Variation in the use of intermittently open estuaries by birds: a study of four estuaries in the Eastern Cape, South Africa.

Thesis presented for the degree of Master of Science

in the Department of Zoology

University of Cape Town

November 2008

by

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ABSTRACT

The main objective of this study was to describe the use of intermittently open estuaries (IOEs) along a section of the Eastern Cape coast by waterbirds, and the factors that influence avifaunal community composition in space and time. The study area consisted of four IOEs of varying sizes within a 40 km stretch of coastline in the warm temperate coastal biogeographical region of South Africa. A total of 58 waterbird counts were conducted under closed and 52 under open estuary mouth conditions at the four study estuaries between December 2005 and November 2006. Habitat composition was a major factor in determining avifaunal species composition and abundance, in particular the area of floodplain and vegetated channel. Diversity was significantly higher under open mouth conditions for all estuaries except Bira. Species composition differed significantly between closed and open mouth conditions on all four estuaries. Each estuary's avifauna responded differently in terms of changes in feeding guild composition when the mouth opened. Community composition differed significantly between estuaries. Changes in water levels significantly influenced the abundance of certain feeding guilds at the East Kleinemonde estuary. Pursuit-swimming piscivore numbers increased with increasing water levels, while wading and aerial-diving piscivores decreased. Waterbird densities varied from 0.5 to 4.2 birds per hectare. Bird abundance changed immediately after breaching at all estuaries. Abundance was significantly higher under open mouth conditions at Bira estuary, was significantly lower at West Kleinemonde due to loss of floodplain habitat, but did not change significantly at East Kleinemonde and Riet. Waterbird activities during daylight hours were monitored at the East Kleinemonde estuary during the period June 2004 to May 2005. The estuary was used mainly for roosting and maintenance (81% of all records), the majority of which was by wading piscivores (50%). There was a significant difference in activity patterns between summer and winter for all feeding guilds except aerial diving piscivores. The arrival and departure of birds at sunrise and sunset suggested that most birds overnighted elsewhere . This study showed that under open estuary mouth conditions waterbird diversity is higher but species composition is significantly different from closed mouth conditions. If the open mouth periods increase then the characteristic avifauna of intermittently open estuaries may be lost and replaced by communities bearing closer resemblance to those of permanently open systems. This must be considered when making management decisions that affect mouth conditions.

ACKNOWLEDGEMENTS

To my supervisor Jane Turpie for being an inspiration, mentor and friend. Thank you for trusting in me, even when times were difficult.

My special gratitude goes to my friend Paul Cowley, without whom I would not be where I am today. Your ideas and input have been extraordinary. You showed me what it means to do a job you love. Thank you also for providing me with the East and West Kleinemonde estuary mouth data.

To Lloyd Gillespie for seeing me through the good times and the bad and for being there for me time and time again. I will be forever grateful for all the fieldwork you did, and I could not have done it without you. Thank you for believing in me always.

My field assistant Kyle Mason-Jones. All those hours on the rivers, blazing hot, wet and cold, carrying boats, cleaning engines. I sincerely enjoyed your company, sense of humour and keen enthusiasm for all things in nature. We will always have great memories of quiet sunsets on still rivers.

To all the others who helped with fieldwork. Warren Potts and Amber Robyn Childs. I can always count on you. Anne Williams for her help, interest and great knowledge on birds. Tom and Anne Hecht for recording the Kleinemonde estuaries daily mouth status. Barry Clarke for taking the time out of your busy schedule and helping me with my stats. Alan Whitfield for supporting me from beginning to end.

Mom and dad, thanks for supporting me in every way and helping me achieve my goals, especially when times got tough.

Finally, thanks to the Water Research Commission and the Percy FitzPatrick Institute NRF Centre of Excellence for funding this project.

PREFACE

Parts of this work have been published as follows:

WHITFIELD, A.K., ADAMS, J.B., BATE, G.C., BEZUIDENHOUT, K., BORNMAN, T.G., COWLEY, P.D., FRONEMAN, P.W., GAMA, P.T., JAMES, N.C., MACKENZIE, B., RIDDIN, T., SNOW, G.C., STRYDOM, N.A., TALJAARD, S., TERÖRDE, A.I., THERON, A.K., TURPIE, J.K., VAN NIEKERK, L., VORWERK, P.D. & WOOLDRIDGE, T.H. 2008. A multidisciplinary study of a small, intermittently open South African estuary, with particular emphasis on the influence of mouth state on the ecology of the system. *African Journal of Marine Science* **30:** 453-473

TERÖRDE, A.I. & TURPIE, J.K. 2007. Birds. In: Whitfield A.K. & Bate, G.C. (eds). A Review of Information on Temporarily Open/closed Estuaries in the Warm and Cool Temperate Biogeographic Regions of South Africa, with Particular Emphasis on the Influence of River Flow on these Systems. *WRC Report No. 1581/1/07.*

TERÖRDE, A.I. & TURPIE, J.K. 2008. Appendix K. Specialist Report: Birds. In: van Niekerk, L., Bate, G.C. & Whitfield, A.K. (eds). *East Kleinemonde Estuary Reserve determination study: Technical report.* Department of Water Affairs & Forestry, Pretoria.

TURPIE, J.K., CLARK, B., COWLEY, P.D., BORNMAN, T. & TERÖRDE, A.I. 2008. Integrated ecological-economic modelling as an estuarine management tool: A case study of the East Kleinemonde estuary. Volume II. Model construction, evaluation and user manual. WRC Report

Part of this thesis was presented at the following conference and was awarded best student oral presentation:

TERÖRDE, A.I. & TURPIE, J.K. 2008. The influence of mouth dynamics on the avifauna of intermittently open estuaries in the Eastern Cape, South Africa. In: *Southern African Marine Science Symposium*, University of Cape Town, Cape Town, South Africa, 29 June – 3 July 2008.

DECLARATION

I know the meaning of plagiarism and declare that all of the work in the document, save for that which is properly acknowledged, is my own.

INTRODUCTION

Estuaries make up a mere 0.56% of the area of South Africa, but form a significant component of the aquatic and coastal habitat in South Africa. As such, they are an important habitat for birds. Indeed, almost a fifth of the species and half of the orders of birds in South Africa are found in estuaries. This relatively high diversity can be attributed to the high variety of habitats that are represented in estuarine ecosystems (Hockey & Turpie 1999a). Moreover, birds often aggregate in high densities within estuaries and therefore tend to constitute a significant proportion of the biomass of estuarine organisms. Consequently, they are believed to play an important ecological role within estuaries, both as consumers or predators and in terms of nutrient cycling (Hockey & Turpie 1999b).

Avifaunal research in South Africa has focused mainly on permanently open estuaries where bird numbers are generally high and statistically meaningful data can be collected (Heÿl & Currie 1985, Williams 1986, Velasquez *et al.* 1991, Kalejta 1993, Kalejta & Hockey 1994, Turpie 1994). The smaller intermittently open estuaries have received very little attention, even though they represent more than 70% of South Africa's estuarine systems (Whitfield 1992), and should therefore be represented in conservation planning. Collectively, small intermittently open estuaries potentially provide a large area of habitat for estuarine birds in the region. Management decisions that affect mouth opening events of these estuaries could therefore have a significant influence on the avifauna. However, to date little information exists on bird populations in these systems and their responses to mouth opening events and changes in water levels. This is largely due to the low numbers of birds present in these systems, which makes any statistical analysis difficult.

Of the total 289 estuaries along the coast only 12.8% are permanently connected to the marine environment (Whitfield 1992) and thus termed permanently open estuaries (POEs). All other systems are cut off from the sea for varying amounts of time by sandbars that form across the estuary mouths in times of low or no river flow and are thus classified as temporarily open/closed estuaries (TOCEs). Estuarine bays and lakes also fall within this category, but the majority of South African estuaries are predominantly closed and thus termed intermittently open estuaries (IOEs) (Whitfield & Bate 2007). Internationally, similar systems are only found in Australia (Young & Potter 2002) so that information about the dynamics and ecology of IOEs is very limited.

The typical IOE is a small system, with a small tidal prism when the mouth is open, and none when the mouth is closed. Floods following periods of high rainfall and freshwater runoff cause the water level in the estuary to rise until it exceeds the height of the sandbar at the mouth. A breaching event then occurs which causes water levels to drop rapidly. This leads to large areas of previously submerged substratum colonised by rich communities of plants and animals to be exposed (Perissinotto *et al.* 2000). When in flood they can start resembling river mouths, but normally behave like typical estuaries when open (Whitfield 1992). When closed, horizontal temperature and salinity gradients are typically absent due to limited freshwater inflow and strong coastal winds which facilitate mixing of the water column (Froneman 2002). The conditions and available habitats within these estuaries not only differ from other estuaries, but differ temporally within these systems.

IOEs in the warm-temperate region of South Africa typically develop behind low-elevation barriers and are restricted to high tide water levels. Contrarily, sub-tropical IOEs develop behind steep beaches and have high berms so that their water level can be maintained above high tide level (Cooper 2001, Harrison 2004). These perched systems are characterised by higher turbidities, lower salinities and warmer water temperatures than the non-perched systems of the warm-temperate region (Harrison 2004).

AIMS OF THE STUDY

The aim of this investigation was to gather baseline information on the avifauna of intermittently open estuaries in the warm temperate region of South Africa. The main objectives were to:

1. Describe the avifauna of a variety of IOEs and identify factors influencing community composition and abundance.

2. Investigate to what extent birds depend on these systems by gathering information on their behaviour and for what purpose they utilise these systems.

Specifically the following key questions were addressed:

- How does habitat structure influence the community composition?

- Does abundance, community composition and diversity change with a change in mouth state?

- How does the bird community respond to changes in water level?

- What characterises the avifauna of intermittently open estuaries?

- How important are IOEs for waterbirds for feeding or non-feeding purposes and at different times of day or year?

LITERATURE REVIEW

AVIFAUNA OF SOUTH AFRICAN ESTUARIES

This review summarises available information on estuarine birds in South Africa which might shed light on the implications of intermittent closure of estuaries on the avifauna they support. Despite a dearth of information, an attempt is made to compare the avifauna of intermittently open estuaries and permanently open estuaries. Some attention is also given to the effects of rapid habitat changes in response to open mouth phases in IOEs. This review places particular emphasis on the piscivorous birds as they are the dominant avifaunal component in IOEs.

Species richness and abundance

Approximately 162 bird species from 36 families and 13 orders are known to frequent South African estuaries. Ninety-six of these species are known to breed in estuaries, of which most are resident in South Africa throughout the year (Hockey & Turpie 1999a).

Approximately 98% of estuary-associated species utilise estuaries as feeding grounds. Of these, 54% of species prey on invertebrates, 26% are mainly piscivorous, 14% are herbivores and only a very small proportion (< 1%) feed mainly on small vertebrates (Hockey & Turpie 1999a).

The total numbers of birds that use South African estuaries are difficult to estimate due to their high mobility and seasonality of their distribution. Hockey & Turpie (1999a) estimated from several sources (Underhill & Cooper 1984, Ryan & Cooper 1985, Martin & Baird 1987, Underhill 1987, Ryan *et al.* 1988, Tree & Martin 1993) that South African estuaries support a minimum of 345 000 non-passerine[1] water-birds during summer. The majority of these (225 000) belong to the Order Charadriiformes (waders, gulls and terns), in turn dominated by waders (150 000), while the remainder are made up of other orders such as wading birds (e.g. herons, egrets), flamingos, rails (e.g. coots), birds of prey and ducks.

A large proportion of the birds present during summer are migratory, particularly among the waders. However, seasonal variations in abundance and occurrence occur not only for migrant species. In winter an influx of cormorants, gulls, egrets and spoonbills into estuarine systems takes place (Heÿl & Currie 1985, Martin & Baird 1987, Cowley 1998, Taylor *et al.* 1999). These species leave the estuaries during their breeding season and return in winter. The influx is therefore not related to prey densities (Martin & Baird 1987). Breeding occurs mainly in spring and summer in the Eastern and Western Cape and in spring and winter (two breeding seasons) in KwaZulu-Natal (Hockey & Turpie 1999a).

Biogeography

South African estuaries fall into three biogeographical regions: the subtropical, warm-temperate and cool-temperate (Whitfield 2000). The exact boundaries separating estuaries into different biogeographic regions have been variously defined in the literature (Day 1981, Maree *et al.* 2000, Whitfield 2000, Harrison 2003). For the purposes of this study the break between the subtropical and warm-temperature zones is taken as the Mdumbi Estuary (31°55'50"S; 29°12'58"E) (Harrison 2003). The break between the warm-temperate and cool-temperate regions occurs at Cape Agulhas. Bird species richness increases from 120 species in the cool-temperate region, to 133 species in the warm-temperate region and 155 in the subtropical region (based on distributions in Hockey *et al.* 2005).

[1] Passerine birds (Order: Passeriformes) are perching birds such as warblers and cisticolas, although they also include wagtails. Although many passerines are associated with aquatic habitats, their habits and habitats (e.g. reedbeds) make them difficult to count, thus studies are typically restricted to non-passerine species.

AVAILABLE INFORMATION ON BIRDS

Internationally, estuarine avifaunal research has focused on the large permanently open systems of the northern hemisphere (Bryant 1979, Prater 1981, Davidson *et al.* 1991, Ysebaert *et al.* 2000, Stillman *et al.* 2005), which are not comparable to the small intermittently open systems that form the majority of estuaries in South Africa.

Bird counting efforts have taken place in South Africa on a regional and national scale (Cooper & Hockey 1981, Underhill & Cooper 1984, Ryan & Cooper 1985, Ryan *et al.* 1988, Tree & Martin 1993, Turpie *et al.* 2004) and the birds of several systems across the country are currently being monitored under the Coordinated waterbird counts (CWAC) and other research programs (Taylor *et al.* 1999).

Much work has been carried out on avifaunal communities and the ecology of certain species in specific estuaries, most of which was conducted on estuarine lakes which are closed to the sea for varying amounts of time (Whitfield 1978, Whitfield & Blaber 1978, Whitfield & Cyrus 1978, Whitfield & Blaber 1979a, Whitfield & Blaber 1979b, Berruti 1980, Fairall 1981, Berruti 1983, Boshoff & Palmer 1983, Heÿl & Currie 1985, Stewart & Bally 1985, Boshoff & Palmer 1988, Boshoff & Palmer 1991, Boshoff *et al.* 1991a, Boshoff *et al.* 1991b, Boshoff *et al.* 1991c, Martin *et al.* 2000). Much information has also been gathered on birds on permanently open estuaries (Every 1970, Blaber 1973, Every 1973, Cyrus 1978, Williams 1986, Martin & Baird 1987, Martin 1991a, Martin 1991b, Velasquez *et al.* 1991, Kalejta 1993, Turpie & Hockey 1993, Kalejta & Hockey 1994, Turpie 1994, Turpie & Hockey 1996, Turpie & Hockey 1997, Martin *et al.* 2000, Pemberton 2000, Turpie 2001). . However, only a few studies were conducted on intermittently open systems and these are summarised below.

AVIFAUNA OF INTERMITTENTLY OPEN ESTUARIES

While several bird counts have included POEs as well as IOEs (Underhill & Cooper 1984, Ryan & Cooper 1985, Ryan *et al.* 1988, Turpie 2004) none have focussed on comparisons between them. Most avifaunal research has been conducted on estuarine lakes and POEs and the only detailed studies of birds on IOEs have been on aspects of the piscivorous birds of some Eastern Cape IOEs (Blaber 1973, Cowley 1998, Beamish 2002, Brown 2003, Terörde 2005). Perissinotto *et al.* (2004) suggested that waders (most of which feed on intertidal invertebrates) would be poorly represented in IOEs compared to POEs, where they tend to dominate the avifauna, and ascribed this to the lack of tidal influence (i.e. intertidal habitats) in IOEs. They found that intertidal habitat in IOEs was even lacking after mouth breaching, since much of the exposed area becomes supratidal rather than intertidal and small shallow-burrowing invertebrates rapidly die due to desiccation. The lack of tidal currents and often greater water clarity in IOEs afford greater foraging opportunities to piscivorous predators. Consequently, piscivorous birds are expected to be an important or dominant component of the avifauna in IOEs. Information on these species in South African estuaries (irrespective of type) is reviewed below.

Classification and status of piscivorous birds

In South Africa there are 41 species of estuarine birds from eight orders whose dominant prey item is fish (Siegfried 1981, MacLean 1993). The majority comprise herons, egrets and bitterns (18 species), followed by pelicans, cormorants and the African Darter (7 species) and terns (7 species). The rest comprise four species of kingfisher, the Great Crested Grebe, the Osprey and African Fish-Eagle, the African Spoonbill and the African Finfoot. A further 32 species of estuarine birds are known to prey on fishes as a minor dietary item.

Thirteen species of piscivores have Red Data Book status (Barnes 2000). Seven are classed globally as near threatened, three as vulnerable, two as endangered (Damara Tern and Saddle-billed Stork) and one as critically endangered (Eurasian Bittern). Three species of piscivores (Caspian Tern, Little Tern and Pink-backed Pelican) are regarded as highly dependent on estuaries. Eighteen species are semi-dependent and 20 species are not dependent on estuaries (Hockey & Turpie 1999a). Only the Common Tern, Sandwich Tern and Little Tern are birds that migrate to South Africa annually from Europe and Asia. All others are residents.

Ecological segregation of piscivorous birds

Segregation by foraging techniques

Piscivorous birds can be classed into three categories by foraging techniques (Whitfield & Blaber 1978, Whitfield & Blaber 1979a, Whitfield & Blaber 1979b; Berruti 1983); those that wade through the water or maintain a position to wait for prey (wading birds), those that dive from the air or a perch (divers) and those that swim and dive for prey from the surface (swimmers). Of the 41 species of estuary-associated piscivorous birds 19 are wading birds[2], 9 are swimmers and 13 are divers. This segregation by foraging technique is a mechanism to avoid potential interspecific competition for food (Hockey & Turpie 1999a). Grey Heron, Goliath Heron and Great Egret feed solitarily, stalking their prey. The Little Egret also uses this foraging technique in low-turbidity water. However, it adopts a very different behaviour in vegetated areas, where it disturbs prey by foot-stirring and running through the water from one area to the next. It also forms feeding associations with other birds such as Reed Cormorants and African Darters that disturb the water while they feed (Fraser 1974, Whitfield & Blaber 1978, Connor 1979). The Little Egret is able to fish in areas with aquatic macrophyte growth that are unavailable to other waders. Reed

[2] The term "wading birds" is used to distinguish these from "waders" which belong to the Order Charadriiformes.

Cormorants and White-breasted Cormorants are known to form feeding associations with pelicans from which the cormorants benefit (Nightingale 1975, Whitfield & Blaber 1979b). Great White Pelicans feed communally in a well-organised manner, while Pink-backed Pelicans feed solitarily (Din & Eltringham 1974).

Segregation by foraging area

Spatial segregation by water depth occurs between wading piscivores, according to their leg length (Whitfield & Blaber 1979a). The relatively small Little Egret has a mean wading depth of 100 mm, the larger Great Egret and Grey Heron have wading depths of 160 mm and 190 mm respectively, and the Goliath Heron has a mean wading depth of 325 mm. This spatial segregation also results in resource segregation, because smaller fish congregate in shallow areas while larger fish are restricted to deeper areas (Whitfield & Blaber 1979a). Spatial segregation occurs between swimming piscivores who fish in different areas of the estuary, e.g. littoral or offshore zone (Whitfield & Blaber 1979b). Diving piscivores reach different depths and those that are able to dive deepest can potentially reach prey unavailable to others. No conclusive data are available on the diving depth of piscivorous birds, but the time spent submerged by diving piscivores has been documented (Whitfield & Blaber 1978).

Temporal segregation

Most piscivorous birds forage during the daytime and roost communally at night. On average they spend 42% of available daylight time foraging (Whitfield & Blaber 1978, Whitfield & Blaber 1979a, Whitfield & Blaber 1979b, Hockey & Turpie 1999a). Two species, the Black-crowned Night Heron and the White-backed Night Heron, forage only at night and some wading piscivores (e.g. Grey Heron, Little Egret) are known to forage at night occasionally (Whitfield & Blaber 1979a, Hockey & Turpie 1999a). Temporal segregation of foraging on a daily scale does not play an important role in most piscivorous birds because they are not dependent on the tides and can forage at low and at high tide. However, some species show peaks in hunting periodicity. Boshoff & Palmer (1983) found that the Osprey hunts more at 09h00-10h30 and 15h00-16h30, while the African Fish-eagle was observed fishing between 09h00 and 17h00 at Lake St. Lucia (Whitfield & Blaber 1978). Pied Kingfishers fish at any time of day (Tjomlid 1973, Whitfield & Blaber 1978). Foraging by egrets and herons at Lake St. Lucia takes place throughout the day but peaks between 06h00-10h00 and 16h00-18h00, which coincides with low wind speeds (Whitfield & Blaber 1979a). Reed Cormorants, White-breasted Cormorants and Great White Pelicans also fish throughout the day but have a peak from 06h00 to 08h00 (Whitfield & Blaber 1979b).

Segregation by prey choice

Piscivorous birds only use a small proportion of available prey species (Whitfield & Blaber 1979a, Whitfield & Blaber 1979b). Prey type is determined mainly by foraging technique and abundance of the prey. The diet is generally dominated by abundant fish species, which may be important for maintaining species diversity in fish communities (Whitfield & Blaber 1978, Hockey & Turpie 1999a). Diving piscivorous birds take fish that are found near the surface while waders are restricted to fish that occur in the littoral zone. Swimming piscivores can prey on fish occurring in offshore areas and deeper waters within their diving range.

Whitfield & Blaber (1978, 1979a, 1979b) conducted a detailed study of the diets of piscivorous birds at Lake St. Lucia. They showed that prey selection is based mainly on prey size and on abundance of prey in the respective foraging area. Size of the water body also plays a role for those species that transport their prey to the shore or a perch. Otoliths in regurgitated pellets, prey remains from breeding colonies, and direct observations of the prey of African Fish-eagle, Pied Kingfisher, Caspian Tern, Great White Pelican, White-breasted Cormorant, Reed Cormorant, Little Egret, Great Egret, Grey Heron and Goliath Heron were used to estimate prey species and size. Also using otoliths, Jackson (1984) found a separation of diets between Pied Kingfisher and White-breasted Cormorant in the Kosi Estuary due to differences in body size and foraging techniques.

Boshoff & Palmer (1983, 1988) obtained data on the spectrum, size and mass of Osprey and African Fish-eagle prey in the Western Cape by direct observations and from prey remains collected below feeding perches. Both were found to prey mainly on mullet.

Piscivorous birds and the estuarine ichthyofauna

The diet and quantification of daily food consumption by piscivorous birds have been studied extensively in Europe and North America. Cormorants are of special interest in these countries, because they are perceived as damaging fisheries (Glahn *et al.* 2000, Lekuona 2002). Kushlan (1976) found a 76% reduction in fish biomass without a loss of species richness by wading bird predation in a seasonally fluctuating pond in Florida. A fish kill, which occurred in a year when wading birds were absent eliminated 93% of fish biomass and the majority of fish species. He demonstrated that wading bird predation may serve as an important function in ponds by preserving fish species richness and cropping fish stocks to levels compatible with their survival during the dry season. Steinmetz *et al.* (2003) demonstrated that avian piscivorous predators can significantly alter the size distribution of prey items.

In South Africa, estuaries are important nursery grounds for many marine-spawning fish species. Therefore, piscivorous birds could potentially have a considerable effect on recruitment into marine fish populations. Blaber (1973) postulated that piscivorous bird densities were related to densities of the Cape Stumpnose in IOEs in the Eastern Cape. Whitfield (1978) showed that the correlation between the number of piscivorous birds and relative densities of fish at Lake St. Lucia was highly significant.

Effects of environmental factors and seasonality of distribution

The population structure and abundance of estuarine birds are influenced by available habitat for feeding, roosting and nesting, as well as prey/food availability and individual migration and distribution patterns. Of the estuary-associated birds, piscivores are probably least affected by changes in hydrological/environmental conditions. Piscivorous birds are not influenced significantly by water level in some estuaries due to their flexible feeding methods (Berruti 1983, Heÿl & Currie 1985). However, Whitfield & Cyrus (1978) showed that a succession of the dominant foraging types occurred under changing hydrological conditions in eulittoral pans at Lake St. Lucia. In general, piscivorous birds also show less seasonal variation in numbers and biomass than the migratory herbivores and invertebrate-feeding waders. Their breeding is also more evenly distributed over the year (Berruti 1983).

STUDY AREA

INTRODUCTION

Four estuaries of varying sizes were selected for this study (Figure 1, Table 1). The sampled estuaries are located on a 40 km stretch of the Eastern Cape coastline between the towns of Port Alfred (33°35'54'S, 26°53'39'E) and Hamburg (33°17'25'S, 27°27'42'E). All estuaries are predominantly closed to the sea and thus termed intermittently open (Whitfield & Bate 2007). A description of these systems follows in this chapter.

