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

Edited by

Alan Whitfield[1] & Guy Bate[2]

[1]South African Institute for Aquatic Biodiversity
[2]Nelson Mandela Metropolitan University and
University of KwaZulu-Natal

Interim report to the Water Research Commission on the Project
"The freshwater requirements of intermittently open Cape estuaries"

WRC Report No 1581/1/07
ISBN 978-1-77005-518-6
Set No 978-1-77005-517-9

February 2007

DISCLAIMER

EXECUTIVE SUMMARY

Along the Eastern Cape coast there are more than 80 temporarily open/closed estuaries (TOCEs) that fall within the warm temperate biogeographical region and 5 in the cool temperate region of the Western Cape. TOCEs are predominantly regulated by the amount of river inflow received, the magnitude of which is governed primarily by catchment size and the regional climate that dictates rainfall patterns.

There is very little published information on the hydrodynamics of TOCEs, hence the approach followed has been to focus on the forces that govern hydrodynamic processes and mouth conditions in estuaries and develop a conceptual model of possible mouth states that can play a role in the control of mouth state. This overview focuses on the similarities and differences between the structure and functioning of TOCEs and permanently open estuaries (POEs) in these regions and the similarities and differences between Cape and KwaZulu-Natal systems. It also aims to inform the Resource Directed Measures (ecological water requirement) process of DWAF, emphasising the importance that needs to be placed on the consequences of reduced river flow/increased closed mouth phases on Cape TOCEs.

Variations in climate, topography and catchment geology give rise to a wide variety of estuarine types, but from a hydrodynamic perspective, all estuaries in South Africa fall into one of two main categories, namely POEs or TOCEs. POEs normally have large catchments and a relatively high runoff throughout the year. Their estuary volume is normally large enough for tidal flow to play a significant role in maintaining open mouth conditions. An examination of the data for all South African estuaries indicates a good relationship between mean annual run-off (MAR) and whether an estuary is a POE or a TOCE, and that a model for indicating this difference is a function of estuary water area x MAR x effective tidal amplitude.

TOCEs are isolated by the formation of a sand berm across the estuary mouth during periods of low or no river inflow. They stay closed until their basins fill up and the berm is breached. Mouth breaching results in the removal of significant amounts of sediment, but infilling by sediment commences once tidal conditions are established. Hence the major forces that maintain open mouth conditions are river and tidal flow and the major closing forces are marine wave energy and sediment availability.

In small and medium size estuaries (<150 ha) tidal flow can maintain open mouth conditions during spring tides but often closure occurs during neap tides. Thus, during periods of low river flow in small to medium sized estuaries, the tidal prism is insufficient to maintain an open mouth. The semi-closed mouth state normally only occurs in small estuaries (<100 ha) with a very limited marine sand supply.

Factors prolonging an open mouth include features that dissipate wave energy and turbulence, which reduce the ability of waves to carry sediment into the mouth. Factors that contribute to

mouth closure include structures or conditions that inhibit river or tidal flow. Strong tidal outflow and the protection of the mouth from wave action by a rocky promontory, if present, play a major roll in maintaining open mouth conditions. Structures that inhibit tidal exchange (e.g. a rocky sill) reduce the scouring ability of the tides and can shorten the time that the mouth remains open. Each estuary is unique because of the various factors that influence its structure and sensitivity to flow, and two similar sized estuaries adjacent to one another can be quite different. At any one time, the mouth of an estuary is either open or closed. However, when closed, some marine 'overwash' may occur during high wave or storm events. There may also be a semi-closed state with only a shallow 'trickle' of water flowing out to sea. This is termed 'overtopping'.

Very little reliable information is available on the hydrodynamics of TOCEs. Even less is known about systems that stay closed for prolonged periods. Hence, to develop an in-depth understanding of the long-term cycles and hydrodynamic processes within TOCEs, data urgently need to be collected on the mouth status of South Africa's smaller estuaries. Most of the studies evaluated in this report indicated that long-term information on estuary mouth status is very limited and that runoff data from small river catchments are of very low confidence. There is therefore an urgent need to improve the quality of the runoff data provided to estuarine scientists.

Two different mechanisms have been proposed for the inlet closure (by sediment) of small estuaries on micro-tidal, wave-dominated coasts with strong seasonal variations in river discharge. The first is the interaction between inlet currents and longshore sediment transport, while the second is the interaction between inlet currents and onshore sediment transport. Both sediment transport mechanisms are likely to be applicable to South African TOCEs. Mouth closure often occurs during sea storms when high sediment loads are entrained by turbulent storm wave action and carried into the estuary and mouth area where it is deposited in the lower energy environment. When this deposition rate exceeds the erosion potential of tidal flow, a net sediment build-up occurs. If this situation continues for long enough, the mouth closes.

Within the coastal zone, there are a number of processes that can transport varying amounts of marine sediments to estuary mouths. Marine sediments that have been transported close to the mouth by such processes are potentially available to be transported into the estuary itself, mainly by means of tidal flow through the mouth but sometimes in conjunction with wave action. There are also a few processes that can transport marine sediment directly into the estuary. Actual net (usually north-easterly) longshore sediment transport of about 400 000 m^3 to 1 200 000 m^3 per annum (on average) is estimated along most of the exposed, open South African coast, while the potential transport (due to wave energy) is sometimes even higher. Along rocky shorelines, or sheltered areas, the net average longshore transport rate is mostly between about 10 000 m^3 and 400 000 m^3 per annum. Extreme cross-shore transport rates are estimated to be as high as 150 000 m^3 over short periods during very large sea storms and a shoreline length of 500 m.

River floods are the most important natural means of eroding and transporting sediments out of estuaries. Large volumes of sediments can be removed in a very short time during major floods with a return period of 1 in 50 years and more. Smaller floods with return periods of 1-2 years can sometimes also have a significant influence, particularly in the estuary mouth region. Floods therefore play a major role in the equilibrium between sedimentation and erosion in estuaries

Depending on factors such as estuary size, beach profile and mouth protection, three different estuary states can occur. These are (a) where the mouth is open to the sea allowing seawater intrusion during flood tides, with river inflow continuing to introduce freshwater into the system under all tidal regimes; (b) where the mouth is semi-closed and the berm prevents seawater intrusion except during high tides; and (c) where the mouth is closed and the height of the berm prevents seawater from entering the system, as well as estuary water draining into the sea. Low volumes of river water could still be entering the estuary and sporadic overwash of seawater can occur, depending on wave conditions at sea and the berm height.

When the mouth of a TOCE is open, a longitudinal salinity gradient normally exists and the position of the haloclines depends on the tidal regime and extent of river inflow. In some systems vertical stratification can also develop, usually in systems where the middle and upper reaches are characterised by deep water (> 3 m). The semi-closed state is typical during periods of low rather than high fresh water input when the mouth will be fully open. If inflowing fresh water is restricted to the surface of the estuary, then more saline water will be 'trapped' in deep areas, thus leading to strong vertical salinity stratification. Entrainment of freshwater into deeper layers and wind mixing causes the water column to gradually change into a homogenous brackish water body. During the closed mouth state, salinity levels throughout the water column are usually similar, although some vertical and longitudinal stratification may be evident immediately after closure.

A decrease in dissolved oxygen is mainly caused by decomposing organic material, which has a high biological oxygen demand. Low dissolved oxygen levels can cause organisms to become stressed or die, with oxygen concentrations less than 3 mg l^{-1} regarded as hypoxic. During the open state, TOCEs normally have > 6 mg l^{-1} oxygen but during the semi-closed state, stratified bottom water may have a concentration of < 3 mg l^{-1}. During the closed state, the water column is expected to become relatively homogenous with no marked vertical stratification. During marine overwash, low oxygen bottom water in closed estuaries can be replaced with fresh well-oxygenated seawater.

The main sources of N and P come from river inflow, seawater intrusion, and remineralisation. Groundwater seepage can also supply variable amounts of inorganic nutrients depending on the catchment characteristics and human activities such as agriculture and pollution. During the open state, the dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) concentrations in the estuary are largely a function of nutrient concentrations from the inflowing river and seawater. Because the measurable level of inorganic nutrients in estuaries is the net result of inputs and transformations, there may not be a direct relationship between the ambient concentration of these variables and the biological response. However, there is more commonly a relationship between flux and biological response, often over very short time scales.

Microalgae form the base of primary production of most estuaries and under open mouth conditions the behaviour of TOCEs may be similar to that of POEs because a channel is maintained due to the high volume of water flowing through the system. After the mouth breaches there is a major outflow of estuarine water to sea, resulting in a rapid drop in the water level. This reduction in water level exposes sand banks that had previously been covered by water for long periods (weeks to years). Exposure of previously inundated sediments has a profound impact on the available microphytobenthic habitat within a TOCE. The reduction in water level also causes a decrease in the volume of water occupied by phytoplankton and limits the potential area for microalgal colonisation as well as overall primary production. The effects of river flow on microalgae include nutrient input, which is particularly effective under low flow conditions when residence time of the water column is increased. Primary production during an overwash period in the Kasouga Estuary was evenly distributed throughout the estuary, ranging between 19 and 26 mg C m^{-2} d^{-1}, and was higher than during the closed phase. Water column productivity during a closed phase ranged between 10 and 19 mg C m^{-2} h^{-1}. Maximum phytoplankton production was recorded during the high river inflow phase when values were 40-65 mg C m^{-2} h^{-1}. Benthic primary production recorded for the oligotrophic Bot Estuary (58 g m^{-2} y^{-1}) was calculated to be below the average of 67-200 g m^{-2} y^{-1} for global estuarine environments. The phytoplankton biomass in TOCEs is generally orders of magnitude lower than that of the microphytobenthic biomass.

Salinity changes are a primary determinant of macrophyte species composition. TOCEs are often dominated by reeds, sedges and submerged macrophytes that favour low salinity, low turbidity, low current levels, more stable sediment and a large nutrient pool. Macrophyte vegetation in POEs is represented by reeds and sedges, salt marsh plants and, in systems along the KwaZulu-Natal east coast, mangrove and swamp forest. A reduction in freshwater supply can increase the frequency and duration of mouth closure that results in increased water levels. Changes in water level and salinity are the major factors causing changes in macrophyte communities. TOCEs are characterized by lower species richness than POEs and the impacts of freshwater abstraction are often greatest in the smaller IOEs. The Klipdrif (Oos) and Slang estuaries in the Eastern Cape Province have changed from intermittently open to almost permanently closed. Little water surface area remains in these systems due to freshwater abstraction, dune encroachment and excessive reed growth. In small systems, floods are important in re-setting the estuary and removing macrophytes from the main channel.

Studies in both KwaZulu-Natal and the Eastern Cape indicate that mouth status plays and important role in structuring zooplankton assemblages. In the absence of any link to the marine environment, estuarine zooplankton diversity is generally low, thus reflecting the reduced contribution of marine and freshwater species to the total zooplankton population. The establishment of a link to the marine environment through overtopping or breaching coincides with an increase in zooplankton diversity, which can be linked to recruitment into the estuary of marine species. The maximum abundance and biomass of zooplankton within TOCEs is attained during the closed phase and appears to be sustained by the extensive microphytobenthic stocks that occur within these systems.

The number of ichthyoplankton species occurring in TOCEs is considerably lower than those in POEs. TOCEs are generally characterized by low larval fish diversity and richness and this is because access by marine species is restricted during periods of closure. The larvae found in Cape TOCEs belong mainly to estuary resident species, especially *Gilchristella aestuaria* and *Glossogobius callidus*, both of which breed within these systems.

The hyperbenthos within Southern African estuaries typically comprises swimming prawns, crabs and shrimps. The numerical importance of the each of these groups exhibits a high degree of spatial and temporal variability. The penaeid prawn fauna in the coastal and estuarine waters of Southern Africa is numerically dominated by five species. These five species are most common in the permanently open subtropical estuaries of KwaZulu-Natal and decline in both numbers and diversity in the warm-temperate waters of the Eastern Cape. Studies indicate that the postlarvae congregate in the near-shore region where they are washed into permanently open estuaries by flood tidal currents, mainly during the night. Peak recruitment of the postlarvae into estuaries takes place during spring and summer. The distribution of the various penaeid prawn species in estuaries appears to be influenced by salinity and to a lesser extent by water temperature and macrophyte distribution. Postlarvae of certain shrimp and prawn species have recruited into TOCEs along the Eastern Cape coastline during overtopping events. Most recruitment of postlarvae has been observed during the estuary open phase, thus demonstrating the importance of breaching to the hyperbenthos of TOCEs.

Freshwater prawns of the genus *Macrobrachium* have been identified, mainly within the subtropical zone of KwaZulu-Natal but with some species extending as far south as the Eastern Cape. Studies suggest that the distribution of most *Macrobrachium* species is strongly correlated to salinity, with maximum abundances near the mouth of streams and points of freshwater inflow into estuaries. Available information suggests an estuarine larval phase for certain species but an absence of any marine phase. Freshwater prawns appear to employ behavioural adaptations to reduce loss of larvae to the marine environment. These data illustrate the importance of freshwater baseflow to ensuring the river-estuary link for the life cycle of these taxa.

The swimming crab, *Scylla serrata*, occurs throughout the subtropical zone of KwaZulu-Natal and extends as far south as the Knysna Estuary within the warm temperate southern Cape. Female *S. serrata* typically spawn at sea with the recruitment of megalopa larvae into estuaries occurring mainly during spring and summer, thus illustrating that the timing of open mouth conditions is important if TOCEs are to act as a habitat for this species. Sexually mature females of *S. serrata* have been known to utilise overwash events to undertake spawning migrations out of temporarily closed estuaries. Studies have further demonstrated that breaching or flood events coincided with a considerable decline in number of mature crabs within estuaries, which could be attributed to the emigration of reproductively active individuals or their intolerance of freshwater conditions associated with river flooding.

Palaemon peringueyi, an estuarine shrimp, is more abundant in permanently open estuaries than in nearby TOCEs. The much lower abundance in TOCEs has been attributed to reduced recruitment opportunities due to the presence of a sand bar across the mouth. Where there is limited habitat availability, in the form of submerged macrophyte beds, populations are further depressed. This shrimp commonly inhabits macrophyte beds where epiphytic diatoms are numerous and supply a large portion of their diet.

The zoobenthos of soft sediments is classified as that group of animals spending most or all of their time buried in sediments. Within the benthos, macrobenthic and meiobenthic organisms are distinguishable. Salinity and substratum type are the major determinants of the benthic community structure in TOCEs, but their relative importance changes between the mouth and upper estuary. It is also important to note that other factors affect community composition and the presence of some species could not be linked to salinity or sediment type. Periods of mouth closure in TOCEs prevent recruitment to estuarine populations of those species that have obligate marine phases of development. Examples of infaunal invertebrates in this category include the mud prawn *Upogebia africana* and numerous species of estuarine crabs. Estuarine mouth closure will also disrupt migration of river crab megalopa belonging to *Varuna litterata. V. litterata* spends most of its life cycle in freshwater but returns to the sea in order to breed. Large numbers of megalopae have been observed passing through estuaries from the sea into rivers.

The prawns *Callianassa kraussi* and *Upogebia africana* are particularly abundant in intertidal sediments of warm and cool temperate estuaries, with each species inhabiting a preferred sediment type. *C. kraussi* generally occurs in sand and *U. africana* in more muddy sediments. Adults of both species have a wide salinity tolerance range but because experimental work on the tolerance levels of estuarine animals has mostly been done on adults, it cannot be assumed that larval stages or juveniles will have equivalent tolerance levels. Adult *C. kraussi* are able to tolerate salinity values as low as 1 PSU, but successful development of eggs and larval stages requires salinity values > 20 PSU. Populations living in areas where salinity values are permanently below 17 PSU are not self-maintaining and must be recruited from elsewhere.

Annual migrations of postlarvae into TOCEs indicate that these life stages act as the dispersal phase for this species, allowing it to spread into areas where it is otherwise unable to breed successfully. Mud prawn larvae require a marine phase of development and are often absent from intermittently open estuaries (IOEs) that are, on average, closed for more than 50% of the time. This observation illustrates the importance of the open mouth phase for these and other zoobenthic species with marine larval phases.

Most fish species found in TOCEs are juveniles of estuary-associated marine taxa, indicating that these systems function as important nursery areas for this group of species. Although TOCEs have been found to have lower ichthyofaunal diversity than POEs, they often have larger populations of estuarine resident species. In addition, certain endemic freshwater taxa and estuarine species are found mainly in TOCEs. Mouth state, particularly the frequency, timing and duration of mouth opening plays a pivotal role in determining species richness, composition, diversity and abundance. Mouth opening, is directly linked to freshwater input, and as such TOCEs in the semi-arid parts of the Eastern, Western and Northern Cape are adversely affected by a reduction in freshwater input. Hypersaline conditions, which can lead to fish kills, are more commonly recorded in TOCEs in the Cape region than in the oligohaline, perched estuaries of KwaZulu-Natal.

The estuaries along the coast of South Africa, and their associated fish assemblages, are not uniformly distributed, but can be grouped according to biological, physical and geographical criteria. Hence, the coast of South Africa has three distinct biogeographic regions, viz. subtropical, warm-temperate and cool-temperate zones. Few fish species occur in all Southern African estuaries and many taxa are confined to specific biogeographic areas, with eographic affinity having a strong influence on the grouping of estuaries. Forty-three species from 20 families were recorded in TOCEs in the warm-temperate region, with an average of 15.5 species recorded per estuary. The dependence of fish species on estuaries in this region ranges from complete to opportunistic. The diversity of fishes in cool-temperate estuaries is low (4.5 species per estuary) when compared with warm-temperate and subtropical systems.

The fish composition in the lower reaches of some estuaries is different from that in the middle and upper reaches. This difference has been attributed sometimes to the distribution of macrophyte beds that are absent from the mouth region where sediment movement is considerable. Mouth condition is regarded as a major determinant of species richness in TOCEs, with higher numbers of marine species being captured in estuaries that open more frequently. In the warm temperate region, results indicate a strong positive correlation between estuary size and species richness. The smaller TOCEs have a much lower species richness and density than larger ones and POEs. The absence, or low numbers, of certain estuary-dependent marine species accounted for these differences. Smaller TOCEs probably have less marine interaction (shorter open mouth phases) and offer less habitat diversity. Large TOCEs have higher nutrient input, positive salinity gradients and higher turbidity than smaller systems and, more importantly, are open for longer periods. Prolonged closed phases in small estuaries result in a low recruitment potential for juvenile marine fish and effectively prevent the emigration of adults back to sea.

Although estuaries only make up 0.56% of the area of South Africa, they form a significant component of the aquatic and coastal habitat in the region. They are an important habitat for birds with almost a fifth of the species and half the orders of birds in South Africa being found in estuaries. This high diversity can be attributed to the high variety of habitats that are represented within estuarine ecosystems. Birds often aggregate in high densities in estuaries and tend to constitute a significant portion of the biomass of estuarine organisms. They are therefore believed to play an important ecological role within estuaries, both as consumers or predators and in terms of nutrient cycling.

An understanding of the marine-estuary interface in South Africa is very limited with respect to data, and important questions remain unanswered on how estuary water, which is released when the mouth opens, influences productivity in the nearshore environment. In the context of TOCEs, data are needed regarding the effect on the nearshore environment of the combined opening of several TOCEs in a given region after extended periods of closure. Existing studies have indicated that large fish and invertebrate populations leave TOCEs when they open. This indicates a large contribution, at least by these taxa, to the biomass and productivity of the marine environment.

Estuary managers must have a good understanding of the manner in which both the physical and biological components interact to provide the conditions supporting the biological components. The Water Act (36) of 1998, inter alia, requires that sufficient water of suitable quality be delivered to estuaries to ensure that they retain a minimum ecological status or class. The Act does not permit an estuary classified in the two lowest classes to remain in either of those classes; they have to be upgraded if possible. Estuary management, which is complex by virtue of the interaction of physical, chemical and biological aspects, becomes more complex due to the difficulties inherent in management being split between different authorities. Possibly the most significant management intervention is the artificial breaching of the mouth, mainly due to poorly planned developments on the estuary floodplain. Breaching of a TOCE is usually triggered when increasing water levels result in the flooding of structures erected on low lying land or too close to the water’s edge.

Residential and industrial developments also have the effect of both lowering natural water flow into estuaries and increasing flood intensity; the former as a result of water abstraction for human, agricultural and industrial use and the latter as a result of run-off from roofs and impermeable areas such as roads and concrete aprons. All these structures should be carefully considered in any local industrial development programme. Sound estuary management is synonymous with sound environmental management. Hence, sound estuary management should always commence with an environmental impact assessment (EIA) that informs the development process.

ACKNOWLEDGEMENTS

The provision of funds by the Water Research Commission for this project is gratefully acknowledged. We also thank the discipline leaders and students from the various institutions for their participation in this study.

ACRONYMS AND ABBREVIATIONS

CSIR	Council for Scientific and Industrial Research
DEE	Daily energy expenditure
DFI	Daily food intake
DIN	Dissolved inorganic nitrogen
DIP	Dissolved inorganic phosphate
DLW	Doubly labelled water
DWAF	Department of Water Affairs and Forestry
ICE	Intermittently closed estuary
IOE	Intermittently open estuary
KZN	KwaZulu-Natal
MAR	Mean annual run-off
MSL	Mean sea level
NTU	Nephelometric turbidity units
POC	Particulate organic carbon
POE	Permanently open estuary
PON	Particulate organic nitrogen
PSU	Practical salinity unit (parts per thousand; $g.l^{-1}$)
RDM	Resource Directed Measures programme of DWAF
SD	Standard deviation
TOCE	Temporarily open/closed estuary
WRC	Water Research Commission

TABLE OF CONTENTS

INTRODUCTION

Alan Whitfield[1] and Guy Bate[2]

[1]South African Institute for Aquatic Biodiversity; [2] Nelson Mandela Metropolitan University, [2]University of KwaZulu Natal

What is an Intermittently Open Estuary and how does it differ from a Temporarily Open/Closed Estuary (TOCE)? Until recently, all South African systems that closed off from the sea due to regular or irregular sand bar development at the mouth were referred to as TOCEs. Although this 'umbrella' description is perfectly adequate for these systems, a further refinement in the existing categorization is necessary to distinguish between those TOCEs that are more closed than open and those that are more open than closed. This has led to a differentiation between intermittently closed estuaries (ICEs) which, on average, have a channel linking the lower reaches to the sea for more than 50% of the time and Intermittently Open Estuaries (IOEs) which, on average, have no link with the sea for more than 50% of the time.

For many TOCEs it is not possible, due to lack of data, to distinguish whether they are IOEs or ICEs and the broader category of TOCEs should therefore be used when assessing these systems. However, for those estuaries where sufficient mouth phase data have been collected to refine their classification, we would encourage scientists to be more definitive on the predominant mouth state. Preliminary indications are that most South African TOCEs are actually IOEs but the average percentage open time for most of these systems is unknown. There are also indications that some previously permanently open estuaries (POEs) are showing increasing signs of becoming ICEs due to increased freshwater abstraction from their catchments. This leads to a dilemma in terms of classifying these estuaries – should one use the natural or current artificial state as the classification benchmark?

Biological evidence suggests that those TOCEs that are closed for prolonged periods differ in their biological community structure from those that are closed for very short periods. Since closure time is often related to the magnitude of catchment run-off, and larger systems tend to have larger estuaries, the apparent separation of IOEs and ICEs may have more to do with estuary size than the duration of the open or closed phase. At present, the default differentiation is set at whether a system is, on average, mostly closed or mostly open. Future research, such as that being carried out in the current WRC study, will no doubt allow us to refine biological and ecological changes under different mouth opening and closing regimes.

One of the aims of this research is to understand the consequences of extended mouth closure (years) on the structure and functioning of these systems. Also, does the timing (seasonality) of a mouth opening event have a major impact on the biota, e.g. is a spring opening more important than an autumn opening for invertebrate and fish migrations? In the final analysis a documentation of detailed biotic and abiotic responses to changing mouth conditions is essential if the impacts of human developments on catchment run-off and other developments are to be properly assessed.

Estuary mouth state is determined by the balance between scouring forces (primarily catchment run-off and tidal prism) and blocking forces (primarily onshore and longshore deposition of sediments). All estuaries have a natural tendency to close as a result of net sediment accumulation on higher velocity flood tides when compared to lower velocity ebb tides. Onshore sand transport is facilitated by the suspension of coastal sediments into surf-zone waves, which then enter the estuary during the flood tide. The calmer waters inside the estuary, especially when flow velocity declines with the onset of high tide, allow for sediment deposition before the ebb tide commences. Although a portion of this sand is re-suspended by the ebb tidal flow, with some sediment being returned to the sea, there is usually a net gain of sand into the estuary during most tidal cycles. The gradual accumulation of sediment in an estuary, especially in the mouth region and lower reaches, can only be reversed by episodic floods that 'reset' the system. Thus, if it were not for intermittent peak flows provided by the upstream river, all bar-built estuaries would eventually close if the time between flood events became too great.

A primary goal of this review is to provide an overview of our current understanding of the structure and functioning of TOCEs in the warm- and cool-temperate biogeographic zones of the Eastern, Western and Northern Cape provinces of South Africa. The review highlights the similarities and differences between TOCEs and POEs in these regions, as well as the similarities and differences between Cape and KwaZulu-Natal TOCEs. Fortunately the participants in this review have been able to draw on a recent Water Research Commission Report (No. 1247/2/04) that provided an overview of past physical, chemical and biological studies in KwaZulu-Natal TOCEs. In addition, the KwaZulu-Natal WRC study undertook a detailed research programme on the Mhlanga and Mdloti estuaries, thus providing new scientific information towards an understanding of the dynamics of these highly threatened ecosystems. A similar focused approach will be implemented during the current Cape TOCE Project, with the East Kleinemonde Estuary being designated as the primary study site.

Past research efforts in South African estuaries have shown that no two systems are the same and that each estuary has to be managed as an entity in its own right. Although much of the knowledge is estuary specific, there are also general principles that have emerged in our understanding of these systems, some of which can be transferred to managers of estuaries that have not yet been studied. In this context, much historic research effort has focused on the larger POEs and there is consequently a greater lack of specific and general information on TOCEs that prevents managers from obtaining a better understanding of these systems. The Cape TOCE study aims to improve this balance by bringing together leading estuarine experts to focus on smaller systems in the Eastern, Western and Northern Cape provinces. The study also intends to inform the Resource Directed Measures (RDM) process of the

South African Department of Water Affairs and Forestry by emphasising the consequences of reduced river flow and of increased closed mouth phases on Cape TOCEs.

An examination of Table 13.1 reveals that the overwhelming majority of South Africa's estuaries are TOCEs. This dominance is the result of these numerous systems having relatively small catchments (mostly < 500 km^2), seasonal rainfall patterns (often punctuated by prolonged droughts), limited tidal prisms when open (mostly < 1 x 10^6 m^3) and a high energy surf-zone (especially along the east and south-eastern coasts) that can move large amounts of sediment into and across estuary mouths. Added to these natural conditions which promote estuary mouth closure are the legitimate demands of farmers and other users to provide fresh water for agricultural, industrial and urban use. This additional freshwater abstraction from catchment streams and rivers means that some of the natural flow that would normally assist ebb tidal flow to keep estuary mouths open is reduced, with the result that normal open periods are of shorter duration and closed phases are more protracted.

Part of the assumption on the effect of a lowered run-off is that if there is to be a reduction in the MAR as a result of human interventions, that the natural periodicity of open/closed conditions will alter and that in most cases the change will be a reduction in MAR reaching the estuary. The Water Act (No. 36 of 1998) requires that the effect of reduced flow has to be assessed with respect to the effect on the natural functioning of these systems. The effect of modifications to water flow has to be assessed by a process known as the Resource Directed Measures (RDM = measures directed at maintaining the aquatic resource), a method which places particular emphasis on establishing the Environmental Reserve (a minimum input of water quantity and quality which ensures the continued ecological functioning of aquatic ecosystems). Usually the Environmental Reserve for a particular system is established separately for the river and estuary using different approaches. In both cases scientists are asked to extrapolate from existing data back in time to the Reference (natural) State, as well as forward to possible future states that usually encompass additional freshwater abstraction scenarios.

Much of the urgency for the information expected from this WRC research programme relates to the anticipated reduction in water flow to estuaries as a result of increasing human use from smaller rivers due to rapid expansion of coastal holiday resorts and towns. In addition, many of the larger perennial river systems are already being fully exploited and in some cases overexploited, thus leading to assessments of possible supplementary freshwater supplies from nearby catchments. Interbasin transfer of fresh water is already a reality in South Africa and is likely to increase in future as human demands on particular systems continue to grow. In addition, climate change is a strong probability in the coming decades and a good understanding of estuarine functioning, especially the small vulnerable systems along our coast, is also required in order to be able to manage TOCEs in the face of changing environmental pressures.

This report comprises a number of sections, some of which are normally disciplines covered in the DWAF RDM proceedings. The literature review has been undertaken with the specific purpose of informing the researchers involved in WRC Project K5/1581 of the most up-to-date information available on TOCEs, derived mainly from research within South Africa, so that existing knowledge is consolidated and does not have to be 'rediscovered'. Since this review is also designed to inform the DWAF RDM process, emphasis has been placed on the consequences of reduced river flow and increased mouth closure on Cape TOCEs. In this context a primary objective of the WRC project will be the collection of data that can subsequently be incorporated into a modelling component that can take our understanding of the functioning of TOCEs and their responses to changing freshwater supplies to a new level, which will be of benefit to management and therefore the long-term environmental health of these systems.

1. HYDRODYNAMICS

Lara van Niekerk

Council for Scientific and Industrial Research, Stellenbosch

INTRODUCTION

This section provides an overview of the hydrodynamics of temporarily open/closed estuaries (TOCEs) in the warm- and cool-temperate biogeographic regions of the Eastern and Western Cape provinces of South Africa. The review focuses on the similarities and differences between the structure and functioning of TOCEs and permanently open estuaries (POEs) in these regions, as well as the similarities and differences between Cape and KwaZulu Natal (KZN) TOCEs based on the WRC report on the KZN temporarily open/closed estuaries (WRC Report 1247/2/04). The review also aims to inform the Resource Directed Measures (RDM) process of the South African Department of Water Affairs and Forestry, emphasising the importance that needs to be placed on the consequences of reduced river flow/increased closed mouth phases on Cape TOCEs.

Due to the paucity of published information on TOCE hydrodynamics the approach has been to provide a focus on the hydrodynamics of estuaries in general. More specifically the approach followed has been to conduct a general review of the forces and processes that govern hydrodynamic processes and mouth conditions in estuaries and develop a conceptual model of the possible mouth states and the driving forces that can play a role in the hydrodynamic control of mouth state in TOCEs.

This review focuses primarily on the following parameters:
Catchment size and river inflow
Mouth status
Salinity
Estuary size and tidal flows
Estuary bathymetry
Water column stratification
Duration of mouth states
Tidal variation and amplitude
Retention/residence time
Ebb- and flood tidal flow channels

Based on available literature and this review, an attempt is made to create a hypothetical TOCE model with which to illustrate and describe important processes that characterize these systems.

HYDRODYNAMIC CLASSIFICATION OF ESTUARIES

The total estuarine area in South Africa is about 600 km^2, of which about 200 km^2 is found along the 2400 km Cape coastline (Turpie et al. 2002). Variations in climate, topography and catchment geology give rise to a wide variety of estuarine types, but from a hydrodynamic perspective all estuaries in South Africa's fall in one of two main categories, namely permanently open estuaries or temporarily open estuaries. TOCEs, estuarine bays, estuarine lakes and estuarine river mouths are all sub-classes of these two types from a hydrodynamic perspective.

Permanently Open Estuaries (POEs)

Only about 25% of South Africa's 250 estuaries are permanently connected to the sea (Whitfield 1998). This category comprises permanently open estuaries, estuarine bays and some river mouths. These POEs normally have large catchments and relatively high runoff throughout the year. The area covered by these estuaries is normally large enough for tidal flow to play a significant role in maintaining open mouth conditions, or if the mouths are protected from high wave energy in the mouth region or little sediment is available for mouth closure. Examples of POEs are the Olifants, Breede and Gamtoos estuaries.

Temporarily Open Closed Estuaries (TOCEs)

About 75% of South Africa's estuaries are temporarily open to the marine environment. These include estuarine lakes and some river mouths (Whitfield 1998). These types of estuaries are isolated from the sea by the formation of a sand berm across the mouth during periods of low river inflow or when river inflow has stopped altogether. Such estuaries stay closed until their basins fill up and the berm is breached, either as a result of high water level or following increased river flow. Mouth breaching may result in the removal of significant amounts of sediment. However, infilling from marine and fluvial sediment following flow reduction can be rapid. Examples of TOCEs include the Groot Brak, Wes Kleinemonde and Mhlanga.

DRIVING FORCES

South Africa's estuaries are sensitive to a reduction in river runoff. The reason is that they generally discharge into a coastline with comparatively high energy and a relatively low runoff that produces rather limited opening forces. Hence the major forces that maintain open mouth conditions are river inflow and tidal flow (van Niekerk 2005, Huizinga and van Niekerk 2005), while the major closing forces are wave energy, of which sand grain size, beach slope, berm height and width of the breaker zone are co-factors that determine the effect of wave energy at the mouth area and marine and fluvial sediment availability.

Factors that assist in prolonging open mouth conditions in medium to small estuaries include: the degree of mouth protection (e.g. rocky headland or reefs in the surf-zone) and sub-tidal mouth protection below the water surface, e.g. rocky shelf running below the surface in the sea (van Niekerk 2005). Mouth protection or submerged rocky shelves assist in dissipating marine wave energy and turbulence. This in turn lessens the ability of waves to carry sediment into the inlet mouth and cause closure.

Factors that contribute to mouth closure include structures that inhibit river or tidal flows, e.g. natural bedform such as sand ripples in the Keurbooms or the artificial causeway over the Seekoei (DWAF 1996, DWAF 2005). Tidal flow, especially the outflow velocity on the ebb tide plays a major role in maintaining open mouth conditions. Structures that inhibit tidal flow reduce the flow velocity and thereby reduce the scouring ability of the ebb tide to remove sediment that entered the system on the flood tide.

It is important to recognise that each estuary is unique in terms of the nature of the various factors that influence its sensitivity to flow, such as bathymetry, run-off and degree of mouth protection. For example, two estuaries could occur adjacent to one another but, due to differences in local coastal conditions, completely different processes could be responsible for maintaining an open mouth.

FACTORS INFLUENCING TOCE HYDRODYNAMICS

Catchment size and river inflow

Catchment size is not necessarily related directly to run-off due to the arid South African climate. Permanently open systems often have larger catchments with significant river flow occurring throughout the year, while TOCEs tend to have smaller catchments (often <100 km^2) and are normally characterised by a strong seasonal variation in runoff (Whitfield 1992).

The Buffels, Spoeg and Groen catchments are examples of large arid catchments that drive mouth status through floods. The Buffels River drains the western edge of Bushmanland and has a catchment area of 9375 km^2 (Heydorn and Tinley, 1980). The Spoeg River has a catchment of 1375 km ^{2} and the Groen River a catchment area of 4500 km^2 (Heydorn and Tinley, 1980). These rivers only flow after substantial rainfall and episodic floods have been recorded for these systems (Heydorn and Grindley, 1981a, 1981b and 1981c). Breaching of these estuaries is mostly linked to flood events and, judging by the frequency of mouth opening, a 1:2 to 1:5 year flood event is required for breaching of these arid region estuaries. Marine overwash of the sand bar might play a role for a few days after mouth closure in modifying the salinity of the water column.

The above catchments are extreme examples of where a rapid increase in runoff following a rain event might flush open the mouth followed by an equally rapid decline in runoff after the rain event. If such an estuary were situated on a high-energy beach, it would tend to close quickly. A semi-closed state normally develops where there is some degree of mouth protection, limited sediment availability or the estuary is of a small size (discussed in more detail later). Sustaining a semi-closed mouth state versus a fully open mouth requires less runoff and smaller catchments can often provide the necessary base flow to create this mouth state.

Mouth status

At any one time, the mouth of an estuary is either open or closed. During the ‘open state’ the system is connected to the sea and seawater can exchange with estuarine water inside the system. During periods of low flow this connection may become constricted, but the connection between the sea and estuary is maintained during the normal tidal cycle. When the mouth is closed, the connection to the sea is severed and the estuary becomes isolated from it even during spring high tides. Some marine overwash may occur during high wave or storm events.

Research conducted in recent years by the CSIR on small systems has highlighted the existence of a third mouth state, the semi-closed state (van Niekerk 2005, van Niekerk et al. 2002, Taljaard et al. 1997; Huizinga et al. 1998; Huizinga and van Niekerk 1998; Huizinga et al. 2000; Huizinga et al. 2001). In the semi-closed state, the mouth is nearly closed with only a shallow, narrow opening allowing water to ‘trickle’ out to sea. The semi-closed mouth is usually perched and too shallow for tidal exchange. However, seawater as overwash may still enter the estuary during spring high tides, thus allowing a brackish, estuarine environment to persist within the system. A semi-closed mouth state is a phenomenon characteristic of many smaller estuarine systems along the South African coastline (e.g. Palmiet, Mngazi and Lourens). In the past, the existence of this semi-closed state was not formally recognized and therefore not seen as especially relevant to the ecology of the estuary. The semi-closed mouth state should not be confused with overwash by big sea waves during storm events or during spring tides, which only occur for short periods or under extreme conditions.

Reductions in river flow can affect the natural variation in the state of an estuary mouth and subsequently the ecological character of the estuary. For example, a small change in river inflow could change the mouth of an estuary from a semi-closed mouth to a closed mouth with its related impact on the ecological functioning.

Recent research conducted on the TOCEs of the KZN region led to the suggestion that if no observations are available on the mouth status of individual systems, ‘residence time’ can be taken as a proxy indicator (Perissinotto et al. 2004). The residence time was calculated as the storage area of the estuary divided by the mean annual runoff (MAR). However, in a detailed evaluation of the Mdloti and Mhlanga estuaries it was shown this is a very crude measure because it does not deal very effectively with the strong seasonal differences between low baseflow, freshettes and floods.

Estuary size and tidal flow

In larger temporarily open estuaries (>150 ha), tidal flow can normally maintain an open mouth state once run-off decreases in the low flow season. Permanently open estuaries, estuarine bays and some river mouths are examples of such systems. An interesting exception to the rule is estuarine lakes, which close despite their significant size due a number of possible factors, e.g. extended low flow, high evaporation rates, high sediment availability, high wave energy, that urgently need further investigation to refine our understanding regarding the interaction between hydrodynamics and sediment dynamics in these systems.

In medium sized estuaries (<150 ha), tidal flow can maintain open mouth conditions during spring tides but often closure occurs during neap tides, e.g. Great Brak and Seekoei (CSIR 2003, DWAF 2005). Thus, during periods of low river flow in small to medium sized estuaries the tidal prism is insufficient to maintain an open mouth, which normally becomes too constricted and then closes.

The semi-closed mouth state normally only occurs in small estuaries. After an extended period of low flow the mouths of large to medium sized estuaries close as the level of the sand berm at the mouth increases in height at a faster rate than the water level in the estuary can rise. In other words, due to their larger volumes, large estuaries require a greater river inflow to maintain high water levels inside the mouth and keep them open during dry periods. It is seldom possible to reach a long-term equilibrium between the closing forces and the river inflow for such large systems during the low flow season and the semi-closed condition occurs for only a few days (if at all) during the transition from an open to a closed mouth state.

A small TOCE, with a relatively small volume, requires less river inflow to increase the water level as high as the sand berm at its mouth. Hence it is possible to reach equilibrium between a sustained or increasing water level in the estuary and the closing forces such as wave action and sediment build-up in the mouth area. A preliminary assessment indicates that this mouth condition in general only occurs in estuaries < 2 km in length or < 100 ha in surface area.

River inflow

River inflow (baseflow) is a major factor that maintains open mouth conditions in South African estuaries. In many TOCEs, it is the only driving force that maintains the mouth in the open state. In larger systems, tidal flow assists in maintaining the open mouth.

The flow regime needed around the coast of South Africa to maintain an open mouth is strongly dependent on sediment availability and wave conditions. For example, on a high energy beach in KZN, the flow required to keep a mouth fully open varies between 5 to 10 $m^3 s^{-1}$, while as little as 1-2 $m^3 s^{-1}$ is needed to maintain an open state along the south-western Cape coast (Huizinga and van Niekerk 2005). By contrast, very little baseflow is required to maintain the semi-closed state. From preliminary assessments at a few estuaries, it appears that a steady outflow of 0.05 to 1 $m^3 s^{-1}$ is needed to maintain a semi-closed state. For estuaries situated on protected or low-energy beaches, such as those along the Western Cape coast, the baseflow required may be as low as 0.2 to 0.05 $m^3 s^{-1}$ (Huizinga et al. 2001). This baseflow requirement would be slightly higher for estuaries situated along high-energy beaches, such as those found along the coast of KZN.

Although the baseflow required to sustain a semi-closed mouth condition is considered to be low, it should still be high enough to compensate for the loss of water by evaporation (negligible in smaller estuaries) and seepage through the berm. The coarser the sand on the beach, the higher will be the loss through seepage, and therefore the higher the baseflow needed to maintain this state. The small increases in baseflow needed to create this state in an estuary may also be produced as a result of return flow from sewage plants, agricultural irrigation schemes and seepage through dam walls, e.g. Nhlabane and Mdloti (DWAF 2002 and 2003b). POE mouths are less sensitive to flow reduction. This is because the runoff and/or tidal flow are high enough to maintain open mouth conditions throughout the year, even during drought periods.

Temporarily open estuaries, including estuarine lakes and some river mouths, exhibit changes in the frequency and duration of mouth closure and modifications in the salinity distribution due to flow manipulation. These systems are very sensitive to base flow reduction, i.e. a small change in runoff can modify the period of mouth closure, e.g. Tsitsikamma in the southern Cape (DWAF 2003a). In extreme cases, fresh water reduction can cause almost permanent mouth closure. For example, the main result of the reduction in MAR from 102 million m^3 to 3 million m^3 into the Isipingo Estuary was that flow through the mouth became too low for most of the time to keep it open. Currently the Isipingo mouth is therefore almost permanently closed (Huizinga and Theron 2002).

While breaching is related to floods at the Buffels and Spoeg, groundwater discharges may play a role in maintaining the water body in the absence of river input from the catchment. The combination of groundwater and seepage through the berm may even reduce the salinity over time, depending on the salinity/conductivity of the inflowing water (Heydorn and Grindley 1981a, 1981b).

Salinity

The salinity distribution of POEs is very sensitive to reductions in seasonal base flow, especially during the low flow period, because this can cause changes in the extent of salinity penetration through the mouth. Permanently open estuaries are often less sensitive to a reduction in the higher flow periods, e.g. 50-100 $m^3 s^{-1}$ because the system will normally be river dominated during these flow ranges. However, floods play a major role in sedimentary processes within South African estuaries and the construction of large dams and/or numerous small farm dams holds severe risks for the long-term sediment equilibrium of estuaries.

In TOCEs, salinity penetration is often reduced during the high river flow periods and the estuary is therefore fluvially dominated during high flow. Once river inflow decreases, saline water can penetrate into the estuary and a well defined longitudinal and or horizontal stratification can develop, i.e. salinity is close to that of seawater at the mouth and fresh at the head of the estuary. As river flow decreases, a 'semi-closed' mouth state can develop that reduces tidal intrusion. As outflow continues through the constricted channel at the mouth, different salinity conditions develop. A further reduction in runoff will lead to the development of the mouth closed state during which the berm will develop to its maximum height and will sever the connection to the sea. Depending on the duration of this closed mouth state, the system can either come progressively fresher, due to limited inflow and seepage through the berm, or more saline as a result of evaporation. Provided the inflow exceeds evaporation and seepage losses, a progressive freshening of the system occurs until such time as rising water levels lead to a breaching of the berm (van Niekerk at al. 2005).

Duration of mouth states

The duration of the various mouth states is strongly dependent on river inflow. Although little evidence is available at present, there is some evidence to indicate that the 'open mouth state' is of short duration (days to weeks) in small TOCEs due primarily to the sporadic nature of the catchment runoff. Both small and arid catchments tend to have short and sharp river flow hydrographs where an increase in runoff is normally of short duration. Generally the hydrograph returns to its baseflow condition within a few hours to days after heavy rainfall events. To distinguish the 'semi-closed' mouth state as a separate condition from the transition phase between open to closed mouth that occurs as river flow decreases, the mouth state should persist for a period of more than 14 days (a neap/spring cycle). This time frame is significant because experience has shown that small estuaries, e.g. Great Brak along the Cape south coast, tend to close during or shortly after a neap tide, when tidal flow becomes too weak to sustain the open mouth condition. Very little data exists on exactly how long this state can occur in various estuaries but preliminary investigations in the Lourens, West Kleinemonde, Mdloti and Mhlanga indicate that it could persist from two weeks up to a few months, depending on the extent of the low flow period in the different regions (Huizinga et al. 2001, DWAF 2002, 2003b).

Retention time

A crude indicator of 'residence' time can be derived by dividing the storage area of the estuary by total inflow (river inflow, direct rainfall, groundwater seepage) minus the total outflow (seepage trough berm and evaporation) (Perissinotto et al. 2004, Dyer 1973). The above-mentioned formula is not sensitive to the dynamic nature of an estuary mouth because TOCEs can vary from a wide open mouth to a very constricted channel, in a very short period (weeks). A more constricted mouth results in less exchange taking place and the residence time will increase. In addition, this approach does not consider effects such as dilution and diffusion that are important processes.

The above formula might be appropriate for very small, shallow TOCEs, but as soon as the bathymetry of the system changes to include deeper areas, stratification often develops under normal flow conditions, i.e. open mouth state and semi-closed mouth state, and the residence time of bottom water can differ substantially from the upper layers. In most cases numerical modelling is often the only way to calculate residence time accurately under these circumstances (van Ballengooyen et al. 2004). Residence time under the ‘close mouth state’ strongly depends on the duration of the state, although some replenishment might be possible due to subsurface groundwater discharge and marine overwash into some systems. The longer the closed state persists, the longer the residence time.

Tidal variation and amplitude

The dominant tide around the South African coast is semidiurnal (12.42 hr period) due to the lunar influence. The diurnal component (24 hr cycle), strongly influenced by the sun, is also important as it generates succeeding tides of variable amplitudes. Because of the relatively straight South African coastline there is very little variation in tide height. Tidal height is the difference between sea levels at high and low tide, with a height of more than 1.0 m above mean sea level (MSL) at spring high tide and as little as 0.25 m at neap high tide (Schumann et al. 1999).

In the open ocean the theoretical tidal variation follows a smooth sinusoidal curve. However, in most South African estuaries the tidal amplitude is dampened due to the constricting effect of the mouth. The more constricted the mouth, the smaller the tidal amplitude and the higher the threshold of the low tides. High tide levels in large open estuaries tend to be similar to that of the adjacent coast.

During the ‘open state’, tidal variation can be >1.5 m after a breaching or flood event, or only a few centimetres in a small ‘perched’ estuary. In POEs the average tidal amplitude varies between ~1.0 m (spring tide) and ~0.3 m (neap tide) during the high flow period, but in certain systems this can be severely reduced during the low flow period. River flooding also dampens the tidal effect as it reduces tidal exchange within the estuary. During the open mouth state in small to medium estuaries the tidal amplitude is often damped by the threshold effect of the mouth which can be perched above the mean sea level and therefore limits low tide levels (Figure 1.1).

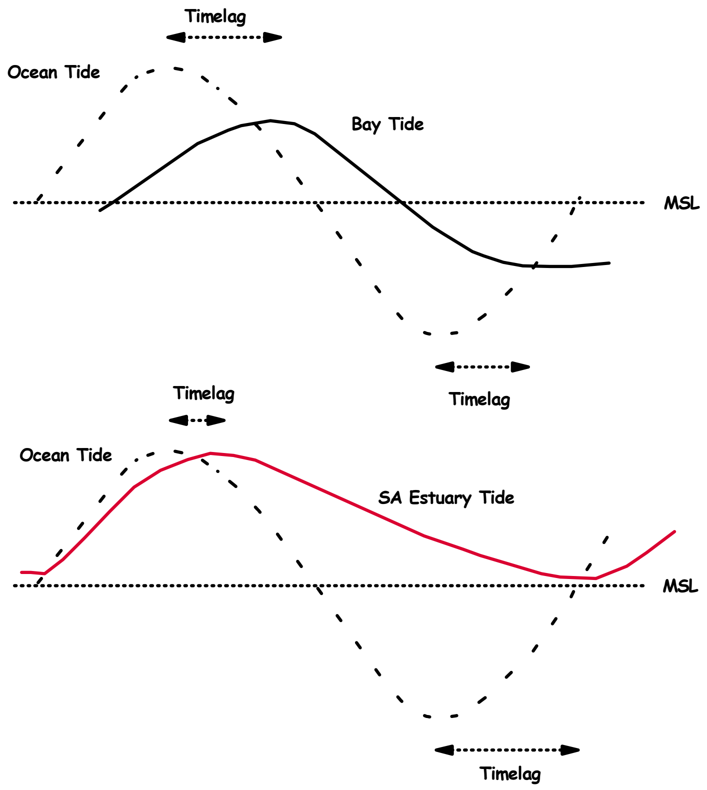


Figure 1.1. Typical tidal variations in a large bay inlet (top) and a small estuarine inlet (bottom) (after Huizinga and van Niekerk 2005).

During the ‘closed mouth state’ no tidal variation occurs. Some estuaries do show an increase in water level during the closed phase due to overwash during storm events or spring tides, e.g. Groot Brak (CSIR 2003). In extreme cases, bar overtopping can even cause the mouth to breach due to a flattening of the sand bar and increased water levels caused by the overwash.

Another consistent characteristic of semi-closed mouth states is that they normally have perched inlets. A perched mouth occurs when it is located high on the beach and above the influence of average wave conditions. A perched mouth usually means that there is limited or no tidal variation in the estuary and a relatively high water level in the estuary (>2.0 m MSL) when the mouth is closed. There are therefore no intertidal areas. Small fluctuations in water level may occur due to changes in river flow, overwash, water losses and variations in berm height (van Niekerk at al. 2002). The outflow channel of a perched estuary still allows wave driven flow (overwash) into the mouth at high sea levels (e.g. high spring tides) and during storm events. The runoff associated with this state is so low that it does not prevent big waves, such as those occurring during a storm, with their high sediment loads from closing the mouth.

In medium and small estuaries the lowest water levels do not occur at spring tides; they occur during neap tides (Huizinga and van Niekerk 2005). This is caused by the restricting effect of the mouth and is stronger at low water levels and weaker at high water levels. During spring tides much more water enters the estuary on the flood tide than leaves the system on the outgoing tide. Once again this is because of the restricting effect of the inlet, regardless the fact that the water level at low tide in the sea is much lower than that in the estuary. Far less water enters the estuary on a neap flood tide than on a spring tide and relatively more water can then drain out during the ebb tide (Huizinga and van Niekerk 2005).

Mouth and outflow channel

During the 'open state' the depth and width of an estuary mouth depends on river and tidal flow. In addition, the head of water available at breaching also plays a significant role because it determines the initial channel configuration. River floods, with their associated high flow rate, can also considerably increase the width of a mouth, but this is often of short duration as the significant closing forces along the South African coastline often reset the system in a matter of weeks.

In the 'semi-closed state' the mouth is normally perched; in other words the mouth is located high on the beach and little interference from wave action occurs. Aerial photographs indicate that the outflow channel is normally only a few meters wide and that it often has extensive meanders. For example, aerial photographs of the Lourens Estuary show such a meandering semi-closed mouth state. Meandering of the mouth is an indication that the semi-closed state has persisted for some time. If strong tidal interaction or strong river flow occurs, the entrance channel is usually relatively straight (Huizinga and van Niekerk 2005). The depth of the outflow channel during the semi-closed mouth state is normally about 0.3 m or less, e.g. Lourens ~0.15m in January 2002 (CSIR unpublished data).

Water column stratification

Stratification in estuaries depends on the extent to which water with different temperatures and salinity mix. Freshwater has a salinity of ~0 PSU (Practical Salinity Units) whereas seawater is approximately 35 PSU. In addition there is normally a difference between the temperature of fresh and seawater. This combination of salinity and temperature difference defines the resultant density of a water mass. For example, a change from 5°C to 25°C will change the density of water with a salinity of 35 PSU by ~0.006 kg m^{-3}, while a change in salinity from 0 to 30 PSU will change the water density by 0.027 kg m^{-3}. Because of limited inflow, most estuaries have a full salinity gradient over the entire range of 0 to 35 PSU and water temperatures which can vary between 5 to 30 °C. Consequently, salinity is generally the dominant factor in determining water density (Schumann et al. 1999). Because of the different densities of seawater, mixed water and fresh water, three types of stratification can be present, namely highly stratified, partially stratified or non-stratified.

Stratification changes in space and time, e.g. an estuary can be highly stratified during high river flow period, but well mixed during the low flow period; well mixed on a spring tide but partially stratified on a neap tide. An estuary may also be stratified in the upper reaches but well mixed near the mouth. In a well mixed estuary, there is usually little density difference between surface and bottom water (Schumann at al. 1999).

Estuary bathymetry

Bathymetry plays a significant role in estuarine circulation because stratification is more likely to develop in systems with deeper basins immediately behind the sand berm than in shallow estuaries, e.g. Palmiet and Kromme (CSIR 2000, 2005; Huizinga and van Niekerk 1999). In TOCEs the saline intrusion, retention and flushing is determined by the constricting effect of the mouth. This reduces flood tide velocity, which allows denser inflowing water to flow below the estuarine water in the deeper channels. On the ebb tide, the deeper saline water is trapped and can only be removed by vertical entrainment. The flow of the river is enhanced by the saline water, both of which are removed by fast, seaward-flowing surface water through entrainment (Largier and Taljaard 1991). Whether stratification will develop under higher flow conditions often depends on the bathymetry of an estuary. In small systems such as the Slang and Klipdrift estuaries, stratification is not likely to develop due to the limited storage area.

Ebb- and flood tidal flow channels

Different ebb- and flood flow channels often develop because of inertia effects. The large volume of water entering the estuary during the flood tide (at a high flow rate) tends to flow straight into the estuary. The flood tidal channel therefore is normally the main channel straight up the estuary (Figure 1.2). A large part of the sediment transported into the mouth on the incoming tide is deposited just inside the inlet, where a flood tidal sand bank is located (Huizinga and van Niekerk 2005).

The ebb-tidal flow is normally of much lower velocity because the period of outflow is of longer duration. The outflow normally takes place through a small ebb-channel, which curves around the flood tidal sand bank inside the estuary (Figure 1.2). This ebb-channel is often connected just inside the mouth to the main channel and is then protected against the sediment transported into the mouth on incoming tide by the berm.

The degree to which the ebb and flood tide channels interact with each other can play a role in the duration of open mouth conditions. A well protected ebb channel often assists in prolonging the open mouth state. An example of such an ebb and flood channel configuration is shown in Figure 1.2.

CONCEPTUAL MODEL

Based on the above review, a conceptual model (Table 1.1) was developed to describe the hydrodynamic characteristics of TOCEs. There are three dominant states in which these systems can exist, State 1, 2 and 3 (see below). Depending on factors such as estuary size, catchment runoff, sediment availability, wave energy and mouth protection, all three of these states (3-mouth state system) can occur in certain TOCEs. Alternatively, some systems may only exhibit the open and closed states (2-mouth state system). Examples of estuaries from both the Cape and KwaZulu-Natal, together with their various states, are outlined in Table 1.2.

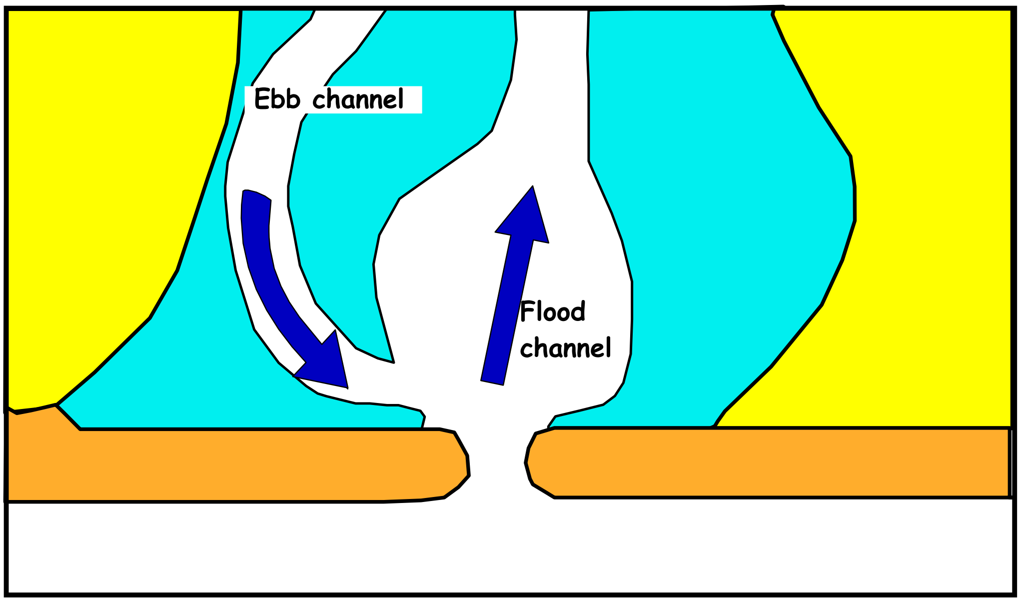
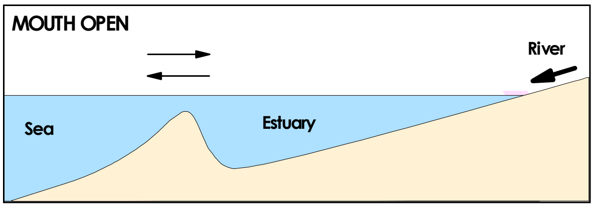


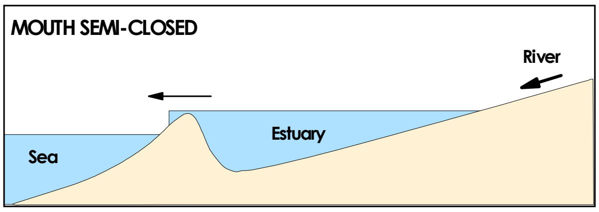
Figure 1.2. Typical configuration of ebb and flood tidal channels in the mouth region of an estuary (Huizinga and van Niekerk 2005).

Table 1.1. Mouth states of temporarily open/closed estuaries.

STATE 1: The 

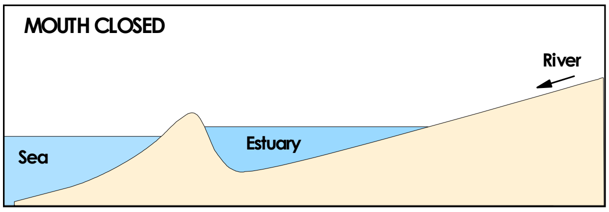
mouth of the estuary is open to the sea, allowing seawater intrusion during high tides, with river inflow introducing freshwater into the upper reaches.

Outflow channel/Mouth depth: The outflow channel will be very well established after floods and freshettes (>2.0 m deep and very wide), but will normally be come more constricted as State 1 persists. In smaller systems the outflow channel can be become only a few meters wide and < 1.0 m deep shortly after a breaching.
Tidal variation: Tidal amplitude varies from ~ 1.0m at spring tide to 0.3 m at neap tides. In smaller estuaries the tides are normally truncated due to the constriction of the outflow channel depth.
Retention time: Residence time is normally only a few days to weeks under this state. In deeper estuaries where stratification may develop, bottom water may have a residence time of a few weeks in the middle to upper reaches.



STATE 2: The formation of a sand berm at the mouth prevents continuous seawater intrusion – during this state seawater intrusion is limited to high tides. However, the berm is still not high enough to prevent water draining from the estuary into the sea.

Outflow channel/Mouth depth: The outflow channel will be 10-30 m wide and only 150-300 mm deep.
Tidal variation: Limited to no tidal variation will occur. Higher spring tides may show variation.
Retention time: Residence of the surface water will be in the order of a few days, while bottom water may be days to weeks.



STATE 3: The height of the sand berm at the mouth of the estuary prevents seawater from entering or water draining from the estuary into the sea through an outflow channel. Although there may still be river water entering the estuary, the flow rate is too little to facilitate breaching.

Outflow channel/Mouth depth: There will be no outflow channel.
Tidal variation: No tidal variation will occur. The water level may increase initially due to overwash during high tides.
Retention time: Residence time is dependent on the duration of the state. Normally it will be weeks to months. Some replenishment may occur due to over washing during this state and outward seepage through the sandbar can also occur.

CONCLUSIONS AND RECOMMENDATIONS

The following conclusions and recommendations can be drawn from the foregoing:
1. Very little reliable information is available on the hydrodynamics of TOCEs. Even less is known about systems that stay closed for prolonged periods.
2. To develop an in-depth understanding of the long-term cycles and hydrodynamic process in TOCEs, data urgently need to be collected on the mouth status of South Africa's smaller estuaries.
3. Most of the studies evaluated indicated that the runoff data were of very low confidence. There is therefore an urgent need to improve the quality of the runoff data provided to estuarine scientists. This includes assessing the MAR of individual smaller estuaries (not just on a quaternary level) and making estimates of the present and reference monthly flow that reached these systems.
4. Monthly flow may not be the most appropriate measure for developing predictive models for small TOCEs. Daily flow data (measured or simulated) should be investigated to see if this information could be provided at a reasonable cost and confidence for the smaller catchments.
5. Estuarine Lakes were not reviewed as part of this study but the mouths of these systems are also known to close off from the sea. This oversight should be addressed as soon as possible in order to understand the continuum from small TOCEs to large estuarine lakes.

Table 1.2. Major hydrodynamic features of selected Cape and KwaZulu-Natal TOCEs.

FEATURE	CAPE TOCE				KZN TOCE	
	EERSTE	**LOURENS**	**PALMIET**	**GROOT BRAK**	**MHLANGA**	**MDLOTI**
Catchment size (km^2)	660	92-140	465 - 539	189	80	484
Size (ha)	10.2	7.1	33	113.9	100.1	58.1
MAR (x 10^6 m^3)	Present: 35 Reference: 22	21	310	Present : 9.84 Reference: 32.76	12.6	83.2
Tidal flow	Negligible, dependent on river flow	Negligible, dependent on river flow	Negligible, dependent on river flow	Can stay open over Springs close on neaps	Negligible, dependent on river flow	Negligible, dependent on river flow
Duration Closed	Nearly always in State 1 due to sewage effluent	State 2 and 3: January - March	State 2 and 3: months at a time during summer	State 3: winter period due to high wave conditions	State 3: 50% of time vs. 80% under reference	State 3: 50% of time vs. 10% under reference
Response to flow	Mouth closed, but some over wash. Estuary will become fresher with time (< 0.1 m^3/s). Semi-closed, some seawater intrusion takes place at spring high tides. The salinity concentrations will normally be slightly higher than at State 3 (0.1 - 3 m^3/s). Mouth open with seawater intrusion. Mouth wide open with estuary being completely fresh (> 3 m^3/s)	Mouth closed, but over wash by seawater occurs occasionally (< 0.05 m^3/s). Mouth semi-open, only outflow occurs. Some seawater intrusion takes place at spring high tides (0.05 - 0.4 m^3/s). Mouth open with seawater intrusion (0.4 - 2.0 m^3/s). Mouth wide open with completely fresh outflow (>2.0 m^3/s).	Closed mouth with no exchange (<0.05 m^3/s). Semi-closed mouth, with no seawater intrusion but outflow to sea (0.05-1.5 m^3/s). Open mouth, with seawater intrusion (1.5 - 10 m^3/s). Open mouth, with limited seawater intrusion, i.e. fluvially dominated (10 - 20 m^3/s) Open mouth, with no seawater intrusion, i.e. fluvially dominated (> 20 m^3/s)	No semi-closed mouth state. Mouth closed at flow <0.5 m^3/s at neap tides.	Predominantly closed (< 0.4 m^3/s). Predominantly semi-closed (0.4 - 0.5 m^3/s) Predominantly open, with marine influence (0.5 - 5 m^3/s). Predominantly open, river dominated (> 5 m^3/s).	Closed, no water exchange with sea (<0.3 m^3/s). Semi-closed, with no seawater intrusion but with water still flowing out to sea (0.3 - 2.0 m^3/s). Open with seawater intrusion (2.0 - 5.0 m^3/s). Open, with no seawater intrusion, i.e. completely fresh (> 5.0 m^3/s)
References	Grindley 1982; Bath 1999; Huizinga et al. 2001	Cliff and Grindley 1982; Huizinga et	Clarke, B.C. 1989; Largier 1986; Taljaard et al. 1986;	Taljaard and Slinger 1993; CSIR 1990, 1992, 1993,	DWAF 2003b; Perissinotto et al. 2004, Begg 1978, 1984	DWAF 2002; Perissinotto et al. 2004, Begg 1978, 1984

FEATURE	CAPE TOCE				KZN TOCE	
	EERSTE	LOURENS	PALMIET	GROOT BRAK	MHLANGA	MDLOTI
		al. 2001; Harrison 1998; Lochner and Brown-Rossouw 1999	Taljaard 1987; Largier et al. 1992; Slinger and Largier 1990; CSIR 2000; Huizinga et al. 1998	1994, 1998, 2000, 2003		

REFERENCES

Bath A (1999) Overview assessment of effluent discharge impacts. Draft Report for Bulk Waste Water Study, Ninham Shand.

Begg GW (1978) The Estuaries of Natal. Part 1. *Natal Town and Regional Planning Report* **41** 657 pp.

Begg GW (1984) The Estuaries of Natal. Part 2. *Natal Town and Regional Planning Report* **55** 631 pp.

Clarke BC (1989) Estuaries of the Cape. Part II. Synopses of available information on individual systems. Report No. 37. Palmiet. *CSIR Research Report* **436**.

Cliff S and Grindley JR (1982) Estuaries of the Cape Part II: Synopses of available information on individual systems (A.E.F. Heydorn and J.R. Grindley, Eds.). Report No. 17: Lourens. (CSW 7) *CSIR Research Report* **416** 39 pp.

CSIR (1990) Great Brak Estuary environmental study with reference to a management plan for the Wolwedans Dam and the Great Brak River mouth. *CSIR Report EMA-C* **9036**. Stellenbosch.

CSIR (1992) Great Brak management programme. Interim Report. Report on the monitoring results for the period April 1990 to March 1992. *CSIR Report EMAS-C* **92083**. Stellenbosch.

CSIR (1993) Great Brak management programme. Interim Report. Report on the monitoring results for the period April 1992 to March 1993. *CSIR Report EMAS-C* **93051**. Stellenbosch.

CSIR (1994) Great Brak management programme. Interim Report. Report on the monitoring results for the period April 1993 to March 1994. *CSIR Report EMAS-C* **940013**. Stellenbosch.

