DYNAMICS OF LARVAL FISH AND ZOOPLANKTON IN SELECTED SOUTH AND WEST COAST ESTUARIES OF SOUTH AFRICA

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GENERAL ABSTRACT

Larval fish and zooplankton assemblages were studied in nine south and west coast estuaries in the cool-temperate and the cool/warm-temperate boundary region between June 2003 and March 2004. This study served to provide new information on previously unstudied estuaries and expand on existing knowledge of larval fish and zooplankton assemblages associated with various estuary types. The south and west coast estuaries sampled in this study showed lower salinities (12.2 - 13.7), lower water temperatures (14.5 - 16.9 °C) and higher turbidities (k = 0.02 - 0.04) in winter and spring while higher salinities (21.7 - 21.8), higher water temperatures (21.7 - 23.1°C) and lower turbidities (k <0.02) were observed in summer and autumn. Mean winter and summer water temperatures in estuaries were lower than those observed in warm-temperate and subtropical systems by other researchers. A total of 49274 larval fishes were caught, comprising 9 orders, 20 families, 29 genera and 47 taxa. The clupeid *Gilchristella aestuaria* (78.8 %) dominated the larval fish assemblages and occurred in all estuaries. The majority (70 %) of identified species are endemic to southern Africa and 96.4 % of larval fishes caught were estuary-resident species. The zooplankton study yielded a total of 44 taxa, comprising 7 phyla, >20 orders and >35 families. The copepod *Pseudodiaptomus hessei* dominated (59 %) the zooplankton and occurred in similar densities to those observed in other South African estuaries. Larval fish and zooplankton varied across seasons, peaking simultaneously in summer although zooplankton showed additional density peaks during the closed phase of some estuaries. Both plankton components were more abundant in the oligohaline and mesohaline zones within the estuaries. Freshwater input, estuary type and the biogeography of the area influenced the composition and structure of larval fish and zooplankton assemblages in these estuaries. The findings suggest that the estuaries are functioning as successful breeding areas for the larvae of endemic estuary-resident fish species and that these estuaries have to be managed to ensure an adequate freshwater supply to maintain the biological integrity of the ecosystem, specially the maintenance of the highly productive River-Estuary Interface (REI) regions.

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DECLARATION

The following thesis has not been submitted to a university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author.

CHAPTER 1
GENERAL INTRODUCTION

Research on estuarine larval fishes and zooplankton in South Africa has been intensive in the subtropical and warm-temperate regions. Historically, this research has focussed on community structure, the role of estuarine environmental conditions and estuary type in characterizing larval fishes and zooplankton assemblages and the effects of freshwater supply variations on estuarine larval fishes and zooplankton communities and dynamics. Despite this comprehensive of work on estuarine plankton in warm-temperate and subtropical systems, no published information is available on the larval fish (Whitfield & Marais 1999) and few published papers are available on zooplankton assemblages (Wooldridge 1999) from the south and west coasts of South Africa, which fall within the cool-temperate biogeographic region and the boundary between this region and the warm-temperate region. On the other hand, the understanding of how the larval fish and zooplankton components interact in South African estuaries is rather poor when compared to other geographical areas. This general introduction is a then a comprehensive list of the studies that have been conducted on larval fish and zooplankton from South African estuaries and it provides comments to the major findings. These findings are then used to build the rationale behind this project. The general introduction is limited to the work conducted in South Africa and only reference to the international literature will be provided within each relevant chapter.

1.1 Estuarine larval fish research in South Africa

The origin of larval fish research in South Africa can be traced back to the early 1900s and the work of J. D. F. Gilchrist on the development of eggs and larvae of South African marine fishes (Gilchrist 1903, 1904, 1916). Descriptions and notes on the larvae of the pilchard *Sardinops ocellata* (Davies 1954), the congrid eel *Gnathophis capensis* (Castle 1968), and the round-herring *Etrumeus teres* (O'Toole & King 1974) followed the work of Gilchrist. However, estuarine larval fish research only started in the late 1970s.

Melville-Smith and Baird (1980) published the first estuarine larval fish study of South Africa. The authors worked on the ecology of larval fish from the warm-temperate Swartkops Estuary. In this study, the round herring *Gilchristella aestuaria* was the most abundant larval fish species. Melville-Smith (1981) also highlighted the importance of the Kromme Estuary as a nursery area for marine species. Subsequent studies described how larval fish use tides to retain their position in (Melville-Smith *et al.* 1981) and/or to enter (Beckley 1985) the estuaries.

Between 1988 and 1997, estuarine larval fish research extended to the subtropical region of South Africa, with several studies taking place in the Kosi, Richards Bay and St Lucia systems. In the Kosi Estuary and Richards Bay Harbour the larvae of the thorny anchovy *Stolephorus holodon* was often the most abundant species (Harris & Cyrus 1997; Harris *et al.* 1995a; Harris *et al.* 1995b) while in the St Lucia Estuary the larvae of the river goby *Glossogobius callidus* dominated the larval fish catches (Harris & Cyrus 1994, 1995). Harris and Cyrus (1996) noted that the presence of reef and oceanic species in catches, attributed to shoreward intrusions of the Agulhas current, enriched the larval fish diversity in subtropical systems.

Estuarine larval fish research continued in the warm-temperate region with studies on the Swartvlei and Sundays systems. Whitfield (1989a) assessed the composition, abundance and seasonality of larval fish in this system. He also studied the nursery function of the surf zone (Whitfield 1989b) and the influence of tidal exchange and adjacent habitats on the larval fish assemblages of the Swartvlei Estuary (Whitfield 1989c). In the Sundays Estuary, Harrison and Whitfield (1990) conducted a baseline study on the structure of estuarine larval fish assemblages.

The first descriptions of larval development of estuary-associated fish from South Africa were published between 1990 and 1999. The early life history stages of *Acanthopagrus berda* (Garrat 1993), *Argyrosomus hololepidotus* (Beckley 1990), *Atherina breviceps* (Neira *et al.* 1988), *G. aestuaria* (Haigh & Whitfield 1993) and *Spondyliosoma emarginatum* (Beckley 1989) were described in this period. The first studies assessing the effects of freshwater input on larval fishes in estuaries also occurred during this period (Martin *et al.* 1992; Whitfield 1994).

The influence of environmental conditions on estuarine larval fish assemblages were the focus of research between 2000 and 2005. Harris and Cyrus (2000) compared the larval fish assemblages of three subtropical estuarine systems that have suffered man-induced alterations of their natural environment. In the same region, Viljoen and Cyrus (2002) studied the temporal recruitment of larval fish into the Mhlathuze Estuary. These two studies suggested that turbidity, water temperature and, more importantly river flow explain the larval fish community patterns in subtropical systems. On the other hand, studies from the warm-temperate systems suggest that additional factors may explain larval fish patterns in these estuaries. Changes of salinity in these systems from altered freshwater inputs (Strydom & Whitfield 2000; Strydom *et al.* 2002), estuarine type (Strydom *et al.* 2003), estuary mouth configuration (Strydom 2003a) and tidal exchange (Strydom & Wooldridge 2005) have been found to affect estuarine larval fish assemblages as well.

In recent years, the surf zones adjacent to estuaries have been the focus of study. Strydom (2003b) assessed the larval fish species occurring in surf zone adjacent to the Van Stadens and Kabeljous estuaries. The trough habitats (Watt-Pringle & Strydom 2003) and over wash events (Cowley *et al.* 2001) occurring on these surf zones and their effects on estuarine larval fish assemblages have also been studied recently. Baseline studies on the community structure of larval fish from South African estuaries (Pattrick *et al.* 2007) and larval fish descriptions of estuarine species (Strydom & Neira 2006) are still taking place, although these studies are more focused on the effects of freshwater deprivation to the ecology of larval fish.

1.2 Estuarine zooplankton research in South Africa

Zooplankton research in South African estuaries can be traced back to the early 1950s and 1960s and the work of Tattersall (1952) and Grindley (1963) describing estuarine mysid and copepods species, respectively. Day (1967) followed with a study on the ecology of the Knysna estuary. However, estuarine zooplankton research in South

Africa only started in the late 1970s with the work of Grindley (1970) on the plankton from 95 estuarine systems.

From 1970 to 1979, many zooplankton baseline studies took place in South African estuaries. The zooplankton from the cool-temperate Langebaan and Saldhana Bay systems (Grindley 1977), the warm-temperate Swartkops (Grindley 1976a) and Wilderness system (Grindley & Wooldridge 1973) and the subtropical Mngazana (Wooldridge 1977a), Msikaba (Wooldridge 1976), Mtentu River (Connell 1974), Richards Bay (Grindley & Wooldridge 1974) and St Lucia (Grindley 1976b) estuaries was assessed in this period. These studies provided information suggesting a dominance of copepods, e.g. *Pseudodiaptomus hessei* and *Acartia longipatella,* and the influence of salinity on the species composition of estuarine zooplankton in South Africa. Descriptions of new species of copepods (Bradford 1976; Connell & Grindley 1974; Grindley 1978a; Wooldridge 1977b) and a guide to the amphipods of southern Africa (Griffiths 1976) supplemented the studies above.

The effect of tidal exchange on zooplankton composition, distribution and migration was also studied in the early days of estuarine zooplankton research, along with spatio-temporal succession of the sympatric copepod species *A. longipatella* and *A. natalensis* in the Swartkops and Sundays estuaries (Wooldridge & Melville-Smith 1979). In the late 1970s, a community structure model for the plankton of west coast estuaries (Grindley 1978b) and for zooplankton vertical migration (Grindley 1972; Hart & Allanson 1976) was proposed.

Between 1980 and 1989, studies on the warm-temperate Swartvlei Estuary (Coetzee 1981) and Wilderness estuarine system (Coetzee 1983) and on the cool-temperate Bot Estuary (Coetzee 1985) were focused on community structure and its relation to physical variables. Perissinotto and Wooldridge (1989) also studied the effects of a power-generating plant on the zooplankton from the warm-temperate Swartkops Estuary. Overall, the studies suggested that zooplankton composition, abundance and biomass vary with freshwater inflow in these estuarine systems. However, Fowles and Archibald (1987) and Wooldridge and Bailey (1982) continued gathering baseline information on estuarine zooplankton from the Mzingazi and Sundays estuaries, respectively. The influence of zooplankton prey on the morphology (Blaber *et al.* 1981) and feeding ecology (Whitfield 1985) of estuarine fish and the use of tides by zooplankton to move within the estuaries (Wooldridge & Erasmus 1980) were also assessed during the 1980s.

A diverse array of research topics on estuarine zooplankton characterized the 1990's. For instance, Jerling and Wooldridge (1991) and Wooldridge (1986) assessed copepod and mysid population dynamics in the Sundays Estuary and under laboratory conditions. Zooplankton feeding interactions (Jerling & Wooldridge 1994; Jerling & Wooldridge 1995a; Jerling & Wooldridge 1995b) and the lunar influence on the distribution of *Pseudodiaptomus hessei* (Jerling & Wooldridge 1992) were studied in the same system. Stable isotopes were used to identify the sources of carbon and to model trophic relations also in the same system (Jerling & Wooldridge 1995c). Froneman and McQuaid (1997) investigated the grazing impact of microzooplankton in the Kariega Estuary, while Schlacher and Wooldridge (1995) considered the tidal and depth effects on zooplankton assemblages in the Gamtoos Estuary. Studies assessing the consequences of anthropogenic changes to freshwater flow regimes on zooplankton assemblages (Jerling 1999; Jerling & Cyrus 1999) also took place.

Zooplankton studies on trophic dynamics in estuaries and on pollution effects gained momentum since 2000. Feeding studies took place in warm temperate (Froneman 2000, 2001a, 2002a, 2002b, 2002d; Perissinotto *et al.* 2000) and subtropical (Kibirige & Perissinotto 2003a; Kibirige *et al.* 2003; Perissinotto *et al.* 2003) estuaries. These studies identified a variety of feeding strategies among zooplankton species that minimize inter-specific competition and hence improve the use of the available food sources (Froneman 2001b; Kibirige *et al.* 2002). Studies on eutrophication in the Mdloti and the Mhlanga estuaries due to pollution (Kibirige *et al.* 2006) and anthropogenic changes to natural freshwater inputs in Richards Bay (Jerling 2003) and Nhlabane (Jerling 2005) estuaries showed the negative impact of estuarine disturbances on the zooplankton community.

1.3 Estuarine larval fish and zooplankton dynamics research in South Africa

The understanding of larval fish and zooplankton dynamics in South African estuaries is rather poor. Wooldridge and Bailey (1982) conducted the first study describing the relationships between the distribution of *G. aestuaria* eggs and larvae and zooplankton biomass and suggesting potential reciprocal feeding interactions between larval fish and zooplankton species in the Sundays Estuary. Whitfield (1985) investigated the feeding on zooplankton by several estuarine larval and juvenile fish species. Grange *et al.* (2000) studied the response of larval fish density and zooplankton biomass to variations in freshwater flow in the Kariega and Great Fish River estuaries, finding a positive response of both components to an increase in river discharge. Froneman (2004) investigated the zooplankton community structure, including larval fish, of the Kasouga Estuary and found that mysid, amphipod and larval fish biomass was higher after overtopping or breaching events. Finally, Kemp and Froneman (2004) studied the recruitment of larval fish and zooplankton into the West Kleinemond Estuary after overtopping events and suggested that such events provide a vector for both the larvae of estuary-dependent marine fish species and predatory zooplankton to enter the estuary.

1.4 Rationale

On the south and east coasts of South Africa, warm-temperate and subtropical estuaries play an important role as breeding, nursery and feeding habitats for commercially, recreationally, ecologically and culturally important aquatic species (Lamberth & Turpie 2003; Whitfield 1996; Wooldridge 1999). For instance, invertebrates used as baits, e.g. *Upogebia africana* (Paula *et al.* 2001; Wooldridge & Loubser 1996) and *Palaemon peringueyi* (Emmerson 1983), and several recreational fishes (Strydom *et al.* 2003; Whitfield 1998) use these estuaries at some point during their life cycles. Vital prey items, i.e. copepods and mysids, for fish and aquatic invertebrates occur in these estuaries as well. Although some information has been published on larval fish of the southeast coast estuaries, few published information are available on zooplankton assemblages (Wooldridge 1999) and none is available on the larval fish (Whitfield & Marais 1999) from south and west coast estuaries of South Africa. This dearth of information has limited the understanding of estuarine functioning in South Africa hence their management and conservation. A study that provides baseline information on either larval fish or zooplankton assemblages from these estuaries will enhance the picture of estuaries as vital breeding and feeding grounds in South Africa.

Clupleidae and Gobiidae estuary-residents species are the most abundant in larval fish assemblages in warm-temperate (Harrison & Whitfield 1990; Strydom *et al.* 2003; Whitfield 1989a; Whitfield 1994), subtropical (Harris & Cyrus 2000; Harris *et al.* 1995a) and subtropical/warm-temperate boundary region estuaries (Pattrick *et al.* 2007). In cool-temperate estuaries, the juveniles of *L. richardsonii*, *M. cephalus R. holubi* and *Heteromycteris capensis* contribute more than 70 % of the total catch. On the other hand, the copepods *Acartia longipatella, A. natalensis* and *Pseudodiaptomus hessei* and the mysids *Mesopodopsis wooldridgei*, *M. africana, Gastrossacus brevifissura, G. gordonae* and *Rhopalophtalmus terranatalis* are the most common species recorded in South African estuaries (Grindley 1981; Wooldridge 1999). The copepods contribute substantially to total zooplankton density (Jerling & Wooldridge 1991; Wooldridge & Callahan 2000), whereas mysids contribute up to 20% of the zooplankton biomass in South African estuaries (Froneman 2001a). Along the South African coast there is a decrease in taxonomic richness from the subtropical north-east (Indian Ocean) toward the temperate west (Atlantic Ocean) coast. Also, it has been found that the west coast and south-west coast estuaries have low numbers of fish species compared to north-east coast estuaries (Harrison 2002) and the percentage endemicity also increases from north-east to west (Whitfield 1998). Therefore, it is expected that the larval fish and zooplankton assemblages in south and west coast estuaries will be composed of few species, with important contributions of the above mentioned species and with a high percentage of endemism.

Regardless of their diet during later stages of their life cycle, virtually all species of larval and early juvenile fishes that occur in estuaries feed on plankton (Baier & Purcell 1997; Whitfield & Marais 1999). This ecological relationship affects reciprocally both zooplankton and larval fish communities (Dagg & Govoni 1996; Sanvicente-Añorve *et al.* 2006; Wooldridge & Bailey 1982). However, South African studies have tried to understand estuarine zooplankton and larval fish communities separately and little is known of the relationships between these two plankton components. Previous studies have shown that larval fishes and zooplankton densities are seasonally synchronized (Harrison & Whitfield 1990; Wooldridge & Bailey 1982; Lara-Lopez and Neira 2008), that there are many trophic relationships between the two components (Chuwen *et al.* 2007; Munk 1997; Sanvicente-Añorve *et al.* 2006) and that these plankton groups can respond similarly to environmental conditions (Grange *et al.* 2000). It is then natural to expected that a combined analysis of the larval fish and zooplankton assemblages from south and west coast estuaries will show similar relationships between the two components

1.5 Objectives

This study aims to provide baseline information on:

- The composition, abundance and distribution of larval fish in selected south and west coast estuaries,
- The composition, abundance and distribution of zooplankton in the same estuaries, and
- Provide some insight into the relationships between these two plankton components in estuarine systems.

The scope of the present study includes nine estuarine systems (five permanently open, two temporarily open/closed, and two estuarine lake systems) from the west (Olifants, Great Berg and Diep estuaries) and south (Lourens, Heuningnes, Breede, Goukou, Bot and Klein estuaries) coast of South Africa. The study ran over a period of 12 months with sampling at seasonal intervals. The focus of study was on the larval fish and zooplankton larger than 200 µm i.e. mesozooplankton and macrozooplankton.

1.6 Thesis Structure

The three main content chapters correspond specifically to the three aims of the thesis. One chapter (Chapter 3) is currently in press in the Journal African Zoology and the remaining two content chapters will also be submitted for publication. This results in a limited degree of repetition in the introduction, methods and study areas of each section. The preceding chapters include a literature review and a detailed description of the physico-chemical environment of the estuaries sampled. A synthesis and conclusions section and a list of references cited throughout the thesis follows the content chapters.

CHAPTER 2
THE PHYSICO-CHEMICAL ENVIRONMENT OF SELECTED SOUTH AND WEST COAST ESTUARIES OF SOUTH AFRICA

2.1 INTRODUCTION

The climatic and oceanographic environment of the region in which an estuary occurs mainly determines its physico-chemical characteristics (Day 1981a). The climate influences the seasonal patterns of freshwater runoff, winds, waves and insolation and in turn these factors cause regular and substantial alterations in estuarine circulation and water column structure (Schumann *et al.* 1999). The large Agulhas and Benguela currents characterise the different oceanic regions off the South African coast, which influence the adjacent coastal and estuarine environment (Harrison 2004; Schumann *et al.* 1999). Specific fluctuations in the physico-chemical conditions of South African estuaries can also occur as a result of estuary type (Strydom *et al.* 2003), episodic events (Cowley *et al.* 2001; Froneman 2002d; Martin *et al.* 1992) and anthropogenic effects (Morant & Quinn 1999; Whitfield & Wooldridge 1994). Of the latter, water abstraction and pollution are the most evident anthropogenic causes of physico-chemical alterations in South African estuaries (O'Keefe *et al.* 1991; Schulz 2001; Whitfield & Wooldridge 1994).

The coastal region of South Africa falls within three oceanographically defined climate regions, namely a cool-temperate, warm-temperate and subtropical region (Harrison 2002; Harrison 2004; Whitfield 1998). Generally, cool-temperate estuaries are characterised by cool, wet winters and hot, dry summers with water temperatures below 20 ºC (Harrison 2004). Winter rainfall results in low salinities accompanied by high turbidities whereas high salinities and low turbidities dominate in summer (Millard & Scott 1954). Autumn and spring rainfall result in low salinities and high turbidities during these seasons (Cowley *et al.* 2001; Perissinotto *et al.* 2000) and annual estuarine water temperatures are usually between 16 - 24 ºC (Harrison 2004; Whitfield 1998) in warm-temperate estuaries. Subtropical estuaries typically have low salinities and high turbidities during the summer rainfall period and estuarine water temperatures usually range between 14 - 26 ºC with a mean above 22 ºC (Harrison 2004; Harrison & Whitfield 2006).

The estuaries of this study fall within the cool- and warm-temperate regions of South Africa. The Olifants, Great Berg, Heuningnes, Breede and Goukou estuaries represented permanently open (PO) estuaries. The Diep and Lourens estuaries represented temporary open/closed (TOC) systems and the Bot and Klein estuaries represented estuarine lake (EL) systems (Figure 2.1). Estuaries were selected based on the paucity of qualitative and quantitative data on zooplankton and larval fish assemblages in each system as well as accessibility of each to sampling gear. This chapter provides a description of the physical environment characterising the nine south and west coast estuaries of this study. A detailed description of the spatial and temporal variability of salinity, temperature and water transparency in these systems is given.

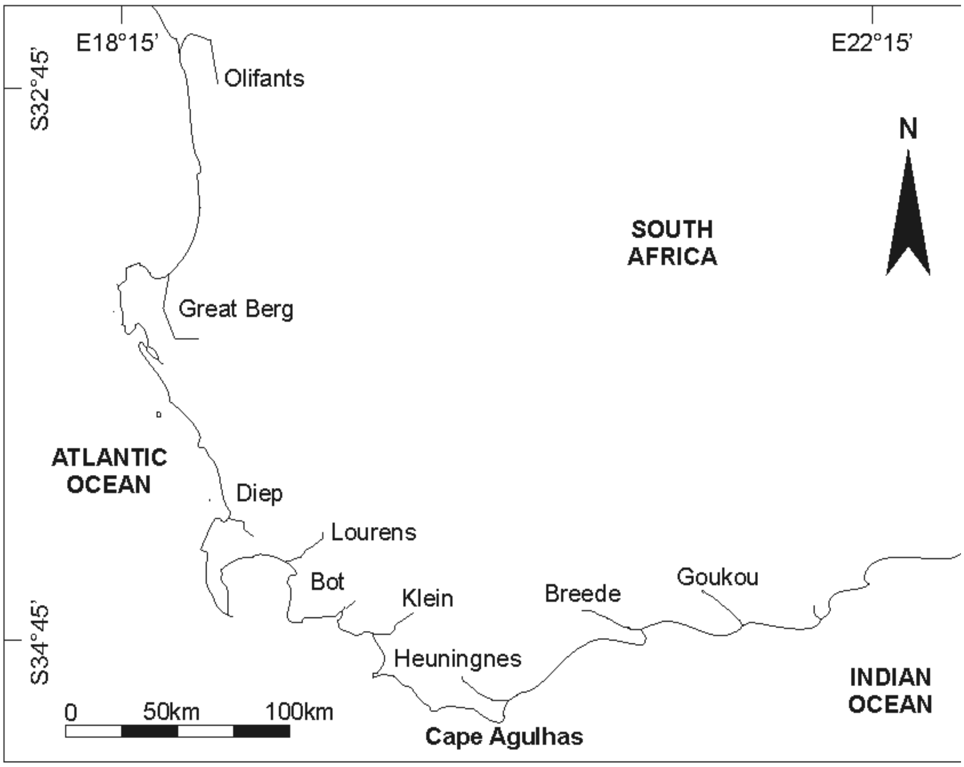

Figure 2.1 Geographical position of estuaries sampled on the south and west coasts of South Africa between June 2003 and March 2004.

2.2 MATERIALS AND METHODS

2.2.1 Field sampling

Physico-chemical surveys of estuaries took place in conjunction with plankton sampling, every three months for one year between June 2003 and March 2004. Collection of data was conducted on predetermined days for each estuary associated with the new moon phase and specific tide state and this sampling protocol was standardised across all fieldtrips. Sampling was conducted after dark at GPS fixed equidistant sites along the navigable length of each estuary. The number of sampling sites varied depending on this navigable length (Table 2.1). Salinity and temperature profiles were obtained at each site using a YSI multiparameter instrument. Recordings were made at 0.5m intervals between the surface and bottom of the water column. Water transparency (extinction coefficient k) at each site was calculated from Secchi disc (20 cm diameter) depth recordings taken at all sites. The formula used is described in Dawes (1981), where $k = 1.7/D$, and D is Secchi depth in cm. Secchi disc readings were taken during the day. The mouth condition (open/closed) of each estuary at the time of sampling was noted.

2.2.2 Data analysis

Contours plots were used to describe the temporal and spatial variation in salinity and temperature and resultant stratification of the water column in each estuary. Contour plots were constructed using data from depth profiling and plotted on SigmaPlot 9. General descriptive statistics were generated for salinity, temperature and water transparency (Table 2.1). A modified Venice system (Strydom et al. 2003) was used to describe the salinity environment within each estuary. Water column salinities obtained from depth profiling were averaged for this purpose.

A stations/variables matrix with all sample units (210) was constructed from averaging water column salinities and temperatures obtained from depth profiling at each individual site. Co-linearity between salinity, temperature and water transparency and the best transformation option were checked using the Draftsman plot routine. Salinity, temperature and water transparency did not correlate with each other. Data were then Log_{10} (x+1) transformed and standardized. A Principal Component Analysis (PCA) was then performed based on this matrix to yield a low-dimensional summary of the inter-relationships between stations based on the physico-chemical variables. PRIMER 5 statistical software package was used to perform the multivariate analyses.

The *a priori* grouping factors i.e. estuaries, estuary types, seasons and biogeographic region were superimposed to assess patterns of association based on these groupings. The differences between the *a priori* groups were assessed by performing a series of ANOSIM routines (analysis of similarities). Because of the uneven sample size of *a priori* groups due to varying estuary size, conclusions from the ANOSIM analysis were accepted only for those cases were $P < 0.01$. Cool-temperate and warm-temperate regions were defined with Cape Agulhas as the boundary (Harrison 2004).

2.3 RESULTS

2.3.1 Permanently open estuaries

Goukou Estuary. In the Goukou Estuary (Figure 2.2), salinities averaged 9.9 and ranged 0 – 34.4 in winter while in summer averaged 29.1 and ranged 19.8 – 35.0 (Figure 2.3). Throughout the study, lower reaches (St 1 – 2) showed euhaline conditions (30.0 – 35.9). Oligohaline (0.5 – 4.9) and fresh (0 – 0.49) conditions were only recorded during winter at upper sites (St 4, 5 and 6). Depth profiles of salinity showed a well mixed estuary throughout the study (Figure 2.4). Water temperatures in winter and spring ranged 12.9 - 18.4 ºC. Summer and autumn temperatures were higher and ranged 21.4 - 24.4 ºC (Figure 2.3). Although, mean temperatures at stations were similar (19.1 – 20.2 ºC), the temperature range was greater in the upper reaches (12.9 – 24.4 ºC) than in the lower reaches (15.7 – 22.6 ºC). During all seasons sampled except winter, lower reaches were colder than upper reaches. During this study, the water temperature of the estuary was well mixed throughout the water column (Figure 2.4). The water was more turbid in winter (k >0.03) than in summer (k <0.02) and the middle and upper reaches (stations 3 – 6) were generally more turbid than the lower reaches, especially in winter (Figure 2.5).

Table.2.1 Salinity, temperature (℃) and water transparency (k) in selected south and west coast estuaries during the entire study period (St = number of sampling sites, D = distance sampled in km).

Estuary	Variables	Mean	Median	Range	St	D
Permanently open estuaries						
Goukou	Salinity	23.33	22.99	0.00-35.06	6	12
	Temperature	19.76	21.37	12.94-24.42		
	Water transparency	0.02	0.02	0.01-0.06		
Breede	Salinity	9.46	4.45	0.00-32.36	10	30
	Temperature	19.27	21.12	14.27-23.25		
	Water transparency	0.03	0.03	0.01-0.05		
Heuningnes	Salinity	26.09	29.88	1.90-35.76	4	8
	Temperature	19.90	20.20	15.82-24.24		
	Water transparency	0.02	0.01	0.01-0.09		
Great Berg	Salinity	13.23	10.95	0.00-34.33	12	30
	Temperature	18.91	16.83	13.01-24.94		
	Water transparency	0.03	0.02	0.07-0.09		
Olifants	Salinity	15.60	16.53	0.00-34.14	10	20
	Temperature	18.80	18.23	12.35-24.83		
	Water transparency	0.02	0.02	0.01-0.03		
Temporary open/close estuaries						
Lourens	Salinity	8.31	0.31	0.00-28.54	2	0.6
	Temperature	18.57	20.94	13.31-23.72		
	Water transparency	0.03	0.02	0.02-0.07		
Diep	Salinity	10.70	3.57	0.66-33.82	3	3
	Temperature	18.48	17.29	13.57-24.82		
	Water transparency	0.04	0.03	0.02-0.09		
Estuarine lake systems						
Klein	Salinity	24.53	31.95	6.68-34.34	4	8
	Temperature	18.76	17.43	13.45-25.22		
	Water transparency	0.01	0.01	0.01-0.03		
Bot	Salinity	26.03	35.00	4.76-38.73	3	6
	Temperature	18.49	21.06	13.18-25.05		
	Water transparency	0.01	0.01	0.00-0.03		

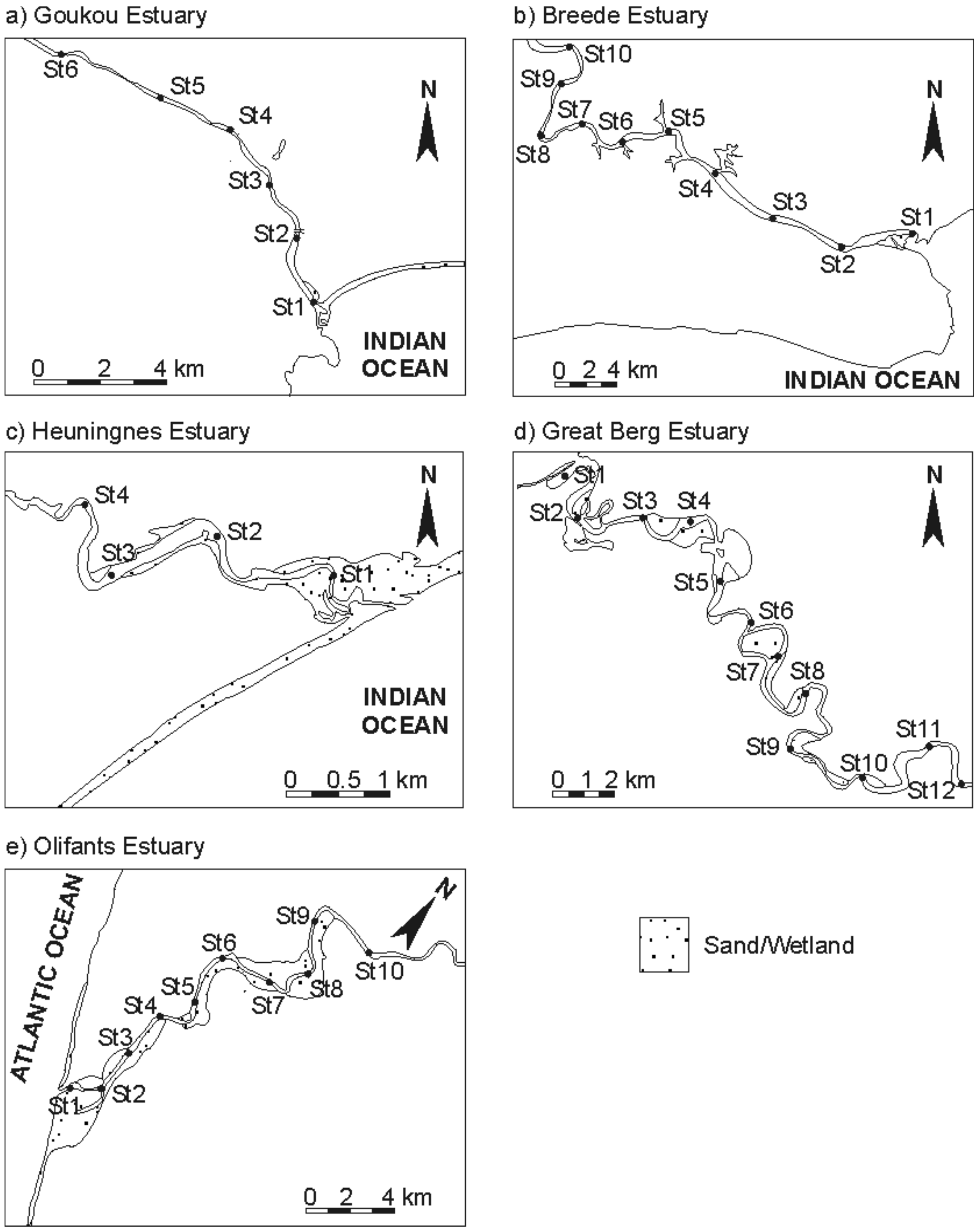

Figure 2.2 Location of sampling stations along selected, permanently open south and west coast South African estuaries.

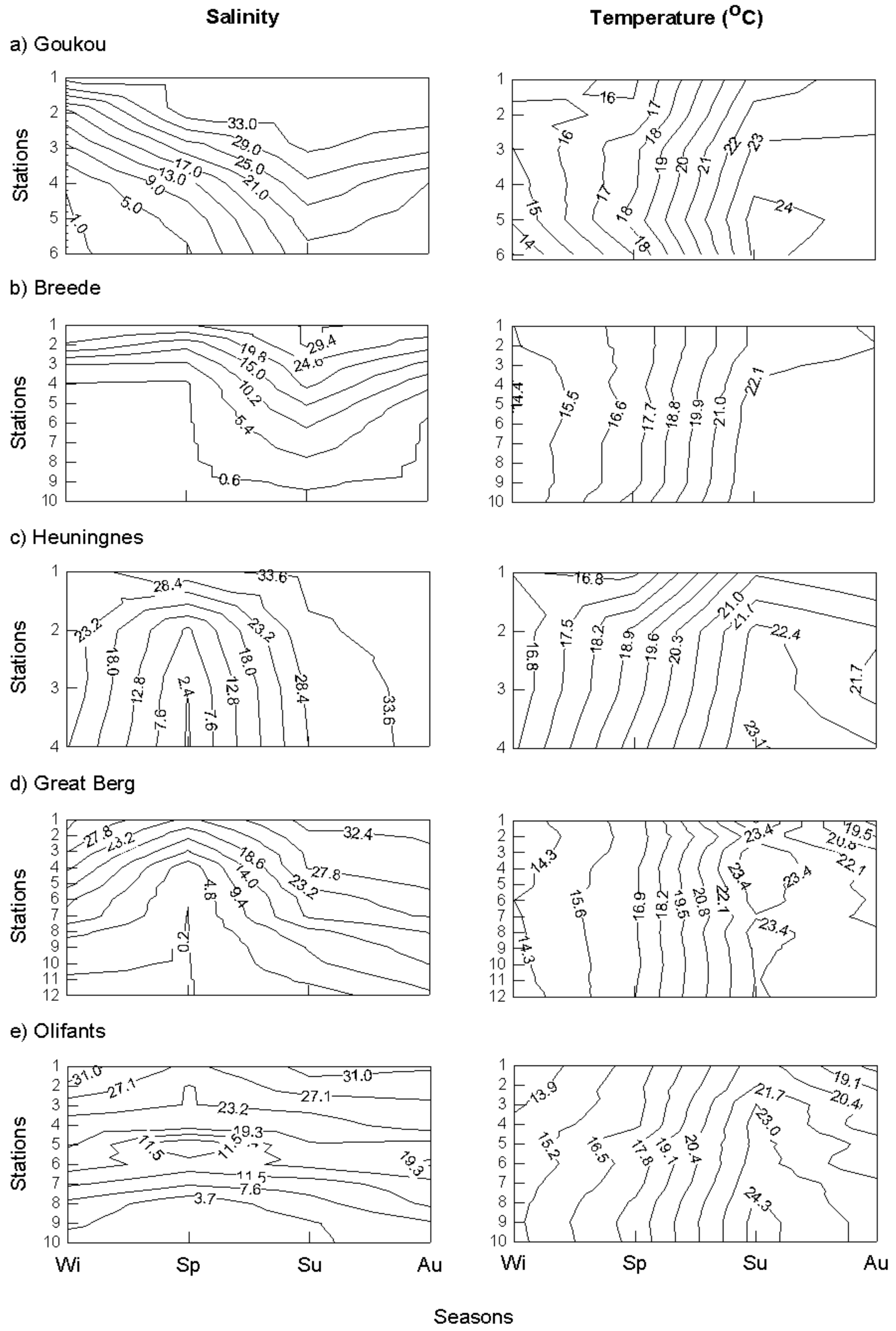

Figure 2.3 Contour plots of average salinity and temperature recorded in selected, permanently open south and west coast South African estuaries in winter (June 2003), spring (September 2003), summer (December 2003), and autumn (March 2004).