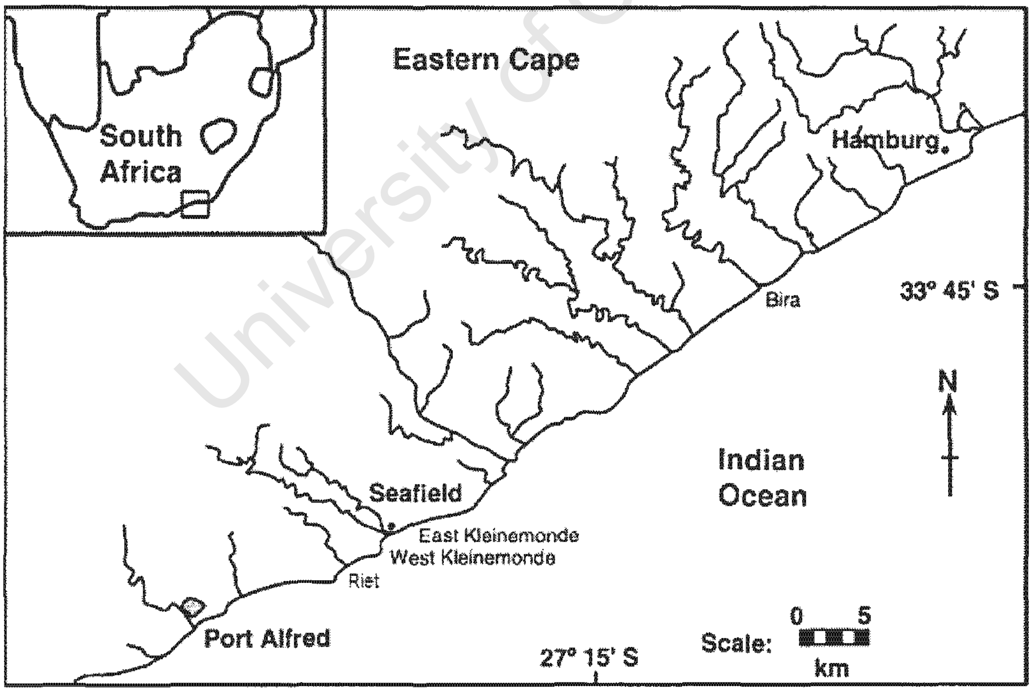

Figure 1. Map of the study area and sampled estuaries (modified from Walton 1984).

Climatic conditions

The Eastern Cape coastline between East London and Port Elizabeth lies within the warm-temperate region of South Africa (Allanson & Baird 1999), which is a transitional zone between the cool temperate region of the western South African coast and the subtropical region of the eastern coast. Rainfall in this region is not as influenced by season as as other parts of the country (Stone 1988). During the study period rainfall occurred in all months, with peaks in October 2004, December 2005 and September 2006 (Figure 2). Rainfall ranged from 7.6 mm in July 2006 to 209.2 mm in August 2006. Mean monthly air temperatures ranged from 7.9°C in July to 26.7°C in February (Figure 3).

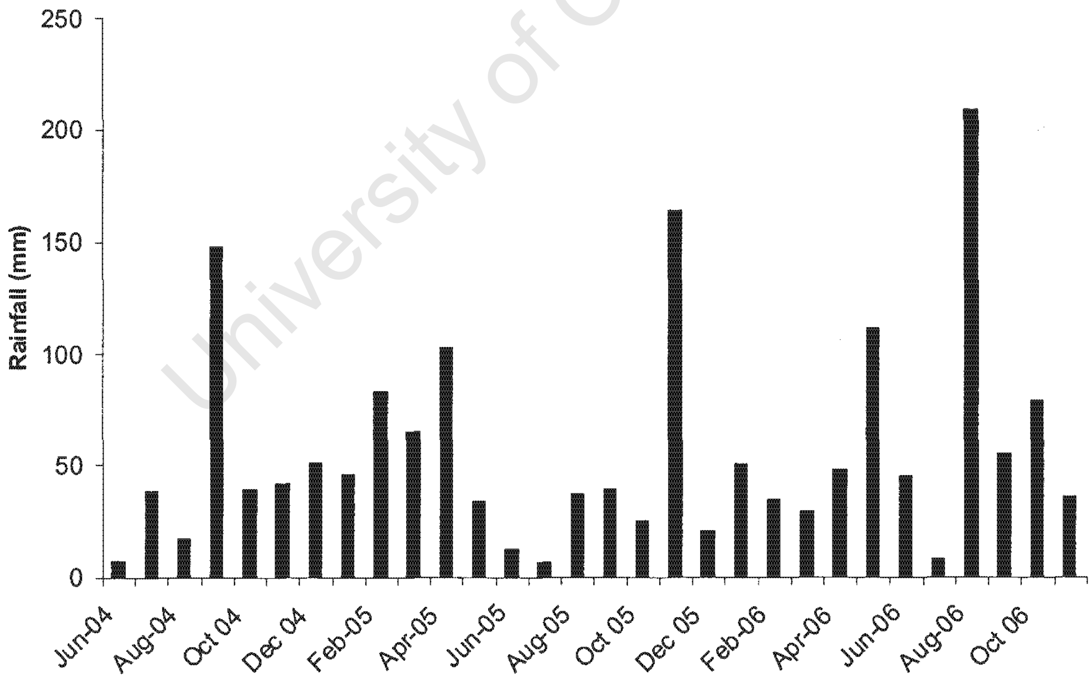

Figure 2. Mean monthly rainfall recorded at Port Alfred weather station from June 2004 to November 2006.

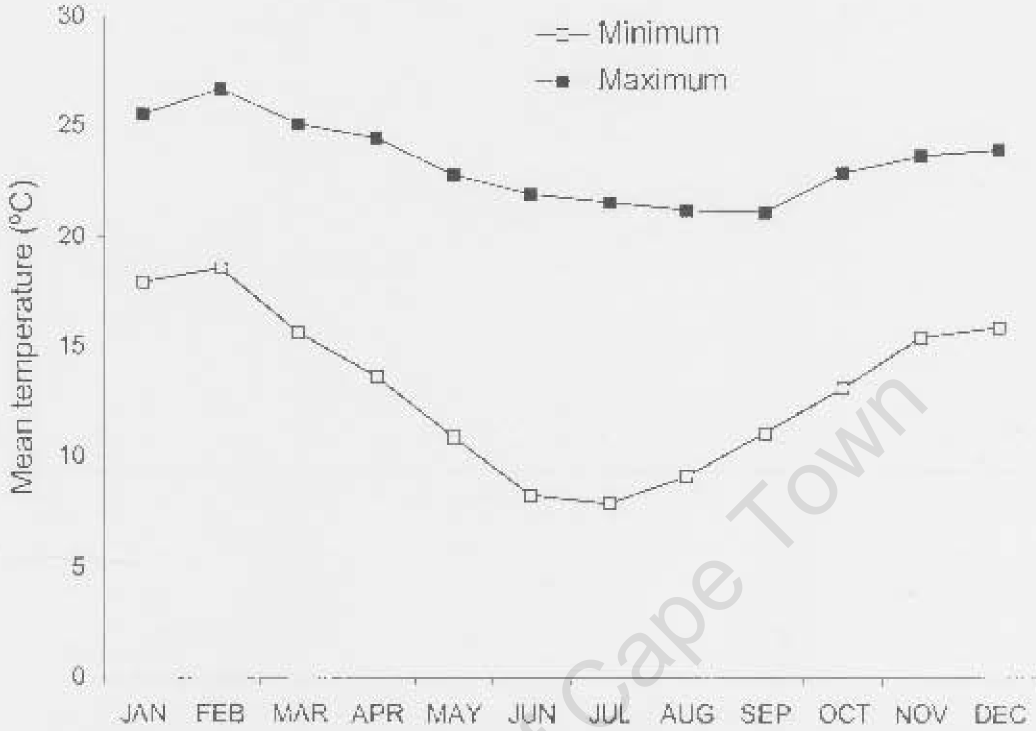

Figure 3. Mean monthly minimum and maximum air temperatures recorded at Port Alfred weather station for 2004 to 2006 (South African Weather Bureau).

RIET ESTUARY

The Riet estuary (33°33'S, 27°00'E) is the smallest estuary that was sampled in the study. It is approximately 1.75 km in navigable length with an approximate maximum channel width of 50 m (Table 1, Figure 4). The surface area of the estuary is approximately 8.94 ha, which includes a floodplain and saltmarsh area of 4.5 ha. No previous data on mouth conditions are available for this system. The catchment of the estuary consists mainly of natural agricultural land used for cattle grazing. The estuary is largely supratidal and only shows tidal influence above the mouth when a deep channel is formed after very heavy rainfalls. Residential housing developments exist on the western bank between the mouth and the bridge. Further developments are planned on the agricultural land on the lower eastern bank.

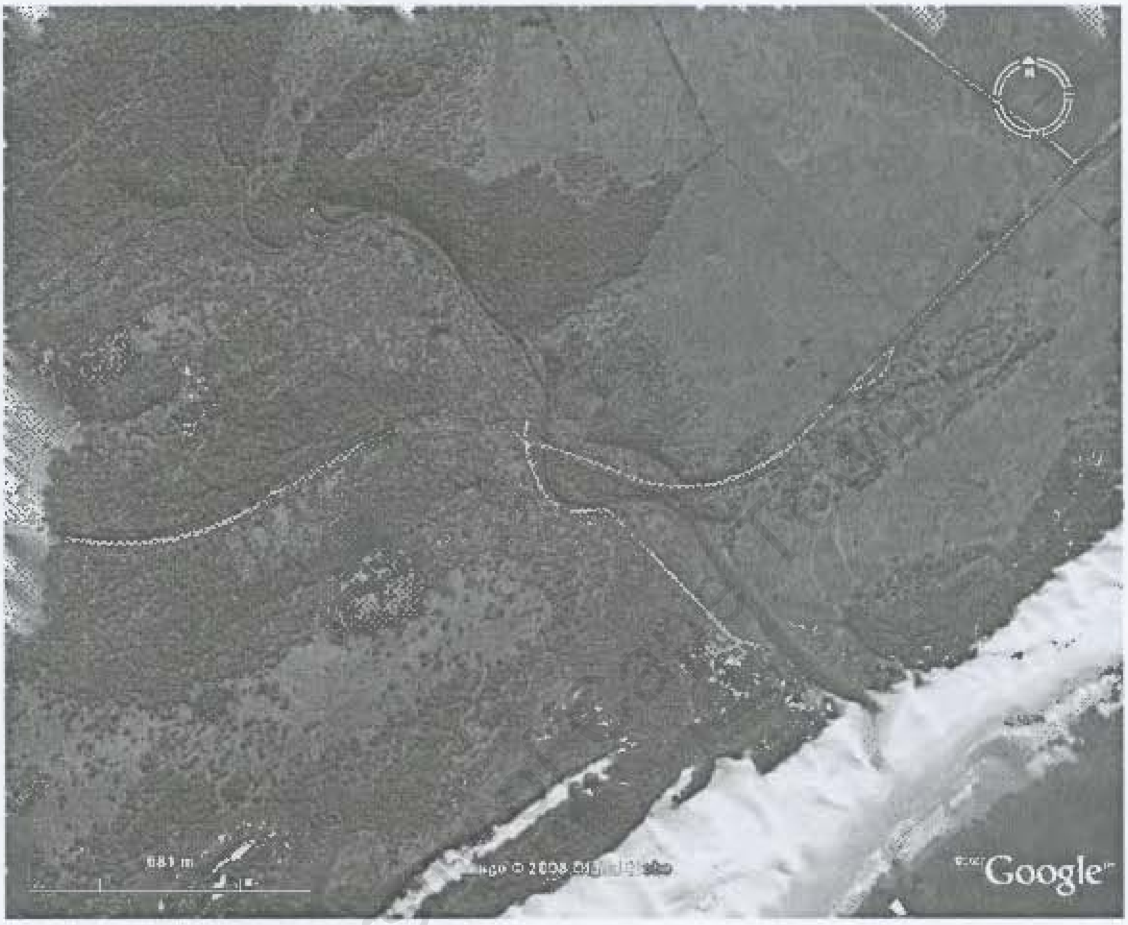

Figure 4. Aerial view of the Riet estuary catchment and estuary.

The estuary was divided into four regions for the purpose of this study.

Region 1 stretched from the mouth 400 m up the estuary (Figure 7). This region was characterised by a saltmarsh on the western bank and housing developments and lawns reaching to the waters edge on the eastern bank. The approximate surface area of this region was 4 ha.

Region 2 was approximately 500 m in length with a surface area of approximately 4.19 ha. The eastern bank in this region was largely flat agricultural land used for cattle grazing. The flat western bank consisted of a saltmarsh and floodplain.

Region 3 was approximately 400 m in length with a surface area of 0.53 ha m^2. Its eastern bank consisted of largely undisturbed valley bushveld vegetation, while the dirt road leading to the housing developments near the mouth ran close to the western bank. The main road (R72) bridge crossed the estuary in this region.

The fourth region comprised the upper reaches of the estuary and was approximately 450 m in length with an approximate surface area of 0.23 ha. The estuary became increasingly narrow and shallow in this region with dense vegetation on the banks and many overhanging trees.

WEST KLEINEMONDE ESTUARY

The West Kleinemonde estuary (33°32'S, 27°02'E) lies adjacent to the East Kleinemonde estuary in the small town of Seafield (Kleinemonde), approximately 15 km north of Port Alfred (Figure 5). It has large areas of floodplains (approximately 58.3 ha) which are inundated when water levels in the estuary are high. The lower banks are developed on both sides with residential units and lawns reaching up to the water's edge. The estuary is utilised by residents for fishing, swimming and power boating and disturbances can be very high, especially during the summer months. The mouth is generally more stable than the East Kleinemonde estuary and often remains closed for periods exceeding one year. Salinity in the estuary under closed conditions ranges from 5‰ - 10‰ in the upper reaches to 25‰ – 30‰ in the lower reaches. Water temperatures show a high variation with a summer range between 22°C and 29°C and a winter minimum of 12°C (Cowley *et al.* 2003).

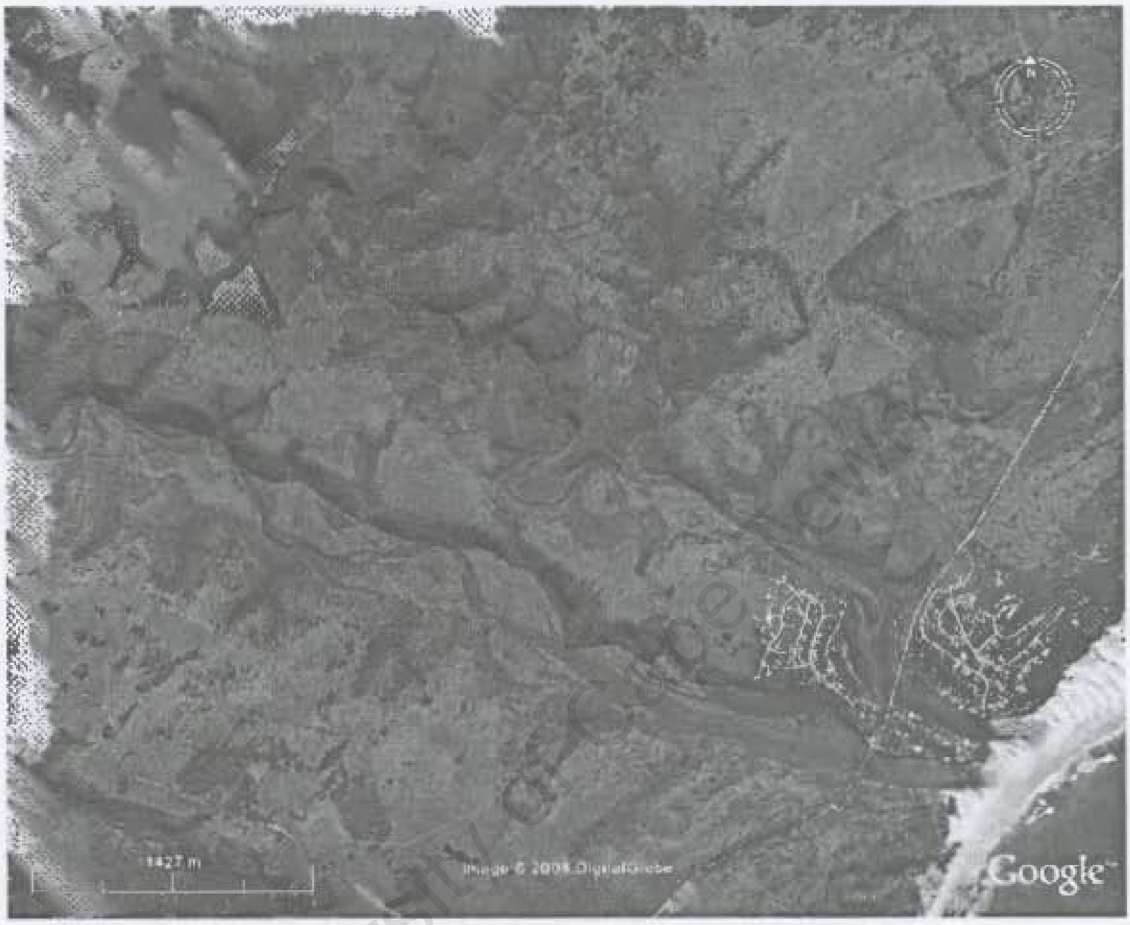

Figure 5. Aerial view of the East Kleinemonde (upper) and West Kleinemonde (lower) estuaries.

The estuary was divided into four regions for this study. Region 1 (Figure 7) reached from the mouth 600 m to the main road bridge. It comprised an area of approximately 7.5 ha. Housing developments flanked both banks with lawns running up to the water's edge. Human disturbance through boating, angling and swimming was highest in this region.

Region 2 was designated from the bridge to 1.6 km upstream. It had a surface area of approximately 40.75 ha, of which approximately 18.0 ha consisted of floodplains that were inundated when water levels were high. The main channel was relatively wide in this region.

Region 3 had a length of 2 km and comprised the major floodplains of this system with a narrowing main channel. It had a total surface area of 48.56 ha of which the majority (40.25 ha) consisted of floodplains.

Region 4 comprised the top section of the estuary where the channel became very narrow and there were no floodplains. This section had a length of 2.3 km and an approximate surface area of 4.38 ha. The vegetation on the banks consisted mainly of valley bushveld on the steeper slopes and thorn veld used for cattle grazing.

The area of the estuary above region 4 was not included in sampling because the estuary became too shallow, narrow and overgrown to navigate by boat or on foot. At the beginning of the study several hikes into this area were conducted but because no waterbirds were found this area was excluded from the study.

EAST KLEINEMONDE ESTUARY

The East Kleinemonde estuary (33°32'S 27°03'E) has an approximate length of 3.5 km and a maximum width of 120 m (Table 1). Tidal influence in this system can be strong after breaching events caused by large river floods which scour a deep channel in the mouth region. The system is mostly shallow with a main channel depth of 1-2 m (Cowley & Whitfield 2002). The land surrounding the estuary is characterised by agricultural land used for cattle and pineapple farming in the middle and upper reaches and human settlements in the lower reaches (Figure 5). An analysis of mouth conditions between 1993 and 2006 showed that the estuary was closed to the sea 74% (van Niekerk *et al.* 2008) and open 15% of the days. Marine overwash events took place 11% of the days. The longest recorded period that the estuary was connected to the marine environment was 32 days in 2004. River base flow and tidal exchange in this system are insufficient to maintain open mouth conditions and the mouth generally closes a few days after river flooding has subsided (van Niekerk *et al.* 2008). The mean monthly salinity of the estuary can range from 0‰ to 25‰, depending on the mouth condition and freshwater inflow (Cowley *et al.* 2003). Average temperatures range from 15°C in winter to 27°C in summer (Cowley *et al.* 2003). The East Kleinemonde estuary was studied extensively during 2005 and 2006 as part of a multi-disciplinary research programme funded by the Water Research Commission. Hydrodynamics, sediment dynamics, macro-nutrients, microalgae, macrophytes, zoobenthos, hyperbenthos, zooplankton, fishes and birds were studied (Whitfield *et al.* 2008). This thesis forms part of this project.

The estuary was divided into four regions (Figure 7). Region 1 extended from the mouth to the main road bridge approximately 800 m. It had an approximate surface area of 8.75 ha and a maximum width of 130 m. It was characterised by human habitation and disturbance, little natural vegetation on the riverbanks and relatively deep water.

Region 2 had an approximate length of 600 m and a surface area of 14.5 ha. This region encompassed an extensive shallow salt marsh area and few human settlements on both banks. The surrounding vegetation was dominated by *Euphorbia* and *Aloe* species on the western bank above the salt marsh, and *Phragmites* reeds on the eastern bank.

Region 3 was approximately 800 m in length. The estuary was narrower in this region with degraded veld on the western slope and valley bushveld on the steeper eastern slope. The maximum width of this region was 55 m with a surface area of approximately 7.0 ha.

Region 4 had a length of 1.2 km and a surface area of approximately 3.75 ha. It comprised the upper reaches of the estuary with relatively undisturbed valley bushveld on the steep eastern slopes and degraded veld used for cattle farming on the flatter western slopes. In the upper reaches of region 4, the western bank becomes very steep and rocky and valley bushveld dominates.

BIRA ESTUARY

The Bira estuary (33°22'S, 27°19'E) is the largest studied system (Figure 6) with an approximate surface area of 116.25.4 ha, a navigable length of approximately 8.9 km under closed conditions and a maximum width of approximately 300 m in the lower reaches (Table 1). The catchment consisted mainly of agricultural land used for cattle farming. Signs of erosion and overgrazing were present. A dam has been built on one of the main tributaries 16.5 km from the estuary mouth. When the estuary mouth opens to the sea it can stay open for extended periods of time (several weeks to months), and once closed usually remains so for several months. Holiday housing developments exist on the eastern bank near the mouth.

Region 1 of the estuary extended from the mouth to approximately 1.7 km upstream and had a total surface area of approximately 40.25 ha (Figure 7). Housing developments were present on the eastern shore near the mouth. When the estuary is open a system of sandbanks is exposed at low tide (Figure 4).

Region 2 of the estuary had a length of approximately 3.1 km. Its surface area was approximately 44.75 ha with a maximum width of 150 m.
The banks were generally flat and exposed and the adjoining vegetation had been used extensively for cattle farming..

Region 3 had a length of 2.3 km and comprised an area of approximately 21.5 ha. The channel had a maximum width of 130 m at the beginning of this region, becoming increasingly narrow towards the top. The banks were mostly exposed or rocky.

Region 4 represented the upper reaches of the system with an increasingly shallow, rocky and narrow channel. It had an approximate surface area of 9.75 ha, a maximum width of 50 m and was 1.8 km in length. The banks in this region were steeper and rockier with a few overhanging trees at the far top.

Figure 6. Aerial view of Bira estuary and catchment.

Table 1. Summary of estuary characteristics (Badenhorst 1988, Vorwerk 2000, Cowley & Whitfield 2002, Whitfield & Bate 2007, Hughes 2008).

	length (km)	max width (m)	survey area (ha)	MAR ($m^3 \cdot yr^{-1}$)	catchment (km^2)
Riet	~2	~50	8.9	2×10^6	48
West Kleinemonde	~7	~330	101.2	4×10^6	94
East Kleinemonde	~3.5	~120	34.0	2×10^6	46
Bira	~9	~300	116.3	13×10^6	255

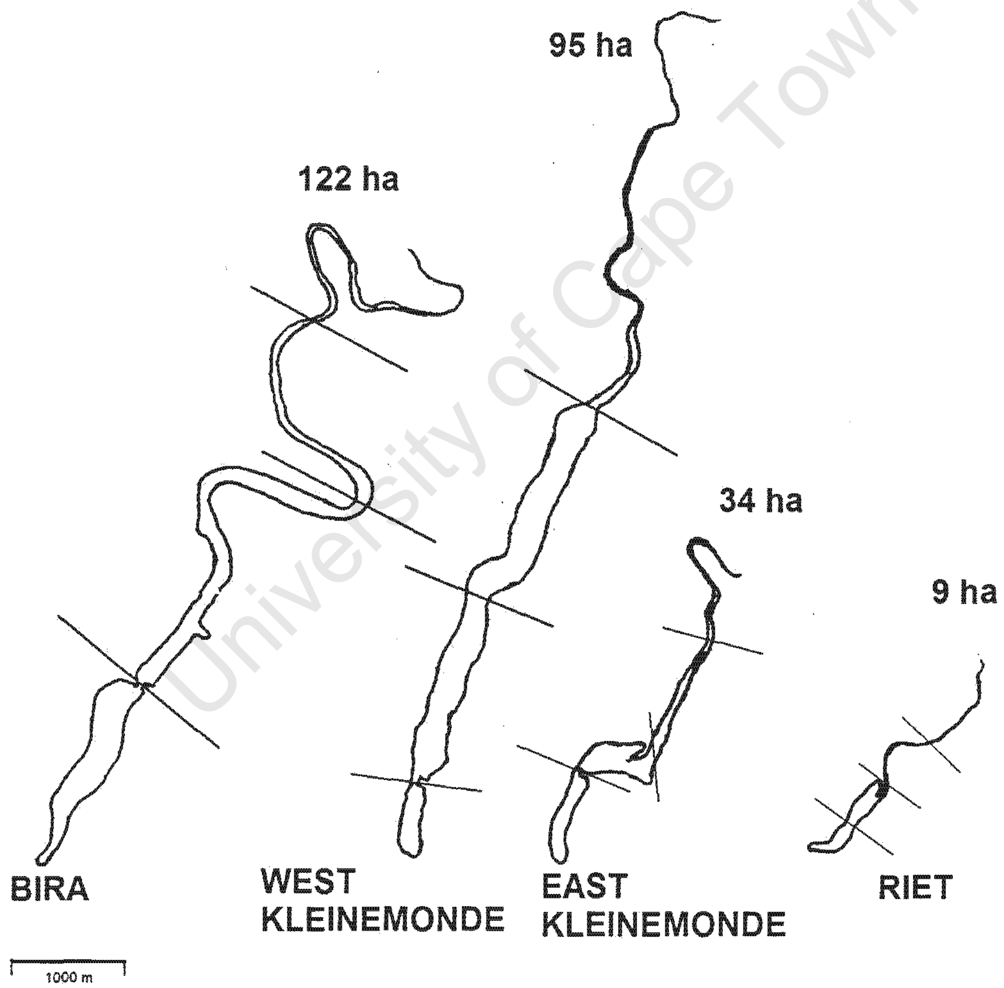

Figure 7. Comparative map of the four studied estuaries with lines marking the described regions.