CSIR (1998). Great Brak management programme. Interim Report. Report on the monitoring results for the period April 1997 to March 1998. *CSIR Report ENV/S-C* **98122**. Stellenbosch

CSIR (2000) Palmiet River Water Resource Management Plan. Summary Report: Requirements of the estuary. *CSIR Report ENV-S-C* **2000-48**. Stellenbosch.

CSIR (2003) Great Brak management programme. Review Report March 2003 *CSIR Report ENV/S-C* **2003-092**. Stellenbosch

CSIR (2005) Department of Water Affairs and Forestry, South Africa. 2005. Kromme/Seekoei Catchments Reserve Determination Study – Technical Component Seekoei . Prepared by CSIR for CES. *CSIR Report ENV/S-C* **2005-061.**

DWAF (1996) Plettenberg Bay Coastal Catchment Study. Keurbooms River Estuary Environmental Work Session. Ninham Shand Consulting Engineers.

DWAF (2002) Rapid determination of the Resource directed Measures of the Mdloti (including preliminary estimates of capping flows for the Mdloti and Mhlanga estuaries. Final Draft Report submitted to the Directorate Resource Directed Measures, February 2002.

DWAF (2003a) Determination of the Preliminary Ecological Reserve on a Rapid Level for the Tsitsikamma (including a desktop assessment on other estuaries in K80 tertiary catchment). Final Report submitted to Directorate Resource Directed Measures, March 2003.

DWAF (2003b) Determination of the Preliminary Ecological Reserve on a Rapid Level for Mhlanga. Final Report submitted to Directorate Resource Directed Measures, DWAF, Pretoria.

DWAF (2005) Kromme/Seekoei Catchments Reserve Determination Study – Technical Component. Kromme . Prepared by CSIR for CES. Report No. KSCR-IR-0001.

Dyer KR (1973) Estuaries: A physical introduction. John Wiley and Sons. London, 140 pp.

Grindley JR (1982) Estuaries of the Cape Part II: Synopses of available information on individual systems (A.E.F Heydorn and J.R. Grindley, Eds.). Report No. 16: Eerste. (CSW 6) *CSIR Research Report* **415** 51 pp.

Harrison TD (1998) A preliminary survey of the coastal river systems of False Bay, south-west coast of South Africa, with particular reference to the fish fauna. *Transactions of the Royal Society of South Africa* **53**(1) 1-31.

Heydorn AEF and Grindley JR (1981a) Estuaries of the Cape. Part II. Synopses of available information on individual systems. Report No. 1. Spoeg. *CSIR Research Report* **400**.

Heydorn AEF and Grindley JR (1981b) Estuaries of the Cape. Part II. Synopses of available information on individual systems. Report No. 2. Buffels (CW3). *CSIR Research Report* **401**.

Heydorn AEF and Grindley JR (1981c) Estuaries of the Cape. Part II. Synopses of available information on individual systems. Report No. 3. Groen. *CSIR Research Report* **401**.

Heydorn AEF and Grindley JR (1980) Estuaries of the Cape. Part I. Synopses of the Cape Coast. Natural features, dynamics and utilisation. *CSIR Research Report* **380**. 97pp.

Huizinga P and Theron AK (2002) Isipingo Mouth – Options to increase tidal exchange. Preliminary investigation. Unpublished report to DAEA.

Huizinga P and van Niekerk L (1998) Nhlabane: Physical aspects. *CSIR Report ENV/S* **98107**. Stellenbosch, South Africa.

Huizinga P and van Niekerk L (1999) The effects of a freshwater release from the Mpofu Dam on salinity distributions of the Kromme Estuary'. *CSIR Report ENV/S-C* **99045**. Stellenbosch, South Africa.

Huizinga P and van Niekerk L (2005) Coastal Engineering Course. University Stellenbosch, September 2005. Mouth dynamics and Hydrodynamics of Estuaries. Unpublished notes.

Huizinga P van Niekerk L and Taljaard S (1998) The effects of future changes in run-off on the Palmiet: Physical Dynamics and Water Quality. *CSIR Report ENV/S-C* **98134**. Stellenbosch, South Africa.

Huizinga P, Harrison TD and van Niekerk L (2000) Fresh Water Requirements of the Mdloti. *CSIR Report ENV/S-C* **2000-132**. Stellenbosch, South Africa.

Huizinga P, Taljaard S, van Niekerk L, Turpie JK and Lamberth SJ (2001) The effects of water abstraction on the estuaries of the Eerste and Lourens rivers. *CSIR report ENV-S-C* **2001-007**

Huizinga P, van Niekerk L and Taljaard S (1998) The effects of future changes in run-off on the Palmiet: Physical Dynamics and Water Quality. *CSIR Report ENV/SC* **98134**. Stellenbosch, South Africa.

Largier JL (1986) Structure and mixing in the Palmiet Estuary, South Africa. *South African Journal of Marine Science* **4** 139-152.

Largier JL and Taljaard S (1991) The dynamics of tidal intrusion, retention, and removal of seawater on a bar-build estuary. *Estuarine, Coastal and Shelf Science.* **33** 325-338.

Largier JL, Slinger JH and Taljaard S (1992) The stratified hydrodynamics of the Palmiet – a prototypical bar-built estuary. In: Dynamics and exchanges in estuaries and the coastal zone. Prandle, D (Ed) Coastal and Estuaries Studies 40. New York, Springer and Verlag. pg 135 – 153.

Lochner P and Brown-Rossouw R (1999) Management plan for the coastal zone between the Eerste and Lourens Rivers. *CSIR Report ENV-SC* **98** 103pp.

Perissinotto R, Blair A, Connell A, Demetriades NT, Forbes AT, Harrison T.H, Lyer K, Joubert M, Kibirige I, Mundree S. Simpson H, Stretch, D, Thomas C, Thwala X, Zietsman I (2004) Contribution to information required for the implemtation of Resource Directed Measures for estuaries (Volume 2). Responses of the biological communities to flow variation and mouth stste in two KwaZulu-Natal temporarily open/closed estauries. *Water Research Commission Report No.* **1247/2/0**.

Schumann E, Largier J and Slinger J (1999) Estuarine hydrodynamics. In Allanson BR and Baird D (eds.) *Estuaries of South Africa*, Cambridge University Press 289-321.

Slinger JH and Largier JL (1990) The evolution of thermohaline structure in a closed estuary. *South African Journal of Aquatic Science* **16** (1/2) 60-77.

Taljaard S (1987) Nutrient circulation in the Palmiet River Estuary: A summer study. *CSIR Research Report* **633**. Stellenbosch.

Taljaard S and Slinger J H (1993) Investigation into the flushing efficiency of 1. A freshwater release and 2. Seawater overwash in the Great Brak. *CSIR Research Report* **713**.

Taljaard S, Eagle GA, Hennig HF-KO (1986) The Palmiet Estuary: A model for water circulation using salinity and temperature measurements over a tidal cycle. *Water SA* **12**(3) 119-126.

Taljaard S, Slinger JH, van Niekerk L and Huizinga P (1997) Topographic and physico-chemical surveys of three Eastern Cape estuaries during August 1996: Mngazi river estuary, Mzimvubu river estuary, Mntafufu river estuary. *CSIR Technical Report ENV/S* **97003.**

Turpie JK, Adams JB, Colloty, BM, Joubert A, Harrison TD, Maree RC ,Taljaard S, van Niekerk L, Whitfield AK, Wooldridge TH, Lamberth SJ, Taylor R, Morant P, Awad A, Weston B and Mackay H (2002) Classification and prioritization of South African estuaries on the basis of health and conservation priority status for determination of the estuarine water reserve. Department of Water Affairs and Forestry, Pretoria.

van Ballegooyen R., Taljaard S, van Niekerk L and Huizinga P (2004) Using 3D modelling to predict physico-chemical responses to variation in river inflow in smaller, stratified estuaries typical of South Africa. *Journal of Hydraulic Research* **42** (6) 563–577.

van Niekerk L, van der Merwe JH and Huizinga P (2005) The hydrodynamics of the Bot River revisited. *Water SA* **31** 73-85.

van Niekerk L (2005) Desktop assessment of the Wild Coast Estuaries: Sensitivity to Flow reduction. *CSIR Report ENV/S-C* **2005-042**.

van Niekerk L, Huizinga P and Theron A (2002) Semi-closed mouth states in estuaries along the South African coastline. In: Environmental Flows For River Systems Proceedings. *Fourth International Ecohydraulics Symposium* **31** 1 (ISSN 0378-4738)

Whitfield, AK (1992) A characterisation of southern African estuarine systems. *Southern African Journal of Aquatic Sciences* **12** 89-103.

Whitfield, AK (1998) Biology and Ecology of Fishes in Southern African Estuaries. *Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology* No. **2** 1-223.

2. SEDIMENT DYNAMICS

Andre Theron

Council for Scientific and Industrial Research, Stellenbosch

INTRODUCTION

The purpose of this document is to provide an overview of the available literature on sediment dynamics of temporarily open/closed estuaries (TOCEs) in the warm-temperate and cool-temperate biogeographic regions of the Eastern and Western Cape provinces. The review focuses on south-eastern and southern Cape estuaries and includes a summary of all available previous sediment dynamics research on TOCEs in the area. Reference is also made to those TOCEs in KwaZulu-Natal for which literature exists. This review also attempts to identify the new datasets that are required in order to make suitable comparisons between Cape and KwaZulu-Natal estuaries. The source for this includes information from published and 'grey' literature.

STUDY SITES

The East Kleinemonde was chosen as the primary study site, with ancillary study estuaries being the van Stadens, Kasouga, Grants Valley and West Kleinemonde. The selected KwaZulu-Natal estuaries are the Mdloti and Mhlanga.

AVAILABLE LITERATURE

The literature review of South African temporarily open/closed estuaries (TOCEs) by Perissinotto et al. 2004 (WRC Report 1247/2/04), was very thorough in identifying literature that addresses sediment dynamics and geomorphology of estuaries on the subcontinent. Only a few relevant publications could be found that were not already included or have been published since. The main South African publications include Beck et al. (2004), Schumann (2003), van Niekerk et al. (2002), Huizinga and van Niekerk (2002), Theron et al. (2002), Theron (2004a) and Vorster (2001). Recent conference presentations (SAMSS 2005) by Bornman and Adams, Froneman, and James et al. appear particularly relevant but have not been published as yet. Publications that have additional relevant information regarding the selected study sites are Badenhorst (1988), Bell et al. (2001) and Froneman (2002).

Publications relating to estuaries on other continents (especially North America, Europe and Asia) are often not very applicable to South African conditions. However, a few publications were found which are considered worthwhile in respect of this review and are discussed below:

Ranasinghe et al. (1999) explained two different mechanisms for inlet closure of small estuaries on micro-tidal, wave-dominated coasts with strong seasonal variations in river discharge.

Mechanism 1: interaction between inlet current and longshore current
The tidal inlet disrupts the longshore current and with it the longshore sediment transport. A shoal will form up-drift of the inlet because sediment is deposited when the ebb current is reduced and diverted by the longshore current. If the river and tidal flows are strong enough to remove the sediment that is deposited in the mouth, the shoal will not grow and the inlet will remain open. However, if the inlet current decreases, such as during months of low river flow, the shoal may grow and eventually block the inlet (see Figure 2.1).

Mechanism 2: interaction between inlet current and onshore sediment transport
Under stormy conditions, sand eroded from the beach and surf zone is carried offshore and stored. When the storm subsides, the stored sand will be transported onshore. If the ebb flow is strong (i.e. due to high river flow or large tidal ranges) the onshore transport will be disrupted. However, if the ebb flow is weak, the continuous onshore transport can cause closure of the inlet (see Figure 2.1).

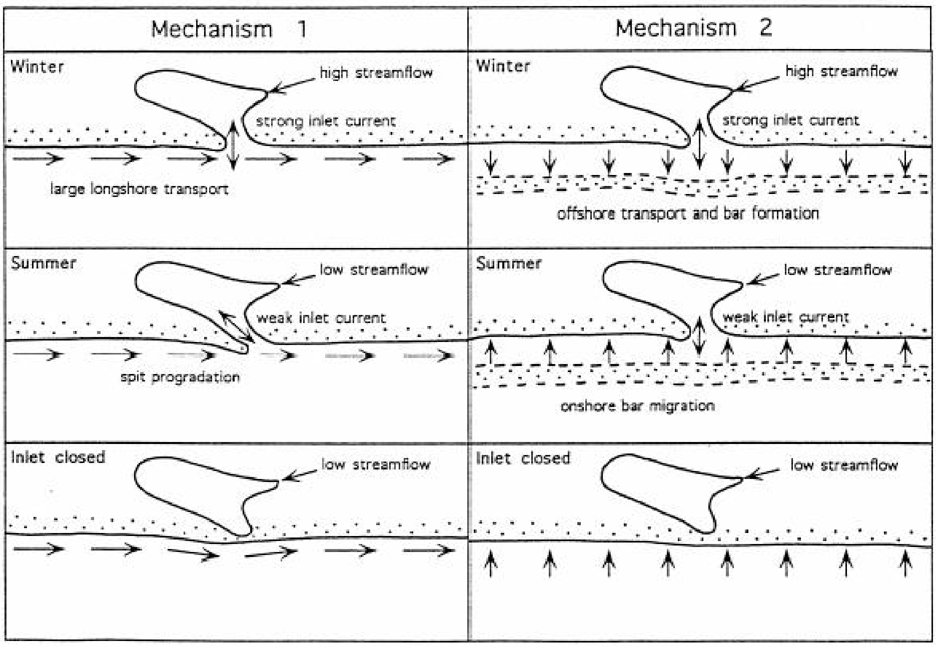


Figure 2.1 Schematic depiction of inlet closure by longshore processes and cross-shore processes.

Aird et al. (2004) elucidate some of the processes responsible for the onshore migration of dynamic sand banks situated adjacent to two United Kingdom estuaries. In these particular cases they found that the sand banks had a net onshore migration, the rates of which were related to the wave energy. Field measurements showed that onshore-directed sediment transport occurs in the inner- to mid-surf zone region at certain times. Short wave stirring suspends sediment, which is then transported by mean flows around the margins of the sand bank in a shoreward direction. The onshore-directed sediment transport is further assisted by the absence of a well-developed undertow on the offshore flank of the sand bank. This can be partially attributed to the typical geometry of the sand bank which is narrow in the longshore direction, enabling the onshore directed momentum flux to be redirected around the sand bank margins, which in turn contributes to the onshore directed mean current along the sand bank margins.

Both of the mouth closure mechanisms described by Ranasinghe et al. (1999) are likely to be applicable to some South African TOCEs. However, in contrast to both the Ranasinghe et al. (1999) Mechanism 2 for mouth closure and the Aird et al. (2004) findings regarding the onshore migration of sand banks, a more direct process is considered to often occur in South African estuaries. In the latter case mouth closure often occurs during sea storms and not some time afterwards when the storm-built bar moves back onshore. High sediment loads are entrained by the turbulent storm wave action and carried into the estuary and mouth area where the sediment is deposited in this lower energy environment (which has a lower sediment carrying capacity). When this deposition rate exceeds the erosion potential of tidal flow, a net sediment build-up occurs. If this situation continues for long enough (sufficient deposition volume), the mouth is closed.

For funnel-shaped estuaries, Prandle (2004) examined how tides and river flow determines size and shape. He also considered how long it takes for bathymetric adjustment, both to determine whether present-day bathymetry reflects prevailing forcing and how rapidly changes might occur under future forcing scenarios. Minimum times for deposition to in-fill estuaries were determined. These times range from a decade for the shortest, shallowest estuaries, to upwards of millennia in longer, deeper estuaries with smaller tidal ranges.

Suprijo and Mano (2004) presented dimensionless parameters for investigating the topography of estuary mouths. Based on the volumetric sediment budget for deposition by littoral drift and removal by river flow and tidal currents, the parameters are obtained from an equation to calculate the time-dependent width of estuary mouths on sandy beaches. The two dimensionless parameters represent the relative importance of actions by river-flows and tides to that by waves. The solutions are examined against estuary mouth data and include a special case that has no river flow.
Other publications from abroad that appear to warrant further investigation are the following: Bryce et al. (1998), Coates et al. (2001), Green and MacDonald (2001), Ranasinghe and Pattiaratchi, (1998) and USACE (2001). Despite the availability of international literature on the topic, there has been a paucity of studies on the hydrodynamics, sediment-dynamics and morphology of South African estuaries. Indeed, only a single limited Cape study on the East and West Kleinemonde estuaries (Badenhorst 1988) covered all the aspects listed above. Overall, the available information on sediment dynamics associated with South African TOCEs is, at best, considered to be poor.

Chapter 1 has already discussed mouth conditions, impacts of river flow and tidal flow, which are all intrinsically related to the sediment dynamics of estuaries. The remaining driver of sediment dynamics in estuaries is linked to coastal processes and this aspect will be examined in more detail below.

LITTORAL SEDIMENT TRANSPORT AND WAVE EFFECTS

Within the coastal zone, there are a number of processes that can transport varying amounts of marine sediments to estuary mouths. Marine sediments that have been transported close to the mouth by such processes are then potentially available to be transported into the estuary itself, mainly by means of tidal flow through the mouth (sometimes in conjunction with wave action). There are also a few processes (such as wind action and wave overwash), which can transport marine sediment directly into the estuary (i.e. tidal flow through the mouth is not necessarily required to facilitate these sediment inputs).

Sediment transport in the nearshore region is usually categorized as longshore (parallel to the shoreline, Figure 2.2) or cross-shore (perpendicular to the shoreline, Figure 2.3). Actual net (usually up-coast) longshore sediment transport of 400 000 - 1 200 000 m^3 per annum (on average) is estimated along most of the exposed, open South African coast, while the potential transport (due to wave energy) is sometimes even higher. Along rocky shorelines or sheltered areas the net average longshore transport rate is mostly between about 10 000 m^3 and 400 000 m^3 per annum (Theron, 2004b).

Extreme cross-shore transport rates are estimated to be as high as 150 000 m^3 over only 2 days for very large sea storms and a shoreline length of 500 m (Theron et al. 2003). Even within the somewhat sheltered Durban Bight, a net cross-shore loss of some 100 000 m^3 has been recorded during a single storm event (Theron 2000a). More typical shorter-term storm net cross-shore rates would be in the order of a few m^3/m per hour for 24 hours. Most southern African sea storms have durations of a few hours to a few days.

On a coastline with an exposed sandy area above the high-water mark, aeolian (wind-blown) sediment transport also plays a role. In general, sediment is very rarely moved by only one mode of transport in the littoral zone; longshore, cross-shore and aeolian sediment transport occurs simultaneously. Even on a long straight shoreline, the current circulation pattern (including rip currents, Figure 2.4) and the associated sediment transport patterns are very complex.

Furthermore, marine sediment transport is dependent on wave and tide conditions with the result that it changes continually, not only in direction and rate, but also in the location where it takes place in the nearshore zone. The sand movements on the seabed near mouths are therefore a complex response to these complex wave and current systems.

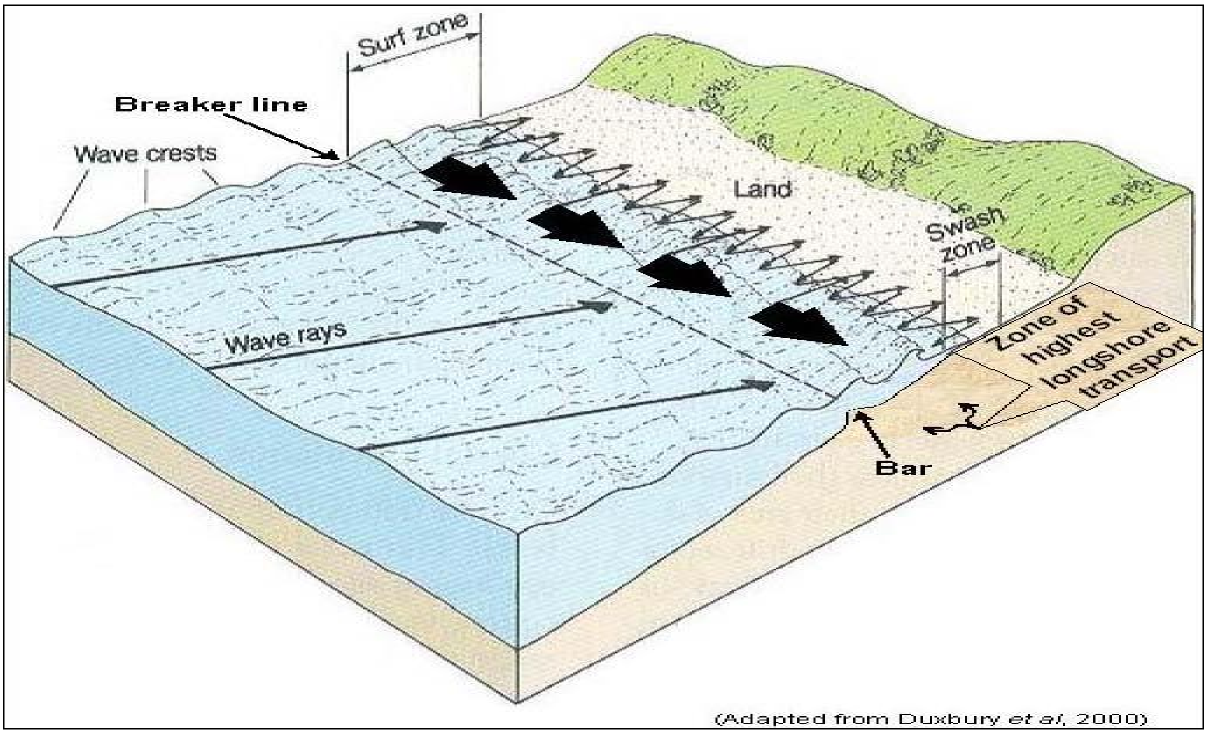


Figure 2.2. Schematic diagram showing longshore transport.

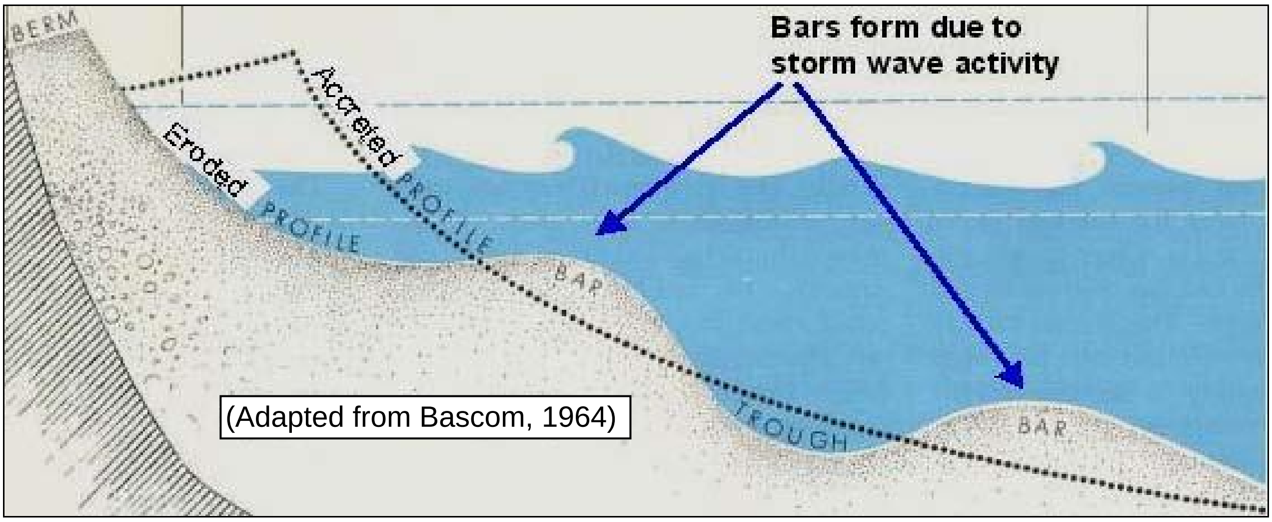
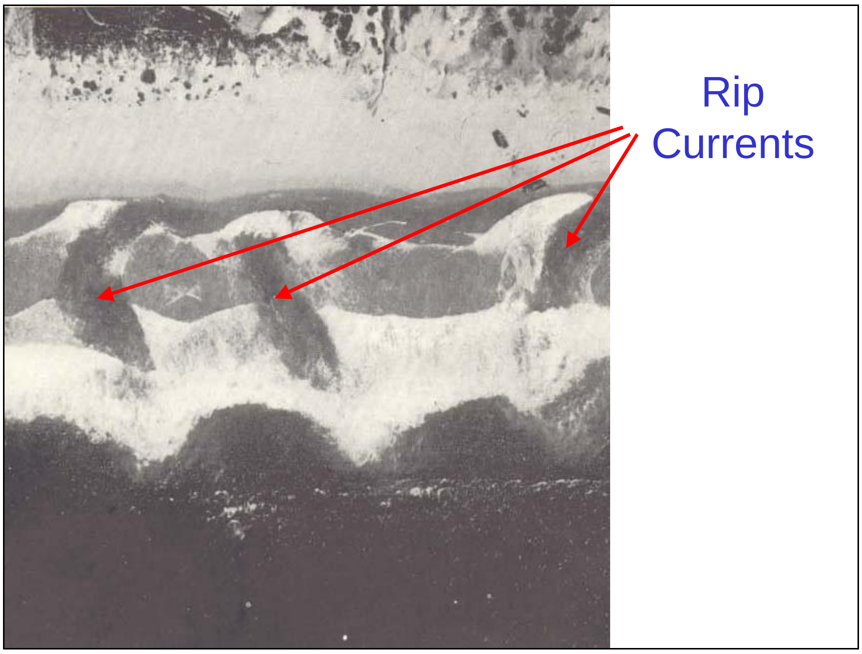


Figure 2.3. Example of cross-shore transport.



(From
http://duedall.fit.edu/
Ocean 1010, Coasts
and Beaches.URL)

Figure 2.4. Aerial photograph showing rip currents.

ORIGIN OF MARINE SEDIMENTS

Sediment found close inshore, including that associated with estuary mouths along the coast, usually originates from fluvial sources and the disintegration of rocks and shells on the seashore, e.g. the dunes around Port Elizabeth comprise mainly $CaCO_3$ (60-90%) derived from marine sources. This does not, of course, mean that the beach sand is not derived from the dunes. It may mean that the dunes themselves are of marine origin and have been uplifted when sea level fell. The major input sources of marine sediment to the inshore area, and thus potentially to estuaries, is beach or dune erosion, possible offshore sources and larger rivers in the region (e.g. Figure 2.5). Periodic flood-derived pulses of sediment are transported to the inshore area from such rivers, but the amounts can vary greatly. Sediment along the coast is continuously being moved and rearranged by wind, wave and current action. Large quantities of sand are moved by wave action, particularly during storms.

In South Africa, high wave energy components usually occur predominantly from the southern quadrant. Under the action of these prevailing wave conditions, sediments can also be moved up coast from river mouth areas towards estuaries located further north (e.g. Figure 2.6).

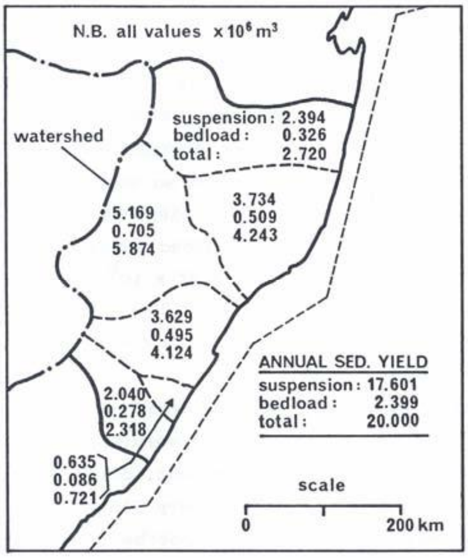


Figure 2.5. Estimates of South African east coast river sediment yield (adapted from Flemming (1981).

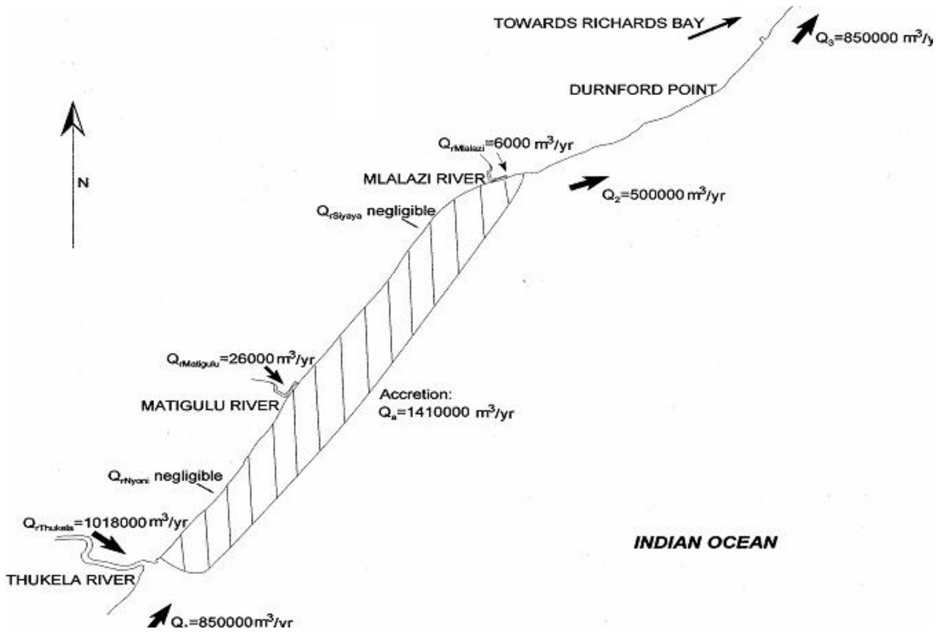


Figure 2.6 Thukela-Mlalazi coastal sediment balance showing the net north-easterly movement of sediments.

When wave directions become more easterly along South Africa’s Indian Ocean seaboard, flood-derived pulses of sediment originating from rivers are likely to be moved south-westward along the coast towards estuaries located further south. Similarly, along South Africa’s Atlantic Ocean seaboard, westerly to north-westerly wave directions could transport fluvial sediments from river mouths towards estuary mouths located further south. However, due to the relatively few river mouths along the west coast, and the mostly large distances between them, the sediment dynamics of an estuary along the west coast is unlikely to be affected significantly by other rivers in the region. If geological time scales are considered, it is of course known that the Orange River used to reach the sea where the Olifants River mouth is presently located and would have influenced sedimentation in that area.

The nature of the drainage areas of large rivers (e.g. Figure 2.7), characterised by rainfall, size, slope, vegetation, farming practices, etc., and the type of sediment source (e.g. easily eroded, fine-grained shale and mudstone, etc.), determines the character of the bulk of the sediments discharged into the sea (e.g. predominantly fine or medium grained). Rivers that drain primarily rocks that are mostly coarse grained and are more resistant to erosion will have considerably lower sediment yields and the sediment supplied to the sea will be largely medium to coarse grained. Most of the sand supplied to the sea will come from the bed load in the river, while relatively little sand will be contributed by the suspended load in the river (as much is too fine). In the sea, the finer particles originating from the river load will be washed out and dispersed (often to deeper water).

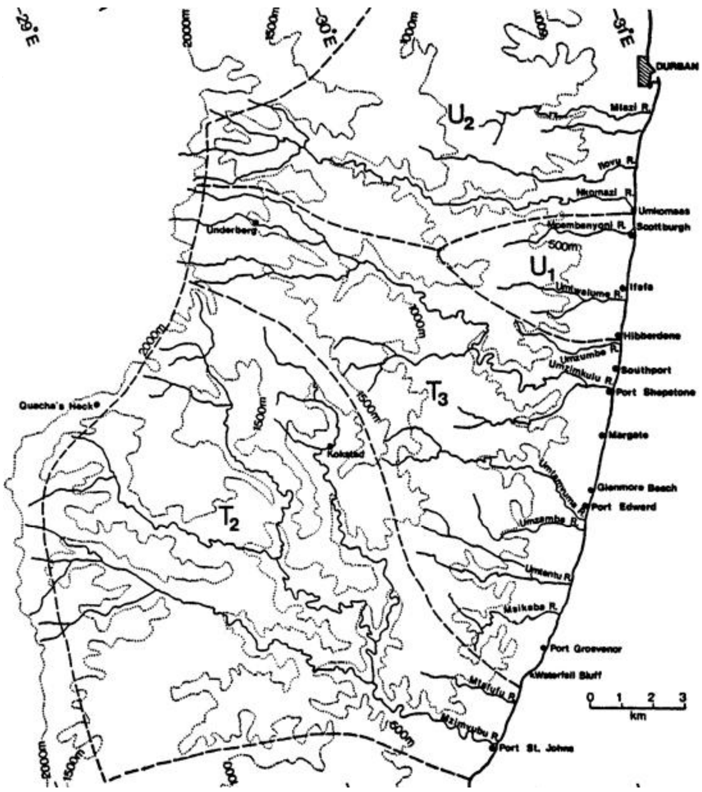


Figure 2.7. KwaZulu-Natal south coast drainage areas

Periodic flood-derived pulses of sediment are also transported into the sea from smaller rivers, but the amounts are usually very small and somewhat intermittent. Some rivers and catchments have been altered by anthropogenic activities (e.g. dams), so that the sediment contribution they made in their natural state has been significantly increased or decreased.

Once deposited in the coastal zone (from various origins as described above) these sediments are now subject to many coastal processes and become marine sediments. From the coastal zone, the marine sediments can once again be transported into estuaries. Therefore, in the long-term, the amount and character of marine sediment transported to estuaries is often ultimately determined by the larger rivers (and the nature of their catchments) within a region. This also implies that ultimately the availability of marine sediment is likely to be affected by progressive changes in river catchments.

MARINE SEDIMENT AVAILABILITY

Marine sedimentation of estuaries is a slow, long-term process. For typical South African estuaries, it is estimated that slight sedimentation rates (the norm) could be in the order of zero to a few thousand $m^3\ y^{-1}$, while extreme rates (very rare cases) may attain 50 000 $m^3\ y^{-1}$ (both total net rates). The latter extreme rates could only occur in large estuaries during exceptional environmental conditions. The total net rate of sedimentation, and even the instantaneous sediment transport rate in an estuary, is orders of magnitude less than typical longshore or cross-shore transport rates (see foregoing sections), which move coastal sediments into the estuary mouth. Even if the longshore transport is sometimes nil, but the coastline at the mouth consists mainly of sand, large amounts of marine sediment is usually stirred up by wave action. A more than ample supply of marine sediment is therefore usually present at estuary mouths, for potential transport into the estuary. Thus, the amount of marine sediment intrusion into an estuary is mainly dependent on the (net) transport capacity of the ebb and flood tidal flows near the mouth, and usually not on the amount of sediment available outside of the mouth. Even the relatively small amounts of direct marine sediment intrusion due to wash over of the berm or aeolian transport could be of the same order of magnitude as the total rate of net long-term sedimentation in some estuaries.

In some estuaries, however, the amount of marine sediment available near the mouth might be very small. This will mostly occur where the shoreline is mainly rocky and little marine sediment is present. Note that a mainly rocky shoreline does not by itself imply that very little marine sediment is present. Significant amounts of sediment could still be moving along such a coast, but, for example, wave conditions are such, that a sand veneer covering the rocks is usually prevented from building up.

In a few instances, the amount of marine sediment available to enter an estuary could also be significantly limited where the estuary mouth is located in a well sheltered area. This will mainly occur in bays and/or in the lee of points/headlands or reefs. In other cases the mouth area may be sandy but little marine sediment is stirred up or transported alongshore due to a lower wave action. In such cases the amount of sediment moving into the mouth is likely to be very low, which means that if the estuary is relatively small the mouth could still take decades to close, even if river flooding rarely occurs.

TIDAL TRANSPORT, FLOOD EFFECTS AND LONG-TERM SEDIMENT BALANCE

Besides river flow, the main hydraulic driver in the estuary is the ocean tide. Tidal sediment transport in estuaries is a result of the interaction of both currents and waves, which is especially important in the mouth region. Inside the estuary, wave action is generally rapidly reduced. Wave-current interaction considerably complicates sediment transport predictions. However, wave action is generally much reduced inside an estuary and traditional river sediment transport equations are often applied.

During neap tides, maximum water velocity within the estuary is low with little sediment transport, while both velocity and transport increase towards spring tides. Most significant, however, is that in some estuaries over this neap to spring period there is a net upstream sediment transport, e.g. in the Goukou (Theron 2004a). In other words, there is a net upstream movement of marine sediment within the estuary. If there is a long-term net ingress of marine sediment (which is often the case), then the only plausible way for a long-term equilibrium to be established is if large river floods, on occasion, flush out this accumulated sediment.

Floods are the most important natural means of eroding and transporting sediments out of estuaries. Large volumes of sediment can be removed in a very short time during major floods with a return period of 1 in 50 years and more. Smaller floods with return periods of 1-2 years can sometimes also have a significant influence. Floods therefore play a major role in the equilibrium between sedimentation and erosion in estuaries (Beck et al. 2004). In this regard it would be very useful to investigate the hydrology of a river and also determine the magnitude of flood required to effectively flush out sediment from the estuary.

The effect of a river flood on a relatively small permanently open estuary (Goukou) was investigated by Theron (2004a). Water levels were recorded in the estuary during a flood that had an estimated return period of about 1 in 10 years. The effect of the flood on the water level was clearly discernible. Of importance is the fact that the maximum water level during this particular flood did not even attain the level reached during spring tides. This means that in the lower part of the estuary, flow velocity and sediment transport potential during this event were not even as high as that during spring tide. It seems that a flood with a significantly greater return period, or extended high river discharge rates due to prolonged heavy rainfall in the catchment, would be required to affect large scale scouring of the sandbanks in the lower Goukou Estuary.

SITE SPECIFIC INFORMATION ON PHYSICAL COASTAL PARAMETERS

Only the main coastal parameters relevant to the present study are discussed here. The near-shore wave climate, which plays an integral role in the generation of near-shore currents and sediment transport, is dependent on the deep-sea wave conditions and the near-shore wave processes. *Wave height* and *period* are two of the parameters that describe the near-shore wave climate. From the wave height data a wave height distribution curve can be determined. The *slope* of the *wave height exceedance curve* gives a relative indication of the severity of wave action at a beach, i.e. the sea is rough more often in areas with steeper wave-height exceedance curves. Wave energy (and associated sediment transport) is the main driving force for mouth closure along the South African coastline. Therefore, the potential closing forces are greatest at estuaries where the wave height gradient is steepest.

The *longshore sediment transport rate* is calculated from the wave climate and also takes into account the sediment *grain size*. A gradient in the longshore transport can result in either the net removal of sediment (if longshore transport increases) or deposition (if longshore transport decreases). For the same amount of input wave energy, fine-grained sand results in much higher rates of longshore transport than coarse sand. This factor is, for example, generally considered to be one of the major reasons for probable differences between KwaZulu-Natal and Cape TOCEs, but needs to be investigated further.

Profile slopes: The type of wave breaking, the extent of near-shore currents and the strength of the backwash are all directly related to the slope of the tidal face of the beach. An increase in this slope will lead to more severe surf conditions, with more sediment entrainment and availability for transport into an estuary mouth. Beach profile slopes can be directly related to *sediment grain sizes* (e.g. Wiegel 1964) and are usually also indicative of the wave energy distribution along the coast. To determine the degree of exposure of a beach, it is important to know both the beach slope and the median grain size, because these parameters are interlinked. Representative surface sediment samples are taken from the beach between the high and low tide line along the study area to assess the energy status of the coastline and to assess the marine and aeolian sediment transport potential.

Beach type: Beaches are globally categorised according to one of six types, viz. dissipative beaches, four classes of intermediate beaches and reflective beaches. Reflective beaches have a steep beach face with surging breakers that are reflected back towards deeper water. Dissipative beaches have flat beach slopes and the wave energy is dissipated gradually in deeper water further away from the beach.

Wave breaker type: The degree and type of wave breaking determines the rate of energy dissipation and is also an important parameter in other near-shore processes. Spilling waves gradually dissipate energy while plunging waves dissipate most of their energy at the breakpoint. Collapsing and surging waves dissipate energy close to the shoreline. The *surf*

zone width influences the amount of energy dissipation in the surf zone. A wide surf zone with many re-breaks means that energy is dissipated over a wider area further away from the shore. These parameters, for example, determine whether the zone of high sediment entrainment is located close to the shoreline, thus enabling easy transport into the estuary (and potential mouth closure), or further offshore, which makes transport into the estuary (and mouth closure) more difficult.
Berm dimensions: Besides also being related to wave conditions and sediment characteristics (and sometimes also aeolian transport), berm formation and berm dimensions obviously have a direct impact on mouth closure/breaching, overwash into estuaries, or seepage (both to and from the sea).

Cusps: Beaches are usually not straight, in that the water line is not straight but made up of a series of cusps. Cusps are defined as a series of low mounds of beach material separated by crescent-shaped troughs spaced at more or less regular intervals along the beach face. These cusps are important indicators of hydraulic processes taking place within the surf-zone. The extent of cuspate formation is also an indication of the strength of nearshore currents, especially *rip currents* near the crests of cusps. The angle between the crest of initial breakers and the local seabed contours (wave incidence angle) has a major effect on near-shore currents. Rip currents and cusps can lead to local offshore directed sediment transport.

AVAILABLE INFORMATION

One of the objects of this review was that it should also focus on the similarities and differences between Cape and KwaZulu-Natal TOCEs. Scant information in terms of sediment dynamics and coastal processes/parameters are available regarding most South African estuaries. However, there are limited data from certain systems and some of the more relevant literature from the East and West Kleinemonde estuaries in the Eastern Cape and the Mdloti and Mhlanga estuaries in KwaZulu-Natal is outlined below.

Information from CSIR (2000) contains sediment and survey data from the East and West Kleinemonde estuaries. Sand samples taken from the mouth areas of these estuaries indicated their sediment grain sizes (Table 2.1).

Typical beach slopes on the western side of the West Kleinemonde mouth (31 January 1988 and 7 July 1988) between 0 and +2 m MSL were about 1 in 18. Badenhorst (1988) also contains sediment and survey data from these estuaries. Beach slopes on the western side of the combined mouth area were calculated to be about 1 in 21, while beach slopes on the eastern side of the combined mouth area were about 1 in 24. Three vibracores taken near the bridge across the West Kleinemonde all showed median grain sizes (D50) of about 250 micron up to depths of about 1.4 m.

Table 2.1 Sediment grain size distribution of samples taken from the combined East and West Kleinemonde mouth area.

Date	D10* (micron)	D50** (micron)	D90*** (micron)
7 July 1988	182	238	290
30 July 1996	195	265	338
9 March 1999	177	249	311

* D10 means that 10% of the sample is equal to or smaller than the given value;
** D50 means that 50% of the sample is equal to or smaller than the given value, i.e. the median grain size;
*** D90 means that 90% of the sample is equal to or smaller than the given value.

To determine the degree of exposure of a beach, it is important to know both the beach slope and the median grain size because these parameters are interlinked. An increase in this slope will lead to more severe surf conditions closer to the shoreline, with more sediment entrainment and availability for transport into the estuary mouth (and therefore potential closure).

Data from KwaZulu-Natal estuaries indicates that those systems typically have steeper beach profiles and are therefore more prone to closure or close sooner than those in the Eastern Cape. In this connection useful information regarding the coastal processes/parameters in these areas is contained in Theron (1992, 2000a, 2000b and 2003) as well as CSIR (1999). Additional relevant information regarding the near shore wave regime in the Eastern Cape is contained in Theron (2004b). Further datasets will certainly contribute to quantitative comparisons between Cape and KwaZulu-Natal estuaries and provide useful relationships between physical parameters and estuarine regimes.

PRELIMINARY CONCLUSIONS

The ecology of an estuary is closely related to its physical character, which is determined by the hydrodynamics, sediment regime and state of the river mouth. Although a good knowledge basis has been laid, there is a dire need for improved understanding of, and especially predictive capabilities regarding, the hydrodynamics and sediment dynamics in estuaries. Through the understanding of these processes and using predictive capabilities, ecologists could be provided with essential information on the physical behaviour of the system. This is also required for the effective implementation of new policies in estuaries, such as those contained in the South African Water Act (No. 36 of 1998).

A more than ample supply of marine sediment is usually present at estuary mouths for potential transport into the system. Thus, the amount of marine sediment intrusion into an estuary is mainly dependent on the (net) transport capacity of the ebb and flood tidal flows near the mouth, and usually not on the amount of sediment available outside of the mouth. Even the relatively small amounts of direct marine sediment intrusion due to berm overwash or aeolian transport could be of the same order of magnitude as the total rate of net long-term sedimentation in some estuaries. In certain estuaries, however, the amount of marine sediment available near the mouth is very small (mostly where the shoreline is predominantly rocky). In a few instances, where the estuary mouth is located in a well sheltered area such as bays and in the lee of points/headlands or reefs, the amount of marine sediment available might also be small.

One of our primary objectives should be to develop techniques to quantify the slow rate of sedimentation due to tidal flows and also the flushing effects of large floods. An integrated approach of selected field measurement techniques combined with appropriate modelling techniques will be the most efficient route to achieve these aims. In the long-term it is not affordable to do extensive field measurements in a great many South African estuaries. Thus, limited key field data should be collected and, using this as input, make use of mathematical models to simulate estuarine sediment dynamics and predict the consequences of changes in the system or impacts of management actions.

Small estuaries, which commonly have narrow mouths, provide a unique area of application where this type of morphological investigation has rarely been attempted (as far as could be ascertained from the literature survey). The results of previous field measurements and modelling proved enlightening and yielded valuable new information regarding the hydro- and sediment dynamics of South African estuaries in general. It appears that we have workable tools to quantify previously unknown, but important, aspects of the sediment dynamic processes in South African estuaries. The focus should now also include:
(a) Quantification of the long-term sediment balance based on extrapolation from shorter term field data and modelling techniques.
(b) Quantify flushing of sediments at estuary mouths during breaching events and during various realistic river flood regimes (i.e. return periods of say 1-in-5, 1-in-20 or 1-in-50 years) from field measurements and modelling.
(c) Develop techniques (modelling, etc.) for predicting estuarine morphology in cohesive sediment environments. The research to date has mainly focused on sediments that have no cohesion, and our understanding of cohesive sediment dynamics (as found in many South African estuaries) is not as well developed.

It seems that limited field investigations, coupled with numerical modelling, is an appropriate tool for studying hydro- and sediment dynamics in South African estuaries. At this stage it appears possible to simulate sediment dynamics reasonably well. A concern, however, is that the expected budgets for many future contracts in this field (e.g. Rapid and Intermediate

Reserve studies) would be too small to enable the amount of effort required for the fieldwork and modelling. The literature shows that the sediment balance in estuaries often relies on a subtle balance between dominant flood and ebb tide flows. It is therefore not correct to simply conclude that sedimentation occurs upstream due to the stronger flood tide since the cross-sections and durations of the flow differ during the two tidal phases. Wave action can be an important stirring mechanism in the mouth and it is important to include suspended sediment transport in modelling work. Although fieldwork and modelling provide a good understanding, there are still additional aspects to include such as time varying roughness changes. For long-term and long reach investigations, one-dimensional (or quasi-two-dimensional) model simulations will also be required in future.

Despite the availability of the above literature, to date there has been a paucity of studies on the hydrodynamics, sediment-dynamics or morphology of South African estuaries, and none (with the exception of one limited study) directed at eastern and southern Cape estuaries in terms of all these aspects. Therefore, overall the available information is at best considered to be poor.

INTERIM RECOMMENDATIONS

Further research is required on the following aspects:

1. For most South African estuaries, very little real data are available regarding sediment transport or estuarine morphology. More detailed, high quality survey data will aid the accurate determination of long-term progressive change in estuarine bathymetry. Regular bathymetric surveys of the whole estuary will provide invaluable information regarding the bathymetry and possible evolution of the system. In order to obtain more quantitative information on flows and sediment transport, further field data should also be collected.
2. The information on the perceived sedimentation in many estuaries needs to be expanded. Only in a few instances has clear evidence of progressive sedimentation actually been obtained. In many cases, it appears that very little has been done to quantify and establish detailed facts on this issue.
3. Modelling and field measurements are required to quantify the effects of a range of river floods on local sediment transport and to determine which floods have any significant effect on the overall sedimentary regime.
4. The combined longer term effects of possibly small net marine sedimentation and river floods on local sediment transport patterns, and ultimately on estuarine morphology, should be investigated further as this will contribute to a more complete understanding of the evolution of estuarine morphology.
5. The integration of field measurements and modelling to predict sediment transport and resultant bottom changes should be expanded. This would be especially useful to quantify the effects on the transport regime of different proposed modifications (e.g. new dams or increased freshwater abstraction, or groynes/breakwaters to ‘stabilise’ estuary mouths) to an existing scenario.

6. Since this project is also designed to inform the DWAF RDM process (DWAF 2004), emphasis needs to be placed on the consequences of reduced river flow/increased closed mouth phases on Cape TOCEs.
7. New datasets are required in order to make suitable comparisons of Cape and KwaZulu-Natal TOCEs.

REFERENCES

Aird NP, Davidson MA and Marino-Tapia IJ (2004) Physical processes associated with onshore sand bank migration adjacent an estuary mouth. Proceedings of the 29th International Coastal Engineering Conference, Lisbon, Portugal. World Scientific Publishing Co. Pty. Ltd., Plymouth, Devon, U.K.

Badenhorst P (1988) Report on the dynamics of the Kleinemonde West and East estuaries (CSE 13 and 14). *CSIR Report EMA-T **8805***, Stellenbosch. 31 pp.

Bascomb WN (1964) Waves and beaches. In: *Beaches*. Doubleday, New York, Chapter IX pp. 184-212.

Beck JS, Kemp A, Theron AK, Huizinga P and Basson GR (2004) Hydraulics of estuarine sediment dynamics in South Africa: Implications for Estuarine Reserve determination and the development of management guidelines. *WRC Report No. 1257/1/04*. Pretoria, South Africa.

Bell KNI, Cowley PD and Whitfield AK (2001) Seasonality in frequency of marine access to an intermittently open estuary: Implications for recruitment strategies. *Estuarine, Coastal and Shelf Science* **52** 327-337.

Bornman TG and Adams JB (2005) Sensitivity of small intermittently open estuaries to freshwater inflow alterations in the Tsitsikamma region. SAMSS Conference, Durban.

Bryce S, Larcombe P and Ridd PV (1998) The relative importance of landward-directed tidal sediment transport versus freshwater flood events in the Normanby River estuary, Cape York Peninsula, Australia. *Marine Geology Journal* **149** (1-4) 55-78.

Coates M.J, Guo Y and Davies PA (2001) Laboratory model studies of flushing of trapped salt water from a blocked tidal estuary. *Journal of Hydraulic Research* **39** (6) 601-609.

CSIR (1999) Durban wave and wind recording annual summary report March 1998 to February 1999. *CSIR Report ENVS-C 99052*, Environmentek, Stellenbosch.

CSIR (2000). South African estuaries; Data report on topographical surveys for selected estuaries: 1985 - 1999, Volume II - Eastern Cape. *CSIR Report ENV-S-C 2000-120B.* Environmentek, Stellenbosch.

Department of Water Affairs and Forestry (DWAF) (2004) Water resource protection and assessment policy implementation process. Resource Directed Measures for protection of water resources: Methodology for the determination of the ecological water requirements for estuaries (Version 2). DWAF, Pretoria.

Flemming BW (1981) Factors controlling shelf sediment dispersal along the southeast African continental margin. *Marine Geology* **42** 259-277.

Froneman PW (2002) Seasonal changes in selected physio-chemical and biological variables in the temporarily open/closed Kasouga , Eastern Cape, South Africa. *African Journal of Aquatic Science* **27** 117-123.

Froneman PW (2005) Significance of overtopping events in Eastern Cape temporarily open/closed estuaries. SAMSS Conference, Durban.

Green MO and MacDonald T (2001) Processes driving estuary infilling by marine sands on an embayed coast. *Marine Geology* **178** (1-4) 11-37

Hay ER (1984) Sediment dynamics on the continental shelf between Durban and Port St Johns (southeast African continental margin). Marine Geoscience Unit, Department of Geology, University of Cape Town, Bulletin No. 13.

Huizinga P and van Niekerk L (2002) The role of river flow in maintaining physical processes in South Africa's estuaries. In: Enviro Flows 2002. Proceedings of the International Conference on Environmental Flows for River Systems, Cape Town.

James, N.C., Whitfield, A.K., and Cowley, P. D. (2005) A long-term study of the fish community of the East Kleinemonde Estuary, South Africa, with evidence for global warming. SAMSS Conference, Durban.

Perissinotto R, Blair A, Connell A, Demetriades NT, Forbes AT, Harrison TD, Lyer K, Joubert M, Kibirige I, Mundree S, Simpson H, Stretch D, Thomas C, Thwala X and Zietsman I (2004) Contribution to information required for the implementation of Resource Directed Measures for estuaries (Volume 2). Responses of the biological communities to flow variation and mouth state in two KwaZulu-Natal temporarily open/closed estuaries. *Water Research Commission Report No. 1247/2/04.*

Prandle D (2004) Review: How tides and river flows determine estuarine bathymetries. *Progress in Oceanography* **61** 1–26.

Ranasinghe R, Pattiaratchi C (1998) Flushing characteristics of a seasonally-open tidal inlet: A numerical study. *Journal of Coastal Research* **14** (4) 1405-1421

Ranasinghe R, Pattiaratchi C and Masselink G (1999) A morphodynamic model to simulate the seasonal closure of tidal inlets. *Coastal Engineering* **34**, 1-36.

Schumann EH 2003 (ed.) Towards the management of marine sedimentation in South African estuaries with special reference to the Eastern Cape. *WRC Report No. 1109/1/03.*

Suprijo T and Mano A (2004) Dimensionless parameters to describe topographical equilibrium of coastal inlets. *Proc. of the 29th International Coastal Engineering Conference, Lisbon, Portugal,* World Scientific Publishing Co. Pty. Ltd., UK.

Theron AK (1992) Natal north and south coast - Beach evaluation. *CSIR Report EMAS-C 92001*, Ematek, Stellenbosch. 16 pp.

Theron AK (2000a) Durban beach monitoring progress report: July 1998 to June 1999, Volume I. *CSIR Report ENV-S-C 2000 – 022A*. Environmentek, Stellenbosch.

Theron AK (2000b) Setback line for the coastal zone: Tongaat Beach - Ohlanga. *CSIR Report ENV-S-2000-071*. Environmentek, Stellenbosch. 42 pp.

Theron AK (2003) Setback line for the coastal zone: Msimbazi to Mahlongwana River mouth, and Mgeni to Ohlanga River mouth. *CSIR Report EMAS-C 2003-088*. Environmentek, Stellenbosch. 47 pp.

Theron AK (2004a) SA estuarine hydro- and sediment dynamics: Marine sediment yields. Goukou fieldwork and workshop proposals. *CSIR Internal Report ENV-S-I 2004-022*. Environmentek, Stellenbosch.

Theron AK (2004b) Sediment transport regime at East London. M.Eng. thesis, University of Stellenbosch, Stellenbosch.

Theron AK, Diedericks GPI, Huizinga P, Basson GR and Kemp A (2002) Measurement and modelling of sediment dynamics in estuaries. In: Enviro Flows (2002). Proceedings of the International Conference on Environmental Flows for River Systems, Cape Town.

Theron AK, Schoonees JS, Huizinga P and Phelp DT (2003) Beach diamond mining design at the rocky Namaqualand coast. Proceedings, 4th Coastal Structures Conference, ASCE, Portland, Oregon.

USACE (2001) Hydrodynamics of tidal inlets. In: Coastal Engineering Manual, Part 2, Chapter 6: 1-73. Engineer Manual 1110-2-1100, U.S. Army Corps of Engineers, Washington, DC. U.S.

Van Niekerk L, Huizinga P and Theron AK (2002) Semi-closed mouth states In Estuaries along the South African coastline. Enviro Flows 2002. Proceedings of the International Conference on Environmental Flows for River Systems, Cape Town.

Vorster JA (2001) Evaluation of hydrological and hydraulic processes on sedimentation of estuaries. MSc thesis, Universities of Lausanne, ETH (Zurich) and Neuchatel. 120 pp.

Wiegel RL (1964). Oceanographical Engineering. Fluid Mechanics Series. Prentice-Hall Inc., Englewood Cliffs. 532 pp.

SELECTED FURTHER READING

Cooper JAG (2002) The role of extreme floods in coastal behaviour: contrasts between river- and tide-dominated microtidal estuaries. *Sedimentary Geology* **150** (1-2): 123-137.

Cooper JAG, Mason TR, Reddering JSV and Illenberger WI (1989) Geomorphological effects of catastrophic fluvial flooding on a small subtropical estuary. *Earth Surface Processes and Landforms* **15**: 25-41.

Flemming BW (1981) Factors controlling shelf sediment dispersal along the southeast African continental margin. *Marine Geology* **42**: 259-277.

Harrison TD Cooper JAG and Ramm AEL (2000) Geomorphology, ichthyofauna, water quality and aesthetics of South African estuaries. *CSIR Report ENV-DC 2000-01*, Environmentek, Congella.

Reddering JSV and Rust IC (1990) Historical changes and sedimentary characteristics of southern African estuaries. *South African Journal of Science* **86**: 425-428.

Van Rijn LC (1993) Principles of sediment transport in rivers, estuaries and coastal seas. Aqua Publications, Amsterdam, The Netherlands.

3. WATER QUALITY

Gavin Snow [1] and Susan Taljaard [2]

[1] Botany Department, Nelson Mandela Metropolitan University, Port Elizabeth; [2] CSIR, Stellenbosch.

INTRODUCTION

The purpose of this review is to provide an overview of the water quality (or biogeochemical) features and characteristics of temporarily open/closed estuaries (TOCEs) in the warm-temperate and cool-temperate biogeographic regions of the Eastern and Western Cape Provinces of South Africa.

To provide focus to this literature review, the following approach was followed:
A simple conceptual (or hypothetical) model on the water quality (or biogeochemical) structure and characteristics of TOCEs in South Africa were developed, based on current understanding. Thereafter available literature on estuaries in the warm-and cool-temperate biogeographic regions of South Africa (Cape systems) was reviewed and assessed against this conceptual model. Finally, preliminary conclusions on whether the water quality structure and characteristics of TOCEs can be explained by such a generic conceptual model are provided. The review focuses on the following water quality parameters: salinity, temperature, pH, dissolved oxygen, turbidity, and inorganic nutrients.

CONCEPTUAL MODEL FOR WATER QUALITY CHARACTERISTICS IN TOCEs

To provide a conceptual model for the water quality characteristics of TOCEs, it is important to provide background on typical abiotic states that can occur within these estuaries. For this perspective, there are three dominant hydrodynamic states in which TOCEs can exist, namely:

Mouth open: In this state the mouth of the is open to the sea allowing seawater intrusion during high tides with river inflow introducing freshwater into the upper reaches.

Mouth semi-closed: In this state the berm height prevents continuous seawater intrusion during high tides, i.e. seawater intrusion is limited e.g. only during spring high tides, called 'overwash'. However, the berm is not high enough to prevent some water draining from the estuary into the sea or the freshwater inflow is sufficient to maintain a continuous outflow.

Mouth closed: In this state the height of the berm prevents seawater from entering the estuary as well as water draining from the estuary into the sea. Low volumes of river water could still be entering the estuary and sporadic overwash of seawater can occur depending on conditions at sea and berm height.

Depending on factors such as estuary size, beach profiles and mouth protection all three of these states can occur (3-phased systems) or only the open and closed states (2-phased systems). These relationships are discussed in further detail as part of the hydrodynamic review. In the following sections possible water quality characteristics associated with each of the above states are provided.

Salinity

The characteristic salinity distribution patterns expected under each of the three states described above are provided below:

Mouth Open: When the mouth is open a longitudinal salinity gradient exists in the estuary (Figure 3.1). The position of the haloclines depends on the extent of river inflow. In some systems vertical stratification can also develop in this state, usually in systems where the middle and upper reaches are characterised by deeper areas, e.g. Palmiet.

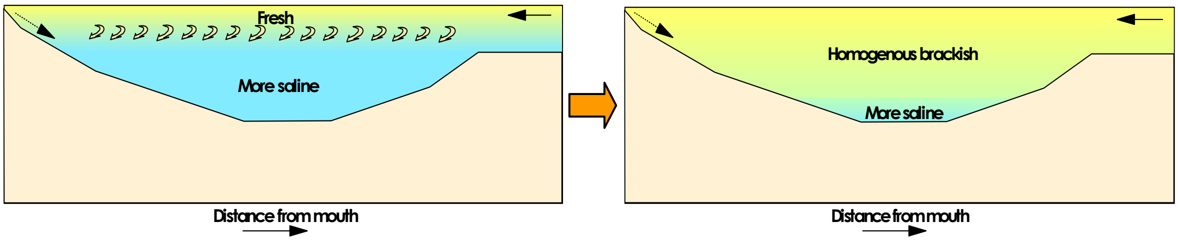


Figure 3.1. Normal salinity conditions in a TOCE when the mouth is open to both seawater and river water (mouth on the left hand side).

Mouth semi-closed: The semi-closed state is typical during periods of low fresh water input, creating a strong longitudinal salinity gradient. Inflowing fresh water is restricted to the surface of the estuary, thus trapping more saline water in deeper areas. At the onset of this state, vertical stratification usually develops as a result of low density freshwater flowing across higher density saline water (Figure 3.2). Through entrainment of freshwater into the more saline bottom layer, as well as wind mixing forces, the estuary gradually changes into a homogenous brackish water body. The duration of the stratified conditions depends on river inflow, the strength of wind mixing force and the depth of the estuary. For example, a shallow system, subject to strong wind mixing, will become a homogenous water body much faster than a deep, wind protected system. Periodic intrusion of seawater (e.g. during spring high tides) may sustain more saline conditions in deeper areas near the mouth. If the semi-closed state persists for a few months at a time and there is little or no overwash, then salinity throughout the estuary may decrease due to entrainment as the fresh water ‘erodes’ into the more saline bottom water or from wind mixing.

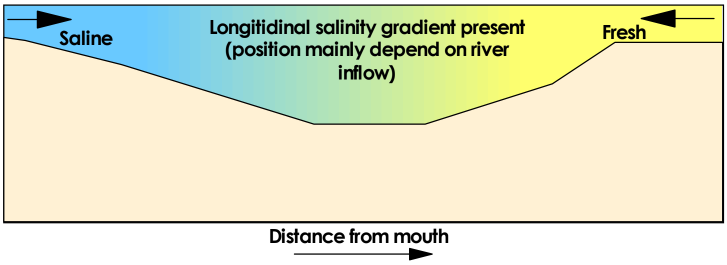


Figure 3.2 Vertically stratified salinity conditions becoming mixed by wind to homogenous brackish in the semi-closed mouth state (mouth on the left hand side).

Mouth closed: In the closed mouth state, salinity throughout the water column is near homogenous (Figure 3.3), although some vertical and longitudinal stratification may be evident immediately after closure. Depending on the height of the berm and conditions at sea, sporadic overtopping of seawater (or seawater overwash) can occur during this closed state.

This results in a change of bottom water, the extent of which depends on the volume of seawater entering the estuary and the bathymetry. Continued river input may result in systems gradually becoming fresher, while the absence of river inflow may result in the system gradually becoming more saline or, in some instances, even hypersaline.

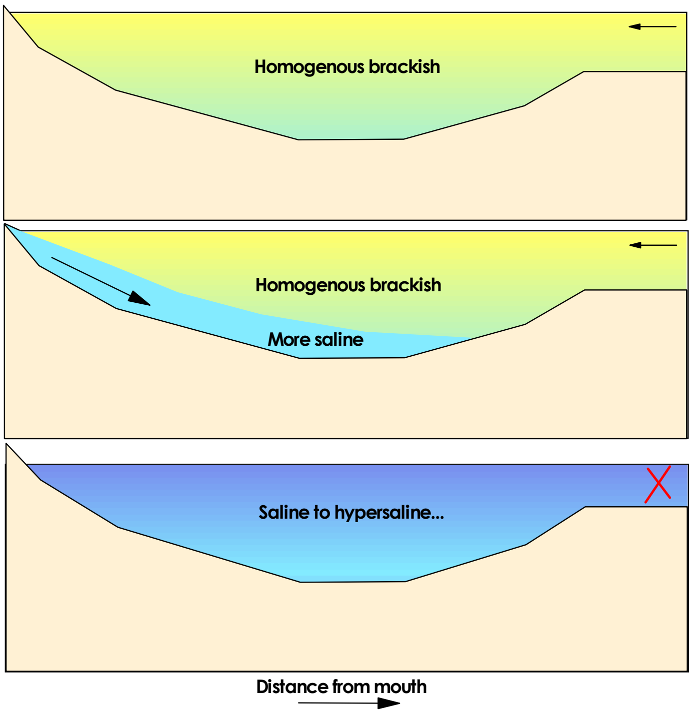


Figure 3.3. Salinity during the closed mouth condition is near homogenous throughout the water column, although some vertical and longitudinal stratification may be evident immediately after closure. Over wash events may introduce more saline water to deeper reaches of the estuary (mouth is on left hand side).

Temperature

In TOCEs, water temperature is usually a function of seasonal trends in atmospheric temperature. Although the achieved temperature will obviously depend on local atmospheric temperature, strong seasonal signals are expected in temporal regions where winter temperature typically ranges between 15-20^{o}C with summer temperatures between 20-25^{o}C.

Water temperature in estuaries is also subject to prevailing sea conditions, particularly during the open mouth state. For example, coastal areas along the cool temperate zone of South Africa, particularly the west coast, are regularly subject to upwelling when cold bottom waters are brought to the surface. The temperature of newly upwelled waters can range between 9 and 14^{o}C, depending on the strength of the upwelling event (DWAF 1995). Along the west coast these events are usually most prevalent during spring/summer (Monteiro and Largier 1999) under off-shore wind conditions. For the foregoing reasons, when estuaries are in the open mouth state, sea conditions (e.g. upwelling) can also influence water temperature, particularly in the lower and middle reaches of the estuary. If this happens, for example in summer, a strong longitudinal temperature gradient can develop with the colder water near the mouth and temperatures becoming significantly warmer upstream.

pH

Typically, the pH of estuarine waters is influenced by the sources flowing in, namely the river and the sea. Seawater pH is known to range between pH 7.9 and 8.2 (DWAF 1995), while that of river water is usually a function of catchment characteristics. For example, rivers draining Table Mountain quartzite are usually rich in humic acids originating from typical vegetation found in these soils) and characterised by low pH levels (~4). However, as a result of the strong buffering capacity of seawater, pH levels in estuarine water are usually within the range 7.0-8.5.

Dissolved oxygen

In estuaries the decrease in dissolved oxygen is mainly caused by the degradation of organic material through bacterial activity, which consumes available oxygen. These can be as a result of natural processes but can also be triggered by anthropogenic sources of nutrients and organic material such as fertilizers applied to agricultural fields, golf courses, and suburban lawns; deposition of nitrogen from the atmosphere; erosion of soil containing nutrients; and sewage treatment plant discharges (United States Geological Survey - http://toxics.usgs.gov).