Breede Estuary. The Breede Estuary (Figure 2.2) showed predominantly oligohaline conditions. Although seawater intrusion increased salinities >30 in summer, they remained <15 during the sampling period (Figure 2.3). Mean salinity in spring decreased to 4 and in summer, the highest value was 14.5. Throughout the study, mesohaline and oligohaline conditions characterized the estuary (St 3 – 10) with only polyhaline conditions recorded at lower reaches (St 1 - 2). In winter and spring, fresh water conditions penetrated down to 12 km from the mouth (St 4) while in summer fresh water conditions were recorded only 30 km (St 10) from the estuary mouth (Figure 2.3). Depth profiles of salinity evidenced a well mixed estuary throughout the study (Figure 6). Water temperatures varied between seasons sampled and increased from winter (range 12.9 - 18.4 ºC) to summer (21.5 – 23.2 ºC). Despite the temporal variation, temperatures along the length of the estuary were similar within each sampling period. During this study, the water temperature of the estuary was well mixed throughout the water column (Figure 2.6). Water transparency was similar between seasons sampled, although the lower reaches tended to be more turbid in spring and winter. The middle and upper reaches showed less variation in water transparency between seasons (Figure 2.5).

Heuningnes Estuary. The Heuningnes Estuary (Figure 2.2) had the highest mean salinity and mean temperature values of all estuaries sampled (Table 2.1). Freshwater reached the lower reaches in spring and salinities decreased to 1.9, whereas in autumn, mean salinity was 35.6 and ranged 35.1 – 35.7 (Figure 2.3). Throughout the study, the lower reaches (St 1) had euhaline conditions whereas middle and upper reaches (St 2 – 4) were predominantly polyhaline. Depth profiles of salinity showed a stratified estuary during winter (Figure 2.7). Mean water temperature in winter was approximately 16 ºC and increased to 23.2 ºC in summer (Figure 2.3). Temperatures were similar between stations, although the upper reaches exhibited higher temperatures (Figure 2.3). During winter, the temperature of the water column was stratified (Figure 2.7). Water transparency was low (k <0.02) and similar between seasons and stations. During spring, however, the freshwater intrusion increased turbidity (k >0.06) at stations 2 – 4 (Figure 2.5).

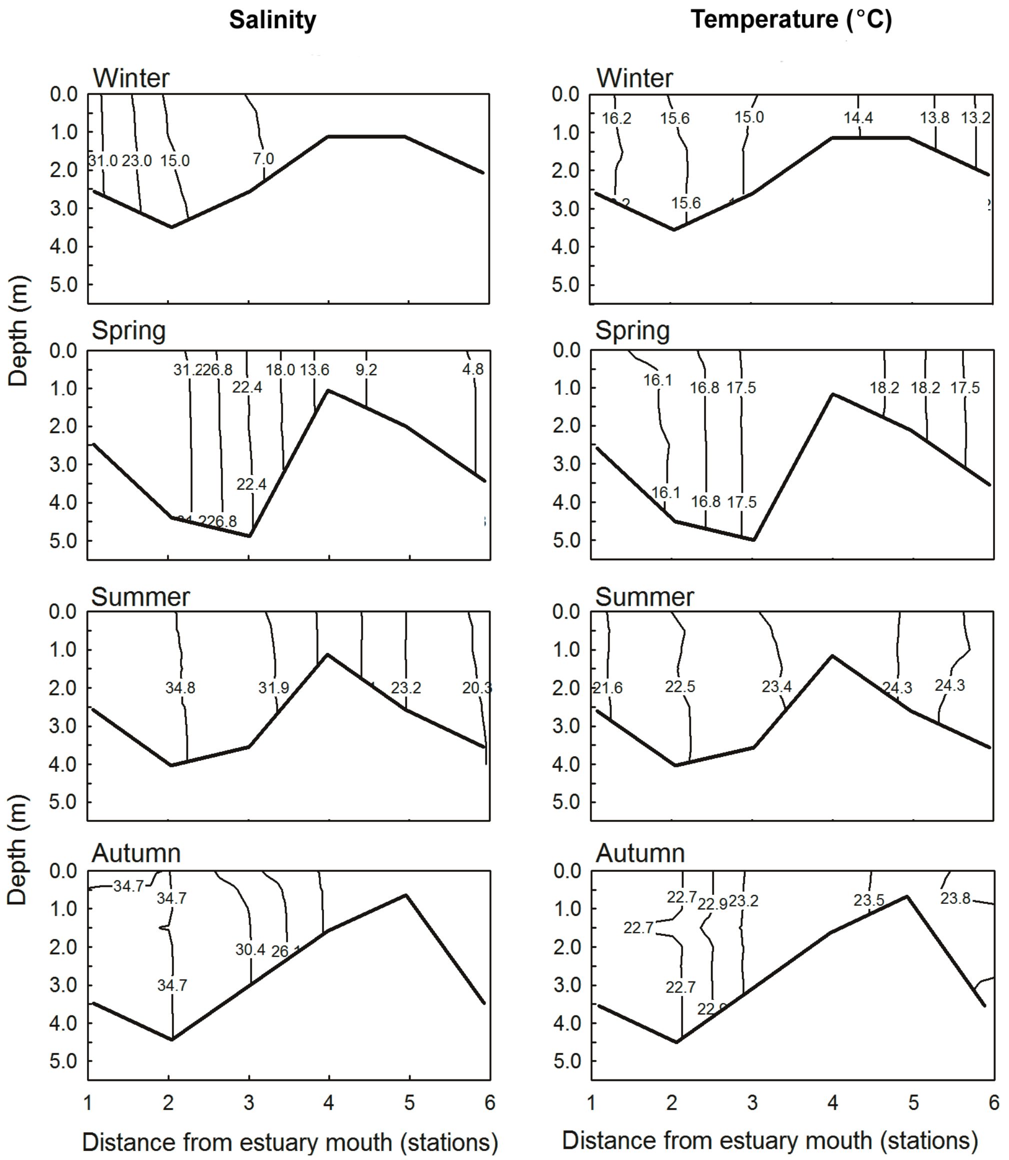

Figure 2.4 Depth profiles of seasonal salinity and temperature recorded at each site in the Goukou Estuary

Great Berg Estuary. In the Great Berg Estuary (Figure 2.2), salinity was similar between seasons except spring when the estuary was predominantly oligohaline (Figure 2.3). The estuary showed a strong salinity gradient from the mouth to the upper reaches. Spring exhibited fresh and oligohaline conditions 8 km from the estuary mouth (St 4) whereas autumn sampling exhibited mesohaline conditions 30 km from the estuary mouth (St 10) (Figure 2.3). Depth profiles of salinity showed a well mixed estuary throughout the study (Figure 2.8). Water temperatures increased from winter (range 13.1 - 14.3 ºC) to summer (22.9 - 24.9 ºC) and did not overlap between seasons (Figure 2.3). Temperatures along the length of the estuary were similar throughout the study. During autumn however, mouth (Station 1) temperatures (<16 ºC) were lower than middle and upper reaches. During this study, the water temperature of the estuary was partially to well mixed (Figure 2.8). Turbidities in spring were higher ($k > 0.06$) than turbidities in winter, summer and autumn, which remained below 0.03 (Figure 2.5). The water was clearer in the lower reaches ($k < 0.03$), notably during autumn when $k < 0.02$ and salinities >20 were recorded up to 16 km from the mouth (St 8). During spring, high turbidities ($k > 0.06$) were recorded 4 km from the estuary mouth and were related to the predominantly fresh and oligohaline conditions observed in the system.

Olifants Estuary. In the Olifants Estuary (Figure 2.2), the salinity was similar between seasons (Figure 2.3) and was predominantly mesohaline. Along the length of the estuary, the salinity decreased steadily from the lower reaches to the upper reaches with freshwater conditions only recorded during spring in the upper reaches (St 9 and 10). The salinity of the estuary was generally well mixed although, some stratification was observed during spring (Figure 2.9). Temperatures increased from winter (range 12.6 – 14.9 ºC) to summer (21.1 – 24.8 ºC) and decreased in autumn (17.3 – 22.4 ºC). Along the estuary (Figure 2.3), temperatures increased from the mouth (12.6 – 21.1 ºC) to the upper reaches (14.8 – 24.8 ºC). The temperature of the estuary was partially mixed and was stratified during spring (Figure 2.9). The water was generally clear ($k < 0.03$) however, the lower and middle reaches were more turbid during summer (Figure 2.5).

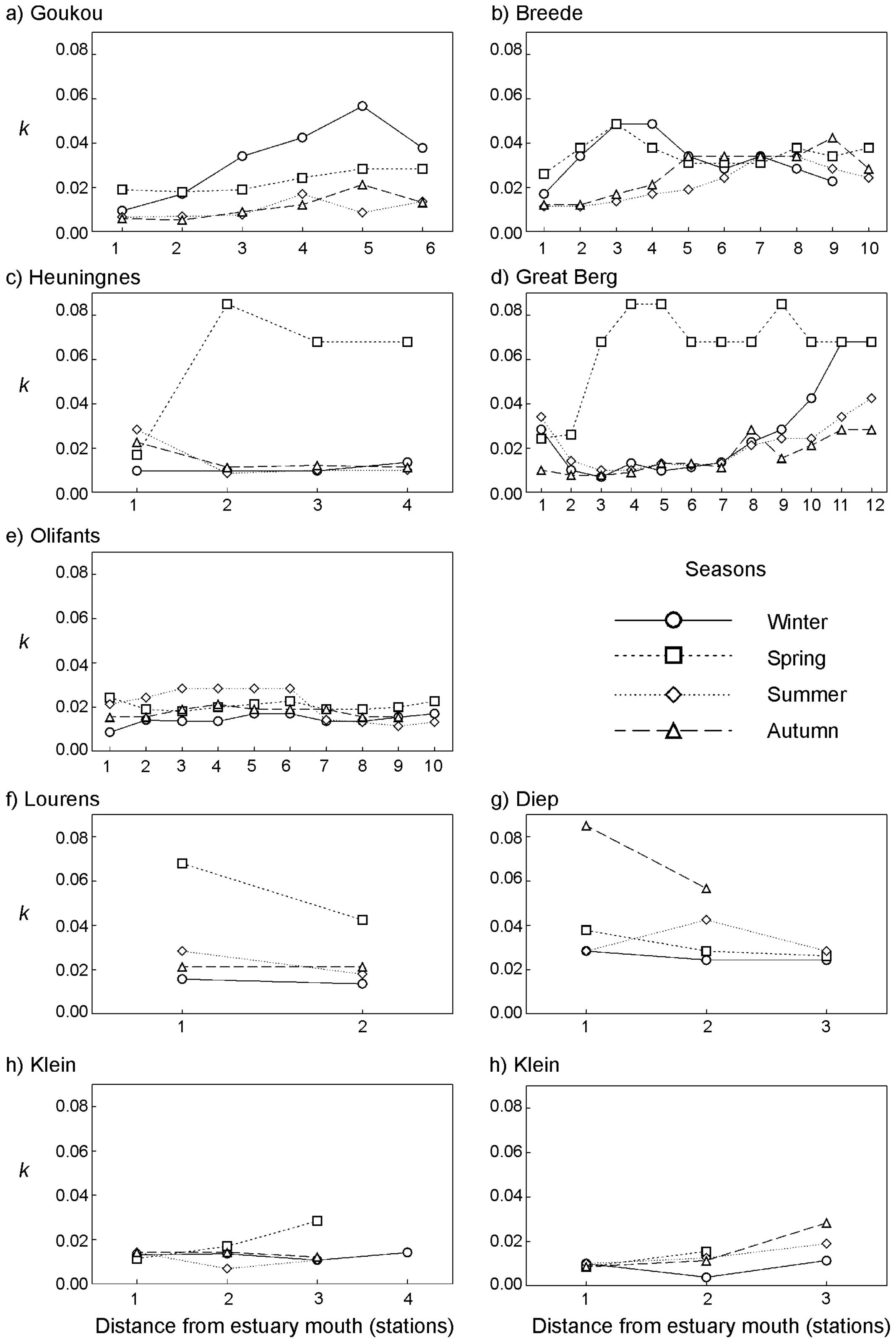

Figure 2.5 Line plots of seasonal water transparency (k) recorded in selected south and west coast South African estuaries.

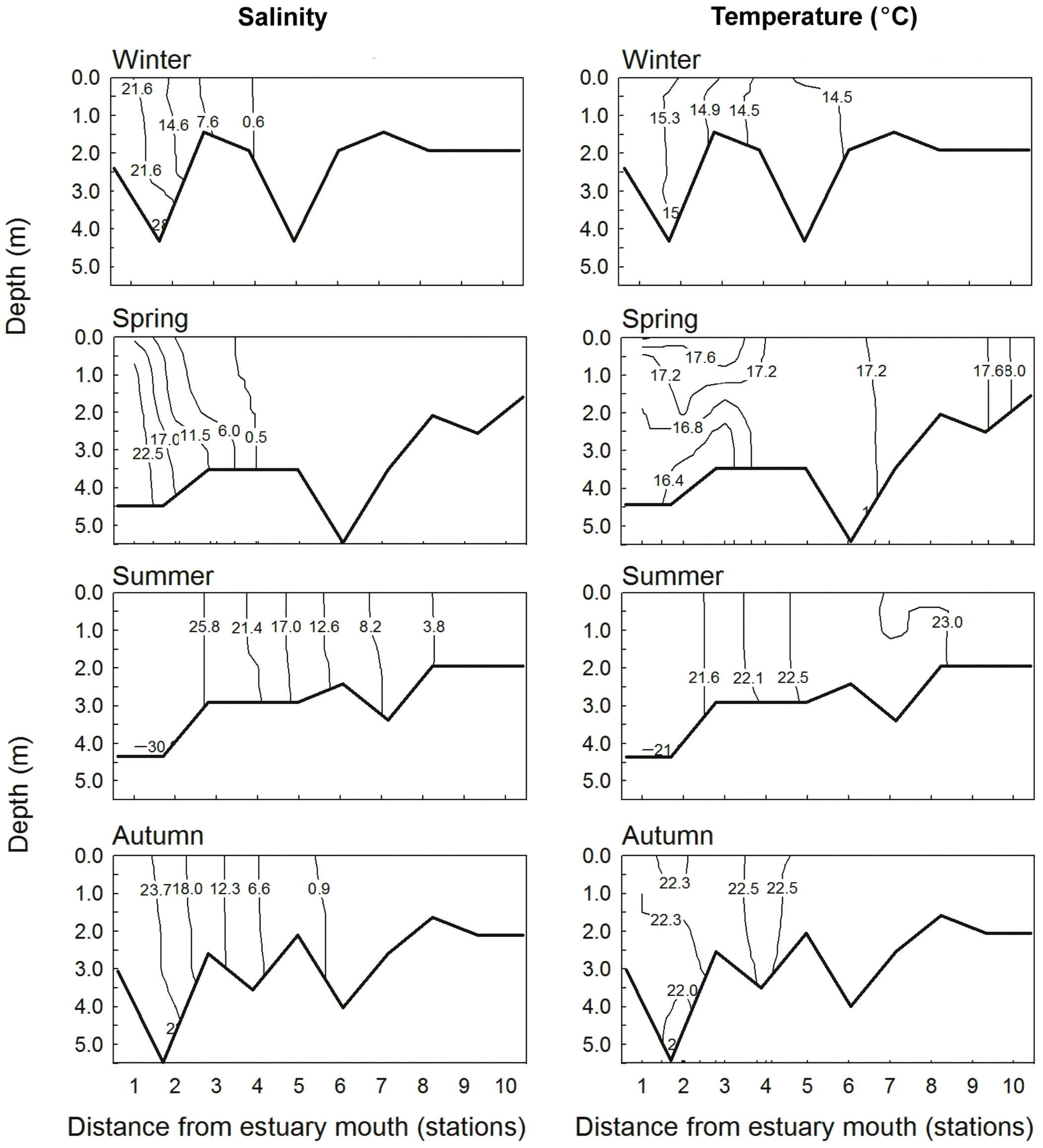

Figure 2.6 Depth profiles of seasonal salinity and temperature recorded at each site in the Breede Estuary.

2.3.2 Temporarily open/closed estuaries

Lourens Estuary. The salinity of the Lourens Estuary (Figure 2.10) varied between seasons (Figure 2.11). Although conditions were predominantly mesohaline (<18), fresh water conditions predominated in spring. During autumn when the mouth was closed, salinity ranged 0.0 – 18.7 whereas the range was smaller in winter (14.5 – 14.6) and summer (6.0 – 6.5). Salinities did not vary much spatially but showed strong vertical stratification (Figure 2.12). Temperatures were considerably different between winter-spring and summer-autumn. Fresh water conditions in spring were accompanied by temperatures ranging 13.3 – 13.6 ºC whereas during the closed phase in autumn, temperatures increased to 21.2 – 22.7 ºC. Temperatures did not vary spatially but showed vertical stratification throughout the study (Figure 2.12). Water was more turbid during spring (0.04> *k* <0.07) than during winter, summer and autumn (Figure 2.5).

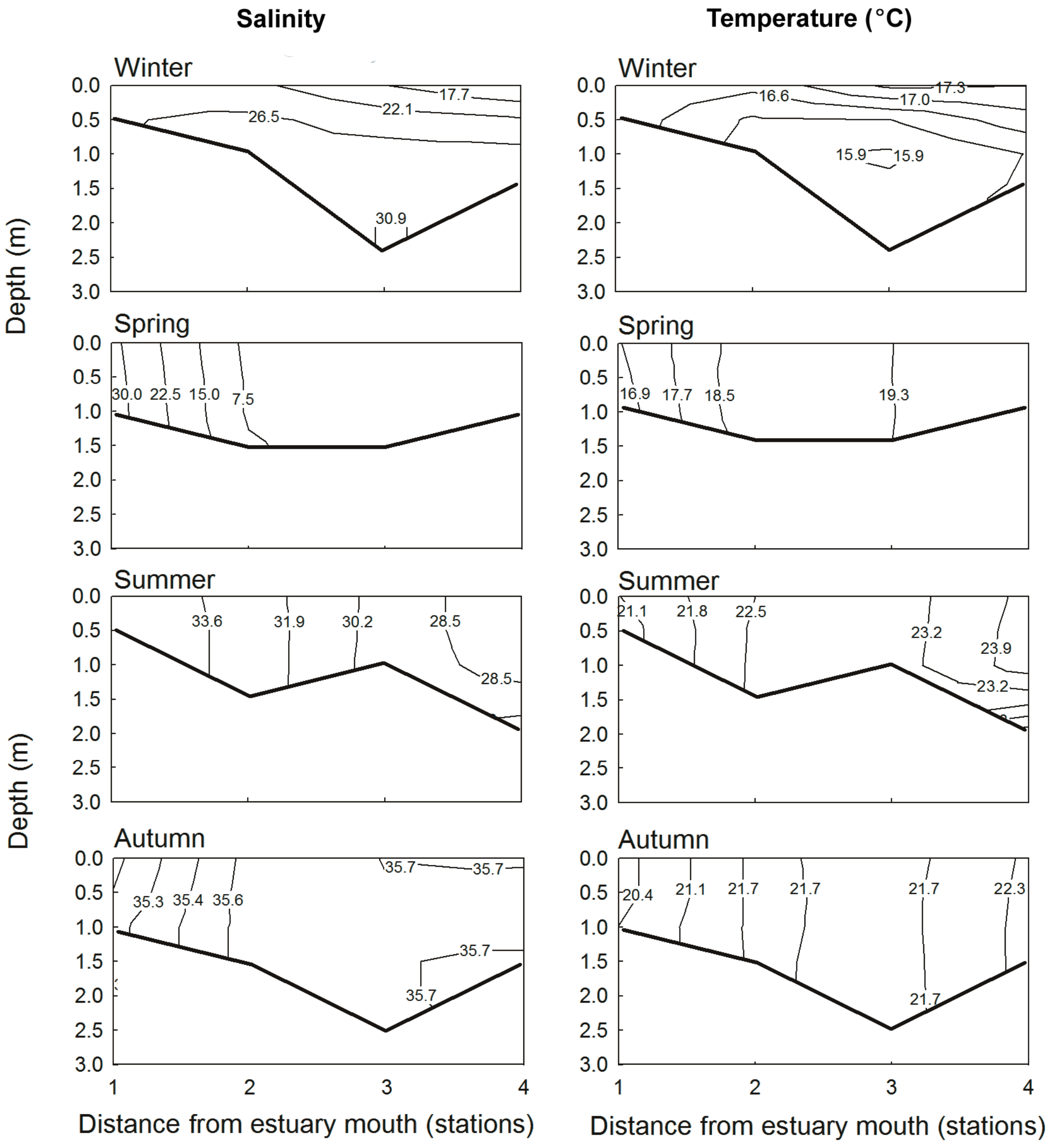

Figure 2.7 Depth profiles of seasonal salinity and temperature recorded at each site in the Heuningnes Estuary.

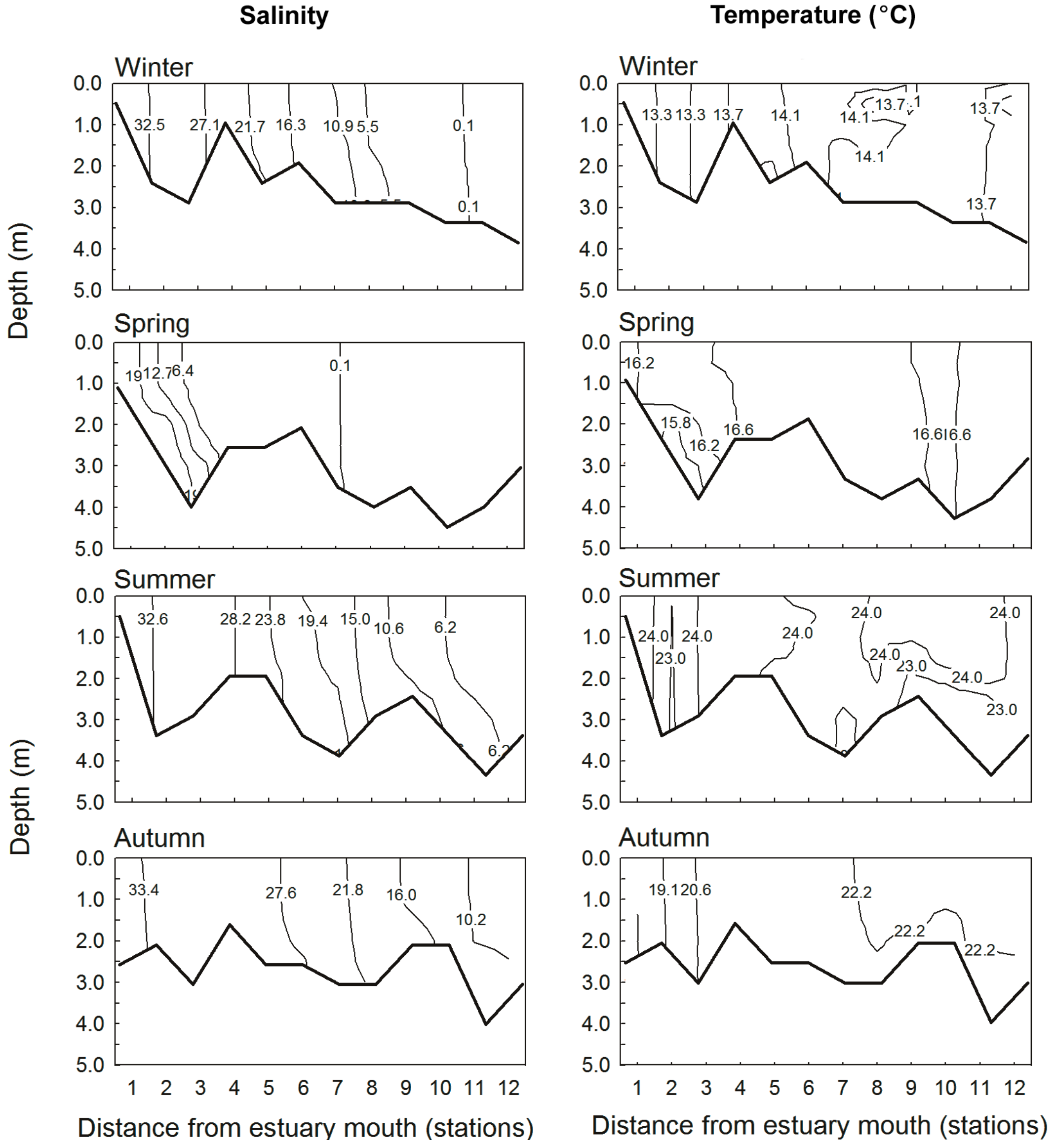

Figure 2.8 Depth profiles of seasonal salinity and temperature recorded at each site in the Great Berg Estuary.

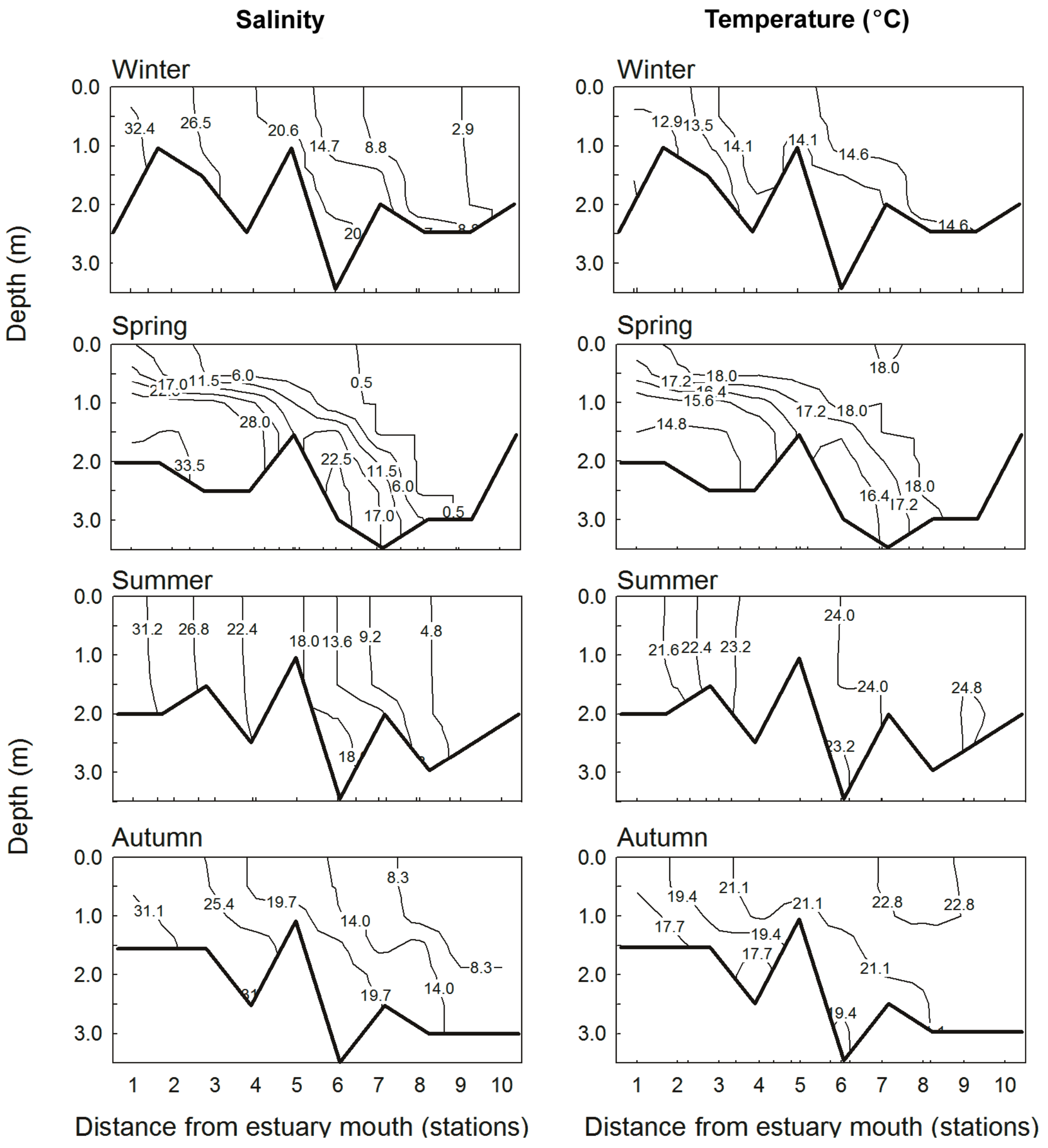

Figure 2.9 Depth profiles of seasonal salinity and temperature recorded at each site in the Olifants Estuary.

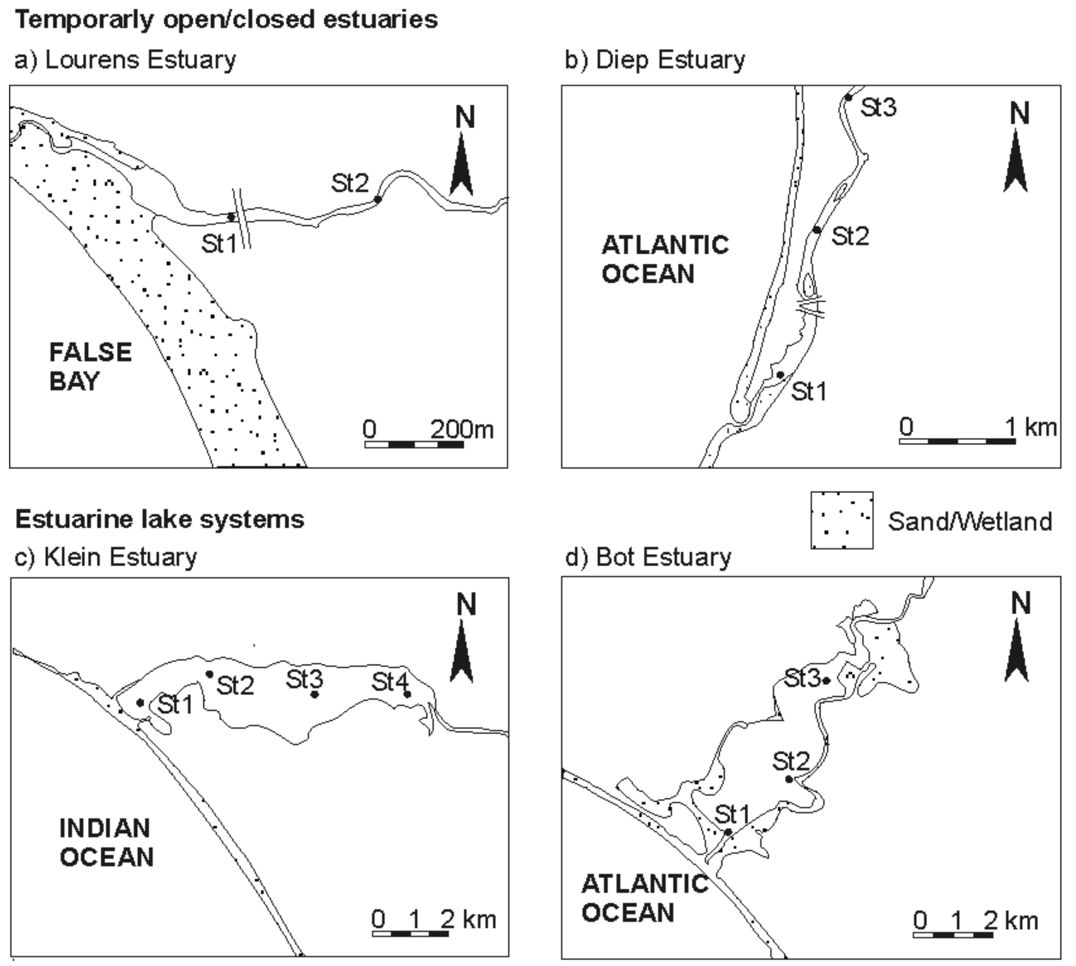

Figure 2.10 Location of sampling stations along selected, temporarily open/closed and estuarine lake systems from the south and west coast South African estuaries.

Diep Estuary. The Diep Estuary (Figure 2.10) was open during sampling. The predominant salinity environment was mesohaline, although, the estuary was entirely oligohaline (salinity range 1.2 – 1.9) during winter and seawater intrusion during summer increased salinities >28 (Figure 2.11). The salinity range at the mouth was 1.7 – 28.2 whereas at the upper site (St 3) was 1.9 – 9.9. Depth profiles of salinity showed a stratified water column in the estuary throughout the study (Figure 2.13). Temperature increased from winter to summer and did not overlap between seasons (Figure 2.11). During winter, temperatures ranged 14.2 – 14.7 ºC whereas during summer increased to 21.4 – 24.7 ºC. Water temperatures did not show spatial variation but showed some stratification (Figure 2.13). This estuary was the most turbid of all estuaries sampled.

Water was considerably more turbid during autumn (*k* >0.05) than during other seasons. The lower reaches tended to be more turbid than the upper reaches, particularly during autumn (Figure 2.5).

2.3.3 Estuarine lake systems

Klein Estuary. In the Klein Estuary (Figure 2.10), salinities varied considerably between seasons and only overlapped between summer and autumn (Figure 2.11). Mesohaline conditions dominated in winter when the estuary was closed (8.7 – 11.2). The mouth opened in spring because of a prior increase in river flow, which allowed seawater to enter the estuary and increased the salinity range from 17.8 to 30.7. Euhaline conditions (32.0 – 34.1) predominated in summer and autumn when the estuary closed again. Salinity along the length of the estuary was homogeneous. The increased river flow, however, was responsible for the spatial variation of salinity observed in spring. Salinities decreased from euhaline conditions at the mouth (St 1) to predominantly mesohaline conditions at the top (St 3) of the estuary (Figure 2.11). During this study, the salinity of the estuary was partially mixed throughout the water column (Figure 2.14). Temperatures increased from winter (<16 ºC) to summer (>23.5 ºC) and showed a 6 ºC increase between spring and summer. Spatially, temperatures showed similar ranges between stations during the entire study. The temperature of the estuary was partially to well mixed in the water column (Figure 2.14). Water transparency was homogeneous (mean *k* = 0.01 - 0.02) between seasons and stations. The open state resulted in more turbid waters during spring (*k* >0.02) and a spatial turbidity gradient (Figure 2.5) was observed. Water transparency decreased from the mouth (*k* <0.01) to the upper reaches (*k* >0.02).

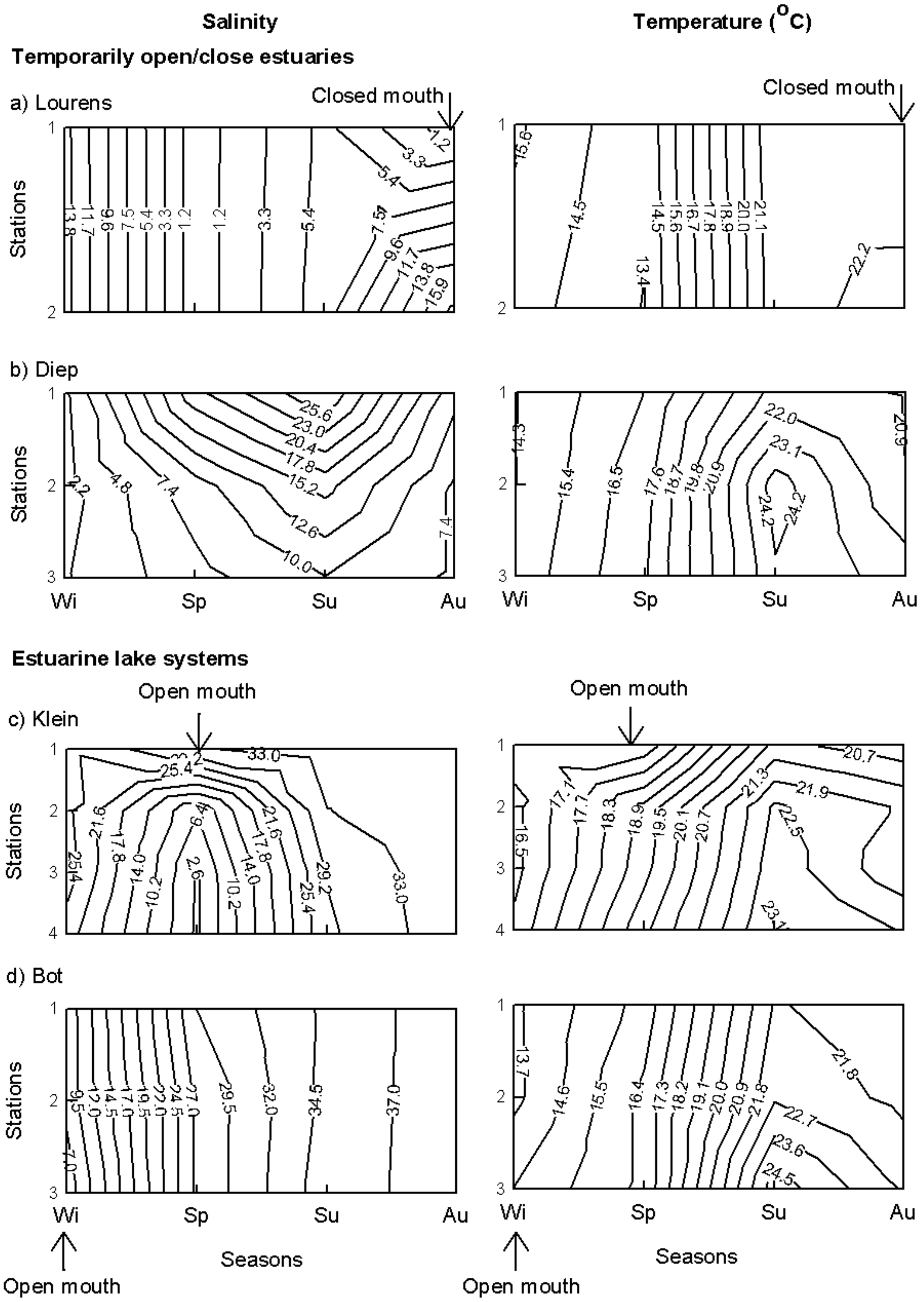

Figure 2.11 Contour plots of average salinity and temperature recorded in selected, temporarily open/closed and estuarine lake south and west coast South African estuaries in winter (June 2003), spring (September 2003), summer (December 2003) and autumn (March 2004).