METHODS

BIRD COMMUNITY COMPOSITION AND THE INFLUENCE OF ESTUARY CHARACTERISTICS AND MOUTH DYNAMICS

Bird counts

All four estuaries were sampled from a motorised boat or on foot along their navigable length. Sampling was carried out from December 2005 until November 2006. All encountered water-associated birds were recorded on a GPS referenced map. Terrestrial-feeding birds such as Black-headed Heron, Cattle Egret and Brown-hooded Kingfisher were excluded from the study. The status of each estuary mouth (breach/open/closed) was recorded daily during the entire study period. Water level measurements for the East Kleinemonde estuary were obtained from the Department of Water Affairs and Forestry (DWAF), which installed a permanent water level recorder at the main road bridge in December 2004. November to April were classified as summer and May to October were classified as winter months, according to the presence or absence of the majority of palearctic-breeding migrants.

A total of 110 waterbird counts were conducted during the study (Table 2) of which 52 and 58 were carried out under open and closed estuary mouth conditions (Appendix I). From March 2005 through November 2005 additional weekly bird counts were conducted at the East Kleinemonde estuary and the combined count data were correlated with water level measurements.

Table 2. Summary of the number of bird counts conducted between December 2005 and November 2006 on all sampled estuaries.

		Number of counts	
	Total	Mouth open	Mouth closed
Riet	22	13	9
West Kleinemonde	33	12	21
East Kleinemonde	34	15	19
Bira	21	12	9
Total	110	52	58

Riet estuary

From December 2005 through February 2006 sampling took place approximately three times per month until six counts were completed (Appendix I). The sampling frequency was then lowered to once per month until a mouth breaching event took place in May. Sampling was then increased to daily until six counts were completed, after which the estuary was sampled bimonthly for two months and after remaining stable and open, monthly until the end of the study in November 2006.

West Kleinemonde estuary

The estuary was sampled at least bimonthly from the beginning of the study to the first breaching event in August (Appendix I). It was sampled daily after the first breaching for six days, even though it closed again on the fifth day after breaching. Four counts were conducted in the week following the second opening, after which bimonthly sampling was continued.

East Kleinemonde estuary

Sampling commenced in December 2005 and was conducted approximately weekly until mid March (Appendix **IError! Reference source not found.**). In this way enough samples were collected during the closed mouth phase before a potential opening event. From March 2006 the sampling frequency was lowered to bimonthly until the major breaching event in August 2006. Bird counts were conducted daily for a week following the mouth opening event. Thereafter sampling continued bimonthly until the end of the study.

Bira estuary

Sampling at Bira estuary was started in January 2006. Six counts were conducted in January and February after which the sampling frequency was lowered to monthly (Appendix I). Within ten days of the breaching event in May 2006 seven counts were conducted, and thereafter sampling continued monthly.

Habitat characteristics

Seven functional habitat types were identified on all estuaries. These were overhanging trees / rocks, exposed banks, reedbeds, inundated floodplains, shallow margins, unvegetated channel and vegetated channel (with submerged macrophytes). Habitat types were identified on the estuaries by field observations. The area of each habitat type in each region of each estuary was estimated using percentage cover estimates from aerial photographs with the aid of a grid.

Data analyses

Avifauna of the four estuaries

Count data were summarised by taxonomic group, species, migratory status and feeding guild over the whole year and by mouth condition.

Species were grouped according to dominant dietary items into piscivores, herbivores (ducks, geese, coots, moorhen) and invertebrate-feeding waders. Piscivores were grouped further according to feeding method into pursuit-swimming piscivores (cormorants, darters, grebes), aerial-diving piscivores (kingfishers, raptors, terns, gulls) and wading piscivores (herons, egrets). Resident birds were defined as species breeding in South Africa although not necessarily breeding on estuaries.

Bird abundance was summarised by overall mean and mouth condition. Differences in mean abundance at each estuary between open and closed mouth phase were tested for using one way ANOVAs. Mean bird densities on each estuary were calculated for the whole year and different mouth states.

Spatial distribution of feeding guilds along the estuaries was analysed according to the regions described above for each estuary in terms of mean numbers and densities.

The degree to which birds frequented the estuaries was analysed in terms of the proportion of counts in which they were present, and the coefficient of variation in numbers on the estuary.

Factors influencing community composition

Multiple regression analyses were done to investigate relationships between feeding guild abundance and habitat sizes in the 16 regions. Because habitat size was calculated for closed conditions, only samples taken under closed and full conditions were used. All 16 regions were treated as independent samples on the basis of the assumptions that (i) the pool of birds that utilise these systems was not limited to the studied estuaries and (ii) birds moved freely between and within these systems and other systems.

Chi^2 tests of independence were used to compare feeding guild composition of the bird community under open and closed estuary mouth conditions.

ANOVAs were used to test for differences in mean feeding guild abundance between open and closed mouth states.

Diversity was calculated as Shannon-Wiener index using PRIMER statistical software. A Bray-Curtis similarity matrix was generated using PRIMER statistical software for each individual estuary and combined estuaries. Clusters in a dendrogram were assessed using group average hierarchical sorting. Non-metric multi-dimensional scaling (MDS) was used to examine relationships between samples for each estuary. ANOSIM was used to test for differences between groups in each analysis. Where significant differences were found, the SIMPER routine was applied to determine the relative contribution of key species to the differences between groups. Only the top 50% of species contributors to each group tested were used in the analysis.

Water level measurements at the East Kleinemonde estuary were correlated to abundance of feeding guilds by mouth condition and season using the combined count data from March 2005 to November 2006.

ACTIVITY PATTERNS OF WATERBIRDS AT THE EAST KLEINEMONDE ESTUARY

A section of the East Kleinemonde estuary in which the majority of waterbirds are found (Terörde 2005) was surveyed. The area corresponds to region 2 of the estuary described above (Figure 7).

Survey techniques

Observations were made from an elevated platform overlooking the estuary. Birds were counted approximately four times per month (Table 3) every 90 minutes from sunrise to sunset from June 2004 to May 2005 (12 months). A total of 397 scans were made. Twenty-four sampling days were in the summer months (November – April) and 22 in the winter months (May – October).

The activities of all waterbirds and their positions were noted on a map. Observations were made using binoculars (Leica 10x40) and a Leica Televid 77 Spotting Scope mounted on a tripod.

Activities were divided into the following categories:

- Resting: sleeping, standing, sunning, lying down
- Feeding: species specific feeding behaviour
- Orientation: flying or swimming from one area to another
- Maintenance: preening, nest-building, mating, territorial behaviour

Table 3. Sampling schedule and mouth conditions of the East Kleinemonde estuary from June 2004 to May 2005. Grey fields indicate sampling dates. o: estuary mouth open T: mouth closed with large overwash; t: mouth closed with small overwash event

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Jun 04																	T														
Jul 04			T	T	T																										t
Aug 04	t															t	t	t													
Sep 04																															
Oct 04										t																	t				
Nov 04																															
Dec 04																							o	o	o	o	o	o	o	o	o
Jan 05	o	o	o	o	O	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	T	T	T
Feb 05	T				T	t	t	t	t	t	t	t	t	t				o	o	o	o	o	o	o	o	o	o	o			
Mar 05	o	o	o	o	O	o	T	o	o	o	o	o	o	o	o	o	o	o	o	o	T	T	o	T	t	T	t	t	t		
Apr 05	t					t	t	t	t	t	o	o	o	o	o	o	o	o	o	o	o	t	T	T	t	t	t	t	t		
May 05			o	o	O	o	T	T	T	t	t	t	t	o	o	o	o	T	t			t	t	T	T	t	t	t	t		

Data analysis

For analysis all recorded birds were divided into feeding guilds according to their feeding method and diet. The used guilds were pursuit-swimming piscivores (darters, cormorants, grebes), aerial-diving piscivores (kingfishers, terns, gulls, raptors), wading piscivores (herons, egrets, spoonbills, hamerkops), invertebrate-feeding waders (waders, ibises, thick-knees) and herbivores (ducks, geese, coots).

The data were not normally distributed and non-parametric tests were used for analysis. The count data were summarised by mean number of individuals, season, month, time of day, feeding guild and activity.

The percentage of birds of a feeding guild recorded for each activity was compared across seasons using Chi-square tests for independence. For this analysis the activities maintenance and resting (non-feeding related activities) and orientation and feeding (feeding related activities) were combined due to low sample sizes in the maintenance and orientation categories.

Activity times were calculated to estimate the amount of time the individuals of a feeding guild spent carrying out each activity on the estuary. Activity times were calculated as the sum of the recorded number of birds of a species performing an activity divided by the maximum number of recorded individuals of that species, multiplied by 90 minutes, for each time period.

RESULTS

BIRD COMMUNITY COMPOSITION, DISTRIBUTION AND DYNAMICS

Avifauna of the four estuaries

Overall abundance

Waterbird abundance varied greatly between the four sampled estuaries (Figure 8). The Riet estuary, the smallest of the four systems, had very low numbers of birds (Table 4, Figure 8) with the number of recorded birds ranging from eight to 22 individuals per count. Abundance was lowest during the first two counts in December and then remained relatively stable for the remainder of the study period. The mean number of birds recorded was 15.8 (SD ± 3.3). The Riet estuary data were normally distributed (Kolmogorov-Smirnov; $d = 0.17$, $p > 0.05$). The difference between the mean number of birds during the closed and open phase was not significant (ANOVA; LSD test; $MS = 9.95$; $df = 20$; $p > 0.05$).

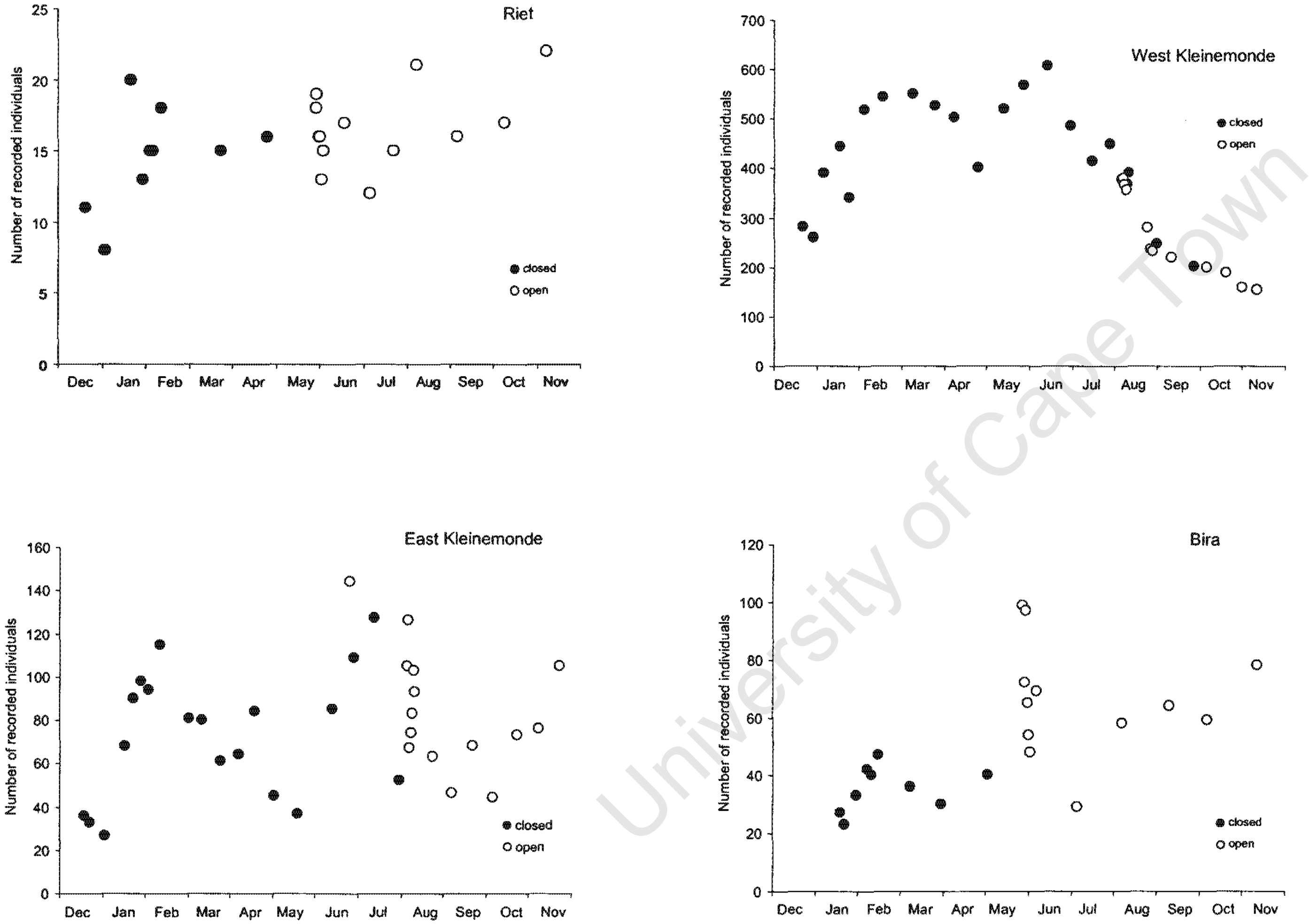

Figure 8. Numbers of waterbirds recorded at the four studied estuaries (December 2005 to November 2006). Note the differences in scales.

Bird abundance at the East Kleinemonde estuary ranged from 27 to 144 individuals, with a mean number of 78.1 (SD ± 29.0). Overall abundance was low at the beginning of the study period in December 2005 and early January 2006 (Figure 8). It then increased, reaching a peak on 10 February 2006, after which it decreased until 18 May 2006. The maximum number of birds was recorded immediately after the first breaching event (N = 144) on 24 June 2006. The data were normally distributed (Kolmogorov-Smirnov; $d = 0.07$; $p > 0.05$) and there was no significant difference in mean bird numbers between open and closed estuary mouth conditions (ANOVA; LSD test; $MS = 830.07$; $df = 32$; $p > 0.05$). Immediately after the breaching of the mouth many dead fish were lying on the previously inundated floodplains at the West and East Kleinemonde estuaries. Many small fish were trapped in receding puddles and small pools of water. At the East Kleinemonde estuary 60 Reed Cormorants were recorded the day after the first breaching event roosting near the floodplain and wading piscivores such as Little Egret and Grey Heron were observed feeding in the puddles and small pools.

The West Kleinemonde estuary had the highest number of birds with a mean of 368.3 (SD ± 132.4) birds per count (Table 4). Bird numbers ranged from 153 to 606. Total waterbird abundance increased from the beginning of the study in December 2005 to June 2006 (Figure 8). It then decreased until the end of the study in November 2006. The data were normally distributed (Kolmogorov-Smirnov; $d = 0.11$; $p > 0.05$) Overall bird abundance was significantly higher when the estuary mouth was closed. (ANOVA; LSD test; $MS = 11230$; $df = 31$; $p < 0.001$).

The Bira estuary, a relatively large system, had a mean of 52.9 (SD ± 21.1) birds with numbers ranging from 23 to 99 individuals (Table 4). Total abundance was low during the closed phase from December 2005 to May 2006 (Figure 8). It then rose considerably once the mouth opened and except for one count with low abundance in July, remained high for the remainder of the study. The data were normally distributed (Kolmogorov-Smirnov; $d = 0.12$; $p > 0.05$). Numbers were considerably lower than at the West Kleinemonde estuary, despite the similar size of the systems. In contrast to the West

Kleinemonde estuary, at Bira bird numbers were generally higher when the estuary mouth was open. This difference in bird abundance between open and closed mouth conditions was highly significant (ANOVA; LSD test; MS = 246, df = 19; $p < 0.001$).

Table 4. Mean bird numbers recorded at the four studied estuaries from December2005 to November 2006.

	All counts		Closed mouth		Open mouth		
	Mean ± SD	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**p-level**
Riet	15.8 ± 3.3	8 - 22	14.6 ± 3.6	8-20	16.7 ± 2.8	12-22	n.s.
West Kleinemonde	368.3 ± 132.4	153 - 606	429.0 ± 115.2	201-606	262.2 ± 86.6	153-380	< 0.001
East Kleinemonde	78.1 ± 29.0	27 - 144	72.9 ± 29.4	27-127	84.7 ± 28.0	44-144	n.s.
Bira	52.9 ± 21.8	23 - 99	35.3 ± 7.8	23-47	66.0 ± 19.5	29-99	< 0.001

The West Kleinemonde estuary had the highest density of waterbirds with a mean number of 3.6 birds per hectare (Table 5), followed by the East Kleinemonde estuary with 2.3 birds/ha. The small Riet estuary had a higher bird density (1.8 birds/ha) than the large Bira estuary which only had a mean number of 0.5 birds/ha. Estuary size was not correlated with bird densities.

Table 5. Waterbird population densities recorded over the entire study and under open and closed estuary mouth conditions at the four sampled estuaries.

		Average density (n/ha) ± SD		
	Survey area (ha)	**All counts**	**Closed**	**Open**
Riet	8.94	1.8 ± 0.4	1.7 ± 0.4	1.9 ± 0.4
West Kleinemonde	101.19	3.6 ± 1.3	4.2 ± 1.1	2.6 ± 0.9
East Kleinemonde	34.00	2.3 ± 1.0	2.1 ± 0.9	2.5 ± 0.8
Bira	116.25	0.5 ± 0.2	0.3 ± 0.1	0.6 ± 0.2

Community composition

Riet estuary had the lowest diversity of waterbirds with 25 recorded species from 13 Families in four Orders (Table 6) and a Shannon's diversity index of 1.85 (Table 9). At Bira and East Kleinemonde estuaries a total of 38 and 37 species were recorded respectively. East Kleinemonde had the second lowest Shannon's diversity index (2.26). West Kleinemonde had the highest diversity of waterbirds and the highest Margalef's species richness score (4.13) with a total of 55 recorded species from 18 Families in 5 Orders. Bira estuary's Shannon diversity score was slightly higher (2.33) than that of the West Kleinemonde estuary (2.32). While the West Kleinemonde estuary had a higher species count and Margalef's species richness score than Bira estuary, the population there was dominated by a few species, namely Yellow-billed Duck and Reed Cormorant.

Table 6. Taxonomic composition of the avifauna at the four sampled estuaries.

Order	Family		Riet	East Kleine-monde	West Kleine-monde	Bira
Anseriformes	Anatidae	Ducks, geese	3	3	7	5
Coraciiformes	Alcedinidae	Alcedinid kingfishers	1	2	2	2
	Dacelonidae	Dacelonid kingfishers	2	2	2	2
Gruiformes	Rallidae	Moorhens, coots	0	0	2	0
Charadriiformes	Scolopacidae	Greenshanks, whimbrels, stints, sandpipers, ruff, turnstones	2	8	10	5
	Rostratulidae	Painted-snipes	0	0	1	0
	Burhinidae	Thick-knees	1	1	1	1
	Haematopodidae	Oystercatchers	1	1	1	0
	Recurvirostridae	Stilts	0	1	1	0
	Charadriidae	Plovers, lapwings	3	5	6	6
	Laridae	Gulls, terns	1	2	7	4
Ciconiiformes	Accipitridae	Typical raptors, ospreys	1	1	2	1
	Podicipedidae	Grebes	1	1	1	1
	Anhingidae	Darters	1	1	1	1
	Phalacrocoracidae	Cormorants	3	3	3	2
	Ardeidae	Egrets, herons	5	5	4	4
	Scopidae	Hamerkop	0	0	0	1
	Threskiornitidae	Ibises, spoonbills	0	2	2	0
	Ciconiidae	Storks	0	0	1	0
		Total number of species	25	38	54	35

Charadriiformes formed the largest Order at the East Kleinemonde (48.6% of recorded species), West Kleinemonde (51.9%) and Bira (50%) estuaries. Ciconiiformes was the largest Order at the Riet estuary (45.8%) (Table 6).

An analysis according to diet showed that piscivorous bird species made up the largest group in terms of species diversity on all four estuaries (Table 7), followed by invertebrate-feeding species and finally herbivorous species.

Table 7. Percentage of recorded species in a dietary guild.

	Piscivorous species (%)	Invertebrate-feeding species (%)	Herbivorous species (%)
Riet	60.0	28.0	12.0
West Kleinemonde	44.4	38.9	16.7
East Kleinemonde	47.4	44.7	7.9
Bira	51.4	34.3	14.3

Piscivorous birds also dominated the avifauna in terms of abundance at Riet, West Kleinemonde and East Kleinemonde estuaries (Table 8). Only at Bira estuary was the proportion of recorded individuals that were invertebrate-feeding waders slightly higher than that of piscivores.

Table 8. Percentage of all recorded individuals in a dietary guild.

	Piscivores (%)	Invertebrate-feeders (%)	Herbivores (%)
Riet	54.0	31.3	14.7
West Kleinemonde	62.3	14.6	23.1
East Kleinemonde	69.8	25.7	4.5
Bira	41.2	47.5	11.3

Table 9. Total number of recorded species, mean Margalef's species richness and mean Shannon diversity indices for the four sampled estuaries.

	No. of species	Species richness (d)	Species diversity (H')
Riet	25	2.49	1.85
West Kleinemonde	54	4.13	2.32
East Kleinemonde	38	3.30	2.26
Bira	35	3.55	2.33

Factors influencing community composition

Influence of habitat on bird communities

A multiple regression analysis of bird numbers under closed conditions with area of habitat types was significant for all feeding guilds (Table 10). Overhanging trees/rocks, exposed bank and unvegetated channel did not show any significant correlations with any feeding guild. Reedbeds showed a significant correlation with aerial-diving piscivores and herbivores, while shallow margins were correlated with aerial-diving and wading piscivores. The size of floodplain was correlated with all feeding guilds except aerial diving piscivores and vegetated channel was correlated with all guilds except wading piscivores.

Estimated habitat sizes and corresponding feeding guild abundance are presented in Appendix II.

Table 10. Multiple regression results of mean bird numbers and habitat sizes under closed mouth conditions. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$

		Regression coefficient (Beta)							
	Overall model	**Intercept**	**Over-hanging trees/ rocks**	**Exposed bank**	**Reed-beds**	**Flood-plain**	**Shallow margins**	**Unvege-tated channel**	**Vege-tated channel**
Pursuit-swimming piscivores	adjusted $R^2 = 0.96$ $F(7,8) = 54.11$ **$p < 0.001$**	-1.03	0.09	-0.15	-0.03	0.34 **	-0.01	0.12	0.81 ***
Aerial-diving waders	adjusted $R^2 = 0.79$ $F(7,8) = 9.23$ **$p < 0.01$**	5.34	-0.05	-0.44	-0.51 **	0.17	0.54 **	-0.10	0.74 *
Wading piscivores	adjusted $R^2 = 0.92$ $F(7,8) = 24.61$ **$p < 0.001$**	-2.32	0.12	-0.32	0.12	1.08 ***	0.42 **	0.14	-0.28
Invertebrate-feeding wader	adjusted $R^2 = 0.93$ $F(7,8) = 31.15$ **$p < 0.001$**	1.68	0.00	0.13	-0.03	1.30 ***	0.11	0.01	-0.60 **
Herbivores	adjusted $R^2 = 0.99$ $F(7,8) = 284.70$ **$p < 0.001$**	2.06	-0.03	0.03	-0.16 ***	1.07 ***	0.05	-0.06	-0.15 *

Influence of mouth condition on community composition

None of the estuary mouths opened during the first five summer months (December 2005 to April 2006) of the study period. All mouths were however open in the next summer month of November 2006. Since only 1 - 2 counts per estuary were conducted in November 2006, and all other sampling dates on open mouth conditions fell within the winter months, the comparison between open and closed mouth conditions was largely a within-winter issue. Details of the mouth dynamics during the study are provided in Appendix III.

Chi^2 tests of independence revealed that feeding guild composition was significantly different under open and closed estuary mouth conditions on all four estuaries (Table 11).

Table 11. Chi-Square test of independence results for feeding guild distribution under open and closed mouth conditions (degrees of freedom = 4).

	Riet	**West Kleinemonde**	**East Kleinemonde**	**Bira**
Chi^2	57.1	495.6	36.3	67.6
p-value	< 0.001	< 0.001	< 0.001	< 0.001

At Riet estuary aerial-diving piscivores formed the majority of the bird population under closed mouth conditions, followed by invertebrate-feeding waders (Figure 9). Pursuit-swimming piscivores and herbivores were largely absent when the mouth was closed, while wading piscivores occurred in low numbers. Under open estuary mouth conditions the proportion of birds that were pursuit-swimming piscivores and herbivores increased considerably.

At West Kleinemonde estuary the bird community was dominated by pursuit-swimming piscivores and herbivores under closed mouth conditions. Under open conditions pursuit-swimming piscivores also formed the largest group, followed by invertebrate-feeding waders (Figure 9). The proportion of herbivores, wading piscivores and aerial-diving piscivores decreased substantially when the estuary mouth was open.