Hypoxia or ‘low oxygen’ levels is the concentration that can cause organisms to become stressed or die. Oxygen concentrations less than 2-3 mg.l-1 can be regarded as hypoxic and often arise following eutrophication within an estuary. Anoxia arises when there is a complete lack of oxygen (0 mg.l^{-1}). Dissolved oxygen concentrations greater than 3 mg.l^{-1} are unlikely to result in the stress or death of organisms. Dissolved oxygen concentrations greater than 3 mg l^{-1} are unlikely to result in the stress or death of organisms. There are characteristic oxygen distribution patterns that are usually expected in under each of the three mouth states:

Mouth open: During the open state, TOCEs are expected to be well oxygenated (levels above 6 mg l^{-1}) because there is good water exchange through tidal flushing and river inflow.

Mouth semi-closed: During the semi-closed state, strong vertical stratification may prevent proper aeration of bottom waters. Depending on the duration of these stratified conditions and the organic load, bottom waters may become low in oxygen (< 3 mg l^{-1}). If vertical stratification is broken down and the water column becomes well mixed again (e.g. wind mixing), oxygenated waters get re-introduced into the bottom layers (Figure 3.4). Lower oxygen levels (< 3 mg l^{-1}) may still occur in the deeper, more saline pools, which are 'cut off' from surface waters as a result of strong vertical stratification persisting at depth (i.e. the winds were not sufficiently strong to 'break down' stratification throughout the water column).

Mouth closed: During the closed state, the water column is expected to be relatively homogenous with no marked vertical stratification. As a result, wind mixing is likely to maintain aerated conditions throughout the water column. However, lower oxygen levels may still occur in deeper, more stagnant pools, depending on factors such as organic loading. During an overwash event, low oxygen bottom water can be replaced with new well-oxygenated seawater, depending on the volume of water that enters the system.

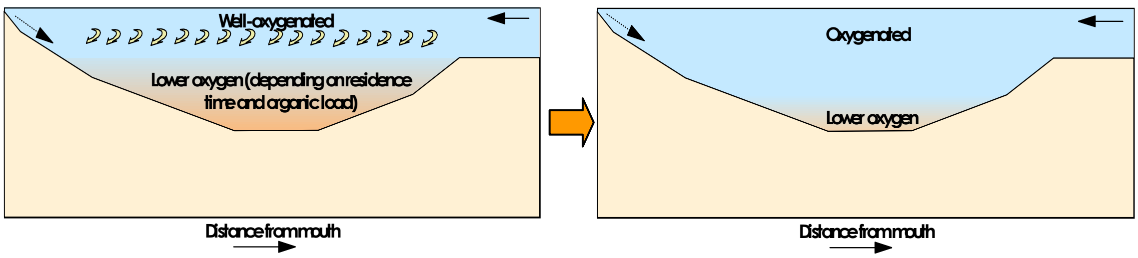


Figure 3.4 Schematic illustration of the progressive change expected in dissolved oxygen characteristics in an TOCE under the semi-closed state.

Turbidity

Estuarine water turbidity, usually reported in NTUs (Nephelometric Turbidity Units), is largely a function of concentrations in the water sources (i.e. the river and the sea), bottom sediment composition (i.e. mud versus sand, water depth and wind mixing. Usually the turbidity levels in seawater entering estuaries along the cool and warm temperate regions of South Africa are relatively low (< 10 NTU). The turbidity of river water flowing into an estuary can vary greatly, depending on catchment geology as well as agricultural practices within the catchment.

Sediment characteristics and physical features within the estuary can also play a role, e.g. wind mixing forces can create turbid conditions in shallow systems, characterised by fine bottom sediments, through re-suspension. Turbidity characteristics of estuaries are therefore site-specific and can be predicted taking into account:

- Turbidity characteristics of river inflow, e.g. based on knowledge of the catchment geology.
- Bathymetry (depth), bottom sediment composite on and wind forces within the estuary (e.g. if an estuary is shallow with bottom sediments being rich in silt and organic fines and subject to strong winds, turbidity levels are likely to be high).

Inorganic Nutrients

For the purposes of this review, the focus will be on dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphate (DIP), considered to be the most important forms of inorganic nutrients in estuaries. A simplified representation of main potential sources of inorganic nutrients to estuaries is provided in Figure 3.5.

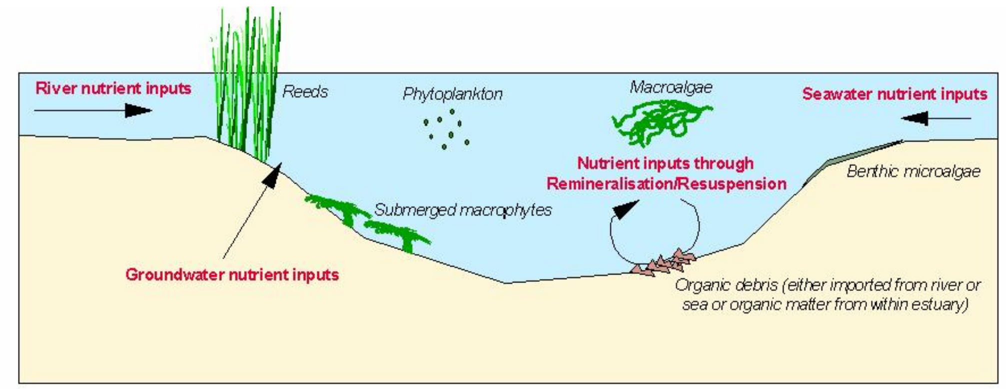


Figure 3.5 A simplified representation of the main potential sources of inorganic nutrients to estuaries.

The key sources of DIN and DIP include:

- River inflow, where inorganic nutrient input concentration in the river water is determined by the catchment characteristics (e.g. rivers draining Table Mountain quartzite are typically low in both DIN and DIP), as well as agricultural and other anthropogenic activities in the catchment.
- Seawater intrusion, where the inorganic nutrient concentrations may be influenced by processes such as upwelling (introducing nutrient rich bottom water into the surface layers of the sea from where it enters estuaries).

- Biochemical processes within the estuary, such as nitrogen fixation and remineralisation (i.e. degradation of organic matter through bacterial activity).
- Groundwater seepage, where inorganic nutrients are again dependent on the characteristics of the catchment from where the water originates. The characteristics of the catchment include human activities such as agriculture and pollution.

The inorganic nutrient concentration in an estuary is largely a function of the concentration in the source waters, i.e. the river, sea and/or groundwater, as well as any physical (e.g. evaporation) or biochemical processes (e.g. biological uptake and remineralisation) that occur within the estuary. Hence, values of DIN and DIP in estuary water do not provide an exact measure of how much is being processed at a given time.

A generalised characterisation of inorganic nutrient sources and processes, under each of the three dominant states, are as follows:

Mouth open: During the open state, DIN and DIP concentrations in the estuary are largely a function of the concentrations in the inflowing river and seawater. Rapid water exchange usually does not allow sufficient residence time within the estuary for marked primary production in the water column particularly in smaller systems, characteristic of many of the South African TOCEs. Although physical and biochemical processes and groundwater input may be important in terms of benthic primary production and for macrophytes taking up nutrients through their roots, these are not considered to be major sources in terms of the overall water column inorganic DIN/DIP pool, although this still needs to be confirmed.

During the open state, the expectation is that there would be a linear relationship between DIN, DIP and salinity, with the concentration of DIN and DIP typically being higher at lower salinity values. Due to the salinity of seawater being very stable (within a few parts per thousand), the relationship between it and DIN and DIP concentrations can be used as a means of characterising the distribution and fate of inorganic nutrients within an estuary (Figure 3.6).

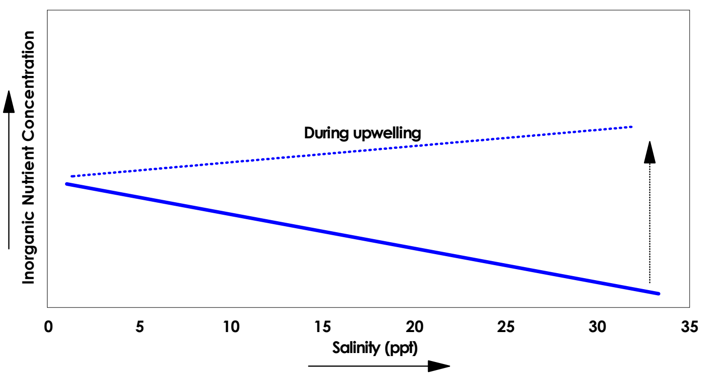


Figure 3.6. Hypothetical relationship between salinity and inorganic nutrient concentrations for the open mouth state.

DIN and DIP introduced through river inflow are usually high compared to that introduced via the sea. However, along the west coast (cool temperate zone) inorganic nutrient concentration (particularly DIN) is also influenced by upwelling, when colder nutrient rich bottom water is advected to the sea surface. This is less common along the warm temperate zone although upwelling is known to also occur along some areas of the south and southeast coasts.

Mouth semi-closed: At the onset of the semi-closed state, DIN and DIP concentrations are largely a function of the concentrations in the inflowing river and seawater at the onset of the semi-closed state. However, higher phytoplankton production, in association with an increase in phytoplankton biomass, is likely to occur as a result of the longer residence time of water leading to a decrease in DIN and DIP concentrations. River inflow is likely to maintain DIN and DIP levels to sustain a certain level of water column primary productivity.

It is expected that biochemical processes and groundwater input will also become important sources of DIN and DIP for primary production in TOCEs during this state. A hypothetical relationship between water column chlorophyll *a* and inorganic nutrient concentrations under the semi-closed state is illustrated in Figure 3.7.

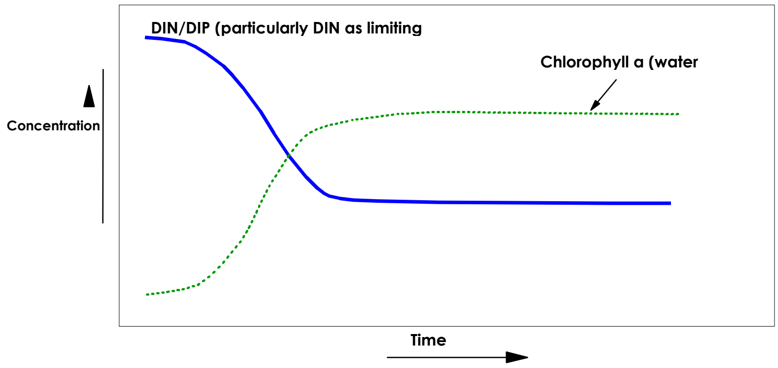


Figure 3.7 A hypothetical relationship between water column chlorophyll *a* and inorganic nutrient concentrations as a function of time in the semi-closed mouth state.

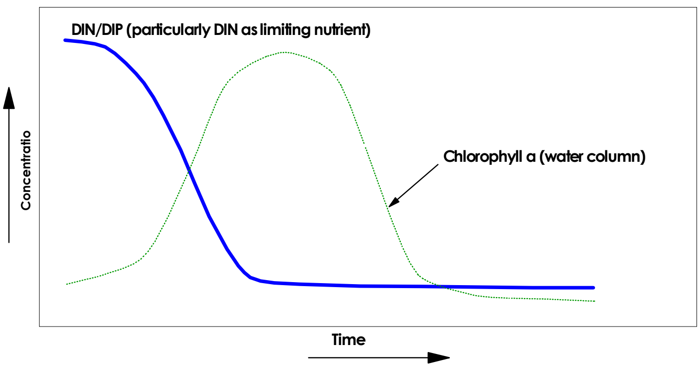


Figure 3.8. A hypothetical relationship between water column chlorophyll *a* and inorganic nutrient concentrations as a function of time in the closed mouth state.

Mouth closed: There are two possible scenarios related to the onset of the closed state a) the mouth is initially open and b) the mouth is initially in the semi-closed state. In both scenarios DIN and DIP concentrations are largely a function of the concentrations in the inflowing river and seawater at the time of closure. If the mouth was initially open, then DIN and DIP concentrations would have been high and chlorophyll *a* concentrations low. Following mouth closure, the longer residence time of water would result in an increase in water column chlorophyll *a* and an associated decrease in DIP and DIN concentrations until such time as the nutrients (DIN in particular) are depleted (Figure 3.8). However, if the mouth was semi-closed then water column chlorophyll *a* would have been high in relation to nutrient concentrations (Figure 3.7). Following mouth closure, residence time would increase further resulting in a short-lived increase in water column chlorophyll *a* before nutrients (DIN in particular) become depleted. This would result in a decrease in water column chlorophyll *a*.

During the closed state it is expected that biochemical processes (e.g. remineralisation) of organic matter in the sediment and groundwater input become important sources of DIN and DIP for benthic microalgal primary production and macrophytes taking up nutrients through their root system. Depending on the rate of these biochemical processes and groundwater input, as well as sediment disturbance (e.g. wind turbulence and infauna), it is expected that these sources may also become important sources of DIN and DIP to the water column. However, very little is known about these biochemical processes in South African TOCEs and will be one of the research focus areas of the current WRC research project.

During over wash of seawater under the closed state, DIN and DIP concentrations in the estuary water column may take on some of the quality characteristics of the seawater, the extent depending on the volume of seawater that enters the system.

As stated before, in assessing the nutrient characteristics, it is important to realise that the influence of inorganic nutrients on estuaries occurs through transformations. As a result of this, there may not be a direct relationship between the ambient concentration of these variables and the biological response, but there is often a relationship between flux and biological response. For example, the concentration of DIN and DIP measured in the water column reflects the net effect of the rate at which these nutrients are taken up by primary producers and the rate at which they are regenerated or replaced. A very low nutrient concentration could therefore indicate that a particular nutrient is essentially depleted from the water column and is therefore limiting primary production, but equally it could simply be the net result of a very rapid uptake and slow remineralisation of the nutrient. (ANZECC 2000).

Organic nutrients

Organic nutrients in this review mainly refer to particulate organic carbon (POC) and particulate organic nitrogen (PON). Sources of organic nutrients in estuaries include the river catchment (introduced through river inflow), sea (e.g. kelp), nutrients introduced through tidal exchange, and debris and leaf litter generated within the estuary.

Local experience on the characteristics and processes influencing organic nutrient concentrations in estuaries (including TOCEs) is limited and it is therefore difficult to put forward a sensible hypothetical model of organic nutrients in TOCEs.

DETAILED ASSESSMENT OF TWO CASE STUDIES

The water quality characteristics measured in two systems within the cool temperate zone, namely the Diep and the Palmiet estuaries, are discussed in more detail in this section in order to give some scientific support to the conceptual water quality model provided above.

Diep

The Diep Estuary is situated about 5 km north of Cape Town and is divided into two distinct regions, namely the Milnerton Lagoon (below the Otto du Plessis Bridge - 33^o 54.5' S 18^o 28' E) and Rietvlei (between the Blaauwberg Bridge and the Otto du Plessis Bridge - 33^o 51' S, 18^{o}29'E). During the rainy winter months the mouth is usually open to the sea. During drier periods (usually in summer), the mouth is closed off by a sandbar (Taljaard et al. 1992). Tidal influence is restricted to the lagoon area, which is the focus of this assessment. The semi-closed mouth state does not occur in the Diep Estuary.

Water quality data were collected from the estuary on two occasions (Taljaard et al. 1992), viz. September 1988 (winter) and February 1989 (summer). Sewage effluent is discharged into the system near the Blaauwberg Bridge. In earlier (1988) studies, the results indicated that reed beds (*Phragmites*) in the immediate vicinity of the discharge provided a very efficient wetland, purifying the effluent before it reached the estuary (Taljaard et al. 1992). However, in recent years, extensive urban development has resulted in an overloading of the wastewater treatment works causing major pollution effects within the estuary.

The Diep Estuary is a 2-phased system, which means that it can occur either in the mouth open or closed states. This is mainly because the system is a medium sized TOCE, while the semi-closed state usually only occurs in smaller systems.

Salinity

Open mouth: During the winter study (September 1988), the estuary mouth was open. Strong river inflow resulted in the estuary being fresh (<1.5 PSU) throughout (Taljaard et al. 1992). However, a plug of saline water (10-25 PSU) was still evident in a deep section (>2 m) near the mouth. Saline bottom water remained trapped in the estuary during neap tides, but on subsequent spring tides it was usually replaced by seawater due to strong tidal flow. This suggests that during the open mouth state, the volume of river inflow largely determines the salinity distribution within the estuary. During higher flows the system will be freshwater dominated, but with strong vertical stratification remaining in the deeper sections near the mouth. Low flow periods will probably be characterised by strong longitudinal and vertical stratification.

Closed mouth: In February 1989 the estuary mouth was closed. Hypersaline conditions existed in the estuary with the salinity ranging from 37 PSU near the mouth, increasing to 43 PSU near the upper reaches (Taljaard et al. 1992), with no vertical stratification evident. In recent years the volume of wastewater from the sewage treatment plant being discharged into the estuary has increased substantially so it is unlikely that hypersaline conditions will occur in the future and mouth closure is less likely to occur. During the closed mouth state, salinity in the Diep Estuary is most likely to be homogenous.

Temperature

During winter (September 1988) temperatures ranged from 13^{o}C near the mouth to 21^{o}C in the upper reaches. During summer (February 1989) temperature was relatively uniform and significantly higher ranging from 24^{o}C near the mouth to 25^{o}C in the upper reaches (Taljaard et al. 1992). The Diep Estuary is situated on the west coast, so upwelling may influence seawater temperatures during summer. Therefore, at times when the open mouth state occurs during the summer period, temperature near the mouth can decline to around 13^{o}C.

Temperature distribution patterns in the Diep Estuary show stronger seasonal correlations, rather than correlations with open/closed mouth states. The temperature regime therefore follows seasonal trends in atmospheric temperatures as might be predicted in a conceptual model.

pH

pH levels in the Diep Estuary during periods of high river inflow (September 1988) were similar to that of the inflowing river water and ranged between 7.4 and 7.6. During February 1989 when the system was hypersaline, it ranged from 8.0 to 8.2 throughout the estuary (similar to that of seawater) (Taljaard et al. 1992). Therefore pH in this estuary appears to be linked to the source water entering the system at the time of measurement, e.g. lower pH during high river flow and higher pH under more saline conditions. However, the overall pH range for the system was within the range proposed by the conceptual model, i.e. 7 and 8.5.

Dissolved oxygen

Open mouth: No dissolved oxygen measurements were taken in the estuary during the winter open state (September 1989), but one would expect that the system would have been well oxygenated, except in the deeper bottom waters (> 2 m) near the mouth (as explained earlier). High total ammonia-N concentrations in this deeper section were also indicative of hypoxic or even anoxic conditions (Taljaard, et al. 1992). This estuary is characterised by strong vertical stratification, particularly in the deeper section near the mouth during its open phase. As a result, deeper bottom waters (> 2 m) have limited exchange with surface waters and the atmosphere.

Closed mouth: Dissolved oxygen concentrations measured in the estuary during the closed state (hypersaline conditions) showed that the system was well oxygenated throughout, with dissolved oxygen saturation levels of about 80% (Taljaard et al. 1992). This suggests that in the absence of strong vertical stratification, wind mixing was sufficient to maintain oxygenated conditions throughout the system.

Turbidity

Turbidity levels in the Diep Estuary appear to be strongly influenced by the characteristics of the source waters, with strong river inflow creating more turbid conditions than under marine dominated or hypersaline conditions. Average suspended solid concentrations measured in the estuary under strong river influence and during the closed state (hypersaline) were 32.4 mg l^{-1} and 11.8 mg l^{-1}, respectively (Taljaard et al. 1992). This suggests that river inflow to the system probably introduces turbidity, resulting in the estuary being more turbid when the system is dominated by freshwater.

Inorganic nutrients

Open mouth: During the open state, DIN concentrations appear to be strongly linked to two sources. In September 1988 strong river inflow resulted in the estuary being almost fresh, with nutrient concentrations resembling that of the river, except in the deeper sections near the mouth (which showed a stronger influence from the lower-nutrient seawater). Nitrite-N levels were less than 100 µg l^{-1}, while nitrate-N concentrations in the fresher shallower sections ranged from 700-980 µg l^{-1} but were about 210 µg l^{-1} in the deeper pools near the mouth. However, total ammonia-N levels were higher in the deeper pools (560 µg l^{-1}) compared with concentrations measured elsewhere in the system (280 µg l^{-1}), probably linked to longer residence time of water in this area. DIP concentrations followed a similar trend to nitrate, where the concentration in the fresher shallower sections ranged between 620 and 899 µg l^{-1}, but decreased to 310 µg l^{-1} in the deeper pools.

Closed mouth: DIN and DIP concentrations during January 1989, when the mouth was closed and the estuary hypersaline, did not show any marked trends throughout the system. DIN concentrations were near depletion (nitrite-N: 2.8 µg l^{-11}, nitrate-N: 12.6 µg l^{-1}, total ammonia-N 70 µg l^{-1}), while DIP concentrations averaged 577 µg l^{-1}.

Palmiet

The Palmiet Estuary (34^{o} 20' S; 18^{o} 59' E), located 75 km southeast of Cape Town, is a small TOCE, 1.67 km in length and some 300 m at its widest point. The head of the estuary is marked by a series of rock sills. The channel meanders between rocky banks in the upper reaches of the estuary and scour holes (4-5 m) are located in the upper reaches. From about 700 m upstream of the mouth, the channel is located close to the west bank with a broad, shallow tidal flat on the east bank. The mouth is close to a rocky bank on the western side with an extensive and mobile sand spit to the east. The Palmiet River is a ‘black water’ system draining mainly Table Mountain quartzite and characterised by low inorganic nutrient concentrations.

The Palmiet Estuary is a 3-phased system, which means that it can occur either in the mouth open, semi-closed or closed states. Data on the water quality characteristics of the estuary are available for the following periods (Largier 1986, Taljaard et al. 1986, Taljaard 1987, Taljaard and Largier 1989, Largier and Taljaard 1991, Slinger and Largier, 1990 and Largier et al. 1992); February 1985 (open), August 1986 (open), February 1988 (closed - only salinity and temperature), January to April 1998 (semi-closed). Water quality characteristics of the systems have also been reviewed previously in CSIR (2000) and most of the information for this review was extracted from that study.

Salinity

Open mouth: The open mouth state during the dry season is marine-dominated owing to extensive seawater intrusion and limited river inflow, probably the dominant state in the system during summer (CSIR 2000). Strong vertical stratification occurs in the estuary, with the bottom waters being replaced or partially replaced by fresh seawater on the flood tides (particularly spring flood tides). During the wet season (winter) the system is river-dominated and can become completely fresh during ebb tides, with some saline intrusion during flood tides.

Semi-closed mouth***:*** The semi-closed mouth state occurs quite often in the late summer. This state was monitored in detail during the summer of 1998 as part of an estuarine flow requirements study (CSIR 2000). At the onset of the semi-closed state the estuary was strongly stratified. Over the following three months the depth of the halocline increased, mainly as a result of the turbulence caused by inflowing river water. At the end of the sampling period the estuary was almost completely fresh, except in the deeper scour holes where a very strong halocline (at about 4 m), still trapped old saline water (32 PSU). The rate at which this process occurs is obviously a function of the river inflow rate and if persisting for long enough (about 5 months) the estuary is likely to become completely fresh in this state.

Closed mouth: During a closed state investigated in February 1988, strong vertical stratification persisted, ranging from 5 PSU in surface waters to 34 PSU in bottom waters (Slinger and Largier 1990, CSIR 2000). Although no data were available, it was anticipated that as long as the mouth remained closed, strong stratification would persist for an extended time, mainly because the estuary is protected from wind, and turbulence associated with river inflow will also be low (CSIR 2000).

Temperature

Open mouth: The open, marine dominated state typically occurs during the drier summer months in the Western Cape. Temperatures in the estuary were largely influenced by the prevailing temperature of the seawater, which varied between 13^{o}C to 17^{o}C at that time of year. Upwelling events, which occur along this section of coast, result in temperatures dropping to 13^{o}C (CSIR 2000). During summer, river water temperatures typically range between 20^{o}C to 25^{o}C. During summer, when the mouth is open, surface waters can be distinctly warmer than those at the bottom or surface waters near the mouth. During the wet season (winter), temperatures in the estuary are largely influenced by that of the river water, averaging about 13^{o}C during winter (CSIR 2000).

Semi-closed and closed mouth: Temperature distribution in the Palmiet Estuary, similar to most other TOCEs, showed a strong seasonal signal. As the closed and semi-closed state usually occurs during summer, temperatures throughout the estuary will be relatively high. Temperature measured in the system under these states ranged from 10^{o}C in winter to 26^{o}C in summer (CSIR 2000).

pH

Open mouth: During the open marine dominated state (summer) pH levels in the estuary generally ranged between 7 and 8. Lower pH values have been measured near the head of the estuary (associated with acidic nature of river inflow), but owing to the weak buffering capacity of the river water, pH levels rapidly increase once it comes into contact with saline estuarine waters (CSIR, 2000). During the strong river inflow (winter), when the estuary becomes river dominated, lower pH levels, between 4 and 6.5 can occur throughout the system (CSIR 2000).

Semi-closed and closed mouth: Although no measurements were taken, it is expected that pH values at the onset of the semi-closed and closed states would range between 7 and 8. As the influence of river water increases, it is expected that pH in the estuary will gradually decrease and may drop to between 4 and 6.5 (CSIR 2000).

Dissolved Oxygen

Open mouth: During both the marine dominated and river dominated open states, the Palmiet Estuary is generally well oxygenated (concentrations > 6 mg l^{-1}). During the marine dominated state, strong tidal flushing regularly replaces bottom waters in this small system, while during the river dominated state the entire estuary is regularly flushed through strong river inflow (CSIR 2000).

Semi-closed mouth: The changes in dissolved oxygen concentration in the Palmiet Estuary were studied in detail in the summer of 1998 (CSIR 2000). At the onset of the semi-closed state, when the main flushing mechanism of bottom water during the dry season was cut off, oxygen levels in the bottom waters decreased. This was attributed to the high oxygen demand of decaying organic matter, mainly originating from kelp debris and *Cladophora* that was present at the time. This trend rapidly increased so that within a week after the onset of the semi-closed state, the water column below the halocline became hypoxic and, in places, anoxic. However, through entrainment of freshwater into the more saline bottom layer, as well as wind mixing forces, low oxygen water was gradually replaced by well-oxygenated river water. Although most of the estuary was largely re-oxygenated after about 2 months (only the deeper scour holes were still anoxic), it is expected that if this state persisted the entire estuary would be re-oxygenated (CSIR, 2000).

Closed mouth: Based on field measurements taken during the semi-closed state, the expectation is that during the closed state a large portion of the bottom water below the halocline will remain hypoxic and even anoxic. This is mainly a result of the high organic loading in the system from the summer when kelp debris entered the open mouth and dense *Cladophora* beds developed within the estuary. This situation is likely to persist, or even worsen, whilst the halocline remains intact (CSIR 2000).

Turbidity

Turbidity is not considered to be a major issue in the Palmiet Estuary since 'black water' systems carry limited suspensoids. However, the dark colour of the humate stained water does affect light penetration. The only measurements that were taken in the estuary were during the semi-closed period (summer 1998) when Secchi disc depths remained at 2 m through the study period (CSIR 2000).

Inorganic nutrients

Open mouth: Under the open states (both marine and river dominated) DIN and DIP concentrations in the estuary were closely associated with salinity, thereby indicating that the nutrient concentrations are mainly influenced by the two water sources. During this state, contribution to the nutrient pool in the water column from other sources (e.g. remineralisation) appears to be relatively unimportant.

During the marine dominated open state, marine upwelling may result in elevated DIN and DIP concentrations being introduced to the estuary. Typical of well-oxygenated systems, nitrite-N and total ammonia-N were low. Nitrate-N concentration ranged between 40 and 190 $\mu g\ l^{-1}$, while DIP concentrations ranged between 12 and 30 $\mu g\ l^{-1}$ (CSIR 2000).

Although under the freshwater dominated open state, concentrations of nitrite-N, total ammonia and DIP were generally similar to that under the marine dominated state, nitrate-N concentrations appeared to be much higher (190 to 1300 $\mu g\ l^{-1}$) and indicate nutrient inputs from the catchment. These inputs are probably associated with agricultural activities since black water systems are typically low in nutrients (CSIR 2000).

Semi-closed mouth: DIN and DIP levels during the semi-closed state displayed interesting patterns. At the onset of this state in the summer of 1998, DIN and DIP concentration were relatively low, similar to that of the marine dominated open state (CSIR 2000). DIN and DIP concentrations in the surface layer remained low throughout the 3 month study period and even became depleted. Bottom waters below the halocline remained low in nitrite and eventually became depleted of nitrate. However, after about one month, total ammonia and DIP concentrations showed a marked increase in the saline bottom water that was still trapped below the halocline. Total ammonia-N concentrations increased from 30 µg l^{-1} to 2 000 µg l^{-1}. Similarly DIP concentrations increased from 30 µg l^{-1} to 300 µg l^{-1} (CSIR 2000). The increase in these nutrient concentrations was attributed to remineralisation.

Closed mouth: No data are available for the closed mouth state. However, it is expected to display similar characteristics to the semi-closed state, where surface water becomes nutrient depleted and remineralisation becomes and important source inorganic nutrients in bottom waters.

BRIEF ASSESSMENT OF OTHER CAPE CASE STUDIES

Water quality related studies were also reviewed for a number of other southern and Eastern Cape estuaries to assess similarities or differences in salinity structure and water quality characteristics to the conceptual model already presented.

Groot Brak (34^{o} 03’ 23’ S; 22^{o} 14’ 25’E): Approximately 7 km long with a causeway located at the head of the estuary. Freshwater inflow to this TOCE has been significantly reduced with the completion of the Wolwedans Dam in 1990s. This resulted in the estuary now closing for longer periods than before. The classic semi-closed state does not occur in the Groot Brak Estuary but during the closed state seawater over wash does occur periodically (typically during major storms). Water quality related studies on the system were undertaken in November 1988 (CSIR 1990), November/December 1990 (Taljaard and Slinger 1993), February 1991 (CSIR 1992), January 1992 (CSIR 1992), May 1992 (Taljaard and Slinger 1993), February 1993 (CSIR 1993), January 1994 (CSIR 1994) and February 1998 (CSIR 1998). Water quality in the estuary was sampled on three occasions in the open state (November 1988, January 1992 and February 1993) and three times during the closed state (February 1991, January 1994 and 24 February 1998). The November/December 1990 study coincided with a fresh water release from the Wolwedans Dam. One seawater over wash event was sampled in May 1992 (Taljaard and Slinger, 1993).

Tsitsikamma (34^{0} 08’ 05’ S, 24^{0} 26’ 25’ E): Drains a relatively small catchment (189 km^2) and lies in a high, all-year, rainfall region of >1000 mm per annum. It is a small intermittently open system; about 3 km long and has a present mean annual runoff (MAR) of about 13.31 x 10^6 m^3, a 33 % reduction from the reference condition (19.90 x 10^6 m^3) (data provided by DWAF). The mouth dynamics are strongly influenced by the presence of exposed sand dunes in the mouth area. The combination of a small estuary, low river runoff because of the small catchment and the adjacent dune field creates a situation in which a semi-closed mouth state persists for the majority of the year. During periods of extreme low flow the estuary will close completely and for limited periods during higher flows it would remain open to tidal intrusion. Information for this review was extracted from Adams et al. (1994), DWAF (2002) and Harrison et al. (1996), which describe conditions during semi-closed conditions in November 1993 and August 2005. No data were available for open or closed states.

Noetzie (34^0 04’ 43’ S, 23^0 07’ 46’ E): The Noetzie River catchment is small, 38.8 km^2, and the estuary is in a near natural condition due to the difficulty in accessing both the estuary and catchment areas. The estuary is a ‘black water’ system that drains predominantly quartzites of the Table Mountain Group and as a result rarely becomes silt laden under natural conditions. In recent years, anthropogenic activities in the catchment have increased the silt load of the Noetzie River and its tributaries. Available information on the Noetzie is limited to water quality data collected in June 1994 and which was published in a national report (Harrison et al. 1995) and a detailed report by Bornman and Adams (2005).

Van Stadens (33^o 58’ 01’’ S, 25^o 13’ 20’’ E): A small river catchment (90 km^2) and largely covered by shrub-thicket vegetation with some areas covered with forests. However, some areas of the catchment are used as farmland primarily for dairy and chicken rearing. A significant portion of the catchment is characterised by very steep gorges of Table Mountain quartzite that is covered by fynbos in the upper and middle regions with valley-bushveld thicket near the coast. Mean estuarine water depth is approximately 3 m with a maximum depth of 8 m. The estuary is only open intermittently throughout the year and remains closed for the majority of the time. Gama et al. (2005) studied the Van Stadens Estuary for the period April 2001 - April 2004.

Maitland (33^o 59’ 02’’ S, 25^o 17’ 4’’ E): A small catchment (60 km^2) of primarily farmland with a relatively small portion of land covered by shrub-thicket vegetation near the coastline designated as a nature reserve. A number of farm dams occur in the catchment and are used to store water for irrigation and for livestock, mainly dairy cattle. The maximum depth of the estuary when the mouth is closed is 2 m whilst the mean depth is approximately 0.9 m. The estuary is only open intermittently throughout the year and remains closed for the majority of the time. Gama et al. (2005) studied this estuary over the period April 2001 - April 2004.

Kasouga (33^o 39' 17’ S, 26 ^{o} 44' 08’ E): A medium sized intermittently open estuary with a surface area of ~22 ha. The system is navigable for approximately 2.5 km, is ~150 m wide at the widest point and is mostly shallow, with depths ranging from 0.5 to 2.0 m in the main channel. As with other TOCEs, the catchment is small (estimated at 39 km^2) and used primarily for cattle farming. The nearby stream and river valleys within the catchment area are, however, relatively undisturbed and covered by Valley Bushveld vegetation. The estuary was studied from September 2000 to December 2001 (Froneman 2002a and b).

Salinity

Open mouth: In general, strong longitudinal and often vertical salinity gradients were present in most of the estuaries during the open state, as observed in the Diep and Palmiet systems. The strength of the gradients was largely a function of estuarine length, bathymetry and the volume of riverine input. A study of a fresh water release in the Groot Brak Estuary showed that as a result of its bathymetry (shallow in the lower reaches becoming deeper in the middle and upper reaches) strong vertical stratification developed in the middle and upper reaches. Consequently, bottom waters in these reaches typically had a longer residence time than surface waters (Taljaard and Slinger 1993). A week after the release and mouth opening, complete flushing of the middle reaches had still not occurred, although the lower reaches of the system (within 4 km of the mouth) experienced active exchange with the sea. The above study indicated that late ebb tide, subsequent to the fresh water release and opening of the mouth, was considered to be the point of maximum flushing as a result of the fresh water release, before the secondary flushing process (i.e. flood tide intrusion) set in (Taljaard and Slinger, 1993).

In the case of the Noetzie Estuary the slightly perched nature of the estuary means that, even during the open state, seawater intrusion is restricted to spring high tides and high sea conditions, i.e. very similar to its semi-closed state. Significant mouth breaching following a flood event is likely to be short-lived before the sandbar at the mouth redevelops, followed by horizontal and vertical salinity gradients becoming re-established.

During a flood event in the Van Stadens Estuary, the mouth opened and high river input resulted in the estuary becoming fresh. However, as the river flow subsided, a saline wedge penetrated upstream and strong horizontal and vertical salinity gradients were established. This stratification persisted for a number of days to weeks before coastal winds mixed the water column thus creating homogenous brackish conditions throughout the estuary.

During the same high rainfall period, a flood event in the Maitlands Estuary scoured sediment from the estuary leading to improved tidal exchange across the sandbar. This resulted in a higher average salinity and strong horizontal and vertical salinity gradients in the estuary.

Semi-closed mouth: The semi-closed state is typical of small TOCEs and does not typically occur in the medium size systems such as the Groot Brak. In the Tsitsikamma Estuary, strong vertical stratification developed during the open mouth state, particularly in the deeper areas (i.e. near the mouth and a deeper area about 1.8 km from the mouth), and occurred when river inflow was low (0.05 - 0.4 $m^3 s^{-1}$). Saline water trapped in the estuary (which penetrated the system during the previous open state) forms a saline bottom layer with freshwater flowing out to sea at the surface. During the semi-closed state, bottom salinity values can also be elevated through over-wash as a result of wave action during spring tides and during storm events. It has been shown elsewhere that over-wash can markedly increase salinity values in small system such as the Tsitsikamma. If this state persists for months at a time with little or no over wash, salinity values in the estuary may progressively decrease through entrainment as the fresh surface layer ‘erodes’ into the more saline bottom layers (as predicted in the TOCE conceptual model), but due to the low flows these effects would not be as significant as was recorded in the Palmiet.

Harrison et al. (1995) recorded salinities of 20-21 PSU in the Noetzie but there was no indication of vertical stratification at the two lower reaches sites. Although data records from the June 1994 survey refer to an open mouth state, it is more likely that the estuary was perched and in a semi-closed state at the time of sampling due to the homogenous water column observed in the lower reaches. Marine over wash combined with a measured total discharge of river water 0.075 m^3 s^{-1} were responsible for creating strong vertical and horizontal stratification in the estuary during the semi-closed state in April 2005 when salinities ranged from 0.2 PSU to 27 PSU.

Overwash occurred frequently in the Van Stadens Estuary and it was therefore difficult to distinguish between closed and semi-closed states (see more detailed discussion under closed mouth below). The neighbouring Maitlands Estuary was most commonly in the semi-closed state (42% of the study period) which was frequently also influenced by over wash events. Marine water introduced through over wash events increased salinity in the estuary but river flow, groundwater seepage and the seepage of estuarine water through the sandbar rapidly dissipated the salinity.

The classic semi-closed state is not expected to occur in the Kasouga Estuary due to a large sand bar that typically develops across the mouth.

Closed mouth: In the Great Brak Estuary, salinity distribution under the closed state is generally homogenous although some vertical stratification remained in the upper sections, the extent depending on the amount of freshwater still entering the system. For example, during a survey in February 1991 the mouth had been closed for 8 weeks. At the time salinity was relatively homogenous throughout the estuary, ranging from 30 PSU near the mouth to 25 PSU in bottom waters near the head, but freshwater inflow still resulted in marked vertical stratification in the upper estuary (CSIR 1992).

In May 1992 large volumes of seawater were introduced over the sandbar into the Great Brak Estuary owing to high wave conditions while the mouth was closed (Taljaard and Slinger 1993). The seawater that had overtopped the berm initially (salinity >35 PSU, temperature <17^{o}C) intruded as a density current along the bottom of the estuary, filling the deeper holes. This intruding water was diluted as mixing occurred and water of salinity 30 PSU reached as far as 5.5 km from the mouth. The density-driven (baroclinic) circulation pattern that was set up resulted in a system uniformly vertically stratified (salinity) (Taljaard and Slinger 1993). Salinity ranged from 20 PSU at the surface to >30 PSU in the deeper areas. Salinity of about 10 PSU in the surface water of the upper reaches indicated a limited fresh water influence. It was concluded that over wash of large volumes of seawater could be a very effective mechanism through which bottom waters in the estuary is renewed during the closed phase (Taljaard and Slinger 1993). However, the extent of renewal of bottom water will be a function of the volume of water being over washed, as well as the bathymetry of the estuary.

Strong vertical and longitudinal salinity stratification was present in the Van Stadens Estuary shortly after mouth closure. However, this condition is generally short-lived (days to weeks) before wind mixes the water column. Strong horizontal and vertical salinity gradients also developed when the closed state was accompanied by strong over wash events. Depending on the duration and intensity of the over wash events, these marked stratifications can be short-lived as the winds that generate and push the swells over the sand bar creating these pycnoclines also assist in mixing the water column, hence aiding in rapidly eroding them. These very dynamic, hydrologically and chemically driven interactions, together with very low river inflow, tend to raise the overall water column salinities to levels that range from 18 PSU in the upper reaches to 20 PSU in the lower reaches. Although freshwater input from the river is generally low during closed mouth periods, flows below 0.1 $m^3 s^{-1}$ were sufficient to maintain horizontal and vertical stratification for periods ranging from days to several weeks.

The water column in the Kasouga Estuary during a closed state (September to November 2000) was well mixed. Extremely low river inflow resulted in the development of hypersaline conditions, with salinity ranging from 35.5 to 37.3 PSU. As predicted in the TOCE conceptual model, such conditions can be expected to develop under the prolonged periods of closure and low freshwater input. An over-wash event sampled in the estuary was found to reduce the salinity in the estuary slightly, resulting in a salinity range of 35.1 to 35.8 PSU. The over wash effectively reduced salinity from hypersaline conditions to salinity more typical of seawater but the lack of fresh water input resulted in the water column remaining well mixed throughout.

Temperature

Water temperature in the above estuaries was largely affected by atmospheric temperature, the temperature of marine and river water entering these systems and the state of the estuary mouth. During the open state, the temperature of seawater and river water strongly influenced the temperature of the lower and upper reaches respectively, frequently resulting in strong longitudinal and vertical temperature gradients. Upwelling of cold water in the marine environment is also expected to result in a further decrease of water temperature in some estuaries. During the semi-closed state, water temperature in the estuaries was largely affected by atmospheric temperature and the temperature of river water entering these systems. Over wash during the semi-closed state generally introduced cooler marine water into the deeper areas of the lower reaches of the estuaries. During the closed mouth state, temperature in the estuaries was closely associated with seasonal trends in atmospheric temperatures.

pH

In most of the systems included in this review, pH generally fell within the range predicted by the TOCE conceptual model, namely 7.0 to 8.5. The leaching of tannins in catchments dominated by fynbos vegetation resulted in the Noetzie River having a relatively low pH (6.3). However, upon entering the estuary pH levels generally fell within the expected range due to the strong buffering capacity of seawater.

Dissolved oxygen

Open mouth: The Groot Brak Estuary is characterised by strong vertical stratification during its open mouth state, mainly attributed to its bathymetry (shallow in the lower reaches becoming deeper in the middle and upper reaches). This results in limited exchange between surface and bottom water, particularly in the middle and upper reaches. As tidal flushing is not sufficient to regularly replenish bottom waters in the middle and upper reaches (> 2 m), these areas often experience hypoxic and even anoxic conditions. For example, during the February 1993 survey, oxygen saturation levels in the surface water ranged between 60-80%, while the concentration in the bottom waters, particularly in the deeper pools of the upper reaches was zero (CSIR 1993). Based on the TOCE conceptual model, low oxygen conditions are generally not expected under the open state. However, the Great Brak is considered to be longer and larger than typical TOCEs, thus reducing the efficiency of tidal flushing.

For the other listed systems, data on dissolved oxygen characteristics during the open state was only available on the Van Stadens and Maitlands estuaries. Dissolved oxygen measurements taken in the Van Stadens exceeded 11 mg l^{-1} during periods of high river input and open mouth conditions. In the Maitlands well-oxygenated conditions were re-established after a flood had opened the mouth, often approaching super saturation particularly when mats of filamentous green algae developed along the bottom of the upper and middle estuary reaches. Both these cases support the TOCE conceptual model prediction for dissolved oxygen during the open state (i.e. well oxygenated).

Semi-closed and closed mouth: During the closed state, oxygen concentrations in the Groot Brak display a more or less similar patterns to the observation made during the open state, namely surface water are generally oxygenated when compared with deeper waters (> 2m) in the middle and upper reaches (which tend to be hypoxic and even anoxic). An over wash event in May 1992, when a large volume of new seawater entered the estuary over the sandbar was found to be very effective in replenishing the dissolved oxygen concentrations in bottom waters (> 2 m) (Taljaard and Slinger 1993) at least up to the middle reaches of the estuary (about 5 km upstream of the mouth).

The Tsitsikamma, Noetzie and Kasouga estuaries are small and shallow systems. As expected oxygen concentrations measured in these systems generally reflected well-oxygenated conditions. Wind mixing and periods of over wash are considered the key factors maintaining oxygen levels in these systems during both the semi-closed and/or closed states.

Although the Maitlands Estuary is also a small and shallow system, decaying organic matter from dense stands of emergent macrophytes has led to anoxic conditions developing in the upper reaches during prolonged periods of low river flow and mouth closure.

In the Van Stadens Estuary, low oxygen concentrations (<3 mg l^{-1}) were recorded in a deep 'hole' (8 m) in the middle reaches of the system during an extended period of low river flow and mouth closure. During this time the estuary was perched behind a well developed sandbar and a strong vertical salinity gradient prevented the mixing of water in this deeper area, as predicted by the TOCE conceptual model.

Turbidity

Most of the estuaries considered in this review have rivers that drain Table Mountain quartzite vegetated with fynbos, resulting in clear water with varying concentrations of tannins. Secchi depth was generally >2 m with low turbidity (<10 NTUs), thus reflecting the source waters (viz. the sea and rivers) which were generally clear. Turbulent river flow re-suspended fine particles at the head of the Noetzie but these quickly settle leaving the rest of the estuary relatively clear.

The Kasouga River drains the Karoo Supergroup, a geological formation high in mudstone. Once eroded, high concentrations of fine sediments enter the estuary and these are easily re-suspended by wind-generated turbulence in the shallow water column. As a result, turbidity in excess of 10 NTUs is likely to be measured frequently in this estuary.

In accordance with the TOCE conceptual model, turbidity in these systems is largely influenced by the levels in source waters and/or the extent of re-suspension of fines by wind-generated turbulence.

Inorganic nutrients

DIN distribution patterns in the Great Brak Estuary showed similar trends for most surveys with no marked difference between the open and closed mouth states. DIN and DIP concentrations were generally low throughout but on occasions limited input of DIN from the sea and river was evident through elevated levels measured at stations near the mouth and head of the estuary respectively. However, high total ammonia and DIP concentrations were frequently measured in the deeper pools (>2 m) of the upper-middle reaches, usually coinciding with anoxic conditions, the result of organic degradation and long residence times. These higher concentrations were most likely associated with remineralisation processes. This was even evident during the open mouth state when strong vertical stratification resulted in 'trapping' of these bottom waters.

The Tsitsikamma and Noetzie estuaries are 'black water' systems so nutrient levels were generally low. It is likely that they should remain low during the open and closed states but further studies are needed to test this.

Nutrient concentrations in the Van Stadens Estuary were generally low (DIP <0.5 μg l^{-1} and DIN <1.0 μg l^{-1}). As the system moved from an open (flows >1.0 $m^3 s^{-1}$) to semi-closed (0.5 $m^3 s^{-1}$) to closed (0 $m^3 s^{-1}$) state, nutrient concentrations peaked and then decreased to very low concentrations (excluding ammonium). There was still a fairly strong ammonium signal (relative to phosphate and nitrate) during extended periods of mouth closure, possibly as a result of the low dissolved oxygen concentrations which led to the ammonification of available oxidised nitrogen (nitrate and nitrite).

Nutrient concentrations in the Maitlands Estuary (<1.0 mg l^{-1} nitrate, <1.2 mg l^{-1} total phosphate) were low, increasing slightly on occasions in response to increased river flow. Low dissolved oxygen concentrations favoured an increase in ammonium concentrations (maximum 11 mg l^{-1}) presumably from remineralisation.

Nutrient concentrations in the Kasouga were extremely low (phosphate and total oxidised nitrogen <1 mg l^{-1}) and generally homogenous throughout the estuary during the closed state (Froneman 2002a). Harrison (unpublished data) recorded phosphate-P, nitrate-N and ammonium-N concentrations of 10-30 μg l^{-1}, 130-240 μg l^{-1} and 0 μg l^{-1} respectively in August 1995.

In general, available data on the inorganic nutrient characteristics of selected southern and Eastern Cape TOCE systems were too limited to properly assess similarities and differences with the proposed TOCE conceptual model. Available data, however, did suggest that during the open state the characteristics of the source water are probably a determining factor (e.g. Great Brak), while processes such as remineralisation could become important during the closed state (e.g. Great Brak and Maitlands estuaries).

CONCLUSIONS AND RECOMMENDATIONS

In general, the estuaries considered in this review fit within the TOCE conceptual model in terms of the predicted structure and water quality characteristics of intermittently open estuaries (TOCEs) under the three dominant states in terms of salinity, temperature, pH, dissolved oxygen, turbidity and inorganic nutrients.

Most of the estuaries existed as 3-phased systems, the only exceptions being the Diep and Groot Brak estuaries, which were 2-phased systems in which the semi-closed state did not occur. This was mainly because these two estuaries were medium sized TOCEs, while the semi-closed state usually occurs in smaller systems. The model appears to be rigid because it describes three independent states but should be regarded as a progression from high flows (open state), to low flows (generally semi-open state) and extremely low or no flow (closed state). If perceived as a progression, it is easier to understand many of the trends in the water quality variables.

A number of anomalies were identified in which measured results deviated from the prediction in the TOCE conceptual model. These are briefly highlighted below:
The conceptual model predicts that during the closed state, TOCEs will become well mixed brackish system possibly becoming more saline, and even hypersaline. In this regard, the model appears to be somewhat biased to southern and western Cape, where rainfall tends to lower and evaporation higher when compared to KwaZulu-Natal TOCEs (Perissinotto et al. 2004). A key difference between the TOCEs in higher rainfall areas compared to those in low rainfall areas with high evaporation, is that the former systems tend to become increasingly fresh during the closed state (e.g. Mdloti) while the latter systems typically become more saline, even hypersaline (e.g. Kasouga).

Salinity distribution in medium sized TOCEs (e.g. Great Brak) also did not fully resemble the predicted salinity distribution patterns under the closed state. Although salinity distribution in these types of estuaries does become more homogenous compared to the open state, some vertical stratification usually remains in the upper sections, the extent depending on the amount of freshwater still entering the system and water depth.

Based on the TOCE conceptual model, low oxygen conditions are generally not expected under the open state. However, in the Great Brak Estuary low oxygen concentrations were common in bottom waters of the middle and upper reaches during this state. This was attributed to the system being longer and larger than most typical TOCE systems, thereby reducing the efficiency of tidal flushing of bottom waters.

Estuaries subject to anthropogenic interferences, for example nutrient enrichment through wastewater discharges, will not necessarily match the prediction in the TOCE conceptual model. For example, the high inorganic nutrient inputs from the wastewater discharge into the Mhlanga Estuary (Perissinotto et al. 2004) are probably masking the variability in nutrient distribution patterns predicted for the closed states in the TOCE model.

In conclusion, this review has emphasised that the largest uncertainties in terms of the biogeochemical (or water quality) characteristics and processes of TOCEs (particularly those in the cool and warm temperate zones) are in terms of inorganic (and organic) nutrients. Further research within this particular field is therefore urgently required if we are to understand water quality changes in TOCEs.

REFERENCES

Adams JB, Bate GC and Wooldridge TH (1994) A biological survey of the Tsitsikamma. In: Algoa Reconnaissance Flow Assessment Work Session on Kouga River, Elands River, Groot River and Tsitsikamma River. Department of Water Affairs and Forestry Report, Pretoria.

ANZECC (2000) (Australia and New Zealand Environment and Conservation Council 2000). Australian and New Zealand guidelines for fresh and marine water quality. *National Water Quality Management Strategy* No **4**. Canberra, Australia.

Bornman TG and Adams JB (2005) Present state of the Noetzie Estuary. Institute for Environmental and Coastal Management, Nelson Mandela Metropolitan University. *IECM Research Report* No. **45**. 43pp.

CSIR (1990) Great Brak. Environmental study with reference to a management plan for the Wolwedans Dam and the Great Brak River mouth. *CSIR Report EMA-C* **9036**. Stellenbosch.

CSIR (1992) Great Brak management programme. Interim Report. Report on the monitoring results for the period April 1990 to March 1992. *CSIR Report EMAS-C* **92083**. Stellenbosch.

CSIR (1993) Great Brak management programme. Interim Report. Report on the monitoring results for the period April 1992 to March 1993. *CSIR Report EMAS-C* **93051**. Stellenbosch.

CSIR (1994) Great Brak management programme. Interim Report. Report on the monitoring results for the period April 1993 to March 1994. *CSIR Report EMAS-C* **940013**. Stellenbosch.

CSIR (1998) Great Brak management programme. Interim Report. Report on the monitoring results for the period April 1997 to March 1998. *CSIR Report ENV/S-C* **98122**. Stellenbosch.

CSIR (2000) Palmiet River Water Resource Management Plan. Summary Report: Requirements of the estuary . *CSIR Report ENV-S-C* **2000-48**. Stellenbosch.

Department of Water Affairs and Forestry (DWAF) (1995) South African Water Quality Guidelines for Coastal Marine Waters. Volume 1: Natural Environment. Pretoria.

Department of Water Affairs and Forestry (DWAF) (2002) Determination of the preliminary Ecological Reserve on a rapid level for the Tsitsikamma (including a desktop assessment on other estuaries in the K80 tertiary catchment). Report prepared by S Taljaard with specialist contributions from Dr J B Adams, P Huizinga, L van Niekerk , Dr A K Whitfield and Prof T H Wooldridge. Pretoria

Froneman PW (2002a) Response of plankton to three different hydrological phases of the temporarily open/closed Kasouga , South Africa. *Estuarine, Coastal and Shelf Science* **55** 535-546.

Froneman PW (2002b) Seasonal changes in selected physico-chemical and biological variables in the temporarily open/closed Kasouga , Eastern Cape, South Africa. *African Journal of Aquatic Science* **27** 117-123.

Gama PT, Adams JB, Schael DM and Skinner T (2005) Phytoplankton chlorophyll *a* concentration and community structure of two temporarily open/closed estuaries. Prepared for Water Research Commission, WRC No. 1255/1/05, Pretoria.

Harrison TD, Cooper JAG, Ramm AEL and Singh RA (1995) Health of South African estuaries, Palmiet – South. Executive Report. Executive Report to Department of Environment Affairs, Pretoria. CSIR, Durban.

Harrison TD, Cooper JAG, Ramm AEL and Singh RA (1996) Health of South African estuaries, Groot (Wes) – Great Fish. Executive Report to Department of Environment Affairs, Pretoria. CSIR, Durban.

Largier JL (1986) Structure and mixing in the Palmiet , South Africa. *South African Journal of Marine Science* **4** 139-152.

Largier JL and Taljaard S (1991) The dynamics of tidal intrusion, retention and removal of seawater in a bar-built estuary. *Estuarine, Coastal and Shelf Science* **33** 325-338.

Largier JL, Slinger JH and Taljaard S (1992) The stratified hydrodynamics of the Palmiet – a prototypical bar-built estuary. In: Dynamics and exchanges in estuaries and the coastal zone. Coastal and Estuaries Studies 40. Prandle D (ed.), pp 135 – 153. Springer and Verlag, New York.

Monteiro PMS and Largier JL (1999) Thermal stratification in Saldanha Bay (South Africa) and subtidal, density-driven exchange with the coastal waters of the Benguela upwelling system. *Estuarine, Coastal and Shelf Science* **49** 877-890.

Perissinotto R, Blair A, Connell A, Demetriades NT, Forbes AT, Harrison TD, Iyer K, Joubert M., Kibirige I, Mundree S, Simpson H, Stretch D, Thomas C, Thwala X and Zietsman I (2004) Contributions to information requirements for the implementation of Resource Directed Measures for estuaries. Volume 2: Responses of the biological communities to flow variation and mouth state in two KwaZulu-Natal temporarily open/closed estuaries. *WRC Report* No. **1247/2/04**.

Slinger JH and Largier JL (1990) The evolution of thermohaline structure in a closed estuary. *Southern Africa Journal of Aquatic Science* **16** (1/2) 60-77.

Taljaard S, Eagle GA and Hennig HF-KO (1986) The Palmiet Estuary: A model for water circulation using salinity and temperature measurements over a tidal cycle. *Water SA* **12**(3): 119-126.

Taljaard S (1987) Nutrient circulation in the Palmiet River Estuary: A summer study. *CSIR Research Report* **633**. Stellenbosch.

Taljaard S and Largier JL (1989) Water circulation and nutrient distribution in the Palmiet River Estuary: A winter study. *CSIR Research Report* **680**. Stellenbosch.

Taljaard S, De Villiers S, Fricke AH and Kloppers WS (1992) Water quality status of the Rietvlei/Milnerton Lagoon system (Diep River Estuary) – 1988/89. *CSIR Data Report EMAS-D* **92007**. Stellenbosch.

Taljaard S and Slinger JH (1993) Investigation into the flushing efficiency of 1. A freshwater release and 2. Seawater overwash in the Great Brak Estuary. *CSIR Research Report* **713**. Stellenbosch.

4. MICROALGAE

Phumelele Gama

Nelson Mandela Metropolitan University, Port Elizabeth

INTRODUCTION

A number of South African estuarine systems are closed off from the sea by a sand bar for varying periods ranging from weeks to years, particularly during drought periods. Mouth closure events normally occur during periods of low river inflow coupled with longshore sand movements in the nearshore marine environment (Day 1981). Of the approximately 250 estuaries recorded along the coastline about 70% are classified as intermittently open. Along the Eastern Cape coast there are more than 80 temporarily open closed estuaries (TOCEs) that fall within the warm temperate biogeographical region and 5 in the cool temperate region of the Western Cape (Whitfield 1992). TOCEs are predominantly regulated by the amount of river inflow received, the magnitude of which is governed primarily by catchment size and the regional climate that dictates rainfall patterns.

Microalgae (i.e. phytoplankton and microphytobenthos) form the base of primary production of most estuaries. Although the South African coastline comprises a large number of TOCEs, our understanding of the ecological functioning of these systems is still poor. It is only recently that there have been studies examining the contributory role of microalgae to estuarine production. A majority of the research has focused on the microphytobenthos associated with bottom sediments and those attached to sand grains and phytoplankton (Robarts 1976, Day 1981, Bally et al. 1985, Adams et al. 1999, Allanson and Baird 1999, Perissinotto et al. 2000, Froneman 2002a and b). Greater detail on the hydrology and physico-chemical characteristics of these estuaries is provided in earlier sections. This chapter deals primarily with the influence of abiotic factors on the microalgae in Eastern and Western Cape TOCEs, based on existing information.

In this review the Mdloti and Mhlanga estuaries in KwaZulu-Natal are used as a basis for comparative case studies to illustrate similarities and differences between these and Cape systems. The KwaZulu-Natal data allows preliminary conclusions to be reached on whether the microalgal biomass distribution patterns and community structures in Cape and KwaZulu-Natal TOCEs show similarities or, if not, to identify the likely factors responsible for any differences that might arise. This information will aid in developing a generic model that can be used to formulate guidelines about microalgae in South African TOCEs.

PRIMARY STUDY SITES

The intermittently open estuaries reviewed in this chapter and representing the different biogeographical regions within the Eastern and Western Cape are shown in Table 4.1.

Table 4.1 TOCEs from the cool temperate and warm temperate biogeographical regions and associated references used in this review.

Biogeographic Region	**Estuary**	**Reference**
Cool Temperate Zone	Bot	Bally et al. (1985)
	Diep	Taljaard et al. (1992)
Warm Temperate Zone	Palmiet	Taljaard (2000)
	Groot Brak	Huizinga et al. (1998)
	Noetzie	Bornman and Adams (2005)
	Tsitsikamma	Bate et al. (1994)
	Kabeljous	Van Hattum (1998)
	Van Stadens	Gama et al. (2005)
	Maitland	Gama et al. (2005)
	Kasouga	Froneman (2002a, 2002b)
	Nyara	Perissinotto et al. (2000)

PHYSICO-CHEMICAL FACTORS

Water flow

Because there is a lack of scientific data from most TOCEs in the cool temperate and warm temperate biogeographic regions, this review will be based on the estuarine systems that have, for the most part, had simultaneous measurements taken of physico-chemical data together with microalgal information over a seasonal cycle or monthly over an annual cycle.

Research from both overseas and local studies on permanently open estuaries (POEs) has demonstrated the significance of freshwater inflow in controlling phytoplankton spatial distribution within these systems (Mostert and Christie 1977, Cloern et al. 1983, Hilmer and Bate 1991, Mallin 1994). In addition, information on nutrient transport (Allanson and Read 1995, Donohue et al. 2001), estuarine circulation (Read 1983) and the structuring of physico-chemical characteristics (Harrison 2004) in relation to river flow into POEs is also available.

Recent South African studies on the influence of freshwater inputs to TOCEs have also demonstrated the importance of river flow in controlling mouth dynamics (Huizinga et al.

1998), structuring physico-chemical characteristics (Bally et al. 1985) and influencing microalgal distribution patterns (Perissinotto et al. 2000, Froneman 2002a and b, Gama et al. 2005).

Mouth condition

Under open mouth conditions the behaviour of TOCEs may be similar to that of POEs as the channel is maintained in the open phase due to the increased volume of water flow arising from seasonal or sporadic rainfall events. Most TOCEs are perched above mean sea level (MSL) when closed. Hence, during the initial stages following mouth breaching there is usually a major outflow of estuarine water to the sea, resulting in a rapid drop in the estuarine water level. The reduction in water level exposes sand banks that had previously been covered by water for long periods ranging from weeks to years. Exposure of previously inundated sediments has a profound impact on the available microphytobenthic habitat within a TOCE that has recently opened.

Coupled with the reduction in water level is a decrease in the volume of water occupied by phytoplankton that limits the potential area for colonisation as well as overall primary production (Day et al. 1989, Nielsen et al. 2004). During this outflow phase limited tidal activity is recorded within the estuary. Once the floodwaters have dissipated, the estuary becomes tidal and behaves in a similar manner to a POE with the establishment of a characteristic longitudinal pycnocline. The interacting forces between tidally regulated dense ocean water and less dense downstream flowing riverine water represent estuarine circulation and mixing processes. As a result of the perched nature of TOCEs the tidal prism is usually limited and often never reaches the upper reaches of the estuary. The open phase ends when river flow declines to a point where the scouring effect of the outflow is overcome by onshore and longshore sediment transport that re-establishes a sand bar across the mouth.

Under low river flow conditions freshwater may continue to maintain estuarine volumes and sustain brackish to oligohaline conditions in the upper reaches (Huizinga et al. 1998, Perissinotto et al. 2000, Gama et al. 2005). During extended droughts river flow can stop altogether. This latter condition may lead to the onset of hypersaline conditions, especially when coupled with high evaporative loss during the hot dry summer periods. Low river flow rates are usually accompanied by low current velocities that extend the residence time of phytoplankton in the water column, thereby enhancing conditions for increased production within the estuary.

The effects of river flow on microalgae include nutrient input, which is particularly effective under low flow conditions when residence time for phytoplankton is increased. Under strong river flows, as normally occurs during floods, there is extensive sediment bed scour, mouth breaching, and flushing of the estuary (Perissinotto et al. 2000, Froneman 2002a and b, Gama et al. 2005). During high flow conditions that lead to mouth breaching events microalgae are removed from the estuary and consequently the estuary will experience low levels of microalgal production. Studies by Froneman (2002a) on the Kasouga Estuary and by Gama et al. (2005) on the Van Stadens and Maitland estuaries showed an increase in chlorophyll a concentrations, particularly the large microphytoplankton fraction from 2-10 weeks following the cessation of river flood conditions. In the Nyara Estuary (Perissinotto et al. 2000) flood conditions (open phase) did not support high microphytoplankton production; instead the nano- and picophytoplankton size fractions contributed most to chlorophyll a biomass.

Marine overtopping

Marine overtopping of the sand bar at the mouth is a common feature of many TOCEs. Water introduced in this manner may represent a formidable augmentation of water into the estuary (Harrison 2004). Marine phytoplankton species are introduced in this manner but may be restricted to the lower reaches of the estuary, especially if river inflow is occurring (Gama et al. 2005). Overwash normally introduces clear marine water that favours the growth of the microphytobenthic community. This is because light penetration is greatly improved, especially in the deeper parts of the estuary. However, turbidity can be increased if sediments within the estuary are resuspended as a result of water movements generated by the overwash event. For example, in the Kasouga Estuary, a marine overtopping event that stirred up estuarine sediments was preceded by predominantly clear waters during the closed phase (Froneman 2002a). Primary production during the overwash period was generally evenly distributed throughout the estuary, ranging between 19.80 and 26.37 mg C m^{-2} d^{-1} and was higher than during the closed phase.

Turbidity

Light transparency in TOCEs is strongly attenuated during river floods or when water movement is sufficiently high to resuspend and shift bottom sediments and associated benthic material. In the Van Stadens Estuary the light attenuation coefficient tracked rainfall, showing increased levels of attenuation with higher rainfall occurrences (Gama et al. 2005). Similar seasonal patterns were recorded in the Kasouga, Nyara, and Swartvlei estuaries, which is indicative of the influence of river flow on light transmittance.

Total suspended solids in the Kasouga reached their highest levels during the river flood phase and were lowest during the closed phase (Froneman 2002a). Levels of suspended matter and turbidity were highest during the flood phase, with microalgal biomass and primary production peaking when compared to all the other phases. Similar observations were made in the Van Stadens and Maitland estuaries, with the microphytoplankton size fraction contributing the most to total chlorophyll a concentration. Even though turbidity was highest during the flood phase, it appears not to have suppressed water column phytoplankton biomass and production in these systems, possibly due to the continuous circulation of phytoplankton cells into surface waters (Cloern 1987).

The closed phase of both the Van Stadens and Maitland estuaries was characterised by an improved euphotic depth favourable for increased photosynthesis, but chlorophyll a concentration was lowest during this phase (Gama et al. 2005). In contrast, during river flood conditions, characterised by increased light attenuation coefficients, the highest nutrient and chlorophyll a concentrations were recorded for both systems. This occurrence has also been observed in other TOCEs within the Eastern Cape (Perissinotto et al. 2000, Froneman 2002a) and KwaZulu-Natal (Nozais et al. 2001). It thus appears that light availability does not limit algal production in TOCEs, although nutrient availability may be limiting, particularly for large sized phytoplankton (Froneman 2002a, Gama et al. 2005).

Salinity

When a TOCE mouth is breached during a flood, river flow introduces large amounts of fresh water, lowering the salinity to less than 5 PSU from the head to the mouth of the estuary. Once the outflow has subsided a tidal regime is normally imposed on the system together with a typical longitudinal salinity gradient. When the mouth closes and the influence of marine water on the estuary is cut off, horizontal salinity gradients begin to break down. Differences between the upper and lower reaches may still remain depending on river flow, groundwater seepage, marine overtopping over the sand bar, as well as seepage from the estuary into the sea.

Oligohaline (0-2 PSU) conditions in the upper reaches are favoured when low flows persist under closed mouth conditions. However, if freshwater input ceases then mesohaline (5-15 PSU) conditions tend to prevail in most TOCEs (Perissinotto et al. 2000, Froneman 2002b, Gama et al. 2005). Phytoplankton community species distribution under oligohaline conditions will favour freshwater tolerant species, including euglenoids and flagellated chlorophytes (although saline tolerant genera like *Tetraselmis* sp. and *Micromonas* sp. will also co-occur). Cyanobacteria, cryptophytes and dinoflagellates show a greater range of salinity tolerance but are more likely to be prevalent under mesohaline conditions (e.g. *Cryptomonas ovata* and *Peridinium quinquecorne*) (Gama et al. 2005).