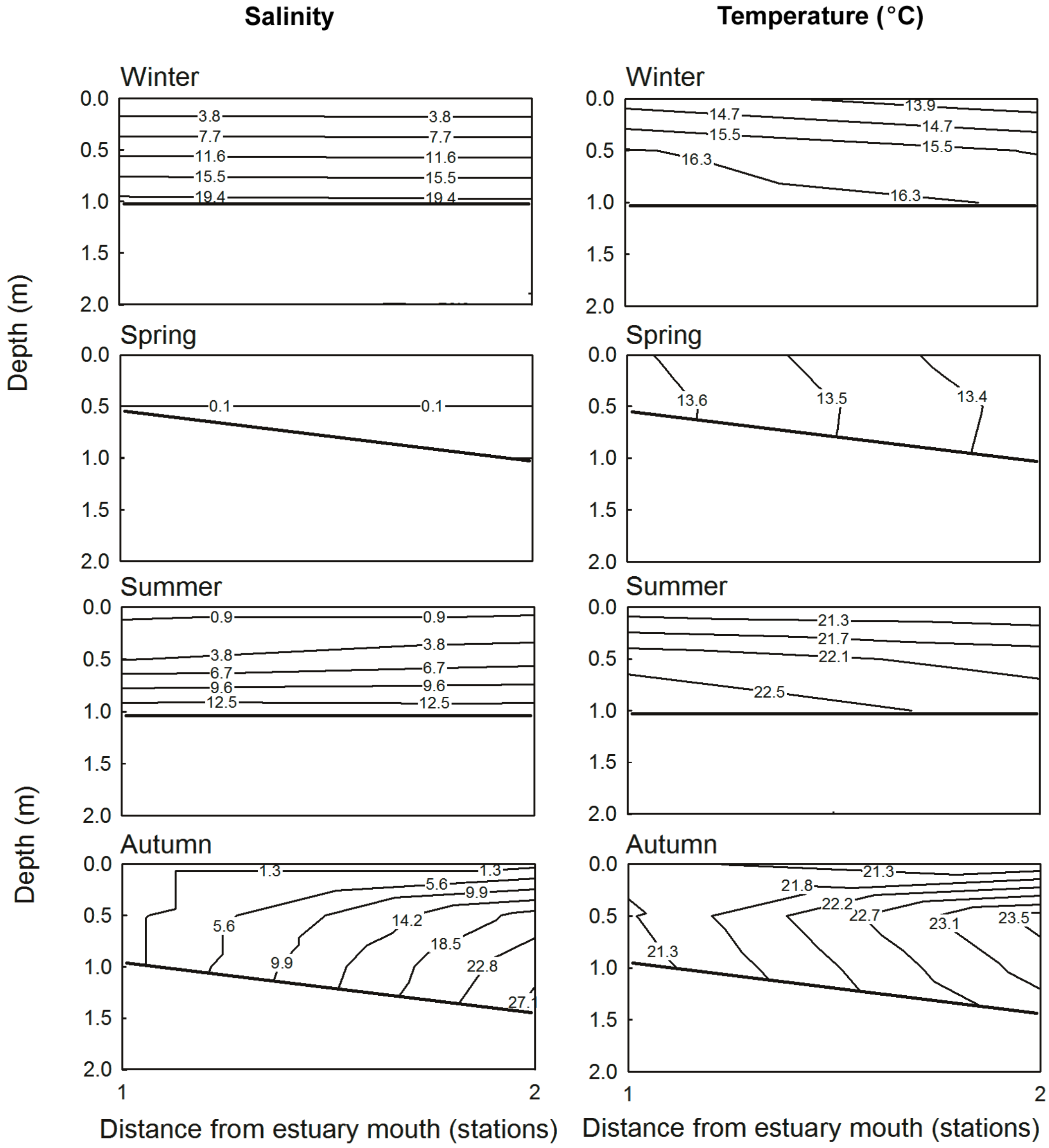

Figure 2.12 Depth profiles of seasonal salinity and temperature recorded at each site in the Lourens Estuary.

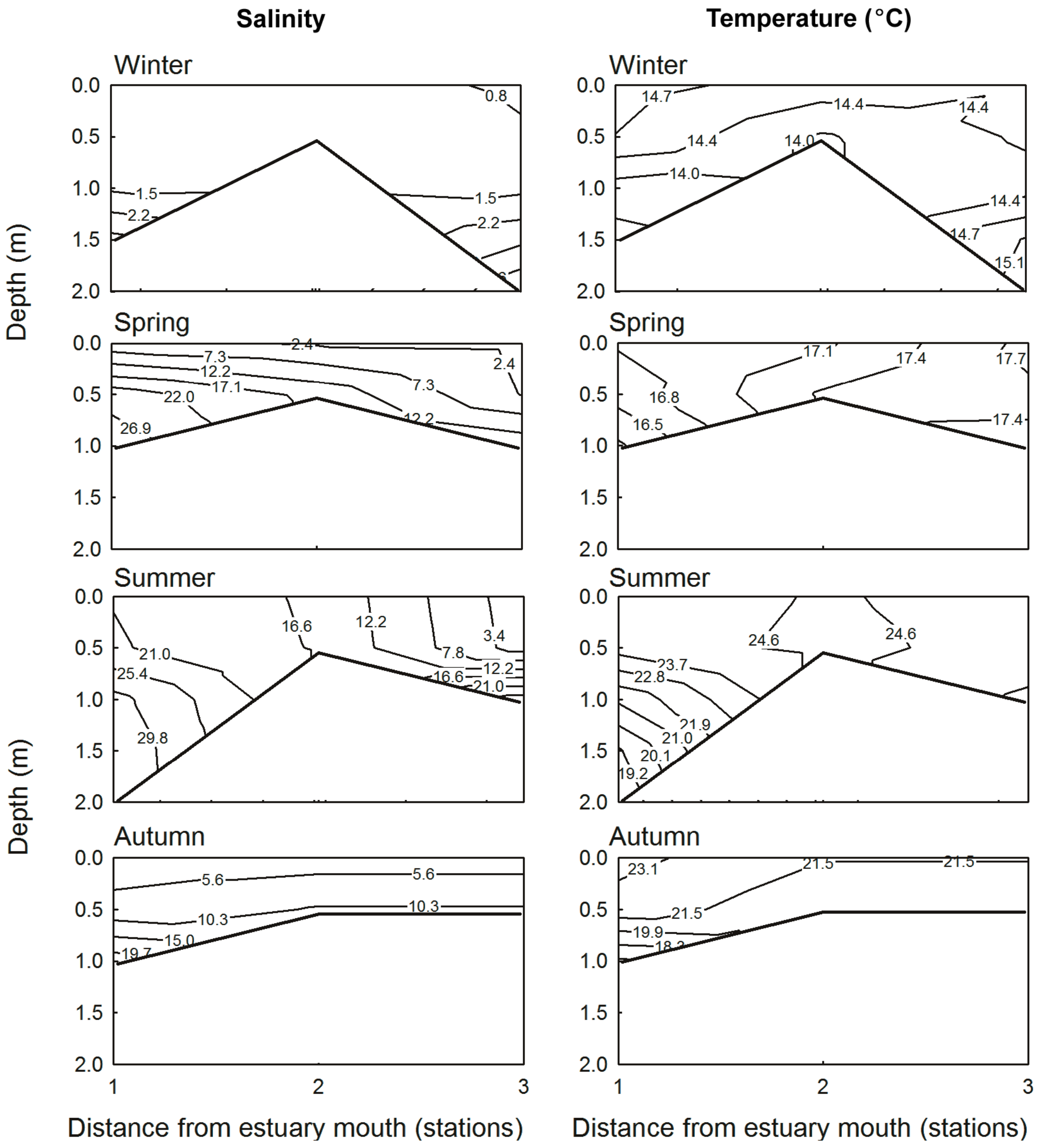

Figure 2.13 Depth profiles of seasonal salinity and temperature recorded at each site in the Diep Estuary.

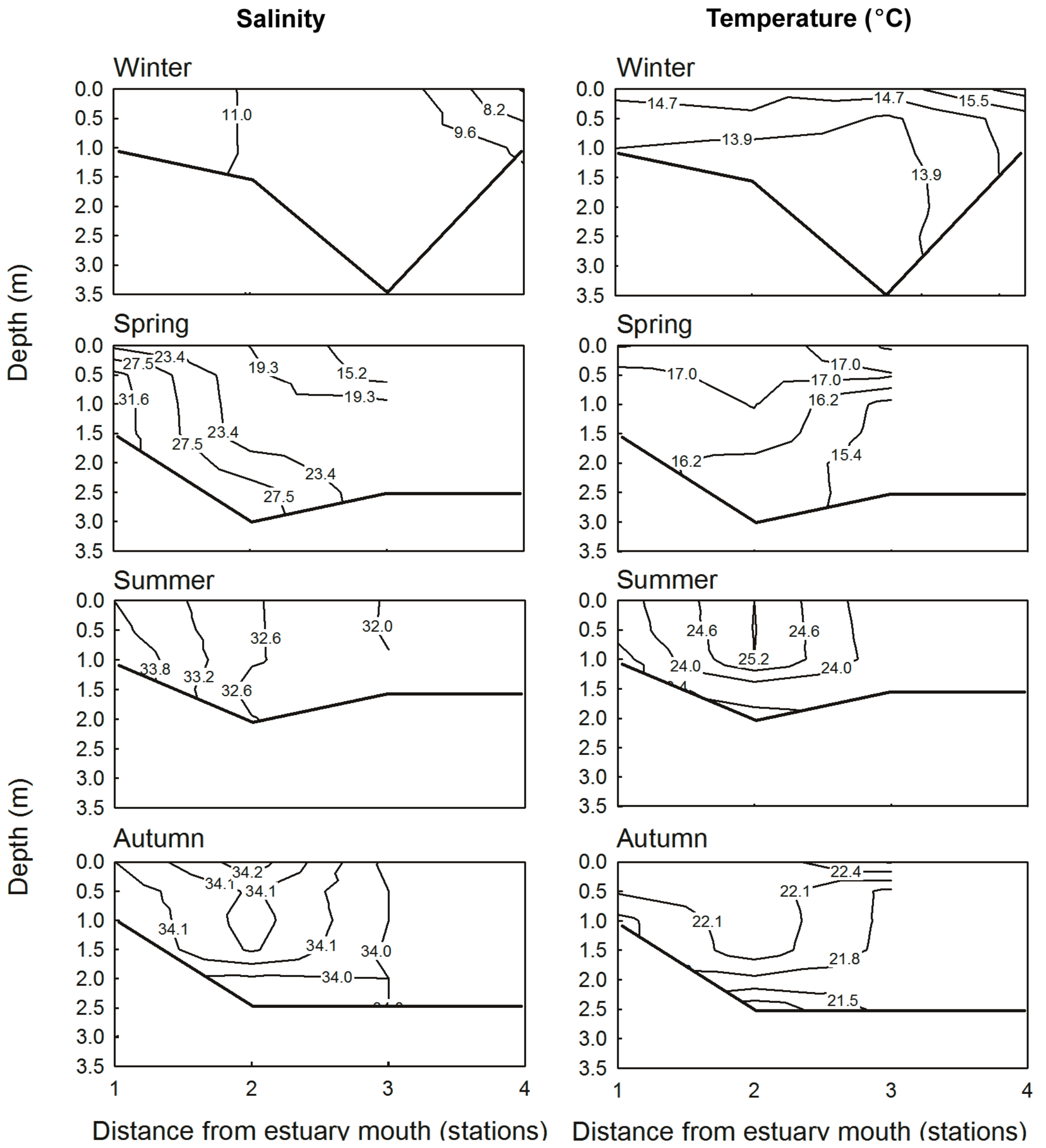

Figure 2.14 Depth profiles of seasonal salinity and temperature recorded at each site in the Klein Estuary. (Note: St 4 was sampled only in winter as the site was not accessible during the rest of the study).

Bot estuary. The Bot Estuary (Figure 2.10) had excessive, dense growth of the pondweed *Potamogeton pectinatus* during the sampling period and made site access difficult. The estuary was predominantly euhaline. However, the mouth opened in winter and mesohaline conditions (5.4 – 8.0) predominated in this season (Figure 2.11). During the closed state of the estuary, salinities increased from polyhaline in spring to hypersaline in autumn. Salinity showed similar ranges and means between stations throughout the study. The salinity of the water column was mixed but the water column showed some salinity stratification during spring (Figure 2.15). Temperatures increased from winter (13.5 – 14.6 ºC) to summer (21.9 – 25.0 ºC). Temperatures were generally higher in the upper reaches than in the lower reaches (Figure 2.11). As with salinity, water temperature was mixed but showed some stratification during spring (Figure 2.15). The estuary was the least turbid (k <0.02) of all systems sampled. Water transparency was similar between stations and seasons, although, larger variations were observed at Station 3 and during autumn (Figure 2.5).

2.3.4 Multivariate analysis

The first two axes of the PCA (Figure 2.16) accounted for approximately 88 % of the variation between the samples. The first PC axis correlated negatively to salinity and positively to water transparency, while the second axis correlated positively to temperature (Table 2.2). Stations from estuaries with high salinities plotted in the left half of the ordination while those with high turbidities plotted in the right half. Stations from estuaries with warmer waters plotted in the lower half of the ordination (Figure 2.16).

The pattern produced by the ordination suggested seasonal variation of physical variables as an important factor influencing the environment in estuaries. A gradient from stations sampled in summer, extreme lower left of the plot, and autumn, lower left-right to centre, to stations sampled in spring, middle left-right to centre, and winter, extreme upper left-right of plot, was observed from the PCA plot (Figure 2.16). The ANOSIM test confirmed the seasonal gradient by suggesting significant differences in the physico-chemical environment between seasons however, the seasonal groups were not well separated (R = 0.1, *P* >0.01).

Although superimposing estuaries in the PCA plot did not suggest a clear pattern for the *a priori* groups estuaries, biogeographic region and estuary type, the ANOSIM tests did show significant differences between estuaries (*P* >0.01) and biogeographic regions (*P* >0.01). Similarly as seasons, these groups were weakly (R = 0.1) separated.

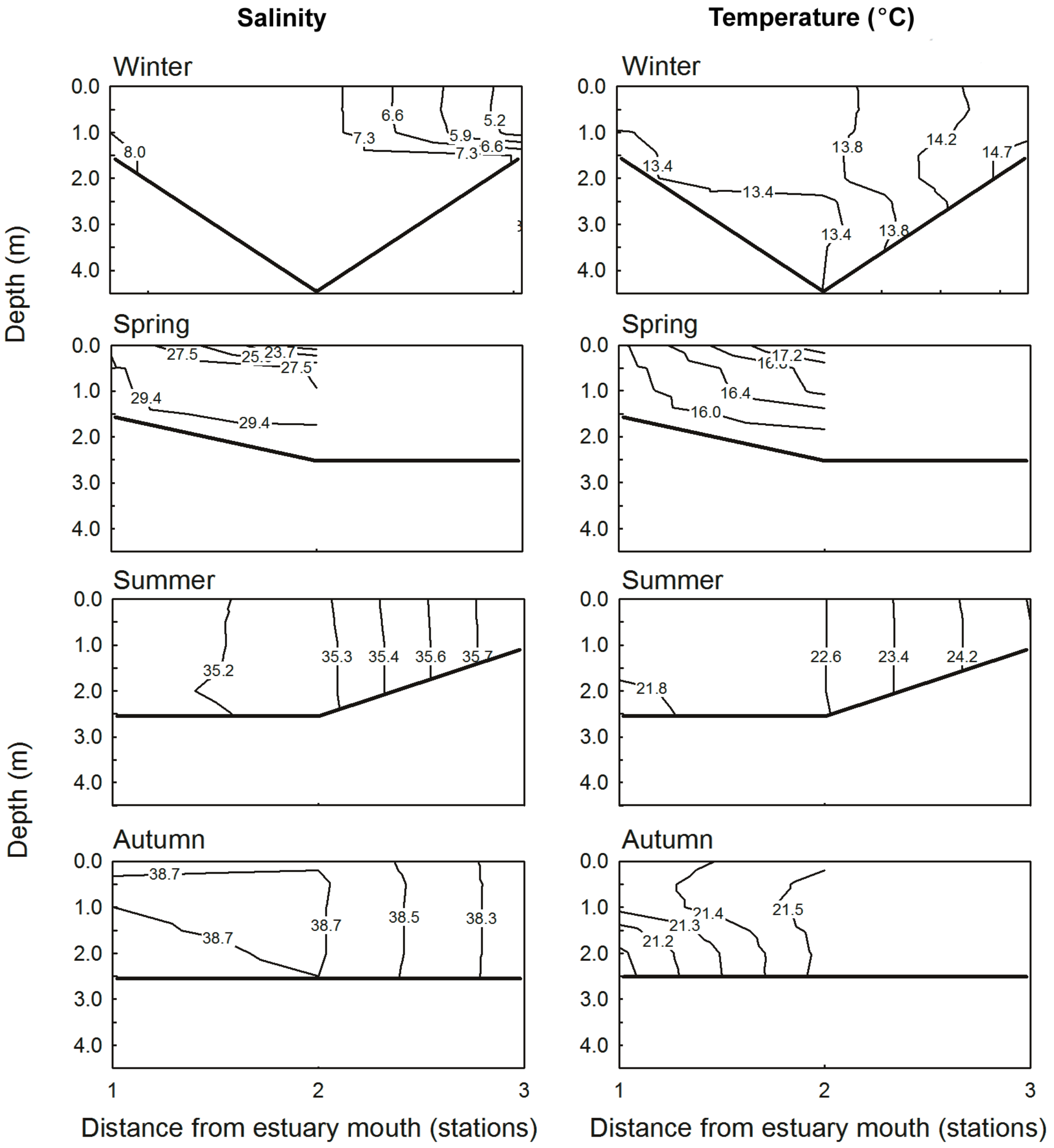

Figure 2.15 Depth profiles of seasonal salinity and temperature recorded at each site in the Bot Estuary. (Note: St 3 was not accessible in spring).

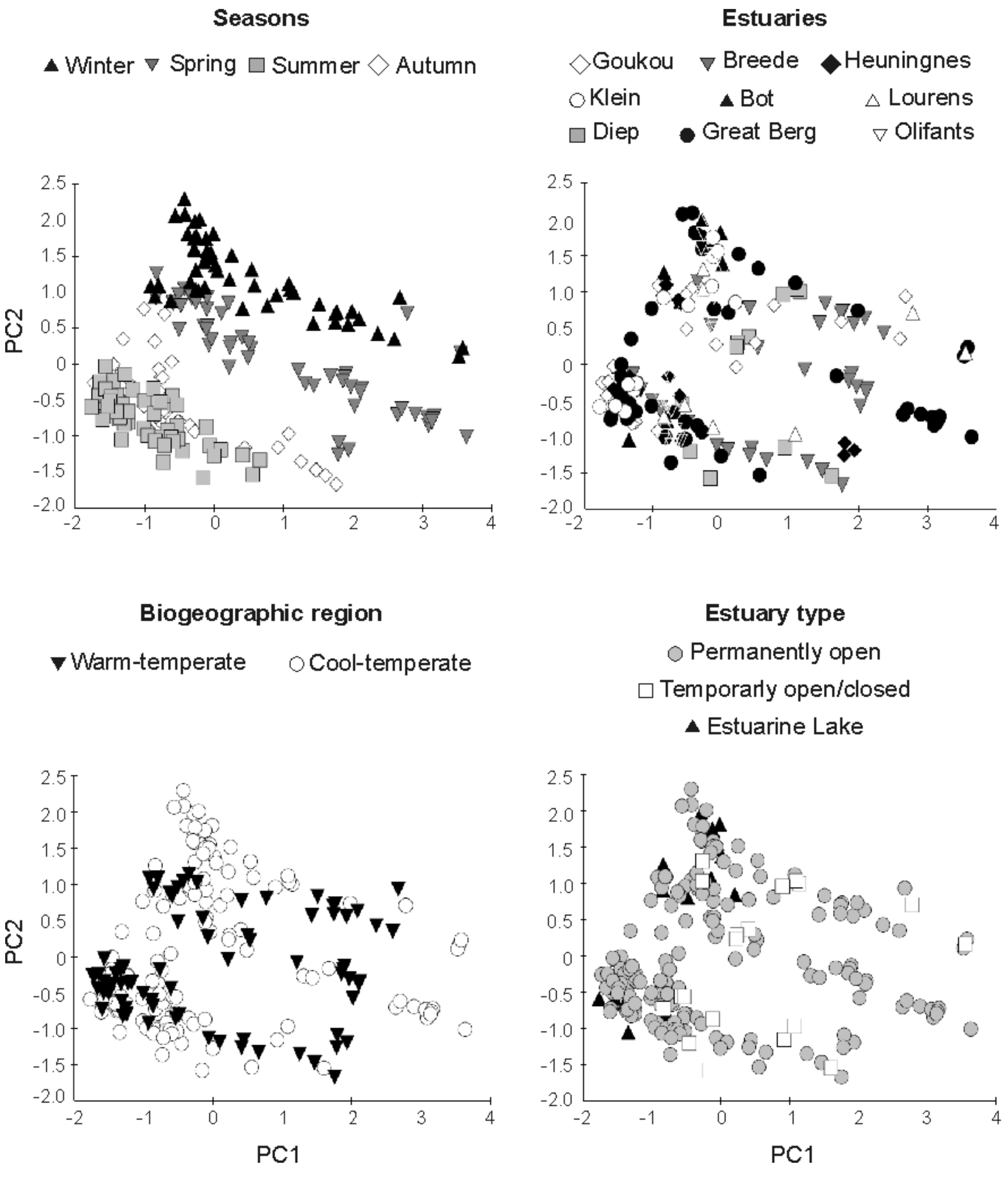

Figure 2.16 PCA ordination plot of physical variables for selected south and west coast South African estuaries. Factors have been superimposed to assess relationship within samples ordination.

Table 2.2 Coefficients in the linear combinations of the physico-chemical variables making up the principal components for selected south and west coast South African estuaries. Percentage variation explained by the principal components is also shown.

Variable	PC1	PC2	PC3
Sal	-0.66	0.2	-0.72
Temperature (ºC)	-0.39	-0.91	0.1
Water transparency (*k*)	0.64	-0.35	-0.68
% Variation	59	28.8	12.2

2.4 DISCUSSION AND CONCLUSIONS

2.4.1 Salinity

The salinity environment in the estuaries studied between 2003 and 2004 is similar to that recorded in previous studies in the same systems (Cliff and Grindley 1982; Carter and Brownlee 1990; Harrison 2004; inter alia). The observed seasonal patterns of salinity reflected in the presence, distribution and extension of salinity zones within estuaries. For instance, hypersaline and euhaline conditions extended throughout the whole Heuningnes, Bot and Klein estuaries in summer and autumn while fresh conditions were recorded in the Lourens Estuary during spring. Mesohaline conditions extended over 14 km in the Olifants Estuary in spring. In the Goukou, Breede, and Great Berg estuaries mesohaline and euhaline conditions were recorded >12 km upstream of the mouths during summer and autumn sampling coinciding with the decrease in river flow (Figure 2.17). On the other hand, homogeneous salinities, as high as 50, have been recorded 12 km upstream of the mouth in the shallow Heuningnes Estuary during open mouth periods (Bickerton 1984). This seasonal variation on salinity zones within estuaries will influence the extension of the highly productive River-Estuary Interface (REI) region (Bate *et al.* 2002).

Salinity was lower in spring rather than in winter. The south and west coast of South Africa is historically characterised by winter rainfall and estuaries exhibit lower salinities during this season (Day 1981b; Harrison 2002). However, in 2003/2004 the Hydrological Information System of the South African Department of Waters Affairs and Forestry (Figure 2.17) registered a higher river flow in the same systems during spring compared to that in any other season. Temporal variations of river flow and rainfall influence the salinity of estuarine waters (Day 1981a; Whitfield & Wooldridge 1994) and dictate the relationship between seasonal salinity and river flow (Schumann *et al.* 1999; Strydom & Whitfield 2000). Therefore, the lower salinities recorded in spring in the estuaries of this study could be the result of the atypical spring river flow registered in the exact same year of sampling.

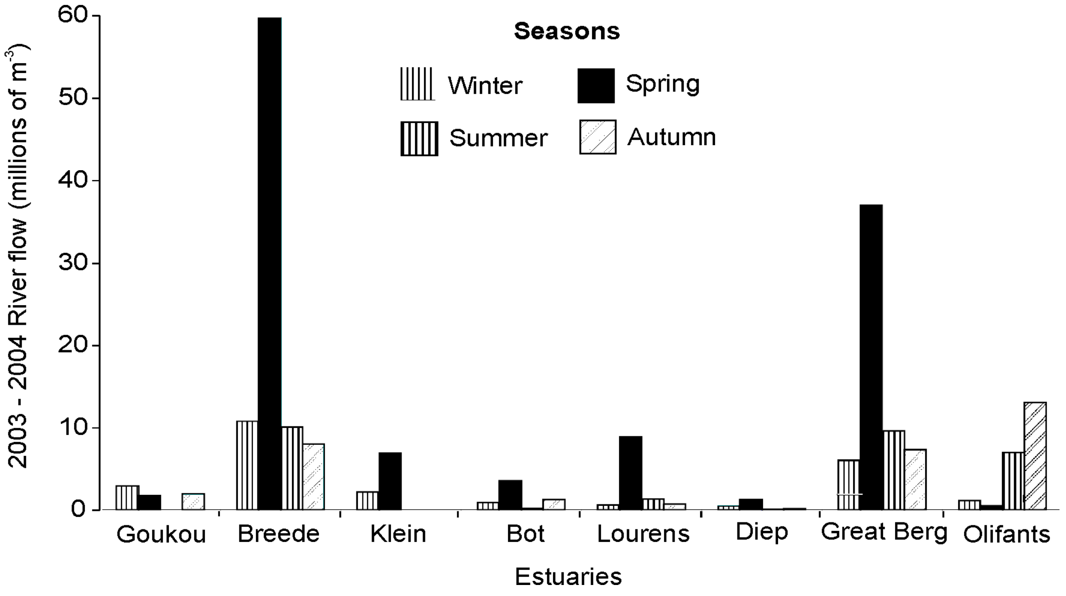

Figure 2.17 2003/2004 river flow in selected south and west coast African estuaries (Data from the Hydrological Information System of the South African Department of Waters Affairs and Forestry).

Mean salinities in PO, TOC and EL systems in this study ranged 9.5 – 26.1, 8.3 – 10.7 and 24.5 – 26.0 respectively and these differences were related to the nature of estuary type. The two TOC estuaries were generally open whereas the two EL systems remained closed during sampling. Physical variables in intermittently open/closed estuaries are dependent on mouth state (Whitfield 1998). During the open state estuaries exhibit lower salinities because of the increase in river flow and during the closed state estuaries exhibit higher salinities because of evaporation. On the other hand, the salinity range in PO estuaries tends to be larger than that of intermittently open systems (Harrison 2004; Strydom *et al.* 2003) because of the regular addition of salt and freshwater (Schumann *et al.* 1999).

2.4.2 Temperature

In this study, summer and winter mean and range temperatures were higher than those recorded in previous studies (see Figure 2.18). Although not statistically confirmed, the increase in South African air temperatures suggested by Kruger and Shongwe (2004) in the last decades coupled with the anomalous event in the Benguela Current system that warmed sea temperatures in 2003 (Rouault & Lutjeharms 2003) may give an explanation to the higher temperatures recorded in the estuaries of this study. Nonetheless, monitoring of estuarine temperatures in these systems is imperative if climate change trends are to be established.

South coast estuaries in this study (Goukou, Breede and Heuningnes) had higher mean temperatures than the west coast estuaries (Olifants, Great Berg and Diep). This is directly attributed to the influence of the cold Benguela Current in the west and the warm Agulhas Current in the south east coast of South Africa (Miller *et al.* 2006; Schumann *et al.* 1999) which give name to biogeographic regions of South Africa (Day 1981c; Harrison 2002).

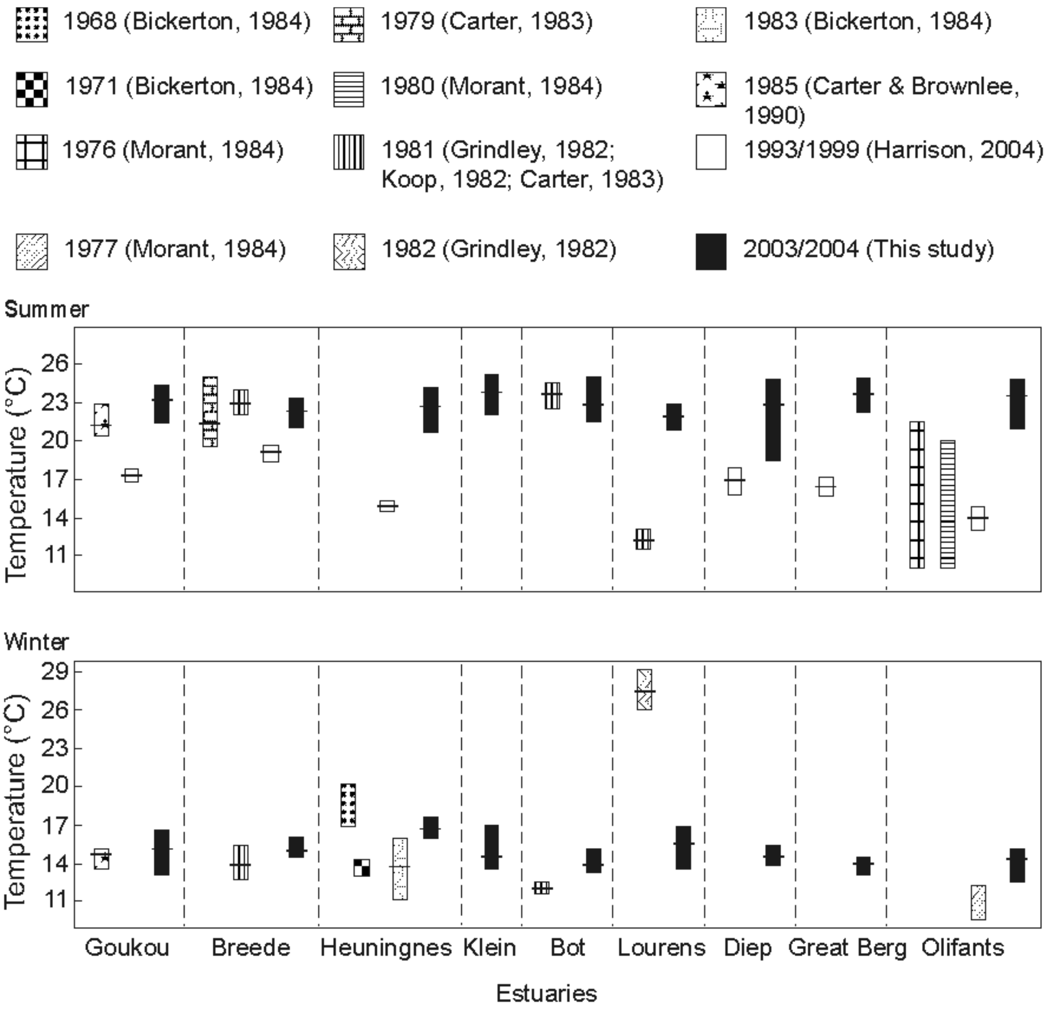

Figure 2.18 Comparison of mean and range for water temperatures recorded in selected south and west coast South African estuaries.

2.4.3 Water transparency

Although comparisons with previous studies need to be done cautiously since Secchi disk readings were not converted to the extinction coefficient (*k*) and the conditions of sampling were not identical, the water transparency results of this study appear to be similar to that from previous studies in the same systems. For instance, after converting previous Secchi disk readings taken in the Breede (Carter 1983), Bot (Grindley 1982), Goukou (Carter & Brownlie 1990), Diep (Grindley & Dudley 1988), Olifants (Morant & Quinn 1984) and Heuningnes (Bickerton 1984) estuaries to the extinction coefficient *k*, the values recorded in the previous studies range 0.001 – 0.09, which is the same water transparency range obtained in this study (Table 2.1). Also, the highest Secchi readings in the literature and in this study are from the Bot Estuary, where Koop (1982) in 1980 recorded underwater visibility of 3 metres or more (k <0.001) and this study recorded a maximum of 4.5 metres. Finally, Grindley and Dudley (1988) note that in the Diep Estuary turbidity was high as a result of siltation steadily increasing in the late 80s and in this study, the Diep estuary was the most turbid of all systems sampled.

Water transparency (k) in this study varied between seasons and appears to be related to changes in mouth condition. For instance, the water column of the EL Klein and Bot systems were clearer than the PO and TOC estuaries (Figure 2.13). Estuarine lake systems are characterised by low river flow (<10 million m^3) and the mouth therefore only opens temporarily during rainy periods (Schumann *et al.* 1999; Whitfield & Bate 2007). In this study, the estuaries remained closed during most sampling trips with exceptions in spring (Klein) and winter (Bot). Therefore, mouth closure resulted in more stable conditions within the systems, which increased water transparency (Day 1981b; Gaughan & Potter 1995). On the other hand, the Olifants Estuary showed clearer waters with no variation between seasons (Figure 2.5). This is attributed to the estuary having more than 30 dams and being one of the most threatened by reduced freshwater input (Whitfield & Wooldridge 1994) since turbidities in estuaries that are subject to damming or water abstraction are typically lower than systems receiving a natural supply of fresh water (Day 1981b).

2.4.4 Multivariate analysis

Salinity and water transparency were the most important variables explaining physico-chemical variability in estuaries sampled. Although based on a single, once-off survey, Harrison (2004) obtained similar results when comparing spring/summer salinity, temperature, dissolved oxygen, water transparency and depth of open and closed systems from the cool-temperate, warm-temperate and subtropical regions. In both studies, temperature did not play an important role explaining the variability amongst systems. River flow affects the salinity and water transparency of estuaries (Day 1981a;

Schumann *et al.* 1999). Therefore, the results support the hypothesis that river flow plays a major influence in defining the physico-chemical environment of South African estuaries (Mallin *et al.* 1993; Morant & Quinn 1999; Schumann *et al.* 1999).

Warm-temperate and cool-temperate estuaries showed unclear differences between their physico-chemical environment in this study. These results agree with those of Harrison (2004) who also found unclear differences between estuaries within these two regions after assessing their physico-chemical characteristics. Nevertheless, Harrison and Whitfield (2006) suggest that due to lower rainfall and runoff, together with the high seawater input and evaporate loss, warm-temperate estuaries generally have higher salinities and are less turbid than cool-temperate. Unlike the study of Harrison (2004) this study includes a temporal dimension that provides a longer data set to compare systems. Consequently, results from this study are not conclusive in delineating or eliminating geographic regions defined by physico-chemical variables alone. The unclear differences between the estuaries in this study can be attributed to the varying boundary between these two regions (Harrison 2002) and to the uneven number of estuaries representing in each region.

Few South African estuaries remain in a near pristine state because of human interference (Morant & Quinn 1999). Grindley and Dudley (1988) note that siltation in the Diep Estuary was steadily increasing in the late 80s and Harrison *et al.* (2000) rated this estuary as being in poor health. Snow and Taljaard (2007) suggest that the volume of wastewater from the sewage treatment plant being discharged into the Diep Estuary has increased substantially. In this study, the Diep estuary was the most turbid of all systems sampled, the mouth never closed and strong odours, indicative of eutrophication of the water column, were present during sampling. Another example is the Heuningnes Estuary that was open during all seasons when under natural conditions the estuary used to behave as a TOC estuary (Bickerton 1984). Throughout the study, the Bot Estuary had excessive growth of the pondweed *Potamogeton pectinatus*, an angiosperm that has been related to water pollution (Ali & Soltan 1996; Demirezen & Aksoy 2006). Although it is difficult in the short term to distinguish human impacts from natural variability in many South African estuaries (Allanson 2001), the previously mentioned characteristics reflect detrimental changes in the natural conditions of the estuaries sampled.