While the change in feeding guild composition was still significant at East Kleinemonde estuary, it was not as pronounced as on the other estuaries (Table 11, Figure 9). The proportion of wading piscivores and herbivores was greater when the estuary mouth was closed than when it was open.

At Bira estuary the avifauna was dominated by invertebrate-feeding waders and aerial-diving piscivores under closed and open mouth conditions. Pursuit-swimming piscivores were virtually absent (single record of African Darter) when the estuary was closed to the sea, but cormorants, darters and grebes were present when the estuary mouth was open.

ANOVAs testing for differences in the mean number of birds of a feeding guild recorded under open and closed mouth conditions varied considerably from estuary to estuary (Figure 9). Aerial-diving and pursuit-swimming piscivores, such as kingfishers and cormorants decreased significantly at Riet estuary under an open mouth state, while they increased significantly at Bira. There were no significant changes in mean numbers of these groups at East and West Kleinemonde estuaries with changes in mouth state. Wading piscivores such as herons and egrets decreased significantly at West Kleinemonde estuary but increased at Bira. They showed no significant change in mean numbers at Riet and East Kleinemonde estuaries (Figure 9). There was no significant change in mean invertebrate-feeding wader numbers at any of the four estuaries (Figure 9). The mean number of recorded herbivorous waterfowl increased on all estuaries except the West Kleinemonde, where it showed a significant decrease. The increase in waterfowl at Bira was however not significant (Figure 9).

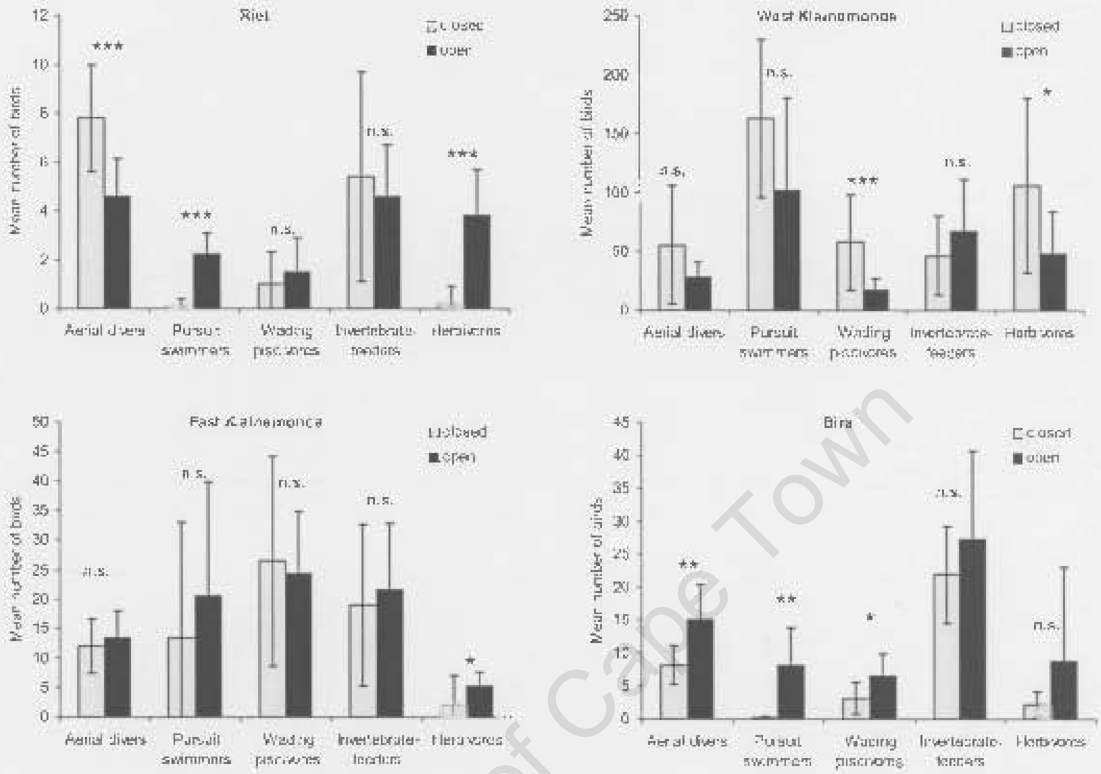

Figure 9. Mean numbers of birds under closed and open mouth conditions.
***: < 0.001;   **: < 0.01;   *: < 0.05;   n.s.: not significant (ANOVA)

The analysis of changes in species composition with mouth state showed that two distinct communities were found under open and closed mouth conditions on all four estuaries (Figure 10 – 19). ANOSIM analysis found these differences to be significant (Table 12). A T-test between open and closed samples on each estuary showed that there was a significant increase ($p < 0.01$) in Shannon's diversity index from closed to open estuary mouth condition on Riet, East Kleinemonde and West Kleinemonde estuaries (Table 12).

Table 12. Comparison of changes in Shannon-diversity and species composition from the closed to open mouth state at the four sampled estuaries.

	Shannon's diversity index (H') T-test	Species composition (ANOSIM)
Riet	increase ($p < 0.01$)	$p < 0.001$
West Kleinemonde	increase ($p < 0.05$)	$p < 0.05$
East Kleinemonde	increase ($p < 0.01$)	$p < 0.001$
Bira	increase (n.s.)	$p < 0.01$

The SIMPER routine showed that at Riet estuary 52% of the dissimilarity between closed and open mouth conditions was accounted for by six species. These were Pied Kingfisher (19%), Yellow-billed Duck (7%), Three-banded Plover (7%), Blacksmith Lapwing (7%), Common Sandpiper (6%) and South African Shelduck (6%). Pied Kingfisher, which was much more abundant when the estuary was closed (Mean closed = 6.6; Mean open = 2.8) is a piscivorous aerial-diving species, while three of the other five species were invertebrate-feeding waders and two herbivorous waterfowl. Pursuit-swimming piscivores accounted for a combined total of 11% of the dissimilarity.

At the West Kleinemonde estuary 52% of the dissimilarity in species composition between open and closed mouth state was accounted for by five species. Reed Cormorant contributed 21% to the dissimilarity, followed by Yellow-billed Duck (17%), African Spoonbill (5%), Common Tern (5%) and Curlew Sandpiper (4%). Only Curlew Sandpiper, an invertebrate-feeding wader, increased its mean abundance from the closed (Mean = 6.0) to the open mouth state (Mean = 13.0), while the other four species decreased in abundance. Wading piscivores contributed a combined 11% to the dissimilarity. Overall the difference in species composition was therefore due to a decrease in Reed Cormorant, Yellow-billed Duck and several species of wading piscivores.

At the East Kleinemonde estuary 54% of the dissimilarity between open and closed conditions was also accounted for by six species, but all of these differed from Riet estuary: Reed Cormorant (14 %), African Spoonbill (12%), Great Egret (10%). Water Thick-knee (6%), Grey Heron (6%) and Little Egret (6%). Except for Reed Cormorant all of these species are wading piscivores. The greatest change was that of African Spoonbill which had a mean abundance of 1.0 when the mouth was closed which increased to 11.9 when the mouth was open. Water Thick-knees and Grey Heron also had a higher abundance when the mouth was open. However, Great Egret's and Little Egret's mean abundance was lower when the mouth was open.

50% of the dissimilarity between open and closed mouth at the Bira estuary was accounted for by 6 species. These were Common Greenshank, White-fronted Plover, Yellow-billed Duck, Three-banded Plover, Pied Kingfisher and Water Thick-knee. Their respective contributions to this dissimilarity were more evenly distributed and ranged from 6% (Water Thick-knee) to 10% (Common Greenshank). All of these species except for Common Greenshank were more abundant under open than under closed mouth conditions.

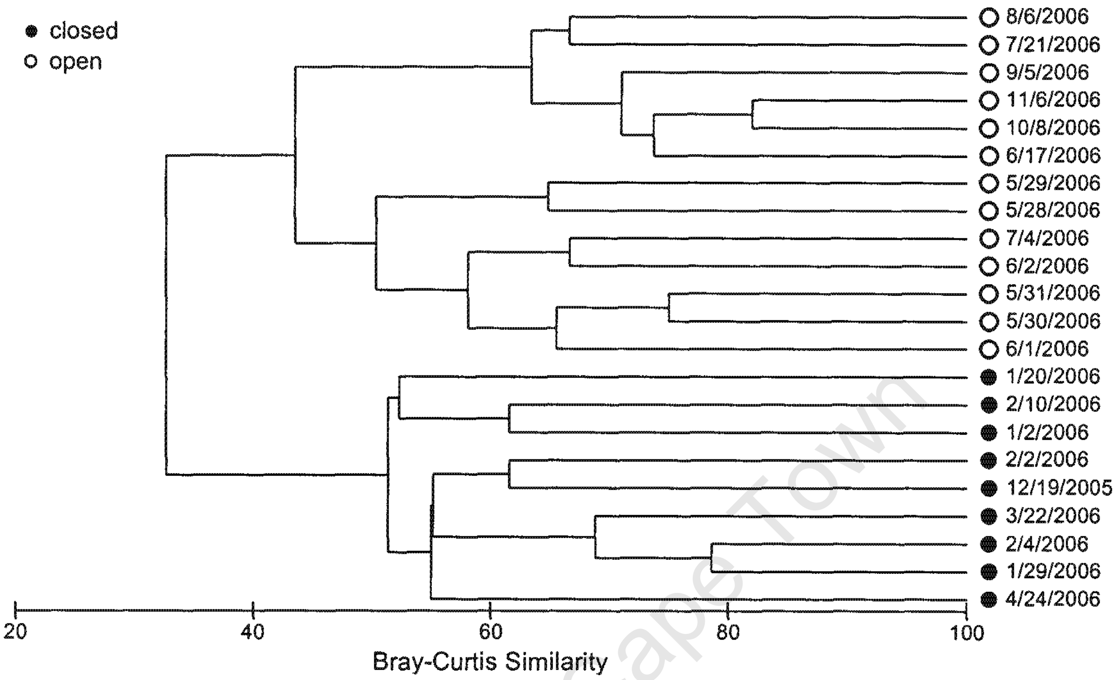

Figure 10. Similarity dendrogram of species composition under closed and open estuary mouth conditions at the Riet estuary.

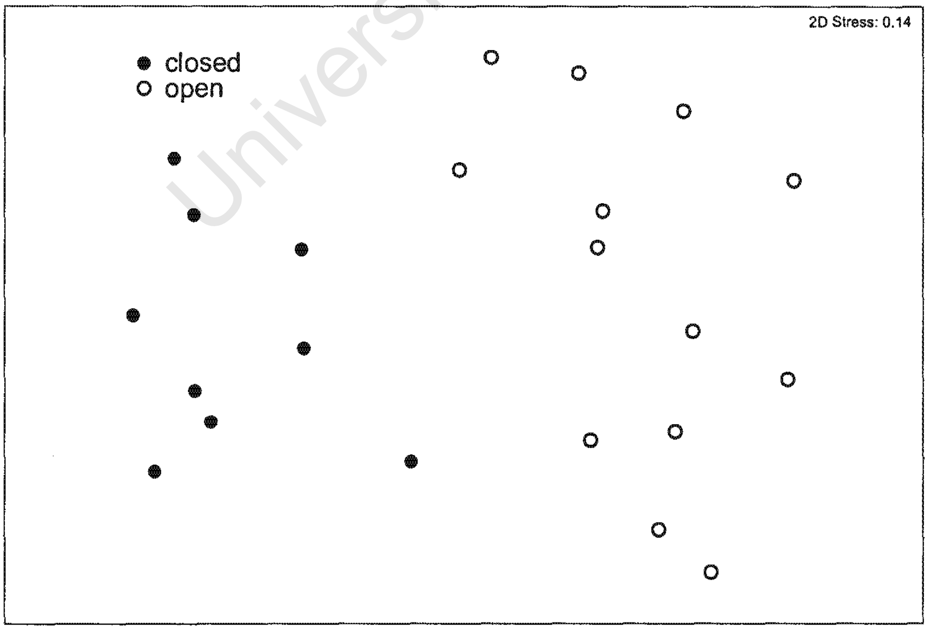

Figure 11. A two dimensional MDS (multi-dimensional scaling) plot of bird count data under closed and open estuary mouth conditions at the Riet estuary.

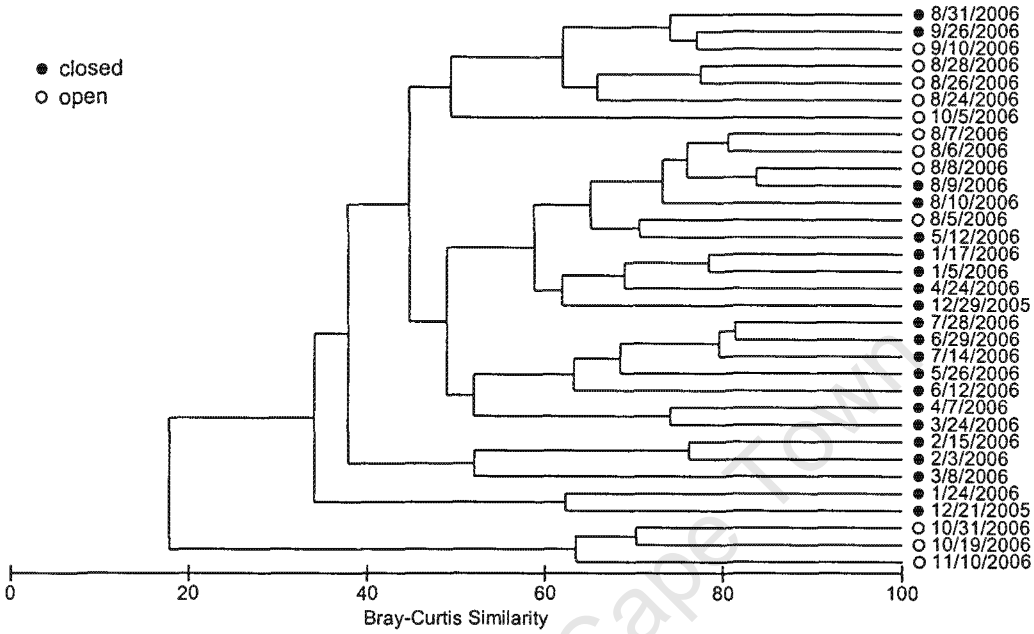

Figure 12. Similarity dendrogram of species composition under closed and open mouth conditions at the West Kleinemonde estuary.

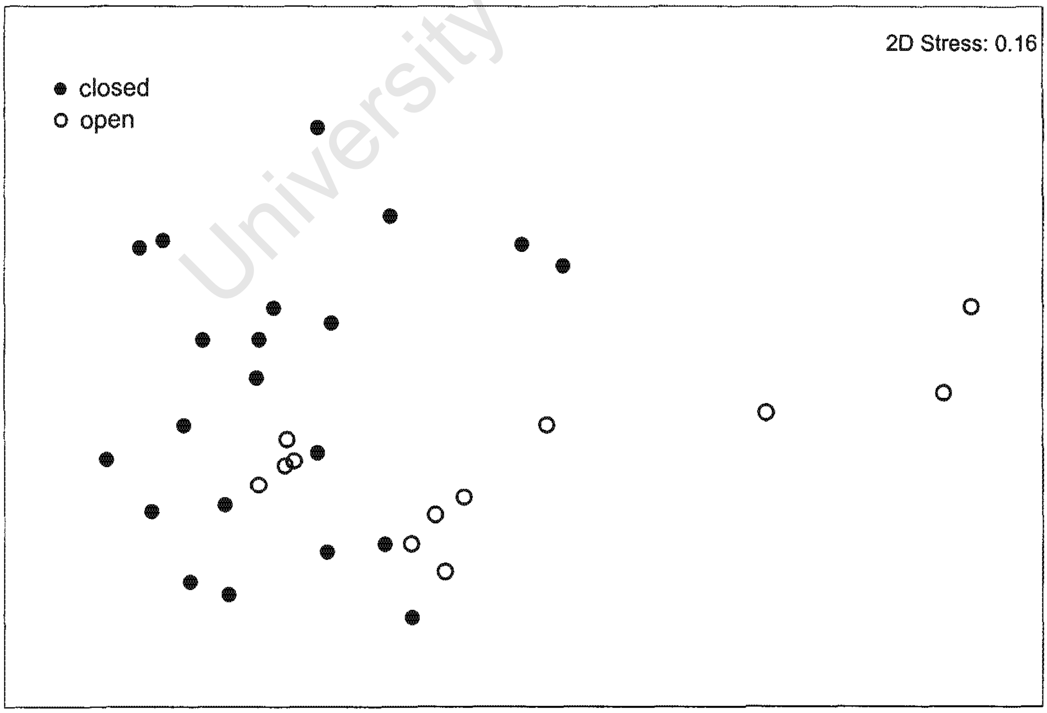

Figure 13. A two dimensional MDS plot of bird count data under closed and open mouth conditions at the West Kleinemonde estuary.

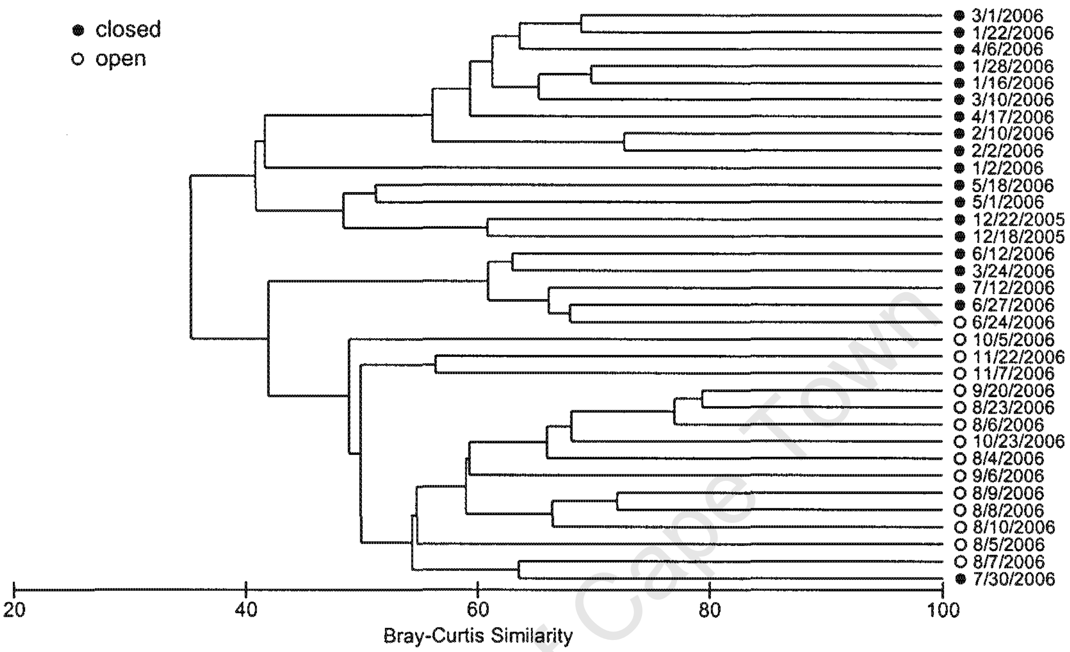

Figure 14. Similarity dendrogram of species composition under closed and open estuary mouth conditions at the East Kleinemonde estuary.

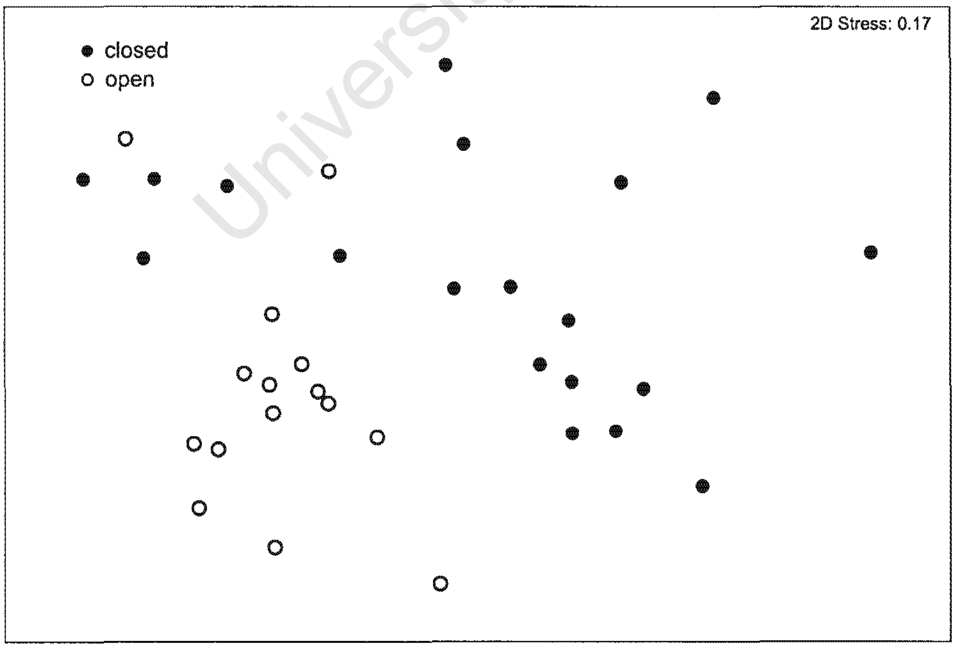

Figure 15. A two dimensional MDS plot of the East Kleinemonde estuary bird count data under closed and open estuary mouth conditions.

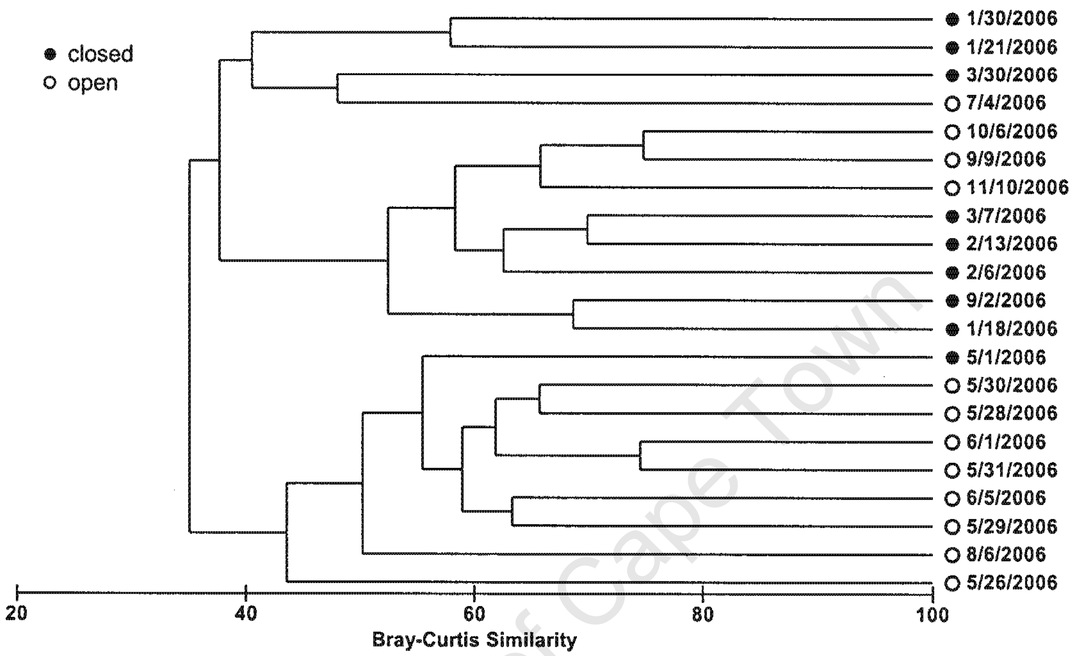

Figure 16. Similarity dendrogram of species composition under closed and open estuary mouth conditions at the Bira estuary.

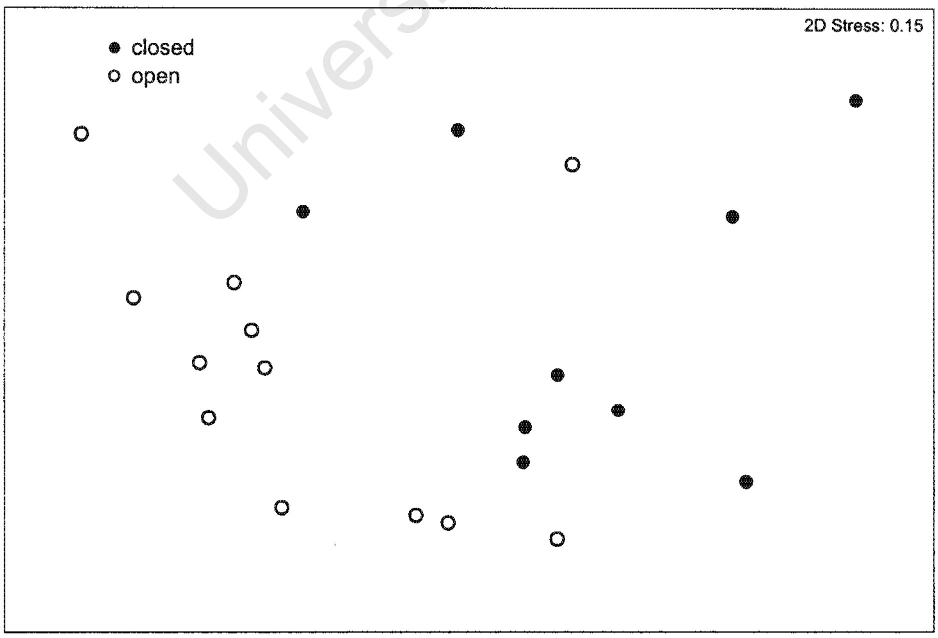

Figure 17. A two dimensional MDS plot of bird count data at the Bira estuary under closed and open mouth conditions.