Overwash and tidally introduced marine water imports mainly marine algal species into the estuary. However, these taxa may be intolerant of low salinity conditions as salt water is rapidly mixed either by wind generated turbulence or estuarine water currents. Marine taxa introduced through overwash remain confined to the lower reaches of an estuary until marine water completely mixes with lower salinity water resulting in the replacement of these species by estuarine forms. Vertical salinity stratification will persist under open mouth condition only if there is an exchange between river inflow and tidal marine water. The horizontal salinity gradient can be short-lived under open mouth conditions in TOCEs and the distribution patterns of the phytoplankton community structure tend to track that gradient. Chlorophytes and euglenoids occur in the upper reaches, possibly extending into the middle reaches, with dinoflagellates and chrysophytes (mainly diatoms) found toward the lower reaches (Gama et al. 2005). Due to the small size and shallowness of these systems mouth closure results in mixing from wind turbulence and estuarine circulation processes such that inflowing water rapidly erodes the salinity and temperature gradients that may be present. Vertical and horizontal stratification can be quickly eroded under closed mouth conditions, thus establishing uniform horizontal and vertical salinity and temperature profiles. Chlorophyll a and phytoplankton community distributional patterns become more uniform throughout the estuary as a result of the mixing forces.

MACRONUTRIENTS

Unlike permanently open systems characterised by a continuous supply of nutrients, TOCEs become depleted of nutrients as flows decline and the nutrient supply decreases or is cut off completely particularly during dry years. River inflow forms the major source of inorganic macronutrients to the water column of most TOCEs. The supply of macronutrients decreases under low flow conditions such that estuarine water column nutrient concentrations decline to levels that limit microalgal production, particularly phytoplankton (Perissinotto et al. 2000, Froneman 2002a). In contrast, increased nutrient concentrations from non-point sources continue to increase under low flow rates in some permanently open estuaries (Snow et al. 2000), a situation not yet recorded in Cape TOCEs.

Following mouth closure, microalgal production is generally driven by phytoplankton because the concentrations of inorganic nutrients are sufficient to support phytoplankton primary production (Froneman 2002a, Gama et al. 2005). Extended periods of mouth closure, however, result in the depletion of water column nutrients thus shifting the primary source of production to the microphytobenthic algae. Under closed mouth conditions light penetration reaches the bottom sediments and seepage from groundwater may supply the nutrients, creating conditions in which micro- and macroalgae are able to thrive. Microphytobenthic chlorophyll a levels recorded for the Kasouga Estuary were highest during the closed phase compared to other phases. Similar patterns were evident in the Maitland, Nyara and Van Stadens estuaries. This suggests that these algae are able to exploit the high light environment under nutrient poor, calm conditions.

Recent studies on the Maitland Estuary indicate that water column macronutrient levels seem to control phytoplankton community composition. Flagellates, including euglenoids and cryptophytes, have been positively correlated with an increase in nitrate. Nutrient availability is important in influencing phytoplankton size structure. Microphytoplankton chlorophyll a concentrations were highest following an increase in the supply of macronutrients 2-10 weeks after the flood phase, in contrast to a water column dominated by pico- and nanophytoplankton size fractions during the closed phase. The supply of macronutrients in Cape TOCEs is closely linked to river runoff such that the microalgal communities respond positively to an increase in nutrient input following heavy rainfall events in the catchment (Froneman 2002a, Gama et al. 2005). The microalgae of some TOCE systems within this region do become limited by light during the river flood phase, when the supply of nutrients is improved beyond levels normally available during the low flow conditions (Perissinotto et al. 2000, 2003).

BIOLOGICAL FACTORS

Phytoplankton biomass

The importance of microalgae to estuarine ecosystem production has been demonstrated for a number of estuarine systems (Day 1981, Cloern et al. 1983, Chan and Hamilton 2001, Bergmann et al. 2002, Nielsen et al. 2004). The contribution by microalgae to total primary production in estuarine ecosystems is well established (Day et al. 1989, Mallin 1994, Adams et al. 1999). A number of physical, chemical and biological factors contribute to the variation in biomass. High river inflow, strong water currents and short residence time results in low biomass in the 'black water' southern Cape estuaries, which is in sharp contrast with those estuaries located northeast of St Francis Bay (Bornman and Adams 2005, Gama et al. 2005). Estuaries in the Western Cape region experience stronger river flow during winter and also exhibit low phytoplankton production as a result of short water retention times. The high humic content, characteristic of many Western Cape systems, stains the river water and limits light penetration within these estuaries, thus influencing water column primary production (Day 1981, Taljaard 2000, Bornman and Adams 2005). Estuaries of the more arid coastal regions of the Eastern Cape display higher production following increased river inflow in response to an increased nutrient load (Froneman 2002a and b, Gama et al. 2005). These higher levels of biomass are generally short lived and subject to the magnitude of river flow. Low river inflow that is normal during summer periods and no-flow conditions (i.e. drought years) tend to result in low phytoplankton biomass. Such conditions have been observed in the Tsitsikamma, Kabeljous, Van Stadens, Maitland and Kasouga estuaries, particularly when nutrients become depleted as river inflow declines.

The phytoplankton biomass in these systems is generally orders of magnitude lower than that of the microphytobenthic biomass, especially under low flow conditions when the mouth is closed. In contrast, POEs show higher water column chlorophyll a levels, which can be attributed mostly to the continuous supply and availability of nutrients (Perissinotto et al. 2000). When considering chlorophyll a distribution patterns that have been fractionated into three size fractions (i.e. pico <3.0µm, nano 3-20µm and micro >20µm) in the Nyara Estuary, they varied both temporally and with size structure. The picophytoplankton were the dominant fraction in winter, while the nanophytoplankton were dominant in the spring and the microphytoplankton contributing ~50% to total chlorophyll a in late summer (Perissinotto et al. 2000). The high concentrations of picophytoplankton occurred during the dry winter period under low flow conditions. This pattern was also evident in the Kasouga, Van Stadens and Maitland estuaries. Data on fractionated chlorophyll a concentrations from estuaries along the southern and south-eastern Cape coast indicate low concentrations of chlorophyll a during periods of low river inflow associated with closed mouth conditions (Bornman and Adams 2005). The microphytoplankton size fraction in these systems (i.e.

Nyara, Kasouga, Van Stadens and Maitland) was the dominant fraction when river influx breached the mouth. This suggests that phytoplankton size structure in these systems is possibly controlled by the supply and availability of allochthonous macronutrients (Perissinotto et al. 2000, Nozais et al. 2001, Froneman 2002a). Although there is temporal variability in chlorophyll a distribution in these systems, seasonality appears not to be the significant physical factor controlling water column concentrations.

Microphytobenthos biomass

The chlorophyll a biomass of the microphytobenthos is normally two or three orders of magnitude higher than in the adjacent water column (Perissinotto et al. 2000). Benthic microalgae contribute a significant portion of the total biomass in estuaries, usually exceeding that of the phytoplankton. Spatial and temporal distribution patterns of microphytobenthic biomass are influenced by nutrient availability, turbidity, salinity, desiccation, water turbulence and sediment composition.

During periods of low river inflow, that are generally associated with mouth closure, estuarine water levels can reach their maximum. Under these conditions, light penetration to the sediment floor usually remains greater than 1% of that at the water surface and is sufficient for microphytobenthic production (Froneman 2002b, Perissinotto et al. 2003). It is under closed mouth conditions that microphytobenthic algal chlorophyll a concentrations reach their maximum and then decline rapidly when surface sediments are removed by seasonal flooding events during the wet period or following heavy sporadic rainfall that causes mouth breaching. Subsequent to these flooding events, microphytobenthic chlorophyll a concentrations decline to their lowest levels.

Although nutrient availability, turbidity, salinity, desiccation, water turbulence and sediment composition may influence horizontal distribution patterns, observations from the Nyara, Kasouga, and Van Stadens estuaries showed no clear spatial distribution. In a study conducted over a seasonal cycle in 2003 in the Van Stadens estuary, microphytobenthic chlorophyll *a* concentrations varied between 0.3 - 5.7 µg g^{-1} sediment. Chlorophyll a distribution remained relatively uniform throughout the length of the estuary over the sampling period and showed no relation to the measured physico-chemical factors, although sediment composition indicated a weak response to chlorophyll a concentrations (Skinner 2005). It has been suggested that the source of nutrients to these systems under closed mouth conditions could be from autochthonous sources following resuspension of the sediment from wind generated turbulence and seepage from groundwater (Perissinotto et al. 2000). These suggestions however, remain to be investigated by examining fluxes at the sediment/water interface.

Data describing the distribution of benthic microalgae suggests that the dominance of the bottom sediments along the length of an estuary by diatom taxa is largely related to mouth state and sediment type. River influx and tidal processes that are dominant at any one time, coupled with wind and current generated turbulence at the sediment surface, determine sediment composition along the length of Cape TOCEs. In the Van Stadens and Maitland estuaries the general spatial distribution of sediment composition did not show variation along the length of these estuaries over a seasonal cycle. However, the general pattern was that coarse sand predominated in the upper reaches and medium to fine sand in the middle and lower reaches of the Van Stadens Estuary (Table 4.2). Preliminary results from this estuary indicate that sediment microalgal biomass did not vary significantly with sediment composition (Skinner et al. 2005).

The recovery of the microphytobenthos following removal by floods is determined by environmental conditions leading to mouth closure. As river inflow subsides to levels that are insufficient to remove sand accumulated by longshore and onshore sediment movements, mouth closure occurs. The increased sediment stability within the estuary is followed by a steady rise in chlorophyll a concentrations, normally about two weeks following mouth closure (Skinner 2005).

Table 4.2 General percent sediment composition of the lower, middle and upper reaches of the Van Stadens Estuary in 2003. (Modified from Skinner 2005).

Site	Silt (<63µm)	Fine sand (63-125µm)	Medium sand (125-50µm)	Coarse sand (250-500µm)	>500µm
Lower	0%	5%	45%	45%	5%
Middle	0%	5%	50%	30%	15%
Upper	0%	2%	10%	65%	23%

Sediment consolidation and stability derived from the production of extracellular organic matter by diatoms is critical to the establishment of an intact and cohesive microphytobenthic community biofilm (Underwood et al. 1995, Tolhurst et al. 2003). Studies on sediment stabilisation by the microphytobenthic algae (e.g. diatoms) in South African TOCEs are still lacking, thus indicating potential gaps in our understanding of the biological mediation that microphytobenthic organisms have on the functioning of these types of estuarine systems.

PRIMARY PRODUCTIVITY

Studies on microalgal primary productivity in TOCEs have often been measured using different methods, thus precluding direct comparison. However, the above measurements do provide an insight into general patterns of carbon sequestration and its potential availability to higher trophic levels within these systems. Studies on water column primary productivity in Cape TOCEs show that phytoplankton productivity is generally higher than that of the microphytobenthic algae (Perissinotto et al. 2000). In the Bot Estuary, however, phytoplankton annual primary production was found to be similar to that of the microphytobenthic algae (Bally et al. 1985).

The effects of different hydrological phases (high river inflow or flood, over-wash, and closed) on phytoplankton primary productivity were investigated in the Kasouga, Maitland and Van Stadens estuaries (Froneman 2002a, Gama et al. 2005). Water column productivity during the closed phase in the Kasouga was the lowest of all three hydrological phases, ranging between 10.92 and 19.83 mg C m^{-2} h^{-1}. On the other hand, during the high river inflow phase (flood) the highest phytoplankton production was recorded, ranging between 40.09 and 64.66 mg C m^{-2} h^{-1}. During this latter hydrological phase the mouth was not breached although the estuary did experience a significant influx of freshwater. The increase in water column nutrient availability associated with the increased river inflow possibly accounted for the observed high productivity levels (Froneman 2002a). In the Van Stadens Estuary the highest phytoplankton productivity occurred both in the spring (13.96 mg C m^{-2} h^{-1}) and summer (13.43 mg C m^{-2} h^{-1}) seasons during an open mouth phase and two weeks following mouth closure respectively. In contrast to the findings in the Kasouga Estuary, where picophytoplankton contributed the most to water column production during the closed and over-wash mouth phases, in the Van Stadens and Maitland estuaries the nanophytoplankton component was the largest contributor to production during both the open and closed phases.

Except for a few studies conducted in different biogeographical regions along the South African coast, microphytobenthic primary productivity data are lacking for most TOCEs. Benthic primary production recorded for the Bot Estuary (58 g m^{-2} y^{-1}) was calculated to be below the average of 67-200g m^{-2} y^{-1} for global estuarine environments reported by Ferguson et al. (1981). However, when considering other systems in South Africa, the level of production for the Bot Estuary was similar to that of other estuaries with sandy sediments (Bally et al. 1985).

Microalgal community structure

There are a few studies that have documented the taxonomic composition and distribution of phytoplankton in TOCEs (van Hattum 1998, Adams et al. 1999, Perissinotto et al. 2000, Walker et al. 2001, Gama et al. 2005). The taxonomic composition in a number of these estuarine systems includes a large range of algal groups (e.g. chlorophytes, dinoflagellates, euglenophytes, cryptophytes, chrysophytes including bacillariophytes and cyanophytes). Seasonal distribution patterns seem to indicate that chlorophytes are dominant during summer, with diatoms and cryptophytes dominant in spring. River flow provides the dominant influence on microalgal community structure and composition because observations show that low cell numbers occur under high flow conditions and low flow can have high cell numbers. Flagellated groups (e.g. dinoflagellates, cryptophytes and euglenoids) are usually dominant during turbid, low light conditions. This suggests that these taxa can tolerate high river flow during floods and are resilient to high-suspended inorganic loads.

A study that investigated the microphytobenthic community composition and structure in the Van Stadens estuary showed that the sediment to be dominated by diatoms (>90% at all sites on each sampling date), with the most abundant species being *Nitzschia closterium*, *Amphora coffeaeformis*, *Pleurosigma aestuarii* and *Navicula gregaria* (Skinner 2005). This study also examined the migratory behaviour of diatoms within the upper layer (0-10 mm) of the bottom sediment matrix and revealed a shift in diatom species composition over a 4-hour daylight period. Five species were found to be dominant, viz. *Amphora coffeaformis*, *Nitzschia dissipata*, *Navicula* sp1, *Navicula* sp2 and *Amphora arcus*. *Amphora coffeaeformis* was dominant in the 0-5 mm layer between 11h00 and 12h00 but migrated deeper into the sediment (5-10 mm) from about 12h00-13h00, resurfacing again into the 0-5mm depth layer. *Navicula* sp.2 showed the opposite behaviour by migrating to the surface at midday and remaining there throughout the sampling period (Skinner 2005).

COMPARISONS BETWEEN CAPE AND KWAZULU-NATAL TOCES

The high variability in the west and southeast Cape regional weather patterns when compared to the more predictable KwaZulu-Natal rainfall events tend to restrict direct comparisons and interpretation of biological responses to these estuarine hydrodynamic processes. Certain responses to physico-chemical factors may reveal possible generic biological outcomes apparent across different estuarine systems. Increased river flow and water turbidity following high rainfall in the catchment reduces light penetration in most TOCEs and may account for the low chlorophyll a levels measured during these events. Although turbidity was also elevated in the Van Stadens and the Kasouga estuaries at times, chlorophyll a concentrations were at their maximum several weeks post the flood phase, suggesting that these systems are nutrient and not light limited as are the KwaZulu-Natal estuaries (Perissinotto et al. 2000, 2003, Froneman 2002a).

Immediately following mouth closure in the Van Stadens and the Kasouga estuaries phytoplankton chlorophyll a increased as underwater light penetration improved. At the same time there was an increase in nutrient availability associated with the mixing of freshwater and marine water as the estuarine water levels gradually increased from the continuous supply of freshwater (Gama et al. 2005). Picophytoplankton (<3μm) comprised the dominant size fraction contributing the most to total chlorophyll a concentrations in KwaZulu-Natal systems whereas microphytoplankton (>20μm) was the major contributor to chlorophyll a in Cape TOCEs. This may mean that microphytoplankton cannot compete with picophytoplankton for nutrients or that turnover rates far surpass microphytoplankton uptake rates in KwaZulu-Natal.

Nutrient depletion generally limits phytoplankton production two weeks after mouth closure. Under closed mouth conditions the combination of low mineral nutrients and grazing become significant factors regulating phytoplankton production (Froneman 2002b, Kibirige and Perissinotto 2003). In KwaZulu-Natal systems, primary production is significantly suppressed during the flood outflow phase. However, the highest primary productivity readings were recorded during the river influx (flood) phase in the Kasouga Estuary when the estuary mouth remained closed (Froneman 2002a). In the Mdloti Estuary, microphytobenthic biomass was related to the high nutrient concentrations during the closed phase (Perissinotto et al. 2003). This was not the case with Cape TOCEs although benthic microalgal biomass did increase following mouth closure.

Water column nutrient levels in TOCEs decline significantly once river inflow is reduced to baseflow levels. Nutrient augmentation is possibly supplied through ground water seepage or dune seepage and may form an essential source for benthic microalgal production. The monitoring of nutrient concentrations entering the Van Stadens Estuary as groundwater did not show a direct link but groundwater macronutrient levels were normally higher than water column concentrations (Gama et al. 2005). For both Cape and KwaZulu-Natal TOCEs average microphytobenthic chlorophyll a concentrations generally exceed water column phytoplankton levels. Spatial distribution patterns of benthic microalgae in Cape estuaries appear not to respond directly to physico-chemical factors along an axial gradient but are influenced by sediment structure within estuaries (Skinner 2005).

CONCLUSIONS

Flood events reduce production by scouring the bottom sediments that destabilises the microphytobenthic layer by dislodging and removing algal cells away from the sediment. This physical disturbance, together with a lowering of the water level following breaching, exposes large previously submersed benthic areas thus leading to a loss of habitat. Extended periods (>4 months) of mouth closure promote the growth of benthic microalgae that can be replaced by macroalgae and macrophytes. The ratio of the euphotic depth to total depth in TOCEs contributes to the high productivity rates of the microphytobenthos. Under the closed mouth phase, estuarine water levels increase and sediment disturbance from wind and water generated turbulence are minimal, thus offering a fairly stable environment for micro and macroalgal growth. When estuarine water levels decline the sediment surface may become prone to destabilisation by wind turbulence and associated water currents.

Although similar characteristics may prevail when the mouth is breached in most TOCEs, features unique to a particular estuary will dictate the ecological functioning of that system. Further research into microalgal responses to changes in physico-chemical factors in Cape estuaries warrants additional investigation, as too few TOCEs have been examined to date. Emphasis and focus should be placed on understanding the role of ground water seepage and nutrient cycling at the sediment water interface. Information from such studies will aid our understanding of the importance of benthic microalgal production under closed conditions and during the open mouth state.

REFERENCES

Adams JB Bate GC and O'Callaghan M (1999) Primary producers. In: Estuaries of South Africa, (eds Allanson BR and Baird D), pp 91-117. Cambridge University Press, Cambridge.

Allanson BR and Baird D eds (1999) Estuaries of South Africa. Cambridge University Press, Cambridge. 340pp.

Allanson BR and Read GHL (1995) Further comment on the response of Eastern Cape Province estuaries to variable freshwater inflows. *Southern African Journal of Aquatic Sciences* **21** 56-70.

Bally R, McQuaid CD and Pierce SM (1985) Primary productivity of the Bot river estuary, South Africa. *Transactions of the Royal Society of South Africa* **45** 333-345.

Bate GC, Adams JB and Wooldridge TH (1994) Tsitsikamma River: A biological survey of the Tsitsikamma river estuary. Department of Water Affairs and Forestry Report No. B33/1/1200 56pp.

Bergmann T, Richardson, TL, Paerl, HW, Pinckney JL and Schofield O (2002) Synergy of light and nutrients on the photosynthetic efficiency of phytoplankton populations from the Neuse River Estuary, *North Carolina. Journal of Plankton Research* **24** 923-933.

Bornman TG and Adams JB (2005) Present State of the Noetzie Estuary. Prepared for the Pezula Private Estate. *Institute for Environmental and Coastal Management Research Report* No **45**.

Chan TU and Hamilton DP (2001) Effects of freshwater flow on the succession and biomass of phytoplankton in a seasonal estuary. *Marine Freshwater Research* **52** 869-884.

Cloern JE (1987) Turbidity as a control of phytoplankton biomass and productivity in estuaries. *Continental Shelf Research* **7** 1367-1381.

Cloern JE, Alpine AE, Cole BE, Wong RLJ, Arthur JF, and Ball MD (1983) River discharge controls phytoplankton dynamics in the northern San Francisco Bay estuary. *Estuarine, Coastal and Shelf Science* **16** 415-429.

Day JH (1981) Estuarine ecology with particular reference to southern Africa. (ed) Day JH A.A. Balkema, Cape Town. 411pp.

Day JW, Hall CS, Kemp WM and Yanez-Arancibia A (1989) Estuarine Ecology. John Wiley and Sons, New York. 558pp.

Donohue R, Davidson WA, Peters NE, Nelson S and Jakowyna B (2001) Trends in total phosphorus and total nitrogen concentrations of tributaries to the Swan-Canning Estuary, 1987-1998. *Hydrological Processes* 15 2411-2434.

Ferguson RL, Thayer GW and Rice TR (1981) Marine primary producers. In: Functional adaptation of marine organisms. (eds Vernberg FJ and Vernberg WB), pp. 9-69. Academic Press, New York.

Froneman PW (2002a) Response of the plankton to three different hydrological phases of the temporarily open/closed Kasouga Estuary, South Africa. *Estuarine, Coastal and Shelf Science* **55** 535-546.

Froneman PW (2002b) Seasonal changes in selected physico-chemical and biological variables in the temporarily open/closed Kasouga estuary, Eastern Cape, South Africa. *African Journal of Aquatic Science* **27** 117-123.

Gama PT, Adams JB Schael DM and Skinner T (2005) Phytoplankton chlorophyll a concentration and community structure of two temporarily open/closed estuaries. *Water Research Commission Report* No. **1255/1/05** 91pp.

Harrison TD (2004) Physico-chemical characteristics of South African Estuaries in relation to the zoogeography of the region. *Estuarine, Coastal and Shelf Science* 61 73-87.

Hilmer T and Bate GC (1991) Vertical migration of a flagellate-dominated bloom in a shallow South African estuary. *Botanica Marina* **34** 113-121.

Huizinga P, Taljaard S and van Niekerk L (1998) Great Brak Estuary Management Programme. Report on the monitoring results for the period November 1997 to November 1998. *CSIR Contract Report ENV/S-C* **98122**: 22pp.

Kibirige I and Perissinotto R (2003) The zooplankton community of the Mpenjati Estuary, a South African temporarily open/closed system. *Estuarine Coastal and Shelf Science* **58** 727-741.

Mallin MA (1994) Phytoplankton ecology of North Carolina Estuaries. *Estuaries* **17** 561-574.

Mostert HSA and Christie ND (1977) Phytoplankton production in the Langebaan Lagoon and Saldanha Bay. *Transactions of the Royal Society of South Africa* **42** 383-398.

Nielsen S L, Banta GT and Pedersen MF (2004) (eds.) Estuarine Nutrient Cycling: The Influence of Primary Producers. Kluwer Academic Publishers. London. 303pp.

Nozais C, Perissinotto R and Mundree S (2001) Annual cycle of microalgal biomass in a South African temporarily-open estuary: nutrient versus light limitation. *Marine Ecology Progress Series* **223** 39-48.

Perissinotto R, Walker DR, Wooldridge TH and Bally R (2000) Relationships between zoo- and phytoplankton in a warm-temperate, semi-permanently closed estuary, South Africa. *Estuarine, Coastal and Shelf Science* **51** 1-11.

Perissinotto R, Nozais C, Kibirige I, and Anandraj A (2003) Planktonic food webs and benthic-pelagic coupling in three South African temporarily-open estuaries. *Acta Oecologica* **24** 307-316.

Read GHL (1983) The effect of a dry and a wet summer on the thermal and salinity structure of the middle and upper reaches of the Keiskamma Estuary, Ciskei. *Transactions of the Royal Society of South Africa* **45** 45-62.

Robarts RD (1976) Primary production of the upper reaches of a South African estuary (Swartvlei). *Journal of Experimental Marine Biology and Ecology* **24** 93-102.

Skinner T (2005) Determination of microphytobenthic biomass and community structure in a temporarily open/closed estuary under different mouth conditions. MSc thesis, Nelson Mandela Metropolitan University, Port Elizabeth.

Snow GC, Bate GC and Adams JB (2000) The effects of a single freshwater release into the Kromme Estuary. 2: Microalgal response. *Water SA* **26** 301-310.

Taljaard S (2000) Palmiet River Water Resource Management Plan. Summary Report: Requirements of the Estuary. *CSIR Report No. ENV/S-C* **2000-48**.

Taljaard S, de Villiers S, Fricke AH and Kloppers WS (1992) Water Quality Status of the Rietvlei/Milnerton Lagoon System (Diep River Estuary). *CSIR Data Report EMAS-D* **92007**.

Tolhurst TJ, Jesus B, Brotas V and Paterson DM (2003) Diatom migration and sediment armouring: an example from the Tagus Estuary, Portugal. *Hydrobiologia* **503** 183-193.

Underwood GJC, Paterson DM and Parkes RJ (1995) The measurement of microbial carbohydrate exopolymers from intertidal sediments. *Limnology and Oceanography* **40** 1243-1253.

Van Hattum T (1998) Effect of mouth closure on microalgal biomass and composition in the Kabeljous estuary in the Eastern Cape, South Africa. MSc thesis. University of Port Elizabeth, Port Elizabeth.

Walker DR, Perissinotto R, and Bally RPA (2001) Phytoplankton/protozoan dynamics in the Nyara Estuary, a small temporarily open system in the Eastern Cape (South Africa). *African Journal of Aquatic Science* **26** 31-38.

Whitfield AK (1992) A characterization of southern African estuarine systems. *South African Journal of Aquatic Science* **18** 89-103.

5. MACROPHYTES

Janine Adams and Taryn Riddin

Department of Botany, Nelson Mandela Metropolitan University, Port Elizabeth

INTRODUCTION

When closed, temporarily open closed estuaries (TOCEs) are characterized by low turbidity, low flow rates, stable sediment and salinity conditions (Adams et al. 1999, Walker et al., 2001; Froneman, 2002). Salinity can decrease if there is a freshwater inflow or it can increase due to evaporation when freshwater inflow is low or absent. These salinity changes determine macrophyte species composition. TOCEs are dominated by reeds, sedges and submerged macrophytes that can withstand low turbidity, low current levels, more stable sediment and salinity environments and a large nutrient pool available in the substrate (Adams et al. 1999). In contrast, permanently open estuaries (POEs) that have regular seawater and freshwater inflows are normally capable of supporting a large phytoplankton biomass and a well-developed pelagic food web (Adams et al. 1999). Macrophyte vegetation in POEs is represented by reeds and sedges, salt marsh (both supratidal and intertidal) and in systems along the KwaZulu-Natal east coast, mangrove and swamp forest.

A study of four Eastern Cape estuaries (Adams et al. 1992) showed that in the Seekoei and Kabeljous TOCEs diversity and cover of emergent macrophytes was lower than that for the nearby POEs (Gamtoos and Kromme). This was attributed to the unavailability of suitable habitat due to fluctuating water levels and periodic hypersaline conditions in the TOCEs.

FACTORS INFLUENCING THE GROWTH AND DISTRIBUTION OF MACROPHYTES ASSOCIATED WITH TOCEs

Macroalgae

Macroalgae are not well represented in South African estuaries and are limited to a small number of genera that can withstand the deposition of silt and the absence of wave action (Day 1981). In permanently open South African marine-dominated estuaries such as the Kromme, Kowie and Kariega, they can contribute a substantial proportion of the total macrophyte biomass (Adams et al. 1992). Species found in TOCEs are considered opportunistic, being able to tolerate fluctuating salinity (Table 5.1). They proliferate during the closed mouth phase and are washed out to sea during the open phase (Adams et al. 1999). Studies in Langstone Harbour (UK) showed that water currents of 1.22 m s^{-1} resulted in *Enteromorpha* being washed out to sea (Lowthion et al. 1985), whereas in Mongeo Estuary (Portugal), Martins et al. (2001) found that currents of 1.4 m s^{-1} removed *Enteromorpha*.

Macroalgae may be intertidal or subtidal, attached or free floating (Adams et al. 1999). Species such as *Enteromorpha*, *Chaetomorpha* and *Cladophora* are common mat forming algae, although they require a firm substrate for initial cell attachment and filament growth.

Table 5.1 Documented salinity ranges for macroalgae.

Species	Salinity (PSU)	Reference
Cladophora albida	2-50	Gordon et al. (1980)
Enteromorpha intestinalis	0-51, although 0 can only be tolerated for 1 to 5 days	Reed and Russell (1979), Pringle (1986), Kamer and Fong (2000), Martins et al. (2001)
Caulerpa filiformis	25-45	Adams (1989)

Good availability of inorganic nutrients (especially N and P) is known to stimulate the abundance of ephemeral and epiphytic macroalgae in shallow coastal waters (Sand-Jensen and Borum 1991, Duarte 1995, Valiela et al. 1997, Karez et al. 2004). *Ulva*, *Enteromorpha* and *Cladophora* often form accumulations due to their filamentous nature and higher nutrient uptake rates than thicker algae (Fletcher 1996, Raffaelli et al. 1998 cited in Karez et al. 2004). These accumulations can reduce the water quality of estuaries, not only by depleting the oxygen in the water column upon decomposition but also causing anoxic sediment conditions when large mats rest on the sediment under low flow conditions (Sfriso et al. 1992). This was shown for *Enteromorpha intestinalis* that filled the shallow water column during bloom events and depleted the water of oxygen (Sfriso et al. 1987, Valiela et al. 1992 cited in Sfriso et al. 1992), causing fish and invertebrate mortality (Sfriso et al. 1992). Additionally, large mats of algae often rest on the benthos at low tide and cause the sediment to become anoxic. A shift to anoxic sediment can change infaunal community structure (Raffaelli et al. 1991, Ahern et al. 1995 cited in Karez et al. 2004) and subsequently affect bird populations (Raffaelli et al. 1989 cited in Karez et al. 2004). *Enteromorpha* has been reported as a problem in the Swartvlei Estuary during summer. Extensive winter growth can rot causing unpleasant sulphide odours in the recreational section of the estuary (Howard-Williams and Allanson 1979). Decaying mats of filamentous algae have been shown to adversely impact the social acceptability of water in the Great Brak and Kleinmond estuaries and are often the reason for the manipulated opening of the mouth (Adams et al. 1999).

Submerged macrophytes

Submerged macrophytes play an essential role in nutrient trapping and recycling in estuaries. In the Wilderness Lakes *Potamogeton pectinatus* contributed more than 70% of the total submerged biomass of the lake (Weisser and Howard-Williams 1982). Similarly in the Bot Estuary submerged macrophytes contributed 72 % of the total production of 13 000 tons dry weight per year (Branch et al. 1985). Aquatic macrophyte populations of brackish waters are characterized by a low species diversity and vulnerability to changes in environmental conditions (Weisser et al. 1992). Studies on the submerged aquatic macrophytes of the

Wilderness Lakes, southern Cape, showed that during the senescence phase, no new macrophytes species invaded the previously occupied littoral zone and recolonisation was limited to five potential species (Weisser et al. 1992).

The distribution of submerged macrophytes is controlled by turbidity, water velocity, salinity, substratum, nutrient availability, temperature and water depth. Light availability and substratum are considered the most important controlling factors (Howard-Williams 1979, Howard-Williams and Allanson 1981, Spence 1982, Weisser et al. 1992). In estuaries where the sediment is constantly being modified by dynamic processes, submerged macrophytes are absent. Ideal conditions favouring the establishment of submerged macrophytes in estuaries are high water clarity, limited sedimentation, low water velocity and a suitable salinity range for each species. For this reason submerged macrophytes are not widely distributed in KwaZulu-Natal estuaries due primarily to low water clarity resulting from high sediment loads.

Light

Light availability and turbidity is determined by the amount of suspended matter and debris brought in by freshwater, by phytoplankton density and by the colonisation of epiphytic algae, especially in nutrient-rich waters (Spence 1982, Adams et al. 1999). Increases in light attenuation may also be directly due to phytoplankton blooms in nutrient-rich water (Crum and Bachman 1973, Andersen 1976, Jupp and Spence 1977a), but also indirectly due to epiphyte and filamentous algal growth, which shades out macrophytes causing their demise (Phillips et al. 1978). Minimum light requirements for submerged macrophytes range from 5 to 29 % of surface light (Duarte 1991) (Table 5.2).

Table 5.2 Documented light requirements of submerged macrophytes.

Species	**Light requirement**	**Reference**
Halophila ovalis	> 2 to 10 % of surface intensity in summ	Hillman *et al.* (1995)
Potamogeton pectinatus	5 to 15 % of surface intensity	Howard-Williams and Liptrot (1980)
P. pectinatus	> 0.2 m secchi transparency	Kantrud (1990)
Ruppia spp.	17.5 to 42.5 ppm suspended sediments	Kantrud (1991)

Light requirements for submerged macrophytes are higher than for other marine plants, presumably because of the high photosynthetic demand to survive in rooted anoxic conditions. However, light requirements can differ during the growth period. Turbid events (floods or storm events) may be tolerated for short periods, although they may have the potential to affect the distribution and abundance of submerged macrophytes. In the case of Ruppia spp., an increase in suspended sediment of 100 mg l^{-1} is likely to have a significant effect (Tyler-Walters 2001) and a 40% reduction in light intensity was reported to result in a

50% reduction in the standing crop of Ruppia spp. (Congdon and McComb 1979 cited in Kantrud 1991). Furthermore, seedling germination is also influenced by light conditions. Most Ruppia seeds occur in the top 5 cm of sediment and can survive in sediment for up to three years and germinate as long as they are not buried by more than 10 cm of sediment (Kantrud 1991).

Water currents and wave action

Generally, currents greater than 1 m s^{-1} result in the removal of submerged plants (Adams et al. 1999). Currents of approximately 0.5 m s^{-1} result in mechanical damage of the plants, and currents less than 0.1 m s^{-1} favour the growth and establishment of macrophytes. In the Swartvlei Estuary, where mixed stands of *Ruppia* and *Zostera* occur, *Zostera* was found at the channel edges and *Ruppia* in the more sheltered sections (Howard-Williams 1980). This is because *Ruppia* has a very delicate, shallow root system making it susceptible to turbulence (Kantrud 1991). The root system of *Ruppia* consists of horizontal runners a few mm below the sediment surface and only 1-2 thin roots per 10-20 cm section along the rhizome (Verhoeven 1979, Kantrud 1991). Verhoeven (1979) noted that the leaf base detaches easily in turbulent water and so avoided damage to the root system. He also suggested that *Ruppia maritima* was particularly intolerant of water currents while *Ruppia cirrhosa* occurred at more exposed but still sheltered sites.

Indirect effects related to water currents are water clarity, sediment and mouth dynamics (Adams et al. 1999). Wave action has been shown to not only reduce the productivity of *Potamogeton pectinatus* through direct damage, but also due to the transport of fine nutrient-rich sediments to more sheltered areas (Jupp and Spence 1977b). Wave action results in coarser sediment and nutrient limited conditions. Where physical removal of plants occurs due to water currents, recovery will depend on the extent or magnitude of damage to the rhizome and root system. Where the rhizomes remain, recovery is likely to be rapid. For example, in subtropical climates wintering waterfowl were reported to consume entire stands of *Ruppia* spp., which re-established within weeks in optimal conditions from rhizomes (Kantrud 1991).

Water depth

The influence of depth is related to turbidity, sediment texture and wave action. *Ruppia* spp. occurs at shallow depths (<1.5 m) on fine, clay sediments but at 2.0 m or more on sand or shell substrata (Tyler-Walters 2001). Sedimentation and a reduction in water depth may result in a change of submerged vegetation to one of reeds and sedges. Submerged macrophytes generally occur in water with a depth greater than 0.5 m and can found in up to 10 m in clear systems (Table 5.3). Adaptation to depth varies greatly within the submerged species. *Ceratophyllum demersum* completes its entire life cycle under water, whereas both *Nymphaea capensis* and *Potamogeton pectinatus* require their flowering structures to be on the water's surface.

Table 5.3 Documented depth distribution of submerged macrophytes.

Species	Depth (m)	Water level change	Reference
Ceratophyllum demersum.	1 to 10		Howard-Williams (1980)
Chara globularis	0.5 to 10		Schwarz and Hawes (1997), Howard-Williams and Allanson (1979)
Lamprothamnium papulosum	0.5 to 0.8		
Myriophyllum spicatum	1 to 10		Howard-Williams (1980)
Najas marina	1 to 10		Howard-Williams (1980)
Najas pectinata	1 to 10		Howard-Williams (1980)
Potamogeton sp.	1.6 to 4.8		Boshoff (1983)
Potamogeton crispus	1 to 10		Howard-Williams (1980)
Potamogeton pectinatus	0.5 to 3.5		Weisser et al. (1987)
Potamogeton pectinatus	1 to 10		Howard-Williams (1980)
Potamogeton pectinatus		0.5 to 1.75 m	Kantrud (1990)
Potamogeton pucillus	1 to 10		Howard-Williams (1980)
Potamogeton schweinfurthii	1 to 10		Weisser et al. (1987), Howard-Williams (1980)
Ruppia maritima	0 to 4.5	Exposure for 1 hour results in die-back	Howard-Williams and Allanson (1979)
Ruppia cirrhosa		Exposure for 3 months results in die-back	Adams and Bate (1996)
Utricularia spp.	1 to 10		Howard-Williams (1980)

Rapid changes in estuarine water depth can leave plants exposed and dry. Verhoeven (1979) stated that the resistance of *Ruppia* spp. to exposure was very low and that after desiccation all plant parts, except ripe seeds, die within a few days. Similarly, Tyler-Walters (2001) reported that exposure for one hour will result in a loss of *Ruppia* stands. This exposure also influences seed germination and *Ruppia* seeds will not germinate in moist soil but need to be covered with water (Kantrud 1991). Adams and Bate (1994a) have shown that when water levels are high, *Ruppia cirrhosa* can germinate rapidly from a large seed bank and complete its life cycle within 3 months.

Salinity

Table 5.4 shows the salinity tolerance ranges of some submerged macrophytes occurring in South African estuaries. The salinity tolerance of each species varies with some species able to survive rapid salinity fluctuations, e.g. *Ruppia* has been reported to survive a drop of at least 14 PSU in 24 h (Kantrud 1991). Studies by Hillman et al. (1995) have shown that *Halophila ovalis* is unlikely to tolerate freshwater conditions for prolonged periods, e.g. during years of prolonged rainfall. A short-term decrease in salinity is unlikely to affect stands of *Ruppia*, whereas prolonged exposure to low salinity or freshwater is likely to result in replacement of the *Ruppia* community by other aquatic plant communities e.g. *P*.

pectinatus. In general, most estuary-associated submerged macrophytes appear to occur where the salinity is between 10 and 20 PSU, with 'freshwater' species favouring the lower end of the range and 'marine' species the upper end.

Table 5.4 Documented salinity ranges of submerged macrophytes in South African estuaries.

Species	Optimum range	Effects of salinity change	Reference
Halophila ovalis	20-35 PSU	< 10 PSU results in stress and senescence at 5 PSU; >50 PSU for 96 hours results in senescence	Hillman et al. (1995), Ralph (1998), Benjamin et al. (1999)
Potamogeton pectinatus	2-15 PSU	≥19 PSU for one year will cause die-back in St Lucia Estuary, South Africa	Ward (1976), Orth et al. (1979), Verhoeven (1980)
Ruppia maritima	0-13 PSU		Verhoeven and van Vierssen (1978)
Ruppia cirrhosa	0-30 PSU, but Can withstand fluctuating levels up to 75 PSU	Growth was reduced between 55-75 PSU, but some remained alive. Although plants grew vegetatively there was no seed germination; seed germination inhibited ≥ 35 PSU	McMillan and Moseley (1967), Adams and Bate (1994b), Verhoeven and van Vierssen (1978)
Zostera capensis	15-35 PSU	0 PSU for 2 weeks results in stress; dies after 3 months of 55 PSU; dies after 1 month of 75 PSU	Iyer and Barnabas (1993), Adams and Bate (1994b, 1996)

Nutrients

Submerged macrophytes are unique in having access to nutrients both in the sediment via root uptake and in the open water via foliar uptake. Experiments with ^{15}N demonstrated that submerged macrophytes could take up inorganic N from both pore water and the water column (Nichols and Keeney 1976, Short and McRoy 1984, Flindt et al. 1999). In evolutionary terms submerged macrophytes have had a reduction in leaf cuticle thickness. This thin cuticle allows the exchange of dissolved ions between their surrounding solution and their photosynthetic tissue. Submerged macrophytes therefore play an important role in nutrient recycling. Estuarine sediments can act as a phosphorus sink. High nutrient conditions in the water column generally have an adverse affect on submerged macrophytes through a reduction in light availability due to increased epiphyte and macroalgal growth and phytoplankton blooms. Twilley et al. (1985) found that epiphyte growth in nutrient enriched conditions reduced the light incident on *Ruppia* leaves by >80%, resulting in significant decreases in macrophyte biomass.

Temperature

The influence of water temperature is physiological, relating to the thermal tolerances and optimum temperatures for photosynthesis, respiration and growth for each species. Temperature increased biomass and seed production in *Potamogeton pectinatus* (Kantrud

1990) with the optimum temperature for the growth of young plants between 23 to 30^{0}C (Spencer 1986). *Ruppia* spp. survive water temperatures of 0-38°C but grow rapidly between 10-30°C (Verhoeven 1979). Temperature also affects seagrass distribution through effects on flowering and seed germination. A decrease in temperature is likely to delay the onset of budding, germination and subsequent reproduction.

EXAMPLES OF PHYSICO-CHEMICAL EFFECTS ON SUBMERGED MACROPHYTES IN SOUTH AFRICAN TOCES

Light

Submerged macrophyte beds grow and expand during closed mouth conditions when the light is favourable following low freshwater and sediment input. In Swartvlei, poor catchment practices such as clearing for agricultural activities resulted in the decline of macrophyte biomass between 1975 and 1980 (Taylor 1983). Similarly, decreased water transparency due to increased silt content of the Wilderness Lakes resulted in a major dieback of submerged macrophytes between 1979 and 1981 (Weisser and Howard-Williams 1982). The input of silt and associated high turbidity limit submerged macrophyte distribution in the Narrows of the St Lucia Estuary (Ward 1976). In the lakes of the same system, wind and the resultant turbid water limit the distribution of submerged macrophytes to waters shallower than 60 cm (Taylor 2006). Only two estuaries in KwaZulu-Natal currently have beds of *Zostera capensis*, namely St Lucia and Richards Bay (Hiralal 2001). *Zostera capensis* was reported regularly from the Umgababa Estuary from the early 1950s until 1989 (Begg 1984, Hiralal 2001). However, it has not been recorded since the latter date in this or other KZN TOCEs (Hiralal 2001), probably due to increased siltation and turbidity.

Examples of physico-chemical effects on submerged macrophytes in South African TOCEs
Light
Submerged macrophyte beds grow and expand during closed mouth conditions when the light is favourable due to low freshwater and sediment input. In Swartvlei, poor catchment practices such as clearing for agricultural activities resulted in the decline of macrophyte biomass between 1975 and 1980 (Taylor 1983). Similarly, decreased water transparency due to increased silt content of the Wilderness Lakes resulted in a major dieback of submerged macrophytes between 1979 and 1981 (Weisser and Howard-Williams 1982). The input of silt and associated high turbidity limit submerged macrophyte distribution in the Narrows of the St Lucia Estuary (Ward 1976). In the lakes of the same system wind and resultant turbid water limit the distribution of submerged macrophytes to waters shallower than 60 cm (Taylor 2006). Only two KwaZulu-Natal estuaries currently have beds of *Zostera capensis*, namely St Lucia and Richards Bay. *Zostera capensis* was reported regularly from the Umgababa Estuary from the early 1950s until 1989 (Begg 1984, Hiralal 2001).
Water Depth
The frequency of mouth opening and the resultant depth determines the abundance of submerged macrophytes. During the closed phase species such as *Ruppia cirrhosa* and *Potamogeton pectinatus* can establish and complete a lifecycle before mouth opening occurs again. *P. pectinatus* occurs

where water is absent for no more than 3 months (Verhoeven 1980; Grillas and Duncan 1986; Coetzer 1987). In the Swartvlei Estuary closure occurs for periods up to 12 months allowing the establishment of submerged macrophytes, *Ruppia cirrhosa* and *Zostera capensis* (Howard-Williams and Liptrot 1980; Whitfield 1988). Extensive beds of *Potamogeton pectinatus* are present in Swartvlei lake where little or no change in water depth occurs (Howard-Williams and Allanson 1979).

Water currents and wave action

Winter water currents in the Palmiet Estuary are greater than 1.14 m s^{-1} and submerged macrophytes are absent. High flow velocities and wave action in the St Lucia Estuary mouth region possibly limit the establishment of submerged macrophytes when the mouth is open. This area is also characterised by soft sediments and high water turbidity.

Salinity

Hypersaline conditions in St Lucia Estuary result in die-back of all three dominant submerged species. When conditions are favourable again *Zostera capensis* is slow to recover compared to *Ruppia cirrhosa* and *Potamogeton pectinatus* that seeds prolifically and hence seems able to respond more rapidly (Taylor 2006). *Ruppia cirrhosa* grows well in TOCEs such as the Seekoei and Kabeljous, even when salinity exceeds 55 PSU. *Zostera capensis* occurs when the salinity is less than 45 PSU and *Potamogeton pectinatus* is dominant when the salinity is less than 15 PSU.

Nutrients

In Zandvlei, nutrient enrichment has been cited as the reason for the dense *Potamogeton pectinatus* beds. The plants in these areas were harvested to provide open areas for recreation (Stewart and Davies 1986). Nutrient enrichment can lead to dense epiphyte and nuisance macroalgal populations (e.g. *Cladophora* spp.), which out compete submerged macrophytes for nutrients and light and cause a decrease in overall species diversity. In Zeekoeivlei *P. pectinatus* was dominant until sewage discharge into the system from the Cape Flats increased, leading to a take-over by macroalgal species (Bickerton 1982).

SALT MARSHES

Salt marshes occur in only certain South African estuaries, being related to specific environmental habitats within each system, which are in turn determined by patterns of salinity and inundation (Adams et al. 1999). Salt marshes perform a number of important functions that include sediment stabilisation, bank protection, filters for sediment and pollutants. They are a source of primary production and provide a habitat and food for a variety of marine and estuarine species.

Although salt marshes are better developed in estuaries with regular tidal exchange, they do occur in some TOCEs, e.g. *Juncus kraussii* occurs in TOCEs such as Kleinmond and Uilkraals. Under these conditions where habitats are seasonally inundated, they survive as short-growing emergent macrophytes. Potential threats to salt marsh communities include altered flooding regimes, land reclamation, dredging, artificial breaching practices and altered salinity regimes (Chapman 1960, Ungar 1962, Tölken 1967, Ungar 1978, Gray 1986, Naidoo and Mundree 1993, Adams and Bate 1995).

Salt marsh vegetation predominates at salinity values between 10 and 35 PSU (Chapman 1960, Day 1981) although certain species can tolerate higher levels than others, providing such high levels are not maintained for long periods (Table 5.5). High salinity levels not only reduce productivity, but also effect flowering and seed germination (Ungar 1962, Ungar 1978, Gray 1986). Under hypersaline conditions, there is a period of adjustment following an initial decrease in biomass. In experiments with *Triglochin maritima*, a change from a treatment of 241 days with dilute seawater to 173 days of pure seawater required a 100 day adjustment period for steady states to be reached in plant biomass. In the St. Lucia system, Ward (1976) found that *Sporobulus virginicus* was more tolerant of higher salinity for longer periods than *Paspalum vaginatum*. In supratidal salt marshes, sediment salinity is possibly controlled more by rainfall and evaporation than by tidal inundation (Adams *et al.* 1992).

Table 5.5 Documented salinity ranges of salt marsh species.

Species	**Optimum range (PSU)**	**Effects of salinity change**	**Reference**
Juncus bulbosus	0.3-1.5		Spence (1982)
Juncus kraussii	< 20		Adams et al. (1999)
Sporobulus virginicus	1-13	Seed germination reduced at > 15 PSU and inhibited at 20 PSU; seedlings older than 3 months showed growth reduction at 20 PSU and inhibition at > 30 PSU	Breen et al. (1977), Marcum and Murdoch (1992), Naidoo and Naidoo (1998)
Sarcocornia perennis	0-15	≥ 35 PSU results in reduced growth	Adams and Bate (1994c)
Sarcocornia natalensis		Fluctuating conditions of 15 to 140 PSU	O'Callaghan (1992)
Sarcocornia pillansii	0-35	> 75 PSU no significant growth	Bornman (2002)
Spartina maritima	0-35	Reduced growth at ≥ 35 PSU for 3 weeks	Adams and Bate (1995)
Spartina alterniflora	0-20	Die-back ≥ 45 PSU	Adams and Bate (1995)
Triglochin bulbosa	6-12	15 PSU delays germination; > 23 PSU for 9 weeks reduced growth	Naidoo and Naicker (1992), Naidoo (1994)
Triglochin striata	6-12	6 PSU reduces seed germination; > 15 PSU reduced growth	Naidoo and Naicker (1992), Naidoo (1994)

Recent studies have indicated groundwater salinity and depth to groundwater as important determinants for supratidal and floodplain salt marsh (Bornman et al. 2002, 2003, 2004). The Olifants Estuary on the dry west coast has the largest area of supratidal (143 ha) and floodplain salt marsh (797 ha) in South Africa. A single species (*Sarcocornia pillansii*) is dominant in this dry saline habitat. Bornman (2002) showed that the survival of the plants was dependent on the utilisation of saline groundwater, particularly during the dry period (8 months) of the year. The cover abundance of *Sarcocornia pillansii* was visibly reduced where the water table was deeper than 1.5m and/or where the electrical conductivity of the groundwater had a high ion concentration (> 80 mS cm^{-1}). Floods to the estuary are important in lowering the salinity of the water column, which then influences groundwater salinity. Any disturbance to this habitat will result in large areas of bare ground as has happened at the Orange River mouth (Bornman et al. 2003, 2004). The conservation value of this vegetation lies in the fact that halophytes are the only plants adapted to grow in these harsh environments and the loss of this vegetation would lead to the formation of bare, dry salt pans that are more easily eroded by wind and water. *Sarcocornia pillansii* occurs in dry, saline elevated areas of TOCEs.

Water level fluctuations

Prolonged inundation slows flowering and subsequent seed production in *S. decumbens* (O'Callaghan 1990a, 1990b). This has serious consequences since, although propagation is predominantly vegetative in salt marsh species, resident seed banks play an important role in the re-establishment of salt marsh communities when water levels drop after protracted flooding, e.g. *Triglochin* spp. in the Great Brak Estuary and *Sarcocornia* spp. in the Seekoei Estuary. *Suaeda fructicosa* was found to be intolerant of water logging (Walsh 1974 in Adams et al. 1992). By contrast, *S. virginicus* grows well under waterlogged conditions as well as being able to withstand long periods of submergence, i.e. 2-3 months (Table 5.6). Where tidal influence stops, as in estuaries that are closed for long periods, salt marsh areas are often colonised by other species such as reeds and sedges which grow under fresher and more inundated conditions.

Table 5.6 Documented influence of water level changes on salt marsh vegetation.

Species	**Influence of water level change**	**Reference**
Cynodon dactylon	Tolerates 28 days flooding	Furness and Breen (1985)
Sporobolus virginicus	Tolerates 42 days flooding	Naidoo and Mundree (1993)
Sporobolus virginicus seedlings ≥ 3 months	Growth improved by inundation of 3 cm for 38 days	Breen et al. (1977)
Sporobolus virginicus seedlings < 3 months	Growth inhibited by inundation of 3 cm for 38 days	Breen et al. (1977)
Sarcocornia perennis	≥ 35 PSU and complete submergence over 2 weeks reduced growth	Adams and Bate (1994c)
Sarcocornia perennis	Inundation with 5 cm water increased/ stimulated growth	Jackson and Drew (1984)
Sarcocornia natalensis	Endures submergence for ≤ 3 months without negative effects	Tölken (1967)

Examples of physico-chemical effects on salt marshes in South African TOCEs
Salinity
Freshwater for too long may eliminate the salt marsh community. O'Callaghan (1990b) has shown how poorly developed the halophytic vegetation is in the False Bay estuaries because of human impacts and reduced saline inputs. O'Callaghan identified restriction of tidal input as a serious threat to Western Cape salt marshes. Salt accumulation due to low rainfall and high water column salinity can result in bare areas in the marsh, e.g. Kromme Estuary (Adams *et al.* 1992).
Water Level Fluctuations
In the Great Brak Estuary water level increased during mouth closure resulting in dieback of *Sarcocornia natalensis* communities during 1989/1992 (Adams *et al.* 1999). This dieback was due to inundation for longer than 2 months.

REED AND SEDGES

Reeds, sedges and rushes occur on soft intertidal or shallow subtidal substrates with their photosynthetic portions partially and/or periodically submersed. These peripheral communities form important habitats for birds, invertebrates and fish species. They also provide an important input of detritus as well as a substratum for periphyton and bacteria. Emergent macrophytes provide bank stabilisation due to their effectiveness in trapping sediments. *Phragmites australis* can form either monospecific stands in wet areas, or mixed stands where it is associated with species such as *Scirpus* sp., *Schoenoplectus* sp., *Typha* sp. and/or *Cladium* sp. (Haslam 1971). Water depth, salinity, sediment type and nutrient availability (Haslam 1971, Barko and Smart 1978), as well as light availability (Haslam 1971, Benfield 1984) have been shown to affect emergent macrophyte distribution and establishment. Alterations of these factors will have ecological implications for the stability of emergent macrophyte communities and the functioning of the estuary.

Water depth and water level fluctuations

Water depth is considered the main regulatory factor for emergent reed and sedge communities (Grime 1979, Haslam 1971, Lieffers and Shay 1981, Grace 1989, Hellings and Gallagher 1992, Squires and Van der Valk 1992, Coops and Van der Velde 1996). The limiting depth of emergent macrophytes appears to be approximately 2 m (Table 5.7). Although *P. australis* has been reported to occur in water depths up to 4 m in Uganda (Haslam 1971), under these inundated conditions Squires and Van der Valk (1992) found that survival was only possible for one or two years. Deeper water not only reduces above and below ground biomass, but also effects reproductive strategies. The vegetative spread of *P. australis* and *S. maritimus* decreases with depth and there is a shift from vegetative growth to seed production (Grime 1979). Increased dormancy and buoyancy of the seeds of these two species increases under prolonged inundation (O’Neil 1972). This is because increased seed production ensures the rapid colonization of open mudflats when water levels decrease.

The timing of water level rises is also crucial. When the Swartvlei Estuary was open, *Phragmites australis* occurred in depths of 0.3 to 0.5 m (Howard-Williams and Liptrot 1980). However, during periods of mouth closure water levels rose so that *P. australis* was subjected to levels of 1.5 m, an increase of 1 m. This increase in water level occurred during the winter months when the aerial parts were dying off and thus the increase had little impact. Submergence during autumn however is likely to have a negative impact since this is when nutrients are remobilised for spring growth. The seedling establishment of *P. australis* is sensitive to submergence (Hellings and Gallagher 1992).

The Mhlanga Estuary in KwaZulu-Natal is characterized by extensive reed and sedge swamps (*P. australis* and *Scirpus scirpiodeus*). In a study to determine the freshwater requirements of the Mhlanga estuary, it was hypothesized that long-term closure of the mouth would result in a reduction of reed and sedge and swamp forest due to the influence of increased water level. Reed encroachment is restricted in the main channel because of high water level during the closed mouth state.

Salinity

Table 5.8 documents the salinity ranges and influence of varying salinity on reed and sedge species. Increased salinity generally results in reduced shoot height and overall reduced plant performance. This is due to a diversion of energy away from active meristematic growth to the maintenance of osmotic balance (Hellings and Gallagher 1992). Some species withstand brackish conditions due to the ability of their rhizomes to remain dormant until normal conditions return as in *Typha domingensis* (Glen et al. 1995). In *Juncus kraussii*, 95 % of plants previously receiving treatments of 15 and 30 PSU recovered after 150 days with treatment of freshwater (Heinsohn and Cunningham 1991).

Tolerance to high salinity also depends on the stage of development, with tolerance increasing with age (Albert 1982, cited in Hartzendorf and Rolletschek 2001). Seedlings of *Sporobulus virginicus* are able to survive *in situ* treatments of 80 PSU for 8 months (Gallagher 1979). This means that although there is little growth during periods of high salinity, seedlings are able to survive hypersaline conditions until rainfall dilutes soil salinity.

Wave action

Because reed and sedge communities associated with estuaries and lakes occur in the littoral zone, wave action has an effect on growth and species distribution. *P. australis* is better adapted morphologically to wave action than *S. scirpiodes* due to its higher bending resistance and lower susceptibility to breaking (Coops and Van der Velde 1996). Nodal stabilisation also reduces the risk of buckling. Water velocity associated with 0.23 m waves was strong enough to uproot and fracture *S. scirpiodes*. Strength and flexibility of emergent stems varies between species as well as seasonally according to the growth stage of the plant. *P. australis* often forms dense stands and this closeness serves to lessen the effects of waves, which is particularly important for new emerging shoots.

Table 5.7 Documented water levels for various reeds and sedges.

Species	**Optimum range**	**Effect of water level change**	**Reference**
Cladium jamaicense	0-2 m		Howard-Williams (1980)
Cyperus natalensis	0-2 m		Howard-Williams (1980)
Cyperus papyrus	0-2 m		Howard-Williams (1980)
Echinochloa pyramidalis	0-2 m		Howard-Williams (1980)
Juncus bulbosus		Survives 1 m variations	Spence (1982)
Phragmites australis	0-2 m	4 m depth only possible over 1 to 2 years	Haslam (1971), Yamasake and Tange (1981), Weisner (1991), Spence (1982)
Phragmites australis		Increase of 35 cm to depth of 80 cm reduced growth; tolerates 80 cm for two growing seasons	Mall (1969), Coops et al. (1996)
Polygonum lopathifolium	0-2 m		Howard-Williams (1980)
Schoenoplectus lacustrus	0.3-1.5 m	Survives1 m variations	Spence (1982)
Scirpus littoralis	0-2 m		Howard-Williams (1980)
Scirpus littoralis	0-1.5 m		Weisser et al. (1987)
Scirpus marimus	0-0.2 m	Increase of 44 cm to 80 cm depth reduced growth	Lieffers and Shay (1981), Coops et al. (1996)
Typha glauca	≤ 0.6 m		McDonald (1955)
Typha latifolia	≤ 0.3 m		McDonald (1955)
Typha latifolia	0-0.5 m		Weisser et al. (1987)
Typha latifolia	0-2 m		Howard-Williams (1980)
Typha latifolia	0-0.95 m		Grace (1989)
Typha capensis		Tolerates 0.15 m for 6-12 months	Mall (1969)

Sediments and nutrients

Sediment and associated nutrient characteristics also determine species composition and distribution of emergent macrophyte species. Fine-textured sediments support a proportionally greater above ground biomass in *Cyperus esculentus* and *Scirpus validus* than do coarser sediments, possibly in response to greater nutrient availability associated with the fine sediments (Haslam 1971, Barko and Smart 1978). Because emergent macrophytes are such effective sediment traps, high rates of sedimentation have had serious effects in some smaller KwaZulu-Natal estuaries (Begg 1978). Left unchecked, these macrophytes build up estuarine sediments into firmer ground thereby accelerating a succession towards coastal forest.

Table 5.8 Documented salinity ranges for various reed and sedges.

Species	**Optimum range (PSU)**	**Effects of salinity change**	**Reference**
Phragmites australis	18-30	> 15 PSU reduced growth; inhibited growth with 20 PSU over 2 weeks; die-back with 30 PSU inundation over 94 days	Adams and Bate (1999), Benfield (1994), Lissner and Schierup (1997)
Juncus kraussii	0-20		Adams et al. (1999)
Sporobulus virginicus		Seedlings can survive 80 PSU for 8 months	Gallagher (1979)
Scirpus lacustris	< 18		
Scirpus maritimus	18-30	From one week 30% mortality and complete dieback after 4 months at 18 PSU	Hootmans and Wiegman (1998)
Schoenoplectus triqueter	0-7		Deegan et al. (2005)
Typha domingensis	0-3	Salinity of ≥ 7 PSU reduced growth Salinity ≥ 10 PSU causes die-back	Beare and Zedler (1987), Glenn et al. (1995)
Typha latifolia	< 18	From one week 70% mortality and complete dieback after 4 months at 18 PSU	Hootmans and Wiegman (1998)

Light

Shading by microbial blooms has been shown to affect peripheral swamp species. *Microcystis* blooms in Lake Teganuma in Japan resulted in a reduction in water transparency and dissolved oxygen (Yamasaki 1993). Withering of bottom leaves of *P. australis* occurred, as well as reduced bud size. In Lake Mzingazi in KwaZulu-Natal, the spread of *P. australis* into the waters edge was prevented as a result of shading by the floating macrophyte *Nymphoides indica* (Boshoff 1983).

Examples of physico-chemical effects on reeds and sedges in South African TOCEs

Water Level Fluctuations

In the Wilderness lakes, emergent macrophytes, namely *P. australis* and *T. capensis* increased in area between 1936 and 1976 (Weisser and Howard-Williams 1982). This increase was related to the lower average water level resulting from artificial opening of the mouth. In the Mzingazi Lake in Zululand, Weisser *et al.* (1987) found that extreme changes in water level resulted in the destruction of littoral stands of *Phragmites mauritianus*. The loss of these macrophyte communities was due to increased wave action on the shore, changed sediment pattern, sedimentation and the release of nutrients that were previously bound by these littoral plants.

Salinity

Field measurements in the Goukou and Keurbooms estuaries showed that the height of *Phragmites australis* decreased from the landward to the seaward edge and that this was associated with an increase in salinity of the interstitial water (Adams and Bate 1994d, 1999).

Sediments and Nutrients

Excessive sedimentation, resulting in reed swamp encroachment, has been observed in many smaller KwaZulu-Natal systems. A classic KwaZulu-Natal example is the Siyaya Estuary. Extensive siltation following mismanagement of the catchment area reduced water depth and encouraged reed swamp encroachment (Begg 1978, Weisser and Parsons 1981). Whereas in 1937 tidal exchange took place

over 3.4 km, by 1996 it was only over the first 500 m. Nutrient enrichment from agricultural activities in the catchment has also accelerated the expansion of *P. australis*. Reed swamp was shown to be expanding at a rate of 0.15 ha per year (Benfield 1984). In the Western Cape, Onrus Lagoon was a deep estuary until the 1940s. When the water upstream was dammed, the annual floods could no longer sweep the estuary clear of silt deposition. The mouth consequently closed, salinity decreased and the silt was colonized by dense growths of *Phragmites* (Branch and Branch 1985, Adams *et al.* 1999).
Light
In the Zinkwazi and Mdlotane estuaries in KwaZulu-Natal, aerial photograph analysis showed that fringing reed and sedge communities have decreased in places due to shading caused by an increase in overhanging swamp forest between 1937 and 1998 (Riddin 1999).

SWAMP FOREST

Swamp forests, unlike mangrove communities, which are associated with saline habitats, are freshwater ecosystems associated with estuaries. Common species include *Syzygium cordatum, Barringtonia racemosa* and *Ficus trichopoda*. Swamp forest plays an especially important role in the attenuation of river floods and riparian erosion control (Wessels 1997). Furthermore, in systems where submerged macrophytes do not exist, lagoon swamp forests play an important role in detritus input (Begg 1978). The Mhlabatshane and Siyaya estuaries are good examples. However, expanding growth of lagoon swamp forest can have adverse effects, e.g. in the Intshambili Lagoon. The freshwater mangrove *B. racemosa* dominates this system and the high detritus input from mainly leaf litter has resulted in deoxygenation of the water and humate staining, adversely affecting the aquatic communities (Begg 1978). Dense stands may also decrease circulation of the water by wind, e.g. the Mbango Estuary. In some systems, overshadowing of reed swamps by lagoon swamp forests has been shown to occur, e.g. in the Siyaya Estuary where Weisser and Parsons (1981) recorded the spread of *Hibiscus tiliaceus* and *B. racemosa* in the upper reaches of the lagoon.

The single most important regulator of species distribution and composition is the length of the hydroperiod (Wessels 1997). Drainage or prolonged inundation, especially with saline water, has adverse effects on swamp forests (Table 5.9). Studies on the effect of salinity on seedling establishment of *B. racemosa* have shown the best growth to occur between 0 and 3.5 PSU (Msibi 1991). After 53 days of 8.7 PSU, seedlings showed signs of stress on their leaves. At 17.5 and 35 PSU growth ceased and death occurred after 53 days.

Table 5.9 Documented salinity ranges for some swamp forest species.

Species	Optimum Range	Effects of Salinity (PSU) Change	Reference
Barringtonia racemosa	0 to 3.5 PSU	Reduced growth at 8.7 PSU for 53 days. Inhibition at ≥ 17.5 PSU for 53 days	Msibi (1991)
Barringtonia racemosa		Die-back ≥ 22 PSU over 6 hrs (high tide)	Cyrus et al. (1997)
Phoenix reclinata		Die-back ≥ 22 PSU over 6 hrs (high tide)	Cyrus et al. (1997)
Hibiscus tiliaceus		Die-back ≥ 22 PSU over 6 hrs (high tide)	Cyrus et al. (1997)

Examples of physico-chemical effects on swamp forests in South African TOCEs

Water Level Fluctuations

In the Mgobezeleni system near Sodwana, large areas of swamp forest around Lake Shazibe were destroyed through prolonged inundation (Bruton and Appleton 1975). Of all the species, *Syzygium cordatum* was more persistent due to its better tolerance of anaerobic conditions. In Lake Mzingazi in Richards Bay, lowered water level had no adverse effects on *F. trichopoda* and *B. racemosa* since these species also occur in terrestrial habitats. However, under these drier conditions, *S. cordatum* is likely to invade their habitat. This is because *B. racemosa* and *F. trichopoda* are poor competitors outside of their natural hydrophytic habitats (Boshoff 1983).

Salinity

In Lake Mzingazi, drought conditions and increased industrial abstraction has resulted in tidal intrusions into the Mzingazi Canal. Groundwater salinity values of 22 to 30 PSU resulted in the die-back of swamp forest species (Cyrus et al. 1997). Similarly, during the construction of the Richards Bay harbour, the artificial opening of a new mouth resulted in an increased tidal range and salinity. This in turn was responsible for a loss of 6 ha of *B. racemosa* and *Phoenix/Hibiscus* communities (Weisser and Ward 1982).