Physico-chemical variables affect the structure of biotic communities in estuaries. For instance, changes in water temperatures alter the structure of faunal and floral communities in estuaries, particularly that of fish communities (Maree *et al.* 2000; Perry *et al.* 2005; Wood & McDonald 1997). Salinity zones define larval fish assemblages in warm- temperate South African estuaries (Strydom *et al.* 2003), limit the distribution of endemic South African fish species (Harrison & Whitfield 2006) and influence primary and secondary productivity in estuaries (Bate *et al.* 2002). On the other hand, turbid waters provide protection from predators to larval and juvenile fishes in estuaries (Cyrus & Blaber 1987). Changes in the physico-chemical characteristics of South African estuaries and surrounding environments are often documented (Morant & Quinn 1999; Whitfield & Wooldridge 1994). Therefore, it is imperative for ecologists to understand the physico-chemical dynamics of estuaries prior to assessing fauna and flora assemblages within estuaries.

CHAPTER 3

DESCRIPTION OF LARVAL FISH COMPOSITION, ABUNDANCE AND DISTRIBUTION IN NINE SOUTH AND WEST COAST ESTUARIES OF SOUTH AFRICA

(This work has been accepted for publication in the journal *African Zoology*)

3.1 INTRODUCTION

Research on estuarine larval fishes in South Africa has mainly focused on systems from the subtropical (Harris & Cyrus 2000; Harris *et al.* 1995a) and warm-temperate (Harrison & Whitfield 1990; Melville-Smith 1981; Melville-Smith & Baird 1980; Strydom & Neira 2006; Strydom *et al.* 2003) regions. This research has focussed on community structure, the role of estuarine environmental conditions and estuary type in characterizing larval fish assemblages and the effects of freshwater supply variations on larval fish communities in estuarine systems. Despite the diversity of work on larval fishes occurring in South African estuaries, no literature exists on larval fishes occurring in estuaries along the south and west coasts. The work by Whitfield (1998) in the Swartvlei Estuary represents the farthest south that such research has taken place, leaving the cool-temperate region of the country, and the boundary region for this climatic zone, unexplored.

Research to date has highlighted the importance of subtropical and warm-temperate estuaries for the late-stage larvae of estuary-associated coastal fish species showing that these larvae contribute significantly to catches (Harris & Cyrus 2000; Strydom *et al.* 2003). Furthermore, this work has stressed how estuary type and associated physico-chemical conditions (Harris *et al.* 2001; Lamberth & Turpie 2003; Viljoen & Cyrus 2002) as well as anthropogenic changes (Strydom & Whitfield 2000; Strydom *et al.* 2002) affect the composition, abundance, distribution and diversity of larval fishes in these estuaries. The role that cool-temperate estuaries, as well as cool/warm-temperate boundary region estuaries, play as nursery areas for larval fishes is unknown. Furthermore, it is unknown to what extent the estuarine dynamics affect these south and west coast larval fish assemblages. This information gap has limited the holistic understanding of larval fish use of estuarine ecosystems along the entire South African coast.

The purpose of this study was to gather baseline information to describe larval fish assemblages in nine south and west coast estuaries and to assess the nursery function of these systems relative to the east and southeast coasts of South Africa. The specific aims were to identify the species composition, abundance and diversity of larval fish assemblages occupying these estuaries, to assess whether larval fish assemblages exhibit the same physical, temporal and spatial patterns as the warm-temperate systems and to provide insights into how biogeographic patterns reflect on larval fish communities. In so doing, this work expects to provide an impetus for further study of planktonic communities occurring in these estuaries.

3.2 MATERIALS AND METHODS

3.2.1 Study area

Estuaries were selected based on the paucity of qualitative and quantitative data on larval fish assemblages in each system as well as accessibility of each to sampling gear. A range of estuary types with differing freshwater input and anthropogenic impact levels were selected (Table 3.1). Permanently open (PO), freshwater-rich (Mean Annual Runoff-MAR >900 $x10^6$ m^3) estuaries included the Olifants, Great Berg and Breede systems while PO, freshwater-deprived (MAR <110 $x10^6$ m^3) estuaries included the Heuningnes and Goukou systems. The Diep and Lourens estuaries represented temporary open/closed (TOC) systems and the Bot and Klein estuaries represented estuarine lake (EL) systems (Figure 3.1).

3.2.2 Fieldwork and laboratory analysis

The study undertook plankton surveys of all estuaries once per season between June 2003 and March 2004. Two modified WP2 plankton nets (570 mm mouth diameter, 200 µm mesh aperture size) fitted with Kalhisco 005 WA 130 flow meters were used. Collection of data was conducted on predetermined days for each estuary associated with the new moon phase and specific tide state and this sampling protocol was standardised across all fieldtrips. Sampling was conducted after dark at GPS fixed equidistant sites along the navigable length of each estuary. Towing speed ranged from 1 - 2 knots and lasted 3 min. Two sub-surface (20 cm below the surface) samples (replicates) were collected per site, per estuary, during all four seasons. Table 3.1 shows the number of sampling sites and the distance sampled in each estuary (see Section 2.3 to view sampling sites along each estuary). The average water volume filtered was 12.21 m^3 (±8.28 SD). Buffered formalin (10%) was used to preserve plankton samples on site.

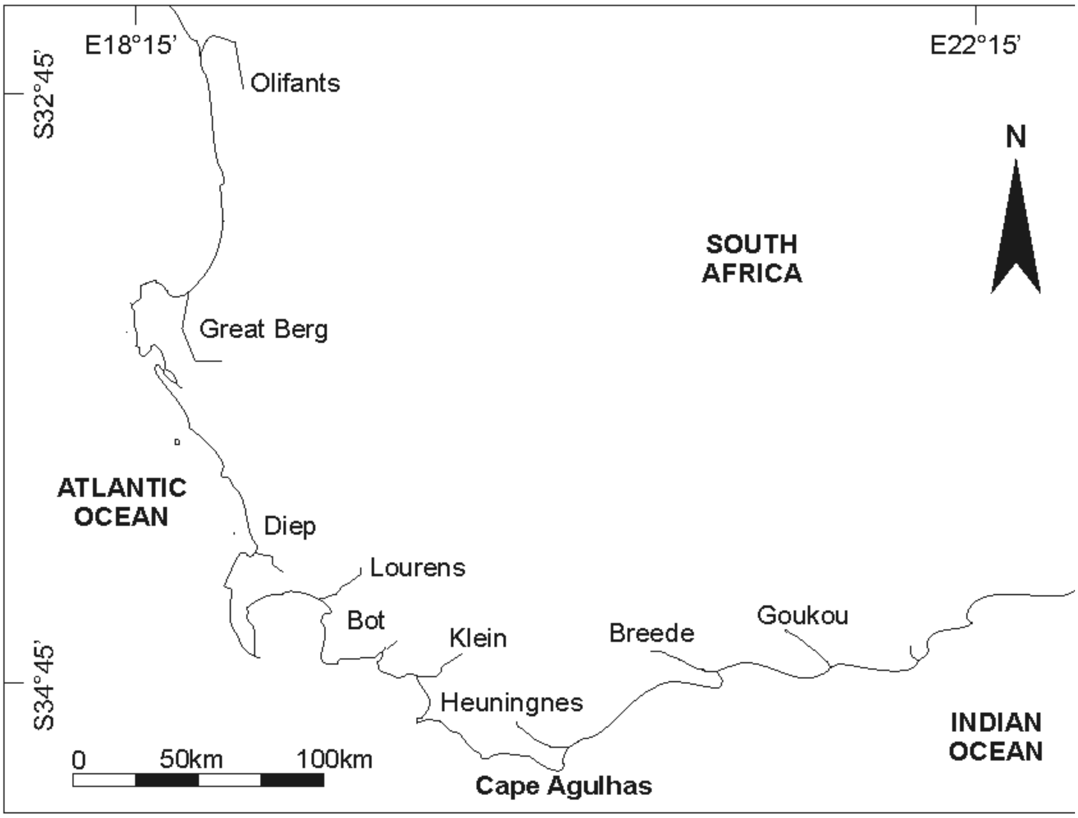

Figure 3.1 Geographical position of estuaries sampled on the south and west coasts of South Africa between June 2003 and March 2004.

Salinity and temperature profiles were obtained at each site using a YSI multiparameter instrument. Recordings were made at 0.5 m intervals between the surface and bottom of the water column. Water transparency (extinction coefficient k) at each site was calculated from Secchi disc (20 cm diameter) depth recordings taken at all sites. The formula used is described in Dawes (1981), where $k = 1.7/D$, and D is Secchi depth in cm. Secchi disc reading were taken during the day. The mouth condition (open/closed) of each estuary at the time of sampling was also noted. Descriptions of the salinity environment within each estuary used a modified Venice System (Table 3.2). Water column salinities obtained from depth profiling at each site were averaged for these description.

In the laboratory, larval and early juvenile fish were removed from the samples. Fish were identified to the lowest possible taxon (Neira *et al.* 1998; Smith & Heemstra 2003). Numbers of individuals per taxa were counted and standardized to number of larvae 100 m^3 of water. The formula used was $D = (N/V) \text{ X } 100 \text{ m}^3$, where D is larval density, N is the number of larvae caught in a specific tow, and V is volume of water filtered on that tow. A maximum of 20 larvae of each species in each sample were measured (N = 5270 individuals) to the nearest 0.1 mm body length and their developmental stage was recorded (Neira *et al.* 1998). Measurements were made using an eyepiece micrometer for larvae <10 mm and Vernier callipers for larger specimens.

Table 3.1 Summary of physical characteristics of selected South African south and west coast estuaries included in this study (source Harrison *et al.* 2000).

	Surface area (ha)	Mean Annual Runoff (m^3)	Bio-geographic region (after Harrison 2005)	Health status			Length sampled (km)	No. sites sampled
				Ichthyofauna	Water quality	Aesthetics	This study	
Permanently open								
Goukou	100	106 $x10^6$	Warm-temperate	Good	Moderate	Good	12	6
Breede	1472	1 873 $x10^6$	Warm-temperate	Good	Good	Good	30	10
Heuningnes	>100	38 $x10^6$	Warm-temperate	Fair	Good	Fair	8	4
Great Berg	6085	913 $x10^6$	Cool-temperate	Fair	Poor	Fair	30	12
Olifants	648	1 008 $x10^6$	Cool-temperate	Fair	Good	Fair	20	10
Estuarine lake								
Klein	>150	40 $x10^6$	Cool-temperate	Good	Good	Good	8	4
Bot	>150	66 $x10^6$	Cool-temperate	Good	Good	Moderate	6	3
Temporarily open/closed								
Lourens	2-150	21 $x10^6$	Cool-temperate	Good	Fair	Poor	0.6	2
Diep	2-150	30 $x10^6$	Cool-temperate	Good	Poor	Poor	3	3

Table 3.2 Modified Venice System for classification of salinity zones for use in south and west coast South African estuaries (from Strydom *et al.* 2003).

Salinity zone	Salinity range
Fresh	0 - 0.49
Oligohaline	0.5 - 4.9
Mesohaline	5.0 - 17.9
Polyhaline	18.0 - 29.9
Euhaline	30.0 - 35.9
Hypersaline	≥ 36.0

3.2.3 Data analysis

Normality and homogeneity of variances assumptions were not met and the Kruskal-Wallis (*H*) ANOVA test was used to assess differences in fish diversity and density between estuaries, estuary types, seasons and salinity zones and within each estuary. Diversity indices were calculated to describe the larval fish assemblages throughout the study, per estuary, per season and per salinity zone. The Margalef's species richness (d) and Shannon-Wiener‘s diversity (H’) indices were used. Spearman Rank Correlation was used to ascertain whether environmental variables displayed any significant relationship with fish density. In these analyses, actual replicate values of fish density per site were used, i.e. no data was averaged prior to statistical test. In all analyses, statistical significance was considered at a level of P <0.05. These analyses were conducted using the PRIMER v5.2.9 and STATISTICA 8.0 statistical software packages.

Group average hierarchical cluster analysis was used to ascertain non-random patterns or structure in larval fish assemblages in estuaries, seasons and salinity zones. The number of species was reduced to those accounting for more than 3 % of the total abundance at any one site, reducing the effects of rare species (Clarke & Warwick 1994). One transformation was to provide information related to the productivity of the estuary and freshwater flow Log_{10} (x+1), i.e. REI regions, and the other one to provide information related the biogeography and estuary type. Species densities were Log_{10} (x+1) transformed or presence-absence transformed. Bray-Curtis similarity matrices were generated for estuaries, seasons and salinity zones. The ANOSIM routine was used to assess differences between *a priori* groups (i.e. estuaries, estuary types, seasons, zones) and groups of larval fish assemblages resulting from cluster analyses. The SIMPER routine was used to establish the contribution of each species to the average dissimilarity between groups of samples. The cut-off for species contribution to the dissimilarity was 50 %. Diversity indices were calculated to describe the larval fish assemblages throughout the study, per estuary, per season and per salinity zone. The Margalef's species richness (d) and Shannon-Wiener‘s diversity (H’) indices were used. These analyses were conducted using the PRIMER v5.2.9 statistical software package.

3.3 RESULTS

3.3.1 Composition and estuary association

A total of 49 274 larval and early juvenile fishes were caught in this study, comprising nine orders, 20 families, 29 genera, and 47 taxa (Table 3.3). Thirty-one taxa were identified to species, three to genus, and 11 to family levels. Two were too small to be identified. The majority (70 %) of identified species are endemic to the southern African coast. The family Gobiidae contributed 10 species to the total catch, and the families Blenniidae, Mugilidae and Sparidae contributed four species each to the total catch. Four families accounted for 98.1 % of the total larvae caught. These were the Clupeidae (78.8 %), predominantly represented by *Gilchristella aestuaria*; Gobiidae (13.7 %), mostly *Caffrogobius* species; Blenniidae (4.5 %), mainly *Omobranchus woodi* and *Parablennius* sp; and Atherinidae (1.9 %), represented by *Atherina breviceps*. Only seven species accounted for 93.4 % of the total catch, namely *G. aestuaria* (78.8 %), *Caffrogobius gilchristi* (6.2 %), *Psammogobius knysnaensis* (3.5 %), *C. nudiceps* (2.5 %), *Parablennius* sp. (2.4 %), *O. woodi* (2.1 %) and *A. breviceps* (1.9 %).

Fishes that were positively identified (31 species) were categorized according to the degree to which the species is dependent on South African estuaries (Whitfield 1998).

Estuary-resident fishes (categories Ia and Ib) contributed 21 % of the species identified and accounted for 96.4 % of the total catch. On the other hand, estuary-dependent marine species (categories IIa, IIb and IIc) accounted for 23 % of the species identified but contributed <1 % of the total catch. Marine stragglers (category III) contributed 17 % of the species identified but were scarce in numbers (<1 % of the total catch). No freshwater migrant (category IV) species were found (Table 3.5) in any of the estuaries sampled and the mullet *Myxus capensis* was the only catadromous migrant (categories Va and Vb) recorded (<1 % of the total catch), although the facultative catadromous species *Mugil cephalus* and *Liza richardsonii* were also recorded. Unidentified taxa contributed 34 % of the total species identified and 3.2 % of the total catch.

All larval fish developmental stages were recorded. Larvae in the preflexion stage were dominant, comprising 59 % of the total larvae measured, followed by the yolk sac (15.3 %), flexion (12.7 %), postflexion (12.0 %) and early juvenile (1 %) stages. Estuary-resident species were found in all developmental stages with 86.4 % being yolk sac, preflexion and flexion stages, 13.0 % postflexion and <1 % early juveniles. Estuary-dependent marine species occurred in all but yolk sac stages. Preflexion and flexion larvae accounted for 56.5 % of the larvae measured, whereas postflexion larvae and early juveniles accounted for 10.2 % and 31.5 % respectively. Leptocephalus and glass eel stages of *Ophisurus serpens* accounted for the remaining 1.8 %. Marine stragglers were predominantly in yolk sac, preflexion and flexion (96.4 %) with a small representation by postflexion larvae (3.6 %). Unidentified taxa in yolk sac, preflexion and flexion stages (94.6 %) accounted for most of the larvae measured while postflexion larvae made a small contribution (5.4 %).

Table 3.3 Species composition, total catch, mean density, mean length and range, developmental stage and estuary association (after Whitfield 1998) for larval and early juvenile fishes in selected south and west coast estuaries of South Africa. +=Endemic to southern Africa.

			Body length (mm)		**Developmental stage**								**Estuary occurrence**								
Taxa	**Total catch (%)**	**Mean density (larvae 100m^{-3})**	Mean	Range	Yolk sac	Preflexion	Flexion	Postflexion	Juvenile	Leptocephalus	Glass eel	**Estuary association**	Goukou	Breede	Heuningnes	Klein	Bot	Lourens	Diep	Great Berg	Olifants
Gilchristella aestuaria+	78.8	1367.8	7.9	1 - 43.1	*	*	*	*	*			Ib	*	*	*	*	*	*	*	*	*
Caffrogobius gilchristi+	6.2	277.1	2.9	1.5 - 29.2	*	*		*	*			Ib	*	*	*	*	*			*	
Psammogobius knysnaensis+	3.5	96.3	2.9	1.4 - 31.3	*	*	*	*	*			Ib	*	*	*	*	*	*		*	*
Caffrogobius nudiceps+	2.5	85.9	3.7	1.7 - 32.3	*	*	*	*	*			Ib	*	*	*					*	*
Parablennius sp.	2.4	391.6	3.7	2 - 10.4	*	*	*	*				?	*	*	*					*	*
Omobranchus woodi+	2.1	174.3	2.9	2.0 - 14	*	*		*				Ia	*	*	*					*	
Atherina breviceps+	1.9	92.5	6.3	3.7 - 47	*	*	*	*	*			Ib	*		*	*	*			*	*
Argyrosomus cf. *japonicus*	<1	34.3	2.2	1.8 - 2.8		*						IIa		*						*	
Austroglossus cf. *pectoralis*	<1	18.0	4.3	-		*						III		*							
Blenniid 1	<1	6.3	2.6	-		*						?	*								
Caffrogobius sp.	<1	5.2	2.4	2.4 - 2.5		*						?	*								
Chorisochismus dentex	<1	33.8	4.2	3.6 - 4.7		*						III	*	*	*						*
Clinus cf. *superciliosus*+	<1	9.3	23.5	18 - 28				*	*			Ib								*	*

Table 3.3 Continued...

			Body length (mm)		**Developmental stage**								**Estuary occurrence**								
Taxa	**Total catch (%)**	**Mean density (larvae 100m^{-3})**	Mean	Range	Yolk sac	Preflexion	Flexion	Postflexion	Juvenile	Leptocephalus	Glass eel	**Estuary association**	Goukou	Breede	Heuningnes	Klein	Bot	Lourens	Diep	Great Berg	Olifants
Clupeid 1	<1	4.9	17.8	-				*				?								*	
Cynoglossus capensis+	<1	7.8	2.9	2 - 3.8		*						III								*	
Cynoglossus zanzibarensis	<1	4.2	2.9	2.8 - 2.9		*						III	*	*							
Diplecogaster megalops	<1	27.3	2.3	1.8 - 2.9		*						III			*						
Diplodus capensis+	<1	10.2	5.8	4 - 7.5			*	*				IIc	*							*	
Eckloniaichthys scylliorhiniceps	<1	8.3	4.3	-				*				III								*	
Engraulis japonicus+	<1	27.4	4.4	2.1 - 7		*	*					III	*	*							
Gobiid 1	<1	28.1	2.8	1.7 - 3.5	*	*						?	*	*	*	*			*		
Gobiid 2	<1	19.0	2.6	1.8 - 4.2		*	*					?	*	*		*					
Gobiid 3	<1	65.4	4.9	2.2 - 8.7	*	*	*	*				?		*						*	
Gobiid 4	<1	6.1	10.8	7.2 - 14.4				*				?			*						
Gobiid 5	<1	3.9	8.5	-				*				?								*	
Heteromycteris capensis+	<1	11.9	2.1	1.7 - 3.2		*	*					IIb		*							
Hyporhamphus capensis+	<1	5.8	5.5	4.8 - 6.2	*		*	*				Ia		*						*	

Table 3.3 Continued...

			Body length (mm)		**Developmental stage**								**Estuary occurrence**								
Taxa	**Total catch (%)**	**Mean density (larvae 100m^{-3})**	Mean	Range	Yolk sac	Preflexion	Flexion	Postflexion	Juvenile	Leptocephalus	Glass eel	**Estuary association**	Goukou	Breede	Heuningnes	Klein	Bot	Lourens	Diep	Great Berg	Olifants
Iso natalensis	<1	6.5	5.3	-		*						III	*								
Liza dumerilii	<1	9.5	21.9	-					*			IIb		*							
Liza richardsonii+	<1	86.5	29.0	20.9 - 57.7		*			*			IIc						*	*		
Monodactylus falciformis	<1	6.4	5.6	5.0 - 6.3			*					IIa			*						
Mugil cephalus	<1	13.7	23.6	17 - 41.1				*	*			IIa		*						*	*
Myxus capensis+	<1	19.6	8.8	6.6 - 9.8				*				Vb		*	*					*	
Omobranchus sp.	<1	11.3	3.6	-	*	*						?		*						*	
Ophisurus serpens	<1	23.9	92.1	89.2 - 97					*	*	*	IIc			*					*	*
Redigobius dewaali+	<1	73.9	2.0	1.4 - 2.7		*						Ib	*	*							
Rhabdosargus holubi+	<1	5.2	9.9	9.5 - 10.4				*				IIa	*		*						
Sillaginid 1	<1	3.9	3.6	-	*							?								*	
Sillago sihama	<1	9.3	4.9	4.5 - 5.3		*	*					IIc	*	*						*	
Solea turbynei+	<1	15.8	3.2	1.9 - 9.4		*	*	*				IIb		*	*					*	*
Sparid 1	<1	7.0	3.0	2.5 - 3.5	*	*	*					?	*							*	

Table 3.3 Continued...

Taxa	**Total catch (%)**	**Mean density (larvae 100m^{-3})**	**Body length (mm)**		**Developmental stage**							**Estuary association**	**Estuary occurrence**								
			Mean	Range	Yolk sac	Preflexion	Flexion	Postflexion	Juvenile	Leptocephalus	Glass eel		Goukou	Breede	Heuningnes	Klein	Bot	Lourens	Diep	Great Berg	Olifants
Sparodon durbanensis+	<1	6.7	9.4	-				*				III		*	*						
Syngnathus temminckii	<1	25.0	15.9	8 - 139.2				*	*			Ib	*	*	*	*	*			*	*
Tetraodontid 1	<1	5.5	2.3	1.4 - 3.2	*	*						?	*	*						*	
Tripterygiid 1	<1	12.9	11.0	5 - 13.9		*	*	*				?	*								*
Unidentified species 1	<1	9.5	2.2	1.9 - 2.5		*						?		*							
Unidentified species 2	<1	15.6	7.0	-			*					?						*			

3.3.2 Temporal and spatial trends in larval fish density

Densities of larval fishes varied between estuaries (H = 47.09, *P* <0.001) with the Great Berg Estuary accountable for 71 % of the total catch predominantly the clupeid *G. aestuaria* (Table 3.4). Larval fish densities also varied between estuary types (H = 7.38, *P* <0.05) where PO estuaries had higher densities than TOC systems (Table 3.4). Fish density was significantly higher (H = 155.33, *P* <0.001) in summer (Table 3.5). Larval fish densities also varied between salinity zones (H = 60.17, *P* <0.001) with the mesohaline zone generally having higher densities than other zones sampled across all estuaries in the region. In the Great Berg and Olifants estuaries, the fresh and oligohaline zones yielded higher larval fish densities and this was attributed to the high numbers of newly hatched clupeid *G. aestuaria.*

3.3.3 Temporal and spatial trends in larval fish diversity

The families Clupeidae and Gobiidae were present in all estuaries sampled (Table 3.3) and these two families together with the families Blenniidae and Mugilidae were present in all seasons sampled. The clupeid *G. aestuaria* was the only species occurring in all estuaries. This species together with the pipefish *Syngnathus temminckii*, the gobies *Caffrogobius nudiceps*, C. *gilchristi, P. knysnaensis* and Gobiid 1 also occurred in all seasons. The estuary-residents *C. nudiceps, Redigobius dewaali, O. woodi*, all estuary-dependent marine species, with the exception of the mullet *Liza richardsonii* and all the marine stragglers in the catch were found exclusively in PO estuaries during the study period (Table 3.3).

Species richness (H = 40.70, *P* <0.01) and species diversity (H = 40.00, *P* <0.001) differed between estuaries. The PO estuaries had richer (H = 18.20, *P* <0.001) and more diverse (H = 14.32, *P* <0.001) larval fish assemblages than TOC and EL systems (Table 4). Species richness (H = 130.58, *P* <0.001) and species diversity (H = 103.29, *P* <0.001) also varied between seasons sampled. Summer had a richer and more diverse larval fish assemblage than other seasons sampled in south and west coast systems. Species richness (H = 97.02, *P* <0.001) and species diversity (H = 97.43, *P* <0.001) also varied between salinities zones. The euhaline zone (30.0 – 35.9) showed a richer and more diverse larval fish community than other zones (Table 3.5).

3.3.4 Community analysis

A cluster analysis of estuaries based on larval fish densities (Figure 3.2) showed strong differences in community structure between estuaries (R = 0.86, *P* <0.01). An arbitrary selected 55 % similarity level yielded five groups. Group 1 was formed by the freshwater-deprived TOC Diep and Lourens estuaries, situated on the west coast. The lack of the blenniid *Parablennius* sp. and the estuary-resident *C. nudiceps,* compounded by the lower density of the clupeid *G. aestuaria* (SIMPER) were responsible for this grouping. Group 2 comprised the PO, freshwater-rich Olifants and Great Berg estuaries, also situated on the west coast. Higher densities of the blenniid *Parablennius* sp, the gobiid *C. nudiceps* and *G. aestuaria,* together with lower densities of the gobiid *C. gilchristi* were responsible for this separation (SIMPER). Groups 3 to 5 included all south coast systems. The PO, freshwater-deprived Heuningnes Estuary formed group 3 and the lower abundance of *G. aestuaria* but higher densities of the *C. gilchristi* (SIMPER) were responsible for this grouping. Group 4 comprised the EL, freshwater-deprived Bot and Klein systems. Group 5 comprised the PO estuaries, freshwater-deprived Goukou and freshwater-rich Breede estuaries. The separation of these two groups was attributed to the higher abundance of *A. breviceps* and *S. temminckii* in the Bot and Klein estuaries and to the exclusive presence of the estuary-residents *O. woodi* (Blenniidae) and *R. dewaali* (Gobiidae) in the Goukou and Breede estuaries (SIMPER).

Table 3.4 Summary of abiotic and biotic characteristics of selected South African south and west coast estuaries sampled from winter 2003 to autumn 2004 (*K* = extinction coefficient).

	Goukou	**Breede**	**Heuningnes**	**Klein**	**Bot**
Estuary Type	Permanently open	Permanently open	Permanently open	Estuarine Lake	Estuarine Lake
Latitude	34°22’41’’ S	34°24’16’’ S	34°42’51’’ S	34°25’07’’ S	34°22’01’’ S
Longitude	21°25’22’’ E	20°50’57’’ E	20°06’54’’ E	19°18’15’’ E	19°05’55’’ E
Environmental variables: mean (range)					
Salinity	21.11 (0.00-35.06)	7.92 (0.00-32.36)	25.92 (1.90-35.76)	24.20 (6.68-34.34)	27.26 (4.76-38.73)
Temperature (°C)	19.58 (12.94-24.42)	19.28 (14.27-23.25)	19.79 (15.82-24.24)	18.73 (13.45-25.22)	19.00 (13.18-25.05)
Water transparency (*k*)	0.02 (0.01-0.060)	0.03 (0.01-0.05)	0.02 (0.01-0.09)	0.01 (0.01-0.03)	0.01 (0.00-0.03)
Diversity: mean (range)					
Total species (Families)	22 (12)	27 (14)	18 (11)	8 (5)	5 (4)
Species richness (d)	0.28 (0.00 - 1.32)	0.24 (0.00 - 1.73)	0.27 (0.00 - 1.40)	0.21 (0.00 - 0.81)	0.06 (0.00 - 0.49)
Species diversity (H')	0.38 (0.00 - 1.51)	0.34 (0.00 - 1.91)	0.49 (0.00 - 1.98)	0.39 (0.00 - 1.44)	0.07 (0.00 - 0.72)
Dominant families (% of total catch)	Gobiidae (58.5)	Clupeidae (77.8)	Gobiidae (89.4)	Clupeidae (60.8)	Clupeidae (79)
	Blenniidae (28.0)	Gobiidae (16.0)	Atherinidae (4.2)	Gobiidae (36.1)	Gobiidae (19.9)
	Clupeidae (12.1)	Blenniidae (4.0)	Blenniidae (3.4)	Syngnathidae (2.1)	Atherinidae (<1)

Table 3.4 Continued...

	Goukou	**Breede**	**Heuningnes**	**Klein**	**Bot**
Dominant species (% of total catch)	*C. gilchristi* (45.5) *O. woodi* (27.7) *G. aestuaria* (12.1)	*G. aestuaria* (77.8) *R. dewaali* (8.9) *O. woodi* (3.8)	*C. gilchristi* (72.9) *P. knysnaensis* (12.5) *A. breviceps* (4.2)	*G. aestuaria* (60.8) *C. gilchristi* (29.2) *P. knysnaensis* (6.6)	*G. aestuaria* (79) *P. knysnaensis* (19.8) *A. breviceps* (<1)
Fish larvae density (larvae 100m^{-3})					
Mean	120	129	103	173	549
Range	0 - 2 696	0 - 4 234	0 - 2 415	0 - 1 666	0 - 5 538
Estuarine association (% of total catch)					
Estuary-resident (I)	98.2	97.4	94.5	99.8	100
Estuary-dependent marine species	0.1	1	1.1	-	-
Marine stragglers (III)	0.2	0.8	0.3	-	-
Catadromous migrants (V)	-	<0.1	0.3	-	-
Unidentified	1.5	0.7	3.6	0.2	-

Table 3.4 Continued...

	Lourens	**Diep**	**Great Berg**	**Olifants**
Estuary Type	Temporarily open/closed	Temporarily open/closed	Permanently open	Permanently open
Latitude	34°06’03’’ S	33°54’28’’ S	32°46’13’’ S	31°42’01’’ S
Longitude	18°48’49’’ E	18°28’19’’ E	18°08’40’’ E	18°11’16’’ E
Environmental variables: mean (range)				
Salinity	7.53 (0.00-28.54)	10.15 (0.66-33.82)	15.17 (0.00-34.33)	16.50 (0.00-34.14)
Temperature (°C)	18.19 (13.31-23.72)	18.76 (13.57-24.82)	18.90 (13.01-24.94)	18.70 (12.35-24.83)
Water transparency (*k*)	0.03 (0.02-0.07)	0.04 (0.02-0.09)	0.03 (0.07-0.09)	0.02 (0.01-0.03)
Diversity: mean (range)				
Total species (Families)	4 (3)	3 (3)	27 (17)	12 (11)
Species richness (d)	0.07 (0.00 - 0.29)	0.02 (0.00 - 0.20)	0.32 (0.00 - 2.33)	0.16 (0.00 - 0.97)
Species diversity (H')	0.22 (0.00 - 0.69)	0.02 (0.00 - 0.28)	0.47 (0.00 - 1.79)	0.25 (0.00 - 1.42)
Dominant families (% of total catch)	Gobiidae (70.6) Clupeidae (24.5) Mugilidae (3.9)	Clupeidae (97.8) Mugilidae (1.2) Gobiidae (<1)	Clupeidae (88.9) Gobiidae (5.2) Blenniidae (2.8)	Gobiidae (37.6) Blenniidae (30.8) Clupeidae (24.2)

Table 3.4 Continued...

	Lourens	Diep	Great Berg	Olifants
Dominant species (% of total catch)	*P. knysnaensis* (70.6) *G. aestuaria* (24.5) *L. richardsonii* (3.9)	*G. aestuaria* (97.8) *L. richardsonii* (1.2) Gobiid 1 (<1)	*G. aestuaria* (88.9) *C. nudiceps* (2.8) *Parablennius* sp. (2.7)	*Parablennius* sp. (30.8) *C. nudiceps* (24.9) *G. aestuaria* (24.2)
Fish larvae density (larva 100m^{-3})				
Mean	83	270	623	45
Range	0 - 608	0 - 2 603	0 - 33 472	0 - 1 744
Estuarine association (% of total catch)				
Estuary-residents (I)	95.1	97.8	96.4	64.9
Estuary-dependent marine species	3.9	1.2	<0.1	2.3
Marine stragglers (III)	-	-	<0.1	1.7
Catadromous migrants (V)	-	-	<0.1	-
Unidentified	1.0	1.0	3.5	31.1

Table 3.5 Temporal and spatial variation in species richness, diversity and density indices for fish larvae assemblages in south and west coast estuaries.

	No. of species	**Species richness (d)**	**Species diversity (H')**	**Density (larvae 100 m^{-3})**		
	Range	**Range**	**Range**	**Mean**	**Median**	**Range**
Season						
Winter	0 - 4	0 - 0.70	0 – 0.19	32	0	0 - 695
Spring	0 - 5	0 - 0.80	0 – 0.47	153	10	0 - 4216
Summer	0 - 20	0 - 2.33	0.09 - 0.81	2211	476	0 - 33472
Autumn	0 - 8	0 - 1.40	0 – 0.88	115	41	0 - 1452
Salinity zone						
Fresh	0 - 3	0 - 0.09	0 - 0.13	64	0	0 - 695
Oligohaline	0 - 3	0 - 0.14	0 - 0.21	295	0	0 - 4234
Mesohaline	0 - 20	0 – 0.50	0 – 0.66	1421	20	0 - 33472
Polyhaline	0 - 8	0 – 0.42	0 – 0.72	333	66	0 - 4534
Euhaline	0 - 12	0.11 - 1.22	0.12 - 1.50	687	109	0 - 6796
Hypersaline	1	-	-	335	33	5 - 1452

The analysis based on species presence or absence showed clear differences in community structures between estuary types (R = 0.944, P <0.01). The TOC Diep and Lourens estuaries separated from the PO and EL systems and formed group 1 (Figure 3.2). The exclusive presence of the estuary-dependent marine species *L. richardsonii* and the lack of the estuary-resident *S. temminckii, A. breviceps* and *C. gilchristi* were the reasons for this separation (SIMPER). The EL Bot and Klein systems formed group 2 (Figure 3.2). This was mainly attributed to the absence of the estuary-residents *C. nudiceps* and *O. woodi,* the estuary-dependent marine species namely, *Solea turbynei* (Soleidae), *Ophisurus serpens* (Ophichthidae), *Mugil cephalus* (Mugilidae), and the marine straggler species namely, *Chorisochismus dentex* (Gobiesocidae) and *Parablennius* sp (SIMPER). The rest of estuaries, all PO systems, clustered together to form group 3, which was characterized by a higher number of species, the presence of estuary-dependent marine species and the estuary-residents *C. nudiceps* and *O. woodi,*

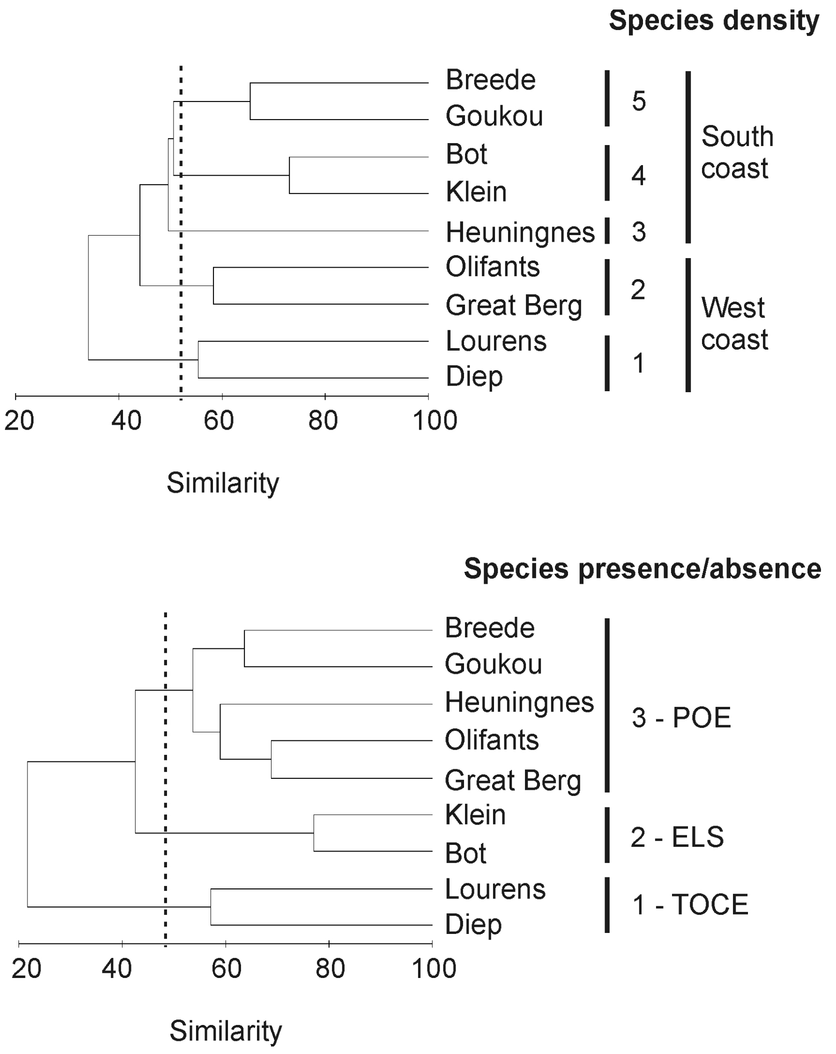

Figure 3.2 Dendrograms showing the clustering of selected south and west coast estuaries based on species density and species presence or absence.