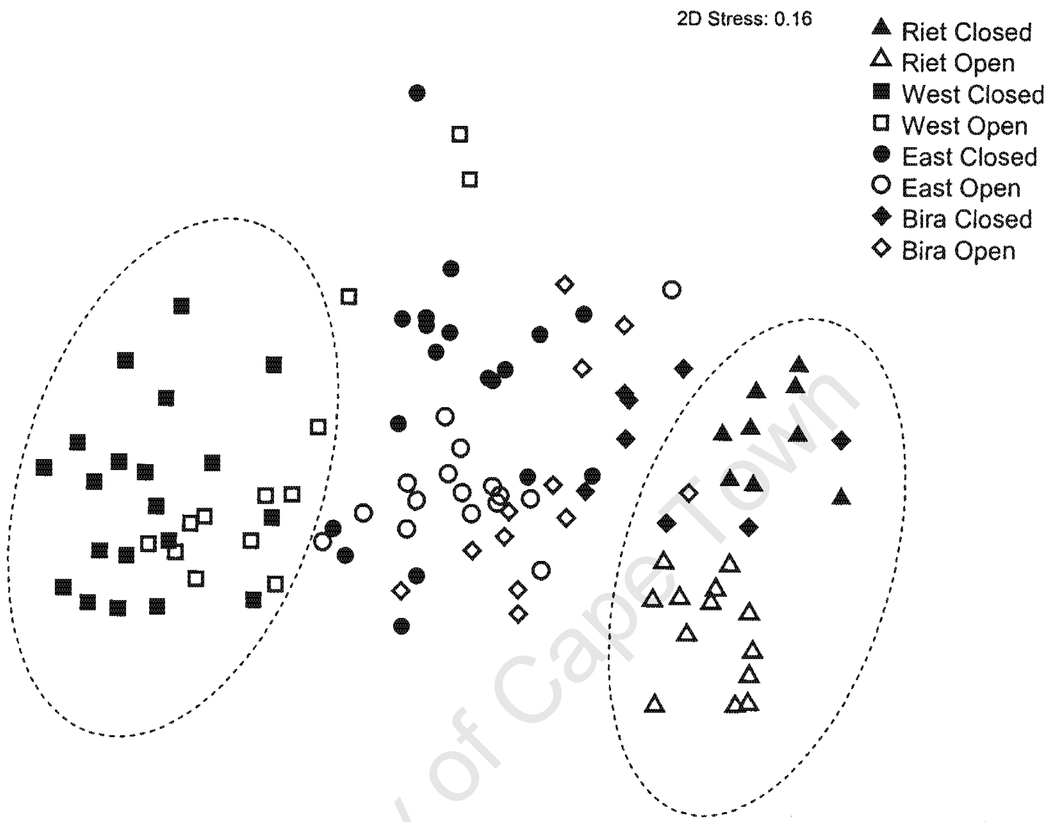

Figure 18. A two dimensional MDS plot of the combined bird count data from all four estuaries under open and closed mouth conditions.

When combining the data from all estuaries and applying a similarity analysis, the West Kleinemonde estuary data under open and closed conditions separated away from the other estuaries and mouth conditions (Figure 12 & Figure 13). There was also a separation of the Riet estuary from the other systems, however the stress on this analysis is relatively high and the results should be considered with caution.

An ANOSIM analysis showed that the separation between rivers was more significant ($R = 0.83$; $p < 0.01$) than the separation between mouth states ($R = 0.36$; $p < 0.01$). Estuary was therefore more important in determining species composition than mouth state. Each estuary had a distinct community composition.

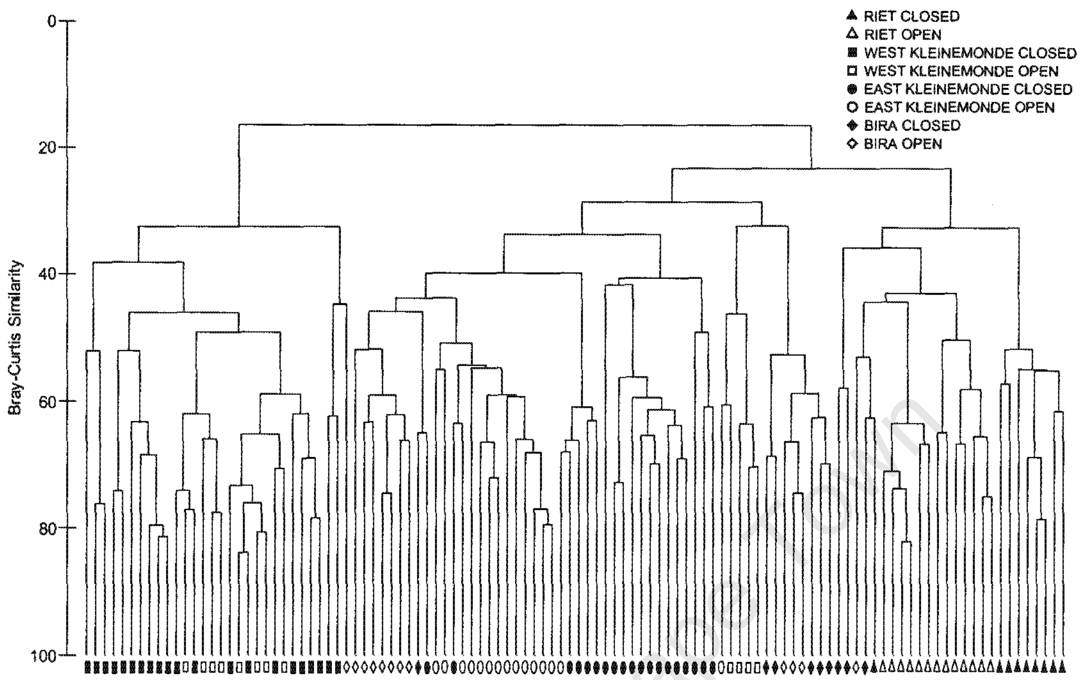

Figure 19. Similarity dendrogram of species composition under open and closed mouth conditions at Riet, East Kleinemonde, West Kleinemonde and Bira estuaries.

Water level and abundance of feeding guilds at East Kleinemonde estuary

There was a significant positive correlation between water level and the number of pursuit-swimming piscivores recorded under closed estuary mouth conditions ($r^2 = 0.1264$; $p < 0.05$; Figure 20). However, the correlation was weak and no correlations were found between water level and pursuit-swimming piscivores under open conditions.

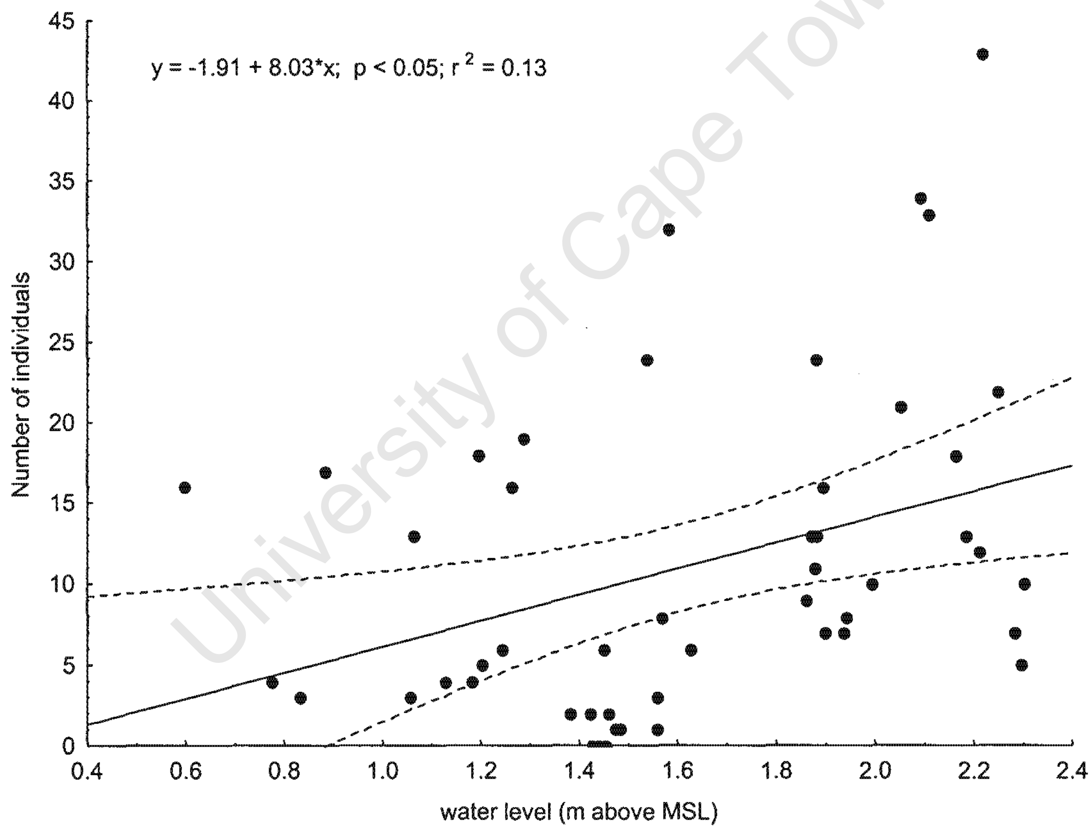

Figure 20. Relationship between pursuit-swimming piscivore numbers and water level at East Kleinemonde estuary under closed mouth conditions.

Overall, wading piscivore numbers decreased significantly with increasing water levels ($r^2 = 0.16$; $p < 0.01$, Figure 21). Under closed estuary mouth conditions (Figure 22) wading piscivore numbers peaked at water levels between 1.4 m and 1.7 m.

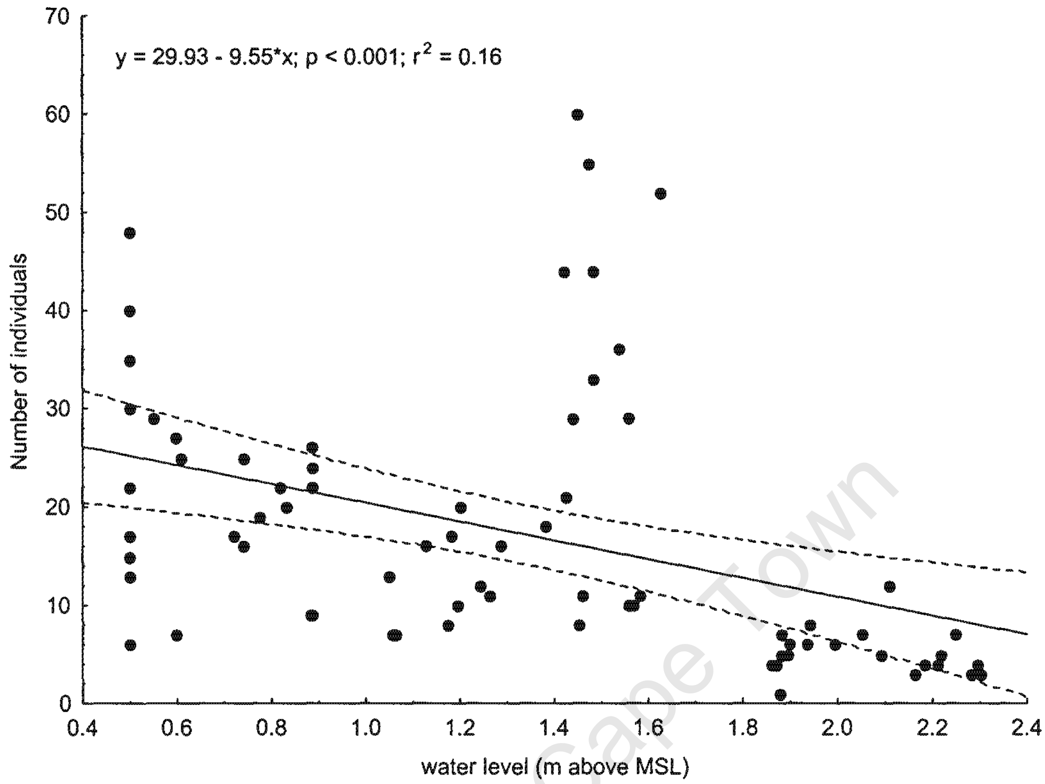

Figure 21. Relationship between wading piscivore numbers and water level at East Kleinemonde estuary.

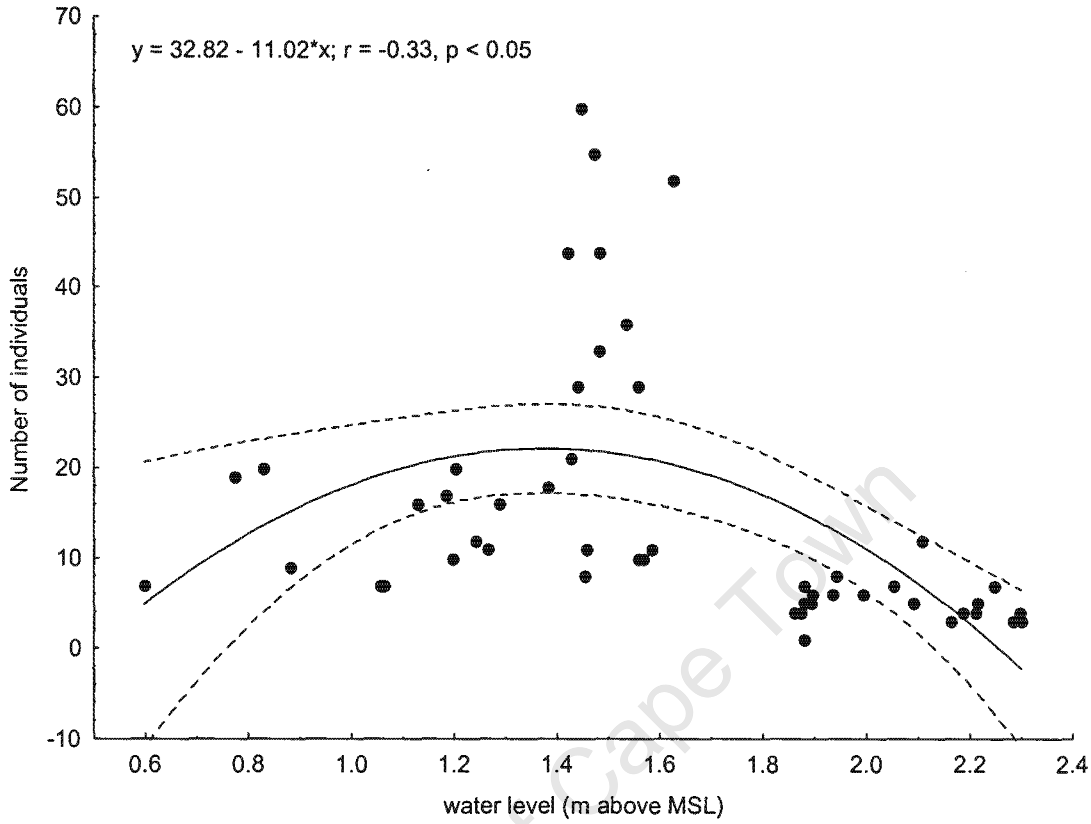

Figure 22. Relationship between wading piscivore numbers and water level at East Kleinemonde estuary under closed estuary mouth conditions.

South African resident waders, such as Black-winged Stilts, Water Thick-knees and White-fronted Plovers were more abundant in the winter months (Mean = 13.3 ± 9.9) than in the summer months (Mean = 6.8 ± 4.9) and their numbers decreased with increasing water levels (Figure 23). When separating the data by season a significant correlation ($r^2 = 0.20$; $p < 0.005$) was found between water level and number of recorded individuals in the winter months. The correlation between water level and abundance was not significant in the summer months ($r^2 = 0.11$; $p > 0.05$).

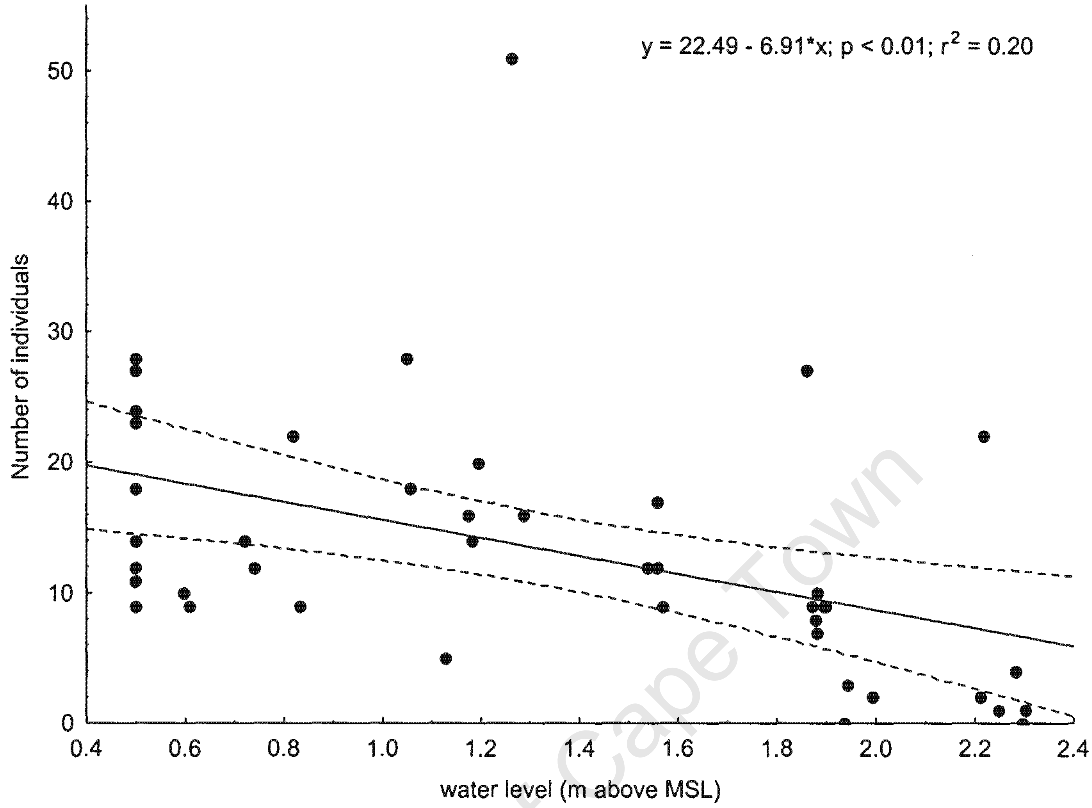

Figure 23. Relationship between resident wader numbers and water level at East Kleinemonde estuary in the winter months.

Aerial-diving piscivores such as kingfishers, terns and raptors showed a significant decrease in numbers with increasing water levels ($r^2 = 0.19$; $p < 0.001$; Figure 24).

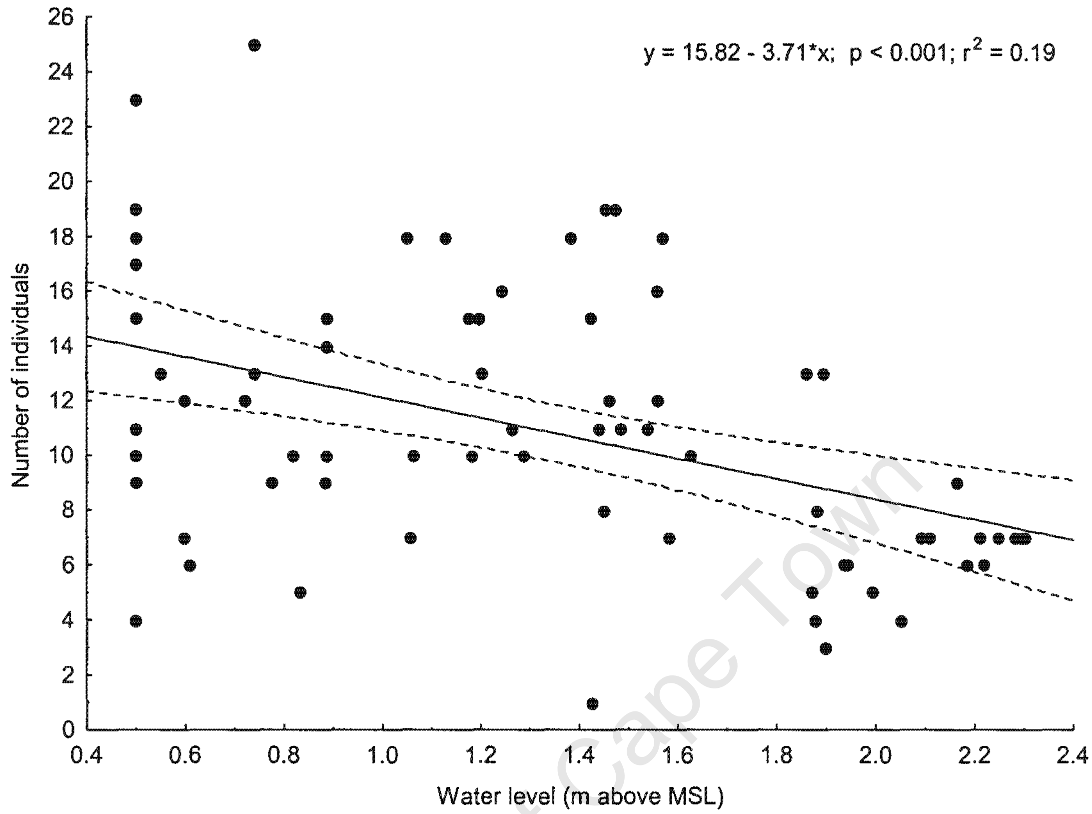

Figure 24. Relationship between aerial-diving piscivore numbers and water level at East Kleinemonde estuary.

Spatial distribution of birds

The highest abundance of birds at the Riet estuary was recorded in regions 1 and 2 (Figure 25), while the density of birds was lowest in these regions. These are the areas that include the floodplain and they were larger in size than regions 3 and 4. Herbivores were most abundant in the floodplain area of region 2, while aerial-diving piscivores and invertebrate-feeding waders were most common around the mouth region of the estuary. Wading piscivores were most abundant in region 3.

At the West Kleinemonde estuary bird densities were highest in region 4 which was the smallest region in size. The highest overall abundance of birds was found in region 3 of the estuary which is the area of the large floodplains (Figure 25). The majority of birds in region 3 were herbivorous waterfowl. Region 2 attracted large numbers of pursuit-swimming piscivores, mainly Reed Cormorant that fed in the wide and deep channel and roosted on the banks of this region. Region 1, which is flanked on both banks by housing developments, showed an overall low abundance of birds, as did the upper reaches of the estuary. In region 4 most recorded birds were pursuit-swimming piscivores, especially White-breasted Cormorants and African Darters.

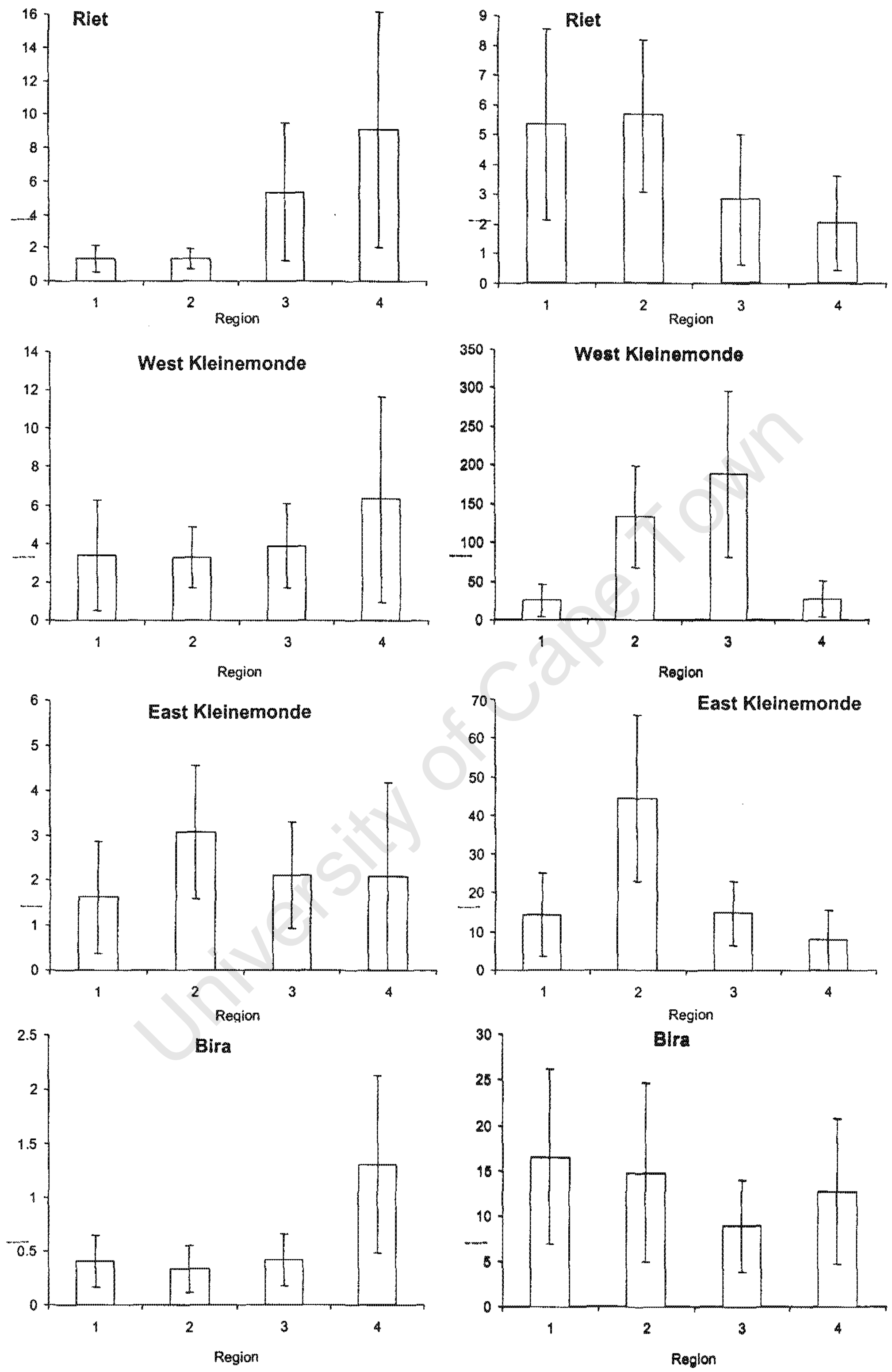

Figure 25. Mean bird densities and numbers in the different regions of the four studied estuaries.