MANGROVES

Mangroves are halophytes that occur as intertidal vegetation in many tropical and subtropical regions (Naidoo 1986). There are five species that typically characterize mangroves in South Africa, namely *Lumnitzera racemosa*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, *Rhizophora mucronata* and *Avicennia marina*. Within an estuary, mangroves establish between mean sea level and the mean high-water spring tide mark; the extent of their inundation varying according to the tidal cycle (Steinke 1995). Conditions favouring the establishment of mangroves are intertidal environments characterized by fluctuating salinity (Table 5.10) and water content, substrata with high silt and clay components, high coastal rainfall and temperature (Naidoo and Raiman 1982, Naidoo 1986). Within an estuary, variation in salinity due to tidal changes, frequency of inundation, seasonal rainfall and river flow pattern effect mangrove spatial distribution and their position along the intertidal gradient (Steinke 1995). Because of their requirement for intertidal conditions mangroves seldom occur in TOCEs.

In the Kosi Bay Estuary, prolonged inundation (154 days) due to mouth closure resulted in the death of predominantly *A. marina*, with deaths among *Ceriops tagal* and *Rhizophora mucronata* also occurring (Breen and Hill 1969). Long-term inundation of pneumatophores due to prolonged mouth closure also caused die back of mangrove populations in Deep Creek, New South Wales, Australia (Whetham 2004).

Potential threats to well established mangroves include altered water flow patterns and altered salinity regimes. Mangrove encroachment is impeded by strong wave action or tidal scour so that sheltered areas often become colonised by extensive forests. Mangroves are also adversely affected by flooding with freshwater and continuous inundation. Examples are the destruction of mangroves in the Kosi Estuary (Breen and Hill 1969), St Lucia Estuary (Steinke and Ward 1989), Mgobezeleni Estuary (Bruton and Appleton 1975), Umlalazi Estuary (Hill 1966) and the Mgeni Estuary (Steinke and Charles 1986). Deposition of silt and the consequent covering of the base of trees also adversely affect mangroves, as in the Mbashe Estuary (West 1944 cited by Steinke 1972). *B. gymnorrhiza* is more tolerant of prolonged basal inundation than *A. marina* and has been reported to colonize periodically closed estuaries. *B. gymnorrhiza* has been found growing in depths of 0.75 m where salinity values of less than 10 PSU have been recorded (Ward 1976).

Because mangroves require a periodic change in water level to aerate the lenticels, which supply oxygen to the roots (Day 1981), Bruton and Appleton (1975) stated that inundation for as little as a fortnight by even a small permanent rise in local water level is enough to kill populations. Furthermore, unlike *B. gymnorrhiza* where propagules are able to survive more than a year immersed in freshwater (Ward et al. 1986), propagules of *A. marina* are intolerant of prolonged immersion (Table 5.11). Timing of inundation is also important because inundation of 2-3 months prior to flowering (October to January in *A. marina*) is sufficient to either kill or potentially threaten parent plants and result in a reduction of viable fruit production, as was found in the Kosi Estuary (Ward et al. 1986). Secondary effects of flooding, i.e. sedimentation left after the subsidence of water, also cause impacts. The consolidation of these sediments produces hard crusts that limit gaseous exchange between the pneumatophores and the water column/atmosphere. Sediments also build up so that the floor of the mangrove community is raised above the tidal influence.

Table 5.10 Documented salinity ranges for various mangrove species.

Species	Optimum range	Effects of salinity change	Reference
Avicennia marina	5-35 PSU	0 PSU for 6 months results in reduced growth; > 20 PSU delayed germination and reduced growth; > 35 PSU caused stunting	Downton (1982), Ball and Farquhar (1984), Burchett et al. (1984), Clough (1984), Naidoo (1987)
Bruguiera gymnorrhiza	≥ 10 PSU	> 35 PSU seed growth and germination reduced and/or senescence	Ward (1976), Steinke and Charles (1986), Naidoo (1990)
Ceriops tagal	5-16 PSU	> 30 PSU for 5.5 months reduced growth and seed germination; > 42 PSU for 5.5 months no seedling growth	Smith (1988)

Table 5.11 Documented water levels for various mangrove species.

Species	Optimum range	Influence of water level change	Reference
Bruguiera gymnorrhiza	0-75 cm		Ward (1976)
Avicennia marina		Die-back from 50 cm increase for 154 days	Breen and Hill (1969)
Ceriops tagal		Die-back from 50 cm increase for 154 days	Breen and Hill (1969)
Rhizophora mucronata		Die-back from 50 cm increase for 154 days	Breen and Hill (1969)

Examples of physico-chemical effects on mangroves in South African TOCEs

Water Level Fluctuations

Mangrove communities were destroyed in the Mgobezeleni Estuary due to inundation caused by a poorly designed bridge built across the estuary in 1971-72 (Bruton and Appleton 1975). For 5 months between 1965 and 1966, mangrove swamps in the Kosi Bay Estuary were inundated with 1.6 m of freshwater due to mouth closure following a cyclone. Mangroves in the lower reaches of the system were destroyed (Moll *et al.* 1971). Similarly, increased water levels of between 1.5 to 2.5 m in the St Lucia estuary after a cyclone also resulted in the die-back of mangroves (Steinke and Ward 1989). The mangrove communities of the Bulungula Estuary on the Transkei coast completely disappeared due to a natural reduction in freshwater inflow and the subsequent closure of the mouth for 5 months (Adams et al. 2004).

Salinity

The construction of a low-level bridge on the Mgobezeleni Estuary in KwaZulu-Natal resulted in salinity dropping to 0.3 PSU and the destruction of mangrove communities (Bruton and Appleton 1975).

DISTRIBUTION OF MACROPHYTES IN SOUTH AFRICAN TOCEs

Botanically, TOCEs in South Africa differ from each other, depending on their freshwater input, duration of mouth opening/closure and latitude. In a botanical survey of estuaries in the Eastern Cape Province, Colloty et al. (2002) found that in the Ciskei area salt marsh, reed and sedge and macroalgal communities were dominant. Submerged macrophytes such as *Ruppia cirrhosa* and *Potamogeton pectinatus* also occurred. Salt marsh was present because of high water column salinity and wide intertidal and supratidal areas. These estuaries were large (15 to 186 ha) and had high salinity of 13-23 PSU, due to overwash of seawater. TOCEs north of the Great Kei Estuary to the Mngazana Estuary had reeds and sedges. These estuaries were small (1- 41 ha) and a salinity range of 11-17 PSU prevailed. North of the Mngazana Estuary swamp forest, reeds and sedges occurred in place of salt marsh. These estuaries were also small (2-50 ha) and had salinity ranges of 10-18 PSU. Submerged macrophytes were not well represented in the KwaZulu-Natal estuaries, due to the high turbidity and sedimentation of these rivers when compared to Cape estuaries (Howard-Williams and Allanson 1979).

Macroalgae

Filamentous green algae are common in most TOCEs around the coast. They have wide salinity tolerance ranges and are often indicative of non-turbulent water (closed mouth conditions) and nutrient enrichment. In the small estuaries of KwaZulu-Natal, Begg (1984) reported that blooms of filamentous algae, e.g. *Chaetomorpha* often occur after flood events. Large mats of *Cladophora* and *Enteromorpha* have been observed in the Cape estuaries of Great Brak, Kabeljous, Seekoei, Van Stadens and East Kleinemonde.

Submerged macrophytes

Representative species are *Potamogeton pectinatus, Ruppia cirrhosa, Zostera capensis* and *Halophila ovalis*. Most of these species are cosmopolitan in their distribution. Verhoeven (1979) noted that *Ruppia* spp. had little ability to compete with other, more vigorous aquatic plants and, therefore, most frequently occurred in environments of variable salinity and temperature that other species could not endure. Many of the Eastern Cape estuaries (e.g. Seekoei and Kabeljous) have extensive submerged macrophyte beds consisting of both *Ruppia cirrhosa* and *Zostera capensis*.

In the St Lucia Estuary in KwaZulu-Natal, submerged macrophytes are only found at depths less than 60 cm (Taylor 2006). This is because the estuary is very turbid. Salinity variations determine the abundance of the dominant species. Under high saline conditions that exceed the tolerance range of *Potamogeton pectinatus*, *Ruppia cirrhosa* and *Zostera capensis* are dominant. *Potamogeton pectinatus* also occurs in some of the cool, temperate TOCEs along the west coast of South Africa, e.g. Groen (Heydorn and Grindley 1981).

Salt marshes

The distribution of salt marsh species is mainly determined by specific environmental habitats associated with periods of tidal inundation and salinity (Adams et al. 1999). In POEs where there is a large intertidal range, zonation tends to be better developed, e.g. Langebaan Lagoon and Knysna Estuary. Where small tidal ranges occur, vegetation forms mosaic patterns rather than definite zonation bands. O'Callaghan (1990a) identified two types of salt marsh communities in Cape estuaries namely, those associated with estuaries where tidal exchange predominates, i.e. POEs and those associated with estuaries that are predominately closed. The marshes associated with closed estuaries e.g. Kleinmond Lagoon had *Cotula coronopifolia* at the lower reaches, with *Sporobolus virginicus*, *Juncus kraussii* and *Samolus* sp. higher up. *Spartina maritima* is absent from most TOCEs because it occurs in areas where there is adequate tidal exchange (Adams and Bate 1995).

North of the Kei Estuary the subtropical climate generally favours the development of mangrove swamps (Adams et al. 1999). Hygrophilous grasses, e.g. *Sporobolus virginicus, Paspalum notatum* and *Cynodon dactylon* are, however, common. These species are often inundated at extremely high spring tides and form borders between estuarine and terrestrial vegetation.

The frequency and duration of open mouth conditions determines the presence of salt marsh. The large supratidal salt marsh areas in the Ncizele Estuary in the former Ciskei region was attributed to high salinity conditions as a result of seawater overwash into the estuary. The Cefane Estuary in the Eastern Cape is a TOCE with wide floodplains and extensive salt marsh (49.5 ha) (Walker 2004). Although this is a TOCE, is it often open and has an average salinity of 21 PSU (Walker 2004).

Reeds and sedges

The reed and sedge plant community types are found in freshwater and brackish zones of estuaries, usually as emergent plants lining the banks. Reeds and sedges occur in most TOCEs throughout South Africa. They are particularly prevalent in KwaZulu-Natal because these estuaries are mostly brackish. Dominant species are *P. australis, S. scirpiodes, Cyperus* spp., *Echinochloa pyramidalis, Leersia hexandra* and *Cyperus papyrus* (Howard-Williams 1979). Many of these species form floating mats.

Swamp forest

Swamp forests occur on the Mozambique Coastal Plain between the Mozambique border and the Msikaba River in the Eastern Cape (Colloty 2000). Swamp forest occurs in many of KwaZulu-Natal's estuaries where they often can be found as isolated patches in the upper reaches of permanently open estuaries (Begg 1978). Their occurrence in the lower reaches can be attributed to the lateral seepage of freshwater from the coastal dunes. Swamp forest is predominant in the smaller, fresher TOCEs of KwaZulu-Natal. Here they seem to be limited to a depth of <0.5 m (Riddin 1999).

Mangroves

Mangroves are found in the larger estuaries of the east coast. The northern limit of their distribution is the Kosi Estuary and their southern limit is at the Nxaxo-Nquisi Rivers (Wavecrest) and the Kobonqaba River (Nahoon River in the south) (Steinke and Ward 1990). In the southern systems they are restricted to isolated trees or small stands. This southern limit appears to be related to temperature with 19^{o}C being the lower limit (MacNae 1963). However there have been reports of significant growth of mangroves in the colder climates of Australia and New Zealand (Bridgewater 1982, Crisp et al. 1990, cited by Steinke 1995). Along the southeast South African coastline other factors that may influence mangrove distribution include the paucity of propagules, mortality rates and restriction of dispersal range (Steinke 1972, Steinke 1986). Mangroves are precluded from the smaller Eastern Cape estuaries due to infrequent mouth opening, continuous flooding of supratidal areas when closed and the difference in physico-chemical properties of TOCEs as opposed to POEs.

CONCLUSIONS

The increase in freshwater abstraction from estuaries can have a major influence on the physico-chemical characteristics of TOCEs. A reduction in freshwater supply can increase the frequency and duration of mouth closure. Increased water level and changes in salinity are the major factors that can cause changes in the macrophyte communities. South Africa has approximately 186 TOCEs. These estuaries are characterized by lower species richness than permanently open estuaries. The impacts of freshwater abstraction are often greatest in the smaller estuaries. The Klipdrif (Oos) and Slang estuaries have changed from intermittently open to almost permanently closed. Little water surface area remains due to freshwater abstraction, dune encroachment and excessive reed growth. In these small systems floods are important in re-setting the estuary and removing macrophytes from the main channel.

In other estuaries, management interventions have mitigated the impacts of freshwater abstraction. For example, in the Great Brak Estuary, a mouth management plan and water releases from the Wolwedans Dam have ensured that the mouth has remained open at important times, i.e. spring / summer. Long-term monitoring in this estuary has shown that the salt marsh is in a healthy condition as a result. Low water levels during the open mouth phase ensure the germination of seeds and growth of seedlings. Both intertidal and supratidal species are found and the salt marshes show distinct zones brought about by tidal inundation. When freshwater releases were not provided, there was a year of prolonged mouth closure. High water level and flooding of the marsh reduced the cover of supratidal (*Chenolea diffusa* and *Sporobolus virginicus)* and intertidal salt marsh species (*Triglochin* spp. and *Cotula coronopifolia*).

Besides salinity and water level fluctuations, other important factors controlling macrophytes in TOCEs are light and nutrient input. The lack of submerged macrophytes in KwaZulu-Natal estuaries on the east coast of South Africa has often been attributed to an increase in both catchment and bank erosion, sedimentation and lack of adequate light penetrating the water column. In some estuaries nutrient input coupled with prolonged mouth closure has resulted in excessive macroalgal growth. Although TOCEs are dynamic, resilient systems, the degradation of macrophytes and species losses can occur in response to changes in freshwater inflow. Since there are a limited number of aquatic macrophyte taxa able to colonise estuaries, the loss of one or two species from an estuary can mean the demise of submerged plants from that system.

Case studies from TOCEs in other parts of the world indicate that these estuaries function similarly and have similar species and macrophyte community types, and are dominated by submerged macrophytes and macroalgae. The majority of these plants can tolerate the fluctuating conditions characteristic of such estuaries.

REFERENCES

Adams JB (1989) The effect of light and salinity on the photosynthetic rates of lower intertidal and estuarine *Caulerpa filiformis* (Caulerpales, Chlorophyta). BSc Hons Project, University of Port Elizabeth, Port Elizabeth.

Adams JB, Knoop WT and Bate, GC (1992) The distribution of estuarine macrophytes in relation to freshwater. *Botanica Marina* **35**: 215-226.

Adams JB and Bate GC (1994a) The tolerance to desiccation of the submerged macrophytes *Ruppia cirrhosa* (Petagna) Grande and *Zostera capensis* Setchell. *Journal of Experimental Marine Biology and Ecology* **183**: 53-62.

Adams JB and Bate GC (1994b) The ecological implications of tolerance to salinity by *Ruppia cirrhosa* (Petagna) Grande and *Zostera capensis* Setchell. *Botanica Marina* **37**: 449-456.

Adams JB and Bate GC (1994c) The effect of salinity and inundation on the estuarine macrophyte *Sarcocornia perennis* (Mill.) A.J. Scott. *Aquatic Botany* **47** 341-348.

Adams JB and Bate GC (1994d) The freshwater requirements of estuarine plants incorporating the development of an estuarine decision support system. Unpublished report to Water Research Commission, Report No. 292/2/94. 73 pp.

Adams JB and Bate GC (1995) Ecological implications of the tolerance of salinity and inundation by *Spartina maritima*. *Aquatic Botany* **52**: 183-191.

Adams JB and Bate GC (1996) Understanding the freshwater requirements of estuarine plants. In: Coastal Management and Habitat Conservation. (eds. Salman, A.H.P.M., Langeveld, M.J. and Bonazountas, M.), pp. 181-192. The Netherlands.

Adams JB, Bate GC and O'Callaghan MO (1999) Primary Producers. In: Estuaries in South Africa. (eds. Allanson, BR and Baird D). Cambridge University Press. pp 91-117.

Adams JB, Colloty BM and Bate GC (2004) The distribution and state of mangroves along the coast of the Transkei, Eastern Cape Province, South Africa. *Wetlands Ecology and Management* **12** 531-541.

Andersen FO (1976) Primary production in a shallow water lake with special reference to a reed swamp. *Oikos* **27** 243-250.

Ball MC and Farquhar GD (1984) Photosynthetic and stomatal responses of two mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, to long-term salinity and humidity conditions. *Plant Physiology* **74** 1-6.

Barko JW and Smart RM (1978) The growth and biomass distribution of two emergent freshwater plants, *Cyperus esculentus* and *Scirpus validus*, on different sediments. *Aquatic Botany* **5** 109-117.

Beare PA and Zedler JB (1987) Cattail invasion and persistence in a coastal salt marsh: the role of salinity reduction. *Estuaries* **10**(2) 165-170.

Begg GW (1978) The Estuaries of Natal. *Natal Town and Regional Planning Report* **41** 657 pp.

Begg GW (1984) The comparative ecology of Natal's smaller estuaries. *Natal Town and Regional Planning Report* **62** 182 pp.

Benfield MC (1984) Some factors influencing the growth of *Phragmites australis* (Cav.) Trin ex Steudal. M.Sc. thesis University of Natal, Durban.

Benjamin KJ, Walker DI, McComb AJ and Kuo J (1999) Structural response of marine and estuarine plants of *Halophila ovalis* (R. Br.) Hook. F. to long-term hyposalinity. *Aquatic Botany* **64** 1-17.

Bickerton IB (1982) Report No. 15: Zeekoe (CSW 5). In: Estuaries of the Cape, Part II. Synopses of Available Information on Individual systems. (eds. Heydorn, A.E.F. and Grindley, J.R.). *CSIR Research Report* No. **414**.

Bornman TG (2002) Freshwater requirements of supratidal and floodplain salt marsh on the West Coast, South Africa. Ph.D. thesis, University of Port Elizabeth.

Bornman TG, Adams JB and Bate GC (2002) Freshwater requirements of a semi-arid supratidal and floodplain salt marsh. *Estuaries* **25** (6B) 1394-1405.

Bornman TG, Adams JB and Bate GC (2003) The influence of floodplain geohydrology on the distribution of *Sarcocornia pillansii* in the Olifants Estuary on the West Coast, South Africa. *Journal of Arid Environments* **56** 603-625.

Bornman TG, Adams JB and Bezuidenhout C (2004) Adaptations of salt marsh to semi-arid environments and management implications for the Orange River mouth. *Transactions of the Royal Society of South Africa* **59**(2) 125 – 131.

Boshoff DN (1983) Die moontlike uitwerking van verlaagde watervlak (1.5 m en 3 m) op die plantegroei in en om die Mzingazimeer. University of Zululand, unpublished report to the Richards Bay Municipality.

Branch M and Branch G (1985) The Living Shores of Southern Africa. C. Struik Publishers, Cape Town: 272 pp.

Branch GM, Bally R, Bennet BA, De Becker HP and Fromme G (1985) Synopsis of the impact of artificially opening the mouth of the Bot river estuary: implications for management. *Transactions of the Royal Society of South Africa* **45** 465-483.

Breen CM and Hill BJ (1969) A mass mortality of mangroves in the Kosi estuary. *Transactions of the Royal Society of South Africa* **38** (3) 285-303.

Breen CM, Everson C and Rogers K (1977) Ecological studies on *Sporobulus virginicus* (L.) Kunth with particular reference to salinity and inundation. *Hydrobiologia* **54** (2) 135-140.

Bridgewater PB (1982) Phytosociology of coastal salt-marshes in the mediteranean climatic region of Australia. *Phytoceanologia* **10** 257-296.

Bruton MN and Appleton CC (1975) Survey of Mgobezeleni lake-system in Zululand, with a note on the effect of a bridge on the mangrove swamp. *Transactions of the Royal Society of South Africa* **41** (3) 283-295.

Burchett MD, Field CD and Pulkownik A (1984) Salinity, growth and root respiration in the grey mangrove, *Avicennia marina. Plant Physiology* **60** 113-118.

Chapman VJ (1960) Salt Marshes and Salt Deserts of the World. Interscience Publishers, New York. 392 pp.

Clough BF (1984) Growth and salt balance of the mangrove *Avicennia marina* (Forsk.) Vierh. and *Rhizophora stylosa* Griff. in relation to salinity. *Australian Journal of Plant Physiology* **11** 419-430.

Coetzer AH (1987) Succession in zooplankton and hydrophytes of a seasonal water on the west coast of South Africa. *Hydrobiologia* **148** 193-210.

Colloty BM Adams JB and Bate GC (2002) Classification of estuaries in the Ciskei and Transkei regions based on physical and botanical characteristics. *South African Journal of Botany* **68** 312-321.

Colloty BM (2000) Botanical importance of estuaries of the former Ciskei/Transkei region. PhD thesis, University of Port Elizabeth, Port Elizabeth 202 pp.

Coops H and Van der Velde G (1996) Effects of waves on helophyte stands: mechanical characteristics of stems of *Phragmites australis* and *Scirpus lacustris*. *Aquatic Botany* **53** 175-185.

Coops H, van den Brink FWB and van der Velde G (1996) Growth and morphological responses of four helophyte species in an experimental water-depth gradient. *Aquatic Botany* **54** 11-24.

Crum G.H and Bachman RW (1973) Submersed aquatic plants of the Iowa Great Lakes region. *Iowa State Journal of Research* **48** 147-173.

Cyrus DP, Martin TJ and Reavell PE (1997) Salt-water intrusion from the Mzingazi River and its effects on adjacent swamp forest at Richards Bay, Zululand, South Africa. CRUZ, University of Zululand.

Day JH (1981) *Estuarine Ecology*. A.A. Balkema, Cape Town.

Deegan B, Harrington TJ and Dundon P (2005) Effects of salinity and inundation regime on growth and distribution of *Schoenoplectus triqueter*. *Aquatic Botany* **81** 199–211.

Downton WJS (1982) Growth and osmotic relations of the mangrove *Avicennia marina*, as influenced by salinity. *Australian Journal of Plant Physiology* **9** 519-528.

Duarte CM (1991) Seagrass depth limits. *Aquatic Botany* **40** 363-377.

Duarte CM (1995) Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* **41** 87-112.

Flindt MR, Pardal MA, Lillebo AI, Martins I and Marques, JC (1999) Nutrient cycling and plant dynamics in estuaries: A brief review. *Acta Oecologica* **20** 237-248.

Froneman PW, (2002) Response of the plankton to three different hydrological phases of the temporarily open/closed Kasouga Estuary, South Africa. *Estuarine, Coastal and Shelf Science* **55** 535-546.

Furness HD and Breen CM (1985) Interactions between period of exposure, grazing and crop growth rate of *Cynodon dactylon* (L.) in seasonally flooded areas of the Pongolo River floodplain. *Hydrobiologia* **126** 65-73.

Gallagher JL (1979) Growth and element compositional responses of *Sporobolus virginicus* (L.) Kunth, to substrate salinity and nitrogen. *The American Midland Naturalist* **102** (1) 68-75.

Glenn E, Thompson TL, Frye R, Riley J and Baumgartner D (1995) Effects of salinity on growth and evopotranspiration of *Typha domingensis* Pers. *Aquatic Botany* **52** 75-91.

Gordon D.M, Birch PB and McComb AJ (1980) The effect of light, temperature and salinity on photosynthetic rates of an estuarine *Cladophora*. *Botanica Marina* **23** 749-755.

Grace JB (1989) Effects of water depth on *Typha latifolia* and *Typha domingensis*. *American Journal of Botany* **76**(5):762-768.

Gray AJ (1986) Do invading species have definable genetic characteristics? *Philosophical Transactions of the Royal Society of London,* Series B **314** 655-674.

Grillas P and Duncan P (1986) On the distribution and abundance of submerged macrophytes in temporary marshes in the Camargue (S. France). In: Proceedings of the 7th International Symposium on Aquatic Weeds, European Weed Research Society and Association of Applied Biologists. Pages 133-141.

Grime J (1979) *Plant Strategies and Vegetation Processes*. Wiley and Sons, Toronto. 222 pp.

Haslam SM (1971) Community regulation in *Phragmites communis* Trin. II. Mixed stands. *Journal of Ecology* **59** 75-88.

Hartzendorf T and Rolletschek H (2001) Effects of NaCl salinity on amino-acid and carbohydrate contents of *Phragmites australis. Aquatic Botany* **69** 195-208.

Heinsohn RD and Cunningham AB (1991) Utilization and potential cultivation of the saltmarsh rush *Juncus kraussii*. *South African Journal of Botany* **57** (1) 1-5.

Hellings SE and Gallagher JL (1992) The effects of salinity and flooding on *Phragmites australis*. *Journal of Applied Ecology* **29** 41-49.

Heydorn AEF and Grindley JR (1981) Estuaries of the Cape. Part II. Synopsis of available information on individual systems, Report No. 3: Groen. (eds. Heydorn, A.E.F. and Grindley, J.R.). *CSIR Report* **402** 40pp.

Hill BJ (1966) A contribution to the ecology of the Umlalazi estuary. *Zoologica Africana* **2** (1) 1-24.

Hillman K, McComb AJ and Walker DI (1995) The distribution, biomass and primary production of the seagrass *Halophila ovalis* in the Swan/Canning Estuary, Western Australia. *Aquatic Botany* **51** 1-54.

Hiralal P (2001) The effects of sedimentation and turbidity on the distribution of the seagrass *Zostera capensis* Setchell in KwaZulu-Natal, South Africa. MSc thesis, University of Durban-Westville, Durban.

Hootmans MJM and Wiegman F (1998) Four helophyte species growing under salt stress: their salt of life? *Aquatic Botany* **62** 81-94.

Howard-Williams C (1979) Distribution, biomass and role of aquatic macrophytes in Lake Sibaya. In: Lake Sibaya. (eds. Allanson, B.R., *et al.*). *Monographiae Biologicae* **36**, Dr W.Junk Publishers, The Hague.

Howard-Williams C and Allanson B R (1979) The ecology of Swartvlei: Research for planning and future management. *Water Research Commission Report*, 26 pp.

Howard-Williams C (1980) Aquatic macrophytes communities of the Wilderness Lakes: Community structure and associated environmental conditions. *Journal of the Limnological Society of southern Africa* **6** (2) 85-92.

Howard-Williams C and Liptrot MRM (1980) Submerged macrophyte communities in a brackish South African estuarine-lake system. *Aquatic Botany* **9** 101-116.

Howard-Williams C and Allanson BR (1981) Phosphorous cycling in a dense *Potamogeton pectinatus* L. bed. *Oecologia* **49** 56-66.

Iyer V and Barnabas AD (1993) Effects of varying salinity on leaves of *Zostera capensis* Setchell. I. Ultrastructural changes. *Aquatic Botany* **46** 141-153.

Jackson MD and Drew MC (1984) Effects of flooding on herbaceous plants. In: Flooding and Plant Growth. (ed. Kozlowski, T.T.) Academic Press Inc. New York, London.

Jupp BP and Spence DHN (1977a) Limitations on macrophytes in a eutrophic lake, Loch Leven. I. Effects of phytoplankton. *Journal of Ecology* **65** 175-186.

Jupp BP and Spence DHN (1977b) Limitations on macrophytes in a eutrophic lake, Loch Leven. II. Wave action, sediments and waterfowl grazing. *Journal of Ecology* **65** 431-446.

Kamer K and Fong P (2000) A fluctuating salinity regime mitigates the negative effects of reduced salinity on the estuarine macroalga, *Enteromorpha intestinalis* (L.) link. *J. Exp. Mar. Biol. and Ecol.* **254** 53–69.

Kantrud H A (1990) Sago pondweed (*Potamogeton pectinatus* L.): A literature review. U.S. Fish and Wildlife Service, Fish and Wildlife Resource Publication 176. Jamestown, ND: Northern Prairie Wildlife Research Center Home Page.
http://www.npwrc.usgs.gov/resource/literatr/pondweed/pondweed.htm .

Kantrud H A (1991) Wigeongrass (*Ruppia maritima* L.): A literature Review. U.S. Fish and Wildlife Service, Fish and Wildlife Research 10. Jamestown, ND: Northern Prairie Wildlife Research Center Home Page.
http://www.npwrc.usgs.gov/resource/literatr/ruppia/ruppia.htm.

Karez RS, Engelbert, P, Kraufvelin MF Pedersen and Sommer U (2004) Biomass response and changes in composition of ephemeral macroalgal assemblages along an experimental gradient of nutrient enrichment. *Aquatic Botany* 78 103-117.

Lieffers VJ and Shay JM (1981) The effects of water level on the growth and reproduction of *Scirpus maritimus* var. *paludosus*. *Canadian Journal of Botany* 59 118-121.

Lissner J and Schierup HH (1997) Effects of salinity on the growth of *Phragmites australis*. *Aquatic Botany* **55** 247-260.

Lowthion D, Soulsby PG and Houston MCM (1985) Investigation of a eutrophic tidal basin: Factors affecting the distribution and biomass of macroalgae. *Marine Environmental Research* **15** 263–284.

MacNae W (1963) Mangrove swamps in South Africa. *Journal of Ecology* **51** 1-25.

Mall RE (1969) Soil-water-plant Relationships of Waterfowl Food Plants in the Suisun Marsh of California. Wildlife Bulletin No. 1, California Department of Fisheries and Game, Sacramento. 59 pp.

Marcum KB and Murdoch CL (1992) Salt tolerance of the coastal salt marsh grass, *Sporobulus virginicus* (L.) Kunth. *New Phytologist* **120** 281-288.

Martins I, Pardal, MA, Lillebø AI, Flindt MR and Marques JC (2001) Hydrodynamics as a major factor controlling the occurrence of green macroalgal blooms in a eutrophic estuary: A case study on the influence of precipitation and river management. *Estuarine, Coastal and Shelf Science* **52** 165–177.

McDonald, ME (1955) Cause and effects of a die-off of emergent vegetation. *Journal of Wildlife Management* **19** 24-35.

McMillan C and Moseley FN (1967) Salinity tolerances of 5 marine spermatophytes of Redfish Bay, Texas. *Ecology* **48** 503-506.

Msibi SP (1991) The effect of salinity on seedling growth of *Barringtonia racemosa*. Honours Thesis, University of Zululand.

Moll EJ, Ward CJ, Steinke TD and Cooper KH (1971) Our mangroves threatened. *African Wildlife* **26** 103-107.

Naidoo G (1986) Responses of the mangrove *Rhizophora mucronata* to high salinities and low osmotic potentials. *South African Journal of Botany* **52** 124-128.

Naidoo G (1987) Effects of salinity and nitrogen on growth and plant water relations in the mangrove *Avicennia marina*. *New Phytologist* **107** 317-325.

Naidoo G (1994) Growth, water and ion relationships in the coastal halophytes *Triglochin bulbosa* and *Triglochin striata*. *Envrionmental and Experimental Biology* **34**(4) 419-426.

Naidoo G and Mundree SG (1993) Relationship between morphological and physiological responses to waterlogging and salinity in *Sporobulus virginicus* (L.) Kunth. *Oecologia* **93** 360-366.

Naidoo G and Naicker K (1992) Seed germination in coastal halophytes *Triglochin bulbosa* and *Triglochin striata*. *Aquatic Botany* **42** 217-229.

Naidoo G and Naidoo Y (1998) Salt tolerance in *Sporobulus virginicus*: the importance of ion relations and salt secretion. *Flora* **193** 337-344.

Naidoo, G and Raiman, F (1982) Some physical and chemical properties of mangrove soils at Sipingo and Mgeni, KwaZulu-Natal. *South African Journal of Botany* **1** 85-90.

Nichols DS and Keeney DR (1976) Nitrogen nutrition of *Myriophyllum spicatum* uptake and translocation of ^{15}N by shoots and roots. *Freshwater Biology* **6** 144-154.

O'Callaghan M (1990a) The ecology of the False Bay estuarine environment, Cape, South Africa. 1. The coastal vegetation. *Bothalia* **20** 105–112.

O'Callaghan M (1990b) The ecology of the False Bay estuarine environments, Cape, South Africa. 2. Changes during the last fifty years. *Bothalia* **20** 113–121.

O’Callaghan M (1992) The ecology and identification of the southern African Salicorniaceae (Chenopodiaceae). South African Journal of Botany 58: 430-439.

O'Neill EJ (1972) Alkali bulrush seed germination and culture. *Journal of Wildlife Management* **36** 649-652.

Orth RJ, Moore KA and Gordon HH (1979) Distribution and abundance of submerged aquatic vegetation in the lower Chesapeake Bay, Virginia. *U.S. Environmental Protection Agency Report* 600/8-79-029/SAV1. 199 pp.

Phillips GL, Eminson D and Moss B (1978) A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquatic Botany* **4** 103-126.

Pringle JD (1986) Swarmer release and distribution of life-cycle phases of *Enteromorpha intestinalis* (Chlorophyta) in relation to environmental factors. *Journal of Experimental Marine Biology and Ecology* **100**(1–3) 97–112.

Ralph PJ (1998) Photosynthetic response of *Halophila ovalis* (R. Br.) Hook. F. to osmotic stress. *Journal of Experimental Marine Biology and Ecology* **227** 203-220.

Reed RH and Russell G (1979) Adaptation to salinity stress in populations of *Enteromorpha intestinalis* (L.) Link. *Estuarine Coastal and Marine Shelf Science* **8** 251-258.

Riddin T 1999. The botanical importance of the Nhlabane Estuary, South Africa. MSc thesis, University of Port Elizabeth, Port Elizabeth.

Sand-Jensen K and J Borum (1991) Interactions among phytoplankton, periphyton and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany* **41** 137-175.

Schwarz A and Hawes I (1997) Effects of changing water clarity on characean biomass and species composition in a large oligotrophic lake. *Aquatic Botany* **56** (3/4) 169-181.

Sfriso A, Pavoni B, Marcomini A and Orio, AA (1992) Macroalgae, nutrient cycles, and pollutants in the Lagoon of Venice. *Estuaries* **15** (4) 517–528.

Short RM and McRoy CP (1984) Nitrogen uptake by leaves and roots of the seagrass *Zostera marina* L. *Botanica Marina* **27** 547-555.

Smith TJ (1988) Differential distribution between sub-species of the mangrove *Ceriops tagal*: competitive interactions along a salinity gradient. *Aquatic Botany* **32** 79-89.

Spence DHN (1982) The zonation of plants in freshwater lakes. *Advances in Ecological Research* **12** 37-125.

Spencer DF (1986) Early growth of *Potamogeton pectinatus* L. in response to temperature and irradiance: morphology and pigment composition. *Aquatic Botany* **26** 1-8.

Squires L and van der Valk AG (1992) Water-depth tolerances of the dominant emergent macrophytes of the Delta marsh, Manitoba. *Canadian Journal of Botany* **70** 1860-1867.

Steinke TD (1995) A general review of the mangroves of South Africa. In: Wetlands of South Africa. (ed. Cowan, G.I.) pp. 53-73. Department of Environmental Affairs and Tourism, Pretoria.

Steinke TD (1972) Further observations on the distribution of mangroves in the eastern Cape Province. *South African Journal of Botany* **38** 165-178.

Steinke TD (1986) A preliminary study of buoyancy behaviour in *Avicennia marina* propagules. *South African Journal of Botany* **52** 559-565.

Steinke TD and Charles LM (1986) Litter production by mangroves. I: Mgeni Estuary. *South African Journal of Botany* **52** 552-558.

Steinke TD and Ward CJ (1989) Some effects of the cyclones Domoina and Imboa on mangrove communities in the St. Lucia estuary. *South African Journal of Botany* **55**(3) 340-348.

Steinke TD and Ward CJ (1990) Litter production by mangroves. III. Wavecrest (Transkei) with predictions for other Transkei estuaries. *South African Journal of Botany* **56**(5) 514-519.

Stewart BA and Davies BR (1986) Effects of harvesting on invertebrates associated with *Potamogeton pectinatus* L. in the Marina da Gama, Zandvlei, Western Cape. *Transactions of the Royal Society of South Africa* **46** 35-50.

Taylor D.I (1983) The effects of a major macrophytes regression upon the primary production in the littoral of Swartvlei. *Archiv für Hydrobiologie* **96**(3) 345-353.

Taylor RH, Adams JB and Haldorsen S (2006) Primary habitats of the St Lucia estuarine system, South Africa, and their responses to mouth closure. *African Journal of Aquatic Science* **31**(1) 31-41.

Tölken HR (1967) The species *Arthrocnemum* and *Salicornia* (Chenopodiaceae) in southern Africa. *Bothalia* **9** 255-307.

Twilley RR, Kemp WM, Staver KW, Stevenson JC and Boynton WR (1985) Nutrient enrichment of estuarine submersed vascular plant communities. Algal growth and effects on production of plants and associated communities. *Marine Ecology Progress Series* **23** 179-191.

Tyler-Walters H (2001) *Ruppia maritima*. Beaked tasselweed. *Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme* [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 06/06/2005].Availablefrom: http://www.marlin.ac.uk/species/Ruppiamaritima.htm.

Ungar IA (1962) Influence of salinity on seed germination in succulent halophytes. *Ecology* **55** 199-201.

Ungar IA (1978) Halophyte seed germination. *Botanical Review* **44** 233-264.

Valiela I, McClelland J, Hauxwell J, Behr PJ, Hersh D and Foreman K (1997) Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* **42** 1105-1118.

Verhoeven JTA and van Vierssen W (1978) Distribution and structure of communities dominated by *Ruppia*, *Zostera* and *Potamogeton* species in the inland waters of 'De Bol', Texel, The Netherlands. *Estuarine Coastal and Marine Science* **6** 417-428.

Verhoeven JTA (1979) The ecology of *Ruppia*-dominated communities in Western Europe. I. Distribution of *Ruppia* representatives in relation to their autecology. *Aquatic Botany* **6** 197-268.

Verhoeven JTA (1980) The ecology of *Ruppia*-dominated communities in Western Europe. II. Synecological classification. Structure and dynamics of the macroflora and macrofauna communities. *Aquatic Botany* **8** 1-85.

Walker DR, Perissinotto R and Bally RPA (2001) Phytoplankton/protozoan dynamics in the Nyara estuary, a small temporarily open system in the Eastern Cape (South Africa). *African Journal of Aquatic Science* **26** 31-38.

Walker DR (2004) Plant and algal distribution in response to environmental variables in selected Eastern Cape estuaries. PhD thesis, University of Port Elizabeth, Port Elizabeth.

Ward CJ (1976) Aspects of the ecology and distribution of submerged macrophytes and shoreline vegetation of Lake St. Lucia. In: (A.E.F. Heydorn, ed.). St. Lucia Scientific Advisory Council workshop - Charters Creek, February 1976. Natal Parks Board, Pietermaritzburg.

Ward CJ, Steinke TD and Ward M.C (1986) Mangroves of the Kosi system, South Africa: their re-establishment since a mass mortality in 1965/66. *South African Journal of Botany* **52** 501-512.

Weisner SEB (1991) Within-lake patterns in depth penetration of emergent vegetation. *Freshwater Biology* **26** 133-142.

Weisser PJ, Whitfield AK and Hall CM (1992) The recovery and dynamics of submerged aquatic macrophyte vegetation in the Wilderness lakes, southern Cape. *Bothalia* **22** 283-288.

Weisser PJ and Howard-Williams C (1982) The vegetation of the Wilderness Lakes system and the macrophyte encroachment problem. *Bontebok* **2** 19-40.

Weisser PJ and Parsons RJ (1981) Monitoring *Phragmites australis* increases from 1937 to 1976 in the Siyayi Lagoon (KwaZulu-Natal, South Africa) by means of air photo interpretation. *Bothalia* **13** (3/4) 553-556.

Weisser PJ and Ward CJ (1982) Destruction of the *Phoenix/Hibiscus* and *Barringtonia racemosa* communities at Richards Bay, Natal, South Africa. *Bothalia* **14** (1) 123-125.

Weisser PJ, Boshoff DN and Van Eeden S (1987) Vegetation and vegetation change at the Mzingazi Lake. In: Proceedings of a symposium on ecology and conservation of wetlands in South Africa. (eds. Walmsley, R.D. and Botten, M.L.). *Occasional Report Series* No. 28, pp. 254-259. Ecosystems Programmes, FRD, CSIR, Pretoria.

Wessels N (1997) Aspects of the ecology and conservation of swamp forests in South Africa. PhD Thesis, Port Elizabeth Technicon, Port Elizabeth.

Whitfield AK (1988) The role of tides in redistributing macrodetrital aggregates within the Swartvlei estary. *Estuaries* **11** (3) 152-159.

Yamasaki S and Tange I (1981) Growth responses of *Zizania latifolia, Phragmites australis* and *Miscanthus sacchariflorus* to varying inundation. *Aquatic Botany* **10** 229-239.

Yamasaki S (1993) Probable effects of algal blooms on the growth of *Phragmites australis* (Cav.) Trin. ex Steud. *Journal of Plant Research* **106** 113-120.

6. ZOOPLANKTON

W. Froneman

Zoology Department, Rhodes University, Grahamstown

INTRODUCTION

The trophodynamics of the larger (> 200µm) zooplankton in Eastern Cape TOCEs has, over the past five years, been the subject of extensive investigation albeit in a limited number of systems (see Table 6.1). However, only two studies have examined the role of microheterotrophs (2-200µm) within TOCEs in the same geographic region. This review therefore covers the main research findings from the spatial and temporal patterns in the community composition and feeding ecology of zooplankton in TOCEs along the Eastern Cape and Western Cape coastlines.

Table 6.1. Major zooplankton studies conducted in TOCEs within the warm temperate and subtropical biogeographical provinces of South Africa

System	Reference
Swartvlei (warm temperate)*	Coetzee (1981)
Touw (warm temperate)*	Coetzee (1983)
Kabeljous (warm temperate)	Schlacher and Woodridge (1995)
Kasouga (warm temperate)	Froneman (2002, 2004a, 2004b, 2004c)
East Kleinemonde (warm temperate)	Kemp and Froneman (2004), Bernard and Froneman (2005)
Nyara (warm temperate)	Perissinotto et al. (2000), Walker et al. (2001)
Mpanjati (subtropical)	Kibirige and Perissinotto (2002), Kibirige et al. (2003), Perissinotto et al. (2003)
Mhlanga (subtropical)	Perissinotto et al. (2004)
Mdloti (subtropical)	Perissinotto et al. (2004)

* Note: Both these systems were separated from the sea by a sand bar at the mouth and are therefore included in this review.

ZOOPLANKTON ABUNDANCE AND BIOMASS

The microheterotrophic component of the zooplankton assemblage in TOCEs along the Eastern Cape coastline has been studied in the Nyara and Kasouga estuaries (Walker et al. 2001, Froneman 2002, 2004). Results of these surveys indicate that the microheterotroph community is numerically dominated by nanoheterotrophs (<20 µm), naked ciliates, tintinnids and dinoflagellates, with densities ranging between 10^3 to 10^5 cells l^{-1} (Walker et al. 2001, Froneman 2004). The highest abundances of microheterotrophs were typically attained during the closed phase of the estuary (Walker et al. 2001, Froneman 2004). Conversely, the lowest abundances were recorded during breaching events. The elevated abundances of microheterotrophs during the closed phase can probably be attributed to the increased residence time of the water body and the low macronutrient concentrations, which promotes the establishment of the microbial loop.

Estimates indicate that the total zooplankton abundance and biomass in TOCEs along the Eastern and Western Cape coastlines is highly variable, reflecting a variety of factors including freshwater inflow, mouth status and seasonality (Coetzee 1981, Froneman 2004a, 2004b, 2004c). Maximum zooplankton abundance and biomass in these TOCEs have generally been recorded during the closed phase (Whitfield 1980, Perissinotto et al. 2000, Froneman 2004a, 2004, 2004c). Under these conditions, the total zooplankton abundance may attain levels of up to 10^6 individuals m^{-3} with a total biomass of up to 2 g dry mass m^{-3} (Perissinotto et al. 2000, Froneman 2004a, 2004, 2004c). Preliminary data indicate that the inflow of marine waters into TOCEs during overtopping events may also contribute to the build-up of zooplankton biomass within these estuaries during the closed phase (Froneman, unpublished data).

There are no apparent horizontal trends in total zooplankton abundance and biomass, possibly due to the virtual absence of horizontal gradients in salinity and temperature within these systems (Schlacher and Wooldridge 1995, Froneman 2004b). In agreement with studies conducted in TOCEs along the KwaZulu-Natal coastline (Whitfield 1980, Perissinotto et al. 2000), breaching events in Eastern Cape TOCEs are associated with a considerable decline in both total zooplankton abundance and biomass (Froneman 2004b, Bernard and Froneman 2005). During these breaching periods, total zooplankton abundance and biomass is normally $< 10^3$ individuals m^{-3} and < 50 mg dry mass m^{-3}, respectively (Froneman 2004b, 2004c). The reduction in total zooplankton abundance and biomass can be linked to the export of zooplankton and associated food resources to the marine environment during river flooding.

ZOOPLANKTON DIVERSITY AND SIZE COMPOSITION

In agreement with studies conducted in a number of TOCEs along the KwaZulu-Natal coastline (Perissinotto et al. 2004), prolonged periods of mouth closure are generally associated with low levels of zooplankton taxonomic diversity in Eastern Cape TOCEs (Froneman 2004a). The reduced levels of taxonomic diversity can be ascribed to the poor representation of typical marine breeding species within the estuary (Froneman 2004a). Analysis of the zooplankton community during the closed phase of the estuary indicate that the total zooplankton community is generally composed of a few euryhaline taxa (generally < 15 species) with 2-3 species generally comprising >90% of the total zooplankton abundance and biomass (Froneman 2002, 2004b). Among the dominant taxa, the various developmental stages of the calanoid copepods, *Pseudodiaptomus hessei* and *Acartia longipatella*, are the most prominent and may account for > 85% of total zooplankton abundance and biomass (Coetzee 1981, 1983, Perissinotto et al. 2000, Froneman 2002, 2004b). Also well represented among the zooplankton are copepod species of the genera, *Oithona* and *Halicyclops*, the cumacean, *Iphinoe truncata*, the amphipod *Grandidierella lignorum*, isopods of the genus *Exosphaeroma* and the mysid, *Mesopodopsis wooldridgei* (Coetzee 1981, 1983, Perissinotto et al. 2000, Froneman 2002, 2004b). The contribution of these species is, however, always <5% of total zooplankton abundance (Coetzee 1981, 1983, Perissinotto et al. 2000, Froneman 2004b). However, in terms of total zooplankton biomass, these species may account for up to 20% of the total.

When compared to larger permanently open estuaries within the same geographic region, zooplankton diversity within TOCE is generally less that that recorded in the former, particularly in those systems characterised by sustained freshwater inflow (Wooldridge 1999). The elevated diversity within the larger permanently open systems can be related to increased contribution of marine breeding species to total diversity and the presence of both freshwater and true estuarine species (Wooldridge 1999). On the other hand, in those permanently open systems, which are freshwater deprived, zooplankton community structure is broadly similar to that found in TOCE's during the closed phase (Froneman 2002).

The establishment of a link to the marine environment through overtopping or breaching events coincides with a considerable increase in the size of zooplankton within the TOCE community and an increase in the taxonomic diversity (Froneman 2004, Kemp and Froneman 2004). The shift can largely be ascribed to the recruitment of larger marine breeding species (including larvae of the caridian shrimp, *Palaemon peringueyi*, the mysids *Gastrosaccus brevifissura* and *Rhapalophthatmus tarrantalis* into the estuary, which are otherwise poorly represented among the zooplankton during the closed phase (Froneman 2004a, 2004b).

ZOOPLANKTON TROPHIC INTERACTIONS

Only a single study has investigated the role of microheterotrophs as grazers of phytoplankton production in TOCEs along the Eastern Cape coastline (Froneman 2004a). The results of a yearlong study indicated that the daily grazing impact of heterotrophic organisms < 200µm ranged between 0.7 and 15.2 mg C m^{-3} d^{-1} that corresponded to a loss of up to 37% (range 7-46%) of the total daily phytoplankton production (Froneman 2004a). Over the same period, the total grazing impact of the mesozooplankton was estimated to range from 0.2 to 24.2 mg C m^{-3} d^{-1}. These ingestion rates were equivalent to the utilisation of between 0.2 and 45% of daily phytoplankton production (Froneman 2004a). Although there were no apparent spatial trends in the grazing impact of the microheterotrophs or mesozooplankton during the study, the highest grazing impact of the mesozooplankton was recorded during the closed phase following freshwater inflow into the estuary. The observed pattern could be linked to the availability of preferred food particle sizes (Froneman 2004a).

The grazing estimates obtained for the larger zooplankton in the Kasouga Estuary are lower than those recorded in TOCEs along the KwaZulu-Natal coastline where the autotrophic consumption by the three dominant species of zooplankton in the Mpenjati estuary between 1998 and 2001 often exceeded 100% of the estimated daily phytoplankton production. (Perissinotto et al. 2003) Differences in the grazing rates of the mesozooplankton between the two estuaries appear to be linked to the size structure of the phytoplankton assemblage. In the Mpanjati estuary, the total phytoplankton biomass is composed mainly of nanophytoplankton (2-20µm), which are readily consumed by copepods. On the other hand, in the Kasouga estuary, picophytoplankton (< 2µm), which are too small to be efficiently grazed by the mesozooplankton, dominated total phytoplankton biomass (Froneman 2004a).

Results of species specific grazing rate studies indicated that the variations in feeding rates of the two dominant copepods in the Kasouga estuary, *Pseudodiaptomus hessei* and *Acartia longipatella*, could be attributed to shifts in the phytoplankton community structure resulting from alterations in freshwater inflow into the estuary (Froneman 2004c). During periods of reduced or no freshwater inflow into the estuary, carbon derived from the consumption of phytoplankton alone was often insufficient to meet the basis metabolic requirements of the two-copepod species (Froneman 2004c). The low contribution of carbon derived from the consumption of the phytoplankton could largely be attributed to the predominance of the picophytoplankton, which is too small to be grazed efficiently by the copepods within the system. Under these conditions, alternative carbon sources including microphytobenthic and protozooplankton are utlised (Froneman 2004c). Indeed, results of stable isotope analysis indicate that microphytobenthic derived carbon represents an important source of carbon for the dominant zooplankton within the Kasouga Estuary (Froneman 2002). This result is consistent with the findings of Kibirige et al. (2002, 2003) within the Mpanjati estuary on the east coast of South Africa. On the other hand, during those periods when the total phytoplankton biomass was dominated by larger nanophytoplankton (2-20µm), carbon derived from the consumption of the phytoplankton was sufficient to meet the basic metabolic requirements of both *P. hessei* and *A. longipatella* (Froneman 2004c). These findings highlight the importance of freshwater inflow through its effect on the phytoplankton size community composition, in determining the feeding dynamics of the dominant zooplankton within Eastern Cape TOCEs.

The variations in the feeding ecology of the numerically dominant zooplankton observed within TOCE's is broadly similar to those recorded in larger permanently open estuaries within the same geographic region (Jerling and Wooldridge 1995; Froneman 2000). In those permanently open systems characterised by sustained freshwater inflow, the zooplankton appear largely to be herbivorous feeding mainly on phytoplankton (Jerling and Wooldridge 1995; Wooldridge 1999). Conversely in those permanently open estuaries with reduced freshwater inflow, the zooplankton appear to derive the bulk of the carbon necessary to meet their basic metabolic requirements from salt marsh vegetation or microphytobethic algae (Froneman 2000).

SUMMARY

Results of studies conducted in TOCE's in both KwaZulu-Natal and Eastern Cape indicate that mouth status plays an important role in structuring the zooplankton assemblages within these systems. In the absence of any link to the marine environment, zooplankton diversity within these systems is generally low reflecting the reduced contribution of marine and freshwater breeding species to total zooplankton in these estuaries. The establishment of a link to the marine environment through overtopping or breaching events coincides with an increase in the zooplankton diversity, which can be linked to recruitment of marine breeding species into the estuary. The maximum abundance and biomass of zooplankton within TOCE's is attained during the closed phase and appears to be sustained by the extensive microphytobenthic stocks that occur within these estuaries. The feeding ecology of the numerically dominant zooplankton within TOCE's is mediated by shifts in the phytoplankton community structure resulting from alterations in freshwater inflow into the estuary. During periods of reduced or no freshwater inflow into the estuary, carbon derived from the consumption of phytoplankton alone is often insufficient to meet the basis metabolic requirements of the two copepod species. The low contribution of carbon derived from the consumption of the phytoplankton could largely be attributed to the predominance of the picophytoplankton, which is too small to be grazed efficiently by the copepods within the system. Under these conditions, alternative carbon sources including microphytobenthic and protozooplankton are utlised. On the other hand, during those periods when the total phytoplankton biomass was dominated by larger nanophytoplankton (2-20μm), carbon derived from the consumption of the phytoplankton was sufficient to meet the basic metabolic requirements of the numerically dominant copepods within TOCE's

REFERENCES

Coetzee DJ (1981) Zooplankton distribution in relation to environmental conditions in the Swartvlei system, southern Cape. *Journal of Limnological Society of Southern Africa* **7** 5-12.

Froneman PW (2000) Feeding studies of selected zooplankton in a temperate estuary, South Africa. *Estuarine, Coastal and Shelf Science* **51** 543-552.

Froneman PW (2002) Food web structure in three contrasting estuaries determined by stable carbon isotope analysis. *African Journal of Aquatic Sciences* **27** 107-115.

Froneman PW (2002) Seasonal variations in selected physico-chemical and biological variables in the temporarily open/closed Kasouga estuary (South Africa). *African Journal of Aquatic Sciences* **27** 117-123.

Froneman PW (2002) Response of the biology to three different hydrological phases in the temporarily open/closed Kasouga estuary. *Estuarine, coastal and Shelf Science* **55** (4) 535-546.

Froneman PW (2004a) Food web dynamics in a temperate temporarily open/closed estuary (South Africa*). Estuarine, Coastal and Shelf Science* **59** 87-95.

Froneman PW (2004b) Seasonal patterns in the zooplankton community structure and biomass in an eastern Cape temporarily open/closed estuary. *Estuarine Coastal and Shelf Science* **60** 125- 132.

Froneman PW (2004c) *In situ* grazing rates of the copepods, *Pseudodiaptomus hessei* and *Acartia longipatella* in a temperate, temporarily open/closed estuary. *South African Journal of Science* **100** 577-583.

Kemp JOG and Froneman PW (2004) Recruitment of ichthyoplankton and macrozooplankton during overtopping events into a temporarily open/closed southern African estuary. *Estuarine Coastal and Shelf Science* **61** 529-537.

Jerling HL and Woodridge TH (1995) Relatively negative $§^{13}C$ ratios of mesozooplankton in the Sundays River estuary, comments on potential carbon sources. *Southern African Journal of Aquatic Sciences* **21** 71-77.

Kibirige I and Perissinotto R (2003) *In situ* feeding rates and grazing impact of zooplankton in a South African temporarily open estuary. *Marine Biology* **142** 357-367.

Kibirige I, Perissinotto R and Nozias C (2002) Alternative food sources of zooplankton in a temporarily open estuary: evidence from $\partial^{13}C$ and $\partial^{15}N$. *Journal of Plankton Research* **24** 1089-1095.

Kibirige I, Perissinotto R and Nozias C (2003) Grazing rates and feeding preferences of the mysid shrimp, *Gastrosaccus brevifissura*, in a temperate temporarily open estuary, South Africa. *Marine Ecology Progress Series 251* 201-210.

Perissinotto R, Blair A, Connell A, Demetriades NT, Forbes AT, Harrison TD, Iyer K, Joubert M, Kibirige I, Mundree S, Simpson H, Stretch D, Thomas C, Thwala X and Zietsman I (2004) Contributions to information requirements for the implementation of resource directed measures for estuaries. Volume 2: Response of the biological communities to flow variation and mouth state in two KwaZulu-Natal temporarily open/closed estuaries. (Ed) Adams JB. *WRC report* No: **K5/1247**.

Perissinotto R, Walker DR, Webb P, Woodridge TH and Bally R (2000) Relationships between zoo- and phytoplankton in a warm-temperate, semi-permanently closed estuary, South Africa. *Estuarine, Coastal and Shelf science* **51** 1-11.

Perissinotto R, Nozias C, Kibirige I and Anandraj A (2003) Planktonic food webs and benthic coupling in three temporarily-open estuaries. *Acta Oecologia* **24** s307-s316.

Schlacher TA and Woodridge TH 1995. Small-scale distribution and variability of demersal zooplankton in a shallow temperate estuary: tidal and depth effects of species-specific heterogeneity. *Cahiers de Biologie Marine* **36** 211-227.

Walker DR, Perissinotto R and Bally RPA (2000) Phytoplankton/protozoan dynamics in the Nyara estuary: a small temporarily open system in the Eastern Cape (South Africa). *African Journal of Aquatic Science* **26** 31-38.

Whitfield AK (1980) A quantitative study on the tropic relationships within the fish community of the Mhlanga estuary, South Africa. *Estuarine, Coastal and Shelf Science* **10** 417-435.

Wooldridge T (1999) Estuarine zooplankton community structure and dynamics. In: *Estuaries of South Africa* (eds) Allanson BR and Baird D. Cambridge University Press, Cambridge, United Kingdom. pp 141-166.

7. LARVAL FISH

Nadine Strydom

South African Institute for Aquatic Biodiversity, Grahamstown

INTRODUCTION

Published and unpublished scientific information dealing with fishes exists for most of the 47 permanently open and at least 80 of the 181 TOCEs in South Africa. These works extend over a range of biological, physiological and ecological aspects of fishes in estuaries (Whitfield 1998, Whitfield 2000). On the other hand, research on larval fishes in these systems has been less intensive. Researchers have either defined the larval fish assemblage in $a particular estuarine system (Wallace 1975, Melville-Smith and Baird 1980, Melville-Smith 1981, Whitfield 1989a, Harrison and Whitfield 1990, Harris and Cyrus 1995, Harris et al. 1995), or have assessed dynamic aspects of larval fishes associated with these single-estuary assemblages such as tidal exchange (Beckley 1985, Whitfield 1989b, Strydom and Wooldridge 2005), tidal current use by a larval fish species (Melville-Smith et al. 1981), recruitment (Harris and Cyrus 1996), ocean-estuary coupling (Harris et al. 2001) and natural and artificial flushing effects (Martin et al. 1992, Strydom and Whitfield 2000; Strydom et al. 2002). Most of these research efforts on larval fishes have been conducted in permanently open estuaries (POEs), predominantly in the warm temperate Eastern Cape region.

Multi-estuary approaches to understanding the composition and dynamics of larval fish assemblages in different types of estuaries are relatively new. Whitfield (1994) and Harris and Cyrus (2000) presented work in which three POEs were compared in the warm temperate and subtropical region respectively. A recent publication by Strydom et al. (2003) compares 12 warm temperate estuaries, five of which were TOCEs (Table 7.1). Research in progress by Strydom (in prep.) includes an assessment of larval fish composition and abundance in nine cool temperate estuaries, two of which are TOCEs, and an additional two in estuarine lake systems that function similarly to TOCEs (Table 7.1).

LARVAL FISH RESEARCH IN INTERMITTENTLY OPEN ESTUARIES

Very little work has been conducted in TOCEs on larval fishes in South Africa. Whitfield (1980) made some preliminary quantitative notes on fish larvae in the subtropical Mhlanga Estuary in terms of overall calorific value. In that study, no actual abundance data or qualitative compositional data were made available but the author noted that fish larvae presented the highest calorific value in the water column during the closed mouth state in late summer. The seaward flushing of larvae during the opening of perched subtropical estuaries like the Mhlanga probably resulted in large losses of larvae and other zooplanktonic organisms to the sea (Whitfield 1980).

Dundas (1994) compared the ecology of the fishes in three TOCEs in the warm temperate region of the Eastern Cape, namely the Seekoei, Kabeljous and Van Stadens, and included a larval fish component in that study. Only two positively identified species of larval fish were recorded in these systems namely, *Gilchristella aestuaria* and *Atherina breviceps*. Gobiidae were also recorded but were cumulatively referred to as unidentified gobies. Dundas (1994) found that densities peaked in summer and the assemblage was dominated by *G. aestuaria*. Species diversity was very low, probably due to the tenuous link with the sea and drought conditions at the time of sampling. Changes in the frequency, nature and duration of opening events was attributed to drought and this negatively affected recruitment of larvae from the marine environment.

The most comprehensive work on larval fishes in South African TOCEs is a five-estuary survey included in Strydom et al. (2003). The authors assessed species composition, estuarine association, species diversity and abundance of larvae occupying seven POEs and five TOCEs characterized by varying physico-chemical and hydrodynamic features. Furthermore, that study assessed the physical, temporal and spatial factors governing those larval fish assemblages and defined the communities and key species contributing to the differences between the systems. The TOCEs studied were the Gqutywa, East Kleinemonde, Old Womans, Van Stadens and Kabeljous. A summary of available information on these latter systems is included below in Tables 7.2 and 7.3.

ESTUARY-DEPENDENT LARVAE IN SURF ZONES

Whitfield (1989c) assessed the nursery function of the surf zone for estuary-associated larval fish species in Swartvlei Bay, adjacent to the Swartvlei Estuary. Harris and Cyrus (1996) conducted the first KwaZulu-Natal surf-zone research and focused on larval and juvenile fishes in the surf adjacent to the St Lucia Estuary. Harris et al. (2001) expanded this and also investigated larval fish diversity along an ocean-estuarine gradient in northern KwaZulu-Natal. They also expanded on the limited available information linking these habitats and highlighting the coupling and importance of these habitats for estuary-dependent larval fishes. Cowley et al. (2001) published information on surf-zone utilisation by larval stages of estuary-dependent species off the intermittently open East Kleinemonde Estuary. This work provided initial evidence of larval fish recruitment, and the seasonal timing thereof (Bell et al. 2001), into closed estuaries during marine overwash events. Kemp and Froneman (2004) also provided additional information on the potential magnitude of estuary-dependent ichthyoplankton recruitment during overwash events. Strydom (2003) supplemented this TOCE related surf research with a year long assessment of larval fishes in the surf zone adjacent to the intermittently open Van Stadens and Kabeljous estuaries. In this latter study, valuable information was gained on the responsiveness of larval fishes to TOCE opening events.

CAPE TOCE CASE STUDY

A study of larval fishes in seven POE's and five TOCE's was conducted between 1998 and 1999 (Strydom et al. 2003). Some results from that study are presented below, with particular emphasis on information about larval fishes in TOCEs (Figure 7.1). The authors found that physico-chemical and hydrodynamic variability within permanently open and intermittently open estuarine systems influence the larval fish communities residing in and utilising these habitats as nursery areas. Although each estuarine system appeared distinct from the next, driven by the physical variables governing each system (Table 7.3), general trends emerged in the spatial and temporal variability in larval fish assemblages and community structure.

Table 7.1 Available information on larval fishes in South African TOCEs and adjacent surf-zones.

Estuary	**Type**	**Ichthyoplankton information**	**Reference**
Boknes	TOCE	Composition and habitat use in adjacent surf	Watt-Pringle and Strydom (2003)
Bot	Lake	Composition, abundance and distribution	Strydom (in prep.)
Diep	TOCE	Composition, abundance and distribution	Strydom (in prep.)
East	TOCE	Composition, abundance and distribution	Strydom et al. (2003)
Kleinemonde		Composition in adjacent surf-zone	Cowley et al. (2001)
		Estuarine access opportunities for larvae	Bell et al. (2001)
West Kleinemonde	TOCE	Recruitment during overtopping of sandbar	Kemp and Froneman (2004)
Gqutywa	TOCE	Composition, abundance and distribution	Strydom et al. (2003)
Kabeljous	TOCE	Composition, abundance and distribution	Dundas (1994)
		Composition, abundance and distribution	Strydom et al. (2003)
		Composition in adjacent surf-zone	Strydom (2003)
Klein	Lake	Composition, abundance and distribution	Strydom (in prep.)
Lourens	TOCE	Composition, abundance and distribution	Strydom (in prep.)
Old Womans	TOCE	Composition, abundance and distribution	Strydom et al. (2003)
Mhlanga	TOCE	Overall calorific value of ichthyoplankton	Whitfield (1980)
Seekoei	TOCE	Composition, abundance and distribution	Dundas (1994)
Swartvlei	Lake	Composition, abundance and distribution	Whitfield (1989a)
		Composition in adjacent surf-zone	Whitfield (1989c)
Van Stadens	TOCE	Composition, abundance and distribution	Dundas (1994)
		Composition, abundance and distribution	Strydom et al. (2003)

Table 7.2 Physical characteristics of five Eastern Cape TOCE's sampled between 1998 and 1999 (after Strydom et al. 2003) (MAR = mean annual runoff).

TOCE	**Kabeljous**	**Van Stadens**	**East Kleinemonde**	**Old Womans**	**Gqutywa**
Length sampled (km)	1.7	1.5	2.5	0.8	2
Width (m)	10 – 100	10 – 30	20 – 62	10 - 20	40 – 70
Channel depth (m)	0.5 – 1.6	1 – 2	1 – 1.5	0.75 – 1.5	0.5 – 1.5
Catchment (km^2)	312	271	46	24	85
MAR (m^3)	27×10^6	21×10^6	2×10^6	1.2×10^6	6×10^6
Sites sampled	3	3	5	2	3

Table 7.3 Salinity (PSU), water temperature (˚C) and water transparency (*k*) measurements taken in selected Eastern Cape Province estuaries during the study period (after Strydom et al. 2003).

TOCE	**Physico-chemical variable**	**Mean**	**Median**	**Range**
East Kleinemond	Salinity	16.93	14.60	10.69-23.71
	Temperature	21.06	23.14	13.28-26.02
	Water transparency	0.02	0.02	0.01-0.03
Old Womans	Salinity	30.72	31.65	16.91-36.28
	Temperature	20.29	21.55	13.27-27.20
	Water transparency	0.01	0.01	0.01-0.02
Gqutywa	Salinity	39.82	39.87	35.66-43.19
	Temperature	21.92	22.79	15.11-28.01
	Water transparency	0.03	0.03	0.02-0.04
Van Stadens	Salinity	13.02	13.27	2.69-18.94
	Temperature	20.10	20.60	11.99-28.64
	Water transparency	0.01	0.01	0.01-0.02
Kabeljous	Salinity	32.76	34.33	19.79-40.57
	Temperature	20.16	20.70	14.33-26.43
	Water transparency	0.02	0.02	0.01-0.04

POEs showed a distinct separation from the small TOCEs sampled in terms of assemblage structure (Figure 7.1). Community analysis identified distinct assemblages of fishes occupying specific estuary types and salinity zones within these estuaries. Estuary-dependent marine species and the estuarine gobiid, *Redigobius dewaali*, which is not found in TOCE's, were responsible for the distinct separation between POEs and TOCEs.