Seasons showed differences in larval fish density. Although seasons were not significantly separated (R = 1, *P* >0.05), winter was only 43 % similar to the other three seasons (Figure 3.3) and this was attributed to very low densities of the estuary-resident *P. knysnaensis*, *Parablennius* sp, and the marine straggler *C. dentex* (SIMPER). Low densities of common estuary-residents, *G. aestuaria, C. gilchristi, R. dewaali* and *A. breviceps* accounted for the separation of spring from summer and autumn (SIMPER). Summer was separated from autumn at the 65 % similarity level and this was mainly attributed to densities of estuary-resident species peaking during this period (SIMPER). The cluster analysis of seasons based on species presence or absence (Figure 3.3) showed similar results (R = 1, *P* >0.05). The lack of common estuary-dependent marine species, i.e. *L. richardsonii, Sillago sihama* (Sillaginidae) and *S. turbynei,* separated (SIMPER) winter from the other seasons. In this cluster analysis, spring was separated from summer and autumn due to the lack of the catadromous *M. capensis,* the estuary-residents *O. woodi* and *R. dewaali* and the estuary-dependent marine sparid *R. holubi* (SIMPER).

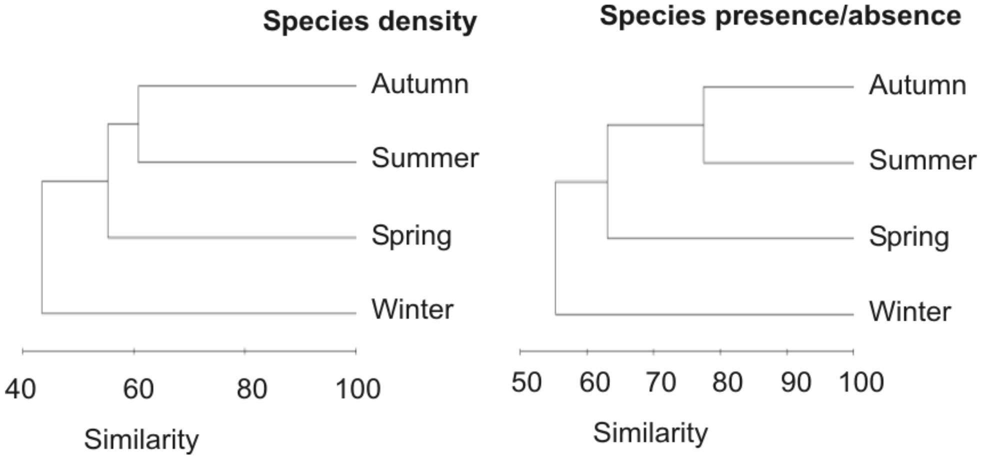

Figure 3.3 Dendrograms showing the clustering of seasons based on species density and species presence or absence.

The salinity environment along the length of each estuary resulted in differences in species density and species presence or absence. Three groups were well separated (R = 0.99, *P* <0.05) in the cluster analysis based on species density: Group 1 comprised the euhaline, polyhaline and mesohaline zones; Group 2 was formed by the fresh zone; and Group 3 linked the hypersaline and oligohaline zones together (Figure 3.4). Group 1 had larger densities of *Parablennius* sp and of estuary-resident species (SIMPER). Group 2 included the fresh zone and was 47 % similar to group 3. The reason for this grouping was a higher density of *P. knysnaensis*, *C. nudiceps* but lower densities of *G. aestuaria* (SIMPER). On the other hand, hypersaline and oligohaline zones, group 3, had considerably high densities of the estuary-resident *G. aestuaria* (SIMPER). The same analysis of zones based on species presence or absence showed similar results (R =

0.99, $P < 0.05$). The hypersaline zone appeared as an outlier (Group 1) (Figure 3.4) due to the absence of most species in this zone except for *G. aestuaria* and *A. breviceps* (SIMPER). The euhaline, mesohaline and polyhaline zones grouped together (Group 2). The high similarity level (67 %) of the fresh and oligohaline zones (Group 3) was attributed to the lack of marine stragglers and estuary-dependent marine species, which occurred only in the euhaline, mesohaline and polyhaline zones (SIMPER).

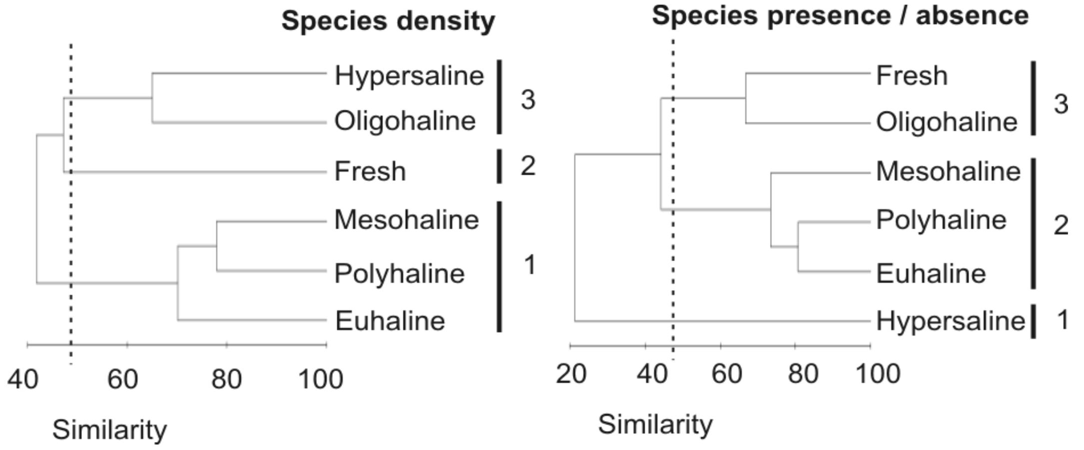

Figure 3.4 Dendrograms showing the clustering of salinity zones based on species density and species presence or absence. The numbers indicated the groups formed at the arbitrary selected similarity level.

3.3.5 Relationships between environmental variables and larval fish assemblages

The Goukou, Heuningnes, Klein and Bot estuaries showed predominantly euhaline conditions whereas the Breede, Lourens, Diep, Great Berg and Olifants estuaries had predominantly mesohaline conditions during the study period (Table 3.4). In general, summer and autumn were characterised by predominantly polyhaline conditions, while winter and spring were characterised by mesohaline conditions in the estuaries sampled. A freshwater pulse in the Great Berg Estuary was recorded during spring with salinities <0.5 found 14 km from the mouth and hypersaline (>35.9) conditions were recorded in the Bot Lake system during summer and autumn. All taxa and individual species densities, species richness and species diversity correlated positively with salinity across all estuaries (Table 3.6). The Breede, Diep and Great Berg estuaries were characterised by higher turbidity and the Goukou, Heuningnes, Klein, Bot and Olifants estuaries had lower turbidity. Very high turbidity occurred in spring and in summer very low turbidity was measured. Larval fish densities, species richness and species diversity) correlated negatively with water transparency across all estuaries (Table 3.6). There were minor differences in temperature between estuaries. Summer - autumn temperatures ranged from 21 – 26 °C and winter – spring temperatures ranged from 13 – 18 °C. Similar to salinity, temperature was correlated positively with all taxa and individual species densities, species richness and species diversity. The salinity and temperature of the water column in the estuaries were partially- to well-mixed. Exceptions were the PO Heuningnes Estuary and the two TOC estuaries that were predominantly stratified. The EL Diep Estuary remained open during sampling and the Lourens Estuary closed during autumn sampling. The two EL systems are artificially breached, every two years in the case of the Bot system (van Niekerk *et al.* 2005), and during this study they were only found open in winter (Bot) and spring (Klein) sampling.

All taxa and individual species densities, species richness and species diversity correlated positively with salinity and temperature and negatively correlated with water transparency across all estuaries (Table 3.6). Separate analyses of each estuary type showed that in PO estuaries, correlations between environmental variables and fish density or diversity indices followed the same patterns as above, however in EL and TOC systems very few correlations were statistically significant (Table 3.6).

Table 3.6 Spearman Rank correlations of diversity indices and larval fish density, for all taxa and individual species recorded, with environmental variables in selected south and west coast estuaries of South Africa. Only species positively identified and with statistically significant (bold) results are shown. sal = salinity; tem = temperature; wtr = water transparency. Significance levels = *P* <0.05.

	All estuaries			**Permanently open**			**Temporarily open/closed**			**Estuarine lake systems**		
	sal	**tem**	**wtr**	**sal**	**tem**	**wtr**	**sal**	**tem**	**wtr**	**sal**	**tem**	**wtr**
Species richness (d)	**0.42**	**0.47**	**-0.24**	**0.47**	**0.48**	**-0.27**	-0.05	**-0.38**	-0.10	**-0.30**	**0.47**	-0.02
Species diversity (H')	**0.42**	**0.41**	**-0.23**	**0.48**	**0.41**	**-0.26**	0.05	**0.39**	-0.13	**0.26**	**0.45**	-0.07
All taxa	**0.37**	**0.49**	**-0.13**	**0.35**	**0.44**	**-0.14**	0.22	**0.70**	0.02	**0.61**	**0.62**	-0.09
Atherina breviceps	**0.29**	**0.39**	**-0.18**	**0.23**	**0.41**	**-0.17**	-	-	-	**0.40**	**0.48**	0.26
Caffrogobius nudiceps	**0.26**	0.10	-0.08	**0.34**	0.09	**-0.12**	-	-	-	-	-	-
Caffrogobius gilchristi	**0.34**	**0.32**	**-0.32**	**0.33**	**0.31**	**-0.32**	-	-	-	0.27	**0.42**	-0.12
Caffrogobius sp.	0.09	0.08	**-0.11**	**0.11**	0.09	**-0.13**	-	-	-	-	-	-
Clinus superciliosus	**0.10**	0.04	0.00	0.11	0.08	0.04	-0.01	-0.01	-0.05	-	-	-
Chorisochismus dentex	**0.11**	-0.05	-0.00	**0.13**	-0.06	-0.01	-	-	-	-	-	-
Engraulis japonicus	**0.11**	0.09	**-0.12**	**0.14**	0.10	**-0.14**	**-**	**-**	**-**	**-**	**-**	**-**
Gilchristella aestuaria	-0.06	**0.44**	0.06	**-0.23**	**0.41**	**0.13**	0.31	**0.68**	-0.07	**0.60**	**0.53**	-0.21
Hyporhamphus capensis	-0.00	**0.13**	0.01	0.00	**0.14**	0.00	**-**	**-**	**-**	**-**	**-**	**-**
Iso natalensis	0.09	0.07	**-0.11**	0.11	0.08	**-0.12**	**-**	**-**	**-**	**-**	**-**	**-**
Monodactylus falciformis	**0.11**	0.02	-0.02	**0.13**	0.02	-0.03	**-**	**-**	**-**	**-**	**-**	**-**
Mugil cephalus	-0.01	0.06	**0.15**	0.00	0.06	**0.16**	**-**	**-**	**-**	**-**	**-**	**-**

Table 3.6 Continued...

	All estuaries			**Permanently open**			**Temporarily open/closed**			**Estuarine lake systems**		
	sal	**tem**	**wtr**	**sal**	**tem**	**wtr**	**sal**	**tem**	**wtr**	**sal**	**tem**	**wtr**
Omobranchus woodi	**0.22**	**0.24**	**-0.24**	**0.26**	**0.26**	**-0.29**	**-**	**-**	**-**	**-**	**-**	**-**
Parablennius sp.	**0.28**	0.05	-0.08	**0.34**	0.05	**-0.11**	**-**	**-**	**-**	**-**	**-**	**-**
Psammogobius knysnaensis	**0.31**	**0.43**	**-0.19**	**0.35**	**0.43**	**-0.20**	-0.18	0.24	-0.20	**0.32**	**0.50**	-0.23
Redigobius dewaali	0.02	**0.26**	-0.05	0.03	**0.28**	-0.07	**-**	**-**	**-**	**-**	**-**	**-**
Solea turbynei	0.04	**0.10**	0.02	0.06	0.11	0.01	**-**	**-**	**-**	**-**	**-**	**-**
Syngnathus temminckii	**0.34**	**0.18**	**-0.24**	**0.34**	**0.18**	**-0.22**	**-**	**-**	**-**	0.01	0.18	0.02

3.4 DISCUSSION

3.4.1 Composition and estuary association

South and west coast estuaries were typically characterised by larvae of estuary-resident species in the families Clupeidae and Gobiidae. In the present study, these two families together with the families Blenniidae and Atherinidae accounted for 98 % of the total catch. These families are also the most abundant in larval fish assemblages in warm-temperate (Harrison & Whitfield 1990; Strydom *et al.* 2003; Whitfield 1989a; Whitfield 1994), subtropical (Harris & Cyrus 2000; Harris *et al.* 1995a) and subtropical/warm-temperate boundary region estuaries (Pattrick *et al.* 2007). Similarly, temperate estuaries worldwide show analogous family dominance (Marques *et al.* 2006; Neira & Potter 1992; Ramos *et al.* 2006). The larvae of *Gilchristella aestuaria*, *Caffrogobius gilchristi*, *C. nudiceps, Psammogobius knysnaensis, Omobranchus woodi*, *Atherina breviceps* (Table 3.3) and *Parablennius* sp. were common in catches. With the exception of the last taxon, these species were also the most important (>70 % of total catches) members of the larval fish assemblages in warm-temperate estuaries from South Africa (Melville-Smith 1981; Strydom *et al.* 2003; Whitfield 1989a). Adults and larvae of *Parablennius cornutus* and *P. pilicornis* have been recorded in warm-temperate estuaries (Potter *et al.* 1990; Strydom 2003a) but the genus is better represented along the South African west coast (Smith & Heemstra 2003) and this distribution accounted for the larger contribution in estuaries in this study.

The distributions of *Argyrosomus japonicus, Hyporhamphus capensis, Omobranchus woodi* and *Sillago sihama* reach south to Cape Point (Smith & Heemstra 2003) and their presence in west coast estuaries may represent a range extension of the estuarine occurrence of these species via their larval stages. The occurrence of these species in the west coast estuaries may be explained by transport and entrapment of their early stages in eddies between the Agulhas and Benguela Current systems (Beckley 1985; Harris *et al.* 1999; Miller *et al.* 2006). More larval fish studies, preferably including DNA methods for species identification are recommended to confirm the presence of resident populations of these species in west coast estuaries and rule out possible misidentification with congeneric species occurring in the same systems.

The contribution of estuary-resident species to larval fish catches appears to differ between the bio-geographic regions in South Africa. In this study, estuary-resident species overwhelmingly dominated the catches of larval fishes in south and west coast estuaries with estuary-dependent marine species contributing <1 % of total catch. In a study of larval fishes from 12 warm-temperate estuaries, Strydom *et al.* (2003) found that estuary-dependent marine species were dominant in open estuaries and comprised 47 % of the total catch, whereas estuary-resident species comprised 50 % of the intermittently open estuary catch. Pattrick *et al.* (2007) found that in the Mngazi Estuary, estuary-resident species comprised the largest portion of the catch (49 %) while estuary-dependent marine species comprised 32 % of total catch. Studies on juvenile and adult fishes also showed that after the estuary-dependent marine *Liza richardsonii* and *Mugil cephalus*, the estuary-residents *A. breviceps* and *G. aestuaria* make important numerical contributions in south and west coast estuaries (Harrison 2005). The important contributions of estuary-resident species in all stages of the life cycle for these species indicate that these estuaries are successful breeding areas.

Despite the low contribution of estuary-dependent marine species to the larval fish assemblages in this study, south and west coast estuaries may still be considered as nursery grounds for the marine species such as *L. dumerilii, L. richardsonii, Mugil cephalus, Ophisurus serpens, A. japonicus, Diplodus capensis and Rhabdosargus holubi*. It is hypothesized that the recruitment of these species is probably taking place predominantly at the juvenile stage unlike the late-larval stage recruitment of estuary-dependent marine species typical of warm-temperate systems (Strydom *et al.* 2003; Whitfield & Kok 1992). The presence of adults of *L. richardsonii, M. cephalus*, *R. holubi* and *Heteromycteris capensis* in the same systems where they dominate numerically or make important contributions to the biomass (Harrison 2005) offers some evidence to support this hypothesis. In addition, the quality of the estuaries of this study has been reduced (Whitfield & Wooldridge 1994; see Table 3.1) and these species may be spawning at sea and then recruiting into estuaries at a later stage in respond to the lack of good quality nursery habitats (Potter *et al.* 1990). The decrease in marine fish taxonomic richness from the north east coast to the south coast of South Africa (Hockey & Buxton 1991) and the eastward migration of some estuary-dependent marine species, e.g. *A. japonicus* and *L. lithognathus* for spawning (Whitfield 1990, 1998) may be further reasons for the lower contribution of estuary-dependent marine species to larvae catches in the present study.

Notable in this study was the absence of larvae of freshwater migrant species (e.g. *Oreochromis mossambicus*), which can be the result of several factors such as biogeography and the resultant decrease in taxonomic richness of freshwater fish in cooler waters (O'Keefe *et al.* 1991; Skelton 2001), reproductive biology (Bruton & Boltt 1975; Skelton 2001) and anthropogenic impacts (Whitfield & Wooldridge 1994; Table 1). In addition, spawning and recruitment of freshwater migrant species may be taking place farther upstream in the systems where sampling was limited by restrictions in estuary navigation.

3.4.2 Temporal and spatial trends in larval fish density and diversity

South and west coast estuaries of this study and other South African systems exhibit similar temporal and spatial trends in larval fish density and diversity. In warm-temperate and subtropical estuaries (Harris & Cyrus 2000; Strydom *et al.* 2003), as well as estuaries from other latitudes (Neira *et al.* 1992; Ramos *et al.* 2006), larval fish densities and richness are higher in summer. This is attributed to most estuary dependent fish species spawning in spring and summer, coinciding with warmer water, and peak recruitment into estuaries also occurring during this period (Potter *et al.* 1990; Whitfield & Marais 1999).

Permanently open estuaries in warm- and cool-temperate South Africa have higher larval fish densities and diversity than intermittently open systems. In the PO estuaries, larval fish density ranged from 0 – 33 472 larvae 100 m^{-3} and the number of species ranged from 18 – 22 whereas in intermittently open systems, larval fish density ranged from 0 – 5 538 larvae 100 m^{-3} and number of species ranged 3 – 8. Similarly, Strydom *et al.* (2003) recorded up to 56 890 larvae 100 m^{-3} and 67 species in warm-temperate, PO estuaries from South Africa, while in intermittently open systems, densities reached 13 881 larvae 100 m^{-3} and only 13 species were recorded. Although the lower larval fish densities and diversity of the TOC Lourens and Diep estuaries can be attributed to the poor quality of these systems, estuary type plays an important role in characterizing larval fish assemblages in warm-temperate systems (Strydom *et al.* 2003) and similar findings have also been obtained for adult fishes in South African estuaries (Harrison 2005).

Larval fish densities in this study were predominantly higher in the river-estuary interface (REI) region, characterized by oligohaline and mesohaline conditions (Bate *et al.* 2002). This supports findings by Strydom *et al.* (2003) in several warm-temperate estuaries and Pattrick *et al.* (2007) in the subtropical/warm-temperate Mngazi Estuary. The REI region has been identified as a highly productive zone (Hilmer & Bate 1990) supporting rich faunal communities (Whitfield & Wood 2003) with a spatial and temporal extension that can vary according to the freshwater flow rate of the estuary (Bate *et al.* 2002). In this study, the freshwater rich Great Berg Estuary differed from all other estuaries in terms of the extremely high densities of *G. aestuaria* (>25 000 larvae 100 m^{-3} per site) recorded in the upper reaches during summer. Strong river flow was recorded during the spring sampling period in this estuary with a completely fresh water column extending to 14 km from the mouth, whereas these conditions usually occur >25 km from the mouth. Adult *G. aestuaria* exhibits pulse spawning in response to freshwater input with high numbers of larvae recorded after small-scale flooding or elevated river flow into estuaries (Martin *et al.* 1992; Pattrick *et al.* 2007; Strydom *et al.* 2002). Data from the present study supports this behavioural response by adult fishes to freshwater input, highlighting the importance of freshwater supply to the productivity of this “food-fish” in estuaries and the resultant importance to piscivores utilizing estuaries.

3.4.3 Community analysis

Temperate south and west coast estuaries have similar patterns in community structure of the larval fish assemblages when compared to warm-temperate estuaries of the southeast coast of South Africa. Typically, estuary types have specific communities of larval fishes utilizing the system. Larvae of estuary-dependent marine species were restricted to PO estuaries. Salinity zones play a definitive role in community structure in terms of species presence or absence and density. Larval fish densities and species richness were higher in summer than in any other seasons sampled. However, there were no statistically significant differences in community structure between seasons. This phenomenon was attributed to the dominance of estuarine residents, which were present in all seasons sampled. Similar findings were obtained by Strydom *et al.* (2003) and Pattrick *et al.* (2007) in estuaries from the southeast coast of South Africa.

The south coast estuaries in this study fall within the cool- and warm-temperate biogeographic boundary region described for South Africa (Allanson & Baird 1999) and only minor changes in species composition and dominance were evident between estuaries falling into these two regions. Besides the larvae of *G. aestuaria* that dominated in both regions, warm-temperate estuaries (Goukou, Breede and Heuningnes) were dominated by the larvae of the gobiid *C. gilchristi,* the blenniid *O. woodi* and the gobiid *R. dewaali,* which was only present in these systems. On the other hand, the gobiid *C. nudiceps* and the blenniid *Parablennius* sp. dominated in cool-temperate, west coast estuaries (Great Berg and Olifants) and the Tripterygiid 1 was only present in systems along this coast. The differences in community structure were not statistically significant and from a larval fish perspective, the patterns observed here do not reflect those of adult fishes. Harrison (2002) found that cool- and warm-temperate estuaries were statistically different in terms of species presence/absence, abundance and biomass. In cool-temperate estuaries, the juveniles and adults of *L. richardsonii* and *M. cephalus* contribute more than 70 % of the total catch. On the other hand, these species together with *A. breviceps*, *R. holubi*, *L. dumerilii*, *Myxus capensis*, *G. callidus*, *L. lithognathus*, among other estuary associated marine species not recorded in this study, make up to 70 % of the total catch in warm-temperate estuaries (Harrison 2005).

The differences between larval, juvenile and adult species composition and abundance can be explained by the fact that estuary-dependent marine species are likely to recruit into south and west coast estuaries at the juvenile stage, which will make them unnoticeable in larval fish studies. In addition, these species may be spawning at sea due to the poor quality of the estuaries sampled (e.g. Lourens and Diep). The high dominance of estuary-resident species in larval fish assemblages and the contrasting dominance of estuary-dependent marine species in juvenile and adult fish assemblages in south and west coast estuaries may also suggest that high mortalities of early recruits of estuary-resident species occur (Whitfield 1999) because of estuary degradation (Bennett 1994; Goodman & Campbell 2007).

3.4.4 Relationships between environmental variables and larval fish assemblages

All three physical and chemical variables measured appear related to larval fish densities. Harris & Cyrus (2000) and Strydom *et al.* (2003) obtained similar results in other South African systems. In these studies, the relationship between environmental variables and larval density tends to be species-specific. However, in this study, all dominant taxa, mostly estuary-resident species, responded similarly to each variable. The reason for this homogeneity could be that the majority of the species found belong to the warm-water and cool-water endemic groups described by Harrison & Whitfield (2006). These groups comprise species that are common in warm- (e.g. Group 3: *G. aestuaria* and *S. turbynei*) and cool-temperate (e.g. Group 4*: A. breviceps, C. gilchristi* and *P. knysnaensis*) estuaries but are less common in subtropical systems. As in this study, these species correlated positively with both temperature and salinity but prefer cooler waters than other fish species (Harrison & Whitfield 2006). Unlike other South African estuaries (Cyrus & Blaber 1987; Harris & Cyrus 2000), water transparency (turbidity) correlated negatively with larval densities. Turbid conditions are registered after winter rains in the southwest Cape estuaries and clearer conditions are often the results of reduced river flow during summer (Day 1981b; Millard & Scott 1954; Schulze 1984). Correlation alone is insufficient evidence to determine the relationship between biotic and abiotic variables, therefore the positive correlation between larval fish densities and water transparency may be the result of lower turbidities and fish spawning coinciding in summer.

This study suggests that in south and west coast estuaries, both river flow and temperature play an important variable characterizing larval fish assemblages. In the present study, larval fish densities and species richness were higher in summer. This seasonal pattern in larval fish density is similar to that described in the warm-temperate and subtropical regions and this is despite major differences in rainfall patterns and therefore salinity regimes between regions. In the subtropical region most rainfall occurs in summer, in the warm-temperate region rainfall occurs almost equally in all seasons, although it is higher in autumn and in the cool-temperate region most rainfall occurs in winter (Schulze 1984). Lara-Lopez & Neira (2008) suggest that marine estuary-spawning fishes may have a fixed spawning period timed to increasing temperatures to ensure a match with abundant microplankton food supply. It is this fixed spawning period that may be producing the apparent similar seasonal pattern in larval fish density between different biogeographic regions as in South African estuaries there is a synchronicity between higher water temperatures and estuarine productivity, both happening generally in summer (Adams & Bate 1999; Froneman 2001a; Wooldridge 1999). This may suggest that summer microplankton food availability for larval fish overrides the seasonality of freshwater inputs and salinity regime. However, in estuaries appropriate freshwater input is required to promote productivity (Bate *et al.* 2002; Grange *et al.* 2000; Snow & Adams 2006) and to trigger fish spawning (Martin *et al.* 1992; Pattrick *et al.* 2007; Strydom *et al.* 2002). Therefore, this study suggests that in south and west coast estuaries appropriate river flow and water temperature act in conjunction to produce the seasonal pattern observed in these larval fish assemblages. King *et al.* (1998) also found that freshwater released from the Clanwilliam Dam in the Olifants River would increase spawning success of *Barbus capensis* only if the water temperatures were above 19 ºC, which the mean summer temperatures (21 ºC) recorded in the present study exceeded.

3.5 CONCLUSIONS

The larval fish assemblages from south and west coast estuaries are dominated by larvae of estuary-resident species and larvae of estuary-dependent marine species are not as numerous in plankton samples when compared to warm-temperate and subtropical South African estuaries. Since endemic species dominate the south and west coast estuaries, they are valuable from a biodiversity perspective in South Africa. The composition and structure of larval fish assemblages from these estuaries is the result of the biogeography of the area, derived from the specific climatic and oceanographic environment (Whitfield & Marais 1999), as well as the nature of estuarine type. Density and species richness of larval fishes appeared higher in freshwater-rich estuaries. The findings support those of other studies that suggest that South African estuaries have to be managed to ensure an adequate freshwater supply to maintain the biological integrity of the ecosystem, specially the maintenance of the highly productive REI regions.

CHAPTER 4

DESCRIPTION OF ZOOPLANKTON COMPOSITION, ABUNDANCE AND DISTRIBUTION IN NINE SOUTH AND WEST COAST ESTUARIES OF SOUTH AFRICA

4.1 INTRODUCTION

Research on estuarine zooplankton in South Africa has been intensive in the subtropical (Grindley 1981; Perissinotto *et al.* 2000; Kibirige & Perissinotto 2003b; inter alia) and warm-temperate (Coetzee 1981; Froneman 2004; Jerling & Wooldridge 1995b; inter alia) regions with relative few studies extending into the cool-temperate region. Historically, this research has focussed on community structure, the role of estuarine environmental conditions and estuary type in characterizing zooplankton assemblages and the effects of freshwater supply variations on estuarine zooplankton community and dynamics. Despite this diversity of work on estuarine zooplankton in warm-temperate and subtropical systems, few quantitative data are available on zooplankton assemblages from the south and west coasts of South Africa (Wooldridge 1999), which fall within the cool-temperate biogeographic region and the boundary between this region and the warm-temperate region. The work by Grindley (1977) on the zooplankton of Langebaan Lagoon and Saldanha Bay and the study of Coetzee (1985) on the zooplankton of the Bot River estuary represent the only published studies focused on the cool-temperate region.

Zooplankton research to date has shown that the copepods *Acartia longipatella, A. natalensis* and *Pseudodiaptomus hessei* and the mysids *Mesopodopsis wooldridgei*, *M. africana, Gastrossacus brevifissura, G. gordonae* and *Rhopalophtalmus terranatalis* are the most common species recorded in South African estuaries (Grindley 1981; Wooldridge 1999). The copepods contribute substantially to total zooplankton density and on occasions can exceed 100 000 ind m^{-3} (Jerling & Wooldridge 1991; Wooldridge & Callahan 2000), whereas mysids contribute up to 20% of the zooplankton biomass in South African estuaries (Froneman 2001a). These zooplankters together with other estuarine planktonic groups (e.g. amphipods, isopods and ostracods) provide the bulk of the diet of many estuary-resident and estuary-dependent marine fish species in South Africa (Bennett 1989; Whitfield 1985; Whitfield 1998).

Freshwater input and mouth condition *per se* seem to be more important than other environmental variables in structuring zooplankton communities in South Africa. For instance, Grange *et al.* (2000) compared the response of two South African estuaries to altered river flow regimes and found that the biomass of various aquatic organisms, including zooplankton, was correlated to the magnitude of freshwater input. Estuaries with reduced freshwater input had considerably lower zooplankton biomass when compared with those systems where strong salinity gradients were present. Whitfield and Bate (2007) suggest that in the absence of any link to the marine environment as is typical in temporarily open/closed (TOC) estuaries, zooplankton diversity is low. In contrast, during the closed phase abundance and biomass of zooplankton attains its maximum in these estuaries. In addition, Wooldridge (1999) suggests that the temporal zooplankton abundance patterns are linked to the frequency of freshwater pulses flowing into an estuary rather than seasonal cycles of environmental variables.

The purpose of this study was to gather baseline information to describe zooplankton assemblages in nine south and west coast estuaries of South Africa. The specific aims were to identify the species composition, abundance and diversity of zooplankton occupying these estuaries, to assess whether zooplankton assemblages exhibit the same physical, temporal and spatial patterns as the warm-temperate systems and to provide insights into the influence of freshwater input and biogeography on the estuarine zooplankton communities. In so doing, the study will provide information needed to facilitate a holistic understanding of estuarine ecosystems along the South African coast. In addition, this work expects to provide an impetus for further study of planktonic communities occurring in these poorly studied estuaries

4.2 MATERIALS AND METHODS

4.2.1 Study area

Estuaries were selected based on the paucity of qualitative and quantitative data on zooplankton in each system as well as accessibility of each to sampling gear. A range of estuary types with differing freshwater input and anthropogenic impact levels were selected (Table 4.1). Permanently open (PO), freshwater-rich (Mean Annual Runoff-MAR >900 x10^6 m^3) estuaries included the Olifants, Great Berg and Breede systems while PO, freshwater-deprived (MAR <110 x10^6 m^3) estuaries included the Heuningnes and Goukou systems. The Diep and Lourens estuaries represented temporary open/closed (TOC) systems and the Bot and Klein estuaries represented estuarine lake (EL) systems (Figure 4.1). The southwest Cape has a Mediterranean climate with cold winters and hot summers, with most rainfall occurring in winter (Schulze 1984).

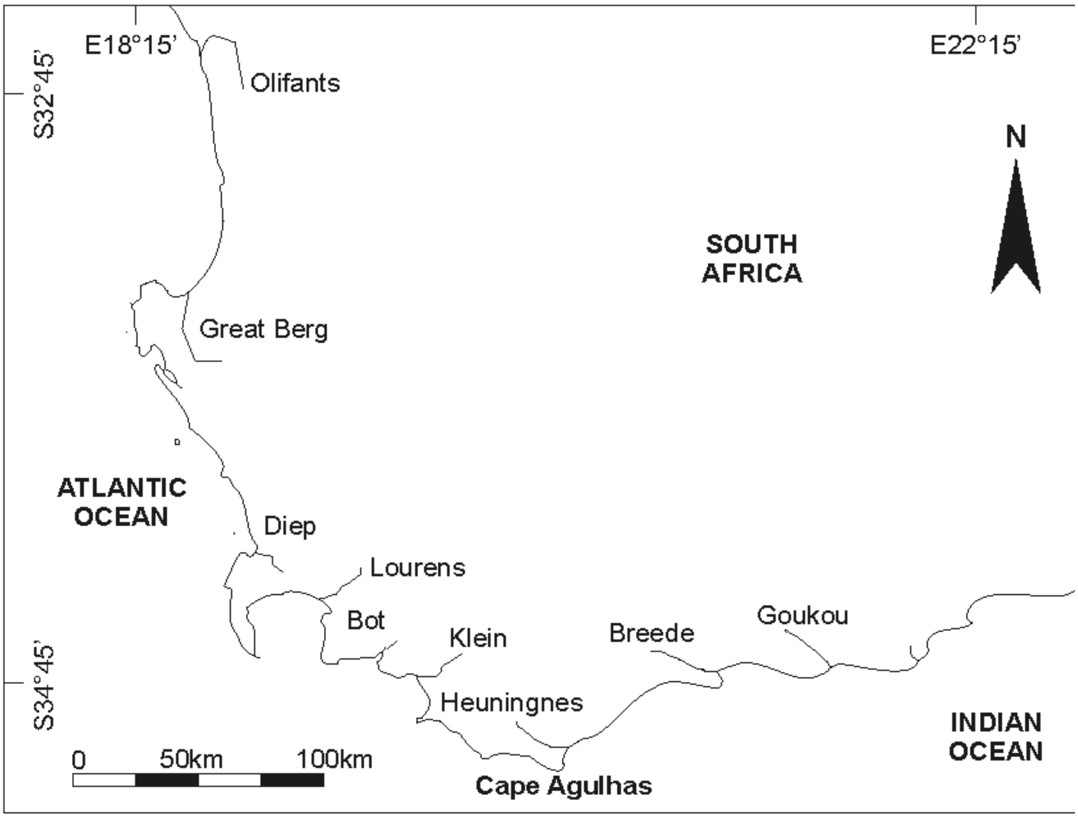

Figure 4.1 Geographical position of estuaries sampled on the south and west coasts of South Africa between June 2003 and March 2004.

4.2.2 Fieldwork and laboratory analysis

The study undertook plankton surveys of all estuaries once per season between June 2003 and March 2004. Two modified WP2 plankton nets (570 mm mouth diameter, 200 µm mesh aperture size) fitted with Kalhisco 005 WA 130 flow meters were used. Collection of data was conducted on predetermined days for each estuary associated with the new moon phase and specific tide state and this sampling protocol was standardised across all fieldtrips. Sampling was conducted after dark at GPS fixed equidistant sites along the navigable length of each estuary. Towing speed ranged from 1 - 2 knots and lasted 3 min. Two sub-surface (20 cm below the surface) samples (replicates) were collected per site, per estuary, during all four seasons. Table 4.1 shows the number of sampling sites and the distance sampled within each estuary. The average water volume filtered was 12.21 m^3 (±8.28 SD). Samples were preserved on site with 10 % buffered formalin.

Salinity and temperature profiles were obtained at each site using a YSI multiparameter instrument. Recordings were made at 0.5 m intervals between the surface and bottom of the water column. Water transparency (extinction coefficient k) at each site was calculated from Secchi disc (20 cm diameter) depth recordings taken at all sites. The formula used is described in Dawes (1981), where $k = 1.7/D$, and D is Secchi depth in cm. Secchi disc reading were taken during the day. The mouth condition (open/closed) of each estuary at the time of sampling was also noted. Descriptions of the salinity environment within each estuary used a modified Venice System (Table 4.2). Water column salinities obtained from depth profiling at each site were averaged for these descriptions.

Table 4.1 Summary of physical characteristics of selected South African south and west coast estuaries included in this study (source Harrison *et al.* 2000).