At the East Kleinemonde estuary overall bird abundance was highest in region 2 of the estuary which encompasses a large floodplain and saltmarsh area. This region also had the highest bird density (Figure 25). The majority of birds in region 2 were wading piscivores, specifically Grey Heron, Great Egret, Little Egret and African Spoonbills. The majority of birds found in region 1, below the main road bridge, were invertebrate-feeding waders. Aerial-diving piscivores were most common in region 3, which is characterised by a wide and relatively shallow channel.

Bira estuary showed a more even distribution of birds along the estuary than the other estuaries (Figure 25). Most birds were recorded in region 1, below the bridge and the majority of these were invertebrate-feeding waders, specifically Water Thick-knees and White-fronted Plovers. The lowest abundance was recorded in region 3, an area with flat sandy banks, a wide and relatively shallow channel and no overhanging vegetation on its banks. Densities were highest in region 4, which was also the smallest area (Figure 25). Aerial-diving piscivores were distributed along the Bira estuary relatively evenly, while wading piscivores preferred region 1. Herbivores were not found in region 1, and were recorded in highest numbers in the top reaches (region 4). The majority of pursuit-swimming piscivores were found in the deep and wide channel of region 2.

Abundance of different species

Pied Kingfisher was the most abundant bird species (Table 13) at Riet and Bira estuaries where overall bird abundance was lowest (Table 4). Pied Kingfisher accounted for 27.3% of all birds at Riet estuary and 13.2% at Bira. The most abundant species at the East Kleinemonde estuary were Reed Cormorant (13.4% of birds) and Pied Kingfisher (10.8%, Table 13). At the West Kleinemonde estuary Reed Cormorant was also the most abundant species (28.9%), followed by Yellow-billed Duck (16.4%).

Table 13. Descriptive statistics of bird count results conducted on the four sampled estuaries between December 2005 and November 2006. The most abundant species is highlighted for each estuary.

	Riet		West Kleinemonde		East Kleinemonde		Bira	
Species	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**
African Darter	0.1 ± 0.35	0 - 1	2.6 ± 3.13	0 - 13	17.9 ± 12.54	0 - 48	1.2 ± 1.86	0 - 6
African Fish Eagle	0.2 ± 0.53	0 - 2	0.3 ± 0.59	0 - 2	1.7 ± 1.08	0 - 4	0.8 ± 0.81	0 - 2
African Oystercatcher	0.4 ± 1.71	0 - 8	0.1 ± 0.50	0 - 2	0.5 ± 1.00	0 - 4		
African Spoonbill			5.8 ± 8.22	0 - 33	15.2± 18.75	0 - 59		
Black Stork					0.3 ± 0.89	0 - 4		
Blacksmith Lapwing	1.6 ± 1.22	0 - 4	2.1 ± 1.8	0 - 9	6.5 ± 2.89	0 - 12	2.2 ± 1.12	0 - 4
Black-winged Stilt			0.1 ± 0.48	0 - 2	4.5 ± 4.49	0 - 19		
Cape Cormorant	0.1 ± 0.29	0 - 1	1.0 ± 1.67	0 - 6	1.7 ± 2.85	0 - 14		
Cape Shoveller					0.0 ± 0.17	0 - 1		
Cape Teal					0.6 ± 1.17	0 - 5		
Caspian Tern	0.0 ± 0.21	0 - 1	0.5 ± 0.71	0 - 3	0.9 ± 1.34	0 - 6	0.5 ± 0.68	0 - 2
Common Greenshank	0.1 ± 0.47	0 - 2	2.3 ± 3.38	0 - 13	9.4 ± 9.56	0 - 44	5.1 ± 5.01	0 - 16
Common Moorhen					0.2 ± 0.36	0 - 1		
Common Ringed Plover			0.2 ± 0.63	0 - 3	3.3 ± 10.93	0 - 49	0.4 ± 0.87	0 - 3
Common Sandpiper	0.5 ± 0.91	0 - 3	1.4 ± 1.46	0 - 6	0.8 ± 1.08	0 - 4	2.0 ± 2.75	0 - 8
Common Tern			0.1 ± 0.38	0 – 2	14.8 33.27	0 - 146	0.2 ± 0.4	0 - 1
Curlew Sandpiper			2.4 ± 7.65	0 - 34	9.1 ± 14.34	0 - 54	0.2 ± 1.09	0 - 5
Egyptian Goose	0.7 ± 0.95	0 - 2	0.8 ± 1.27	0 - 4	6.5 ± 4.28	0 - 13	0.3 ± 0.73	0 - 2
Giant Kingfisher	0.7 ± 0.65	0 - 2	1.1 ± 0.78	0 - 3	1.8 ± 1.50	0 - 5	1.1 ± 1.28	0 - 4
Goliath Heron	0.0 ± 0.21	0 - 1	0.0 ± 0.17	0 - 1			0.8 ± 0.60	0 - 2
Great Egret	0.2 ± 0.39	0 - 1	5.9 ± 7.03	0 - 24	7.0 ± 7.15	0 - 15		
Great CrestedTern					0.2 ± 0.89	0 - 5		
Greater Painted-snipe					0.0 ± 0.17	0 - 1		
Grey Heron	0.6 ± 0.85	0 - 3	8.4 ± 5.08	0 - 23	9.1 ± 5.36	1 - 24	2.6 ± 2.06	0 - 8
Grey Plover					0.2 ± 0.66	0 - 3	0.3 ± 0.73	0 - 2
Grey-headed Gull					0.1 ± 0.24	0 - 1		
Half-collared Kingfisher	0.6 ± 0.58	0 - 2	0.7 ± 1.09	0 - 4	2.2 ± 2.38	0 - 8	1.3 ± 1.59	0 - 5
Hamerkop							0.5 ± 0.98	0 - 4
Kelp Gull			1.3 ± 1.30	0 - 5	6.3 ± 9.61	0 - 41	0.8 ± 0.87	0 - 2
Kittlitz's Plover			0.1 ± 0.34	0 - 2	0.1 ± 0.38	0 - 2	0.1 ± 0.44	0 - 2
Little Egret	0.3 ± 0.72	0 - 3	4.9 ± 6.00	0 - 29	11.2 ± 17.79	0 - 72	1.1 ± 1.30	0 - 4
Little Grebe	0.4 ± 0.73	0 - 2	0.3 ± 1.14	0 - 6	3.2 ± 4.14	0 - 16	0.3 ± 0.58	0 - 2
Little Stint					0.2 ± 0.86	0 - 4		
Little Tern					4.5 ± 12.12	0 - 61	0.0 ± 0.22	0 - 1
Malachite Kingfisher			0.1 ± 0.44	0 - 2	0.4 ± 0.61	0 - 2	0.3 ± 0.46	0 - 1
Marsh Sandpiper			0.1 ± 0.28	0 - 1	0.0 ± 0.17	0 - 1		
Osprey					0.0 ± 0.17	0 - 1		
Pied Kingfisher	**4.3 ± 2.44**	1 - 11	8.5 ± 3.47	0 - 16	11.8 ± 5.11	1 - 23	**6.1 ± 3.74**	1 - 12
Purple Heron			0.2 ± 0.48	0 – 2	0.0 ± 0.17	0 - 1	0.0 ± 0.22	0 - 1
Red-billed Duck					7.9 ± 7.33	0 - 33	0.2 ± 0.6	0 - 2
Red-knobbed Coot					0.0 ± 0.17	0 - 1		
Reed Cormorant	0.6 ± 0.91	0	**10.4 ± 14.84**	0 - 60	**104.1 ± 64.83**	0 - 289	2.0 ± 2.56	0 - 8
Ruddy Turnstone					0.5 ± 2.62	0 - 15		
Ruff			0.1 ± 0.70	0 - 4	8.1 ± 19.88	0 - 83		
Sacred Ibis			0.9 ± 1.54	0 - 6	2.5 ± 5.26	0 - 6		
Sanderling			0.2 ± 0.84	0 - 4	0.7 ± 2.21	0 - 7	0.2 ± 0.54	0 - 2
Sandwich Tern					0.5 ± 2.31	0 - 13		
South African Shelduck	0.7 ±1.16	0 - 4	0.7 ± 1.09	0 - 4	10.6 + 8.11	0 - 32	0.6 ± 0.93	0 - 2
Three-banded Plover	1.0 ± 1.17	0 - 4	1.6 ± 2.31	0 - 9	1.5 ± 2.25	0 - 7	5.0 ± 3.13	0 - 9
Water Thick-knee	0.8 ± 0.92	0 - 3	6.9 ± 5.15	0 - 19	0.4 ± 1.09	0 - 5	2.3 ± 3.65	0 - 11
Whimbrel					0.2 ± 0.64	0 - 3	0.1 ± 0.48	0 - 2
White-breasted Cormorant	0.1 ± 0.35	0 - 1	2.2 ± 5.36	0 - 29	14.2 ± 12.99	0 - 52	1.1 ± 3.31	0 - 15
White-fronted Plover	0.5 ± 0.91	0 - 3	1.3 ± 2.94	0 - 14	2.9 ± 3.91	0 - 17	5.1 ± 4.34	0 - 14
Wood Sandpiper			0.1 ± 0.36	0 - 1	2.3 ± 3.25	0 - 14		
Yellow-billed Duck	0.9 ± 1.23	0 - 4	2.0 ± 3.67	0 - 18	59.2 ± 64.59	0 - 233	3.9 ± 9.64	0 - 43

Frequency of occurrence of different species

There was no definite common pattern in distribution stability within feeding guilds. However, invertebrate-feeding waders tended to be less stable in terms of their occurrence than other feeding guilds. Eleven of 20 species of invertebrate-feeding waders were recorded on less than 25% of occasions on all four estuaries, while this was only the case for 5 out of 12 species of aerial-diving piscivores and for 3 of 9 species of herbivores and 3 of 9 wading piscivores (Table 15). Only one species (Pied Kingfisher) occurred on more than 75% of observations on all four estuaries. Five species occurred on more than 50% of observations on all estuaries. These were three aerial-diving piscivore species, one invertebrate-feeding wader and one wading piscivore.

All four estuaries had a high proportion of rarely recorded species (< 25% of occasions,Table 14). The West Kleinemonde estuary showed the highest proportion of regularly recorded species (31.5%) but also the lowest proportion of occasionally recorded species (9.3%). The proportion of frequently recorded species ranged from 13 - 20% on all estuaries.

Table 14. Summary of frequency of occurrence of species at the four sampled estuaries. Regular: > 75% of occasions. Frequent: 50-74.9% of occasions. Occasional: 25-49.9% of occasions. Rare: < 25% of occasions

	Regular species	**%**	**Frequent species**	**%**	**Occasional species**	**%**	**Rare species**	**%**	**Total number of species**
Riet	1	4.0	4	16.0	9	36.0	11	44.0	25
West Kleinemonde	17	31.5	9	16.7	5	9.3	23	42.6	54
East Kleinemonde	8	21.1	5	13.2	11	28.9	14	36.8	38
Bira	6	17.1	7	20.0	10	28.6	10	28.6	35

Table 15. Frequency of occurrence as a percentage of total observations.
Lightest grey: recorded on ≥75% of counts (regular), Light grey : 50-74.9% of counts (frequent visitors), dark grey: 25-49.9% of counts (occasional visitors), Black: < 25% of counts (rare visitors)

Species	Riet	West Kleinemonde	East Kleinemonde	Bira
African Darter	13.6	94.1	[illegible]	12.9
African Fish Eagle	18.2	79.4	26.5	57.1
African Oystercatcher	4.5	20.6	8.8	
African Spoonbill		58.8	58.8	
Black Stork		17.6		
Blacksmith Lapwing	72.7	94.1	79.4	85.7
Black-winged Stilt		76.5	5.9	
Cape Cormorant	9.1	50.0	35.3	
Cape Shoveller		2.9		
Cape Teal		23.5		
Caspian Tern	4.5	50.0	[illegible]	[illegible]
Common Greenshank	9.1	82.4	52.9	90.5
Common Moorhen		14.7		
Common Ringed Plover		11.8	8.8	23.8
Common Sandpiper	[illegible]	[illegible]	[illegible]	47.6
Common Tern		[illegible]	5.9	19.0
Curlew Sandpiper		[illegible]	14.7	4.8
Egyptian Goose	36.4	55.3	35.3	19.0
Giant Kingfisher	[illegible]	79.4	76.5	57.1
Goliath Heron	4.5		2.9	71.4
Great Crested Tern		8.8		
Great Egret	[illegible]	91.2	82.4	
Greater Painted-snipe		2.9		
Green-backed Heron	[illegible]			
Grey Heron	45.5	97.1	97.1	90.5
Grey Plover		14.7		19.0
Grey-headed Gull		5.9		
Half-collared Kingfisher	59.1	67.6	38.2	52.4
Hamerkop				[illegible]
Kelp Gull		79.4	67.6	52.4
Kittlitz's Plover		5.9	2.9	4.8
Little Grebe	27.3	[illegible]	8.8	[illegible]
Little Egret	22.7	79.4	85.3	[illegible]
Little Stint		5.9		
Little Tern		20.6		4.8
Malachite Kingfisher		32.4	11.8	[illegible]
Marsh Sandpiper		2.9	2.9	
Osprey		2.9		
Pied Kingfisher	100.0	97.1	97.1	100.0
Purple Heron		2.9	17.6	4.8
Red-billed Duck		85.3		9.5
Red-knobbed Coot		2.9		
Reed Cormorant	[illegible]	88.2	[illegible]	[illegible]
Ruddy Turnstone		5.9		
Ruff			5.9	
Sacred Ibis		58.8	41.2	
Sanderling		11.8	5.9	19.0
Sandwich Tern		8.8		
South African Shelduck	[illegible]	85.3	32.4	28.6
Spur-winged Goose		5.9		4.8
Three-banded Plover	45.5	50.0	47.1	95.2
Water Thick-knee	50.0	14.7	79.4	33.3
Whimbrel		8.8		9.5
White-breasted Cormorant	13.6	82.4	[illegible]	[illegible]
White-fronted Plover	[illegible]	61.8	29.4	76.2
Wood Sandpiper		50.0	14.7	
Yellow-billed Duck	[illegible]	94.1	47.1	42.9

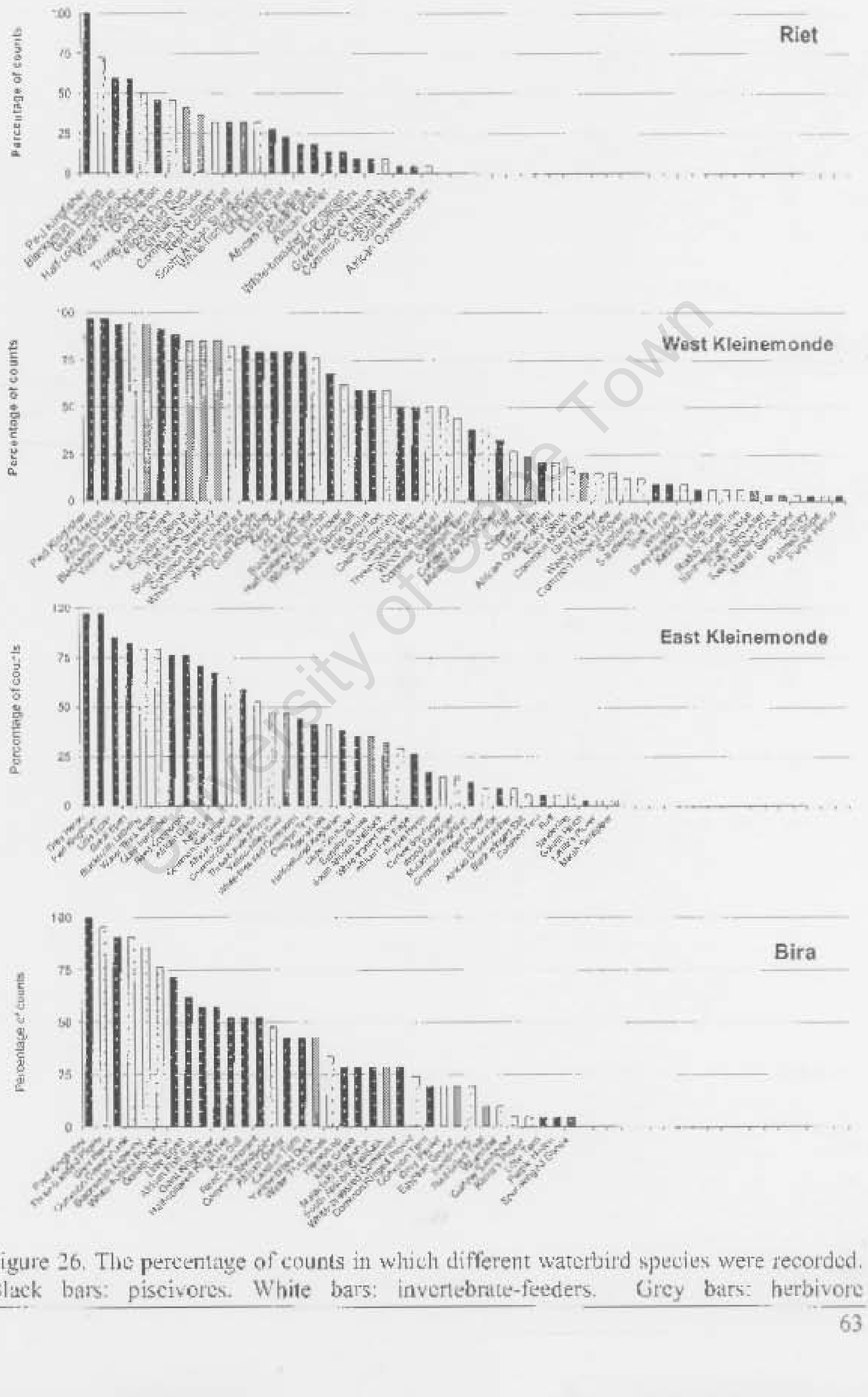

Figure 26. The percentage of counts in which different waterbird species were recorded. Black bars: piscivores. White bars: invertebrate-feeders. Grey bars: herbivore

ACTIVITY PATTERNS OF WATERBIRDS AT THE EAST KLEINEMONDE ESTUARY

The estuary mouth was closed to the sea on 27 sampling days and open on 12 days. Large overwashing events took place on two count days while small overwashings occurred on five count days.

Wading piscivores were the most numerous group making up 62.7% of all recorded individuals (Table 16), followed by pursuit-swimming piscivores (23%). Invertebrate-feeding waders, aerial-diving piscivores and herbivores (7%, 4% and 3% respectively) only contributed 14% to the total number of recorded individuals.

Table 16. Summary of bird count results from June 2004 to May 2005 at the East Kleinemonde estuary.

Feeding guild	Median ± SE	Mean ± SD	Range	% of total
Pursuit-swimming piscivores	0 ± 0.1	1.7 ± 4.5	0 - 42	23
Aerial-diving piscivores	0 ± 0.0	0.3 ± 1.0	0 - 18	4
Wading piscivores	1 ± 0.3	4.7 ± 11.1	0 - 106	63
Invertebrate-feeding waders	0 ± 0.1	0.5 ± 2.3	0 - 34	7
Herbivores	0 ± 0.0	0.3 ± 1.0	0 - 11	3
All birds	0 ± 0.1	1.5 ± 5.7	0 - 106	100

Overall, 70% of all birds were resting, followed by feeding birds (15%). 11% of birds were performing maintenance and only 4% were recorded in the orientation category.

The predominant use of the estuary was for resting by wading piscivores which made up 50% of all records. The second most important use was as a roost site for pursuit-swimming piscivores (16%). In general, the estuary was used more for non-feeding (resting & maintenance) than for feeding purposes (feeding & orientation), with maintenance and resting making up 81% of all records (Table 17).

Table 17. Summary of activity counts for feeding guilds at the East Kleinemonde estuary.

		Mean	Median	Standard error	Range	% of total
Pursuit-swimming piscivores						
	Resting	4.6	1	0.4	0 - 42	66.7
	Maintenance	0.2	0	0	0 - 4	2.9
	Feeding	0.8	0	0.1	0 - 32	11.6
	Orientation	1.3	0	0.2	0 - 23	18.8
Aerial-diving piscivores						
	Resting	0.3	0	0.1	0 - 18	27.3
	Maintenance	0.2	0	0	0 - 4	18.2
	Feeding	0.6	0	0.1	0 - 18	54.5
	Orientation	0	0	0	0 - 2	0.0
Wading piscivores						
	Resting	14.7	9	0.9	0 - 106	79.9
	Maintenance	0.4	0	0.1	0 - 30	2.2
	Feeding	1.5	1	0.2	0 - 61	8.2
	Orientation	1.8	0	0.2	0 - 28	9.8
Invertebrate-feeding waders						
	Resting	0.6	0	0.1	0 - 30	31.6
	Maintenance	0.1	0	0	0 - 5	5.3
	Feeding	1.1	0	0.2	0 - 34	57.9
	Orientation	0.1	0	0	0 - 5	5.3
Herbivores						
	Resting	0.2	0	0	0 - 8	20
	Maintenance	0.3	0	31	0 - 11	30
	Feeding	0.4	0	0.1	0 - 11	40
	Orientation	0.1	0	0	0 - 4	10

Seasonal trends

Bird numbers were significantly higher in summer than in winter (Mann-Whitney U test; $p < 0.001$, $z = 7.79$, $U = 6961597$). While the average number of birds performing feeding, orientation and maintenance activities decreased significantly from winter to summer this was outweighed by a highly significant increase of resting wading piscivores from winter to summer (Table 18, Table 19). A heronry was established on the estuary at the end of winter and a number of Great Egret, Black-headed Heron and Grey Heron bred there successfully. These birds mainly utilised the survey area for nesting and roosting but went elsewhere to feed.

Table 18. Mann-Whitney U test results for changes in average bird numbers between summer and winter months. (+/-) indicates an increase/decrease from winter to summer.

	Pursuit-swimming piscivores	**Aerial-diving piscivores**	**Wading piscivores**	**Invertebrate-feeders**	**Herbivores**	**All birds**
Resting	n.s.	n.s.	$p < 0.01$ (+)	$p < 0.01$ (-)	$p < 0.05$ (-)	$p < 0.001$ (+)
Feeding	$p < 0.01$ (-)	n.s.	n.s.	n.s.	$p < 0.001$ (-)	$p < 0.001$ (-)
Orientation	$p < 0.01$ (-)	$p < 0.01$ (-)	n.s.	n.s.	$p < 0.05$ (-)	$p < 0.001$ (-)
Maintenance	$p < 0.05$ (-)	n.s.	n.s.	$p < 0.01$ (-)	n.s.	$p < 0.001$ (-)

Pursuit-swimming and wading piscivores recorded on the estuary spent the majority of their time in resting and maintenance activities in both seasons (Figure 27), while aerial-diving piscivores and herbivores spent most of their time at the estuary in feeding and orientation activities in summer and winter. Invertebrate-feeding waders spent 85% of their time in feeding and orientation activities in winter but this decreased to 50% in summer.

A Chi-Square test of independence for each feeding guild showed that there was a significant difference in the distribution of feeding and non-feeding activities between summer and winter for all feeding guilds except aerial diving piscivores (Table 19).