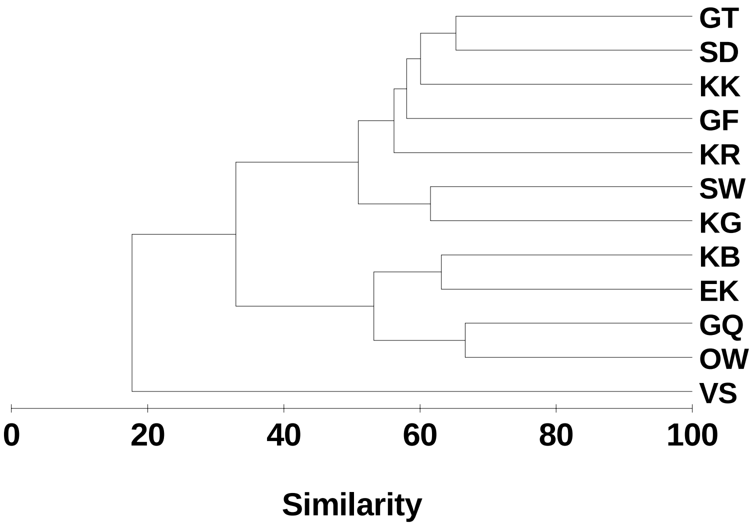


Figure 7.1 Bray-Curtis similarity dendrogram showing classification of selected Eastern Cape Province estuaries based on the presence or absence of larval fishes (GT = Gamtoos, SD = Sundays, KK = Keiskamma, GF = Great Fish, KR = Kromme, SW = Swartkops, KG = Kariega, KB = Kabeljous, EK = East Kleinemonde, GQ = Gqutywa, OW = Old Womans, VS = Van Stadens) (after Strydom et al. 2003).

Salinity zones also appeared to be a defining factor affecting larval and early juvenile distribution in these systems and also reflects the varying salinity preferences of larval fishes utilizing estuarine nurseries. Fish density was found to be an ineffective means of defining an estuarine community because densities varied significantly between open and temporarily open systems. On occasion, densities of certain species, such as *Gilchristella aestuaria*, in TOCEs were higher than catches of the same species made in POEs. Species presence or absence appeared to be the most effective means of defining estuaries in terms of the larval fish assemblages in these systems.

The number of species occurring in TOCEs is considerably lower than those in POEs. TOCEs were characterized by low species diversity and richness and this is directly attributed to the nature of these small systems where access is limited during extended periods of closure (Table 7.4). The larvae found in TOCEs belong mainly to estuary resident fish species, predominantly *Gilchristella aestuaria*, *Glossogobius callidus* and *Psammogobius knysnaensis* (Table 7.5).

Table 7.4 Species richness and diversity indices for larval fish assemblages in five TOCE's sampled between 1998 and 1999 (after Strydom et al. 2003).

Estuary	No. of species	Species richness (d)	Species diversity (H')
Kabeljous	9	2.63	1.22
Van Stadens	4	0.78	0.40
East Kleinemonde	10	1.21	1.08
Old Womans	5	0.67	0.93
Gqutywa	4	0.51	0.19

Table 7.5 Species composition, total catch, length, estuary association (after Whitfield 1998) and developmental stage of larval fishes caught in the plankton of five TOCE's sampled between 1998 and 1999 (after Strydom et al. 2003). Ys = yolk sac, Pr = preflexion, F = flexion, Po = postflexion, Ju = early juvenile, Ge = glass eel.

Family	Species	Catch	Body length (mm)		Developmental stage	Estuary association
		No.	Mean	Range		
Blenniidae	*Omobranchus woodi*	15	3.7	2.7 – 13.6	Ys,Pr,Po	Ia
Clupeidae	*Gilchristella aestuaria*	8437	13.3	2.2 – 31.8	Pr,F,Po, Ju	Ia
	Etrumeus whiteheadi	1	19.3	10.9 – 23.3	Po	III
Gobiidae	*Caffrogobius gilchristi*	574	3.5	2.2 – 10.4	Pr,Po	Ib
	Caffrogobius sp. 1	3505	3.8	2.0 – 17.2	Ys,Pr,Po	-
	Caffrogobius sp. 2	707	3.2	2.0 – 3.7	Ys,Pr	-
	Glossogobius callidus	336	6.7	2.2 – 22.9	Ys,Pr,F,Po	Ib
	Psammogobius knysnaensis	74	2.9	1.7 – 15.5	Ys,Pre,Po	Ib
	Gobiid 2	2	2.9	2.6 – 4.8	Ys,Pre	-
	Gobiid 6	2	3.3	1.9 – 4.4	Pre	-
	Rhabdosargus holubi	2	11.4	8.8 – 17.9	Po	IIa
Syngnathidae	*Syngnathus acus*	1	13.3	9.7 – 21.5	Po,Ju	Ib

The presence of marine postflexion larvae of *Rhabdosargus holubi* and *Etrumeus whiteheadi* recorded on one occasion in the temporarily open East Kleinemonde Estuary, during the closed mouth phase, indicated that certain species are also entering closed estuaries via overwash events during high seas and surviving the overwash process. This phenomenon was initially noted by Dundas (1994) and recorded by Cowley et al. (2001).

Catches of fish larvae were highest in spring and summer in these five TOCEs, with the main contributer being the estuary-resident *Gilchristella aestuaria*. Larvae were often recorded in densities far greater than those observed in POEs. Mesohaline zones were also found to support the highest densities of larvae in POEs as well as TOCEs (Table 7.6).

Table 7.6. Mean density for larval fishes recorded in different seasons and salinity zones in five TOCEs sampled between 1998 and 1999 (after Strydom et al. 2003).

	Density (number per 100 m^3)		
	Mean	Median	Range
Season			
Summer	1372	314	0 - 5346
Autumn	65	34	0 - 313
Winter	3	0	0 - 19
Spring	1099	26	0 - 13881
Salinity zone			
Fresh	-	-	-
Oligohaline	14	14	11 - 17
Mesohaline	1505	121	0 - 13881
Polyhaline	116	6	0 - 2590
Euhaline	379	10	0 - 2612
Hypersaline	176	33	0 - 2355

Mesohaline regions in estuaries have been associated with river estuary interface (REI) regions and generally become regions of high primary and secondary productivity (Wooldridge and Bailey 1982, Jerling and Wooldridge 1991, Snow et al. 2000). This salinity zone may have feeding implications for larval fishes and may explain the higher densities in the mesohaline regions of these estuaries.

CONCLUSIONS

Estuarine type, largely governed by river flow, and associated environmental conditions, determines the composition of larval fishes utilising these systems. This influence of river flow rate spans both POEs and TOCEs (Strydom et al. 2003). TOCEs appear to have a characteristic larval assemblage associated with them, both in the Eastern Cape and Western Cape (preliminary data from Strydom in prep.). Estuary resident larvae dominate TOCEs in both regions.

Despite the understanding we now have on the dynamics of larval fishes in the plankton of these systems, we know very little about the effects of extended mouth closure or opening events on Cape TOCEs. No detailed information exists for the dynamics of recruitment of marine larval fishes that are dependent on the estuary as a nursery area. In particular, we do not know how mouth conditions affect recruitment qualitatively and quantitatively, how opening channel dimensions and associated hydrodynamic features affect larval recruitment, or how conditions within the estuary during different mouth conditions affect larval survival. Much information will be gained by focusing on littoral larval and early juvenile fish communities in TOCEs during both closed and open phases, in both the estuary and the mouth region, to assess the effects of freshwater supply and intensity on mouth dynamics and the use (timing and duration) of the entrance channel by larval fishes.

REFERENCES

Beckley LE (1985) Tidal exchange of ichthyoplankton in the Swartkops Estuary mouth, South Africa. *South African Journal of Zoology* **20** 15-20.

Bell KNI, Cowley PD and Whitfield AK (2001) Seasonality in frequency of marine access to an intermittently open estuary: implications for recruitment strategies. *Estuarine, Coastal and Shelf Science* **52** 327-337.

Cowley PD, Whitfield AK and Bell KNI (2001) The surf zone ichthyoplankton adjacent to the mouth of a predominantly closed Southern African Estuary, with evidence of recruitment during marine overwash events. *Estuarine, Coastal and Shelf Science* **52** 339-348.

Dundas A (1994) A comparative analysis of fish abundance and diversity in three semi-closed estuaries in the Eastern Cape. M.Sc. thesis, University of port Elizabeth, Port Elizabeth. 81 pp.

Harris SA and Cyrus DP (1995) Occurrence of fish larvae in the St Lucia Estuary, KwaZulu-Natal, South Africa. *South African Journal of Marine Science* **16** 333-350.

Harris SA and Cyrus DP (1996) Larval and juvenile fishes in the surf zone adjacent to the St Lucia Estuary mouth, Kwa-Zulu-Natal, South Africa. *Marine and Freshwater Research* **47** 465-482.

Harris SA and Cyrus DP (2000) Comparison of larval fish assemblages in three large estuarine systems, KwaZulu-Natal, South Africa. *Marine Biology* **137** 527-541.

Harris SA, Cyrus DP and Beckley LE (2001) Horizontal trends in larval fish diversity and abundance along an ocean-estuarine gradient on the Northern KwaZulu-Natal coast, South Africa. *Estuarine, Coastal and Shelf Science* **53** 221-235.

Harris SA, Cyrus DP and Forbes AT (1995) The larval fish assemblage at the mouth of the Kosi Estuary, KwaZulu- Natal, South Africa. *South African Journal of Marine Science* **16** 351-364.

Harrison TD and Whitfield AK (1990) Composition, distribution and abundance of ichthyoplankton in the Sundays River estuary. *South African Journal of Zoology* **5** 161-168.

Jerling HL and Wooldridge TH (1991) Population dynamics and estimates of production for the calanoid copepod Pseudodiaptomus hessei in a warm temperate estuary. *Estuarine, Coastal and Shelf Science* **33** 121-135.

Kemp JOG and Froneman PW (2004) Recruitment of ichthyoplankton and macrozooplankton during overtopping events into a temporarily open/closed southern African estuary. *Estuarine, Coastal and Shelf Science* **61** 529-537.

Martin TJ, Cyrus DP and Forbes AT (1992) Episodic events: The effects of cyclonic flushing on the ichthyoplankton of St Lucia Estuary on the southeast coast of Africa. *Netherlands Journal of Sea Research* **30** 273-278.

Melville-Smith R (1981) The ichthyoplankton of the Kromme River Estuary. *South African Journal of Zoology* **16** 71-72.

Melville-Smith R and Baird D (1980) Abundance, distribution and species composition of fish larvae in the Swartkops Estuary. *South African Journal of Zoology* **15** 72-78.

Melville-Smith R, Baird D and Wooldridge TH (1981) The utilisation of tidal currents by the larvae of an estuarine fish. *South African Journal of Zoology* **16** 10-13.

Snow GC, Adams JB and Bate GC (2000) Effect of river flow on estuarine microalgal biomass and distribution. *Estuarine, Coastal and Shelf Science* **51** 255-266.

Strydom NA (2003) Occurrence of larval and early juvenile fishes in the surf zone adjacent to two TOCEs, South Africa. *Environmental Biology of Fishes* **66** 349-359.

Strydom NA (in prep) Composition, abundance and distribution of larval fishes in warm and cool temperate estuaries of South Africa.

Strydom NA and Whitfield AK (2000) The effects of a single freshwater release into the Kromme Estuary. 4: Larval fish response. *Water SA* **26** 319-328.

Strydom NA and Wooldridge TH (2005) Diel and tidal variations in larval fish exchange on a neap and spring tide in the mouth of the Gamtoos Estuary, South Africa. *African Journal of Aquatic Science* **30** 131-140.

Strydom NA, Whitfield AK and Paterson AW (2002) Influence of altered freshwater flow regimes on abundance of larval and juvenile *Gilchristella aestuaria* (Pisces: Clupeidae) in the upper reaches of two South African estuaries. *Marine and Freshwater Research* **53** 431-438.

Strydom, NA, Whitfield AK and Wooldridge TH (2003) The role of estuarine type in characterising early stage fish assemblages in warm temperate estuaries, South Africa. African Zoology **38** (1) 29-43.

Wallace JH (1975) The estuarine fishes of the East Coast of South Africa. III. Reproduction. Oceanographic Research Institute Investigational Report No. 41: 51 pp

Watt-Pringle P and Strydom NA (2003) Habitat use by larval fishes in a temperate South African surf zone. *Estuarine, Coastal and Shelf Science* **58** (4) 765-774.

Whitfield AK (1980) A quantitative study of the trophic relationships within the fish community of the Mhlanga Estuary, South Africa. *Estuarine and Coastal Marine Science* **10** 417-435.

Whitfield AK (1989a) Fish larval composition, abundance and seasonality in a southern African estuarine lake. *South African Journal of Zoology* **24** 217-224.

Whitfield AK (1989b) Ichthyoplankton interchange in the mouth region of a southern African estuary. Marine Ecology Progress Series **54** 25-33.

Whitfield AK (1989c) Ichthyoplankton in a southern African surf zone: nursery area for the postlarvae of estuarine associated fish species? *Estuarine, Coastal and Shelf Science* **29** 533-547.

Whitfield AK (1994) Abundance of larval and 0+ juvenile marine fishes in the lower reaches of three southern African estuaries with differing freshwater inputs. *Marine Ecology Progress Series* **105** 257-267.

Whitfield AK (1998) Biology and Ecology of Fishes in South African Estuaries. *Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology*, No. **2** 223 pp.

Whitfield AK (2000) Available scientific information on individual South African estuarine systems. *Water Research Commission Report* No. **557/3/00** 217 pp.

Wooldridge TH and Bailey C (1982) Euryhaline zooplankton of the Sunday estuary and notes on trophic relationships. *South African Journal of Zoology* **17** 151-163.

8. HYPERBENTHOS

William Froneman[1] and Lukhanyiso Vumazonke[2]

[1]Zoology Department, Rhodes University, Grahamstown;
[2]South African Institute for Aquatic Biodiversity, Grahamstown

INTRODUCTION

The hyperbenthal is the transition zone between the benthos and the plankton (Boyson 1975). The hyperbenthos is defined as the fauna living in the water column but more or less dependent on the proximity of the bottom (Beyer 1958). A variety of organisms occupy the hyperbenthal zone. Permanent hyperbenthic organisms (e.g. amphipods and mysids) spend their entire life cycle in the hyperbenthic zone. Organisms that spend only a part of their life cycle (e.g. fish and larvae of decapods) in the hyperbenthic zone are termed, 'temporary hyperbenthos' (Mees and Hamerlynck 1992). For the purpose of this review, only the macroplankton (> 2 cm) component of the hyperbenthos will be reviewed. The recruitment and population dynamics of the smaller (< 2 cm) components of the hyperbenthos consisting mainly of mysids are briefly discussed in Chapter 6. The hyperbenthos within southern African estuaries typically comprises prawns, crabs and shrimps. The relative importance of each of these groups displays a high degree of spatial and temporal variability (see review of De Villiers et al. 1999).

PRAWNS

The penaeid prawn fauna in the coastal and estuarine waters of southern Africa is numerically dominated by five species, *Penaeus indicus*, *P. japonicus*, *P. semisulcantus*, *P. monodon* and *Metapenaeus monoceros* (De Villiers et al. 1999). The five species of prawn are most common in the permanently open subtropical estuaries of KwaZulu-Natal and decline in numbers in the temperate waters of the Eastern and Western Cape. The life history patterns of the penaeid prawns have been studied extensively, particularly in Durban and Richard Bay as well as in the Kosi Bay and St Lucia systems (see review of De Villiers et al. 1999). Results of these studies indicate that post-larvae (carapace length < 5.0 mm) congregate in the near-shore region where they are washed into permanently open estuaries by tidal currents mainly during the night (De Villiers et al. 1999). A peak in recruitment of the post larvae into estuaries takes place in early summer and autumn with abundances attaining levels of up to 1.5 individuals m^{-3} (Forbes and Benfield 1986; Forbes and Cyrus 1991). It is worth noting that the various species of penaeid prawn show species specific variations in the spatial and seasonal patterns in recruitment into permanently open estuaries (Demetriades and Forbes 1993). The distribution of the various penaeid prawn species in estuaries appears to be influenced by salinity and to a lesser extent water temperature as well as macrophyte distribution (Walsh and Mitchell 1998).

To the authors knowledge there have been no studies on the population dynamics of penaeid prawns in TOCE's within the warm subtropical zone of southern Africa. A recent study by Kemp and Froneman (2004) demonstrated that the post larvae of unidentified prawn species recruited into the East Kleinemonde estuary along the Eastern Cape coastline during overtopping events. Similarly, Froneman (2004) demonstrated that recruitment of the post larvae of prawns into the Kasouga Estuary occurred after it had breached. The recruitment of the prawns into the estuary was largely mediated by incoming tides.

A review of published literature indicates that the penaeid prawns can largely be regarded as benthic omnivores (De Villiers et al. 1999). Their diet consists mainly of crustaceans, crabs and detritus. The predation impact of the prawns on the benthic food species has to date not been quantified (De Villiers et al. 1999). According to Bickerton (1989), local species of the genus *Macrobranchium* can be considered as omnivorous benthic feeders. The predation impact or the role that these species play in structuring the benthic communities within southern African estuaries is presently unknown.

Seven species of the freshwater prawns of the genus *Macrobrachium* have been identified, mainly within the subtropical zone of KwaZulu-Natal. (De Villiers et al. 1999). Bickerton (1983), however, found that *M. petersi* extended its distribution as far south as the Keiskama River in the Eastern Cape. The decline in numbers of species towards the temperate region can be ascribed to the tropical affinity of the genus. Apart from the study on the taxonomic distribution of the seven species by Barnard (1950), information on the biology of these species has been restricted to the St Lucia system (Bickerton 1989). Results of this study suggest that distribution of the prawn was strongly correlated to salinity. Maximum abundances occurred at the mouth of streams and points of freshwater inflow. Egg production occurred mainly in summer and available information suggests an absence of any marine phase (Read 1985 cited in De Villiers et al. 1999). It has been suggested that the shrimp employ behavioural adaptations to reduce loss of larvae to the marine environment (Read 1985 cited in De Villiers et al. 1999).

CRABS

The swimming crab, *Scylla serrata*, occurs throughout the warm tropical zone of KwaZulu-Natal and extends as far south as the Knysna estuary within the warm temperate zone of southern Africa (Day 1974). Maximum abundances of *S. serrata* are recorded within the subtropical zone whereas their abundance becomes erratic at the southern limit of its range (Robertson 1996). Considerable research has been conducted on the swimming crab within permanently open estuaries along both the south and east coasts of southern Africa (Roberstson 1987). Results of these studies indicate that abundances of crab are highly variable ranging from < 0.01 up to 0.339 individuals in 100 m^{-3} (De Villiers et al. 1999). The distribution of the crab within permanently open estuaries varies according to size with juveniles recorded within the inter-tidal region and adults within the water column (Robertson 1987). Female *S. serrata* typically spawn at sea with the recruitment of megalope into estuaries occurring mainly during spring and summer.

The abundance, breeding and growth of *S. serrata* have been investigated in the permanently open Kowie and temporarily open Kleinemonde estuaries along the Eastern Cape coastline (Hill 1975). The estimates of abundance of S. *serrata* in the Kowie and Kleimonde estuaries ranged from 1 and 10 individuals per 10 traps, and between 0 and 7.5 per 10 traps, respectively (Hill 1975). The elevated abundances of the crab recorded in the permanently open Kowie estuary could be related to continuous recruitment of the megalope into the estuary. Results of study further indicated that sexually mature female *S. serrata* utlised overtopping events to emigrate out of the estuary. The study further demonstrated that breaching or flood events coincided with a dramatic decline in the number of mature crabs within the two estuaries. This was attributed to the outflow of estuarine rich water into the marine environment (Hill 1975).

The gut contents of *S. serrata* indicate that the crab consumes mainly gastropods and bivalves and to a lesser extent crustaceans (Hill 1976). Again, the predation impact of *S. serrata* on prey species in southern African estuaries is presently unknown.

SHRIMPS

The published literature indicates that while extensive investigations on the ecological role of *Palaemon peringueyi* in permanently open estuaries have been undertaken (see for example Emmerson 1983, 1987), studies on their role in TOCEs are limited to the Grant's and West Kleinemonde estuaries in the warm temperate zone (Kemp and Froneman 2004, Bernard and Froneman (2005), Froneman (submitted) along the Eastern cape coast.

Estimates of the abundance and biomass of *P. peringueyi* in the temporarily open West Kleinemonde Estuary range between zero and 14.3 individuals m^{-2} and between zero and 1.2g dry mass m^{-2}, respectively (Bernard and Froneman 2005). These estimates are substantially lower than the values reported in permanently open estuaries within the same geographic region. For example, in the Swartkops and Kromme river estuaries, *P. peringueyi* attained abundance levels of 200-400 individuals m^{-2} with a dry biomass equivalent to between 3 and 6 g dry mass m^{-2} (De Villiers et al. 1999 and references therein). The low values recorded in the West Kleinemonde Estuary were attributed to lower recruitment opportunities due to the presence of a sand bar at the mouth and limited habitat availability, which were mainly beds of submerged macrophytes (Bernard and Froneman 2005). The presence of a sand bar at the mouth prevented tidal exchange that also contributed to the lack of any seasonal recruitment into TOCEs as demonstrated in larger POEs within the same region (de Villiers et al. 1999, Bernard and Froneman 2005).

The abundances and biomass of *P. peringueyi* in TOCEs is highly variable, which reflects mouth opening phase and the establishment of a link to the marine environment through overtopping (Kemp and Froneman 2004; Bernard and Froneman 2005). Peaks in the abundance of the shrimp occur following breaching events that can be linked to the mass recruitment of juveniles into the estuary. Minor peaks in abundance were also associated with storm surge overtopping events, although the magnitude of the recruitment was substantially less than those recorded during the breaching events (Kemp and Froneman 2004, Bernard and Froneman 2005, Froneman in press). This result is consistent with a recent study conducted in the small Grant's TOCE located some 5 km north of Kenton-on-Sea. These facts indicate that breaching events represent the main recruitment opportunity of *P. peringueyi* into Eastern Cape TOCEs. On the other hand, the peak in total biomass of *P. peringueyi* was recorded following a period of extended mouth closure (four months), which could be related to growth of the juveniles trapped within the estuary (Bernard and Froneman 2005).

A distinct spatial pattern in the abundance, biomass and community structure of *P. peringueyi* in Eastern Cape TOCEs has been observed. The highest abundance of the shrimp was recorded in the lower reaches of the estuary where juveniles dominated both in abundance and biomass (Bernard and Froneman 2005, Froneman in press). The maximum biomass values of *P. peringueyi* were recorded in the middle reaches of the estuary where adult shrimp were found to be closely associated with beds of submerged aquatic macrophytes (Bernard and Froneman 2005, Froneman in press). The shrimp was virtually absent from the upper reaches of the estuary.

The feeding ecology of *P. peringueyi* was investigated by Emmerson (1987) within the permanently open Swartkops estuary along the Eastern Cape coastline. Results of this study suggest tidal mediated changes in the main prey items consumed by the prawn. During the high tide, shrimp moved into eelgrass beds, which resulted in a high contribution of epiphytic diatom *Cocconeis* and naviculoid diatoms. During the ebb flow, the diet consisted mainly of detritus with a small contribution by nematodes.

CONCLUSIONS

Review of the published literature indicates that while extensive studies have been conducted on the hyperbenthos within permanently open estuaries both along the south and eastern coast line of southern Africa, virtually no information is available for these organisms within TOCEs within the same geographic region. Preliminary data suggest that recruitment of marine breeding hyperbenthic species into TOCEs takes place during breaching events and to a lesser extent during overtopping events. The ecological role of the hyperbenthos within TOCEs is presently unknown.

REFERENCES

Barnard KH (1950) Descriptive catalogue of South African decapod crustacea (crabs and shrimps). *Annals of the South African Museum* **38** 1-837.

Bernard ATF and Froneman PW (2005) Population dynamics of the caridian shrimp, *Palameon peringeuyi*, in a temperate, temporarily open closed southern African estuary. *Estuarine, Coastal and Shelf Science* **63** 73-81.

Beyer F (1958) A new bottom living *Trachymedusa* from Oslofjord. *Nytt Mag Zoology* 121-143.

Bickerton IB (1989) Aspects of the biology of the genus *Macrobrachium* (Decapoda: Caridea: Palaemonidae) in the St Lucia system. MSc thesis, University of Natal.

Boyson HO (1975) Seasonal variations in abundance of hyperbenthic animals in the Kiel Bight. *Meretutkimuslait* **239** 206-212.

Day JH (1974) A guide to marine life of South African shores. AA Balkema, Cape Town. Pp 300

Demitriades NT and Forbes AT (1993) Seasonal changes in species composition of the penaeid prawn catch on the Tugela Bank, Natal, South Africa. *South African Journal of Marine Science* **13** 317-322.

De Villiers C, Hodgson AN Forbes A (1999) Studies on estuarine macroinvertebrates. In: Estuaries of South Africa (eds) Allanson BR, Baird D. Cambridge University Press, United Kingdom. Pp 167-208.

Emmerson WD (1983) Tidal exchange of two decapod larvae, *Palaemon pacificus* (caridea) and *Upogebia africana* (Thalassinidae) between the Swartkops river estuary and adjacent coastal waters. *South African Journal of Zoology* **18** 326-330.

Emmerson WD (1987) Tidal migration and feeding of the shrimp, *Palaemon pacificus* (Stimpson). *South African Journal of Science* **83** 413-416.

Forbes AT and Benefield MC (1986) Penaeid prawns in the St Lucia Lake system: post larvae recruitment and bait fishery. *South African Journal of Zoology* **21** 224-228.

Forbes AT and Cyrus DP (1991) Recruitment and origin of penaeid prawn post larvae in two southeast African estuaries. *Estuarine, Coastal and Shelf science* **33** 281-289.

Froneman PW (in press) Population dynamics of the caridian shrimp, *Palaemon peringueyi*, in a small intermittently open southern African estuary. *African Journal of Aquatic Science*

Hill BJ (1975) Abundance, breeding and growth of the crab, *Scylla serrata* in two south African estuaries. *Marine Biology* **32** 119-126.

Hill BJ (1976) Natural food, foregut clearance rate and activity of the crab, *Scylla serrata* in an estuary. *Marine Biology* **34** 109-116.

Hill BJ (1980) Effects of temperature on feeding and activity in the crab *Scylla serrata*. *Marine Biology* **59** 189-192.

Kemp JOG, Froneman PW (2004) Recruitment of ichthyoplankton and macrozooplankton during overtopping events into a temporarily open/closed southern African estuary. *Estuarine Coastal and Shelf Science* **61** 529-537.

Mees J and Hamerlynck O (1992) Spatial community structure of the winter hyperbenthos of the Schelde estuary, The Netherlands, and adjacent coastal waters. *Netherlands Journal of Sea Research* **29** 357-370.

Robertson WD (1987) Biology of the mangrove crab, *Scylla serrata*. *Oceanographic Research Institute Poster Series* No. 8.

Robertson WD (1996) Abundance, population structure and size at maturity of *Scylla serrata* (Forskal)(Decapoda: Portunidae) in Eastern Cape estuaries, South Africa. *South African Journal of Zoology* **31** 177-185.

Walsh CJ and Mitchell BD (1998) Factors associated with variations in the abundance of epifaunal caridian shrimps between and within seagrass meadows. *Marine and Freshwater Research* **49** 769-777.

9. ZOOBENTHOS

Tris Wooldridge

Nelson Mandela Metropolitan University, Port Elizabeth

INTRODUCTION

Benthic invertebrate research in South African estuaries has gone through a series of phases, with earlier work concentrating mostly on qualitative descriptions, density or biomass estimates of populations and physiological adaptations of species. It was not until the mid 1980s that the focus of research expanded to include response of organisms to environmental fluctuations or the role of benthic organisms in energy flow through systems (de Villiers et al. 1999). A further emphasis developed from the mid 1990s when research focused on subtidal communities and species response to environmental drivers.

The zoobenthos of soft sediments is classified as that group of animals spending most or all of their time buried in sediments. Within the benthos, macrobenthic and meiobenthic organisms are distinguished, usually on the basis of mesh aperture size of the sieving gear used to retain or allow organisms to pass through. Past researchers (e.g. McLachlan 1974, Day 1981, Hanekom et al. 1988) used relatively coarse mesh sieves (1-4 mm) and these studies usually focused on macrobenthic intertidal organisms. Over the past ten years, data on the subtidal zoobenthos have been collected using much finer sieves. These communities often consist of a high proportion of peracarid crustaceans and polychaete worms (Schlacher and Wooldridge 1996b, Teske and Wooldridge 2001) that may be very different in composition and structure when compared to the intertidal benthos.

Smaller mesh sizes become significantly advantageous when population density estimates are the prime goal, although coarser sieves (1 mm mesh) may also be suitable if biomass estimates are the main focus (Schlacher and Wooldridge 1996b, 1996c). This would suggest that earlier studies seriously underestimated species abundance of small zoobenthic species. The subtidal benthos of local estuaries is now recognized as a rich community, attaining high species richness and high levels of abundance. Since large proportions of many of these species are small and include juveniles, a mesh size of 500 microns is used to retain organisms. Nine replicates per sampling site are also collected and this ensures that species representation per site is maximized. It is important to include as many rare species as possible in the final analysis of samples, as rare species are critical for accurate community studies and bioassessment (Cao et al. 1998). Although additional replicates may provide more information, time spent in the analysis of the additional samples becomes prohibitive.

ZOOBENTHOS OF SOFT SEDIMENTS IN TEMPERATE ESTUARIES

Burrowing prawns such as *Callianassa kraussi* and *Upogebia africana* are important in many South African estuaries (Day 1981, Emmerson 1983, de Villiers et al. 1999), although they are sometimes present in subtropical estuaries at very high abundance levels (e.g. Blaber et al. 1983). *C. kraussi* and *U. africana* are particularly abundant in intertidal sediments of warm and cool temperate estuaries, with each species inhabiting a preferred sediment type. Mixed populations are documented, but *C. kraussi* generally occurs in sand and *U. africana* in muddy sediments. Adults of both species have a wide salinity tolerance range and *U. africana* for example, can molt successfully in 3.4 PSU (Hill 1981). Forbes (1978) reported populations of *C. kraussi* living in the upper reaches of Swartvlei and Keurbooms estuaries where salinity values are sometimes below 5 PSU. However, experimental work on the tolerance levels of estuarine animals has mostly been done on adults and it cannot be assumed that larval stages or juveniles will have an equivalent tolerance level (Hill 1981).

The sand prawn (*C. kraussi*) has an abbreviated larval life without planktonic stages (Forbes 1973). Adult *C. kraussi* are able to tolerate salinity values as low as 1 PSU, but successful development of eggs and larval stages requires salinity values > 20 PSU (Forbes 1978). Populations living in areas where salinity values are permanently below 17 PSU are not self-maintaining and must be recruited from elsewhere. Forbes (1978) recorded annual migrations of post larvae in the temporary open/closed Swartvlei and East Kleinemonde systems and suggested that these life stages act as the dispersal phase in this species allowing it to spread into areas where it is otherwise unable to breed successfully.

More recently, Vorsatz (1999) investigated *C. kraussi* life history strategies in the laboratory and recorded larval development times of about 14-15 days at a salinity of 16 PSU and at a temperature of 16^{o}C. At 28^{o}C, larval development was completed in three days at salinity values of 24 and 35 PSU. Although larval development occurred at the lower salinity threshold documented by Forbes (1978), sand prawns collected for experimental purposes by Vorsatz (1999) had embryos with well developed eyespots and most of the development of larvae had taken place in an estuary where salinity values were >20 PSU. Severe floods flushed the Gamtoos Estuary study site in November 1996 (Vorsatz 1999), removing the entire population from sandbanks in the upper reaches. Two years prior to the flood, *C. kraussi* was present in high densities (107 ± 2.9 individuals m^{-2}) on these sandbanks (Schlacher and Wooldridge 1996d). After the flood, recolonisation of the upper Gamtoos by *C. kraussi* was slow (7 months), with adult prawns preceding the appearance of post larval stages. Thus, dispersal and recruitment may not be confined to the postlarval stage; with both adults and juveniles probably being involved.

Upogebia africana is common in muddy substrata of many estuaries around southern Africa. It is endemic to the region (Day 1981), with its distribution up the east coast of Africa probably curtailed by high water temperatures (Hill and Allanson 1971). The species is often abundant on mud banks in permanently open estuaries and may account for a major part of the intertidal macrofaunal biomass. For example, Hanekom et al. (1988) noted that *U. africana* accounted for > 80% of the biomass on mud banks in the Swartkops Estuary. Day (1981) noted that mud prawns were absent from estuaries that had closed off from the sea for 'extended periods' and suggested that its absence from closed estuaries was linked to the lack of water movement that transported detritus across the mud banks. Allanson et al. (1992) also noted the lack of tidal currents as a possible factor excluding *U. africana* from closed estuaries, particularly from the point of view of energy supplementation for feeding and respiration.

Focus on the larval life history strategies have now shown that mud prawn larvae require a marine phase of development, with first-stage larvae migrating from the estuary in highest numbers on the crepuscular ebb tide. After a period of development at sea, postlarvae return to estuaries in highest numbers on the crepuscular flood tide (Wooldridge 1991, Wooldridge 1994, Wooldridge and Loubser 1996). Maximum release of Stage 1 larvae and the return of postlarvae therefore follow a semi-lunar rhythm. Peak emigration of larvae is synchronized to the start of the ebb tide at sunset (shortly after maximum spring tide amplitude) and the time of peak return of postlarvae is synchronized to the start of the flood at sunset (Figure 9.1). Maximum immigration of postlarvae is therefore before maximum spring tide amplitude. The timing of emigration of larvae and immigration of postlarvae relative to the state of the moon is not fixed, but will shift between winter and summer as the time of sunset changes between seasons.

Analysis done on zooplankton samples collected in the mouth of the Swartvlei Estuary provided an estimate of the emigration of Stage 1 larvae on the ebb tide and the return of postlarvae on the flood tide (Table 9.1). Plankton data were collected over 24 hrs on each occasion and are integrated with computed water volumes moving in and out of the estuary over the same 24 h period (Huizinga 1987). The data in Table 9.1 replicates the same semi-lunar pattern of behaviour shown in Figure 9.1. At the time of sampling (October), over 5 x 10^6 Stage 1 larvae were exported from Swartvlei Estuary on a single nocturnal ebb tide. A week later, over 0.2 x 10^6 postlarvae recruited back to Swartvlei on a single nocturnal flood tide to potentially settle on the estuarine mud banks. Over the period of the breeding season (months) the efflux and influx of larvae must be considerable, provided the tidal prism is not constrained through mouth constriction or closure.

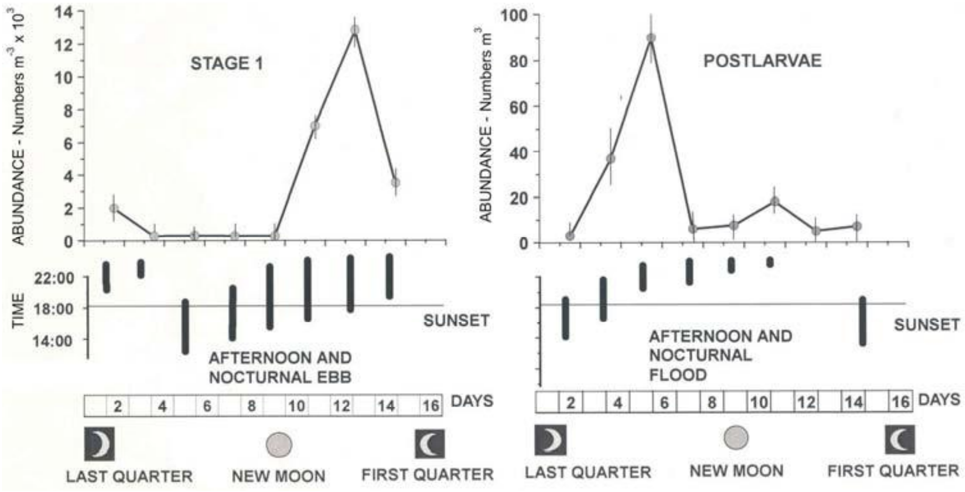


Figure 9.1 Maximum export of *U. africana* Stage 1 larvae over the lunar cycle occurs when the start of the ebb tide coincides with sunset. Maximum return of postlarvae occurs when the start of the flood tide coincides with sunset. Zooplankton was collected in the mouth of the Gamtoos Estuary, sampling every second night for 16 days (sunset shortly after 18:00 during the exercise). Data points shown above represent the mean of all samples (±1SD) collected on the flood or ebb tide every second night.

Table 9.1 Flux of *U. africana* Stage 1 larvae and postlarvae across the mouth of the Swartvlei Estuary during two 24 h sampling series (22-23rd October 1986, three days after maximum spring tide and 29-30th October 1986, three days after maximum neap tide). Water volumes were computed using the 1-dimensional hydrodynamic model of Huizinga (1987). Hourly flow volumes were integrated with larval abundance collected from the plankton (after Wooldridge 1994). Note that maximum export of Stage 1 larvae occurs around spring tides and not neap tides and maximum import of postlarvae is associated with neap tides when the start of the flood is crepuscular.

	Stage 1 larvae		Postlarvae	
	Day	Night	Day	Night
Spring tides				
Flood	0	817	7613	88 367
Ebb	0	540 528	0	0
Net export (-) or import (+)	-	539 711	+	95 980
Neap tides				
Flood	0	0	0	202 455
Ebb	0	9 843	0	2 175
Net export (-) or import (+)	-	9 843	+	200 280

Stage 1 larvae do not metamorphose through subsequent larval stages if trapped in estuaries and this probably accounts for the absence of the species in closed systems (i.e. most TOCEs in warm and cool temperate regions). The continued existence of *Upogebia africana* in TOCEs is directly dependent on the relationship between open and closed phases of the tidal inlet. Opening of the mouth during the breeding season may still enable populations of *U. africana* to survive over time in some estuaries (e.g. Great Brak). However, should the mouth remain mostly closed during the breeding season (summer), recruitment ceases and estuarine mud prawn densities decline or even become locally extinct. The construction of the Wolwedans Dam on the Great Brak River is an example of how estuarine populations of *U. africana* can be affected by changes in the natural opening and closing of the mouth (Figure 9.2).

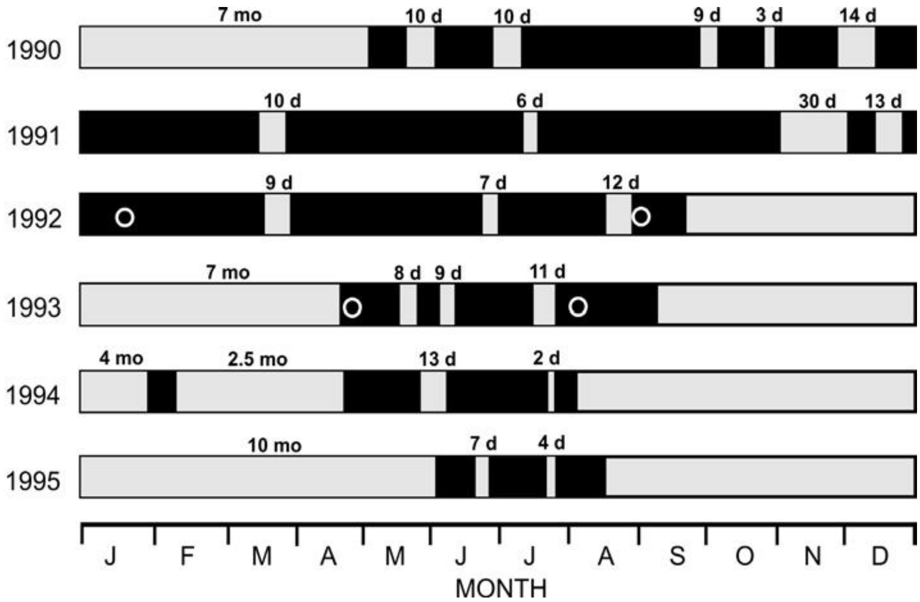


Figure 9.2 Opening and closing of the mouth in the Great Brak between 1990 and 1995. Light bars indicate when the mouth was open, dark bars indicate times of mouth closure. The duration of mouth opening is indicated in days (d) or months (mo). Circles indicate when the estuarine mud prawn population was sampled in 1992 and 1993 (after Wooldridge 1999).

The Wolwedans Dam (maximum capacity 24 x 10^6 m^3) was completed at the end of summer in 1990 (March-April). Little freshwater reached the estuary over the following 28 months as the dam filled. During this time the estuary remained mostly closed, opening occasionally for a few days. In November 1991 the estuary opened for 30 days. The dam reached the designed storage level in the spring of 1992 (September). Thereafter, a management plan that included planned releases of freshwater from the dam when required, ensured that the estuary returned to the typical pattern of opening in summer and closing during the dry season.

The impact of extended mouth closure over the 28 months following completion of the dam is clearly seen in Figure 9.3. Recruitment to the estuarine *Upogebia africana* population ceased during this period resulting in discontinuous distribution of size classes. Integration of mud prawn growth rate (Hanekom and Baird 1992) and the lower size limit of the smallest cohorts shown in Figure 9.3 A-E provide an indication when recruitment last took place each time the estuary was sampled. Recruitment only occurred when the mouth was open to the sea. In Figure 9.3A for example, the smallest cohorts (16-18 mm carapace length) sampled in January of 1992 were about 17-21 months old, indicating that recruitment last occurred in April 1990, shortly before the period of extended mouth closure (Figure 9.2). Some recruitment occurred in November 1991 when the mouth opened for 30 days; reflected in the three smallest size classes (12-14 mm carapace length) shown in Figure 9.3B. Good recruitment occurred after the mouth again opened during most of the summer of 1993 (Figure 9.3C and D).

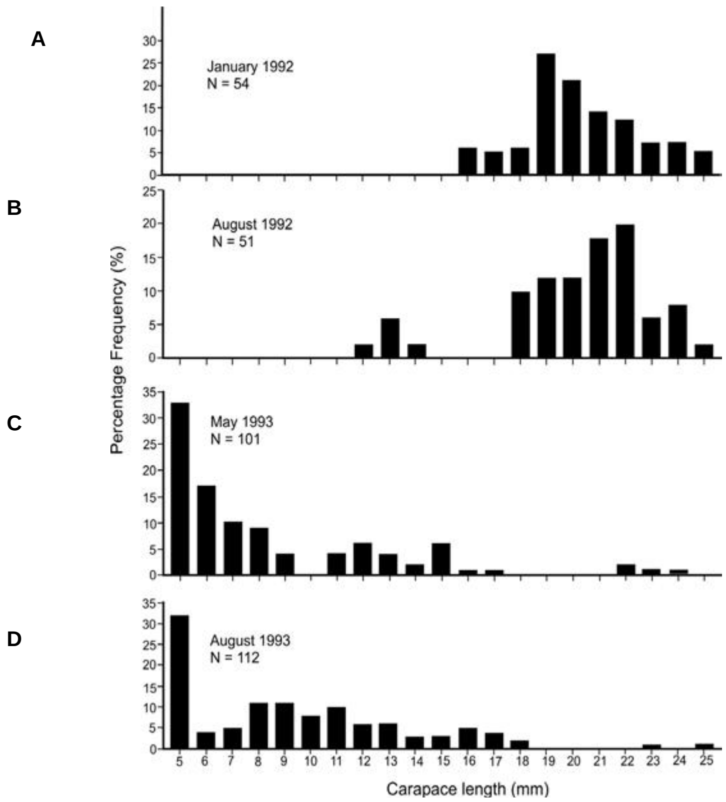


Figure 9.3 Size class distribution (based on carapace length) of *U. africana* population in the Great Brak Estuary on each of the four sampling dates (see Figure 9.2). The relatively small sample size shown in A and B is a reflection of the very low density of prawns in the estuary (see Figure 9.4). Note the growth rate and ultimate mortality of cohorts as the population aged. The maximum age of mud prawns is about 3-4 years (Hanekom and Baird 1992), although the current data suggest that it is nearer three years. The smallest prawns in the substratum have a carapace length of about 5 mm.

Population recovery (expressed as changes in prawn density over time) after the extended period of mouth closure in 1990 and 1991 (Figure 9.2) in the Great Brak Estuary was relatively slow and was monitored over four years (1992-1995, Figure 9.4). Recovery was exponential, with no recruitment to the population during winter (non-breeding period) when the mouth was closed (reflected in the similarity in prawn density within each year sampled, Figure 9.4). Data from the adjacent permanently open Klein Brak Estuary are provided for comparative purposes.

There are also other estuarine organisms that have a similar lifestyle to *Upogebia africana* and include numerous crab species (Hill 1975, Pereyra Lago 1993, Papadopoulos et al. 2002). These populations are therefore also dependent on the state of the mouth with respect to recruitment to estuarine populations. Unlike *U. africana*, *Callianassa kraussi* does not have a marine phase during its life cycle and is not dependent on the state of the mouth in order for recruitment to take place.

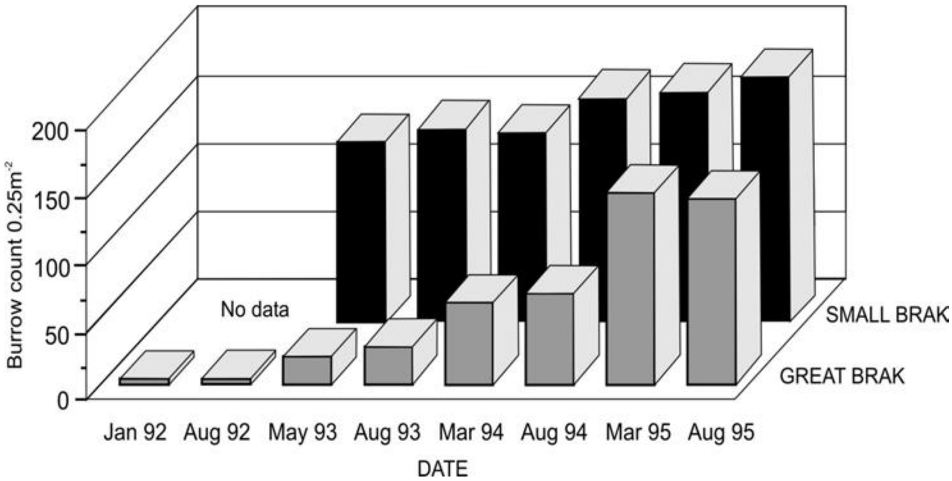


Figure 9.4 Recovery of the *Upogebia africana* population over 4 years following the extended period of mouth closure (1990-1991) in the Great Brak Estuary (see Figure 9.2). Data are compared to prawn density in the adjacent Klein (Small) Brak Estuary that remained permanently open during the monitoring period.

In addition to several benthic species having both a marine and estuarine phase during their respective life cycles, others undergo their entire life cycle in estuaries. Numerous species of crustaceans and polychaetes are widely distributed around the South African coastline and are often common inhabitants of the benthos in both TOCEs and permanently open systems. A common characteristic of these species is their wide tolerance to salinity. Hill (1981) reported on the ability of the amphipod *Grandidierella lignorum* to moult and grow in freshwater. Similarly, the crown crab *Hymenosoma orbiculare* is able to tolerate freshwater, although larvae did not survive below 5 PSU (Broekhuysen 1955). Other benthic species common in TOCEs in the warm and cool temperate regions have also been shown to tolerate low salinity values as they are recorded from the freshwater Lake Sibayi (Hill 1981). These species include the polychaete worm *Ceratonereis keiskama,* the tanaeid *Apseudes digitalis* and the amphipods *Corophium triaenonyx* and *Grandidierella lignorum*. The amphipod *Melita zeylanica* is also common in temperate TOCEs and is able to tolerate salinity values above 49 PSU and below 1 PSU (Millard and Broekhuysen 1970, Scott et al. 1952).

Extensive quantitative investigations of molluscs in TOCEs in the warm or cool temperate regions of South Africa have not been undertaken, although the group is fairly well studied in permanently open systems. According to Day (1951), bivalve molluscs are relatively scarce in South African estuaries and they do not reach the high densities recorded in Europe (McLachlan 1974). However, *Dosinia hepatica* attains relatively high densities in the middle reaches of the Swartkops Estuary (McLachlan and Grindley 1974, Hanekom et al. 1988) and in the Kromme Estuary (Hanekom 1982). In the Swartkops, *D. hepatica* was more common subtidally, but in the Kromme Estuary it was more common at intertidal sites. *Solen capensis* and *S. cylindraceus* were also locally common in the Swartkops and Kromme, with the former species present in sandy substrata and *S. cylindraceus* occurring in muddy areas. Both *Solen* species tended to concentrate around the inter- and sub-tidal interface. In the Kariega Estuary, *S. cylindraecus* has also been recorded at high densities (Hodgson 1987). A fourth species of estuarine mollusc *Macoma litoralis* is mainly an intertidal species, but in the Swartkops and Kromme it was uncommon (Hanekom 1982, Hanekom et al. 1988). The growth rates of local estuarine molluscs is described as moderate, with the more common species such as *Dosinia hepatica* and *Macoma litoralis* growing to a maximum age of about six years, while *Solen cylindraceus* lives to about five years (McLachlan 1974).

In terms of somatic production, molluscs can be important contributors to the macrobenthos in permanently open tidal estuaries. Collectively, molluscs contributed about 25% (crustaceans 75%) towards total macroinvertebrate production averaged for the Swartkops, Kromme and Sundays estuaries (Winter and Baird 1988). If individual mollusc species and estuaries are considered (Table 9.2), *Assiminea bifasciata* was the second most important contributor (27%) in the Swartkops Estuary, while *Nassarius kraussianus* was the most important contributor in the Sundays Estuary (44%). Production estimates are currently not available for smaller macrobenthic organisms. The above general discussion suggests that in permanently open estuaries, molluscs are important contributors to the benthic invertebrate community.

Since the mid 1990's, investigations on the subtidal macrozoobenthos have focused on both TOCEs and permanently open systems. Sampling is undertaken with a grab that bites to a sediment depth of about 10 cm. Animals are then sieved through a 500 micron mesh sieve, significantly finer than the coarser meshes used prior to the 1990's. However, a grab sampler may not be efficient in capturing larger bivalve molluscs (the longer siphon allows the organism to burrow deeper), although McLachlan (1974) documents that maximum density of *Dosinia hepatica* and *Macoma litoralis* in the Swartkops Estuary for example, occurred at a sediment depth of <10 cm.

Table 9.2 Percent contribution and cumulative percent contribution to macrofaunal production in the Swartkops, Kromme and Sundays estuaries (after Winter and Baird 1988).

	Swartkops		Kromme		Sundays	
	%	Cum. %	%	Cum. %	%	Cum. %
Crustaceans:						
Callianassa kraussi	-	-	8	8	9	9
Upogebia africana	34	34	13	21	33	42
Palaemon perengueyi	-	-	32	53	8	50
Sesarma catenata	23	57	22	75	-	-
Molluscs:						
Assiminea bifasciata	27	84	-	-	-	-
Macoma litoralis	-	-	10	85	-	-
Nassarius kraussianus	-	-	-	-	44	94

Estuaries that remain permanently open or remain open for most of the time have richer macrobenthic communities compared to estuaries that open occasionally (de Villiers et al. 1999). Hodgson (1987) reported over 100 species from both inter- and subtidal sites in the permanently open Kariega Estuary using a 1mm mesh sieve. This estuary is described as a freshwater starved system, with the upper reaches regularly reaching hypersaline levels in summer (Hodgson 1987, Allanson and Read 1995, Grange et al. 2000). In the nearby temporary open/closed Kleinemonde Estuary, < 35 species were present (Brown 1953 quoted in de Villiers et. al. 1999). In the temporarily open Bot Estuary on the Cape south coast only 18 macrobenthic species were recorded (Koop et al. 1983). Table 9.3 summarizes recent studies on the subtidal macrobenthos (using a 0.5 mm mesh sieve) in all estuaries sampled around the South African coast. The data indicate the same trend described by de Villiers et al. (1999) for the macrobenthos in general, with TOCEs having fewer species compared to permanently open systems. However, permanently open estuaries that are freshwater dominated also support relatively few species (Table 9.3).

Frequent floods or strong flushing events exclude the establishment of marine associated zoobenthic communities (e.g. in the Great Fish and Keiskamma, Table 9.3) and only hardy types tolerant of wide salinity fluctuations are able to survive. Floods or strong flushing events have previously been shown to act as important regulatory mechanisms that influence distribution and behaviour of macrobenthic species in the short to medium term (McLachlan and Grindley 1974, Hanekom 1989, Read and Whitfield 1989, De Villiers et al. 1999).

In both marine and freshwater dominated permanently open estuaries, species richness declines in an upstream direction (Branch and Grindley 1979, Hodgson 1987, Schlacher and Wooldridge 1996a), contrary to the more uniform distribution of species in TOCEs (e.g. Koop et al. 1983). Factors such as the variability of the horizontal salinity gradient and the extent and persistence of marine dominance interact and influence the dynamics of species, as shown for estuarine zooplankton populations (Wooldridge and Winter 2006).

Periods of mouth closure in TOCEs will obviously prevent any recruitment to estuarine populations that have obligate estuarine and marine phases of development. Examples of invertebrates already mentioned include *Upogebia africana* and numerous species of estuarine crabs (Pereyra Lago 1993, Wooldridge and Loubser 1996, de Villiers et al. 1999, Papadopoulos et al. 2002) and possibly some of the polychaetes and molluscs (de Villiers et al. 1999). Estuarine mouth closure will also disrupt migration of megalopae of the crab *Varuna litterata*. Although *V. litterata* invades freshwater, it returns to the marine environment in order to breed and large numbers of megalopae have been observed passing through estuaries from the sea (Connell and Robertson 1986, Cyrus 2000). This species extends southwards to at least the Mngazana Estuary (Branch and Grindley 1979). Population densities of all these species are likely to fluctuate more widely in TOCEs compared to their respective abundance levels in permanently open systems. If an estuary closes or remains closed for extended periods during the breeding season, recruitment ceases and estuarine population densities will decrease. In extreme cases, populations may become locally extinct. This may partly explain the reduced number of species in TOCEs (Table 9.3), although fluctuations in salinity after mouth closure and the exclusion of more marine associated fauna must also play a role.

Variability and structure of the salinity regime in estuaries (temporal and spatial) is a key abiotic factor that regulates presence or absence of species in estuaries. However, the influence of salinity is not necessarily of equal importance to all communities along the salinity gradient. In general, salinity is more important as a regulatory factor at the extremes of the horizontal salinity gradient. The degree of marine dominance affects the species assemblage in the lower estuary, while at the head freshwater inflow influences the assemblage in the brackish-freshwater zone (Teske and Wooldridge 2003). Both these communities may be absent in TOCEs during the closed phase and/or when euryhaline conditions persist throughout the estuary. The brackish-freshwater group may also be absent in estuaries that are freshwater starved, e.g. in the Kariega and Kromme estuaries.

By contrast, the euryhaline or true estuarine benthic species assemblage may be relatively independent of salinity in the surrounding water, although larvae of these euryhaline species generally have a narrower salinity tolerance range compared to adults of the same species (e.g. *Callianassa kraussi*). This true euryhaline assemblage is characterised by having a relatively low number of species compared to the marine and freshwater associated faunas (Remane and Schlieper 1958 quoted in McLusky and Elliott 2004, Day 1981). The pattern of relatively few species under euryhaline conditions also manifests itself in the freshwater rich systems and TOCEs investigated in the present study (Table 9.3). Although fewer species are usually present in TOCEs, the density of the macrobenthos can be higher compared to permanently open systems (Teske and Wooldridge 2001).

Table 9.3 Number of species recorded in the subtidal benthos in permanently open and temporarily open-closed systems, using a 500 μm mesh sieve. Description of the degree of marine or freshwater dominance in POEs is based on salinity values provided in the references. No sub-categories are shown for TOCEs because salinity is variable and linked to the state of the mouth.

	Number of species	References
Permanently open estuaries		
Strong marine influence		
Mngazana	61	Thwala (2004)
Kariega	48	Teske and Wooldridge (2001)
Kromme	48	Teske and Wooldridge (2001)
Swartkops	42	Teske and Wooldridge (2001)
Strong freshwater influence		
Great Berg	32	Wooldridge (unpublished data)
Great Fish	22	Teske and Wooldridge (2001)
Keiskamma	23	Teske and Wooldridge (2001)
Olifants	23	Wooldridge (unpublished data)
Sundays	23	Teske and Wooldridge (2001)
Temporary open/closed estuaries		
East Kleinemonde	30	Teske and Wooldridge (2001)
Gqutywa	29	Teske and Wooldridge (2001)
Kabeljous	28	Teske and Wooldridge (2001)
Mngazi	29	Wooldridge (unpublished data)
Mpekweni	29	Teske and Wooldridge (2001)
Mtati	24	Teske and Wooldridge (2001)
Old Womans	21	Teske and Wooldridge (2001)
Van Stadens	24	Teske and Wooldridge (2001)

Sediment type is also a key factor that structures estuarine benthic communities (e.g. Boesch 1973, Day 1981). In a study of 13 South African estuaries having widely different abiotic attributes (state of the mouth, salinity distribution, etc.), Teske and Wooldridge (2003, 2004) concluded that the composition of the euryhaline subtidal benthic assemblage was mainly influenced by the nature of the substratum. Two groups were distinguished; an estuarine sand fauna and an estuarine mud fauna. Thus, the importance of water salinity appears to decrease away from the mouth but increase again towards the head where freshwater dominates the salinity regime. Although some species colonise the benthos at both salinity extremes, their presence near the mouth and in the upper estuary is conditional on the occurrence of a sandy substrate, e.g. the sand prawn *Callianassa kraussi* (Forbes 1978, Vorsatz 1999). Salinity and substratum type are therefore major determinants of the benthic community structure, but their relative importance changes between the mouth and upper estuary. It is also important to note that other factors affecting community composition play a role, as the presence of some species could not be linked to salinity or sediment type (Teske and Wooldridge 2003).

REFERENCES

Allanson BR and Read GHL (1995) Further comment on the response of Eastern Cape Province estuaries to variable freshwater inflows. *South African Journal of Aquatic Science* **21** 56-70.

Allanson BR, Skinner D and Imberger J (1992) Flow in prawn burrows. *Estuarine, Coastal and Shelf Science* **35** 253-266.

Blaber, SJM, Kure NF, Jackson S and Cyrus DP (1983) The benthos of South Lake, St Lucia following a period of stable salinities. *South African Journal of Zoology* **18** 311-319.

Boesch, DF (1973) Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. *Marine Biology* **21** 226-244.

Branch, GM and Grindley JR (1979) Ecology of South African estuaries. Part XI. Mngazana: a mangrove in Transkei. South African Journal of Zoology **14** 53-91.

Broekhuysen GJ (1955) The breeding and growth of *Hymenosoma orbiculare*. *Annals of the South African Museum* **41** 313-343.

Cao Y, Williams DD and Williams NE (1998) How important are rare species in aquatic community ecology and bioassessment? *Limnology and Oceanography* **43** 1403- 1409.

Connell AD and Robertson W (1986) Recent records of megalopae of the crak *Varuna litterata* (Fabr.) entering Natal estuaries. *South African Journal of Zoology* **21** 184-185.

Cyrus D (2000) A preliminary assessment of impacts on estuarine associated fauna recruiting from an intra-basin transfer and freshwater abstraction from aquatic systems in the Richards Bay area of KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* **26** 115-120.

Day JH (1951) The ecology of South African estuaries. Part 1. A review of estuarine conditions in general. *Transactions of the Royal Society of South Africa* **33** 53-91.

Day JH (1981) The estuarine fauna. In: Estuarine Ecology with particular reference to southern Africa (ed. Day, J.H.), pp. 147-186. A.A. Balkema, Cape Town.

De Villiers,C, Hodgson A and Forbes AT (1999) Studies on estuarine macrobenthos. In: Estuaries of South Africa (eds Allanson, B.R. and Baird, D), pp. 167-207. Cambridge University Press, Cambridge.

Emmerson WD (1983) Tidal exchange of two decapod larvae *Palaemon perengueyi* (Caridea) and *Upogebia africana* (Thalassinidae) between the Swartkops River and adjacent coastal waters. *South African Journal of Zoology* **18** 326-330.

Forbes AT (1973) An unusual abbreviated larval life in the estuarine burrowing prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassinidea). *Marine Biology* **22** 361-365.

Forbes, AT (1978) Maintenance of non-breeding populations of the estuarine prawn *Callianasa kraussi* (Crustacea, Anomura, Thalassinidea). Zoologia Africana **13** 33-40.

Grange N, Whitfield AK, De Villiers CJ and Allanson BR (2000) The response of two South African east coast estuaries to altered river flow patterns. Aquatic Conservation: *Marine and Freshwater Ecosystems* **10** 155-177.

Hanekom N (1982) An ecological study of the Zostera beds in the Kromme estuary. *University of Port Elizabeth Zoology Department Report Series* No. 18 205 pp.

Hanekom N (1989) A note on the effects of a flood of medium intensity on macrobenthos of soft substrata in the Swartkops estuary, South Africa. *South African Journal of Marine Science* **8** 349-355.

Hanekom N and Baird D (1992) Growth, production and consumption of the thalasinnid prawn *Upogebia africana* (Ortmann) in the Swartkops. *South African Journal of Zoology* **27**130–139.

Hanekom N, Baird D and Erasmus T (1988) A quantitative study to assess standing biomasses of macrobenthos in soft substrata of the Swartkops , South Africa. *South African Journal of Marine Science* **6** 163-174.

Hill BJ (1975) Abundance, breeding and growth of the crab *Scylla serrata* in two South African estuaries. *Marine Biology* **32** 119-126.

Hill BJ (1981) Adaptations to temperature and salinity stress in southern African estuaries. In: Estuarine Ecology with particular reference to southern Africa (ed. Day, J.H.), pp. 187-196. A.A. Balkema, Cape Town.

Hill BJ and Allanson BR (1971) Temperature tolerance of the estuarine prawn *Upogebia africana* (Anomura, Crustacea). *Marine Biology* **11** 337-343.

Hodgson AN (1987) Distribution and abundance of the macrobenthic fauna of the Kariega. *South African Journal of Zoology* **22** 153-162.

Huizinga P (1987) Hydrodynamic model studies of the Swartvlei. *CSIR report T/SEA* 8709.

Koop K, Bally R and McQuaid CD (1983) The ecology of South African estuaries. Part XII: The Bot River, a closed in the south-western Cape. *South African Journal of Zoology* **18** 1-10.

McLachlan A (1974) Notes on the biology of some estuarine bivalves. *Zoologica Africana* **9** 15-20.

McLachlan A and Grindley JR (1974) Distribution of macrobenthic fauna of soft substrata in Swartkops , with observations on the effects of floods. *Zoologia Africana* **9** 211-233.

McLusky DS and Elliott M (2004) The estuarine ecosystem, ecology threats and management. pp.214. Oxford University Press, Oxford.

Millard NAH and Broekhuysen GJ 1970. The ecology of South African estuaries. Part 10: St Lucia, a second report. *Zoologia Africana* **5** 277-307.

Papadopoulos I, Wooldridge TH and Newman BK (2002) Larval life history strategies of sub-tropical southern African estuarine brachyuran crabs and implications for tidal inlet management. *Wetlands Ecology and Management* **10** 249-256.

Pereyra Lago R (1993) Tidal exchange of larvae of *Sesarma catenata* (Decapoda, Brachyura) in the Swartkops, South Africa. *South African Journal of Zoology* **28** 182-191.

Read, GHL and Whitfield AK (1989) The response of *Grandidierella lignorum* (Barnard) (Crustacea: Amphipoda) to episodic flooding in three Eastern Cape Estuaries. *South African Journal of Zoology* **24** 99-105.

Schlacher TA and Wooldridge TH (1996a) Axial zonation patterns of subtidal macrozoobenthos in the Gamtoos , South Africa. *Estuaries* **19** 680-696.

Schlacher TA and Wooldridge TH (1996b) How accurately can retention on benthic macrofauna by a particular mesh size be predicted from body size of organisms? *Hydrobiologia* **33** 149-154.

Schlacher TA and Wooldridge TH (1996c) How sieve mesh size affects sample estimates of estuarine benthic macrofauna. *Journal of Experimental Marine Biology and Ecology* **201** 159-171.

Schlacher TA and Wooldridge TH (1996d) Origin and trophic importance of detritus – evidence from stable isotopes in the benthos of a small, temperate estuary. *Oecologia* **106** 382-388.

Scott KMF, Harrison AD and Macnae W (1952) The ecology of South African estuaries. Part 2: The Klein River , Hermanus. *Transactions of the Royal Society of South Africa* **33** 283-331.

Teske PR and Wooldridge TH (2001) A comparison of the macrobenthic faunas of permanently open and temporarily open/closed South African estuaries. *Hydrobiologia* **464** 227-243.

Teske PR and Wooldridge TH (2003) What limits the distribution of subtidal macrobenthos in permanently open and temporarily open/closed South African estuaries? Salinity vs sediment particle size. *Estuarine, Coastal and Shelf Science* **57** 225-238.

Teske PR and Wooldridge TH (2004) Affinities of some common estuarine macroinvertebrates to salinity and sediment type: empirical data from Eastern Cape estuaries, South Africa. *African Zoology* **39** 183-192.

Thwala NN (2004) The subtidal zoobenthos of the Mngazana estuary. MSc dissertation, University of Port Elizabeth, Port Elizabeth.

Vorsatz J (1999) Life history strategies in the estuarine sandprawn *Callianassa krausii*. MSc dissertation, University of Port Elizabeth, Port Elizabeth.

Winter PED and Baird D (1988) Diversity, productivity and ecological importance of macrobenthic invertebrates in selected Eastern Cape Estuaries. In: Towards an environmental plan for the Eastern Cape (eds Bruton, M.N. and Gess, F.W.), pp. 149-154. Rhodes University, Grahamstown.

Wooldridge TH (1991) Exchange of two species of decapod larvae across an estuarine mouth inlet and implications of anthropogenic changes in the frequency and duration of mouth closure. *South African Journal of Science* **87** 519-25.

Wooldridge TH (1994) The effect of periodic inlet closure on recruitment in the estuarine mudprawn, *Upogebia africana*. In: Changes in fluxes in estuaries: Implications from science to management (eds Dyer, K.R. and Orth, R.J.), pp. 329-333. Olsen and Olsen, Fredensborg.

Wooldridge TH (1999) Estuarine zooplankton community structure and dynamics. In: Estuaries of South Africa (eds Allanson, B.R. and Baird, D), pp. 141-166. Cambridge University Press, Cambridge.

Wooldridge TH and Loubser H (1996) Larval release rhythms and tidal exchange in the estuarine mudprawn, *Upogebia africana*. *Hydrobiologia* **337** 113-21.

10. FISH

Nicola James[1], Paul Cowley[2], Alan Whitfield[2] and Steve Lamberth[3]

[1]Rhodes University; [2]South African Institute for Aquatic Biodiversity; [3]Marine and Coastal Management

INTRODUCTION

This section provides an overview of available published information on the fish communities of temporarily open/closed estuaries (TOCEs) in the Eastern and Western Cape Provinces and compares the information to that for permanently open estuaries (POEs). The review focuses on:

Biogeography of fishes in Eastern and Western Cape estuaries
The distribution of fish in estuaries
Fish length composition in estuaries
The differences between fish assemblages in POEs and TOCEs
Influence of mouth state and estuary size on fish communities
Fishes and river flows in estuaries
Similarities and differences between Cape and KwaZulu-Natal TOCEs are briefly discussed in different sections.