	Surface area (ha)	**Mean Annual Runoff (m^3)**	**Bio-geographic region (after Harrison 2005)**	**Health status**			**Length sampled (km)**	**No. sites sampled**
				Ichthyofauna	**Water quality**	**Aesthetics**	**This study**	
Permanently open								
Goukou	100	106 $x10^6$	Warm-temperate	Good	Moderate	Good	12	6
Breede	1472	1 873 $x10^6$	Warm-temperate	Good	Good	Good	30	10
Heuningnes	>100	38 $x10^6$	Warm-temperate	Fair	Good	Fair	8	4
Great Berg	6085	913 $x10^6$	Cool-temperate	Fair	Poor	Fair	30	12
Olifants	648	1 008 $x10^6$	Cool-temperate	Fair	Good	Fair	20	10
Estuarine lake								
Klein	>150	40 $x10^6$	Cool-temperate	Good	Good	Good	8	4
Bot	>150	66 $x10^6$	Cool-temperate	Good	Good	Moderate	6	3
Temporarily open/closed								
Lourens	2-150	21 $x10^6$	Cool-temperate	Good	Fair	Poor	0.6	2
Diep	2-150	30 $x10^6$	Cool-temperate	Good	Poor	Poor	3	3

Table 4.2 Modified Venice System for classification of salinity zones for use in south and west coast South African estuaries (from Strydom *et al.* 2003).

Salinity zone	**Salinity range**
Fresh	0 - 0.49
Oligohaline	0.5 - 4.9
Mesohaline	5.0 - 17.9
Polyhaline	18.0 - 29.9
Euhaline	30.0 - 35.9
Hypersaline	≥ 36.0

In the laboratory, samples were diluted to known volumes (up to 5 ℓ on average) and subsamples drawn off until counting 300 individuals of each taxon. Zooplankton taxa were identified and enumerated using a stereo dissecting microscope. Living or dead bivalve and gastropod spat could not be accurately discerned therefore were not counted to avoid overestimation of zooplankton density by counting empty shells. Although isopods and amphipods are not part of the plankton, they were considered since they have been found to be part of the gut contents of juvenile fish (Whitfield 1985; Froneman &Vorwerk 2003). Zooplankton abundance was expressed as individual numbers per m^3 of water filtered.

4.2.3 Data analysis

Statistical data analysis was performed using Statistica 8.0. Tests for normality and homogeneity of variances were carried out and suggested a not normal data set. The Kruskal-Wallis (*H*) ANOVA test was used to assess differences in total zooplankton density and diversity between estuaries, seasons and salinity zones. Spearman Rank Correlation was used to ascertain whether environmental variables displayed any significant correlation with zooplankton density and diversity. The correlation analysis was conducted using total zooplankton density per sample and individual taxa density per sample. In these analyses, actual replicate values of fish density per site were used, i.e. no data was averaged prior to statistical test. The Shannon-Wiener‘s diversity indices (H’) were calculated in the statistical package PRIMER v5.2.9 while the non-parametric ANOVAs and correlation analyses were performed in STATISTICA 8.0 software package.

Group average hierarchical cluster analysis was used to ascertain non-random patterns or structure in zooplankton assemblages. Taxa densities per sample were Log_{10} $(x+1)$ transformed and the Bray-Curtis similarity index used. The number of species was reduced to those accounting for more than 3 % of the total abundance at any one site, reducing the effects of rare species (Clarke & Warwick 1994). Three different matrices were created from the general matrix of species – samples by averaging zooplankton density by estuaries, seasons and salinity zones, respectively. A cluster analysis was performed with each matrix to determine similarities among the different levels of each of the *a priori* groups (i.e. estuaries, seasons and salinity zones). One-way ANOSIM tests were used to determine the significant differences between these. For each group, similarity matrices were calculated using the Bray-Curtis similarity index on Log_{10} $(x+1)$ transformed data. The SIMPER routine was used to identify the taxa contributing to the similarity of the groups. The cut-off level of contribution to the similarity was 50 %. These analyses were conducted using the PRIMER v5.2.9 statistical software package.

4.3 RESULTS

4.3.1 Zooplankton composition

Forty-four taxa were recorded in south and west coast estuaries, with copepods clearly dominating the zooplankton from a numerical perspective (Table 4.3 and 4.4). The calanoid copepod *Pseudodiaptomus hessei* was by far the most abundant taxon, contributing 58.9 % of the total zooplankton catch. The calanoid copepod *Acartia africana* (12.0 %) was the second most abundant taxon. Decapod larvae, mainly that of *Hymenosoma orbiculare*, *Upogebia africana* and *Sesarma catenata* (6.1 % of the total zooplankton catch), were the third most abundant taxa in the study. The calanoid copepod *Acartia longipatella* (3.5 %) was the other copepod of numerical importance

(Table 3). Marine calanoid (5.7 %) and cyclopoid (4.4 %) copepods also made notable contributions to the overall catch. Calanoid species included *Calanoides carinatus, Centropages* spp, *Candacia* spp, *Nannocalanus minor* and *Rhincalanus nasutus* whereas cyclopod species included *Halicyclops pondolensis, Oithona* spp, *Hemicyclops* spp, *Saphirella* spp and *Coryaceus* spp. *Mesopodopsis wooldridgei* (1.6 %) was the only mysid with a significant contribution to the total zooplankton density. Larval fish of estuary-resident species namely *Gilchristella aestuaria, Caffrogobius gilchristi, C. nudiceps, Psammogobius knysnaensis, Omobranchus woodi* and *Atherina breviceps* dominated the ichthyoplankton.

4.3.2 Spatial and temporal trends in zooplankton density and diversity

Inter-estuary trends

Total zooplankton densities varied between estuaries (H =28.07, *P* <0.001) and peaked in the Klein estuary, with a maximum density of 100 421 ind m^{-3} in a single station (Table 4.4). However, this was the result of high numbers of *Pseudodiaptomus hessei* in this estuary during the winter sampling when the estuary was closed. During the sampling seasons when the estuary was open, *P. hessei* densities did not exceeded 40 ind m^{-3}. The Lourens and Bot estuaries exhibited a similar pattern in total zooplankton and *P. hessei* numbers. In these estuaries, density was higher during the seasons when the estuary mouth was closed and lower when the mouth was open. Permanently open estuaries and the Diep Estuary, that was open during sampling, had similar mean densities that ranged 3 877-8 890 ind m^{-3} (Table 4.4).

The copepods *Pseudodiaptomus hessei* and *Acartia longipatella* occurred in all estuaries whereas *A. africana* only occurred in the south coast Goukou, Breede and Heuningnes systems were it contributed substantially to the total density (Figure 4.2). *Gastrossacus brevifissura* was the only mysid recorded in all estuaries sampled but in low densities and only exceeding 16 ind m^{-3} in the Goukou, Breede, Klein and Olifants systems. *Mesopodopsis wooldridgei* was recorded in all estuaries but the EL Diep system. This mysid was very abundant in the Great Berg Estuary with mean and maximum density of 470 and 9 637 ind m^{-3}, respectively (Figure 4.3).

Species diversity differed (H =41.11, *P* <0.001) between estuaries. South coast estuaries (i.e. Goukou, Breede and Heuningnes) were more diverse, mean *H'* ranged 1.14-1.37, than west coast estuaries, mean *H'* ranged 0.74-0.98. However, the composition of the zooplankton remained similar throughout the study, as the majority of the species were recorded in all seasons.

Temporal trends

Permanently open estuaries and the EL Diep system exhibited summer zooplankton maxima and winter or spring zooplankton minima while intermittently open systems showed zooplankton maxima during the closed phases and zooplankton minima during the open phases. The differences observed in total zooplankton density between seasons were significant (H =38.46, *P* <0.001). However, the mean densities of *Pseudodiaptomus hessei* were similar in all seasons while those of *Acartia africana* and *A. longipatella* varied among seasons. Spring mean densities of the two species were <20 ind m^{-3} whereas summer mean densities reached 2 260 and 730 ind m^{-3}, for *A. africana* and *A. longipatella*, respectively (Figure 4.2). The mean density of *G. brevifissura* and *R. terranatalis* was similar throughout the seasons sampled. On the other hand, *M. wooldridgei* density showed some seasonal variation as it increased from winter to summer (Figure 4.3) by two orders of magnitude.

Species diversity (H = 28.16, *P* <0.001) varied between seasons sampled. Mean zooplankton diversity was higher in spring (*H'* = 1.22) and autumn (*H'* = 1.07) than in winter (*H'* = 0.93 and summer (*H'* = 0.83).

Spatial (salinity zones) trends

Total zooplankton densities varied between salinity zones (H = 37.65, *P* <0.001) with the oligohaline, mesohaline and polyhaline zones having higher densities. *Pseudodiaptomus hessei* and *Acartia africana* dominated in polyhaline to oligohaline zones, with a combined maximum mean density of 97 962 ind m^{-3} in the mesohaline (Figure 4.2). In contrast, *A. longipatella* was more abundant, maximum mean density 9

705 ind m^{-3}, in polyhaline to hypersaline conditions (Figure 4.2). *Gastrossacus brevifissura, Mesopodopsis wooldridgei* and *Rhopalophtalmus terranatalis* were abundant in the mesohaline zone (Figure 4.3).

Table 4.3 Density of the most abundant zooplankton taxa (>0.1% of the total) collected in nine south and west coast estuaries of South Africa between June 2003 and March 2004.

Taxa	**Mean density (Ind m^{-3})**	**Maximun density (Ind m^{-3})**	**Percentage of total**
Cnidaria	16	1526	0.19
Copepoda			
Calanoida			
Pseudodiaptomus hessei	4070	94990	58.9
Acartia africana	810	49930	12
Acartia longipatella	240	9075	3.5
Other calanoids (mainly nauplii)	386	24084	5.7
Cyclopoida	289	6989	4.4
Harpacticoida	98	3223	1.5
Poecilostomatoida	87	5386	1.3
Cladocera	69	2507	1.1
Ostracoda	18	879	0.3
Cumacea	13	965	0.2
Mysida			
Mesopodopsis wooldridgei	107	9637	1.6
Gastrossacus brevifissura	18	658	0.3
Rhopalophtalmus terranatalis	20	633	0.3
Isopoda			
Exosphaeroma hylecoetes	10	325	0.1
Amphipoda			
Grandidierella lutosa	54	3199	0.8
Corophium triaenonyx	52	2448	0.8
Melita zeylanica	13	1247	0.2
Decapoda			
Hymenosoma orbiculare	7	175	0.1
Decapoda larvae	495	27742	6.5
Polychaeta	10	256	0.1
Pisces	6	324	0.1

Table 4.4 Summary of abiotic and biotic characteristics of selected South African south and west coast estuaries sampled from winter 2003 to autumn 2004 (*K* = extinction coefficient).

	Goukou	**Breede**	**Heuningnes**	**Klein**	**Bot**
Estuary Type	Permanently open	Permanently open	Permanently open	Estuarine Lake	Estuarine Lake
Latitude	34°22’41’’ S	34°24’16’’ S	34°42’51’’ S	34°25’07’’ S	34°22’01’’ S
Longitude	21°25’22’’ E	20°50’57’’ E	20°06’54’’ E	19°18’15’’ E	19°05’55’’ E
Environmental variables: mean (range)					
Salinity	21.11 (0.00-35.06)	7.92 (0.00-32.36)	25.92 (1.90-35.76)	24.20 (6.68-34.34)	27.26 (4.76-38.73)
Temperature (°C)	19.58 (12.94-24.42)	19.28 (14.27-23.25)	19.79 (15.82-24.24)	18.73 (13.45-25.22)	19.00 (13.18-25.05)
Water transparency (*k*)	0.02 (0.01-0.06)	0.03 (0.01-0.05)	0.02 (0.01-0.09)	0.01 (0.01-0.03)	0.01 (0.00-0.03)
Species diversity (H')	1.09 (0.06 – 2.30)	1.18 (0.18 - 2.41)	1.34 (0.46 – 2.29)	0.71 (0.06 - 1.36)	0.88 (0.05 - 1.70)
Dominant groups (% of total density)	Copepoda (82.2) Decapoda (13.4) Cumacea (1.4)	Copepoda (89.3) Amphipoda (4.7) Decapoda (2.1)	Copepoda (81.5) Amphipoda (6.1) Cladocera (5.1)	Copepoda (98.9) Mysida (0.4) Decapoda (0.4)	Copepoda (97.7) Decapoda (0.4) Amphipoda (0.4)
Dominant taxa (% of total density)	*A. africana* (45.9) *P. hessei* (34.3) Decapoda larvae (13.2)	*A. africana* (63.1) *P. hessei* (19.7) *G. lutosa* (4.5)	*P. hessei* (44.1) Cyclopoida (22.3) Harpacticoida (8.5)	*P. hessei* (92.3) Harpacticoida (2.2) Cyclopoida (1.9)	*P. hessei* (69.4) *A. longipatella* (19.2) Harpacticoida (4.9)
Zooplankton density (ind m^{-3})					
Mean	6 175	4 049	3 877	24 135	4 658
Range	3 – 50 454	14 – 30 556	344 – 17 654	573 – 100 421	16 – 29 527

Table 4.4 Continued...

	Lourens	**Diep**	**Great Berg**	**Olifants**
Estuary Type	Temporarily open/closed	Temporarily open/closed	Permanently open	Permanently open
Latitude	34°06’03’’ S	33°54’28’’ S	32°46’13’’ S	31°42’01’’ S
Longitude	18°48’49’’ E	18°28’19’’ E	18°08’40’’ E	18°11’16’’ E
Environmental variables: mean (range)				
Salinity	7.53 (0.00-28.54)	10.15 (0.66-33.82)	15.17 (0.00-34.33)	16.50 (0.00-34.14)
Temperature (°C)	18.19 (13.31-23.72)	18.76 (13.57-24.82)	18.90 (13.01-24.94)	18.70 (12.35-24.83)
Water transparency (*k*)	0.03 (0.02-0.07)	0.04 (0.02-0.09)	0.03 (0.07-0.09)	0.02 (0.01-0.03)
Species diversity (H')	0.89 (0.23 - 1.61)	0.85 (0.25 – 1.58)	0.97 (0.13 – 2.00)	0.81 (0.03 - 1.89)
Dominant groups (% of total density)	Copepoda (94.9) Cladocera (3.6) Insecta (0.9)	Decapoda (45.6) Copepoda (45.0) Cladocera (8.2)	Copepoda (78.6) Decapoda (10.2) Mysida (7.6)	Copepoda (94.4) Amphipoda (3.1) Decapoda (0.8)
Dominant taxa (% of total density)	*P. hessei* (83.3) Cyclopoida 10.8) Cladocera (3.6)	Decapoda larvae (45.5) *P. hessei* (39.5) Cladocera (8.2)	*P. hessei* (44.6) Marine Calanoida (9.5) Decapoda larvae (10.0)	*P. hessei* (76.5) Cyclopoida (8.3) Marine Calanoida (4.0)
Zooplankton density (ind m^{-3})				
Mean	8 890	5 501	6 841	6 269
Range	100 – 72 954	54 – 33 707	29 – 54 617	48 – 38 632

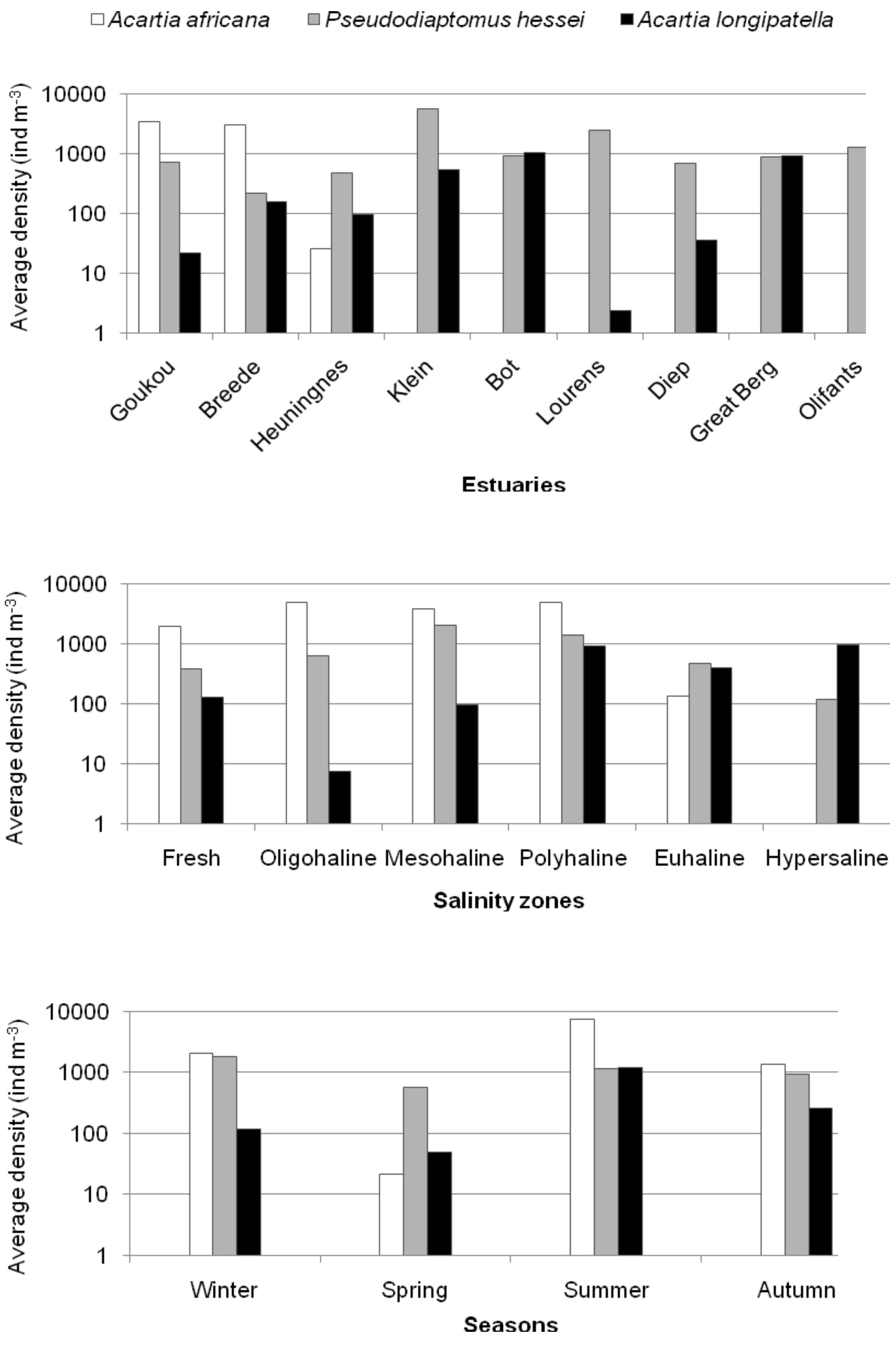

Figure 4.2 Spatial and temporal distribution of the three most abundant calanoid copepods from selected south and west coast estuaries.

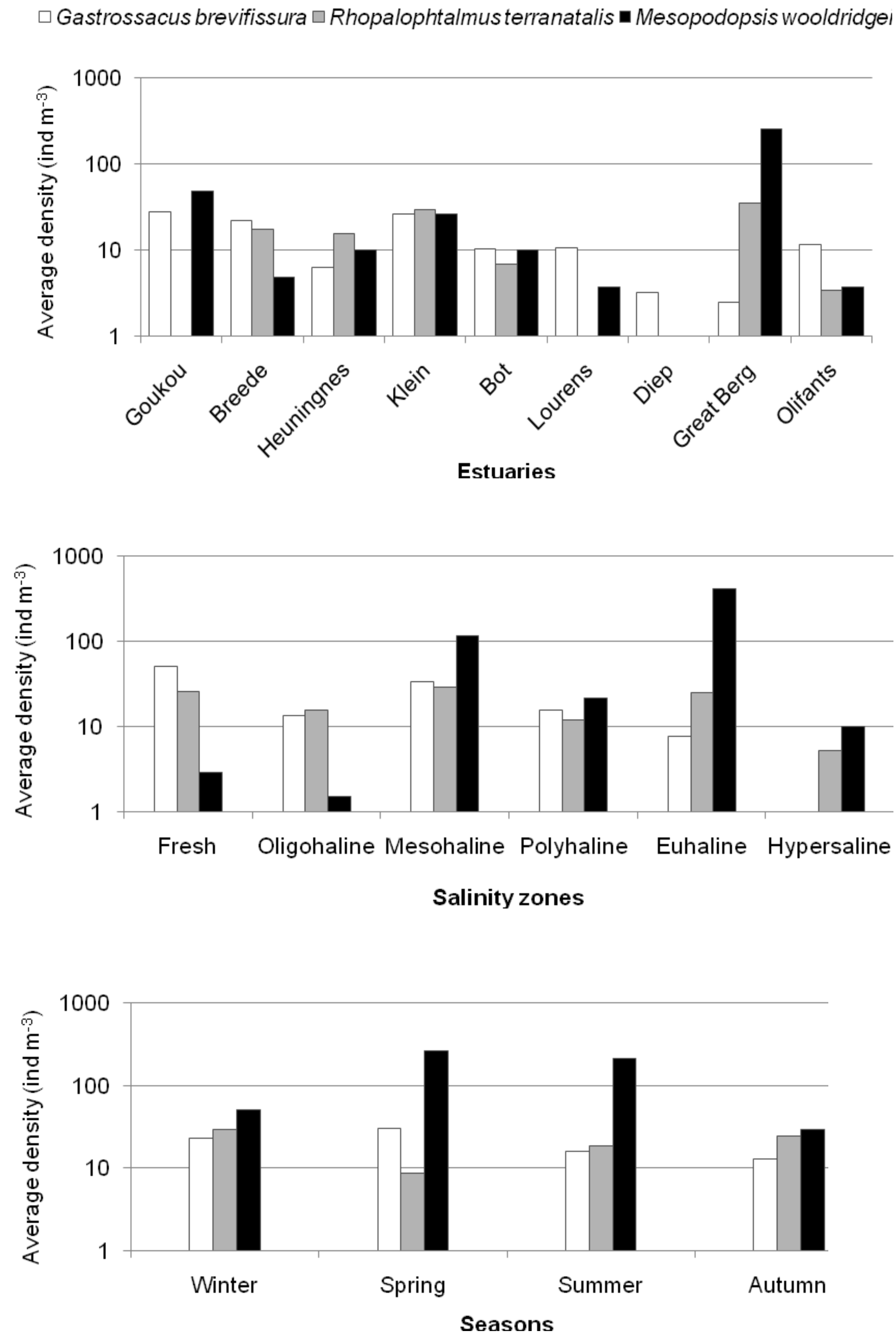

Figure 4.3 Spatial and temporal distribution of the three most abundant mysids from selected south and west coast estuaries.

Species diversity (H = 34.49, *P* <0.001) also varied between salinities zones. The euhaline zone showed more diverse, mean *H'* >1.20, zooplankton than any other zone.

4.3.3 Community analysis

The hierarchical cluster analysis of estuaries showed three major groups at an arbitrarily selected similarity level of 68.5 % (Figure 4.4). The ANOSIM test showed that estuaries were significantly different (Global R = 0.89, *P* <0.01) their zooplankton assemblages. At this similarity level, the two TOC estuaries grouped together forming the first group. Three taxa accounted for over 50 % of the similarity within this group and these were *Pseudodiaptomus hessei*, cladocerans and cyclopods. The south coast Goukou and Breede estuaries grouped together and seven taxa accounted for over 50 % of the similarity within this group. These were *Acartia africana, P. hessei*, *Grandidierella lutosa, Gastrossacus brevifissura,* decapod larvae, marine calanoids and cladocerans. The rest of the estuaries, i.e. Bot, Klein, Heuningnes, Great Berg and Olifants, formed group 3. Six taxa accounted for over 50 % of the similarity within this group and these *P. hessei*, *A. longipatella*, cyclopods, harpacticoids, decapod larvae and marine calanoids. However, within this group, two subgroups were formed: the EL Klein and Bot systems grouped together and the PO Heuningnes, Great Berg and Olifants formed a second subgroup. Taxa accounting for this separation included marine calanoids, poecilostomatoida copepods, *Sagitta* sp. and *G. lignorum* whose densities peaked in the PO estuaries.

Cluster analysis of the average density of taxa for each salinity zone divided the zones into three groups at an arbitrarily similarity level of 79 % (Figure 4.4). The ANOSIM test showed that salinity zones were significantly different (Global R = 0.91, *P* <0.01) in their zooplankton assemblages. The hypersaline zone was grouped on its own. A higher abundance of *A. longipatella* within this zone was responsible for the separation. The typically estuarine zones, i.e. euhaline, polyhaline and mesohaline, grouped together with an average similarity of 81.4 %. Nine taxa accounted for over 50 % of the similarity within this group and these were *P. hessei, A. africana, A. longipatella,* decapod larvae, marine calanoids, cyclopods, harpacticoids, poecilostomatoids and cladocerans. The last two zones, oligohaline and fresh, grouped together with an average similarity of 83.9 %. Six taxa accounted for over 50 % of the similarity within this group and these were *P. hessei*, *A. africana*, *G. lutosa, Corophium triaenonyx,* cyclopods and cladocerans.

Differences in zooplankton assemblages were not apparent (Global R = 1, *P* >0.05) between seasons and this was attributable to *P. hessei* accounting for over 50 % of the similarity within each season and to the fact that most species were present in all seasons. Despite this, the density of some taxa (e.g. *A. africana, A. longipatella, Mesopodopsis wooldridgei,* decapod larvae and marine calanoids) differed between seasons, with summer showing higher densities.

4.3.4 Environmental variability

The Goukou, Heuningnes, Klein and Bot estuaries showed predominantly euhaline conditions whereas the Breede, Lourens, Diep, Great Berg and Olifants estuaries had predominantly mesohaline conditions during the study period (Table 4.4). A freshwater pulse in the Great Berg Estuary was recorded during spring with salinities <0.5 found 14 km from the mouth and hypersaline (>35.9) conditions were recorded in the EL Bot system during summer and autumn. The Breede, Diep and Great Berg estuaries were characterised by higher turbidity and the Goukou, Heuningnes, Klein, Bot and Olifants estuaries had lower turbidity. Temperature was not different between estuaries. The salinity and temperature of the water column in the estuaries were partially- to well-mixed. Exceptions were the PO Heuningnes Estuary and the two TOC estuaries, which were predominantly stratified. The Diep Estuary remained open during sampling and the Lourens Estuary closed during autumn. The two EL systems are artificially breached, every two years in the case of the Bot system (van Niekerk *et al.* 2005), and during this study they were only found open in winter (Bot) and spring (Klein) sampling.

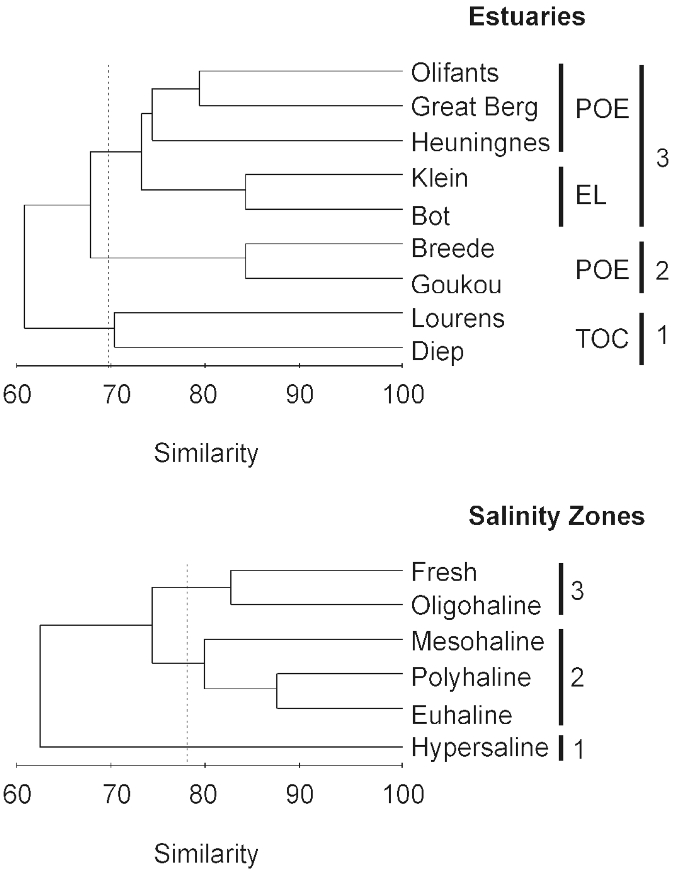

Figure 4.4 Results of the cluster analysis of selected south and west coast estuaries and salinities zones based on zooplankton density. The numbers indicated the groups formed at the arbitrary selected similarity level.

Environmental variables and total density were not significantly (P >0.05) correlated in TOC and EL systems. However, in the PO estuaries salinity and temperature were positively correlated (P <0.05) to zooplankton density whereas water transparency was negatively correlated (P <0.05) to zooplankton density. Table 4.5 shows significant correlation statistics between density and environmental variables. Correlation analyses between zooplankton density in individual estuaries and environmental variables indicated that salinity was positively correlated (P <0.05) to zooplankton density in the Breede, Great Berg and Olifants estuaries but negatively correlated (P <0.05) in the Klein Estuary. Temperature was positively correlated (P <0.05) to total density in the Goukou, Diep and Great Berg estuaries and negatively correlated (P <0.05) in the Klein Estuary. Water transparency was correlated positively (P <0.05) to total density in the

Olifants Estuary and negatively ($P < 0.05$) in the Goukou and Great Berg estuaries. Species diversity was also correlated to environmental variables. Salinity ($P < 0.05$) and temperature ($P < 0.05$) were found to be positively and negatively correlated, respectively, with diversity in PO estuaries.

4.4 DISCUSSION

Species of copepods, mysids, amphipods and decapod larvae dominate numerically the zooplankton assemblages of south and west coast estuaries. The calanoid copepods *Pseudodiaptomus hessei, Acartia africana, A. longipatella,* the mysids *Mesopodopsis wooldridgei, Gastrossacus brevifissura* and *Rhopalophtalmus terranatalis,* and the amphipod *Grandidierella lutosa* were common in catches. With the exception of *A. africana* and *A. longipatella,* these species were also dominant in the zooplankton assemblages in other estuaries in South Africa (Grindley 1981; Wooldridge 1999). *Acartia longipatella* and *A. africana* have been recorded in warm-temperate and subtropical estuaries but the species are better represented along the South African west coast (Coetzee 1985; Wooldridge 1999, 2005) and this distribution accounted for the larger contribution in estuaries in this study.

Table 4.5 Spearman Rank correlations for zooplankton densities versus environmental variables for all taxa and individual species recorded in selected south and west coast estuaries of South Africa. Only taxa with statistically significant (bold) results are shown. sal = salinity; tem = temperature; wtr = water transparency. Significance levels = *p* <0.05.

	Permanently open			**Temporarily open/closed**			**Estuarine lake systems**		
	sal	**tem**	**wtr**	**sal**	**tem**	**wtr**	**sal**	**tem**	**wtr**
Species diversity (H')	**0.16**	**-0.12**	-0.03	-0.25	-0.23	0.01	0.15	0.21	0.02
All taxa	**0.26**	**0.30**	**-0.16**	0.24	0.18	-0.02	0.14	-0.13	0.12
Acartia africana	-0.07	**0.16**	0.02	-	-	-	-	-	-
Acartia longipatella	**0.41**	**0.21**	**-0.26**	**0.38**	0.29	-0.03	**0.60**	**0.55**	0.13
Cladocera	-0.04	-0.08	0.05	**-0.57**	**-0.62**	0.07	**-0.53**	**-0.45**	0.00
Corophium triaenonyx	**-0.42**	**0.16**	**0.20**	0.03	-0.04	0.01	-0.05	-0.22	-0.25
Cumacea	**0.42**	0.09	**-0.28**	-	-	-	0.20	0.17	0.26
Cyclopoida	**0.20**	**-0.12**	**-0.12**	-0.26	-0.12	-0.12	-0.10	-0.15	**0.30**
Decapoda larvae	**0.56**	**0.29**	**-0.39**	**0.48**	**0.63**	0.25	0.27	0.21	0.00
Eurodyce longicornis	**0.23**	**-0.23**	-0.05	0.11	-0.03	-0.03	-	-	-
Exosphaeroma hylecoetes	**0.32**	**-0.16**	**-0.18**	-0.09	0.17	0.01	-0.20	-0.07	0.09
Gastrossacus brevifissura	**-0.19**	0.01	-0.07	-0.13	-0.01	0.18	-0.05	-0.06	0.07
Grandidierella lutosa	**-0.25**	-0.07	**0.28**	0.10	0.05	-0.14	0.15	0.13	-0.15
Harpacticoida	**0.46**	**0.12**	**-0.30**	**0.40**	**0.35**	**-0.52**	0.18	0.23	-0.03
Hymenosoma orbiculare	**0.15**	0.09	**-0.11**	0.01	0.28	0.16	-0.10	-0.01	0.01

Table 4.5 Continued…

	Permanently open			**Temporarily open/closed**			**Estuarine lake systems**		
	sal	**tem**	**wtr**	**sal**	**tem**	**wtr**	**sal**	**tem**	**wtr**
Insecta	**-0.44**	**-0.14**	**0.29**	-0.23	**-0.34**	-0.29	**-0.45**	-0.28	0.05
Marine Calanoida	**0.45**	**-0.22**	**-0.18**	-0.11	**-0.34**	0.06	-0.16	-0.13	0.19
Medusae	**0.38**	**-0.19**	**-0.23**	-0.02	-0.01	-0.06	0.03	-0.12	-0.21
Paramoera capensis	**0.23**	-0.05	0.01	0.06	0.23	0.01	-0.17	-0.01	-0.21
Mesopodopsis wooldridgei	**0.16**	0.07	-0.05	0.16	-0.12	-0.28	0.03	0.02	0.27
Ostracoda	**0.34**	0.01	**-0.17**	-0.18	**-0.41**	-0.13	**-0.52**	**-0.41**	0.05
Pisces	**0.35**	**0.45**	**-0.14**	0.26	**0.70**	0.03	**0.59**	**0.66**	-0.02
Polychaeta	**0.24**	0.01	**-0.15**	-0.23	-0.30	**0.51**	0.00	0.07	0.23
Pseudodiaptomus hessei	**-0.22**	0.16	**0.13**	**0.63**	**0.63**	-0.30	-0.28	**-0.30**	-0.06
Rhopalophtalmus terranatalis	-0.07	-0.01	0.05	-	-	-	0.17	0.06	**0.35**
Sagitta spp	**0.43**	-0.01	**-0.20**	-	-	-	-	-	-
Sesarma catenata	0.15	-0.06	-0.06	-	-	-	-	-	-

Mean and maximum zooplankton densities of the dominant *P. hessei* observed at the nine estuaries sampled compare well with mean and maximum values reported from temperate estuaries in South African. In this study, *P. hessei* had mean and maximum density of 4 070 and 94 990 ind m^{-3}, respectively. Wooldridge (2005) in the freshwater-rich Olifants Estuary and Wooldridge and Callahan (2000) in the freshwater-deprived Kromme used a similar mesh size WP2 plankton net providing the only two comparable studies from South African. In the Olifants Estuary, mean and maximum densities of *P. hessei* were 5 030 and 41 000 ind m^{-3} whereas in the Kromme Estuary mean and maximum densities of the copepod exceeded 1 500 and 100 000 ind m^{-3}. The mean density of the dominant mysid *M. wooldridgei* from this study (107 ind m^{-3}) also compares well with the mean reported from the two previous studies conducted in the Olifants and Kromme estuaries. In the Olifants Estuary, greatest mean density was 4 ind m^{-3} per station (Wooldridge 2005) whereas in the Kromme Estuary mean density was 143 ind m^{-3} (Wooldridge & Callahan 2000). The apparent higher densities of *P. hessei* and *M. wooldridgei* in the freshwater-deprived Kromme Estuary are the result of a positive zooplankton response to an artificial freshwater release into the estuary.

The maximum density of this mysid recorded in the present study (9 637 ind m^{-3}) appears to be related to an increase in freshwater inflow. *Mesopodopsis wooldridgei* maxima were found in the Great Berg Estuary during spring and summer sampling when oligohaline and mesohaline conditions predominated throughout the estuary because of an increase in river flow during the same seasons. The river-estuary interface (REI) region, characterized by oligohaline and mesohaline conditions (Bate *et al.* 2002), has been identified as a highly productive zone (Hilmer & Bate 1990) supporting rich phytoplankton (Snow & Adams 2006) and zooplankton (Jerling & Wooldridge 1991) communities. Estuarine populations of *M. wooldridgei* feed extensively on phytoplankton but can feed on microzooplankton if abundant (Froneman 2001a; Jerling & Wooldridge 1995a). Therefore, *M. wooldridgei* could have been exploiting the ready availability of phytoplankton and microzooplankton in the Great Berg Estuary that is typical for an extended REI region. In South Africa, this same species is known to migrate onshore in large concentrations (15 000 ind m^{-3}) to exploit accumulations of the diatom *Anaulus australis* in Algoa Bay (Webb & Wooldridge 1990) and showed high numbers in the Mpenjati Estuary as a result of its opportunistic behavioural response to low salinity caused by freshwater runoff (Kibirige & Perissinotto 2003b).