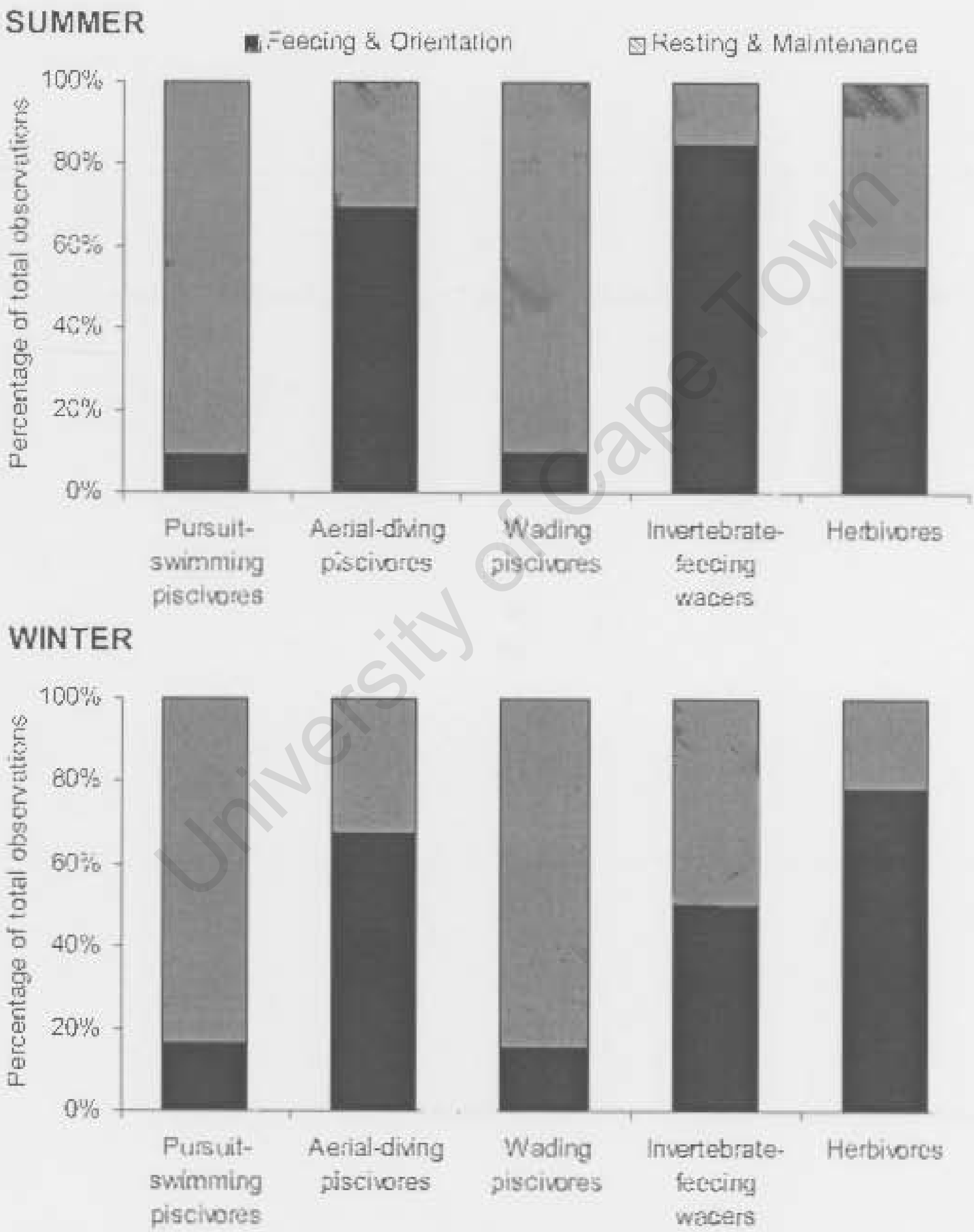

Figure 27. Percentage of total observations of different feeding guilds performing feeding and non-feeding related activities in summer (Nov – Mar) and winter months (Apr – Oct).

Table 19. The average number of birds recorded in summer (Nov – Mar) and winter (Apr – Oct). Chi^2 tests were done to compare summer and winter ratios.

SUMMER	**Pursuit-swimming piscivores**	**Aerial-diving piscivores**	**Wading piscivores**	**Invertebrate-feeding waders**	**Herbivores**	**Total**
Resting	1.9	0.3	22.0	0.2	0.1	**24.5**
Maintenance	0.4	0.0	2.6	0.0	0.0	**3.0**
Feeding	1.2	0.7	2.0	1.0	0.1	**8.0**
Orientation	0.1	0.1	0.6	0.0	0.2	**1.0**
Total	3.6	1.1	27.2	1.2	0.4	36.5
WINTER						
Resting	8.1	0.4	5.4	1.2	0.3	**15.4**
Maintenance	2.5	0.0	0.7	0.3	0.1	**3.6**
Feeding	1.7	0.6	0.9	1.3	0.9	**5.4**
Orientation	0.4	0.3	0.2	0.1	0.5	**1.5**
Total	12.7	1.3	7.2	2.9	1.8	**25.9**
Chi^2 value	**19.2**	**0.2**	**31.8**	**89.8**	**18.2**	
p-value	**< 0.001**	**n.s**	**< 0.001**	**< 0.001**	**< 0.001**	

Daily trends

Mean bird abundance was lower during the first and last count of the day than during the day in summer and winter (Figure 28), indicating that many birds probably did not use the study area for overnight roosting. They could however be utilising other regions of the estuary at night. There was no significant difference between count numbers in summer (Kruskal-Wallis test; $H = 9.7$; df: 9; $N = 4480$; $p > 0.05$), but the difference between counts was significant in winter (Kruskal Wallis test; $H = 17.2$; df: 9; $N = 3460$; $p < 0.05$).

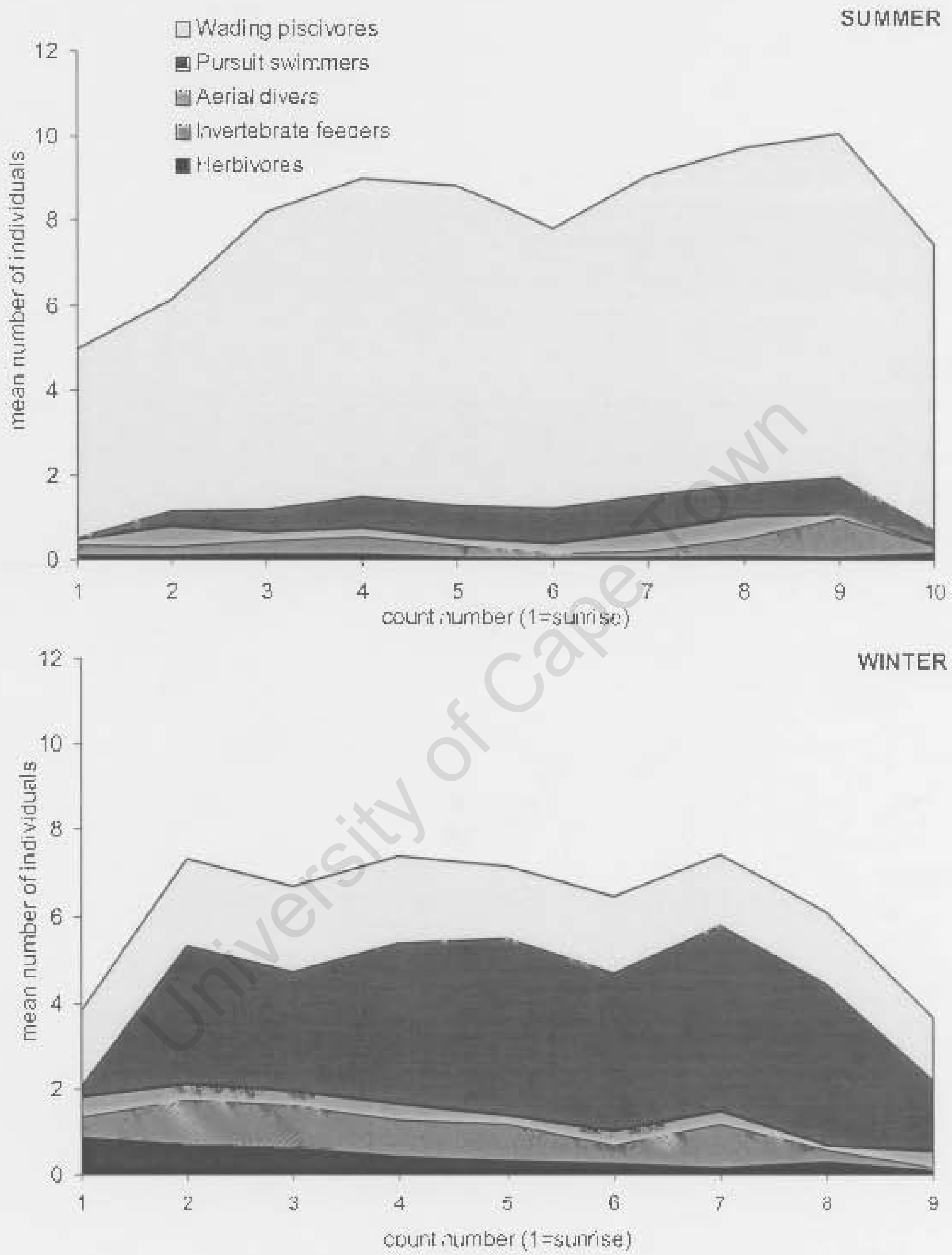

Figure 28. Mean number of individuals of different feeding guilds recorded every 1.5h from sunrise (1) to sunset in summer and winter.

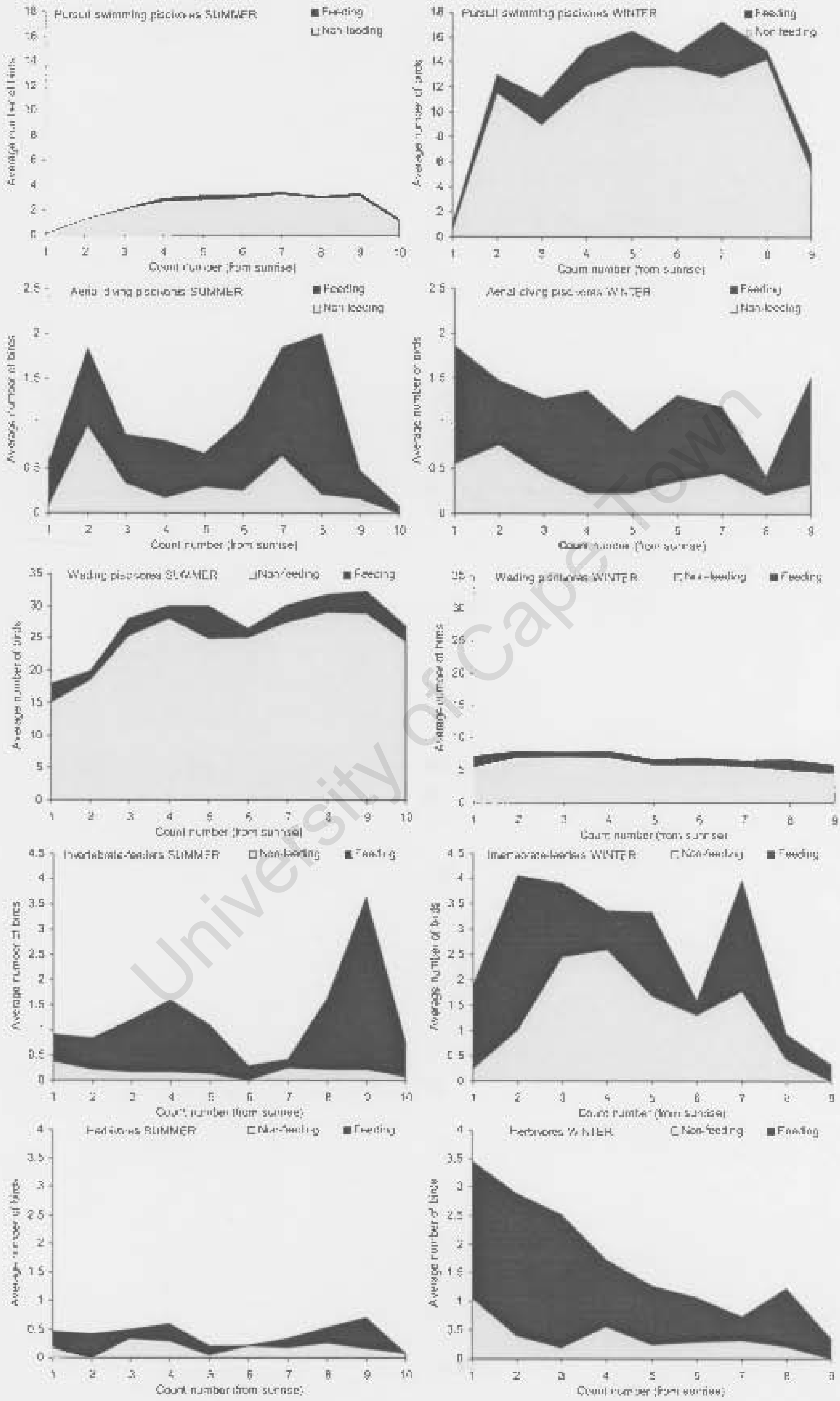

Figure 29. Average numbers of feeding guilds from sunrise (1) to sunset in summer and winter.

In summer mean pursuit-swimming, aerial-diving and wading piscivore numbers increased after sunrise (Figure 29). In winter there was an increase in mean pursuit-swimming piscivore, wading piscivore and invertebrate-feeding wader abundance after sunrise.

Changes in abundance over the course of the day were significant in summer only for pursuit-swimming piscivores. In winter, mean pursuit-swimming piscivore, aerial-diving piscivore and herbivore abundance changed significantly over the course of the day (Table 20).

Table 20. Chi^2 test results of changes in feeding guild abundance over time of day. Degrees of freedom 9 (summer) and 8 (winter).

	SUMMER		WINTER	
	Chi^2	p-value	Chi^2	p-value
Pursuit-swimming piscivores	24.0	**< 0.01**	48.7	**< 0.001**
Aerial-diving piscivores	11.6	n.s.	17.5	**< 0.05**
Wading piscivores	4.7	n.s.	3.9	n.s.
Invertebrate-feeding waders	10.6	n.s.	11.5	n.s.
Herbivores	4.4	n.s.	20.0	**< 0.05**

The proportion of orientation activities was highest at sunrise when birds were observed flying into the survey area, and lowest in the middle of the day (Figure 30) when the proportion of birds resting was highest. The percentage of birds observed performing maintenance activities remained relatively stable. Feeding activity was lowest 7.5 h after sunrise.

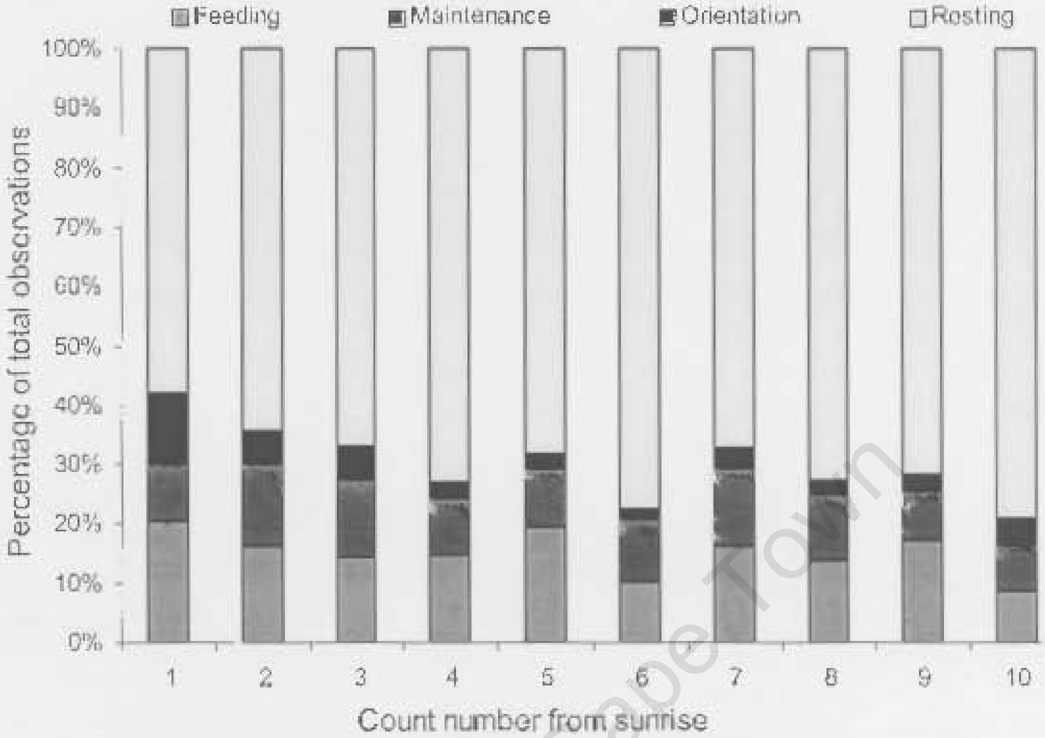

Figure 30. Percentage of total observations that birds were recorded performing different activities. Birds were recorded every 90 minutes from sunrise (1) to sunset at East Kleinemonde estuary between June 2004 and May 2005.

Activity times

The activity time results give an estimate of the amount of time the average bird spends on the estuary on an average day performing the different activities.

Overall waterbirds at East Kleinemonde estuary spent the majority of their day with resting activities, followed by feeding, maintenance and orientation.

In winter on average more time was spent on the estuary per day by waterbirds than in summer. This increase was significant for all activity groups (Table 21).

Table 21. Estimated mean daily activity times (minutes per individual spent with an activity) at East Kleinemonde estuary in summer and winter months during daylight hours.

	TOTAL		**SUMMER**		**WINTER**		**Mann-Whitney**
	Mean ± SD	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**U test**
Resting	156.5 ± 167.3	0 - 654	150.4 ± 190.0	0 - 654	163.1 ± 139.1	0 - 578	**p < 0.05**
Maintenance	28.5 ± 43.9	0 - 210	23.9 ± 40.7	0 - 144	33.6 ± 46.9	0 - 210	**p < 0.05**
Feeding	78.2 ± 78.9	0 - 450	73.1 ± 90.9	0 - 450	83.7 ± 63.3	0 - 315	**p < 0.01**
Orientation	25.1 ± 37.6	0 - 180	17.9 ± 35.5	0 - 180	33.1 ± 38.5	0 - 180	**p < 0.01**

Pursuit-swimming piscivores spent significantly more time at the estuary per day in winter than in summer (Table 22, Figure 31). This increase was due to significant increases in orientation and feeding activities in winter. The increase in time spent with resting and maintenance activities was not significant.

Overall, aerial-diving piscivores did not increase their time spent at the estuary significantly from summer to winter (Table 22). There was however a significant increase in orientation time in winter.

Wading piscivores spent the most amount of time on the estuary per day out of all feeding guilds in summer, as well as in winter and the majority of this time was spent resting (Figure 31). In summer resting and maintenance time was significantly higher than in winter (Table 22) but the decrease in time spent at the estuary per day from summer to winter was not significant.

Invertebrate-feeding waders significantly increased time spent at the estuary from summer to winter. Increases in resting and maintenance activities in winter were also significant (Table 22).

Herbivores also spent significantly more time at the estuary in winter than in summer. Increases in resting, feeding and orientation activities were significant (Table 22).

Table 22. Mann-Whitney U test results between summer and winter activity times.

	Pursuit-swimming piscivores	**Aerial-diving piscivores**	**Wading Piscivores**	**Invertebrate-feeding waders**	**Herbivores**
Resting	n.s	n.s.	$p < 0.01$	$p < 0.01$	$p < 0.05$
Maintenance	n.s	n.s.	$p < 0.01$	$p < 0.01$	n.s.
Feeding	$p < 0.01$	n.s.	n.s.	n.s	$p < 0.001$
Orientation	$p < 0.001$	$p < 0.01$	n.s.	n.s.	$p < 0.05$
All activities	$p < 0.001$	n.s.	n.s.	$p < 0.001$	$p < 0.001$

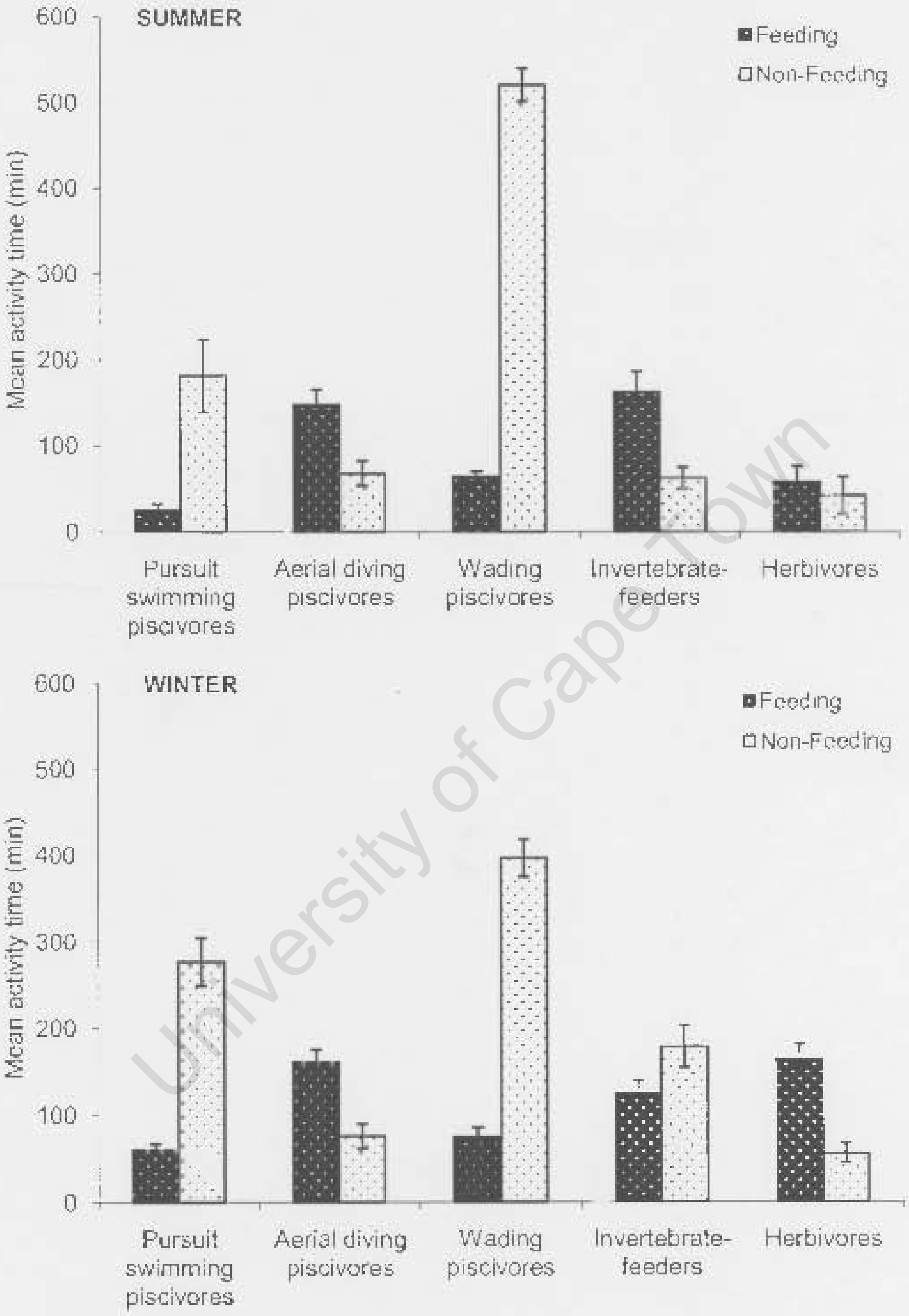

Figure 31. Estimated mean time per bird of a feeding guild spent with different activities during daylight hours at East Kleinemonde estuary in summer and winter months. Error bars mark standard errors.

DISCUSSION

Very limited information exists on bird communities in intermittently open estuaries and it is thus difficult to make any predictions on how they are affected when changes in their environment take place. Urbanisation and industrial development pose a threat to the health of estuaries in South Africa. Also, increasing retention of freshwater by dams for domestic, industrial and agricultural purposes causes the frequency and duration of mouth opening events to decrease (Reddering & Rust 1990, Whitfield 1992, Cooper *et al.* 1999). It is therefore important to have baseline information on how future management decisions will influence the avifauna. Since bird numbers on intermittently open estuaries are very low compared to large permanently open systems statistical analysis is very difficult. These systems have therefore been largely ignored by researchers in the past, despite their potential collective importance in terms of habitat for South African coastal birds.

How does habitat structure influence community composition?

Habitat diversity within and between wetland systems is known to influence waterbird diversity (Brock *et al.* 1999), as different species can occupy more niches in a diverse mosaic habitat (Perrings *et al.* 1992, Gray 1997). As mentioned above, each estuary had a distinct bird community composition. The results of this study indicate that habitat structure is a major factor in determining the community composition of intermittently open estuaries, through effects on the abundance of different feeding guilds.

Floodplain habitat had the strongest influence on bird abundance. The West Kleinemonde estuary, which had the highest abundance and diversity of birds also had the largest area of floodplain. In addition, the channel was vegetated with submerged macrophytes, which was the habitat that correlated with bird abundance the second strongest. By contrast, the Bira estuary which had the lowest abundance and density of birds, had no visible submerged macrophyte growth in its channel and also only a small area of floodplain habitat. The East Kleinemonde estuary had the second most diverse and dense bird community and also had a relatively large floodplain area. While submerged macrophyte growth in the channel was low, wading and aerial-diving piscivores were attracted by the shallow margin habitat, which covered a large portion of the estuary.

Pursuit-swimming piscivores abundance was strongly correlated with vegetated channel habitat and was also correlated with floodplain habitat. The most abundant pursuit-swimming piscivore species was Reed Cormorant, which prefers to fish in water 30 – 200 cm deep (Whitfield & Blaber 1979b). Possibly the concentration of prey fish is higher in waters with submerged macrophytes as they provide shelter and refuge .

Aerial-diving piscivores showed the weakest overall relationship to habitat (adjusted $R^2 = 0.79$). Many of these species (for example terns and gulls) can feed over the entire water surface area and are therefore less reliant on the availability of specific habitat types. Prey availability possibly plays a greater role in this feeding guild.

Wading piscivores were strongly correlated with floodplain habitat and less strongly with shallow margins, both habitats in which they are able to feed. Wading piscivores have a maximum wading depth (Whitfield & Blaber 1979a) and this result was therefore expected.