BIOGEOGRAPHY OF FISHES IN CAPE ESTUARIES

Whitfield (2000) identified 186 estuaries along the coastline of the Eastern, Western and Northern Cape extending from the Namibian border at the Orange (Gariep) Estuary on the Atlantic coast in the west to the Mtamvuna Estuary on the south-eastern coast. Along this stretch of coast, 125 estuaries are classified as TOCEs and despite their predominance, most ichthyological research has focussed on large POEs (Vorwerk et al. 2001).

The estuaries along the coast of South Africa, and their associated fish assemblages, are not uniformly distributed, but can be grouped according to biological, physical and geographical criteria (Maree et al. 2000). Hence, the coast of South Africa has three distinct biogeographic zones, a subtropical zone, warm-temperate zone and cool-temperate zone. Few fish species occur in all southern African estuaries and many taxa are confined to specific biogeographic zones, with geographic affinity having a strong influence on the grouping of estuaries (Marais 1988, Harrison 2002). Researchers, however, have disagreed on the position of the boundaries between these zones. Harrison (2002) conducted an extensive survey of the fish communities of 109 estuaries along the South African coastline, of which 67 were TOCEs. Based on the fish communities, Harrison (2002) identified the break between the warm-temperate and subtropical zones for POEs at the Mdumbi Estuary, south of Port St Johns. The break was slightly different for TOCEs, occurring in the vicinity of the Mbashe Estuary and this was attributed to the lack of TOCEs sampled in this region (Harrison 2003). The break identified by Harrison (2002) between the warm-temperate and cool-temperate regions occurred at Cape Agulhas (Figure 10.1).

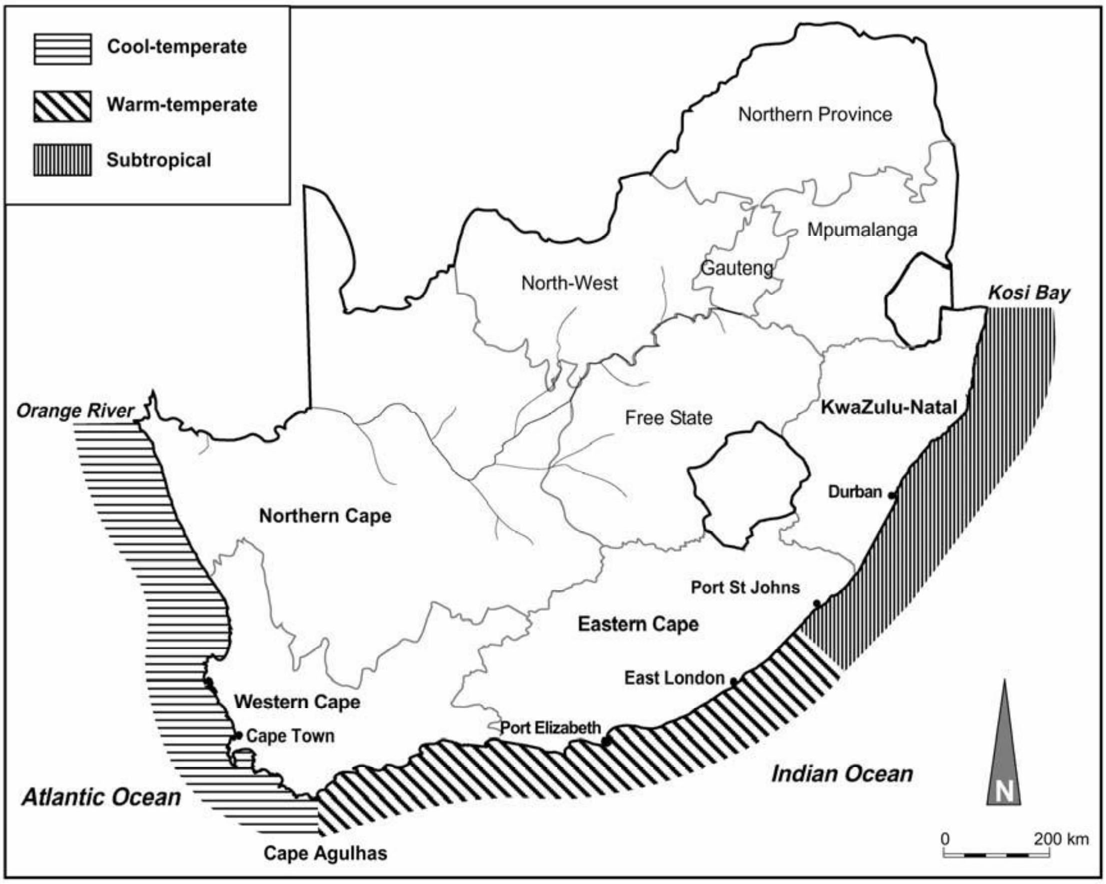


Figure 10.1. Map of South Africa indicating the three biogeographic provinces, based on estuarine fish communities (after Harrison 2002).

Harrison (2003) recorded differences in estuarine fish assemblages around the South African coastline. The gradual decrease in taxonomic richness from east to west was attributed to a decreasing number of tropical marine species, associated with the warm Agulhas Current. Maree et al. (2000) noted a decrease in the number of fish species recorded west of the permanently open Swartkops Estuary. This was attributed to the Agulhas Current moving further offshore in the region of the Swartkops Estuary and consequently tropical species reaching the southern limit of their distribution.

Despite a gradual loss of tropical species, the proportion of endemic species increases south of KwaZulu-Natal before declining again along the southwest (Cape Columbine to Cape Agulhas) and west coasts (Orange River to Cape Columbine). The diversity of cosmopolitan and temperate taxa is low around the entire coast (Harrison 2003).

WARM TEMPERATE ESTUARIES

Fish assemblages

Harrison (2003) used seine and gill nets to sample 109 TOCEs and POEs in South Africa between 1993 and 1999. Sampling occurred in spring or early summer and each system was sampled until no new fish species were recorded or until all obvious habitats within the estuary had been covered. Forty-three species from 20 families were recorded in TOCEs in the warm-temperate region, with an average of 15.5 (SD=4.85) species recorded per estuary. Important taxa in terms of the frequency of occurrence, numerical contribution and biomass in warm temperate estuaries included *Gilchristella aestuaria, Lithognathus lithognathus, Liza dumerili, Liza richardsonii, Liza tricuspidens, Mugil cephalus, Myxus capensis* and *Rhabdosargus holubi.*

From seine and gill netting in eight TOCEs on the southeast coast (Ngculura, Gqutywa, Bira, Mgwalana, Mtati, Mpekweni, Klein Palmiet, East Kleinemonde), Vorwerk et al. (2001) recorded 45 species in total. Two estuarine resident species *G. aestuaria* and *Atherina breviceps* were numerically dominant in the catches, comprising more than 60% of the catch in all estuaries except the Ngculura. The third most abundant species recorded was *R. holubi,* which comprised between 5% and 25% of the overall catch in all systems. Mugilids, particularly *L. richardsonii, M. capensis and M. cephalus* together comprised a minimum of 5% of the catch in most systems.

Mugilids are among the most abundant marine spawning fish found in estuaries in both South Africa and Australia (Potter et al. 1990). Most mugilids are strongly euryhaline, have extended spawning seasons and are able to recruit into estuaries under a range of mouth conditions (Blaber 1987, Cowley and Whitfield 2001a). As an adaptation to the estuarine environment, females have been recorded reabsorbing their eggs if they cannot escape to the sea (Wallace 1975). In addition, the different species of mullet tend to select food associated with different sediment particle sizes, thereby reducing interspecific competition and allowing different species to occur in the same estuary (Blaber 1977).

Cowley and Whitfield (2001b) used seine nets and mark-recapture techniques to estimate fish population sizes in the East Kleinemonde Estuary. Estuarine spawning species were numerically dominant, with *G. aestuaria*, *Glossogobius callidus* and *A. breviceps* the dominant species. Although not numerically dominant, *R. holubi* contributed 56.7% of the biomass and 74% of the production in the East Kleinemonde Estuary (Cowley and Whitfield 2002). *R. holubi* comprised ~75% and ~80% of the catch of marine species in this estuary during 1994 and 1995, with a total population size varying between 12 833 to 107 629 individuals.

Using only seine nets, Dundas (1994) recorded 11, 12 and 6 species in the Kabeljous, Seekoei and Van Stadens Estuaries respectively. Numerically, the important species were *A.*

breviceps, G. aestuaria, R. holubi and *L. richardsonii*, which together comprised more than 80% of the catch in all three systems. Further west the fish community changes slightly. Harrison (1999a) surveyed the small Blinde Estuary, which is situated on the southwest coast, using seine and gill nets. A total of eight species were recorded in this system with *G. aestuaria* and *L. richardsonii* being numerically important. Only four species were recorded in the nearby Klipdrifsfontein Estuary, with mugilids *L. richardsonii*, *M. cephalus* and *M. capensis* dominating catches by number and mass. *Monodactylus falciformis* was also recorded in small numbers (Harrison 1999a). Catches in this estuary are typical of a freshwater dominated system.

The dependence of fish species on estuaries ranges from complete to opportunistic. Whitfield (1998) divided South Africa's estuary-associated species into five categories depending on their degree of dependence on estuaries (Table 10.1).

Table 10.1 Estuary-association categories of southern African fish fauna (after Whitfield 1998).

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

Harrison (2003) found that estuary-dependent marine species (category II) contributed 38% of species recorded in warm-temperate estuaries and in terms of biomass these species comprised 87% of the fish recorded. Important estuary-dependent marine species included *Argyrosomus japonicus*, *Elops machnata, Lichia amia, L. lithognathus, L. dumerilii, L. richardsonii, L. tricuspidens*, *M. cephalus, M. capensis, Pomadasys commersonnii* and *R. holubi.* Estuarine species were found to contribute between 14% and 42% of the number of species recorded. However, in terms of numerical abundance, estuarine species (category I) dominated fish communities, comprising 59% of fishes recorded. The dominant estuarine resident species recorded included *A. breviceps, G. aestuaria*, *G. callidus* and *Psammogobius knysnaensis*.

Although there are only a few species that are able to breed and complete their entire life cycle within an estuary (Day et al. 1981), these species are well adapted to the estuarine environment and occur in large numbers. *A. breviceps* and *G. aestuaria*, two endemic zooplankton feeders that often reach high numbers in TOCEs, are shoaling species that are strongly euryhaline and are able to breed throughout the year, with a peak in spring and summer (Whitfield 1998). Estuary resident species often show reproductive adaptations, for example gobies produce sticky eggs that are attached to stones and guarded (Day et al. 1981). *A. breviceps* produces eggs with adhesive filaments that are attached to submerged plants and other objects (Neira et al. 1988). *G. aestuaria* spawns in the upper reaches of estuaries, to prevent loss of eggs and larvae to the marine environment (Blaber 1979, Talbot 1982).

Cowley and Whitfield (2001a) frequently recorded the estuarine pipefish, *Syngnathus watermeyeri* in the East Kleinemonde Estuary. This small estuarine species was first described in 1963 by JLB Smith and was found in the permanently open Bushmans and Kariega estuaries and the temporarily open/closed Kasuka Estuary in association with submerged aquatic macrophytes (Whitfield 1995). However, freshwater deprivation in the former two systems has led to the disappearance of the estuarine pipefish, which was declared provisionally extinct in 1993 (Whitfield and Bruton 1996). Three years later a healthy population was discovered in the East Kleinemonde Estuary, which has a relatively undisturbed catchment and extensive aquatic macrophyte beds (Cowley 1998).

Vorwerk et al. (2001) found that estuarine residents, particularly *G. aestuaria* and *A. breviceps* were numerically dominant in catches in the temporarily open/closed Gqutywa, Bira, Mgwalana, Mpekweni, Klein Palmiet and East Kleinemonde estuaries on the south-east coast (comprising >70% of the catch). However, estuary-dependent marine species, most notably *R. holubi* was dominant in catches by mass. Similarly, Dundas (1994) found that estuary-dependent marine species, *R. holubi* and *L. richardsonii*, were dominant in catches by mass in the Kabeljous, Seekoei and Van Stadens Estuary, while the estuarine resident, *G. aestuaria* was numerically dominant.

Marine stragglers (category III), which are mainly stenohaline species and not dependent on estuaries, do not contribute significantly to the ichthyofauna of TOCEs in warm temperate areas. In contrast, marine stragglers have regularly been recorded in the mouth area of POEs within this region (Whitfield 1998).

The dominance of estuary-dependent *R. holubi* and *L. richardsonii* in TOCEs in temperate areas has been attributed to a range of specialized life-history characteristics (Cowley and Whitfield 2001a). Both species have an extended breeding season and are serial spawners. They have been shown to use wave overwash events to enter estuaries during closed mouth conditions in the East Kleinemonde, Bira and Haga Haga estuaries (Cowley et al. 2001, Whitfield 1992). *R. holubi* were also shown to be the most abundant larval species in the surf-zone adjacent to the East Kleinemonde Estuary throughout the year (Cowley et al. 2001). This allows *R. holubi* to make use of open mouth conditions and wave overtopping events to enter the East Kleinemonde when they occur (Cowley and Whitfield 2001a). Cowley (1998) proposed that this strategy prevents recruitment failure and accounts for the dominance of this species in the East Kleinemonde and possibly other TOCEs.

Both *L. richardsonii* and *R. holubi* are endemic to southern Africa. *L. richardsonii* is known to occur from the Kunene River in Namibia to the St Lucia Estuary in KwaZulu Natal, but is less abundant in warmer waters (Smith and Heemstra 1990), while *R. holubi* is most abundant in the warm-temperate and subtropical estuaries of South Africa (Blaber 1973a).

Oreochromis mossambicus is the only freshwater species recorded in most TOCEs, particularly on the south-east coast (Whitfield 1998). *O. mossambicus* is endemic to southern Africa, but does not occur naturally south of the Bushmans Estuary in the Eastern Cape, although it has been introduced extensively into systems south of the Bushmans Estuary. *O. mossambicus* is most abundant in TOCEs during the closed phase (Whitfield and Blaber 1979).

COOL TEMPERATE ESTUARIES

Fish assemblages

The diversity of fishes in cool-temperate estuaries is low when compared with warm-temperate and subtropical systems (Harrison 2003). The coast west of Cape Infanta (S 34^{o} 26' E20^{o} 52') is characterised by a Mediterranean climate with most rainfall occurring during winter. As a consequence, TOCEs in this region usually breach between June and September, often following heavy rainfall in the catchment (Harrison 1999b). Harrison (2003) surveyed four TOCEs in the cool-temperate region (Sand, Krom, Wildevoël and Diep) in which a total of 11 species from eight families were recorded, with an average of only 4.5 species per estuary. It is, however, noteworthy that these four estuaries are highly altered urban systems with wastewater treatment works discharging into their river systems and, as such, are possibly no longer typical TOCEs. Juveniles of *L. richardsonii* were the most frequently captured species and were dominant in the catches by number (57%) and mass (50%). Another mugilid, *M. cephalus*, numerically contributed 18% (14% by mass) to the overall catch. Other important species included *A. breviceps, Caffrogobius nudiceps, G. aestuaria* and *L. amia.*

In the area between Cape Agulhas and Cape Point, Bennett (1989) recorded 18 fish taxa in the Kleinmond Estuary. The dominant species captured were *A. breviceps, P. knysnaensis* and *L. richardsonii*, which is very similar to the dominant species recorded in the Onrus and Ratel estuaries (Heinecken and Damstra 1983, Harrison 1999b). Seven TOCEs enter False Bay, (Eerste, Lourens, Silwermyn, Sand, Sir Lowrys Pass, Rooiels and Buffels Oos); Harrison (1998) surveyed all these estuaries and found that *L. richardsonii* was numerically dominant, comprising more than 90% in all systems. The second most abundant species was *P. knysnaensis.*

Clark et al. (1994) conducted an intensive fish survey of the Sand and Eerste estuaries, recording 15 and 13 species in the two systems respectively. *G. aestuaria* was found to be numerically dominant in the Sand Estuary followed by *L. richardsonii* and *A. breviceps*. In the larger Eerste Estuary, catches were numerically dominated by *L. richardsonii* followed by *L. dumerili* and *M. cephalus*. Small numbers of the endemic southern African sparid *Rhabdosargus globiceps* were recorded in the Sand Estuary (Clark et al. 1994). This temperate species prefers colder water compared to *R. holubi* and is therefore absent from subtropical estuaries and most warm-temperate systems (Whitfield 1998).

Harrison (1997) surveyed the fish fauna of the TOCEs west of Cape Columbine. *L. richardsonii* was the dominant species by both number and mass in the Krom, Wildevoël and Diep estuaries. Other researchers also recorded *L. richardsonii* to be the most common species in the Diep (Millard and Scott 1954) and Wildevoël (Heinecken 1985) estuaries.

Within the cool-temperate region, certain estuarine residents, e.g. *G. aestuaria, A. breviceps* and *C. nudiceps* were only recorded in the Diep and Sand estuaries (Harrison 2003). Estuary-dependent marine species (category II) were dominant in cool-temperate estuaries, comprising 80% of the number of taxa recorded. Estuary-dependent marine species also dominated the ichtyofauna numerically (75%) and by mass (99%).

The importance of estuary-dependent sparids, particularly *R. holubi*, decreases on the south-western coast and the mugilid, *L. richardsonii*, becomes dominant in catches both by number and mass (Harrison 1998).

No marine migrants (category III) were recorded in the estuaries entering False Bay (Harrison 2003). Two indigenous freshwater species, *Galaxias zebratus* and *Sandelia capensis* were recorded in the Sand (Morant and Grindley 1982) and Onrus estuaries

(Harrison 1999b). Both these species are common in Cape coastal rivers and streams (Skelton 1993). Several other freshwater species, including *O. mossambicus*, were recorded in the Sand, Eertste and Lourens estuaries, but all are introduced species and are possibly competing with estuarine species (Morant and Grindley 1982, Morant 1991, Clark et al. 1994, Harrison, 1999b).

DISTRIBUTION OF FISH IN ESTUARIES

Although Vorwerk et al. (2001) found no clear evidence of an overall longitudinal fish distribution pattern in different warm-temperate estuaries on the south-eastern Cape coast; on an individual species basis there were distinct trends. *A. breviceps* were generally more abundant in the lower reaches of estuaries and *G. aestuaria* tended to be more abundant further upstream. The freshwater species, *O. mossambicus*, exhibited a preference for the upper reaches of estuaries, with 43% of individuals being caught in this zone. Similarly, the mugilid *M. capensis* was also more abundant in the upper reaches.

Van der Elst (1978) found that primary consumers i.e. species that feed on organisms low down in the food chain, such as plankton, epiphytic algae and detritus, were common in the lower reaches of the Kobole Estuary, while tertiary feeders (i.e. predators such as *Caranx ignobilis*) predominated in the upper reaches.

Classification and ordination of large and small seine catches in the East Kleinemonde Estuary (33º 32´S; 27º 03´E) showed that the fish composition in the lower reaches differed significantly from that in the middle and upper reaches (Cowley and Whitfield 2001a). This difference was attributed mainly to *A. breviceps*, *P. knysnaenis*, *R. holubi*, *L. lithognathus*, *L. dumerili* and *L. richardsonii* showing a preference for the lower reaches of the estuary, with an increase in catches of *G. aestuaria*, *G. callidus*, *M. capensis*, *M. falciformis* and *O. mossambicus* in an upstream direction.

R. holubi is normally closely associated with macrophyte beds (Hanekom and Baird 1984, Beckley 1983, Whitfield 1984). Juvenile *R. holubi* consume *Zostera* and *Ruppia* leaves in order to digest the epiphytic diatoms, with the leaves passing through the alimentary canal undigested (Blaber 1974a). *R. holubi* is also known to feed on macroalgae. Cowley and Whitfield (2001a) speculated that the high abundance of *R. holubi* in the lower reaches of the East Kleinemonde Estuary, where there are few macrophyte beds, might be linked to the presence of filamentous algal mats that develop in the lower reaches between late winter and early summer.

L. lithognathus shows a preference for the lower reaches of the East Kleinemonde Estuary, this may be attributed to the abundance of sand prawns (*Callianassa kraussi*) in this area (Cowley and Whitfield 2001a). *L. richardsonii* and certain other mugilid species are known to be common in the lower and middle reaches of estuaries where a variety of substratum types are present and where particulate organic matter, algae (including diatoms) and decaying macrophytic plant material is readily available (Whitfield 1998).

M. falciformis is more abundant in the upper reaches of the East Kleinemonde Estuary (Cowley and Whitfield 2001a). This species has also been caught in significantly higher numbers around macrophytes in the Kromme, Swartkops and Swartvlei estuaries (Beckley 1983, Hanekom and Baird 1984, Whitfield 1984). Macrophyte beds are more abundant above the road bridge in the East Kleinemonde Estuary, which may account for the increased abundance of *M. falciformis* in the middle and upper reaches. Juvenile *M. falciformis*, in particular, occur in the vicinity of aquatic plants, as they not only provide a refuge from predators, but also a source of epifauna and planktonic invertebrates for food (Whitfield 1984).

M. capensis, which is endemic to South Africa, is termed facultatively catadromous because of its attraction to riverine areas as a juvenile. Although this species spawns at sea, the 0+ juveniles move rapidly into rivers or the upper reaches of estuaries, only returning to the sea to breed. High numbers of *M. capensis* have often been recorded in the upper reaches of estuaries where the rivers are either inaccessible or too small for colonisation (Cowley and Whitfield 2001a).

O. mossambicus, a freshwater cichlid, is well adapted to the estuarine environment and is tolerant of a wide range of salinity (0-117‰), temperature (12-38ºC) and turbidity (Whitfield and Blaber 1979). Although common in TOCEs, it is known to retreat to the upper reaches of TOCEs under open mouth conditions (Whitfield and Blaber 1979). Prolonged closed conditions in TOCEs often result in the flooding of marginal areas, which with the absence of water currents creates a favourable breeding habitat for *O. mossambicus* .

Estuarine resident species show distribution affinities in TOCEs. *A. breviceps* generally prefers the lower reaches, with large populations also occurring in the nearshore marine environment (Whitfield 1998). *P. knysnaensis* usually also predominates in the mouth region of the East Kleinemonde Estuary, which is characterised by a sandy substratum, which this species favours (Cowley and Whitfield 2001a). In contrast, *G. aestuaria* is most abundant in the middle and upper regions of estuaries and is known to spawn there (Talbot 1982).

The use of acoustic telemetry can provide a better understanding of the movement patterns and distribution affinities of fish in estuaries. For example, Kerwath et al. (2005) showed that acoustically tagged *P. commersonnii* in the East Kleinemonde Estuary preferred the lower reaches where they made repeated and prolonged use of some areas. Furthermore, Childs (2005) showed that daily changes in temperature, salinity and turbidity had a significant effect on the change of position of individually tagged *P. commersonnii* in the permanently open Great Fish Estuary.

FISH LENGTH COMPOSITION IN ESTUARIES

Most fish species found in estuaries are juveniles of marine taxa that breed at sea and enter the estuary to utilise the sheltered waters and abundant food resources (Day et al. 1981). TOCEs in the Cape, although closed for most of the year, also provide important nursery areas for these species (Whitfield 1998).

The majority of *R. holubi* recorded in Eastern Cape estuaries are less than one year old (Blaber 1974b, Vorwerk et al. 2001). In TOCEs on the south-western Cape coast, several different size classes of the dominant *L. richardsonii* were recorded although the majority were 0+ juveniles, indicating that these estuaries are important nursery areas for the species (Harrison 1999a).

Vorwerk et al. (2001), surveying TOCEs and POEs in the south-eastern Cape, found that although the length frequency of *P. commersonnii* was similar in all estuaries, larger individuals were found in TOCEs (maximum size = 562mm SL) when compared to POEs (maximum size = 421mm SL). These authors recorded a greater proportion of larger *L. dumerili* and *L. richardsonii* individuals in closed systems. Similarly, Kok and Whitfield (1986) determined that both the average and maximum size of most marine fish species in the Swartvlei Estuary was greater during the closed mouth phase compared to the open phase. These data are explained by the inability of large individuals to return to the sea due to a lack of access (i.e. closed mouth state).

Vorwerk et al. (2001) found that the mean size of estuarine resident species was slightly larger in POEs than in TOCEs, which was attributed to a higher survival rate of larvae and early juveniles in closed systems because larvae and early juveniles may be lost from open systems due to ebb tidal flushing. In contrast, Kok and Whitfield (1986) found very little difference in the size class distribution of *A. breviceps* between the open and closed mouth phases in the Swartvlei Estuary.

DIFFERENCES BETWEEN FISH ASSEMBLAGES IN POES AND TOCES

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

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

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

INFLUENCE OF MOUTH STATE AND ESTUARY SIZE ON FISH COMMUNITIES

Mouth condition is regarded as the major determinant of species richness in TOCEs, with higher numbers of marine species being captured in estuaries that open more frequently (Whitfield 1998). In the warm-temperate region, results of the study by Vorwerk et al. (2003) indicated a strong positive correlation between estuary size and species richness. The smaller TOCEs had a much lower species richness and density than larger TOCEs and POEs. The absence or low numbers of certain estuary-dependent marine species accounted for these differences. Smaller TOCEs probably have less marine interaction (shorter open mouth phases) and offer less habitat diversity.

Large TOCEs have higher nutrient input, positive salinity gradients and higher turbidity than smaller systems and, more importantly, are open for longer periods. Prolonged closed phases in small estuaries result in a low recruitment potential for juvenile marine fish and effectively prevent the emigration of adults back to sea. In addition, during a prolonged closed phase, salinity may either decrease due to freshwater input or increase due to evaporation, allowing only strongly euryhaline species to tolerate these conditions (Vorwerk et al. 2003).

During extended closed phases, fish populations may also decrease considerably due to predation. Blaber (1973b) determined the size of the *R. holubi* population in the West Kleinemonde Estuary when it closed on two separate occasions in 1971 and 1972. In 1971 a population of *R. holubi* consisting of 55 360 individuals decreased to 11 485 individuals after six months, while in 1972 a new stock of 14 674 individuals decreased to 12 000 over a seven month period. The difference was attributed mainly to predation by piscivorous birds, particularly cormorants, darter and heron. Despite heavy predation, Day et al. (1981) using data from Blaber (1973b, 1974b) estimated that the biomass of *R. holubi* in the West Kleinemonde increased in 1971 from 1.7 g m^{-2} to 2.7 g m^{-2} and from 0.46 g m^{-2} to 2.8 g m^{-2} in 1972 at which time the mouth opened. The predation impact by piscivorous birds on a closed estuary fish population has also been quantified in the East Kleinemonde Estuary. Cowley (1998) recorded a 70% reduction in the marine-spawning fish population following an unusual invasion of Cape cormorants during the winter of 1994.

Kok and Whitfield (1986) sampled the fish community of the Swartvlei Estuary during open and closed phases using seine and gill nets. Generally, species were found to increase in size during the closed phase as no new recruits entered the population, while resident species grew. Catch per unit effort of most marine species, particularly those belonging to the Mugilidae, decreased during the closed phase, again because no new recruits entered the population. Cowley and Whitfield (2001a) also recorded significantly higher numbers of estuary-dependent marine species following an extended open-mouth event in the East Kleinemonde Estuary.

Timing, duration and frequency of mouth opening events plays an important role in species composition, diversity and seasonality in TOCEs (Kok and Whitfield 1986, Bennett 1989). The Swartvlei Estuary is frequently closed during winter and open during summer when recruitment of 0+ juveniles into southern Cape estuaries is at a peak. As a consequence, the closed phase is thought to have little impact on the immigration of larvae and juveniles into this system. In fact, Kok and Whitfield (1986) and Whitfield and Kok (1992) suggested that the closed phase is beneficial to estuary-dependent marine species because inundation of the estuary during the closed phase results in the flooding of intertidal and supratidal habitats, thus increasing foraging area considerably and providing protection from predators.

Bennett (1989) sampled the fish community of the seasonally open Kleinmond Estuary, and found that using classification and ordination there were marked seasonal changes in the fish assemblages. The mouth of the estuary opened during July (1980) and remained open during spring and early summer. Estuary-dependent marine species in the Western Cape breed primarily in spring and recruit into estuaries during spring and early summer. Larvae and small juveniles were therefore able to enter the Kleinmond Estuary during spring and summer and remain there during the subsequent closed phase. Similar seasonal fish migration patterns were observed in the adjacent permanently open Palmiet Estuary (Bennett 1989). The timing and duration of mouth opening in the Kleinmond Estuary meant that the closed phase had little impact on the typical seasonal patterns that occur in temperate estuaries.

In the region between Port Elizabeth and East London on the Eastern Cape coastline, rainfall occurs almost equally during all seasons and there is no clear seasonal pattern to mouth opening events. Consequently, Vorwerk et al. (2001) found no seasonal difference in the numbers of individuals caught in TOCEs in this region.

A comparative study of the ichthyofauna composition of the neighbouring Mngazi and Mngazana estuaries by Mbande et al. (2005) revealed that species diversity was higher (66 versus 49 species) in the latter system due to greater marine influence (larger permanently open mouth) and higher habitat diversity. However, the numerical abundance of estuarine-spawning fishes was 18% higher in the Mngazi Estuary, which was attributed to the reduced tidal flow caused by a narrow mouth opening.

FISHES AND RIVER FLOW IN ESTUARIES

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

Mouth opening events are often linked to periods of high river flow. Cowley and Whitfield (2001a) analysed daily mouth condition data collected over a four year period at the East Kleinemonde Estuary and showed that the duration, frequency and seasonality of open phases was highly variable. Although river flow is a primary driver in initiating the open mouth condition, the duration of the open phase is strongly influenced by sediment transport within the mouth region. For example, short open mouth conditions in the East Kleinemonde Estuary were attributed to the predominantly north east bound aeolian and longshore sediment movement (Cowley and Whitfield 2001a).

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

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

In TOCEs, mouth opening and closing is directly linked to freshwater input. Reduced river inflow leads to prolonged mouth closure and shorter open phases, which inhibits immigration and emigration of marine fish species between estuaries and the sea (Whitfield and Wooldridge 1994), thus resulting in a reduction in species richness and abundance (see section on mouth state and estuary size).

TOCEs in the warm-temperate region develop behind low elevation barriers on gently sloping beaches. As a consequence, when these systems are closed the water level is at or close to high tide level. When they open, there is no great reduction in water level (Harrison 2004). In contrast, TOCEs in the subtropical region are 'perched' above mean sea level and develop behind steep beaches and have high berms. This means that the water level in these ‘perched’ systems is often well above the high tide level and they tend to drain almost completely on opening. After closing, the water level in the estuary rises and adjacent floodplains often become inundated (Harrison 2004).

In cool-temperate systems, high winter runoff results in low salinity in TOCEs. Warm-temperate estuaries typically experience high salinity when closed due to low freshwater input, high evaporation rates and seawater introduction through wave overtopping (Harrison 2004). As a consequence, freshwater deprivation, particularly during droughts, can lead to the development of hypersaline conditions in these estuaries (Whitfield and Bruton 1989).

In small warm-temperate TOCEs, salinity extremes during droughts are more marked than in POEs in the same region. Salinity values of up to 98 ‰ have been recorded in the freshwater deprived Seekoei Estuary, compared with a maximum of 29 ‰ in the Boknes Estuary, which has no dams in its catchment (Whitfield and Bruton 1989). During the drought of 1988/89, hypersaline conditions developed in the middle and upper reaches of the Seekoei Estuary and an extensive fish kill, involving at least 6000 individuals and 11 species, was recorded from the end of March 1989 (Whitfield and Bruton 1989). In the adjacent Kabeljous Estuary, which has fewer farm dams in the catchment, salinity during the drought never exceeded 55 ‰ and no substantial fish mortalities were recorded (Whitfield and Bruton 1989).

In contrast, high rainfall and limited seawater input into perched subtropical systems means that these systems typically experience low salinity and are less susceptible to the development of hypersaline conditions (Harrison 2004). Hypersalinity in KwaZulu-Natal estuaries have only been recorded in the St Lucia system, compared with the frequent occurrence of hypersaline conditions in certain Eastern and Western Cape estuaries (Whitfield and Wooldridge 1994).

Although marine fish are well adapted to low salinity (Day et al. 1981), fish kills have been recorded during low salinity conditions. Bennett (1985) recorded an extensive fish kill involving over 7000 fish from nine species in the Bot Estuary in October 1981, when temperatures were low and salinity in the system fell below 2-3 ‰. Prolonged mouth closure in certain Eastern and Western Cape estuaries could lead to similar salinity reductions and therefore pose a threat to marine fish species trapped within these systems.

One of the major effects of impoundements in catchment areas is to reduce the amplitude of floods in rivers and estuaries (Whitfield and Bruton 1989). Freshwater may also play an essential role in attracting larval and juvenile estuary-dependent marine species into estuaries. Indirect evidence suggests that fish trace land-based cues back to an estuary by following the olfactory concentration gradient (Whitfield 1994).

Whitfield (1994) also hypothesised that larvae and juveniles of estuary-dependent species orientate towards temporarily open/closed estuaries when closed, by using dissolved organic or inorganic olfactory cues present in the estuarine water that seeps through the sand bar at the mouth of these systems. Once an estuary mouth is breached, riverine and estuarine waters are flushed out, forming extensive plumes in the marine environment that seem to be attractive to recruiting fish larvae (Strydom 2003).

Without the proposed cues associated with estuarine and freshwater discharge, migratory fishes might have difficulty locating estuaries which, if true, would have serious consequences for their life cycles. Grange et al. (2000) speculated that the higher ichthyoplankton densities in the Great Fish Estuary, compared to the freshwater deprived Kariega Estuary was due to a combination of stronger olfactory cues and elevated food stocks.

CONCLUSIONS

The coast of South Africa can be divided into three distinct biogeographic zones and although species richness is at its lowest in cool-temperate estuaries, these estuaries still provide important nursery areas for the juveniles of marine species, especially *L. richardsonii*. Certain fish species in TOCEs show distinct trends in longitudinal distribution, for example *A. breviceps* are generally more abundant in the lower reaches of estuaries and *G. aestuaria* tend to be more abundant further upstream. Most species found in TOCEs were juveniles of estuary-dependent marine taxa, indicating that these systems function as important nursery areas for these species.

Although TOCEs have been found to have lower ichthyofaunal diversity than POEs in the Cape region, they often have larger populations of estuarine resident species, particularly *A. breviceps* and *G. aestuaria*. In addition, certain endemic freshwater taxa (e.g. *O. mossambicus*) and estuarine species (e.g. *S. watermeyeri*) are found mainly in TOCEs.

Mouth state, particularly the frequency, timing and duration of mouth opening plays a pivotal role in determining species richness, composition, diversity and abundance in TOCEs. Mouth opening, is directly linked to freshwater input and, as such, TOCEs in the semi-arid parts of the Eastern, Western and Northern Cape are adversely affected by a reduction in the natural freshwater input, primarily caused as a result of the construction of dams in the catchment. Hypersaline conditions, which can lead to fish kills, are more commonly recorded in TOCEs in the Cape region than in the perched estuaries of KwaZulu Natal.

Finally, it is important to understand the structure and functioning of fish assemblages in Cape TOCEs because this provides a tangible picture in the understanding of the effects of disturbance, particularly variation in freshwater input, on the biota of these important systems.

REFERENCES

Bate GC, Whitfield AK, Adams JB, Huizinga P and Wooldridge TH (2002) The importance of the river-estuary interface (REI) zone in estuaries. *Water SA* **28** 271-279.

Beckley LE (1983) The ichthyofauna associated with *Zostera capensis* Setchell in the Swartkops estuary, South Africa. *South African Journal of Zoology* **18** 15-24.

Bennett BA (1985) A mass mortality of fish associated with low salinity conditions in the Bot River estuary. *Transactions of the Royal Society of South Africa* **45** 437-448.

Bennett BA (1989) A comparison of the fish communities in nearby permanently open, seasonally open and normally closed estuaries in the south-western Cape, South Africa. *South African Journal of Marine Science* **8** 43-55.

Blaber SJM (1973a) Temperature and salinity tolerance of juvenile *Rhabdosargus holubi* (Steindachner) (Teleostei: Sparidae). *Journal of Fish Biology* **5** 593-598.

Blaber SJM (1973b) Population size and mortality of juveniles of the marine teleost *Rhabdosargus holubi* in a closed estuary. *Marine Biology* **21** 219-225.

Blaber SJM (1974a) Field studies of the diet of *Rhabdosargus holubi* (Pisces: Teleostei: Sparidae). *Journal of Zoology, London* **173** 407-417.

Blaber SJM (1974b) The population structure and growth of juvenile *Rhabdosargus holubi* (Steindachner) (Teleostei: Sparidae) in a closed estuary. *Journal of Fish Biology* **6** 455-460.

Blaber SJM (1977) The feeding ecology and relative abundance of mullet (Mugilidae) in Natal and Pondoland estuaries. *Biological Journal of the Linnean Society* **9** 259-275.

Blaber SJM (1979) The biology of filter feeding teleosts in Lake St Lucia, Zululand. *Journal of Fish Biology* **15** 37-59.

Blaber SJM (1987) Factors effecting recruitment and survival of mugilids in estuaries and coastal waters of southeastern Africa. *American Fisheries Society Symposium* **1** 507-518.

Childs AR (2005) Movement patterns of spotted grunter, *Pomadasys commersonnii* (Haemulidae), in the Great Fish Estuary, South Africa. MSc thesis, Rhodes University, Grahamstown.

Clark BM, Bennett BA and Lamberth SJ (1994) A comparison of the ichthyofaunas of two estuaries and their adjacent surf zones, with an assessment of the effects of beach-seining on the nursery function of estuaries for fish. *South African Journal of Marine Science* **14** 121-131.

Cowley PD (1998) Fish population dynamics in a temporarily open/closed South African estuary. PhD thesis, Rhodes University, Grahamstown.

Cowley PD and Whitfield AK (2001a) Ichthyofaunal characteristics of a typical temporarily open/closed estuary on the southeast coast of South Africa. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* **71** 1-19.

Cowley PD and Whitfield, AK (2001b) Fish population size estimates from a small temporarily open/closed estuary in South Africa, based on mark-recapture techniques. *Marine and Freshwater Research* **52** 283-290.

Cowley PD and Whitfield AK (2002) Biomass and production estimates of a fish community in a small South African estuary. *Journal of Fish Biology* **61** (Supplement A) 74-89.

Cowley PD, Whitfield AK and Bell KNI (2001) The surf zone ichthyoplankton adjacent to an temporarily open/closed estuary, with evidence of recruitment during marine overwash events. *Estuarine, Coastal and Shelf Science* **52** (3) 339-348.

Day JH, Blaber SJM and Wallace JH (1981) Estuarine fishes. In: Estuarine ecology with particular reference to southern Africa. (ed Day, J.H), pp. 197-221. A.A. Balkema, Cape Town.

Dundas A (1994) A comparative analysis of fish abundance and diversity in three semi-closed estuaries in the Eastern Cape. MSc thesis, University of Port Elizabeth, Port Elizabeth.

Grange N, Whitfield, AK, De Villiers CJ and Allanson BR (2000) The response of two South African east coast estuaries to altered river flow regimes. Aquatic Conservation: *Marine and Freshwater Ecosystems* **10** 155-177.

Hanekom N and Baird D (1984) Fish community structures in *Zostera* and non-*Zostera* regions of the Kromme estuary, St Francis Bay. *South African Journal of Zoology* **19** 295-301.

Harrison TD (1997) A preliminary survey of coastal river systems on the South African west coast, Cape Columbine - Cape Point, with particular reference to the fish fauna. *Transactions of the Royal Society of South Africa* **52** 323-344.

Harrison TD (1998) A preliminary survey of the coastal river systems of False Bay, south-west coast of South Africa, with particular reference to the fish fauna. *Transactions of the Royal Society of South Africa* **53** 1-31.

Harrison TD (1999a) A preliminary survey of the estuaries on the south coast of South Africa, Cape Agulhas-Cape St Blaize, with particular reference to the fish fauna. *Transactions of the Royal Society of South Africa* **54** 285-310.

Harrison TD (1999b) A preliminary survey of the estuaries on the south-west coast of South Africa, Cape Hangklip-Cape Agulhas, with particular reference to the fish fauna. *Transactions of the Royal Society of South Africa* **54** 257-283.

Harrison TD (2002) Preliminary assessment of the biogeography of fishes in South African estuaries. *Marine and Freshwater Research* **53** 479-490.

Harrison TD (2003) Biogeography and community structure of fishes in South African estuaries. PhD thesis, Rhodes University, Grahamstown

Harrison TD (2004) Physico-chemical characteristics of South African estuaries in relation to the zoogeography of the region. *Estuarine, Coastal and Shelf Science* **61** 73-87.

Heinecken TJE and Damstra KSJ (1983) Report No. 24: Onrus (CSW 14). In: Estuaries of the Cape. Part 2. Synopses of available information on individual systems. (eds Heydorn, A.E.F. and Grindley, J.R.). *CSIR Research Report* No. **423** 37 pp.

Heinecken TJE (1985) Wildevoëlvlei/Noordhoek (CW 28). In: Estuaries of the Cape. Part 2. Synopses of available information on individual systems. (eds Heydorn, A.E.F. and Grindley, J.R.). *CSIR Research Report* No. **426** 58 pp.

Kerwath SE, Götz A, Cowley PD, Sauer WHH and Attwood CG (2005) A telemetry experiment on spotted grunter *Pomadasys commersonnii* in and African estuary. *African Journal of Marine Science* **27b** (2) 389-394.

Kok,HM and Whitfield AK (1986) The influence of open and closed mouth phases on the marine fish fauna of the Swartvlei estuary. *South African Journal of Zoology* **21** (4) 309-315.

Marais JFK (1988) Some factors that influence fish abundance in South African estuaries. *South African Journal of Marine Science* **6** 67-77.

Maree RC, Whitfield, K and Booth AJ (2000) Effect of water temperature on the biogeography of South African estuarine fish species associated with the subtropical/warm temperate subtraction zone. *South African Journal of Science* **96** 184-188.

Mbande S, Whitfield AK and Cowley PD (2005) The ichthyofaunal composition of the Mngazi and Mgazana estuaries: a comparative study. *Smithiana Bulletin* **4** 22pp.

Millard NAH and Scott KMF (1954) The ecology of South African estuaries. Part 6: Milnerton estuary and the Diep river, Cape. *Transactions of the Royal Society of South Africa* **34** 279-324.

Morant PD (1991) The estuaries of False Bay. *Transactions of the Royal Society of South Africa* **47** 629-640.

Morant PD and Grindley JR (1982) Report No. 14: Sand (CSW 4). In: Estuaries of the Cape. Part 2. Synopses of available information on individual systems. (eds Heydorn, A.E.F. and Grindley, J.R.). *CSIR Research Report* No. **413** 70 pp.

Neira FJ, Beckley LE and Whitfield AK (1988) Larval development of the Cape silverside, *Atherina breviceps* Cuv. and Val., 1835 (Teleostei, Atherinidae) from southern Africa. *South African Journal of Zoology* **23** 176-183.

Potter IC, Beckley LE, Whitfield AK and Lenanton RCJ (1990) Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and Southern Africa. *Environmental Biology of Fishes* **28** 143-178.

Skelton PH (1993) Freshwater Fishes of Southern Africa. Struik Publishers, Cape Town.

Smith MM and Heemstra PC (1990) Smiths sea fishes. Southern Book Publishers, Johannesburg: 1047 pp.

Strydom, NA (2003) Occurrence of larval and early juvenile fishes in the surf zone adjacent to two temporarily open/closed estuaries, South Africa. *Environmental Biology of Fishes* **66** 349-359.

Strydom NA, Whitfield AK and Wooldridge TH (2003) The role of estuarine type in characterizing early stage fish assemblages in warm temperate estuaries, South Africa. *African Zoology* **38** (1) 29-43.

Talbot MMJF (1982) Aspects of the ecology and biology of *Gilchristella aestuarius* (G and T) (Pisces: Clupeidae) in the Swartkops estuary. MSc thesis, University of Port Elizabeth, Port Elizabeth.

Ter Morshuizen LD, Whitfield AK and Paterson AW (1996) Influence of freshwater flow regime on fish assemblages in the Great Fish River and Estuary. *South African Journal of Aquatic Science* **22** (1/2) 52-61.

van der Elst RP (1978) Notes on the teleost fauna of the Kobole estuary, Transkei. South African *Journal of Wildlife Research* **8** 83-85.

Vorwerk PD, Whitfield AK, Cowley PD and Paterson, AW (2001) A survey of selected Eastern Cape Estuaries with particular reference to the ichthyofauna. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* **72** 1-52.

Vorwerk PD, Whitfield AK, Cowley PD and Paterson AW (2003) The influence of selected environmental variables on fish assemblage structure in a range of southeast African estuaries. *Environmental Biology of Fishes* **66** 237-247.

Wallace JH (1975) The estuarine fishes of the east coast of South Africa. III. Reproduction. *Investigational Report of the Oceanographic Research Institute, Durban* **41** 51pp.

Whitfield AK (1984) The effects of prolonged aquatic macrophyte senescence on the biology of the dominant fish species in a southern African coastal lake. *Estuarine, Coastal and Shelf Science* **18** 315-329.

Whitfield,AK (1992) Juvenile fish recruitment over an estuarine sand bar. *Ichthos* 3**6** 23.

Whitfield AK (1994) Abundance of larval and 0+ juvenile marine fishes in the lower reaches of three southern African estuaries with differing freshwater inputs. *Marine Ecology Progress Series* **105** 257-267.

Whitfield AK (1995) Threatened fishes of the world: *Syngnathus watermeyeri* Smith, 1963 (Syngnathidae). *Environmental Biology of Fishes* **43** 152.

Whitfield A. (1998) Biology and ecology of fishes in Southern African estuaries. *Icthyological Monograph of the J.L.B. Smith Institute of Ichthyology* (**2**) 1-223.

Whitfield AK (2000) Available scientific information on individual South African estuarine systems. *Water Research Commission Report* **577/3/00** 217 pp.

Whitfield AK (2005) Fishes and freshwater in southern African estuaries - A review. *Aquatic Living Resources* **18** 275-289.

Whitfield AK and Blaber SJM (1979) The distribution of the freshwater cichlid *Sarotherodon mossambicus* in estuarine systems. *Environmental Biology of Fishes* **4** 77-81.

Whitfield AK and Bruton MN (1989) Some biological implications of reduced freshwater inflow into eastern Cape Estuaries: a preliminary assessment. *South African Journal of Science* **85** 691-694.

Whitfield AK and Bruton MN (1996) Extinction of the river pipefish *Syngnathus watermeyeri* in the Eastern Cape Province, South Africa. *South African Journal of Science* **92** 59-60.

Whitfield AK and Kok HM (1992) Recruitment of juvenile marine fishes into permanently open and seasonally open estuarine systems on the southeast coast of South Africa. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* **57** 1-39.

Whitfield AK and Paterson AW (1995) Flood-associated mass mortality of fishes in the Sundays Estuary. *Water SA* **21** 385-389.

Whitfield AK and Paterson AW (2003) Distribution patterns of fishes in a freshwater deprived Eastern Cape estuary, with particular emphasis on the geographical headwater region. *Water SA* **29** 61-67.

Whitfield AK, Paterson AW and Ter Morshuizen LD (2003) An investigation into the structure and functioning of the ichthyofaunal associated with the REI zone in two Eastern Cape estuaries with differing freshwater inputs. *Water Research Commission Report* **756/1/03** 260-309.

Whitfield AK and Wooldridge TH (1994) Changes in freshwater supplies to southern African estuaries: some theoretical and practical considerations. In: Changes in Fluxes in Estuaries: Implications from Science to Management (eds Dryer K.R. and Orth, R.J.), pp. 41-50. Olsen and Olsen, Fredensborg.

Whitfield AK, Paterson, AW, Bok AH and Kok HM (1994) A comparison of the ichthyofaunas in two permanently open eastern Cape estuaries. *South African Journal of Zoology* **29** 175-185.

11. BIRDS

Anja Terörde[1], Jane Turpie[1] and Paul Cowley[2]

[1]University of Cape Town; [2]South African Institute for Aquatic Biodiversity

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 and 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 and Turpie 1999b).

Some 193 of South Africa's approximately 258 estuaries are classified as temporarily open/closed estuaries (TOCEs) and another six are classified as estuarine lakes. All of the estuaries in the former and most of those in the latter category are closed from time to time, creating conditions that are distinctly different from those of open systems. The conditions and available habitats within these estuaries not only differ from other estuaries, but differ temporally within these systems.

This review summarises available information on estuarine avifauna 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 temporarily open/closed estuaries (TOCEs) and permanently open estuaries (POEs). Some attention is also given to the effects of rapid habitat changes in response to open mouth phases in TOCEs. This review places particular emphasis on the piscivorous birds as they are the dominant avifaunal component in TOCEs.

AVIFAUNA OF SOUTH AFRICAN ESTUARIES

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 and 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.

The total numbers of birds that use South African estuaries is difficult to estimate due to their high mobility and seasonality of their distribution. Hockey and Turpie (1999a) estimated from several sources (Underhill and Cooper 1984, Ryan and Cooper 1985, Ryan et al. 1988, Martin and Baird 1987, Underhill 1987, Tree and 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 is 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 and Currie 1985, Martin and 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 and 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 and 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 et al. 1981, Maree et al. 2000, Whitfield 2000, Harrison 2003).

For the purposes of this review we have adopted the boundaries defined by Harrison (2003), where the break between the subtropical and warm-temperature zones is situated in the region of the Mdumbi Estuary (S 31^{o} 55' 50'; E 29^{o} 12' 58'). 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 MacLean 1993).

[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

Cool temperate region

Bird counts have been conducted on 17 of the 24 estuaries that occur in this region. Ryan et al. (1988) undertook a study that included 14 estuaries in this region. Since 1993 co-ordinated waterbird counts (CWAC) are conducted twice yearly at the Olifants, Berg, Rietvlei, Wildevoëlvlei, Sand, Bot/Kleinmond and Heuningnes estuaries. Ryan and Cooper (1985) surveyed the coast between the Orange and Olifants river mouths and recorded the highest density of waders reported for any region of the southern African coastline. Two of the four most important wetlands in terms of bird abundance in South Africa are located within the cool-temperate region: Langebaan Lagoon is the most important (Cooper and Hockey 1981) while the Orange River mouth is the fourth most important. The Orange River mouth is also an important breeding site for Cape cormorants, Damara terns and Caspian terns (Ryan and Cooper 1985). More detailed studies on the avifauna of single estuaries in relation to environmental features have been conducted at the Orange River mouth (Williams 1986), Berg Estuary (Velasquez et al. 1991, Kalejta 1993, Kalejta and Hockey 1994, Turpie 1994) and Bot Estuary (Heÿl and Currie 1985). Studies on the biology of certain species occurring in this region were conducted on the Giant Kingfisher (Arkell 1979) at Eerste Estuary and the Red-knobbed Coot at Bot Estuary (Stewart and Bally 1985).

Warm-temperate region

A set of once-off summer counts of 72 of the 111 estuaries was conducted in the summers of 1979/80 and 1980/1981 by Underhill and Cooper (1984) and part of those data have been published by Ryan et al. (1988). Turpie et al. (2004) conducted bird counts on 16 estuaries in the warm-temperate region of the Transkei Wild Coast and a total of 31 species of estuarine birds were recorded from those systems. The abundance of estuarine birds was low compared to the rest of the South African coast and was ascribed to the relatively small size of estuaries in this region (Turpie *et al.* 2004).

Currently, CWAC are being conducted twice yearly in five POEs (Zandvlei, Kleinmond, Heuningnes, Keurbooms, Kromme), one estuarine bay (Knysna) and three estuarine lakes (Bot, Wilderness, Swartvlei) within the warm-temperate region. The avifauna of the Swartkops Estuary was counted by Every (1973), Martin and Baird (1987), Martin (1991a) and Tree and Martin (1993). Boshoff and Palmer (1991) and Boshoff et al. *(*1991a, 1991b) conducted several bird counts on the Wilderness-Sedgefield Lakes complex. Every (1970) counted the birds at Coega Estuary and Martin et al. (2000) conducted twelve waterbird counts at the Knysna Estuary between 1993 and 1998.

Studies on the biology of certain species in this region have been conducted on the Osprey (Boshoff and Palmer 1983), the African Fish Eagle (Boshoff and Palmer 1988) and the Red-knobbed Coot (Fairall 1981). Blaber (1973) and Cowley (1998) included counts of the piscivorous bird populations of the East and West Kleinemonde TOCEs in their studies on the fish populations. Terörde (2005) studied temporal and spatial variations in the piscivorous bird population of the East Kleinemonde Estuary. Martin (1991b) and Turpie (1994) undertook detailed studies of the feeding ecology of migrant waders in the Swartkops Estuary (also see Turpie and Hockey 1993, 1996, 1997) and another detailed study of waders took place on the Breede estuary (Pemberton 2000, Turpie 2001).

Subtropical region

There are 120 estuaries in the subtropical region of South Africa of which 93 are TOCEs. A once off bird count of all estuaries from Mbashe to Mtentwana (48 systems) was undertaken by Turpie et al. (2004). The 1979/1980 and 1980/81 counts conducted by Underhill and Cooper (1984) included 67 estuaries in the sub-tropical region and the results of 65 of these are published in Ryan et al. (1988). CWAC counts currently cover 17 estuaries in this region. The avifauna of St. Lucia was studied by Berruti (1980, 1983), Whitfield (1978), Whitfield and Blaber (1978, 1979a, 1979b) and Whitfield and Cyrus (1978). These studies included counts, aspects of the ecology, as well as relationships to prey populations. In more recent years only the avifauna of the Mhlathuze Estuary (Cyrus 2001) and Mdloti and Mhlanga estuaries (Perissinotto et al. 2004) have been studied in the subtropical region of South Africa.

AVIFAUNA OF TOCES

While several bird counts have included POEs as well as TOCEs (Ryan and Cooper 1985, Ryan et al. 1988, Turpie 2004, Underhill and Cooper 1984) none have focused on comparisons between them. Most avifaunal research has been conducted on POEs and the only detailed studies of birds on TOCEs have been on aspects of the piscivorous birds of the West Kleinemonde (Blaber 1973) and East Kleinemonde estuaries (Cowley 1998, Terörde 2005). Perissinotto et al. (2004) suggested that waders (most of which feed on intertidal invertebrates) would be poorly represented in TOCEs compared to POEs, where they tend to dominate the avifauna, and ascribed this to the lack of tidal influence (i.e. inter-tidal habitats) in TOCEs. They found that intertidal habitat in TOCEs was even lacking after mouth breaching, since much of the exposed area become supra-tidal rather than inter-tidal and small shallow-burrowing invertebrates rapidly die due to desiccation. The lack of tidal currents and often greater water clarity in TOCEs afford greater foraging opportunities to piscivorous predators. Consequently, piscivorous birds are expected to be an important or dominant component of the avifauna in TOCEs. Information on these species in South African estuaries (irrespective of type) is has been conducted at Lake St. Lucia (Whitfield 1978, Whitfield and Cyrus 1978, Whitfield and Blaber 1979a, 1979b), Swartvlei Estuary (Whitfield 1986), East Kleinemonde Estuary (Cowley 1998, Terörde 2005), West

Kleinemonde Estuary (Blaber 1973), Swartkops Estuary (Martin and Baird 1987) and Kosi Estuary (Jackson 1984). All but the latter two are systems that close at least periodically.

CLASSIFICATION AND STATUS

In South Africa there are 41 species of estuarine birds from eight orders whose dominant prey item is fish (MacLean 1993, Siegfried 1981). The majority comprises herons, egrets and bitterns (18 species), followed by the 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 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 and 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

Segregation by foraging techniques

Piscivorous birds can be classed into three categories by foraging techniques (Berruti 1983); those that wade through the water or maintain a position to wait for prey (waders), 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 and 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 and Blaber 1978, Connor 1979). The Little Egret is able to fish in areas with aquatic macrophyte growth that are unavailable to other waders. Reed Cormorants and White-breasted Cormorants are known to form feeding associations with pelicans from which the cormorants benefit (Whitfield

---

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

and Blaber 1979b, Nightingale 1975). Great White Pelicans feed communally in a well organized manner, while Pink-backed Pelicans feed solitarily (Din and Eltringham 1974).

Segregation by foraging area

Spatial segregation by water depth occurs between wading piscivores, according to their leg length (Whitfield and Blaber 1979a). The relatively small Little Egret has a mean wading depth of 100mm, the larger Great Egret and Grey Heron have wading depths of 160mm and 190mm respectively, and the Goliath Heron has a mean wading depth of 325mm. This spatial segregation also results in resource segregation, because smaller fish congregate in shallow areas while larger fish are restricted to deeper areas (Whitfield and Blaber 1979a). Spatial segregation occurs between swimming piscivores who fish in different areas of the estuary, e.g. littoral or offshore zone (Whitfield and 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 and 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 and Blaber 1978, 1979a, 1979b, Hockey and 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 and Blaber 1979a; Hockey and 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 and 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 and Blaber 1978). Pied Kingfishers fish at any time of day (Tjomlid 1973, Whitfield and 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 and 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 and Blaber 1979b).

Segregation by prey choice

Piscivorous birds only use a small proportion of available prey species (Whitfield and Blaber 1979a, 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 (Hockey and Turpie 1999a; Whitfield and Blaber 1978). 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 and 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 and 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.

EFFECTS OF PISCIVOROUS BIRDS ON 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 those countries, because they are perceived as damaging fisheries. 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 TOCEs 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.

ASSESSING DAILY FOOD INTAKE

In South Africa several piscivorous bird species have been studied regarding their daily food intake (DFI). Junor (1972) estimated the DFI of piscivorous birds at a lake in Zimbabwe by conducting hand-rearing experiments. He obtained a DFI estimate of 16% of body weight for African Darter, Reed Cormorant, Grey Heron and Goliath Heron. Hand-rearing experiments are problematic because they are very time-consuming and the effects of captivity on feeding behaviour cannot be estimated. Berruti (1983) calculated the mean energy consumption of piscivorous birds at Lake St. Lucia to be 6477 x 10^3 kJ day^{-1}. He multiplied the estimated standard metabolic rate of Lasiewski and Dawson (1967) by a factor of four to correct for additional costs of free-living birds. This factor was then corrected to two (non-breeding) and three (breeding) by Guillet and Furness (1985), which emphasises the bias associated with these calculations.

Jackson (1984) analysed otoliths in regurgitated pellets from Pied Kingfishers and White-breasted Cormorants in the Kosi Estuary and calculated daily energy consumption estimates from those data. For the reasons mentioned above, regurgitated pellets are not always considered a reliable method of estimating daily food intake.

A more valuable approach is to base DFI estimates on daily energy expenditure (DEE) by constructing time energy budgets. Data on time-budgets (time spent with different behaviour) are collected and energy costs are assigned to each behaviour. This has been done for the Great White Pelican in the Western Cape (Guillet and Furness 1985). The estimated DFI of this species was 8.4% of body mass. Before this study, 10% of body mass was commonly used to estimate DFI. This method still contains inaccuracies and bias regarding the time budget allocation.

A more direct and accurate way to estimate daily energy expenditure is the doubly labelled water (DLW) technique. The DLW method has been applied to only two species of piscivorous birds that occur in South African estuaries: the Pied Kingfisher and the Common Tern (Nagy 2001). An equation for 'Marine Birds' or for 'All Birds' was developed by Nagy (2001) to estimate DFI of species not studied by the DLW method. These equations have an average error of 28% and 40% respectively. Terörde (2005) used these equations to estimate biomass consumption of piscivorous birds at the intermittently open East Kleinemonde Estuary. Cowley (1998) estimated piscivorous bird predation in the same estuary using Nagy's (1987) earlier equation for 'All Birds'.

EFFECTS OF ENVIRONMENTAL FACTORS AND SEASONALITY OF DISTRIBUTION

The population structure and abundance of estuarine birds is 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 (Heÿl and Currie 1985, Berruti 1983). However, Whitfield and 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-feeders. Their breeding is also more evenly distributed over the year (Berruti 1983).

REFERENCES

Arkell GBF (1979) Aspects of the feeding and breeding biology of the Giant Kingfisher. *Ostrich* **50** 176-181.

Barnes KN (2000) The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. Birdlife South Africa, Johannesburg. 169 pp.

Berruti A (1980) Status and review of waterbirds breeding at Lake St. Lucia. 1980. *The Lammergeyer* **28** 1-19.

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

Blaber SJM (1973) population size and mortality of the marine teleost *Rhabdosargus holubi* (Pisces: Sparidae) in a closed estuary. *Marine Biology* **21** 219-225.

Boshoff AF and Palmer NG (1983) Aspects of the biology and ecology of the Osprey in the Cape Province, South Africa. *Ostrich* **54** 189-204.

Boshoff AF and Palmer NG (1988) Notes on the abundance, breeding and prey of fish eagles in the southern Cape Province. *Bontebok* **6** 20-25.

Boshoff AF and Palmer NG (1991) Monthly counts and breeding data for some waterbirds in the Wilderness-Sedgefield Lakes Complex, southern Cape Province. *Bontebok* **7** 36-39.

Boshoff AF and Palmer NG and Piper SE (1991a) Spatial and temporal abundance patterns of waterbirds in the southern Cape Province. Part 1: Diving and surface predators. *Ostrich* **62** 156-177.

Boshoff AF and Palmer NG and Piper SE (1991b) Spatial and temporal abundance patterns of waterbirds in the southern Cape Province. Part 3: Wading birds. *Ostrich* **62** 197-214.

Connor MA (1979) Feeding association between Little Egret and African Spoonbill. *Ostrich* **50** 118.

Cooper J and Hockey PAR (1981) The atlas and site register of South African coastal birds. Part 2 – the atlas. Unpublished report. University of Cape Town, Percy Fitzpatrick Institute of African Ornithology, Cape Town.

Cowley PD (1998) Fish population dynamics in a temporarily open/closed South African estuary. PhD Thesis, Rhodes University, Grahamstown.

Cyrus DP (2001) Aquatic avifauna of the coastal lakes of the Mhlathuze River system. African Journal of Aquatic Science **26** (2) 77-83.

Day JH (1981) The estuarine fauna. In: Estuarine Ecology with particular reference to southern Africa (Ed. Day J.H.), pp. 147-178. AA Balkema, Cape Town.

Din NA and Eltringham SK (1974) Ecological separation between White and Pink-backed Pelicans in the Ruwenzori National Park, Uganda. Ibis **116** 28-43.

Every B (1970) The birds of the Coega River mouth. Eastern Cape Naturalist **40** 22-23.

Every B (1973) Wintering waders on the Swartkops river. Bee-eater **24**(3) 7.

Fairall N (1981) A study of the bioenergetics of the red-knobbed coot *Fulica cristata* on a South African estuarine lake. *South African Journal of Wildlife Research* **11** (1) 1-4.

Fraser W (1974) Feeding association between Little Egret and Reed Cormorant. The *Ostrich* **45** 262.

Guillet and Furness RW (1985) Energy requirements of a Great White Pelican (*Pelecanus onocrotalus*) population and its impact on fish stocks. Journal of Zoology **205** 573-583.

Harrison TD (2003) Biogeography and community structure of fishes in South African estuaries. PhD thesis, Rhodes University, Grahamstown.

Heÿl CW and Currie MH (1985) Variations in the use of the Bot River estuary by water-birds. *Transactions of the Royal Society of South Africa* **45** 397-417.

Hockey PAR and Turpie JK (1999a) Estuarine birds in South Africa. In: Estuaries of South Africa (Eds. B.R. Allanson and D. Baird), pp. 235-268. Cambridge University Press, Cambridge.

Hockey PAR and Turpie JK (1999b) Waders and their estuarine food supplies: are predatory impacts or predator behaviour the key to understanding carrying capacity? In: Proceedings of the XXIX International Ornithological Congress, Durban, August 1999. Compact Disk.

Jackson S (1984) Predation by Pied kingfishers and Whitebreasted cormorants on fish in the Kosi estuary system. *Ostrich* **55** 113-132.

Junor FJR (1972) Estimation of the daily food intake of piscivorous birds. *Ostrich* **43** 193-205.

Kalejta B and Hockey PAR (1994) Distribution of shorebirds at the Berg River estuary, South Africa, in relation to foraging method, food supply and environmental features. *Ibis* **136** 233-239.

Kalejta B (1993) Diets of shorebirds at the Berg River estuary, South Africa: Spatial and temporal variability. *Ostrich* **64** 123-133.

Lasiewski RC and Dawson WR (1967) A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* **68** 13-23.

MacLean GL (Ed) (1993) Roberts' Birds of Southern Africa. John Voelcker Bird Book Fund, Cape Town. 871 pp.

Maree RC, Whitfield AK and Booth AJ (2000) Effect of water temperature on the biogeography of South African estuarine fish species associated with the subtropical/warm temperate subtraction zone. *South African Journal of Science* **96** 184-188.

Martin AP (1991a) Numbers and feeding habits of birds on the Swartkops estuary. *The Naturalist* **35** 27-31.

Martin AP (1991b) Feeding ecology of birds on the Swartkops estuary, South Africa. PhD thesis, University of Port Elizabeth, Port Elizabeth.

Martin AP and Baird D (1987) Seasonal abundance of birds on the Swartkops estuary, Port Elizabeth. *Ostrich* **58** 122-134.

Martin AP, Von Korff J and Watt L (2000) Abundance and distribution of waterbirds on the Knysna estuary. *Transactions of the Royal Society of South Africa* **55** 215-222.

Nagy KA (1987) Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monograph* **57** 111-128.

Nagy, K.A. (2001) Food requirements of wild animals: predictive equations for free-living mammals, reptiles, and birds. *Nutrition Abstracts and Reviews* (Series B) **71** 21-31.

Nightingale D (1975) Pelican fishing behaviour. *African Wildlife Research Foundation* **10** (3) 7-10

Pemberton C (2000) Use of habitats by waders on the Breede estuary. Honours thesis, Department of Zoology, University of Cape Town.

Perissinotto R, Blair A, Connell A, Demetriades NT, Forbes AT, Harrison TD, Iyer, K, Joubert M, Kibirige I, Mundree S, Simpson H, Stretch D, Thomas C, Thwala X and Zietsman I (2004) Responses of the biological communities to flow variation and mouth state in two temporarily open/closed KwaZulu-Natal estuaries. In: Contributions to Information Requirements for the Implementation of Resource Directed Measures for Estuaries (Ed. Adams, J.B.). WRC report No. 1247/2/04. pp. 56-162.

Ryan PG and Cooper J (1985) Waders (Charadrii) and other coastal birds of the northwestern Cape Province, South Africa. *Bontebok* **4** 1-8.

Ryan PG, Cooper J, Hockey PAR and Berruti A (1986) Waders (Charadrii) and other water birds on the coast and adjacent wetlands of Natal 1980-81. *Lammergeyer* **36** 1-33.

Ryan PG, Underhill LG, Cooper J and Waltner M (1988) Waders (Charadrii) and other waterbirds on the coast, adjacent wetlands and offshore islands of southwestern Cape Province, South Africa. *Bontebok* **6** 10-19.