In this study, zooplankton density generally exhibited winter minima and summer maxima although in the Klein Estuary exhibited winter maxima and the Lourens Estuary exhibited autumn maxima. Despite changes in species density across seasons, the composition of the zooplankton assemblages displayed little variation. In addition, the REI regions (mesohaline conditions) registered the highest concentrations of zooplankton. Similar to this study, Wooldridge (1999) indicates that in South African estuaries zooplankton density exhibit winter minima and summer maxima. Coetzee (1985) and Grindley (1981) suggest that the zooplankton composition tends to show little variability, due to well-established estuarine populations, except during periods where there is a contribution of marine or freshwater species as a result of changes in freshwater inflow. The REI region in South African estuaries is known to be associated with increased phytoplankton (Bate *et al.* 2002), zooplankton (Wooldridge 1999) and larval fishes (Strydom *et al.* 2003). Therefore, it seems estuarine zooplankton from south and west coast estuaries exhibit the same spatial and temporal variability as east coast estuaries of South Africa.

A spatial pattern between the sympatric species *A. longipatella* and *A. africana* recorded in this study was evident and it is similar to that described for *A. longipatella* and *A. natalensis* in the South African Gamtoos and Swartkops estuaries (Wooldridge 1999). The species co-occurred in the Heuningnes, Goukou and Breede estuaries. In these systems, *Acartia longipatella* reached maximum densities in the salinity range 18 – 36 whereas *A. africana* reached maximum densities in the salinity range 0.5 – 17.9 (Figure 4.2). In the Swartkops and Gamtoos estuaries, *Acartia longipatella* is more common in the lower and middle reaches of the estuaries and *A. natalensis* is more common in the middle and upper reaches of the estuaries (Wooldridge 1999; Wooldridge & Melville-Smith 1979). This spatial pattern has been related to the salinity tolerance of the two species (Coetzee 1985). The positive correlation between *A. longipatella* density and salinity in all estuary types in the present study (Table 4.5) supports this hypothesis. A seasonal succession of the two species has also been described (Wooldridge & Melville-Smith 1979). In the Swartkops Estuary, *A. longipatella* appeared in winter while *A.*

natalensis occurs predominantly in summer. Although this seasonal succession was not observed in this study for the two acartiids recorded, *A. africana* densities increased substantially from winter to autumn while *A. longipatella* densities were relatively homogeneous throughout the study period. Temporal variability in the occurrence of acartiids has been attributed to the reproductive biology of *Acartia* species (Wooldridge 1999).

Changes in mouth condition, in relation to estuary type, influenced zooplankton density. Density maxima were recorded in the seasons when the intermittently open Klein, Bot and Lourens estuaries were closed, while density minima were registered in the seasons when the estuaries were open. This is in agreement with findings from other intermittently open estuaries in South Africa (Coetzee 1985; Froneman 2004; Perissinotto *et al.* 2000) and from Australian seasonally closed (Gaughan & Potter 1995) estuaries. Wooldridge (1999) suggests that temporal abundance patterns do not necessary follow seasonal cycles of physical variables but are instead linked to the frequency of freshwater pulses flowing into an estuary. In addition, the increase in densities of zooplankton in temperate TOC estuaries seems to be related to the stability of the estuarine water during the closed seasons (Gaughan & Potter 1995; Kibirige & Perissinotto 2003b). Results from this study supports these findings since zooplankton abundance changed according to mouth status, total zooplankton density in the TOC and EL systems were not correlated with any environmental variables, and the water column of the estuaries was predominantly stratified during the study period, which is indicative of more stable conditions within these systems (de Villiers & Hodgson 1999).

Estuary type and biogeography influenced the community structure in temperate south and west coast estuaries as well. On one hand, PO estuaries exhibited higher contributions of stenohaline and euryhaline marine species (e.g. decapod larvae, marine calanoids and chaetognaths) when compared to that in the TOC and EL systems. In the TOC estuaries, fewer taxa made up the majority of the contribution. More species contributing to the zooplankton assemblages in PO estuaries could be attributed to the fact that these systems provide a wider axial salinity gradient compared to TOC estuaries, which is known to positively influence the structure of the plankton community in estuaries (Wooldridge 1999) by allowing higher contributions of marine and freshwater species to the zooplankton (Whitfield & Bate 2007).

The south coast estuaries in this study fall within the cool- and warm-temperate biogeographic boundary region described for South Africa (Allanson & Baird 1999) and changes in species composition and dominance were evident between estuaries falling into these two regions. The copepod *Acartia africana* and the amphipod *Grandidierella lignorum* were exclusive to south coast estuaries, with the former making substantial contributions to total density. *Acartia natalensis*, the acartiid that dominates on the east coast (Grindley 1981; Wooldridge 1999) was absent from the estuaries in this study. Also, south coast estuaries exhibited higher diversity indices and the community analysis showed that the difference in community structure between south and west coast estuaries was statistically significant. Similar differences between the cool- and temperate regions of South Africa have been found for adult fishes (Harrison 2002) and marine invertebrates (Emanuel *et al.* 1992).

Although this is a once-off study, has not included all zooplankton groups or their vertical or tidal variation, the findings of this study suggest that zooplankton assemblages from south and west coast estuaries comprised a mix of endemic species and lack unique species. Freshwater input, derived from the nature of estuary type, as well as the biogeography of the area influenced the composition and structure of zooplankton assemblages from these estuaries. These findings support those of other studies that suggest that South African estuaries must be managed to ensure an adequate freshwater supply to maintain the biological integrity of the ecosystem, especially the highly productive REI regions. Further studies on these systems should be focused on the effects of freshwater deprivation on zooplankton communities and detail checklists of zooplankton composition to elucidate the existence of biogeographic regions along the South African coastline based on estuarine zooplankton communities.

CHAPTER 5

LARVAL FISH AND ZOOPLANKTON INTERACTIONS IN SELECTED SOUTH AND WEST COAST ESTUARIES OF SOUTH AFRICA

5.1 INTRODUCTION

The larvae of several commercially, recreationally and ecologically important fish species use estuaries as nursery habitat since these systems provide a rich source of food, e.g. copepods and mysids, and a shelter from predators, e.g. other fish, chaetognaths and jellyfish. Owing to this function, estuaries are considered an important ecosystem for the early stages of fishes in South Africa (Allanson & Baird 1999; Strydom *et al.* 2003; Whitfield 1999) and worldwide (Beck *et al.* 2001; Kerstan 1991; Potter *et al.* 1990; Ramos *et al.* 2006).

From a fish perspective, the larvae of endemic estuary-resident species, namely *Gilchristella aestuaria*, *Caffrogobius gilchristi, C. nudiceps, Psammogobius knysnaensis, Omobranchus woodi* and *Atherina breviceps* dominates south and west coast estuaries in South Africa (Chapter 3). As in other estuaries of South Africa as well as estuaries from other latitudes (e.g. Harris & Cyrus 2000; Neira *et al.* 1992; Ramos *et al.* 2006; Strydom *et al.* 2003), larval fish densities and richness are typically higher in summer. In the south and west coast region of South Africa, permanently open (PO) estuaries have higher larval fish densities and diversity than intermittently open systems which is consistent with findings from other geographic regions (Harris & Cyrus 2000; Strydom *et al.* 2003). Larval fish densities in estuaries from the same region are predominantly higher in the river-estuary interface (REI) region, characterized by oligohaline and mesohaline conditions (Bate *et al.* 2002), and this is related to the high productivity found in the REI region (Hilmer & Bate 1990; Whitfield & Wood 2003). Similarly to previous studies in other systems (e.g. Harris & Cyrus 2000; Strydom *et al.* 2003), the relationship between environmental variables and larval density in south and west coast estuaries is species-specific and is affected by the climate of the area (Chapter 3).

On the other hand, the copepod *Pseudodiaptomus hessei* dominates the zooplankton assemblages from south and west coast estuaries of South Africa. There is a lack of subtropical species and the community comprises a mix of endemic species (Chapter 4). The copepods *Acartia africana, A. longipatella,* the mysids *Mesopodopsis wooldridgei, Gastrossacus brevifissura* and *Rhopalophtalmus terranatalis,* and the amphipod *Grandidierella lutosa* are common in catches. In this region, zooplankton density in estuaries generally exhibit winter minima and summer maxima although in intermittently open systems zooplankton maxima can be reached during stable conditions associated with mouth closure. Despite changes in species density across seasons, seasonally the zooplankton composition varies little. Spatially, the REI region is characterized by the highest zooplankton concentrations. The copepods *Acartia longipatella* and *A. africana* exhibit a spatial pattern with the former species more common in the lower and middle reaches of these estuaries, while the latter is more common in the middle and upper reaches. Spatial and temporal patterns in zooplankton density and occurrence in south and west coast estuaries are consistent with findings from other South African systems (Coetzee 1985; Grindley 1981; Wooldridge 1999; Wooldridge & Melville-Smith 1979).

Virtually all species of larval and early juvenile fishes that occur in estuaries feed on zooplankton (Buskey *et al.* 1993; Gill & Potter 1993; Whitfield & Marais 1999). In South African estuaries, the copepod *P. hessei* is one of the most important food items for zooplanktivorous animals (Bennett 1989; Froneman & Vorwerk 2003; Whitfield 1985; Wooldridge & Bailey 1982). On the other hand, chaetognaths prey on and compete with larval fish in the marine (Baier & Purcell 1997) and estuarine environments (personal observation) and *R. terranatalis* consumes *P. hessei, G. aestuaria* (larvae) and *M. wooldridgei* (adults and juveniles) in South African estuaries (Wooldridge & Bailey 1982). Food composition in larval fishes changes with development of the larvae and may reduce feeding competition with other zooplankters, including competition with other developmental stages of the same species and other larval fish species (Chuwen *et al.* 2007; Munk 1997; Sanvicente-Añorve *et al.* 2006). In addition, warm-temperate studies in South Africa indicate that the seasonal abundances of larval fish and zooplankton are positively correlated (Harrison & Whitfield 1990;

Wooldridge & Bailey 1982) and that these plankton groups respond similarly to environmental conditions (Grange *et al.* 2000).

Integrated assessments of spatio-temporal patterns in the estuarine plankton community in South Africa and worldwide are lacking despite the obvious predatory and competitive interactions that exist. The very few integrated studies on zooplankton and larval fish dynamics suggest that relationships between these two groups can be positive, negative or random depending on small-scale biological processes, such as competition, predation, and intraguild predation (Sanvicente-Añorve *et al.* 2006). Dagg and Govoni (1996) found that even if larval fish feed strongly on copepods, they rarely have any significant effect on copepod population dynamics in estuaries. Blaber *et al.* (1997) found that in the Sarawak and Sabah estuaries (Malaysia) the abundance of larval fish and zooplankton biomass are related. In Australia, Newton (1996) found that in the Hopkins River Estuary the spawning of some estuary-associated fish species coincided with times of high density of food items available to larval fishes. Bonecker *et al.* (1995), in the Estuarine System of Ilha-Grande Bay, and Lopes *et al.* (2006), on the southern Brazilian shelf, studied the zooplankton and larval fish distribution and found that oceanic currents exert a strong seasonal influence on these communities. Marques *et al.* (2006) investigated the spatio-temporal patterns of zooplankton and larval fish communities in the Mondego Estuary (Portugal) and found that the hydrological circulation pattern and human impacts that occur in the estuary strongly influenced the abundance of both plankton components. In the Parana River (Argentina), Paulocci *et al.* (2007) found larval fish benefitting from a new food source, by feeding on the larvae of a bivalve invasive species. Lara-Lopez and Neira (2008) studied the synchronicity between larval fish density and zooplankton biomass using acoustic methods and found a coupled seasonal peak in both components.

Studies assessing the response of larval fish and zooplankton communities to environmental change are common internationally and contribute to the management of estuarine systems, specifically to assess the consequences of anthropogenic disturbances on these systems (see Bednarski & Morales-Ramirez 2004; Browman 2003; Browman *et al.* 2000; Kuhn *et al.* 2000).

In this chapter, an attempt was made to analyze and discuss the relationships between larval fish and zooplankton abundance observed during a plankton study conducted in nine south and west coast estuaries of South Africa. Particular attention was directed towards the interactions of the combined larval fish and zooplankton assemblages as well as those of the dominant species in larval fish and zooplankton groups. The specific aims were to describe the spatio-temporal patterns of the whole plankton community, to assess the influence of the dominant species in this spatio-temporal variability and to provide insights into the potential trophic interactions taking place in these systems. In so doing, this work expects to provide an impetus for further integrative studies of planktonic communities occurring in these estuaries.

5.2 STUDY AREA AND METHODS

5.2.1 Study area

The estuaries of this study fall within the south and west coast of South Africa (Figure 5.1). The area, from Cape Agulhas to Walvis Bay, has a Mediterranean climate with cool wet winters and dry hot summers with water temperatures below 20 ºC (Schulze 1984). Estuaries were selected based on the paucity of qualitative and quantitative data on larval fish and zooplankton as well as accessibility of each to sampling gear. Permanently open (PO) estuaries were represented by the Olifants, Great Berg, Heuningnes, Breede and Goukou estuaries; temporary open/closed (TOC) systems were represented by the Diep and Lourens estuaries; and the Bot and Klein estuaries were included to represent estuarine lake (EL) systems (Figure 5.1).

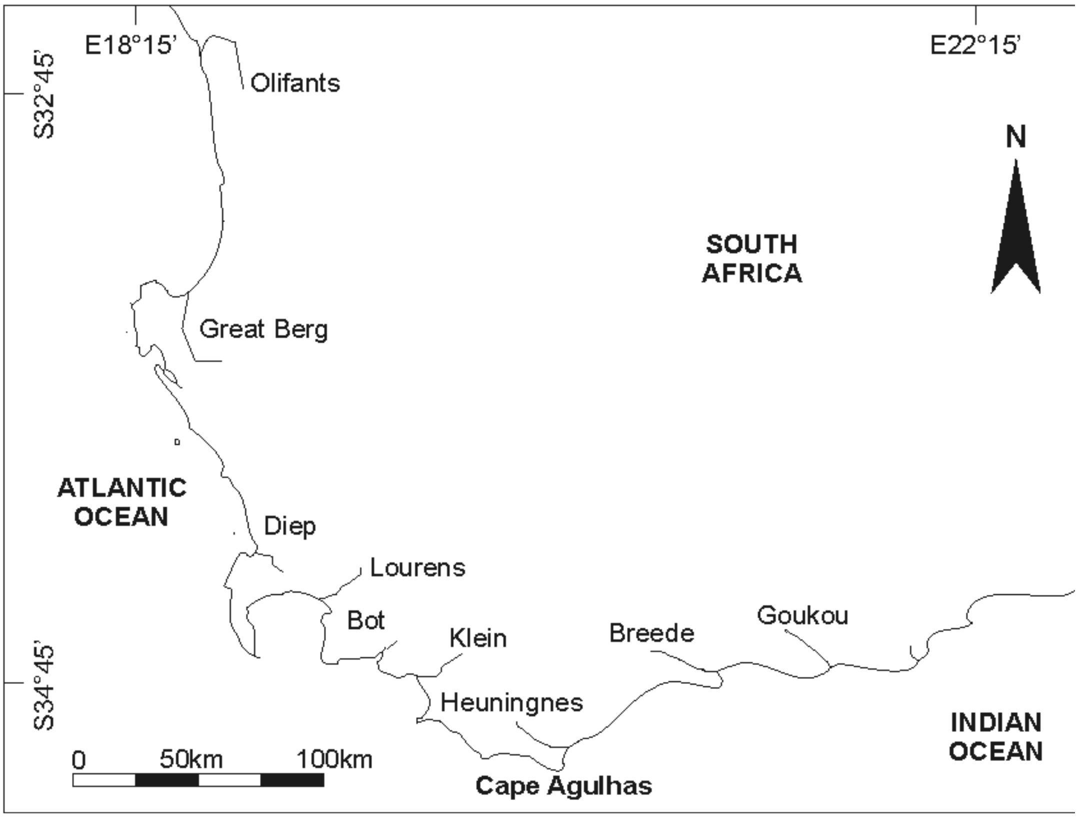

Figure 5.1 Geographical position of estuaries sampled on the south and west coasts of South Africa between June 2003 and March 2004.

The Diep Estuary remained open during sampling, the Lourens Estuary closed during autumn sampling and the mouths of the two EL systems were only open in winter (Bot) and spring (Klein) sampling. A freshwater pulse in the Great Berg Estuary was recorded during spring with salinities <0.5 found 14 km from the mouth and hypersaline (>35.9) conditions were recorded in the Bot Lake system during summer and autumn. The Breede, Diep and Great Berg estuaries were characterised by higher turbidity and the Goukou, Heuningnes, Klein, Bot and Olifants estuaries had lower turbidity. Spring displayed very high turbidity and summer very low turbidity. Summer - autumn temperatures ranged from 21 – 26 °C and winter – spring temperatures ranged from 13 – 18 °C. For a detailed physico-chemical description of the estuaries sampled see Chapter 2.

5.2.2 Sampling and laboratory methods

This study undertook plankton surveys once per season between June 2003 and March 2004. Collection of data was conducted on predetermined days for each estuary associated with the new moon phase and specific tide state and this sampling protocol was standardised across all fieldtrips. Sampling was conducted after dark at GPS fixed equidistant sites along the navigable length of each estuary. Salinity, water temperature and turbidity were also obtained by profiling the water column at each station. Two WP2 plankton nets (570 mm mouth diameter, 0.2 mm mesh aperture size) fitted with Kalhisco 005 WA 130 flow meters were used and two samples (replicates) were collected per station in each estuary. Four hundred and twenty samples were collected in the entire study. In the laboratory, larval fish and zooplankton were identified to the lowest taxon possible and enumerated using a stereo dissecting microscope. See Chapters 3 and 4 for a detailed description of the methods and checklist of species collected.

The copepod *Pseudodiaptomus hessei* was divided into two classes: adults and copepodids. Mysids species were also divided into two classes: juveniles – secondary sexual characteristics not developed – and adults. A maximum of 20 larvae of each fish species in each sample were measured (N =5270 individuals) to the nearest 0.1 mm body length and their developmental stage was recorded (Neira *et al.* 1998). Measurements were made using an eyepiece micrometer for larvae <10 mm and Vernier callipers for larger specimens. Copepod nauplii and fish eggs were excluded since these were not efficiently sampled due to aperture size of the mesh used in nets.

5.2.3 Data analysis

Abundance of both larval fish and zooplankton were standardized to numbers per cubic meter of water filtered. All samples taken, including replicates of each station, from all estuaries were considered as separate data samples and the total sample size was 396. Interactions between larval fish and zooplankton were investigated using total larval fish and total zooplankton densities (total = all species included) as well as using only the dominant estuarine copepod species, *P. hessei* and the dominant estuarine larval fish species, *Gilchristella aestuaria,* taken in plankton tows. These two species together with the chaetognath *Sagitta* sp., the mysids *Mesopodopsis wooldridgei* and *Rhopalophtalmus terranatalis,* and the second-most frequent larval fish species, the goby *Psammogobius knysnaensis,* were used to investigate inter-specific relationships, including several trophic interactions.

Statistical analysis of the data was performed using Statistica 8.0. Tests for normality and homogeneity of variances were carried out and suggested a Log_{10} $(x+1)$ transformation of the raw data. Graphical and correlation analyses were performed on the raw or transformed data (when appropriate) to determine the relationship between larval fish and zooplankton densities.

5.3 RESULTS

5.3.1 Relationships in larval fish and zooplankton distribution

Temporal distribution

Although total zooplankton density was similar throughout most seasons, an inter-estuary analysis of total larval fish and zooplankton density showed that both components peaked simultaneously in spring and summer in PO estuaries and the TOC Diep Estuary (Figure 5.2). Larval fish appeared to maintain this spring-summer peak in intermittently open estuaries however, in the EL Bot (4 larvae m^{-3}) and the TOC Lourens (2 larvae m^{-3}) systems mean larval fish density peaked in autumn when the mouths of these two estuaries was closed. High abundances of *Gilchristella aestuaria* in the EL Bot system and of this species together with *Psammogobius knysnaensis* in the TOC Lourens Estuary were responsible for these autumn peaks. In intermittently open estuaries, the zooplankton exhibited maxima (mean over 3000 ind m^{-3}) in winter and autumn in the Klein and Lourens estuaries when the mouths were closed and exhibited minima in winter and spring in the EL Klein and Bot estuaries when the mouths were open. Total larval fish and zooplankton densities were positively correlated (P <0.05) in all but the Heuningnes and Klein estuaries (Table 5.1).

Table 5.1 Pearson's correlation between larval fish and zooplankton. Only significant correlations are given.

	Goukou	Breede	Bot	Lourens	Diep	Great Berg	Olifants
r	0.45	0.56	0.64	0.50	0.62	0.44	0.23
n	45	76	22	16	21	88	76

Pseusodiaptomus hessei and *Gilchristella aestuaria* were generally more abundant in summer (Figure 5.2). However, *Pseudodiaptomus hessei* showed the same trend as total zooplankton, exhibiting density maxima (mean >7500 ind m^{-3}) in the estuaries and seasons where the mouths were closed. Correlation of the two species within each estuary showed that *P. hessei* and *G. aestuaria* were positively correlated ($0.42< r >0.66$, $P <0.05$) in the Bot, Lourens, Great Berg and Olifants estuaries.

Spatial distribution

Overall both zooplankton and larval fish densities across the salinity zones of the estuaries were dome-shaped (Figure 5.3). Zooplankton was concentrated (>60 % of the total density) in the polyhaline and mesohaline zones. Larval fish density was concentrated in the mesohaline (>50 % of the total density). Nonetheless, highest mean densities of larval fish (8 larvae m^{-3}) and zooplankton (610 ind m^{-3}) were recorded in the mesohaline zone.

Pseudodiaptomus hessei and *Gilchristella aestuaria* showed a dome-shaped distribution across salinity zones as observed for total zooplankton and larval fish densities. Both species were concentrated in the mesohaline zone (>50 % of their total density) and showed mean densities of 2021 ind m^{-3} for *P. hessei* and 32 larvae ind m^{-3} for *G. aestuaria* (Figure 5.3).

5.3.2 Larval fish and zooplankton relationships with physico-chemical variables

Salinity

A small but significant correlation ($P < 0.05$) between total larval fish and zooplankton densities with salinity was found (Figure 5.4). Although both plankton components were spread over the whole range of salinities, total larval fish and zooplankton were more abundant in the areas were salinities were in the range 5 to 15, the mesohaline zone (Figure 5.4). Significant correlations ($P < 0.05$) between salinity and total larval fish ($r = 0.23$) and total zooplankton ($r = 0.26$) densities were found. Analysis of the two selected species suggests that *Pseudodiaptomus hessei* and *Gilchristella aestuaria* exhibit a similar salinity distribution with overlapping peaks in the 5 - 20 salinity range.

Temperature

Larval fishes were recorded in higher numbers in the 21 - 24 °C range whereas zooplankton showed peaks of abundance in two temperature ranges 13 - 16 °C and 21 - 24 °C (Figure 5.5). Significant correlations ($P < 0.05$) between temperature and total larval fish ($r = 0.50$) and total zooplankton ($r = 0.24$) densities were found. Analysis of the two dominant species yielded very similar results (Figure 5.5). *Pseudodiaptomus hessei* was found over a wide range of temperatures and was more abundant at higher temperatures however, the winter samples of the EL Klein system exhibited high density peaks (40 - 110 ind m^{-3}) of this copepod in the 14 - 16 °C range. *Gilchristella aestuaria* displayed higher densities at higher temperatures and showed a correlation ($r = 0.37$; $P < 0.05$) with temperature.

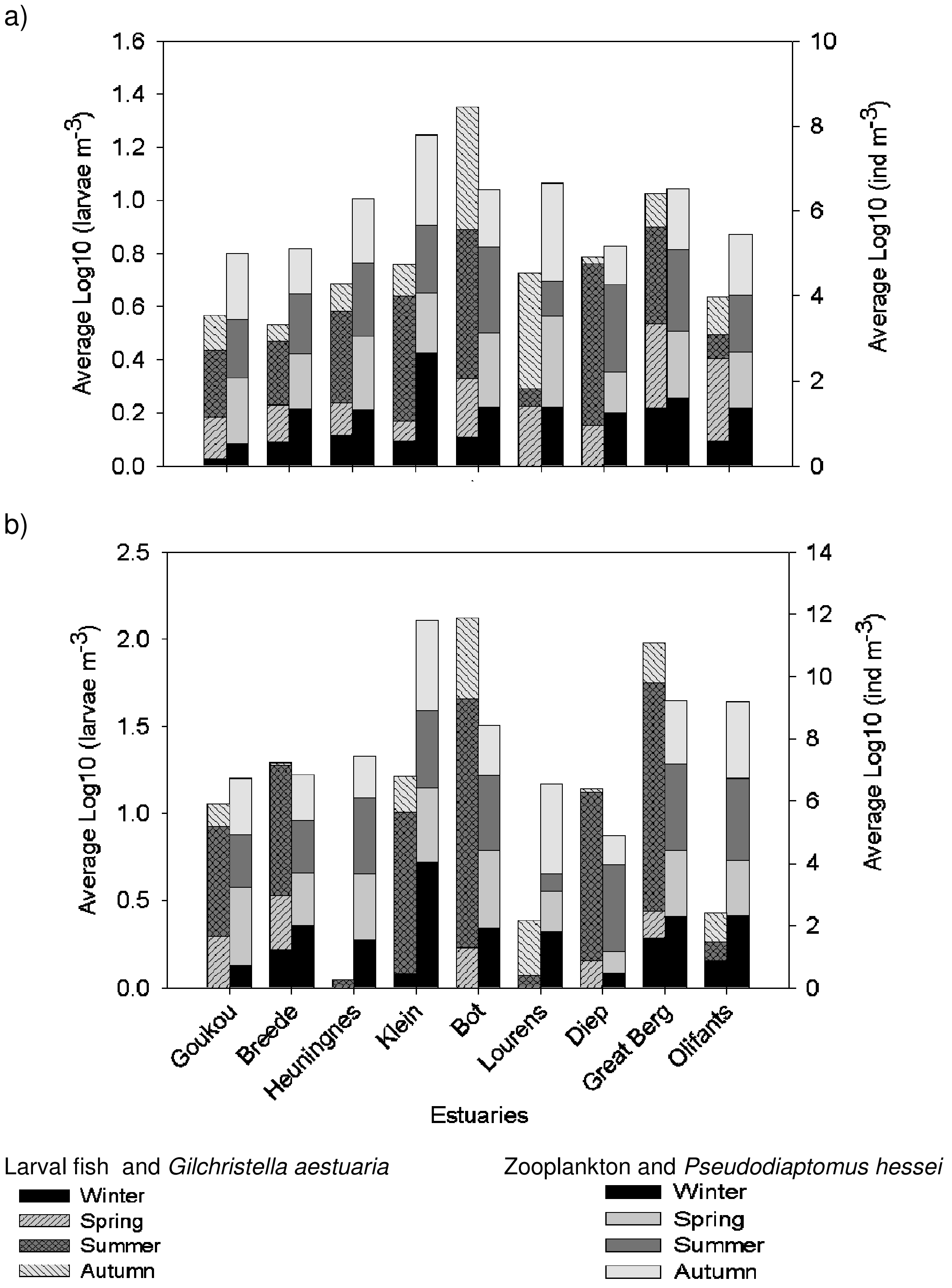

Figure 5.2 Spatial (estuaries) and temporal (seasons) variability in mean density of a) total zooplankton and larval fish and b) the dominant copepod and larval fish species in selected south and west coast estuaries.

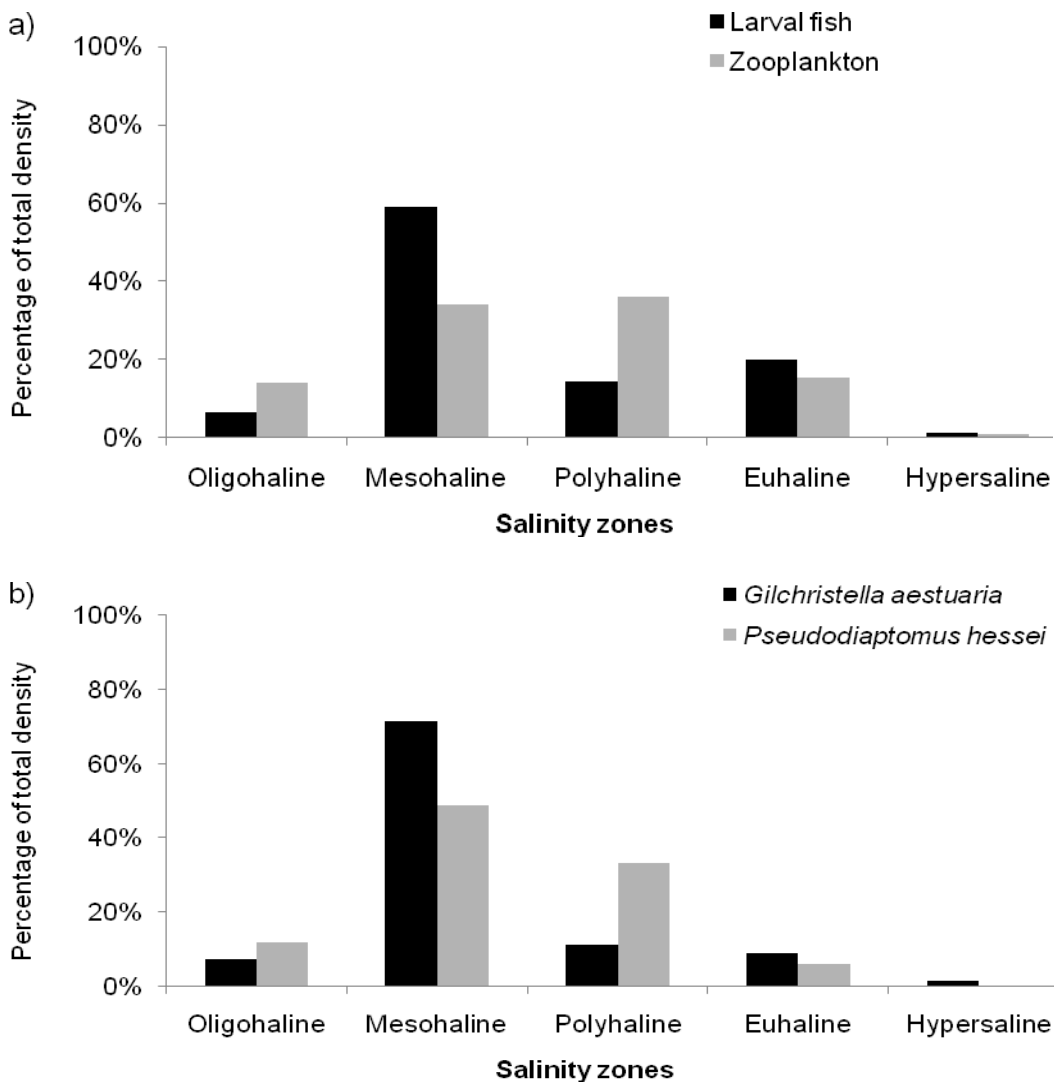

Figure 5.3 Percentage concentration (numbers m-3) of a) zooplankton and larval fish density and b) the dominant copepod and larval fish species in selected south and west coast estuaries of South Africa at different Venice salinity zones.

Turbidity

Total larval fish and zooplankton and dominant species densities peaked in lower water transparency coefficients (clear waters) and in general, the plankton was less abundant in higher water transparency coefficients (turbid waters). Both total larval fish (r = -0.11) and zooplankton (r = -0.18) were negatively correlated (P <0.05) to water transparency, although correlations were weak (Figure 5.6). None of the dominant species were significantly correlated to water transparency.

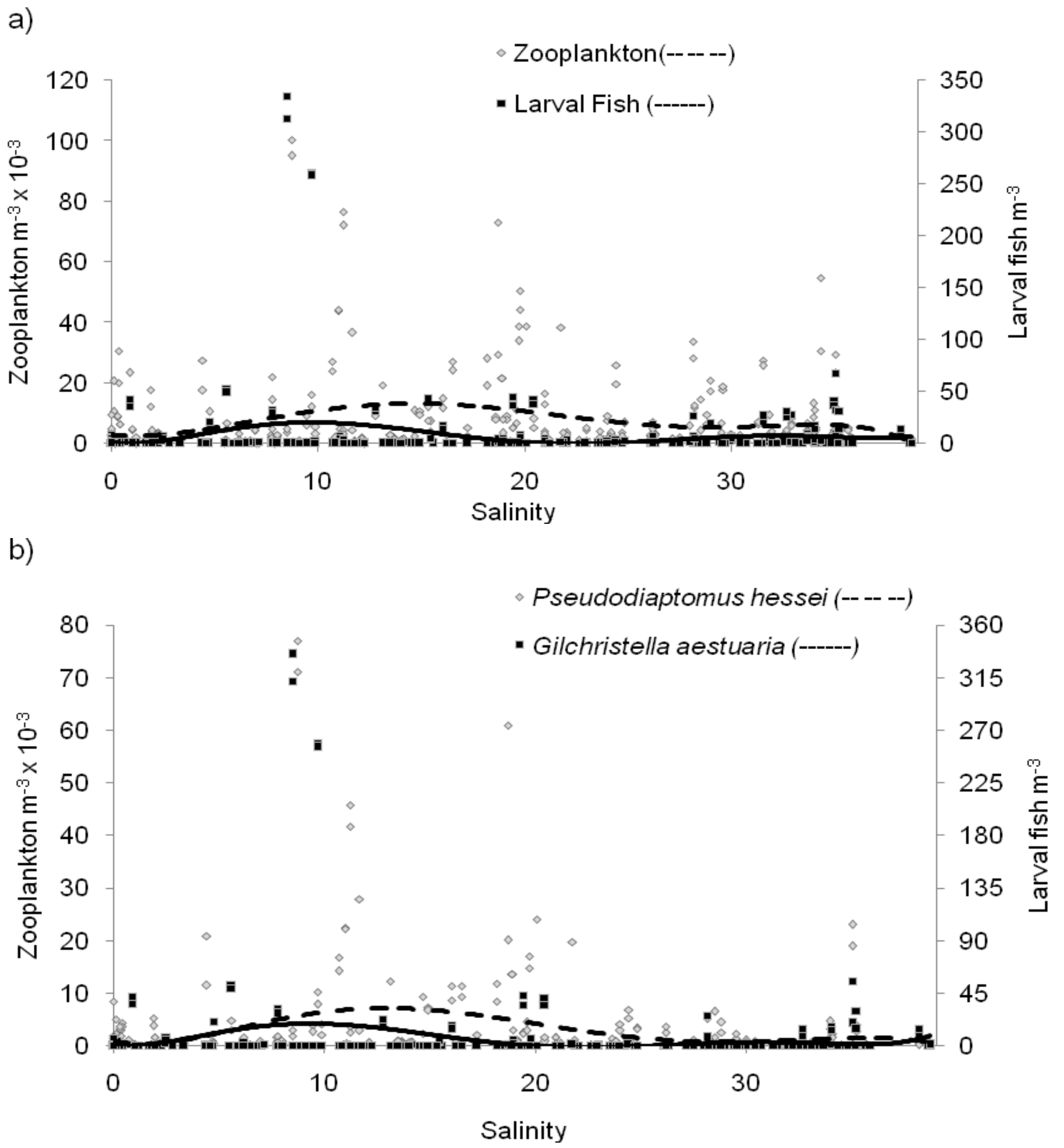

Figure 5.4 Scatter plots of a) total zooplankton and larval fish density and b) the dominant copepod and larval fish species in selected south and west coast estuaries of South Africa over the entire salinity range sampled during the study. Lines represent the general trend of relationship.

5.3.3 Inter-specific relationships

Figure 5.7 and 5.8 display the results of the correlation analysis between the developmental stages of *G. aestuaria* and *P. knysnaensis* and the selected zooplankton species. Positive correlations were found between the different developmental stages of *G. aestuaria* and *P. knysnaensis* and the developmental stages of *P. hessei, M. wooldridgei* and *R. terranatalis*. A negative correlation occurred between the chaetognath *Sagitta* sp. and the preflexion, flexion and postflexion stages of *G. aestuaria,* juveniles and adults of *R. terranatalis* and copepodids and adults of *P. hessei*. In contrast, the preflexion stage of *P. knysnaensis* was positively correlated with the chaetognath *Sagitta* sp.

5.4 DISCUSSION

In this study, zooplankton and larval fish densities showed a positive correlation, which was significant in most estuaries. Chaetognaths, a zooplankton group considered to cause significant mortality of fish larvae in the marine environment (Baier & Purcell 1997), and gelatinous species (cnidarians), another zooplankton group that preys on and competes with larval fish (Purcell & Arai 2001), are much less abundant than larval fish in south and west coast estuaries (Chapter 4). In contrast, copepods, a primary food item for larval fish (Dagg & Govoni 1996; Whitfield & Marais 1999), dominate (>80 % of total density) the zooplankton assemblages in the estuaries of this region (Chapter 4). Sanvicente-Añorve *et al.* (2006) suggest that a positive relationship between zooplankton and larval fish abundance will occur in the absence of major predators on ichthyoplankton and the presence of enough suitable food for larval fish. These conditions were typical in the estuaries of this study during the sampling period, hence the positive relationship observed between zooplankton and larval fish density.