Invertebrate-feeding waders were most strongly correlated with floodplain habitat. Water levels in the floodplains on the studied estuaries varied greatly, so that very shallow water and margins provided a suitable feeding ground for these species. It is interesting to note that they were not correlated with exposed banks, which are relatively unproductive in these largely non-tidal systems.

Herbivorous waterfowl correlated strongly with reedbeds and floodplain habitat, but also with vegetated channel. Since waterfowl are reliant on macrophyte and other plants for feeding this was also an expected result. The floodplain in the West Kleinemonde estuary in which most waterfowl occurred was well vegetated and reedbeds provide shelter .

How do breaching events and mouth condition affect the avifauna of IOEs?

As the estuary mouth breaches and water levels drop, communities of plants and animals colonising the substratum can be exposed (Perissinotto *et al.* 2000). Fish and invertebrates can be stranded on floodplains and immigration of fish and invertebrates into remnant pools occurs, providing highly concentrated feeding opportunities for waterbirds (Kushlan 1976). The increase in bird numbers immediately following breaching events on the Riet, East Kleinemonde and Bira estuaries demonstrates that birds are initially attracted to intermittently open estuaries following mouth breachings and utilise these highly unpredictable events as feeding opportunities.

However, bird numbers decreased immediately following the first breaching event at the West Kleinemonde estuary, and decreased further as the estuary mouth remained open. The West Kleinemonde estuary has large areas of floodplains which were inundated when the estuary mouth was closed and water levels were high. Macrophyte cover was visibly high during the closed phase of the study as the estuary had been closed to the sea for an extended period of time before the beginning of the study. Herbivorous waterfowl such as Yellow-billed Duck and Red-billed Duck favour feeding in the littoral zone where aquatic vegetation is closest to the surface and thus easily accessible (Whitfield & Cyrus 1978), while wading piscivores such as Grey Heron and Great Egret hunt for prey in shallow waters of a maximum depth (Kushlan 1976). These feeding guilds were attracted to the floodplains of the West Kleinemonde estuary in high numbers during the closed phase. As the estuary mouth opened these floodplains drained within a very short period of time and a large area of wading and feeding habitat was lost. Herbivorous waterfowl and pursuit-swimming and wading piscivores departed. The tidal influence was low at the West Kleinemonde estuary and water levels were extremely low, even at low tide, so that the water surface area of the system was greatly reduced. Thus, the initial influx of birds which was recorded at the other three studied estuaries was outweighed by the loss of available feeding habitat on this estuary. The overall high abundance and density of birds (3.6 birds/ha) at the West Kleinemonde estuary can therefore be attributed to the extensive floodplains found in this system. As no other water bodies in the area are known of by local bird watchers in which waterfowl occur in similar numbers (A. Williams, pers. comm.), the West Kleinemonde estuary could potentially be of regional importance for herbivorous waterfowl.

At Bira estuary a strong initial influx of birds was recorded when the mouth opened, and bird numbers then dropped again but settled at a higher level than when the mouth was closed. Bira estuary showed a high tidal influence reaching approximately 10 km up the estuary, and water levels remained relatively high at high tide. The drop in water levels and tidal influence at Bira could have led to an increase in available wading habitat for birds with a maximum wading depth, such as egrets and herons, as deeper areas in the channel became shallower. The strong tidal influence is also likely to be the reason that pursuit-swimming piscivores were attracted to the estuary after the mouth opened, as a narrower channel leads to a higher concentration of fish, making it easier to hunt underwater.

While there was a sharp initial influx of birds at the East Kleinemonde estuary, bird abundance dropped thereafter to a similar level as when the estuary mouth was closed. While there was a loss of floodplain wading habitat after the opening, this did not affect overall abundance. The floodplain, which lacks significant pans, did not attract the large numbers recorded at the adjacent West Kleinemonde and so this loss of wading habitat did not seem to have made an impression on overall numbers. In addition a heronry of Great Egret and Grey Heron was in use near the road during the opening events and this obviously kept wading piscivores from leaving the area. They were observed flying in and out to feed, but remained at the estuary to breed as they had the previous summer.

Waterbird abundance did not increase significantly when the mouth opened at the Riet estuary. This differed from the other systems in that when it opened to the sea, no deep channel was formed at the mouth and tidal influence was minimal, because the system was more perched. The water level dropped only slightly, with water trickling out at the mouth at a rate probably similar to water running in from the top. Most of the exposed sandbanks became supra-tidal rather than inter-tidal, which causes the food items of waders (small shallow-burrowing invertebrates) to desiccate (Perissinotto *et al.* 2004). Only a limited intertidal area was therefore available for invertebrate-feeding waders and wading piscivores to utilise as a feeding ground. Since the water level did not change substantially after opening, there was no drastic changes in habitat available to waterbirds.

This study demonstrates that responses to mouth opening events are highly variable and differ from system to system. The key factor which influences the abundance of birds in these systems is how habitat availability changes with changes in mouth condition. Birds are highly mobile organisms and are attracted to estuaries for a variety of reasons. Seasonal migration patterns, food availability, lack of disturbance, as well as habitat availability all play a role (Ntiamoa-Baidu *et al.* 2000). The occurrence of birds on a system are likely to be influenced by conditions elsewhere as well as conditions on the estuary itself. Piscivorous birds, waterfowl and wader numbers increased abruptly and significantly on the Oosterschelde estuary after the artificial closure of the adjacent Grevelingen estuary (Doornbos 1984, Lambeck *et al.* 1989, Slob 1989).

The results indicate that each estuary has a distinct avifaunal community, which is related to the unique morphology and habitat composition of each estuary, which was therefore investigated further. Also, species compositions at one estuary under open and closed conditions resemble one another more closely than species compositions of the same mouth condition at different estuaries. Species composition and feeding guild composition changed significantly from the closed to the open mouth state, and two distinct communities were found at each estuary. There was a shift from a piscivore dominated community to a more diverse community with an increased proportion of invertebrate feeding waders at the Riet, West Kleinemonde and East Kleinemonde estuaries. Only at Bira were more piscivores attracted to the estuary under open conditions, which can be attributed to the prevailing geomorphological conditions and greater fish recruitment arising from a prolonged marine connection. While a significant change in species composition still took place when the mouth opened, diversity was not increased significantly. Generally however the intermittently open estuarine (IOE) avifauna is a piscivore dominated community, which changes towards the type of community typical of permanently open estuaries when the mouth opens. If an increase in open mouth phase duration takes place it can be expected that the typical IOE avifauna will be replaced. It is unknown to what degree waterbirds, particularly piscivores rely on intermittently open estuaries as feeding and roosting grounds and where they move if conditions become unfavourable.

How does the bird community respond to changes in water level?

Water level fluctuations affect available feeding habitat as well as prey availability and species exhibit different responses to changes in water level (Kushlan 1976, Kushlan 1986, Dimalexis & Pyrovetsi 1997). The correlations found between water level and bird abundance at the East Kleinemonde estuary highlight that different feeding groups respond in different ways to changing water levels. An increase in water level at the estuary increased available diving habitat and led to an increase in pursuit-swimming piscivores. Wading piscivore numbers peaked at a water level between 1.4 and 1.7 m above mean sea level which leads to the conclusion that wading habitat was maximised at this water depth. Resident invertebrate-feeding waders also exhibited a decrease in numbers with increasing water levels, as the water became too deep for them to wade in. Aerial-diving piscivores also declined when water levels increased above a threshold of approximately 1.6 m above mean sea level. Prey concentration possibly was reduced too much when water levels were too high and easier fishing conditions could have prevailed at other nearby estuaries. Overall these correlations were not very strong due to the high variability in numbers and the multitude of factors influencing abundance, such as weather conditions at the site and elsewhere and seasonal migration patterns.

How do densities of birds on intermittently open estuaries compare with other types of estuaries?

Overall waterbird densities ranged from 0.46 birds/ha at the Bira estuary to 3.64 birds/ha at the West Kleinemonde estuary. Few analyses of total waterbird densities on South African estuaries exist (Hockey & Turpie 1999a), with many studies focussing only on invertebrate-feeding waders (Martin & Baird 1987, Hockey *et al.* 1992). Large permanently open systems generally have higher waterbird densities than the intermittently open systems studied here. Martin & Baird (1987) recorded 11.5 birds/ha on Swartkops estuary, while Smits (1981) found densities of 8.5 birds/ha on the Wadden Sea in Europe. At Langebaan Lagoon high densities (15.9 birds/ha) were recorded in summer of which the large majority (14.7 birds/ha) were waders, with densities dropping to 4.5 birds/ha in winter (Underhill 1987), due to the departure of migrating waders. Martin *et al.* (2000) recorded 2.7 birds/ha at Knysna estuary, a large estuarine bay, but attribute this relatively low abundance to high levels of recreational disturbance and low availability of macrobenthic invertebrates. The high bird densities in permanently open systems are largely due to high numbers of invertebrate-feeding waders that utilise these systems, especially in the summer months (Martin & Baird 1987, Underhill 1987, Martin *et al.* 2000). Invertebrate-feeding wader numbers did not increase significantly during open mouth phases at the intermittently open estuaries in this study. However, the estuary mouths were all closed during the majority of the summer months and were only open in October and November and therefore unlikely to attract many summer migrants. Moreover, resident intertidal-feeding waders were not attracted by open mouth conditions and seem to prefer the more stable and predictable environment of permanently open estuaries and shoreline habitats. Small intermittently open estuaries therefore probably do not play an important role for intertidal-feeding waders.

The avifauna of all four studied systems was dominated by piscivorous resident (non-migrating) species. Despite the low densities of birds recorded in this study, compared to permanently open estuaries mentioned above, IOEs collectively provide a large area of feeding, roosting and breeding habitat for piscivorous birds in South Africa. The degree to which they rely on these habitats requires further investigation.

For what primary use do birds utilise intermittently open estuaries?

The East Kleinemonde estuary was used more for non-feeding than for feeding purposes. Aerial-diving piscivores, invertebrate-feeding waders and herbivores present at the East Kleinemonde estuary spent the majority of their time with foraging activities, while wading piscivores and pursuit-swimming piscivores spent the majority of their time with roosting and maintenance. It has been shown that foraging time is inversely related to body size in marine, shore and estuarine birds (Pearson 1968, Engelmoer *et al.* 1984, Zwarts *et al.* 1990, Ntiamoa-Baidu *et al.* 1998) and that foraging time is also related to feeding guild in waterbirds (Ntiamoa-Baidu *et al.* 1998). The pursuit-swimming piscivores and wading piscivores at the East Kleinemonde estuary were generally much larger in body mass than members of the other three guilds. In addition, these guilds were often observed flying from their roosting sites towards the adjacent West Kleinemonde estuary. This in combination with the relative decrease in energy expenditure with increase in body mass can explain the difference in foraging times between feeding guilds.

A heronry was established at the East Kleinemonde estuary in 2005. It was in use during the summer months of the study period. It was situated on the western bank adjacent to the northern side of the main road bridge. Black-headed Heron, Grey Heron and Great Egret successfully bred there during the study. Reed Cormorant, African Darter and Little

Egret also used the heronry for roosting but did not nest there. Breeding birds were often observed returning from the West Kleinemonde estuary and regurgitating food for their young. Many of the roosting birds also flew from the heronry across to the West Kleinemonde estuary in the mornings, returning in the afternoons. Many birds therefore used the East Kleinemonde estuary for breeding and roosting but fed elsewhere. The presence of this heronry possibly confounded some results of this study to some degree, but it also highlights the importance of these systems for non-feeding related activities.

Many studies make inferences from bird abundance to the amount of biomass removed from a system (Cowley 1998, Beamish 2002, Brown 2003, Terörde 2005), but the findings of this study suggest that this approach can overestimate consumption rates. The majority of birds utilised the East Kleinemonde estuary primarily for roosting purposes during the day. Due to the small size of most IOEs, birds move frequently between adjacent systems to feed and roost and it is thus difficult to estimate the amount of biomass removed without including an analysis of time spent at the estuary.

Many waterbirds, especially intertidal-feeding waders, have clear feeding patterns in tidal estuaries (Hockey & Turpie 1999a). However, piscivorous birds do not show a distinctive pattern in foraging activity over the course of the day as they can feed independent of the tides (Whitfield & Blaber 1978, Whitfield & Blaber 1979a, Whitfield & Blaber 1979b, Hockey & Turpie 1999a). In this study the proportion of birds feeding showed a flat pattern over the course of the day, probably due to the absence of a tidal regime and the fact that piscivorous species dominated the community.

CONCLUSIONS

This study has shown that habitat structure plays the most important role in determining bird community composition in intermittently open estuaries. Water levels influence bird abundance by changing habitat availability. It has demonstrated that changes in mouth state influence avian community composition and diversity. Breaching events attract waterbirds and provide feeding opportunities. Intermittently open estuaries are important habitats for waterbirds not only for foraging but also for roosting.

While diversity increased when the mouth of the studied estuaries opened, species composition also changed. An increase in mouth opening events could therefore lead to the distinct intermittently open estuarine avifauna being replaced by communities resembling those of permanently open estuaries.

In order to make informed management decisions about particular IOEs baseline information as provided by this study needs to be gathered for individual estuaries. This study has demonstrated that variation between estuaries is great in terms of bird abundance and responses to changes in environmental variables. Therefore we need information not just on system size, geographic location and mouth condition, but more detailed information on the ichthyofauna, bathymetry, vegetation, habitat diversity and tidal influence of the estuary to predict how prey and habitat availability will change in future scenarios. Since the perched intermittently open estuaries of KwaZulu-Natal differ from warm-temperate estuaries in having extensive reedbeds and oligohaline conditions for much of the year, a comparative study between these two types would be of value.
More comprehensive studies over a wider geographic region are necessary to establish how important intermittently open estuaries are collectively for waterbirds in South Africa and to what degree birds depend on the health and integrity of these systems, both in terms of food and habitat availability. For this it is important to understand movements between these systems and other wetlands to establish their degree of dependence on intermittently open estuaries.

The possibility of using estuarine avifaunal community structure as an indicator for estuarine health should be explored further. This study has shown that there is no typical species composition characteristic of intermittently open estuaries in general, but that each estuary has a distinct avifaunal community influenced by a variety of factors. To enable us to make predictions about the impact of future developments on the health of estuaries, it is necessary to know their natural state and how global and regional changes in the environment affect these systems. Therefore, long term monitoring studies should be conducted that document the changes in diversity, abundance and community structure that arise naturally as well as of a result of anthropogenic influences.

While this study has contributed to the understanding of population dynamics of waterbirds in intermittently open estuaries in a small region of the Eastern Cape of South Africa, much information is still needed to fully understand and protect the estuarine avifauna in South Africa.

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APPENDICES

Appendix I. Sampling days at the Riet (R), East Kleinemonde (E), West Kleinemonde (W) and Bira (B) estuaries November 2005 to December 2006.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Dec 05																		E	R		W	E							W		
Jan 06		R	E													E	W	B		R	B	E		W				E	R	B	
Feb 06		R	E/W	R	W	B			B	R/E			B		W																
Mar 06		E					B	W		E												R		E/W						B	
Apr 06						E	W										E							R/W							
May 06	B	E										W						E								W/B		R/B	R/B	R/B	R/B
Jun 06	R/B	R/B										E/W					R							E			E		W		
Jul 06				R/B								E		W							R							W		E	
Aug 06				E	E/W	R/E/W/B	E/W	E/W	E/W	E/W													E	W		W		W			W
Sep 06					R	E			B	W										E						W					
Oct 06					E/W	B		R											W				E								W
Nov 06						R	E			W/B												E						W			

Appendix II. Habitat sizes and feeding guild abundance in the different regions of the four studies estuaries.

		Mean number of birds					Estimated area covered (m^2)						
Estuary	Region	Pursuit-swimming piscivores	Aerial-diving piscivores	Wading piscivores	Inverte-brate feeding waders	Herbi-vores	Over-hanging trees / rocks	Exposed bank	Reedbeds	Vegetated floodplain	Shallow margins	unvegetated channel	vegetated channel
Riet	1	0.0	2.2	0.4	2.1	0.0	0.0	2000.0	2000.0	16000.0	4000.0	8000.0	8000.0
	2	0.1	1.8	0.7	2.1	0.0	837.5	1256.3	4187.5	25125.0	418.8	5025.0	5025.0
	3	0.0	2.4	0.2	0.8	0.2	1056.0	264.0	528.0	0.0	528.0	1584.0	1320.0
	4	0.0	1.3	0.1	0.4	0.0	1125.0	112.5	0.0	0.0	225.0	675.0	112.5
West Kleinemonde	1	3.4	15.9	0.9	1.8	3.9	0.0	7500.0	0.0	0.0	37500.0	7500.0	22500.0
	2	75.0	13.7	14.7	6.1	23.1	12225.0	40750.0	4075.0	146700.0	40750.0	0.0	163000.0
	3	69.7	19.2	43.7	38.7	89.7	4856.3	19425.0	0.0	339937.5	24281.3	0.0	97125.0
	4	19.8	8.2	2.0	1.0	0.7	8750.0	2187.5	437.5	0.0	2187.5	13125.0	17062.5
East Kleinemonde	1	0.4	1.0	0.4	6.3	0.0	4375.0	21875.0	2625.0	0.0	21875.0	21875.0	14875.0
	2	5.1	3.7	27.0	8.6	1.1	7250.0	8700.0	4350.0	29000.0	55100.0	40600.0	0.0
	3	1.7	3.8	1.6	3.4	0.1	7000.0	8400.0	0.0	0.0	1400.0	53200.0	0.0
	4	0.9	2.9	0.1	0.7	0.0	11250.0	2625.0	0.0	750.0	375.0	22500.0	0.0
Bira	1	0.0	1.8	1.7	7.4	0.2	0.0	12250.0	875.0	3500.0	5250.0	65625.0	0.0
	2	0.0	2.0	0.7	4.4	0.7	1450.0	37700.0	0.0	0.0	23200.0	82650.0	0.0
	3	0.1	1.2	0.1	5.1	0.3	2150.0	32250.0	0.0	0.0	25800.0	154800.0	0.0
	4	0.0	3.1	0.7	4.9	0.9	23400.0	23400.0	0.0	0.0	17550.0	33150.0	0.0

Appendix III

Riet estuary

The estuary was closed to the sea at the beginning of the study on 19 December 2005 (Table 23). According to residents of the area it had been closed for several months. The estuary remained closed until 29 May 2006 when it breached after heavy rainfall. It remained open until the middle of September 2006. During this time water continued to flow out of the estuary into the sea at a very low rate, but water levels remained relatively stable. At times there was only a trickle of water out of the system in a narrow and shallow channel. The tidal influence in this estuary was very low during this period. The estuary remained closed for two full weeks and breached again on 4 October 2006. This breaching caused the mouth to open widely and a deeper channel was formed. The estuary mouth remained open beyond the end of the study period in November 2006. The tidal influence during the second open phase was slightly stronger due to the deeper channel, but the intertidal area was still restricted to a small region around the mouth.

West Kleinemonde estuary

The West Kleinemonde estuary was closed to the sea from the beginning of the study in December 2005 to 4 August 2006 (Table 23) when the mouth breached after a major flood. This was followed by a series of opening, closing and overwashing events, with the estuary staying open for two to five days at a time. On 4 October 2006 it reopened and remained so until 12 November 2006. The estuary then remained closed to the sea for the remainder of the study period.

East Kleinemonde estuary

The estuary was closed to the sea from the beginning of the study in December 2005 to June 2006 (Table 23). During this time five major and 27 minor overwashing events occurred. Water trickled out of the estuary over the sandbar on 3 June, 5 June and 7 June. The estuary mouth breached on 24 June 2006 and remained open for only 3 days. After closure minor overtopping events took place regularly. The mouth breached on 4 August 2006 following a major flood. A deep channel was scoured at the mouth. The estuary mouth closed after 48 days on 20 September 2006 but reopened, after daily overwashing events, on 27 September 2006. It remained open for 5 days, was closed for another 2 days, during which minor overwashing events took place. On 3 October 2006 it opened and remained open for 36 days until 8 November 2006. After 5 days of closure with overwashing events it reopened briefly for three days, closed again for two days, reopened for four days and then remained closed for the remainder of the study. Tidal influence was very strong during the two long open phases, as the major flood in August had scoured a deep channel at the mouth.

Bira estuary

The estuary was closed to the sea from the beginning of the study in December 2005 to 24 May 2006. It remained open to the sea for the remainder of the study period. A deep channel was formed at the mouth and tidal influence was strong in this system.

Table 23. Mouth conditions and sampling dates (grey fields) of the four sampled estuaries (Dec '05 - Nov '06). **O**: open mouth, **t**: small overwashing **T** : large overwashing (P. Cowley, unpublished data). No overwashing data were collected for Riet and Bira estuaries.

Riet estuary

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
D																															
J																															
F																															
M																															
A																															
M																												O	O	O	O
J	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
J	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
A	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
S	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O													
O				O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
N	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	

East Kleinemonde estuary

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
D																t	t														
J																												t			t
F			t	t												t										t	t	t			
M	t	t	t												t		t	t	t	t	t	t	t	t	t	t	t	t			
A																		t							t						
M																							t				t	t	t		
J			t		t		O			t	t	t	t	t									t	t	O	O	t	t	t	t	
J	t	t	t	t	t	t	t	t	t	t	t	t		t	t				t				t	t	t	t	t			t	t
A	t	t	t	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
S	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	t	t	T	t	t	t	O	O	O	O	
O	O	t	t	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
N	O	O	O	O	O	O	O	O	T	t	t	t	t	O	O	O	T	T	O	O	O	O	t					O	O	t	

West Kleinemonde estuary

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
D																															
J																t															
F																												t			
M			t																												
A																		t													
M																												T			
J																															
J																															
A				O	O	O	O	O	T	T	t	t	t									t	O	O	O	O	O	O	O	t	T
S	O	O	t	T	O	O	t	t	O	O	O	t	t	O	O	O	t	t	t	t	T	t	t	t	t	t	t				
O				O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
N	O	O	O	O	O	O	O	O	O	O	O	O	t	O	O	t	t	t	t	t	T	t	t							t	

Bira estuary

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
D																															
J																															
F																												t			
M	t	t	t																												
A																															
M																								O	O	O	O	O	O	O	O
J	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
J	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
A	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
S	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
N	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	

Appendix IV. Common and scientific names of birds recorded at the Riet, West Kleinemonde, East Kleinemonde and Bira estuaries during the study period (according to Birdlife International 2009).

Common name	Species name
African Darter	*Anhinga rufa*
African Fish Eagle	*Haliaeetus vocifer*
African Oystercatcher	*Haematopus moquini*
African Spoonbill	*Platalea alba*
Black Stork	*Ciconia nigra*
Blacksmith Lapwing	*Vanellus armatus*
Black-winged Stilt	*Himantopus himantopus*
Cape Cormorant	*Phalacrocorax capensis*
Cape Shoveler	*Anas smithii*
Cape Teal	*Anas capensis*
Caspian Tern	*Sterna caspia*
Common Greenshank	*Tringa nebularia*
Common Moorhen	*Gallinula chloropus*
Common Ringed Plover	*Charadrius hiaticula*
Common Sandpiper	*Actitis hypoleucos*
Common Tern	*Sterna hirundo*
Curlew Sandpiper	*Calidris ferruginea*
Egyptian Goose	*Alopochen aegyptiaca*
Giant Kingfisher	*Megaceryle maxima*
Goliath Heron	*Ardea goliath*
Great Egret	*Casmerodius albus*
Great Crested Tern	*Sterna bergii*
Greater Painted-snipe	*Rostratula benghalensis*
Green-backed Heron	*Butorides striata*
Grey Heron	*Ardea cinerea*
Grey Plover	*Pluvialis squatarola*
Grey-headed Gull	*Larus cirrocephalus*
Half-collared Kingfisher	*Alcedo semitorquata*
Hamerkop	*Scopus umbretta*
Kelp Gull	*Larus dominicanus*
Kittlitz Plover	*Charadrius pecuarius*
Little Egret	*Egretta garzetta*
Little Grebe	*Tachybaptus ruficollis*
Little Stint	*Calidris minuta*
Little Tern	*Sterna albifrons*
Malachite Kingfisher	*Alcedo cristata*
Marsh Sandpiper	*Tringa stagnatilis*
Osprey	*Pandion haliaetus*

Appendix IV (cont.). Common and scientific names of birds recorded at the Riet, West Kleinemonde, East Kleinemonde and Bira estuaries during the study period (according to Birdlife International 2009).

Common name	Species name
Pied Kingfisher	*Ceryle rudis*
Purple Heron	*Ardea purpurea*
Red-billed Duck	*Anas erythrorhyncha*
Red-knobbed Coot	*Fulica cristata*
Reed Cormorant	*Phalacrocorax africanus*
Ruddy Turnstone	*Arenaria interpres*
Ruff	*Philomachus pugnax*
African Sacred Ibis	*Threskiornis aethiopicus*
Sanderling	*Calidris alba*
Sandwich Tern	*Sterna sandvicensis*
South African Shelduck	*Tadorna cana*
Spur-winged Goose	*Plectropterus gambensis*
Three-banded Plover	*Charadrius tricollaris*
Water Thick-knee	*Burhinus vermiculatus*
Whimbrel	*Numenius phaeopus*
White-breasted Cormorant	*Phalacrocorax carbo*
White-fronted Plover	*Charadrius marginatus*
Wood Sandpiper	*Tringa glareola*
Yellow-billed Duck	*Anas undulata*