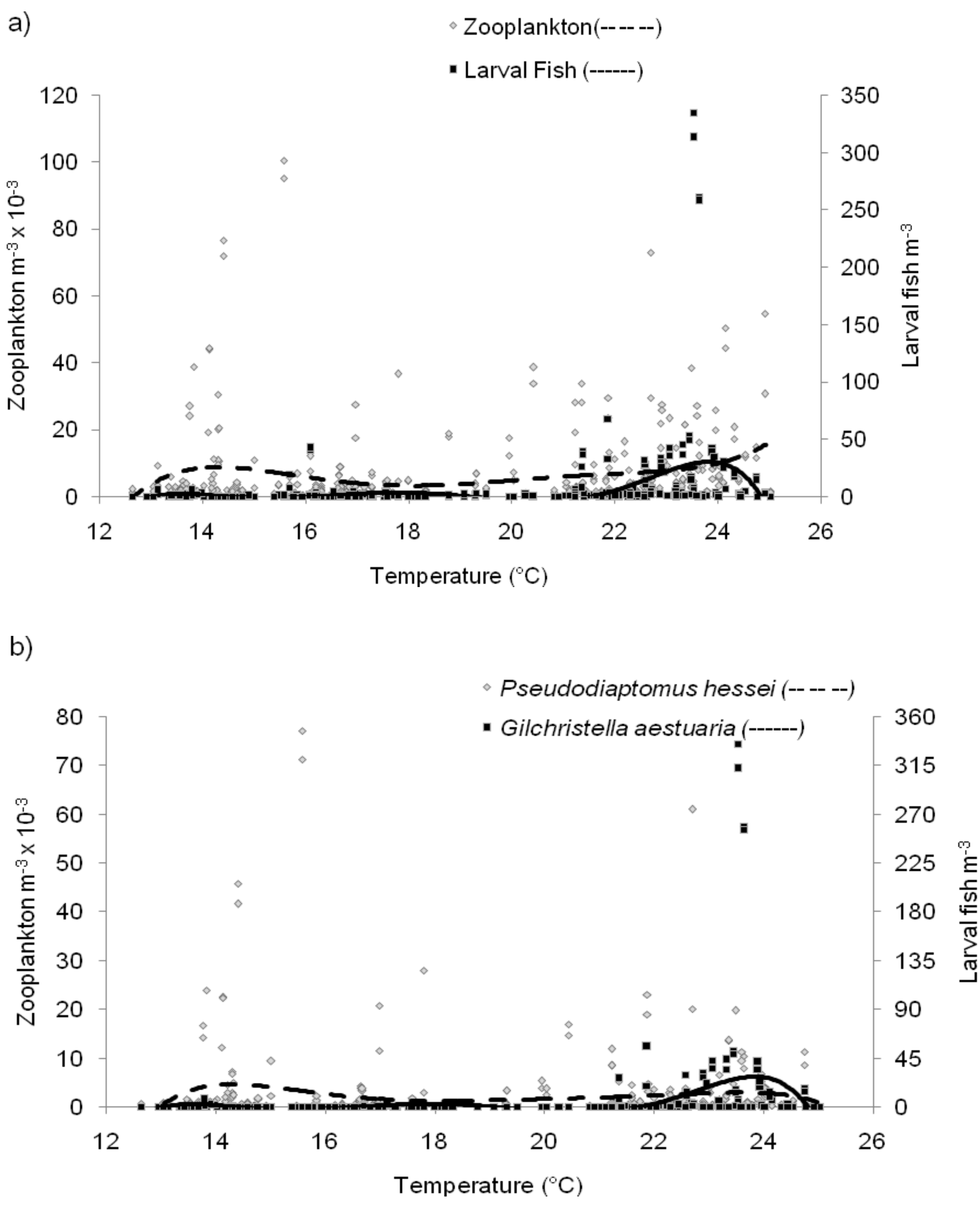

Figure 5.5 Scatter plots of a) total zooplankton and larva fish density and b) the dominant copepod and larval fish species in selected south and west coast estuaries of South Africa over the entire temperature range sampled during the study. Lines represent the general trend of relationship.

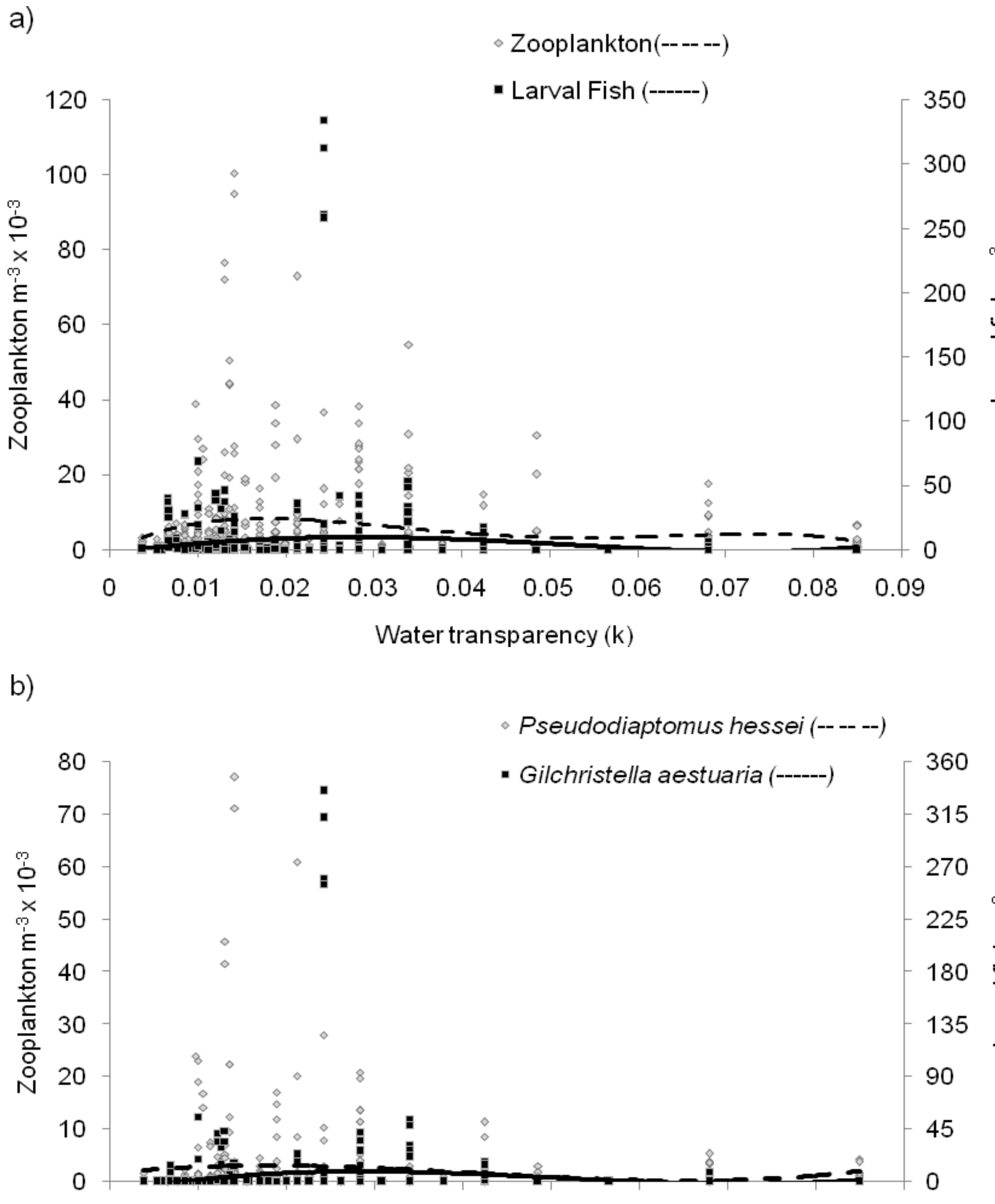

Figure 5.6 Scatter plots of a) total zooplankton and larval fish density and b) the dominant copepod and larval fish species in selected south and west coast estuaries of South Africa over the entire water transparency range sampled during the study. Lines represent the general trend of relationship.

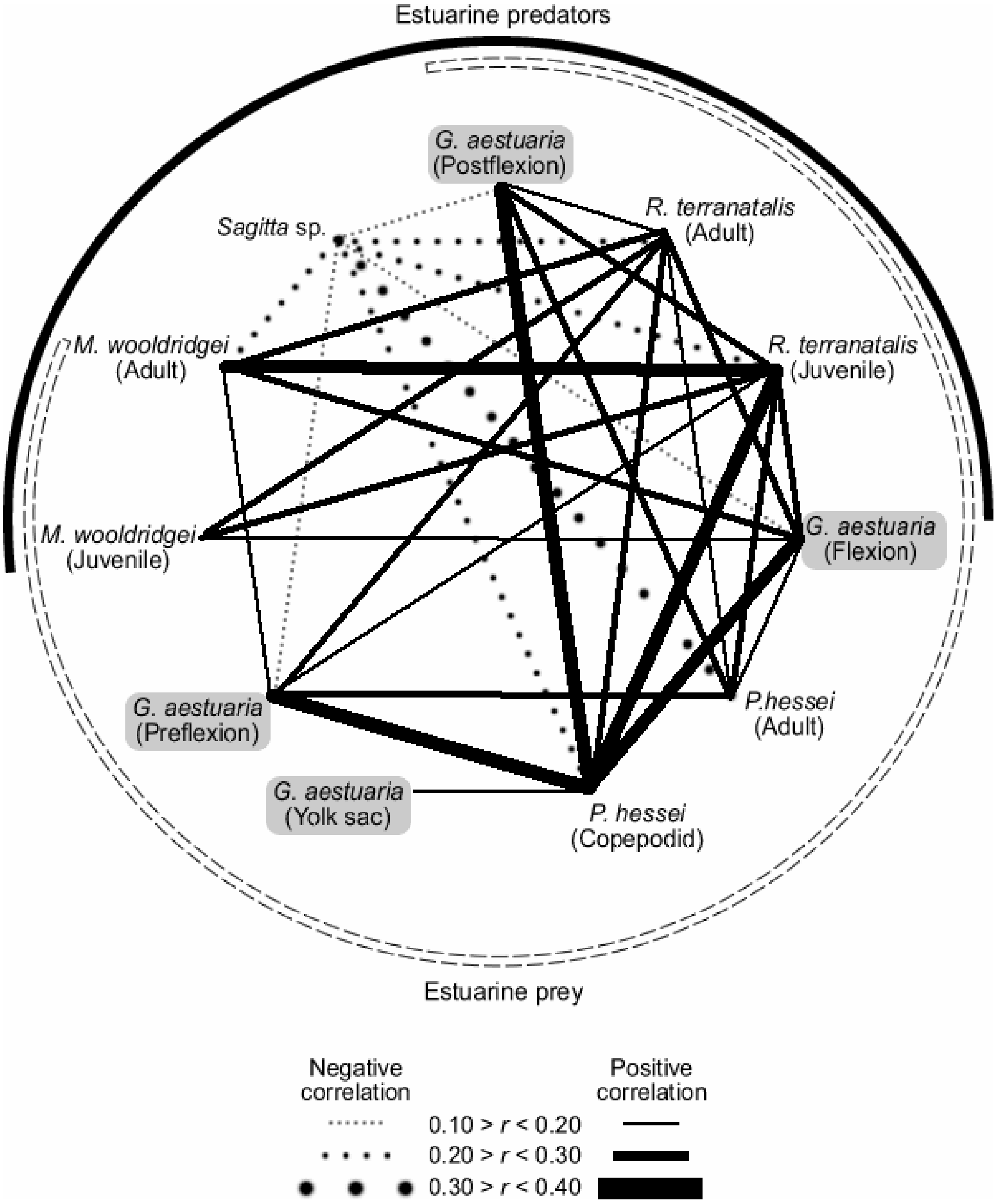

Figure 5.7 Graphical display of the significant correlations between *Gilchristella aestuaria* and the species selected to represent several potential trophic interactions within the estuaries sampled. Significant correlations between conspecifics are excluded.

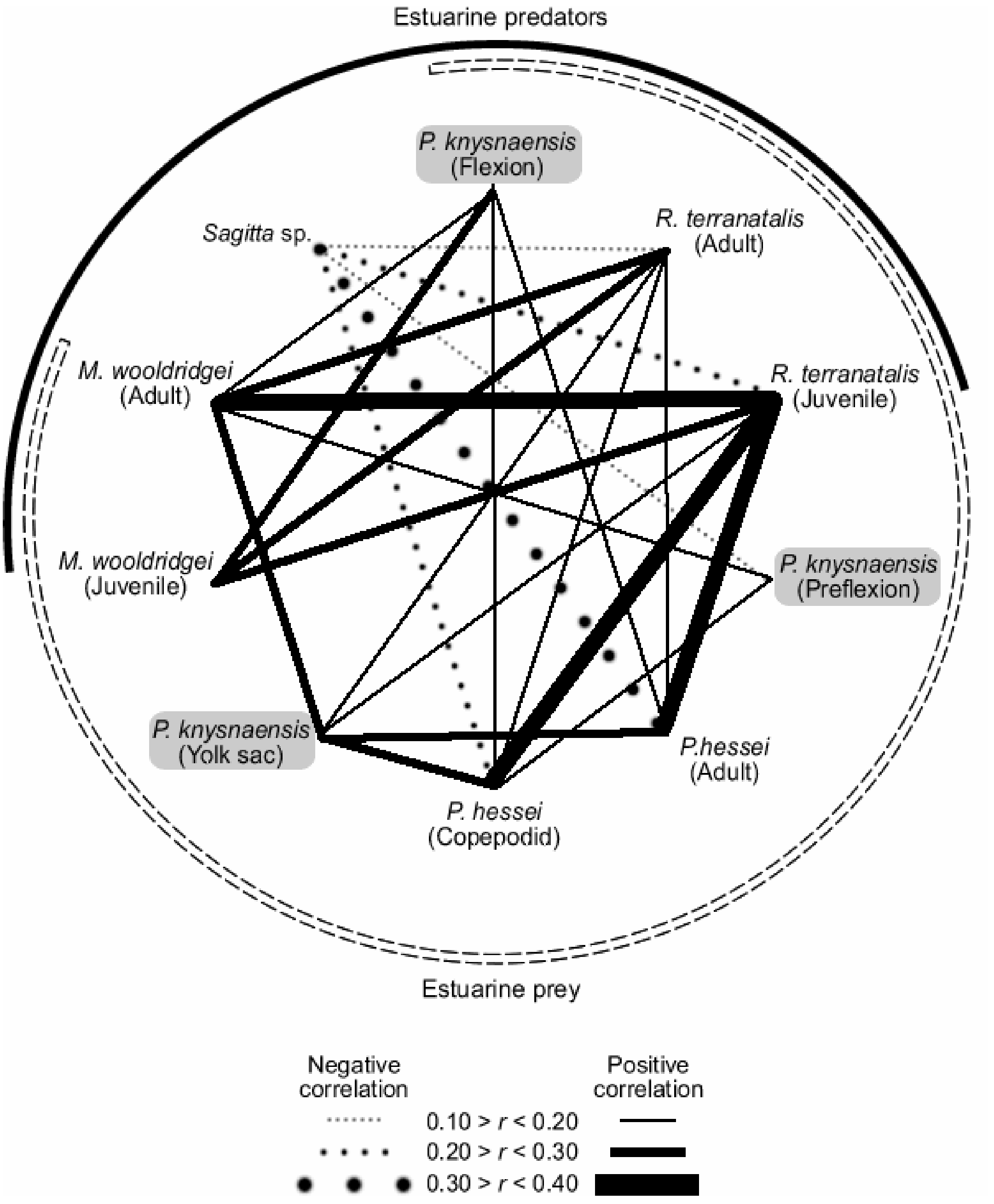

Figure 5.8 Graphical display of the significant correlations between *Psammogobius knysnaensis* and the species selected to represent several potential trophic interactions within the estuaries sampled. Significant correlations between conspecifics are excluded.

The positive relationship between larval fish and zooplankton densities is also attributed to their temporal and spatial synchronicity. Both plankton components in this study exhibited higher densities in summer and in the mesohaline zone. The temporal synchronicity is the result of not only the peak of ocean spawning fishes providing estuary recruits in summer but also estuary-spawning fishes coupling their reproductive strategies to exploit cyclical peaks in abundance and size spectrum of the food available for their larvae (Lara-Lopez & Neira 2008; Newton 1996). Lara-Lopez & Neira (2008) suggest that estuary-associated fishes may have a fixed spawning period timed to increasing temperatures to ensure a match with abundant microplankton food supply. In South African estuaries, primary and secondary production generally peaks in summer (Adams & Bate 1999; Froneman 2001a; Wooldridge 1999) providing ideal feeding conditions for both estuarine and marine plankton utilizing the estuary. The spatial synchronicity observed in this study is related to both components using the high productivity of the river-estuary interface (REI) region (Hilmer & Bate 1990). This region is characterized by oligohaline and mesohaline conditions (Bate *et al.* 2002) and it is in this region that larval fish and zooplankton species find a rich source of food and therefore exhibit density maxima in these salinity zones (Pattrick *et al.* 2007; Chapters 3 & 4; Strydom *et al.* 2003).

Sanvicente-Añorve *et al.* (2006) propose two additional relationship patterns between ichthyoplankton and zooplankton namely, a negative pattern and a random pattern. The former will occur if predation, competition and intraguild predation (predation between two competing species) are detrimental to larval fish, a situation that is unlikely to occur in south and west coast estuaries given the low density of potential larval fish predators and competitors (Chapter 4). The same authors suggest that the random pattern is the result of high water turbulence and gradual shifts between positive and negative patterns.

It is hypothesized that the random pattern described above occurred in the estuaries where larval fish and zooplankton total densities were not correlated. The temporal asynchrony between zooplankton and larval fish density observed in the estuaries where mouth condition changed, thereby creating a disturbance, offers some evidence to support this hypothesis. Wooldridge (1999) suggests that temporal abundance patterns of zooplankton do not necessarily follow a seasonal cycle but are instead linked to the frequency of freshwater pulses flowing into an estuary. Pulse spawning by adult *G. aestuaria* is known to occur in response to freshwater input with high numbers of larvae being recorded after small-scale flooding or river flow into estuaries (Martin *et al.* 1992; Pattrick *et al.* 2007; Strydom *et al.* 2002). A random pattern in the relationship between larval fish and zooplankton in estuaries, especially in intermittently open systems such as those included in this study, could occur. Instead of turbulence being the disturbance factor as proposed by Sanvicente-Añorve *et al.* (2006), in the present context, estuary mouth closure would be the disturbance factor at play.

Both larval fish and zooplankton densities were similarly correlated with the environmental variables measured in this study. The two plankton components were positively correlated to salinity and temperature and negatively correlated to turbidity. Estuarine studies from the warm-temperate region and subtropical region of South Africa have also found that these three variables are often correlated with plankton density (Harris & Cyrus 2000; Harris *et al.* 2001; Strydom *et al.* 2003). In such studies, plankton components tend to be positively correlated to water temperature and turbidity and negatively correlated to salinity. The apparent different directions in the association of the salinity and turbidity and the plankton components are attributed to differences in the climate of the three biogeographic regions. Generally, cool-temperate estuaries are characterised by wet winters that result in higher turbidities and dry summers where low turbidities often occur; warm-temperate estuaries experience autumn and spring rainfall that result in low salinities and high turbidities, and subtropical estuaries typically have low salinities and high turbidities during the summer rainfall (Harrison 2004; Harrison & Whitfield 2006). In turn, temperature is positively correlated to both plankton components and this is attributed to the synchrony between seasonal variation of water temperature and the peak breeding period of most fish species (Whitfield 1990; Whitfield & Marais 1999) and estuarine productivity across South Africa (Adams & Bate 1999; Froneman 2001a; Wooldridge 1999) and worldwide (Lara-Lopez & Neira 2008; Newton 1996).

The relationships between the densities of the dominant species of copepod, *Pseudodiaptomus hessei,* and larval fish, *Gilchristella aestuaria*, and the abiotic variables measured in this study were not as clear. Significant correlations were only found between *G. aestuaria* and temperature. *Gilchristella aestuaria* breeding period correspond to late spring and summer (Whitfield 1998) when temperatures increase and this explains the positive relationship observed. The peak of *P. hessei* in colder waters observed in this study correspond to a single event in winter in the Klein Estuary, which appears to be typical for zooplankton during mouth closure. There is a general increase in zooplankton density in temperate TOC estuaries during closed mouth periods (Gaughan & Potter 1995; Kibirige & Perissinotto 2003b) characterized by more stable physico-chemical conditions. The lack of correlation between both the estuarine copepod and the estuarine larval fish with both salinity and turbidity is attributed to the capacity of these species to tolerate a wide range of salinities (Whitfield 1998; Wooldridge 1999) and the reduced influence of turbidity *per se* in structuring larval fish and zooplankton assemblages in south and west coast estuaries (Chapter 3 & 4).

The correlations obtained in the inter-specific analysis may be a reflection of feeding interactions among estuarine species. In the present study, adults of the mysid *R. terranatalis* were positively correlated to densities of juveniles of *M. wooldridgei,* copepodid and adult stages of *P. hessei* and of the different developmental stages of the *G. aestuaria* and *P. knysnaensis*. These significant relationships could be related to the feeding of *Rhopalophtalmus terranatalis* on juveniles of *M. wooldridgei*, on the copepod *P. hessei* and on larval fish, e.g. *G. aestuaria* (Jerling & Wooldridge 1995a; Wooldridge & Bailey 1982; Wooldridge & Webb 1988). Developmental stages of *G. aestuaria* and *P. knysnaensis* were positively correlated with the developmental stages *P. hessei, R. terranatalis* and *M. wooldridgei* in this study. These findings can be attributed to the copepod and mysids species contributing substantially to the food composition of the fish species in warm-temperate estuaries (Wooldridge & Bailey 1982). Chaetognath density was negatively correlated to most potential prey items, including postflexion larvae of *G. aestuaria*. As mentioned earlier, chaetognaths are important marine predators that can enter estuaries in search for food. Therefore, two potential reasons for the negative correlations are 1) that detrimental competition and intraguild predation interactions between chaetognaths and zooplankton species is taking place in these systems producing the negative pattern as proposed by Sanvicente-Añorve *et al.* (2006), and 2) being a marine species, chateognaths would prefer the lower reaches of the estuaries in comparison to estuarine species. However, only feeding studies could answer these questions.

The positive correlation observed in this study between the chaetognath density and the preflexion stage of *P. knysnaensis* may provide evidence to support reason number two above as well as the theory of a positive relationship between zooplankton and larval fish communities in the estuaries of this study. The early stages of *Psammogobius knysnaensis* were more abundant in the lower reaches of the estuaries of this study, which is in agreement to previous studies that suggest that the species is particularly abundant in the lower reaches of estuaries (Whitfield 1998). Despite the preference for the same habitat as its potential predator chaetognaths, the two species still showed a positive relationship, which supports the hypothesis that predation, competition or intraguild predation are not detrimental to larval fish in south and west coast estuaries given the low density of potential larval fish predators and competitors (Chapter 4).

Although larval fish and zooplankton densities (including all species) can be used to investigate the dynamics between these two plankton components, this study has shown that a species approach provides finer detail. Indeed, differences were observed in the results of the correlation analyses between densities of the two major plankton components (positive correlations) and between dominant estuarine species densities (negative correlations). However, the dominant species of each component, *P. hessei* and *G. aestuaria*, markedly influenced the results of analysis of total densities with both analyses on occasion, showing an almost identical response (see Figures 5.4 – 5.6). In analyses of these cases, subgroups within the plankton community must be created in order to reduce the masking effect of dominant species. For example, estuarine plankton can be grouped into estuary resident, marine migrant or marine straggler species and analyzed by subgroups.

Although the once-off nature of this study warrants precaution on the extrapolation of its findings, south and west coast estuaries of South Africa could probably exhibit complex feeding relationships between zooplankton and larval fish species. These feeding interactions are relevant to understand ichthyoplankton and zooplankton communities and the influence of population dynamics of one component upon the other in response to changing physical environment. Correlation alone is insufficient to adequately assess detailed relationship patterns between the two plankton components, therefore trophic and feeding studies at the species level are recommended for future research in these estuarine systems to supplement the broad-scale pattern observed in the present study.

CHAPTER 6

SYNTHESIS AND CONCLUSIONS

Analyses of aquatic biota in South Africa suggest three main biogeographic provinces namely the subtropical, warm-temperate and cool-temperate regions (Harrison 2002, 2005). The estuaries within the warm-temperate and subtropical estuaries of South Africa have been well studied and are known to play an important role for both the larval and early juvenile stages of many commercially, recreationally and ecologically important marine and estuarine fish species (Beckley 1985; Harris & Cyrus 2000; Strydom *et al.* 2003). Larval fish species find in these warm-temperate and subtropical estuaries a favourable habitat for development, protection and feeding (Potter et al. 1990; Whitfield & Marais 1999). On the latter function, estuaries provide larval fish with a readily available source of zooplanktonic food comprising copepods, ostracods, cladocerans and many other planktonic groups (Wooldridge & Bailey 1982; Whitfield & Marais 1999). In South Africa, the use of south and west coast estuaries by larval fish and the composition and abundance of zooplankton in these estuaries is poorly understood due to the lack of published information on larval fish (Whitfield & Marais 1999) and the few quantitative data available on zooplankton assemblages (Wooldridge 1999). Quantitative data on the composition and abundance of larval fish and zooplankton assemblages occurring in south and west coast estuaries will allow for a better understanding of the estuary use by these plankton groups along the cool-temperate and warm/cool-temperate boundary region of South Africa.

Besides providing food to larval fish, estuaries also support larval fish predators and competitors that affect and are affected by larval fish assemblages as in the marine environment (Dagg & Govoni 1996; Sanvicente-Añorve *et al.* 2006). South African studies have tried to understand estuarine larval fish and zooplankton assemblages separately. As a consequence, little is known about the relationships between these two plankton components. Studies that assess both larval fish assemblages and zooplankton assemblages simultaneously and that investigate the interactions between the two components are imperative to reduce the gap in the understanding of plankton dynamics in South African estuaries.

The present study assessed the composition, abundance and spatio-temporal variability in larval fish and zooplankton assemblages in nine south and west coast estuaries, which belong to the cool- and warm-temperate regions of South Africa. The characteristics of these assemblages were found to be related to the physico-chemical environment characterizing these estuaries. In addition, the relationships between larval fish and zooplankton were assessed and revealed similar responses to environmental variables and potential feeding interactions.

In the present study (Chapter 2), the south and west coast, cool- and warm-temperate, estuaries showed physico-chemical characteristics that were related to the climate and oceanographic conditions typical of the south and west coasts of South Africa. Winter and spring showed lower salinities, lower water temperatures and higher turbidities while summer and autumn showed higher salinities, higher water temperatures and lower turbidities. Generally, south and west coast cool-temperate estuaries are characterised by cool, wet winters and hot, dry summers with water temperatures below 20 ºC (Harrison 2004). Winter rainfall results in low salinities accompanied by high turbidities whereas high salinities and low turbidities dominate in summer (Millard & Scott 1954). On the other hand, mean winter and summer water in estuaries were typically lower than those observed in warm-temperate and subtropical systems by other researches. This is directly attributed to the influence of the cold Benguela Current in the west and the warm Agulhas Current in the south east coast of South Africa (Miller *et al.* 2006; Schumann *et al.* 1999) which in turn, defines the biogeographic regions of South Africa (Day 1981c; Harrison 2002). The estuaries in this study exhibit distinct physico-chemical characteristics that separate them from warm-temperate and subtropical estuaries as has been proposed by Harrison (2004). Since physico-chemical and hydrodynamic variability within estuarine systems influences the biotic communities residing in and utilizing these habitats (Grindley 1981; Strydom *et al.* 2003; Whitfield & Marais 1999; Wooldridge 1999), it would be expected that south and west coast cool-temperate and boundary region estuaries have larval fish and zooplankton assemblages that will also differ from that of typical warm-temperate and subtropical estuaries.

The larval fish assemblages from south and west coast, cool- and warm-temperate boundary region, estuaries comprised 9 orders, 20 families, 29 genera and 47 taxa (Chapter 3). The larvae of the estuary-resident species *Gilchristella aestuaria, Caffrogobius gilchristi, Psammogobius knysnaensis*, *Redigobius dewaali, Omobranchus woodi* and *Atherina breviceps* dominated (>96 % of the total catch) in this study and have also been recorded in earlier estuarine larval fish (Harris & Cyrus 2000; Melville-Smith & Baird 1980; Strydom *et al.* 2003; Whitfield 1989a) and adult fish studies (Harrison 1997a, 1997b, 1998, 1999a, 1999b). Estuary-dependent marine species, namely *Rhabdosargus holubi*, *Diplodus capensis, Heteromycteris capensis*, *Solea turbynei, Liza richardsonii*, *Monodactylus falciformis, Myxus capensis* and *Argyrosomus japonicus* were recorded as far west as the Olifants and Great Berg estuaries, in very small numbers (<1 % of the total catch). These species also contribute significantly to larval fish catches in warm-temperate estuaries (Melville-Smith & Baird 1980; Strydom *et al.* 2003; Whitfield 1989a) and in warm-temperate and subtropical boundary estuaries (Pattrick *et al.* 2007). Estuary-resident species were found in several developmental stages from yolk sac to juveniles while estuary-dependent marine species were predominantly found in late developmental stages, from flexion to early juveniles. Larvae of freshwater migrant species were absent in this study.

The zooplankton from south and west coast, cool- and warm-temperate, estuaries comprised 44 taxa belonging to 7 phyla, >20 orders and over 35 families (Chapter 4). Typical larval fish prey items, namely copepods (87 % of total catch) and decapods larvae (6.5 %), dominated the zooplankton. The calanoid copepods *Pseudodiaptomus hessei, Acartia africana, A. longipatella* and the mysids *Mesopodopsis wooldridgei, Gastrossacus brevifissura* and *Rhopalophtalmus terranatalis* were common in catches and are common in other South African estuaries (Grindley 1970, 1976a, 1976b; Jerling & Wooldridge 1995b; Wooldridge 1977b). The copepod *Pseudodiaptomus hessei* dominated (59% of the total catch) the zooplankton and occurred in similar densities to those observed in other South African estuaries (Wooldridge 2005; Wooldridge & Callahan 2000) despite biogeographic boundaries and temperature differences.

Biogeography did, however, play a role in the zooplankton composition in the south and west coast estuaries. The copepod *Acartia africana* and the amphipod *Grandidierella lignorum* were exclusive to south coast estuaries, with the former making substantial contributions to total density. *Acartia natalensis*, the acartiid that dominates on the east coast (Grindley 1981; Wooldridge 1999) was absent from the estuaries in this study. In addition, south coast estuaries exhibited higher diversity indices and the community analysis showed that the difference in community structure between south and west coast estuaries was statistically significant.

These findings suggest south and west coast, cool- and warm-temperate boundary region, estuaries have distinct larval fish assemblages that are characterized by high endemism, significant contributions of estuary-resident species and a reduced contribution of estuary-dependent marine species and freshwater migrant species. However, adults of estuary-dependent marine species have been recorded in the estuaries and therefore it appears that the reduced contribution of them may be due to these fishes recruiting in as early juveniles. In contrast, southeast and east coast estuaries, belonging to the warm-temperate and subtropical regions, have larval fish assemblages that exhibit important contributions of both the larvae and early juveniles of estuary-resident fishes and the larvae of estuary-dependent marine species (Harris & Cyrus 2000; Strydom *et al.* 2003; Whitfield 1989a; Whitfield 1994). Larval stages of freshwater genera such as *Labeo* and *Eleotris* also appear in larval fish catches from warm-temperate estuaries of South Africa (Strydom *et al.* 2003). On the other hand, the findings also suggest that zooplankton assemblages from south and west coast, cool- and warm-temperate boundary region, estuaries lack unique species and comprise a mix of endemic species occurring in many South African systems. The zooplankton assemblages in these estuaries are also less diverse than their warm-temperate and subtropical counterparts. For instance, the copepods *Tortanus capensis, Temora* spp, *Pseudodiaptomus charteri* and the mysids *Mesopodopsis africana* and *Gastrossacus gordonae* are common in zooplankton catches from east coast estuaries in South Africa but were absent in the south and west coast estuaries sampled in this study.

The differences between plankton assemblages from the south and west coast (this study) and from those in warm-temperate and subtropical estuaries on the south and east coast are the result of differences in the climate, oceanographic characteristics of the region, and differences in the tropical and subtropical marine fish faunas of the highly diverse east coast compared to the less diverse south coast fauna (Grindley 1981; Harrison 2002; Hockey & Buxton 1991). These differences explain the low contribution of larvae of estuary-dependent marine fish species and the absence of copepods and mysids species that are common in warmer estuaries. Zooplankton species in warm-temperate and subtropical estuaries tend to be positively related to turbidity and this is attributed to the protection and feeding aid that these waters provide them (Cyrus & Blaber 1987; Harris & Cyrus 2000; Strydom *et al.* 2003). However, in the present study clearer water conditions coincided with summer peaks in zooplankton abundance and in general zooplankton species were negatively correlated to turbidity. This additional difference between zooplankton assemblages from the estuaries of this study and other warm-temperate and subtropical estuaries is attributed to the climate of the area (Chapter 2). The southwest Cape, from Cape Agulhas to Cape Columbine, generates low turbidities during summer and higher turbidities during winter when rainfall increases (Harrison 2004; Millard & Scott 1954). From this it is evident that holistic views of estuarine plankton dynamics are needed prior to assigning priority to certain physico-chemical variables. Essentially, turbidity *per se* is merely a surrogate for freshwater inflow which is essentially the key driver in estuarine ecosystems.

Clear relationships between larval fish and zooplankton density were evident in south and west coast estuaries (Chapter 5). Total larval fish density was positively correlated to total zooplankton density and the dominant larval fish *Gilchristella aestuaria* and the dominant copepod *Pseudodiaptomus hessei* showed the same positive relationship. The low density of typical larval fish predators (e.g. cnidarians and chaetognaths) and the abundance of suitable food for larval fish in the estuaries explained this positive relationship (Sanvicente-Añorve *et al.* 2006). Two additional reasons for the positive relationship between larval fish and zooplankton densities are their temporal and spatial synchronicity. Both plankton components in this study exhibited higher densities in summer and in the mesohaline zone. Summer correspond to a peak in primary and secondary productivity in estuaries (Adams & Bate 1999; Froneman 2001a; Wooldridge 1999) and the mesohaline zone corresponds to the highly productive River-Estuary Interface (REI) region (Hilmer & Bate 1990). The density of *Gilchristella aestuaria* larvae was positively correlated with *P. hessei* density as well as the density of juveniles of *R. terranatalis*. Also, the density of *R. terranatalis* was positively correlated to densities of juveniles of *M. wooldridgei,* copepodid and adult stages of *P. hessei* and of the different developmental stages of the *G. aestuaria.* These results suggest the existence of the same trophic interactions between the larval fish and zooplankton species that have been identified in previous studies from warm-temperate estuaries between these two components (Froneman & Vorwerk 2003; Whitfield 1985; Wooldridge & Bailey 1982). The role that estuary type and river flow play in characterizing larval fish and zooplankton assemblages in South African estuaries was evident in this study. Both plankton components showed higher diversity in PO estuaries and higher densities during periods of increased river flow (Chapter 3 and 4). Similar findings have been obtained in previous studies from the warm-temperate and subtropical region (Strydom & Whitfield 2000; Strydom *et al.* 2003; Wooldridge 1999).

In conclusion, the estuaries of the south and west coast of South Africa, within the cool-temperate and warm-temperate biogeographic regions, are functioning as successful breeding areas for endemic estuary-resident species. Since the dominant zooplankton species in these estuaries are important food components in the diets of larval and early juvenile endemic fish species (e.g. *Atherina breviceps, Gilchristella aestuaria* and *Rhabdosargus holubi*) (Bennett 1989; Froneman & Vorwerk 2003; Whitfield 1985), south and west coast estuaries play a valuable ecological role in sustaining estuary-resident fish populations, which in turn provide a valuable food source for other faunal groups (adult fishes and birds). The estuaries also serve as nursery areas for estuary-dependent marine species of recreational and commercial fishes. The recruitment of these species is, however, probably taking place predominantly at the juvenile stage unlike the late-larval stage recruitment of estuary-dependent marine species typical of warm-temperate systems (Strydom *et al.* 2003; Whitfield & Kok 1992). This is probably related to the fair health status of south and west coast estuaries and to their distance from the warmer spawning grounds of fishes further up the coast off Kwazulu-Natal and the Eastern Cape. However, more dedicated studies are recommended to further evaluate the nursery function of these estuaries for marine species. Freshwater input as well as the biogeography of the area strongly influenced the composition and structure of larval fish and zooplankton assemblages in these estuaries. The findings in this study support those of other studies that suggest that South African estuaries have to be managed to ensure an adequate freshwater supply to maintain the biological integrity of the ecosystem, in particular the maintenance of the highly productive REI region.

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