Siegfried WR (1981) The estuarine avifauna of southern Africa. In: Estuarine Ecology with particular reference to southern Africa. (Ed. Day, J.H.) pp. 223-250. AA Balkema, Cape Town.

Stewart BA and Bally R (1985) The ecological role of the red-knobbed Coot *Fulica Cristata* Gmelin at the Bot River Estuary, South Africa: A preliminary investigation. *Transactions of the Royal Society of South Africa* **45** 419-426.

Taylor PB, Navarro RA, Wren-Sargent M, Harrison JA and Kieswetter SL (1999) TOTAL CWAC Report. Coordinated waterbird counts in South Africa, 1992-97. Avian Demography Unit, University of Cape Town. 251 pp.

Terörde AI (2005) Aspects of the population dynamics of piscivorous birds at the East Kleinemonde estuary, South Africa. Honours thesis. Department of Zoology and Entomology, Rhodes University, Grahamstown. 47 pp.

Turpie JK (1994) Comparative foraging ecology of two broad-ranging migrants, Grey Plover *Pluvialis squatarola* and Whimbrel *Numenius phaeopus* (Aves: Charadrii) in tropical and temperate latitudes of the Western Indian Ocean. PhD thesis, University of Cape Town.

Turpie JK (2001) Breede River Estuary EFR/RDM study – specialist report on Avifauna. Report to CSIR Environmentek.

Turpie JK (2004) Existing data on area, plants, invertebrates, fish and birds of South African estuaries. *WRC report* No. **1247/1/04** pp. 7-36.

Turpie JK and Hockey PAR (1993) Comparative diurnal and nocturnal foraging behaviour and energy intake of Grey Plovers *Pluvialis squatarola* and Whimbrels *Numenius phaeopus*. *Ibis* **135** 156-165.

Turpie JK and Hockey PAR (1996) Foraging ecology and seasonal energy budgets of estuarine Grey Plovers *Pluvialis squatarola* and Whimbrels *Numenius phaeopus* at the southern tip of Africa. *Ardea* **84** 57-74.

Turpie JK and Hockey PAR (1997) Adaptive variation in the foraging behaviour of Grey Plovers *Pluvialis squatarola* and Whimbrels *Numenius phaeopus*. *Ibis* **139** 289-298.

Turpie JK, Martin AP and Pemberton C (2004) A field count of the birds of the Transkei coast and estuaries: January-February 2002. *WRC Report* No. **1247/1/04** 37-44 pp.

Tree T and Martin AP (1993) Report on the Jan/Feb 1993 CWAC counts in the Eastern Cape. *Bee-eater* **44** 18-26.

Tjomlid SA (1973) Food preferences and feeding habits of the Pied Kingfisher *Ceryle rudis*. *Ornis Scandinavia* **4** 145-151.

Underhill LG (1987) Waders (Charadrii) and other waterbirds at Langebaan Lagoon, South Africa, 1975-1986. *Ostrich* **58** 145-155.

Underhill LG and Cooper J (1984) Counts of waterbirds at southern African coastal wetlands. Western Cape Wader Study Group and Percy Fitzpatrick Institute of African Ornithology, Cape Town (unpublished report).

Velasquez CR, Kalejta B and Hockey PAR (1991) Seasonal abundance, habitat selection and energy consumption by waterbirds at the Berg River estuary, South Africa. *Ostrich* **62** 109-123.

Whitfield AK (1978) Relationship between fish and piscivorous bird densities at Lake St. Lucia. *South African Journal of Science* **74** 478.

Whitfield AK (1986) Predation by White-breasted Cormorants on fishes in a southern Cape estuarine system. *Ostrich* **57** 248-249.

Whitfield AK (2000) Available scientific information on individual South African estuarine systems. *WRC Report* No. **577/3/00** 217 pp.

Whitfield AK and Blaber SJM (1978) Feeding ecology of piscivorous birds at Lake St Lucia, Part 1: Diving birds. *Ostrich* **49** 185-198.

Whitfield AK and Blaber SJM (1979a) Feeding ecology of piscivorous birds at Lake St Lucia, Part 2: Wading birds. *Ostrich* **50** 1-9.

Whitfield AK and Blaber SJM (1979b) Feeding ecology of piscivorous birds at Lake St Lucia, Part 3: Swimming birds. *Ostrich* **50** 10-20.

Whitfield, A.K. and Cyrus, D.P. (1978) Feeding succession and zonation of aquatic birds at False Bay, Lake St. Lucia. *Ostrich* **49** 8-15.

Williams AJ (1986) Wetland birds at the Orange River mouth and their conservation significance. *Bontebok* **5** 17-23.

12. ESTUARINE/MARINE INTERACTIONS

Paul Vorwerk, Mike Jennings and William Froneman

Rhodes University, Grahamstown

INTRODUCTION

Estuarine and marine interactions have only been briefly discussed in the South African scientific literature, with relatively few publications dealing with the interface between these two environments. Due to the nature of the interface area, discussions on these factors have been broken into two separate sections, biological and physico-chemical interactions.

Exchange between TOCEs and the adjacent marine environment may take place in four ways:

- via barrier overwash, whereby saline water is introduced into the closed estuarine environment through a combination of high swell conditions, favourable winds and a rising tide;
- by seepage through the sandbar, in either a landward or seaward direction depending on relative levels in the estuary and the tide state of the sea;
- by overspilling, whereby estuarine water flows into the sea across the barrier without enough force to cut a deep channel into the sandbar; and
- by channelised seaward flow or breaching where river discharge results in the water level inside the estuary being higher than that of the tide level of the sea, and the sandbar is eroded and a seaward flow of estuarine water results (Cooper et al. 1999).

BIOLOGICAL INTERACTIONS

In South Africa, biological interactions between the marine environment and estuaries are generally poorly understood (see Table 12.1). Some work does appear in the grey literature, but this information is difficult to access. For this reason, the review is based on the published literature listed in Table 12.1.

Most of the literature that discusses biological interactions between estuaries and the marine environment considers recruitment of the larvae of marine fish species that use estuaries as nursery areas. There are several publications that cover this aspect, with the best summary being Whitfield (1998). The study of fish recruitment into estuaries has been investigated in both TOCEs and POEs. Initially, the main recruitment of fish larvae into TOCE's was thought to take place during open mouth periods, although several studies have indicated the relevance of overwashing events as a recruitment opportunity for certain fish species (Bell et al. 2001, Cowley et al. 2001, Kemp and Froneman 2004, Vivier and Cyrus 2001).

Table 12.1. Available scientific literature on estuarine/marine interactions.

System	Estuary Type*	Reference	Feature Studied
Kasouga	TOCE (Eastern Cape)	Froneman (2002, 2004).	Zooplankton communities within estuaries and responses to overwash events
East Kleinemonde	TOCE (Eastern Cape)	Bell et al. (2001), Bernard and Froneman (2005), Cowley et al. (2001), Kemp and Froneman (2004)	Fish recruitment during breaching and overwash events; macrozooplankton recruitment during overwash events and breaching.
Nyara	TOCE (Eastern Cape)	Perissinotto et al. (2000)	General zooplankton community with comment on overwash.
Mhlanga	TOCE (KwaZulu Natal)	Harrison and Whitfield (1995), Whitfield (1980)	Factors influencing fish community structure (mouth condition is of relevance); effect of mouth opening events on zooplankton community
Damba	TOCE (KwaZulu Natal)	Harrison and Whitfield (1995)	Factors influencing fish community structure (mouth condition is of relevance)
Zotsha	TOCE (KwaZulu Natal)	Harrison and Whitfield (1995)	Factors influencing fish community structure (mouth condition is of relevance)
Nhlabane	TOCE (KwaZulu Natal)	Vivier and Cyrus (2001)	Fish recruitment through overwash events.
St Lucia	Estuarine Lake (KwaZulu Natal)	Harris et al. (2001)	Fish larval community structure in the marine environment adjacent to the Estuary
Thukela	POE (KwaZulu Natal)	DWAF (2004)	Effect of freshwater outflow on the Thukela banks

*TOCE = Temporarily Open/Closed Estuary; POE = Permanently Open Estuary

Bell et al. (2001), Cowley et al. (2001) and Kemp and Froneman (2004) demonstrated that overwashing events are very important for recruitment of marine breeding fish species into TOCEs, particularly in the Eastern Cape Province, where relatively low sandbars and a high frequency of large southerly swells culminate in a high frequency of overwash events. For example, in the East Kleinemonde Estuary, overwashing events occurred 25% of the time over a period of two years (Cowley and Whitfield 2001). Kemp and Froneman (2004) indicated that during seven different overwash events, the minimum and maximum number of recruits estimated to enter the East Kleinemonde Estuary during a one-hour period were 8000 and 33500 individuals, respectively. Similarly, Cowley et al. (2001) indicated that in the same estuary the highest densities of larvae of specific species were associated with overwashing events rather than open mouth periods.

On the other hand, Vivier and Cyrus (2001) have found that although important in allowing some recruitment into the subtropical Nhlabane Estuary during drought conditions, overwash events do not appear to be the major recruitment method of fish larvae in this region of South Africa. In a study of three KwaZulu Natal estuaries, Harrison and Whitfield (1995) found that the fish communities within these small TOCE's varies according to their mouth condition. Harrison and Whitfield (1995) linked the mouth condition to the habitat availability within these estuaries and determined that although directly responsible for allowing movement of fishes into these estuaries, mouth status additionally influenced the fish communities by altering the habitat availability.

In contrast to the relatively large amount of information available on fish recruitment and the effect of marine-estuarine-interactions (MEIs) on fish communities, the influence of these events on invertebrate communities is poorly documented. A number of publications document the recruitment techniques of specific invertebrate species (Bernard and Froneman 2005, Forbes et al. 1994, Wooldridge 1994), but the effect of MEIs on invertebrate community structure within estuaries has not been well studied in southern Africa. Whitfield (1980) noted changes in the zooplankton and zoobenthic communities in the Mhlanga estuary after mouth opening events, while Froneman (2004, 2002) investigated the effects of overwash events on the zooplankton community in the Kasouga estuary and Kemp and Froneman (2004) studied the macrozooplankton recruiting into the East Kleinemonde during overwash events. The inflow of marine waters during overwash events generally coincides with the recruitment of marine breeding species into the estuary, which contributes to increased diversity in zooplankton and ichthyofauna within these systems. In addition, overwash events contribute to increases in abundance and biomass of the various components of the food web within TOCEs, thus reflecting the recruitment of marine breeding species into the system. Alternatively, breaching events generally coincide with a reduction in plankton and ichthyofaunal biomass within these systems as estuarine water flows into the marine environment reducing both food and habitat availability.

Sixteen species of macrozooplankton were recorded recruiting into the East Kleinemonde during overwash events, with three species, *Palaemon perengueyi*, *Mesopodopsis wooldridgei* and *Eurydice longicornis* accounting for the majority of individuals (Kemp and Froneman 2004). Similarly, Froneman (2004) found that the zooplankton community structure in the Kasouga Estuary was strongly linked to breaching and overwash events. These events caused a change in the community structure, from a copepod-dominated to a mysid- and amphipod-dominated community that recruited from the marine environment and persisted for a short period after these interactions. Consequently, shifts in the zooplankton community structure and species composition have been linked to overwash events (Froneman 2002, 2004). Whitfield (1980) and Perissinotto et al. (2000) identified a large reduction in the numbers and biomass of zooplankton and zoobenthos upon breaching of the Mhlanga and Nyara estuaries. This reduction was attributed to the rapid loss of estuarine water to the marine environment upon opening resulting in the flushing of the majority of the zooplankton community (Perissinotto et al. 2000), and the harsh conditions during the open phase due to sand movement and exposure of intertidal banks causing the loss of zoobenthos (Whitfield 1980). Immediately after opening, the zooplankton numbers recovered rapidly, but a completely different community formed relative to the closed phase, mostly representative of larval marine fishes (Whitfield 1980).

Few biological studies have been published that examined the influence of the marine–estuarine interface zone within the nearshore environment. The exact position of this zone depends on the estuary under discussion, with it occasionally occurring in the surf-zone while on other occasions it extends further offshore. Harris et al. (2001) examined the changes in ichthyoplankton communities along the ocean-estuarine gradient opposite the St Lucia Estuary. The DWAF (2004) report identified potential links between outflow of freshwater from the Thukela River and the linefish communities in the marine environment in northern KwaZulu Natal. More recently, Forbes and Demetriades (2005) demonstrated the importance of freshwater cues for the recruitment of penaeid prawns into estuaries. These publications are crucial as they demonstrated for the first time the links between freshwater entering the marine environment and the communities or species that occur in the ocean. Harris et al. (2001) also investigated the larval fish communities associated with the St Lucia Estuary and adjacent surf-zone and nearshore environment. Their results showed distinct communities related to each of these zones that appeared to separate based on the turbidity occurring within each zone. The DWAF (2004) report indicated that the freshwater flow rates entering the marine environment from estuaries in northern KwaZulu Natal, and the Thukela Estuary in particular, influence the productivity of the adjacent Thukela Banks. This was evident for several linefish species whose recruitment could be related to the flow volume from adjacent estuaries, with good recruitment to the linefishery following years of high flow. The relationships between river flow and the linefish densities on the Thukela Bank were thought to be a combination of high flow rates providing nutrient inputs to the region and conditions conducive to successful spawning aggregations.

This literature on the ichthyofauna in the nearshore environment and their relationship to adjacent estuaries needs to be expanded for estuarine scientists to better understand the influence of estuaries on the marine environment. Similar studies need to be conducted to identify the influence of the marine-estuarine interface on invertebrate communities as there is no published information available.

MACRO-NUTRIENT AND ORGANIC MATERIAL INTERACTIONS

This component of the review focuses on both dissolved and particulate organic material as well as inorganic macro-nutrient transfer between estuaries and the marine environment. Once again the South African literature demonstrates a lack of information about MEIs, this time with regard to the transfer of organic material and macro-nutrients between estuaries and the sea.

The 'outwelling' hypothesis has long been associated with estuaries, the idea being that estuarine systems produce more material (both dissolved and particulate) than can be utilised or degraded within the system, and that excess material is exported to the coastal marine environment where it may contribute to coastal marine productivity (Winter and Baird 1991). This theory has been extensively studied in permanently open systems as well as from salt marshes and mangrove swamps (Baird and Winter 1989). The relevant publications are listed in Table 12.2.

Table 12.2. Publications relating to macro-nutrient and organic material interactions between the marine and estuarine environments.

System	Estuary Type*	Reference	Feature Studied
Swartkops	POE (Eastern Cape)	Winter et al. (1996), Baird et al. (1987)	Flux of particulate matter and dissolved inorganic and organic carbon between the estuary and the sea.
Kasouga, Nyara	TOCE (Eastern Cape)	Froneman (2002), Perissinotto et al. (2000)	Effect of overwash events on macro-nutrient concentrations
Kasouga	TOCE (Eastern Cape)	Froneman (2002), Jennings (2002)	Effect of increased freshwater discharge on macro-nutrient concentrations. Macro-nutrient concentrations during three hydrological phases of a TOCE.
Marine water adjacent to Alexandria dune fields	Marine nearshore area	Campbell and Bate (1998)	Changes in nearshore macro-nutrient concentrations due to groundwater seepage from dunes

*TOCE = Intermittently Open Estuary; POE = Permanently Open Estuary

The available information on carbon flux and inorganic and organic particulate matter transfer between estuaries and the sea has largely been restricted to a study on the Swartkops Estuary near Port Elizabeth (Baird et al. 1987, Winter et al. 1996). Baird et al. (1987) identified that water mass exchanges in the lower reaches of the Swartkops are dominated by tidal exchange and that there was an annual net export of 5306 tonnes of total suspended particulate matter, with the main sources of particulate carbon being the salt marshes and invertebrate production. This result demonstrated that the Swartkops Estuary has an outwelling role and could support marine inshore productivity. Similarly, Winter et al. (1996) identified a total annual carbon (including dissolved organic, dissolved inorganic and particulate organic carbon) export of 4755 tonnes from the Swartkops Estuary. Due to the fact that the study identified that more than 80% of the carbon leaving the estuary was dissolved inorganic carbon, they speculated that this carbon originated from the highly productive macroinvertebrate and phytoplankton components of the estuary.

In terms of macro-nutrients, the duration and extent of connection between estuaries and the sea greatly influences concentrations within the estuary. The inflow of marine waters over the sand bar that separates estuaries from the sea (overwashing) is thought to increase macro-nutrient levels within TOCEs through re-suspension of sediments containing a large nutrient pool available in the substratum (Perissinotto et al. 2000). An increase in macro-nutrient concentrations during the overwash phase was reported in the intermittently open Kasouga Estuary, relative to the closed phase (Froneman 2004). Macro-nutrient concentrations of the overwashing water within the coastal zone are influenced by factors such as proximity to nutrient-rich POEs and the presence of marine upwelling cells. The persistence of upwelled water along the landward edge of the Agulhas Current has been reported offshore of Port Alfred, influencing the macro-nutrient status of the water in this region (Lutjeharms et al. 2000).

Outflow of nutrient-rich estuarine waters following a breaching event will likely promote phytoplankton growth in the nearshore environment as several studies have demonstrated that the marine water along the south-eastern coastline of southern Africa is nutrient poor. However, no studies have been conducted on the response of the phytoplankton in the surf-zone, and indeed near-shore water, to the increased concentrations of nutrients that coincide with breaching events. This is clearly a priority area for further research.

Olfactory cues via seepage through the sand bar are believed to account for fish gathering opposite TOCEs (Whitfield and Marais 1999), with dissolved organic material and/or inorganic macro-nutrients being possible signals in the percolating water. Campbell and Bate (1998) reported the seepage of nutrient-rich water into the surf-zone via groundwater discharge from the Alexandria dunefields aquifer. The discharge occurred in a pulsing fashion, highest during spring tides and lowest during neap tides. The importance of seepage from TOCE’s as a supply of dissolved organic material and macro-nutrients to the adjacent marine environment has been poorly documented, but depends mainly on concentrations within the estuary which are determined primarily by river discharge (Grange and Allanson 1995, Allanson and Read 1995, Grange et al. 2000).

The impoundment of water in dams has resulted in a decreased number of breaching events in many TOCEs, as well as associated problems such as reduced sediment scour, shallower channels and rapid mouth closure after breaching (Whitfield and Bruton 1989). Lowered fluvial discharge into estuaries can culminate in ‘overspilling’ (Cooper et al. 1999) occurring where previously a deep channel would have been cut into the sand barrier during a breaching event. Jennings (2002) reported macro-nutrient concentrations approaching eutrophic levels in the Kasouga Estuary during a river flood, but these conditions were short lived as persistent rains and river discharge meant the estuary breached and drained into the sea. After breaching, the estuary became tidal and the modifying effect of the saline water diluted and lowered macro-nutrient concentrations. According to the results of the Land Ocean Interactions in the Coastal Zone (LOICZ) budget, the estuary acted as a net sink for dissolved inorganic phosphate (DIP) during all three phases (flood, breach and tidal) and as a sink for dissolved inorganic nitrogen in the flood and tidal phases, and as a net source of DIP in the breach phase.

In TOCE's, the degree of influence of an estuary on the marine environment, or vice versa, depends primarily on the magnitude and time between breaching and/or overwashing/ overspill events. In addition, seepage is thought to occur continuously depending on the nature of the sand bar and the relative water heights on either side of the bar.

CONCLUSIONS

At present our understanding of MEIs in South Africa is limited, particularly in the Eastern and Western Cape. Several important questions remain unanswered such as, what is the effect of water released from estuaries to the marine environment and, more specifically, how does this water influence productivity in the nearshore environment? In the context of TOCEs, what is the effect on the nearshore environment of the combined opening of several TOCEs in a given region after extended periods of closure? Prior to opening, these systems have represented a sink in terms of nutrients entering from both the marine environment (overwash events) and the catchments, as well as being a sink for ichthyofaunal and invertebrate larvae that have entered through overwash events, matured and subsequently available to recruit back to the sea.

Studies by Cowley and Whitfield (2001) and Lukey et al. (2006) have indicated large populations (between 18000 and 133000 fish in the East Kleinemonde and approximately 12000 fish in the Grants Valley Estuary) of fish trapped within TOCEs that appear to leave these systems upon opening. This indicates a large contribution by fishes in TOCEs to the biomass and productivity of the marine environment. Further study is required to identify the relative contributions that these systems provide to the nearshore productivity along our coastline, both in terms of migrating biota as well as dissolved and particulate organics and macro-nutrient inputs.

REFERENCES

Allanson BR and Read GHL (1995) Further comment on the response of Eastern Cape Province estuaries to variable freshwater inflow. *Southern African Journal of Aquatic Sciences* **21** 56-70.

Baird D and Winter PED (1989) Annual flux budget of dissolved inorganic nutrients through a well mixed estuary. In: Coastal and Estuarine Studies 36: Estuarine Water Quality Management: Monitoring, Modelling and Research (ed. Michaelis, W.), pp. 335-340. Springer-Verlag, New York.

Baird D, Winter PED and Wendt G (1987) The flux of particulate material through a well-mixed estuary. *Continental Shelf Research* **7** 1399-1403.

Bell KNI, Cowley PD and Whitfield AK (2001) Seasonality in frequency of marine access to an intermittently open estuary: Implications for recruitment strategies. *Estuarine, Coastal and Shelf Science* **52** 327-337.

Bernard ATF and Froneman PW (2005) population dynamics of the caridean shrimp *Palaemon perengueyi* in a temperate temporarily open/closed southern African estuary. *Estuarine, Coastal and Shelf Science* **63** 73-81.

Campbell EE and Bate GC (1998) Tide-induced pulsing of nutrient discharge from an unconfined aquifer into an *Anaulus australis*-dominated surf-zone. *Water SA* **24** (4), 365-370.

Cooper JAG, Wright CI and Mason TR (1999) Geomorphology and sedimentology. In: Estuaries of South Africa (eds. Allanson, B.R. and Baird, D.), pp. 5-25. Cambridge University Press, Cambridge, U.K.

Cowley PD and Whitfield AK (2001) Fish population size estimates from a small intermittently open estuary in South Africa, based on mark-recapture techniques. *Marine and Freshwater Research* **52** 283-290.

Cowley PD, Whitfield AK and Bell KNI (2001) The surf-zone ichthyoplankton adjacent to the mouth of a predominantly closed southern African estuary, with evidence of recruitment during marine overwash events. *Estuarine, Coastal and Shelf Science* **53** 339-348.

DWAF (Department of Water Affairs and Forestry, South Africa) (2004) Thukela Bank: Impacts of flow scenarios on prawn and fish catch report – Reserve Determination Study – Thukela River System. *DWAF Report No.* **PBV000-00-10310.**

Forbes AT, Demetriades NT (2005) A review of the commercial shallow water prawn resource of South Africa.: Status, fisheries, aquaculture and management. Specialist Report. 64 pp.

Forbes AT, Niedinger S and Demetriades NT (1994) Recruitment and utilization of nursery grounds by penaeid prawn postlarvae in Natal, South Africa. In: Changes in fluxes in estuaries: Implications from science to management (eds. Dyer, K.R. and Orth, R.J). *ECSA 22/ERF Symposium*. Olsen and Olsen, Fredensborg.

Froneman PW (2002) Response of the plankton to three different hydrological phases of the temporarily open/closed Kasouga Estuary, South Africa. *Estuarine, Coastal and Shelf Science* **55** 535-546.

Froneman PW (2004) Zooplankton community structure and biomass in a southern Africa temporarily open/closed estuary. *Estuarine, Coastal and Shelf Science* **60** 125-132.

Grange N and Allanson BR (1995) The influence of freshwater inflow on the nature, amount and distribution of seston in estuaries of the Eastern Cape, South Africa. *Estuarine, Coastal and Shelf Science* **40** 403-420.

Grange N, Whitfield AK, De Villiers CJ and Allanson BR (2000) The response of two South African east coast estuaries to altered river flow regimes. *Aquatic conservation: Marine and Freshwater Ecosystems* **10** 155-177.

Harris SA, Cyrus DP and Beckley LE (2001) Horizontal trends in larval fish diversity and abundance along an ocean-estuarine gradient on the northern KwaZulu Natal Coast, South Africa. *Estuarine, Coastal and Shelf Science* **53** 221-235.

Harrison TD and Whitfield AK (1995) Fish community structure in three temporarily open/closed estuaries on the Natal coast. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* **64** 80pp.

Jennings ME (2002) The response of hydrochemical variables in the Kasouga estuary under contrasting meteorological conditions and associated physical forcings. BSc (Hons) Project, University of Cape Town, Cape Town.

Kemp JOG and Froneman PW (2004) Recruitment of ichthyoplankton and macrozooplankton during overtopping events into a temporarily open/closed southern African estuary. *Estuarine, Coastal and Shelf Science* **61** 529-537.

Lukey JR, Booth AJ and Froneman PW (2006) Fish population size and movement patterns in a small intermittently open estuary. *Estuarine, Coastal and Shelf Science* 67 10-20.

Lutjeharms JRE, Cooper J and Roberts M (2000) Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research* **20**(7) 737-761.

Perissinotto R, Walker DR, Webb P, Wooldridge TH and Bally R (2000) Relationships between zoo- and phytoplankton in a warm-temperate, semi-permanently closed estuary, South Africa. *Estuarine, Coastal and Shelf Science* **51** 1-11.

Vivier L and Cyrus DP (2001) Juvenile fish recruitment through wave-overtopping into a closed subtropical estuary. *African Journal of Aquatic Science* **26** 109-113.

Whitfield AK (1980) A quantitative study of the trophic relationships within the fish community of the Mhlanga Estuary, South Africa. *Estuarine Coastal and Marine Science* **10** 417-435.

Whitfield AK (1998) Biology and Ecology of Fishes in Southern African Estuaries. *Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology*, No. **2**, 223 pp.

Whitfield AK and Bruton MN (1989) Some biological implications of reduced fresh water inflow into eastern Cape estuaries: a preliminary assessment. *South African Journal of Science* **85** 691-694.

Whitfield AK and Marais H (1999) The ichthyofauna. In: Estuaries of South Africa (eds. Allanson BR and Baird D), pp.209-233. Cambridge University Press, Cambridge, U.K.

Winter PED and Baird D (1991) The exchange of phosphate between the Swartkops estuary and Algoa Bay. *South African Journal of Science* **87**: 192-197.

Winter PED, Schlacher TA and Baird D (1996) Carbon flux between an estuary and the ocean: a case for outwelling. *Hydrobiologia* **337** 123-132.

Wooldridge TH (1994) The effect of periodic inlet closure on recruitment in the estuarine mudprawn, *Upogebia africana* (Ortmann). In: Changes in fluxes in estuaries: Implications from science to management (eds. Dyer, K.R. and Orth, R.J). ECSA 22/ERF Symposium. Olsen and Olsen, Fredensborg.

13. ESTUARY MANAGEMENT

Guy Bate

Nelson Mandela Metropolitan University and University of KwaZulu-Natal

INTRODUCTION

The primary objectives of estuary management are to:

Maintain an acceptable standard of natural ecological function.

Provide estuary services, which involve both economic and social values.

Sound estuary management implies that the manager must have a good understanding of the manner in which both the physical and biological components interact to provide the conditions supporting the biological components. It is humans that are managing estuaries and ultimately, this management is for the benefit of humans. However, we realise that we do not exist in isolation and that the interaction with other biological organisms and systems is essential for our quality of life and for our very survival.

Estuarine organisms react primarily to the physical and chemical components within the estuary environment, but those estuarine organisms also modify the physical and chemical conditions spatially, so that a continuum of physico-chemical states prevails from the head of the estuary to the mouth. There are certain attributes that biological organisms can modify and other attributes that they cannot. Plants are able to take up the macronutrients that arrive in river water at the head of the estuary, which means that high concentrations of important nutrients may be found at the head of the estuary but these decrease towards the mouth depending upon river flow and estuary length. Plants do not take up significant amounts of salt, hence a change in salinity along the length of the estuary is not a function of plant uptake. Rather it is the result of purely physical processes of mixing and the speed of the flowing water.

Each estuary has its own physical characteristics, to which biological components respond in a complex manner. Fauna also respond to the activities of other fauna and the importance of these interactions is that no two estuaries are the same. The effect of this is that although there are general ways in which estuaries respond, each has to be understood and managed according to the biological, social and economic requirements and values that have been set for it.

The South African Department of Environmental Affairs and Tourism (DEAT) and the Department of Water Affairs and Forestry (DWAF) have the prime responsibility of ensuring that the environmental condition of estuaries is acceptable and that this acceptability continues in perpetuity to be a sustainable resource of biodiversity and social and economic services. The Water Research Commission (WRC) provides a research capability through interaction with hydrologists, engineers and physical and biological scientists (WRC 2004). The data from these research activities are available and should be implemented in the normal course of estuary management. The implication is that estuary managers must keep up-to-date with new information.

The management of estuaries is the legal mandate of DEAT but the provision of adequate water to sustain estuaries is the legal mandate of DWAF. Since the amount of water flowing into estuaries, together with its quality, are the two major physical and chemical factors affecting the estuary environment, much of the primary responsibility for estuary condition devolves to DWAF.

The Water Act (36) of 1998, inter alia, requires that sufficient water of suitable quality be delivered to estuaries to ensure that they retain a minimum ecological status or class. The ecological classes into which estuaries may be classified fall into A – F with Class A being pristine or near pristine and F severely degraded. The Water Act does not permit an estuary classified either an F or an E to remain in that class, with the lowest permitted class being a D. However, although one of the main reasons for an estuary being degraded is the lack of adequate water entering at the head, it is not the only reason. Other causes of degradation include human use, industrial and agricultural pollution. Estuaries are prime areas of human settlement and associated infrastructural, industrial and commercial development. Management of all environmental aspects within a town or city falls directly under the local municipality. Hence, estuary management, which is complex by virtue of the interaction of physical, chemical and biological aspects, becomes more complex due to the difficulties inherent in management being split between different authorities.

The aim of coastal zone management (CZM) is to promote the inevitable development of the coastal zone, in such a way as to benefit the greatest number of people possible, while at the same time safeguarding the intrinsic environmental features and maintaining the natural ecological processes of the coast. This aim promotes wise use of the coast and its resources and encompasses the concepts of optimal utilisation and protection of the coastal environment (Fuggle and Rabie 1992). These authors stated that the objectives of CZM in South Africa have been defined by the Council for the Environment and specifically include protection of ecologically sensitive coastal features such as estuaries, together with the natural processes governing their functioning.

Legislation and research on estuaries in the past have been aimed at both POEs and TOCEs. However, much of the research in the past has centred on POEs because they are generally larger than TOCEs and, by virtue of their larger river volumes, are more important in supplying freshwater for agricultural, industrial and urban development use. The different sections of this review have been dedicated specifically to understanding the individual components of TOCEs that comprise what is now seen to be a very important part of the whole estuarine environment. Management options are available within each of these functional areas and the following sections are an attempt to focus on the management aspects relating to each. The comments are drawn from participants at a WRC Project K5/1581 research meeting held at the Nelson Mandela Metropolitan University on 25th January 2006. Important management issues are discussed under individual headings for convenience.

KNOWLEDGE BASE

Managers of individual estuaries must have an adequate knowledge of the manner in which estuaries function. While there is a wealth of information in the scientific and popular literature, not all of this is available to non-specialist municipal managers. Where no estuarine specialist is available, problems should be addressed in consultation with accredited estuarine scientists. Most accredited estuarine scientists are members of the Consortium for Estuarine Research and Management (CERM) under whose management the current research is being undertaken. The WRC will also be able to provide contact details of experienced estuarine scientists from whom advice can be obtained.

Important components of knowledge are the historical data sets available in both the peer-reviewed literature but also in the 'grey literature' of popular articles as well as student theses and project reports. The WRC bibliographic report by Whitfield (2000) detailing available scientific information on South African estuaries provides a useful starting point for any literature search.

HYDROLOGY AND SEDIMENT MANAGEMENT

Sediment management is an integral part of catchment hydrology management, which must ensure that adequate water arrives at the estuary mouth to keep the TOCE open for the correct period and at the correct time of the year (Hay, Huizinga and Mitchell 2005). In the case of TOCEs, mouth opening is most often a response to river flooding.

When water is in short supply, certain options are available. The mouths of all TOCEs will close at certain times of the year and for certain lengths of time. There will be an individual normal range within which mouth closure occurs (frequency and duration). From a management perspective, if closure falls within the averages, no hydrological actions are required. But if closure falls outside the norms, action of some sort may be required such as artificial breaching or increasing freshwater inflow (van Niekerk, van der Merwe and Huizinga 2005). This implies a knowledge-base regarding the run-off regime from the catchment and any changing catchment management and its influence (DWAF 2002; 2003a; 2003b; 2003c; 2004a, 2004b). Hence, the hydrological management of a TOCE does not end at the defined boundary of the estuary in question. There will be an average frequency of closure and an average length of closure.

Possibly the most significant management intervention is the artificial breaching of the mouth. This is commonly because of low-lying developments within the estuarine floodplain which, with increasing water levels during closed mouth conditions, can result in potential pollution from septic tanks and sewage systems. Unfortunately, artificial breaching causes a significant buildup of sediments in the long-term in estuaries as it prevents a sufficient head of water from building-up behind the berm. This in turn prevents effective scouring of sediments from the estuary during a breaching event (Huizinga, van Niekerk and Whithers 1997; Huizinga and van Niekerk 1998, 1999).

LAND USE

The geographical boundary of an estuary is usually the 5m AMSL mark and no development or structures should be permitted below this mark (DWAF 2004c). Unfortunately, there are already many structures that have been constructed below this level, which give rise to management actions that are contrary to sound estuary management.

Residential and industrial developments have the effect of both lowering natural water flow into estuaries and increasing flood intensity. The former is a result of water abstraction for human, agricultural and industrial use and the latter as a result of run-off from roofs and impermeable areas such as roads and concrete aprons. All these structures should be carefully considered in any local IDP (Van Niekerk and Taljaard 2003).

Because TOCEs can close naturally when ebb tidal flow (normally coupled to reduction in freshwater inflow and/or increase in wave action) falls below a minimum level, any structures (e.g. jetties, bridges, causeways etc.) or activities that cause excessive vegetation growth or reduce estuary depth and natural flow volume or rate should be carefully examined for their potential to cause an unacceptable alteration in ebb-flow rate (van Niekerk, Chapter 1 of this document). These activities are more likely to cause adverse impacts in small TOCEs than in large ones because the latter are more resilient.

River inflow at the head of the estuary and water level records near the mouth of the estuary are essential data required to understand the hydrology and sedimentation attributes of TOCEs. Equipment and long-term data are essential to managing these systems. As a result, all estuary management authorities are encouraged to install the necessary equipment to monitor these aspects of the physical environment (Taljaard et al. 2003). Regional classification of the catchment is available from DWAF and the number and geographical distribution of all inflow channels should be carefully recorded especially when new developments are being planned.

MICROALGAE AND WATER QUALITY

Microalgae are at the base of the food web and provide nutrition for all the small fauna that are eaten by larger animals, including fish and birds. Being microscopic, they have not received as much scientific attention as larger animals and plants. However, it is important for managers to understand that they support the base of the food web i.e. where the food for the primary consumers comes from and they are therefore of major importance to the ecological functioning of every estuary (Soo Park and Marshall 2000, Froneman 2002b).

Microalgae receive their nutrition from minerals in the water that arrives from both land and sea (Piehler et al. 2004). The action of mixing between seawater and fresh water also has a big effect on the availability of minerals for these microscopic plants. Too small (oligotrophic) or too great (eutrophic) a supply of minerals has the effect of low productivity and the growth of nuisance or harmful microalgae respectively. Under natural conditions, low levels of nutrients (oligotrophy) were more normal with very high levels (eutrophy), a rare event probably associated with the periodic congregation of large herbivores, extensive natural veld fires and/or natural erosion following infrequent severe flooding. Agriculture in the catchment causes high mineral loads to arrive in estuaries together with herbicides that have unknown effects on primary producers both in terms of productivity and species diversity (Paterson et al. 2003, Chambers et al. 2006). Agricultural mineral pollution also arises from irrigation schemes where the fertiliser is leached by the irrigation water and enters the river via groundwater. Possibly the major difference between past natural eutrophic conditions and those of today is the retention period. Today, pollution of inflowing river water is permanent whereas in the past it was episodic, especially in TOCEs where the water would tend to become saline following the cessation of inflow. This would force large herds of animals to reject it as a drinking water supply.

Municipal sewage effluent and septic tank effluent flowing into estuaries results in eutrophication. In TOCEs, especially, this can take the form of nuisance algal growths that are unsightly, smelly and can even be toxic under certain circumstances. Municipal sewage works can increase normal estuary flow, especially where interbasin water transfer schemes are used to augment supply to the urban area supplying the sewage (Perissinotto et al. 2004). Both a reduction below and an increase above natural flows can have serious effects on a TOCE to the extent that its condition may impact on the management class allocated to it in terms of the Water Act (No. 36) of 1998. The implication is that even past activities may have to be reversed in order to make the condition of the resource comply with the Act.

Most estuarine ecologists believe that TOCEs should be left to open and close naturally. However, conditions may become so altered that this is no longer possible because local impacts have considerably altered water supply or pollution levels. Under these extreme conditions artificial opening may be necessary while under most conditions TOCEs should be left closed, for years if necessary. Conditions that indicate the necessity for an artificial breach are oxygen levels that have decreased steadily over a period of months to a level of ~ 2 mg O_2 l^{-1}, the excessive growth of large beds of nuisance and aesthetically unpleasant macroalgae such as *Enteromorpha*, the presence of very green water where the chlorophyll-a level is > 300 µg l^{-1} or where the benthic microalgal mats have become very dense with a chlorophyll-a level > 500 µg l^{-1}.

When an estuary mouth closes after a flood, the benthic microalgal population builds up over a period of weeks to months. This benthic material is probably the most important plant food in the estuary. For this reason if an estuary opens frequently, i.e. more often than once in 3 months as a result of manipulations of water inflow, the benthic microalgae may not reach their optimum density and diversity. This will mean that the ecology may not be functioning optimally.

MACROPHYTE VEGETATION

Macrophyte vegetation is an important component of the natural environment in and around estuaries and especially small TOCEs. These visible plants grow in the estuary (emergent, floating and submerged vegetation) and next to the estuary (fringing vegetation) e.g., reeds, sedges, salt marsh plants and mangroves. Fringing vegetation provides storm water control and natural bank stabilization, in addition to reducing lateral erosion and littoral water velocities during river flooding (Wessels 1997). They also provide sites of refuge for juvenile fishes and substrata for microalgal growth that supply higher trophic levels within the estuary (Petr 2000, Martin-Smith 1993, Humphries et al.1992, Whitfield 1984).

Stable calm conditions during the closed mouth phase will promote the growth of submerged macrophytes. If the mouth is closed for long enough they can grow and expand to occupy the entire water column where the habitat is suitable, i.e. calm with adequate mineral nutrition. Some sources feel that thick macrophyte beds can become too dense and may have a negative impact on the fauna. However, plants seem to initiate their own self-thinning when they grow very densely (Riddin, T. Pers Com) . Submerged macrophytes will start to grow if the mouth has been closed for at least 3 months (Riddin, T. Pers Com). This allows *Ruppia cirrhosa* and other submerged plants time to develop, flower and set seed. Also, if a TOCE normally has an area of salt marsh vegetation, extended mouth closure resulting from excessive freshwater abstraction, may cause the salinity to drop sufficiently for the salt marsh to disappear. This would constitute a serious loss of biodiversity.

The implication for management of the macrophyte vegetation within TOCEs relates especially to how long these plants can survive prolonged mouth closure with high water levels and high or low salinity. Because TOCEs are naturally closed systems, which also open for part of the year, there is concern regarding the length of time that seeds and other propagules can survive abnormal flooding, exposure or inundation, depending on the species (Naidoo and Naicker 1992, O'Callaghan 1990, Ungar 1978, O'Neil 1972, Steinke 1972, Ungar 1962, Chapman 1960). Propagule survival is essential for the re-setting of the estuary after the mouth has been breached. Mouth closure for greater than three years would likely result in the decomposition of submerged seeds. Loss of propagules will result in a change in the biotic structure of the estuary, which in turn will increase the deviation from the natural condition. This in turn will result in a reduction in the management class allocated to the estuary with implications attendant upon such a reclassification. From the foregoing one can see that although TOCEs should as far as possible be left to open and close naturally, there may be conditions that argue in favour of artificial breaching. This should not be undertaken lightly and only with a specific end product as the goal. A specific condition in a TOCE that would give rise to the possibility of artificial breaching is if submerged macrophyte and/or macroalgal beds cover the entire water surface area and their die-back has resulted in anoxic conditions.

The importance of baseflow is that it results in a salinity gradient along which different macrophyte communities are distributed and is therefore important in maintaining biodiversity. Baseflow also promotes water movement, thus preventing anoxia and ensuring adequate nutrient exchanges between the plants, sediment and water column. Salinity stratification, if present, tends to be broken down by baseflow, thus promoting efficient nutrient exchanges between the water column, sediments and plants.

Floods that open the mouth are very important because they flush out sediment accreting from the sides thus preventing sedimentation and reed encroachment into the channel. Floods also remove accumulated plant biomass and organic matter, thus reducing the possibility of anoxia as a result of decomposition. Floods and the subsequent reduced salinity promotes the germination of salt marsh plants. However, floods can also remove the top layers of sediment, thus removing the potential seedbank available for recolonisation. Floods also physically remove submerged macrophytes. For example a flow rate >0.1m s^{-1} is sufficient to remove certain submerged plants and *Zostera* seeds have an erosion threshold of 0.7 cm s^{-1}, above which they are washed away

Intertidal salt marsh takes approximately 6 months to become established ((Riddin, T. Pers Com)) and therefore in estuaries where the mouth has been closed for long enough to destroy or seriously weaken salt marsh, the mouth should be allowed to remain open for at least that length of time. This can be expensive both in terms of water requirements and finance. Hence, in TOCEs where salt marsh is present, care is needed to ensure that it is not degraded. The loss of the salt marsh vegetation from an estuary would result in a very significant drop in its biodiversity condition and any score that it may have. In perched estuaries where reeds and sedges are dominant the duration of open mouth conditions is considered to be of little significance (Riddin, T. Pers com).

Overwash of seawater may result in the introduction of propagules and vegetative plant fragments from adjacent estuaries. In some estuaries, such as the Palmiet system in the

Western Cape, marine algae (e.g. kelp) are introduced during these events. This can also be a significant allochthonous input of organic matter (Riddin, T. pers. comm.). Overwash increases the salinity of the estuary, which is important in maintaining salt tolerant communities such as salt marsh. Overtopping of the berm during higher than normal freshwater inflow and subsequent opening of the mouth causes the removal of plant material and nutrients from the estuary. However, overtopping may sometimes occur without complete breaching of the mouth being triggered.

Managers need to understand the life-cycle of the dominant macrophyte species, i.e. time of flowering, time of seed set, time to maximum biomass, etc. as well as the tolerance ranges for optimal growth, e.g. salinity, water level fluctuations, light. This will allow managers at any given time to predict what species are likely to occur and what changes in species composition and cover will take place in the event of one or more of the controlling variables changing. It is also important to have an understanding of the successional changes in plant species during low flow (just after mouth opening), too high water levels (just prior to breaching), their rate of change and their importance in terms of habitat availability to faunal assemblages. This will allow managers to understand if changes taking place are natural or in response to some altered physico-chemical property. Reference to historical changes in a system will assist this understanding.

Managers need to know what vegetation is and has been present in the system under natural conditions. They also need to know the optimum growth requirements and tolerance ranges for all vegetation types present in a TOCE. This will permit predictions of change under varying hydrological conditions, e.g. changing mouth status. The life-cycle and seasonality of the vegetation is also important so that timing and frequency of any artificial mouth breaching will be appropriate. Changes in plant communities and biodiversity are indications that ‘things are going wrong’ in a TOCE. This can take the form of an increase in some components (e.g. reed encroachment in response to either increased sedimentation or localised nutrient inputs), through catchment mismanagement or excessive freshwater abstraction (e.g. the disappearance of *Potomgeton pectinatus* with high salinity). The presence of exotic submerged macrophytes is also indicative of perturbations to the estuary and will almost certainly decrease the species richness of the system.

Houses built too near an estuary can alter the distribution and density of TOCE macrophytic vegetation, especially if there is nutrient input into the system from septic tanks and fertiliser wash (e.g. increase in littoral reed growth). Often, residents remove vegetation, especially reeds and submerged macrophytes in order to improve their view and boating access respectively. These actions do not consider the ecological role of such habitats and should therefore be prevented; the best way being not to allow construction in low-lying areas alongside the estuary.

Boats and jetties influence macrophytes directly through anchor damage, mooring damage, propeller damage, or indirectly through increasing turbidity, through waste disposal (fuel or oil spillage), shoreline erosion and through the introduction of alien species. Where uprooting of macrophytes occurs, the rate of organic production can be decreased and bank erosion increased. Mass decomposition of macrophytes and macroalgae can lead to anoxic conditions which result in fish kills and unpleasant odours. Negative effects of boating can be minimised by zoning the estuary for different activities and reducing speed limits.

Bridges shade out plant communities, causing community fragmentation and the alteration of local hydrology. Changes in flow can cause some areas, not previously inundated, to become so, and visa versa. Salt marsh areas may be inundated with surface runoff from the roads, decreasing salinity of the area. By contrast, freshwater seepage that would naturally maintain low salinity levels for brackish plant communities may be cut off.

Increased growth of macro- and microalgae may cause shading out of submerged macrophyte communities. Increases in nutrients also indirectly influence shading by increasing plant cover. The subsequent increase in epiphyte growth may eventually shade out the host plants.

The trampling of vegetation by bait collectors or cattle can either physically destroy plants, or damage roots and rhizomes. Furthermore seed loss may occur and trampling can bury seed to depths that are not suitable for successful germination.

From the foregoing, managers should prevent excessive nutrient input, clearing of riparian zones, infrequent or too frequent mouth breaching. Monitoring the estuary by means of aerial photographs allows an assessment of changes over time and is essential for good vegetation management.

ZOOPLANKTON AND HYPERBENTHIC FAUNA

Any alteration to natural freshwater flow, either as baseflow, freshettes or floods will alter the normal recruitment of zooplanktonic or hyperbenthic fauna which require open mouth conditions in order to migrate to and from the sea. Artificial opening of the mouth is not as satisfactory as a natural breach because more water flows into the adjacent surf-zone during a natural breaching than under an artificial one. The greater the volume of water entering the sea, the greater the attractant signal(s) to incipiently migrating fauna and the longer the mouth is likely to remain open. Artificial breaching can be condoned if none would otherwise occur, but this is normally only recommended as a ‘rescue’ situation. The better option is not to restrict freshwater supply to the estuary to a level where artificial breaching becomes necessary.

LARVAL FISHES

Larval fishes, like zooplankton and hyperbenthic invertebrates, also require the mouth of TOCEs to be open for some time – usually one or more times per year. Recruitment is maximised when opening events coincide with adult spawning periods, predominantly over the spring and early summer months. Research has shown that moderate amounts of water are required to flow into the surf-zone to get quite large migrations of larval fish into an estuary (Strydom 2003). Freshwater flowing from the estuary into the sea results in an increase in surf-zone productivity, which in turn has a beneficial effect on the extent of larval fish survival and recruitment into estuaries (Strydom 2003). Research has also shown that up to 80% of all juvenile fish recruitment into estuaries by estuary-associated fishes take place predominantly during the late larval stage (Strydom et al. 2003).

A semi-closed state can be achieved in some estuaries by a continual base flow of between 50-100 l s^{-1} but the actual flow needs to be determined for each estuary. In many estuaries this semi-open state may cease as a result of freshwater abstraction from the river feeding the estuary, thus denying larval fish extended access to those systems that have lost this phase.

TOCEs provide a nursery to new stocks of larvae and juveniles after every opening event. Every year that goes by without opening is a loss to this potential nursery function. Artificial opening events should only be considered when anthropogenic change has considerably altered flood and natural opening events and then they should be based on historical information of river floods, baseflow etc. Long period of closure (years) and loss of productivity and water quality are indications that artificial breaching may be necessary. However, artificial openings are not going to benefit productivity of larval fishes as much as natural openings because freshwater input plays a major role in driving productivity. Artificial openings only deal with one half of the problem and if an artificial opening is deemed necessary in times other than during a prolonged natural drought, it is a clear indication that the natural freshwater supply needs to be addressed.

Base flow is essential even during times when the mouth is closed because it brings in nutrients that fuel primary productivity which in turn serves as the food resource for young fishes that are using the estuary as a nursery. Large floods also serve to supply nutrients to the estuary and nearshore marine environment and permit fish recruitment while the mouth is open. Natural opening events drive the nursery function of the estuary, which is essential to the survival of many estuary-dependent fishes like stumpnose, leervis, spotted grunter, white steenbras etc., that are important recreational angling species.

When a TOCE is closed there is still a benefit from the overtopping of estuary water out to sea. Cues from the estuary enter the marine environment and possibly aid in accumulation of larvae off the closed mouth prior to a potential opening event. This in turn supplements recruitment of larval fishes into the estuary, especially during the spawning season when larval numbers are high in the surf zone. Overwashing of seawater into an estuary is also an opportunity for the ingress of fish larvae and other planktonic organisms and nutrients from the surf zone.

Management of TOCEs requires an understanding of life cycles of fishes, particularly the economically important species, and understanding the role that freshwater and estuaries play in these life cycles. These facts are all interlinked and dependent upon one another. Managers should familiarise themselves with basic estuary function and the environmental importance and use of scientific information on which to base management decisions. Mismanagement of land around estuaries, the estuary itself and the freshwater supply has major repercussions for the success of coastal fish populations dependent on estuaries.

If marginal vegetation is removed and artificial channelling is introduced, problems often follow. Steep sided channels increase current velocity along the margins and exclude larval fishes from their preferred habitat, i.e. shallow marginal areas. The natural shallow area of estuary margins is the ideal shelter habitat for larvae and juvenile fish. Boating disturbs sheltering young fishes and certain structures (e.g. small-boat harbours) alter the natural state of marginal habitats that affects the nursery function of the estuary.

Bridges and jetties adversely affect hydrodynamics by changing currents flow patterns and causing unnatural sand scour and deposition. This creates extensive shallow areas that may alternate with deep holes, both of which will affect water temperatures in parts of the estuary. Temperature changes or the lack of suitable temperature environments results in distribution shifts by fishes that could result in increased predation on larvae. Although jetties provide shelter for some species of fish, this advantage is outweighed by the negative effects on estuarine hydrodynamics.

It is not easy to know when things are going wrong in an estuary, but public users usually note changes first. On many occasions, anglers are the first to record problems because fish catches decline. Therefore warnings bells should ring when the public start submitting complaints and hence strong links with local angling and conservation groups need to be maintained.

MACROZOOBENTHOS

Breaching of TOCEs due to river flooding often has a negative effect on the epibenthos due to sediment scour that is followed by prolonged aerial exposure of supratidal sediments. Research has shown that this mouth breaching often results in a population crash of the invertebrates that only recovers once the mouth closes and all the sediments are inundated (De Decker and Bally 1985, Morant and Quinn 1999). Hence, if artificial breaching is necessary for other reasons, bait collection of macrozoobenthos should be restricted until populations recover.

FISH

Healthy populations of marine-spawning fishes in TOCEs are maintained by periodic connections with the sea, preferably by natural freshettes or floods. These periodic connections allow for the emigration of adults to the sea and the recruitment of larvae and juveniles into the estuary (Whitfield 1998). However, the high abundance of certain taxa (e.g. *Rhabdosargus holubi* and members of the Mugilidae) in TOCEs is ascribed to their ability to also recruit during marine overwash events (Cowley et al. 2001). In contrast, prolonged closed phases are more suitable for the estuarine-spawning species due to more stable physical (e.g. water level) and physico-chemical (e.g. salinity) conditions (Bennett *et al.* 1985). Anoxic conditions created by excessive inputs of organic matter, or as a result of excessive algal growth following hypertrophic conditions have been reported to result in major fish kills (Begg 1978). This type of problem is easily avoided with appropriate management.

The available records for East Kleinemonde estuary (13 year data set) reveal that the maximum period that the mouth has been closed is about 14 months. Hence, undesirable consequences due to prolonged closure have not been documented in this estuary. Artificially breaching should only be considered if undesirable conditions occur, i.e. poor water quality as indicated by fish kills. However, to allow for emigration of marine species, artificial breaching might be considered in other TOCEs that have remained closed for a very long time. The question of what constitutes ‘a long time’ should not be answered with reference to time, rather the answer is provided by historical records of mouth phase and estuary condition.

The benefits to fish of flooding in a TOCE are that it permits recruitment of small fishes but also that it facilitates the emigration of larger marine fish. However, an open mouth is not the only way that an estuary can benefit by connection to the sea. Overtopping, although a rare occurrence in non-perched estuaries like the East Kleinemonde, does provide opportunities for marine-spawning species to recruit into the estuary and, depending on the depth of the out- flowing water, larger individuals of certain species may emigrate from the estuary.

The over wash of seawater into estuaries during high tide and storm conditions is known to be of value. There is conclusive evidence that a number of species make use of over wash conditions to recruit into estuaries. The frequency of over wash conditions (i.e. the number of days per year) is approximately double the number of ‘open’ condition days in the East Kleinemonde estuary. As a consequence, the species (e.g *Rhabdosargus holubi* and mugilids) that make use of over wash conditions as a recruitment strategy, tend to dominate the species composition in this estuary.

Managers need to realise that estuaries are an economic asset that provide a range of goods and services. They should also know that estuaries are important nursery habitats for many fishes, including targeted fishery species. It is vital that estuary managers understand the laws that govern activities in and around estuaries and, most importantly, that they ensure that the laws are enforced.

BIRDS

Bird populations within TOCEs show considerable variability, with migrant waders being discouraged during closed mouth conditions because there is no inter-tidal area for foraging. Bird populations are an important indicator of TOCE health, but the natural condition needs to be known. Large populations of birds indicate the availability of abundant food resources and changes in the populations are indicative of changes in the state and health of the system. Managers should encourage bird-watching but should ensure that appropriate data are recorded and made available so that any significant changes are noted.

ESTUARY MARINE INTERACTIONS

When freshwater and seawater mix there is an enrichment of the system and primary productivity has been shown to increase (Froneman 2002a, 2004). In POEs the richest area is at the mixing interface, known as the river-estuary-interface (REI) region (Snow et al. 2000a, 2000b). In TOCEs, there is no REI because when the mouth opens the water inside the estuary flows directly into the surf-zone with little or no mixing within the estuary (Perissinotto et al. 2004). The value of mouth opening is then transferred out of the estuary into the nearshore region where increased primary productivity results from the mixing of river water, estuary water and seawater. The increase in surf-zone primary productivity is important because it adds to the total capacity of nearshore zone to support valuable fish stocks. The accumulated benefits of numerous TOCEs flowing into the Eastern Cape surf-zone are believed to be substantial in terms of the marine line-fishery in these coastal waters (Lukey et al. 2006).

GENERAL

There are certain principles that are well established for undertaking activities in high-risk areas of the coastal zone. To this end, the Council for the Environment identified two types of high-risk areas in the coastal environment that need to be taken into account:
(1) High-risk areas caused by natural processes, including naturally dynamic beach-dune areas, tidal regions of estuaries and/or river mouths, floodplains adjacent to rivers and steep slopes subject to slumping or rock falls.

(2) High-risk areas caused by human activity. Such areas frequently coincide with those mentioned under (1) above, but where vulnerability to damage is often enhanced by human activity, e.g. where the dynamic equilibrium of river mouths and estuaries is disturbed.

There is a need to protect the environment against unnecessary damage as well as developers and investors against loss. Planning of developments should therefore not be based on average conditions but on extreme events that may occur only once in 50 or 100 years. The massive damage to private property and infrastructure in KwaZulu-Natal during the floods of 1987 provides a graphic example of the role estuaries play in our lives (Fuggle and Rabie 1992).

Sound estuary management is synonymous with sound environmental management. Hence, sound estuary management should commence with an environmental impact assessment (EIA). This applies even if the estuary surroundings have already been developed. The EIA should consider the conditions prior to any development and the adverse impacts, if any, should be identified. The procedures of DEAT should be followed and public support for the initiative should be obtained. This is initiated by public scoping where interested and affected parties are identified.

When the EIA has been completed, an Environmental Management Plan (EMP) should be drawn up, again with public participation, because it is very important that the affected public be included and 'buy in' to the management plans. The best option for implementing an EMP is for the managing authority to become ISO 14001 compliant. Where municipalities are the managing authority, implementation of ISO 14001 is important because external auditing is required in order to maintain certification. Should certification not be maintained, the reasons will become apparent and the public will become aware and take the necessary action. Environmental management, and estuary management in particular, is a very public matter because so many people are involved or affected.

Estuary mouths always tend to close as a result of sediment accumulation. The reason for this is that wave action in the surf-zone causes sediment to go into suspension. Tidal inflow carries this sediment into the mouth where the calmer conditions cause it to settle out, thus blocking the mouth. Slow moving water within the estuary is not effective in suspending sediments during the ebb tide and the net result of tidal action is for estuary mouths to close up due to sediment accumulation. When rivers flood, there is more water leaving the estuary and water flow is more rapid at the mouth, causing scour and the removal of sediment from the mouth into the surf-zone. Thus it follows that the difference between POEs and TOCEs is driven primarily by the balance between tidal inflow and tidal outflow plus freshwater outflow.

An examination of the data for all South African estuaries shows that there appears to be a good relationship between MAR and whether an estuary is a POE or a TOCE, and that a model for estimating this might be a function of water area x MAR x tidal amplitude. The data for all South African POEs and TOCEs treated this way are shown in Table 13.1.

Table 13.1. The relationship between MAR, tidal amplitude and water surface area and the classification of the estuary as either a POE or a TOCE. The spring tidal amplitude is taken as 1.8 m for all estuaries.

System	Catchment (km^2)	MAR (m^3 x 10^6)	Size (water area) (ha)	Tidal volume (areax1.8)	Whitfield classification	Tidal volume x MAR
Breë	12384	1751	371	667	POE	1168404
Berg	7715	1035	522	940	POE	973429
Great-Kei	20566	1064	189	341	POE	362744
Olifants	46220	1016	164	295	POE	300154
Mzimkulu	6745	1478	74	133	POE	196692
Gamtoos	34635	503	215	388	POE	194794
Mbashe	6030	836	89	161	POE	134185
Great Fish	30366	525	140	251	POE	131951
Mkomazi	4310	1036	63	113	POE	117175
Gourits	45715	539	92	165	POE	88792
Keiskamma	2745	170	278	500	POE	85271
Mtata	2585	357	102	184	POE	65836
Keurbooms	1080	177	192	346	POE	61173
Mgeni	4432	683	48	86	TOCE	58986
Sundays	20990	202	145	261	POE	52887
Matigulu/Nyoni	995	201	122	220	POE	44176
Mtamvuna	1553	304	46	82	TOCE	24993
Kromme	1085	123	103	185	POE	22791
Mlalazi	492	117	96	173	POE	20194
Swartkops	1303	76	135	243	POE	18410
Buffalo	1279	91	98	176	POE	16011
Diep	1495	80	100	180	TOCE	14451
Duiwenhoks	1340	90	73	131	POE	11780
Goukou	1550	106	48	86	POE	9154
Qora	700	76	65	117	POE	8862
Xora	438	49	91	165	POE	8112
Palmiet	535	201	21	39	POE	7743
Mtentu	965	121	35	63	POE	7593
Mdloti	527	117	33	59	TOCE	6952
Ngqusi/Inxaxo	134	28	124	224	POE	6290
Klein Brak	550	60	50	90	TOCE	5360
Mzamba	505	73	38	68	POE	4940
Tyolomnqa	441	30	88	158	TOCE	4727
Mngazana	285	48	46	82	POE	3908
Gqunube	665	47	40	72	POE	3390
Mgwalana	200	12	154	278	TOCE	3332
Mdumbi	2338	37	46	82	POE	3010
Bira	255	13	122	220	TOCE	2865
Nahoon	584	34	47	85	POE	2865

Groot Brak	190	39	38	69	TOCE	2684
Heuningnes	1400	38	39	71	POE	2663
Mtati	130	8	180	324	TOCE	2595
Msikaba	1011	131	11	20	POE	2574
Kabeljous	276	18	77	139	TOCE	2462
Seekoei	224	14	83	150	TOCE	2150
Lovu	893	112	10	19	TOCE	2112
Kowie	800	26	43	78	POE	2027
Quko	157	34	31	56	TOCE	1893
Mhlali	304	49	21	38	TOCE	1867
Sand	83	10	97	175	TOCE	1824
Kwelera	418	38	27	48	POE	1813
Groot (Wes)	119	30	28	50	TOCE	1516
Mngazi	561	65	13	23	POE	1454
Mhlanga	118	26	30	54	TOCE	1405
Fafa	231	24	30	54	TOCE	1306
Bushmans	2675	38	15	26	POE	1000
Ntlonyane	74	18	29	53	TOCE	928
Eerste	710	195	2	4	TOCE	843
Shixini	332	41	11	20	POE	837
Kobonqaba	321	42	11	20	POE	833
Kariega	685	16	27	49	POE	811
Gwaing	185	44	10	18	TOCE	783
Goukamma	235	53	7	13	TOCE	685
Uilkraals	390	18	21	38	POE	685
Gxulu	105	12	31	56	TOCE	672
Van Stadens	271	21	17	31	TOCE	671
Mbizana	145	30	12	22	TOCE	660
Mntafufu	178	48	8	14	POE	660
Sout	34	9	42	76	POE	660
Maalgate	177	27	14	24	TOCE	647
Kwenxura	144	18	18	33	TOCE	580
Kaaimans	107	40	8	14	POE	569
Zinkwasi	73	15	20	37	TOCE	567
Qinira	90	9	34	62	TOCE	559
Lourens	140	122	2	4	TOCE	549
Mpenjati	100	26	12	21	TOCE	533
Mbokodweni	283	36	7	13	TOCE	464
Mpekweni	65	4	63	114	TOCE	457
Tsitsikamma	225	55	5	8	TOCE	445
Gqutywa	85	6	38	69	TOCE	411
Maitland	187	15	11	21	TOCE	303
Klipdrif (Oos)	169	33	5	9	TOCE	296
Buffels (Oos)	24	11	12	22	TOCE	246
Morgan	31	7	20	36	TOCE	243
Ncera	77	7	17	30	TOCE	226
Mpambanyoni	562	52	2	4	TOCE	217
Wildevoël	20	4	30	55	TOCE	215
Mtentweni	50	15	8	14	TOCE	210
Zotsha	57	14	7	13	TOCE	189
Cefane	38	5	23	41	TOCE	187

Piesang	96	12	8	15	TOCE	180
Kasuka	140	6	15	28	TOCE	167
Sinangwana	64	16	6	10	TOCE	166
Steenbras	74	46	2	3	POE	155
Bulura	47	4	19	35	TOCE	148
Goda	44	6	14	24	TOCE	147
Ku-Bhula	49	12	7	13	TOCE	147
Qolora	77	11	7	13	TOCE	147
Hartenbos	205	5	16	28	TOCE	141
Wes-Kleinemonde	94	4	19	35	TOCE	140
Ngqwara	30	7	10	18	TOCE	135
Gxara	30	5	14	26	TOCE	133
Cintsa	46	6	13	23	TOCE	129
Mahlongwa	92	12	6	11	TOCE	128
Ratel	405	7	10	18	TOCE	127
Riet	48	2	36	65	TOCE	118
Boknes	200	10	7	12	TOCE	118
Mapuzi	30	7	8	15	TOCE	111
Nenga	43	11	6	10	TOCE	110
Mdlotane	43	9	6	11	TOCE	104
Cebe	33	8	8	14	TOCE	101
Matjies	22	6	10	18	TOCE	101
Manzimtoti	39	8	7	12	TOCE	98
Sir Lowry’s Pass	49	30	1	3	TOCE	77
Krom	40	8	5	9	TOCE	71
Noetsie	39	5	8	14	TOCE	69
Jujura	45	11	3	6	TOCE	68
Oos-Kleinemonde	46	2	18	32	TOCE	64
Mhlangeni	38	10	4	6	TOCE	62
Nyara	38	5	7	13	TOCE	61
Sezela	20	3	9	16	TOCE	48
Kiwane	48	3	9	16	TOCE	48
Sandlundlu	16	6	4	7	TOCE	46
Mhlabatshane	47	8	2	4	TOCE	33
Intshambili	33	10	2	3	TOCE	30
Mtana	30	2	7	13	TOCE	29
Schuster	16	3	5	9	TOCE	28
Ngcura (Koega)	625	7	2	4	TOCE	28
Bilanhlolo	21	5	3	5	TOCE	26
Rooiels	21	10	1	3	TOCE	25
Mtendwe	15	3	4	8	TOCE	24
Damba	25	7	2	3	TOCE	22
Old Woman’s	24	1	11	19	TOCE	22
Haga-Haga	39	8	1	3	TOCE	21
Umhlangankulu	9	2	6	10	TOCE	21
Bokramspruit	11	2	5	9	TOCE	19
Tongazi	17	7	1	3	TOCE	17
Sipingo	51	6	1	3	POE	16
Mcantsi	23	2	4	7	TOCE	16
Siyai	18	5	1	3	TOCE	13
Kongweni	20	5	1	3	TOCE	13

Silwermyn	26	5	1	3	TOCE	13
Mzimayi	31	5	1	3	TOCE	12
Kandandlovu	9	4	2	3	TOCE	12
Nqinisa	11	1	9	16	TOCE	11
Rufane	32	1	5	9	TOCE	11
Mkumbane	28	4	1	3	TOCE	11
Kaba	11	2	2	4	TOCE	11
Little Manzimtoti	18	4	1	3	TOCE	10
Blinde	36	1	10	18	TOCE	10
Mhlangamkulu	11	3	1	3	TOCE	8
Onrus	59	3	1	3	TOCE	8
Hickmans	10	1	3	6	TOCE	7
Cwili	13	3	1	3	TOCE	7
Mlele	15	1	3	5	TOCE	7
Hlozi	17	2	1	3	TOCE	6
Uvuzana	8	2	1	3	TOCE	5
Mvutshini	7	2	1	3	TOCE	5
Klipdrifsfontein	27	1	5	9	TOCE	5
Ngculura	15	1	1	3	TOCE	3
Lilyvale	11	1	2	3	TOCE	3
Blind	7	1	1	3	TOCE	1
Cunge	4	0	1	3	TOCE	1
Hlaze	6	0	1	3	TOCE	1
Slang	26	5		0	TOCE	0
Mpande	19	6		0	TOCE	0
Shelbertsstroom	10	1		0	TOCE	0
Ross' Creek	8	1		0	TOCE	0
Mtentwana			10	18	TOCE	0
Nkanya			8	14	TOCE	0
Bulolo			6	11	TOCE	0
Mtumbane			5	10	TOCE	0
Ncizele			5	10	TOCE	0
Ngogwane			5	8	TOCE	0
Ntlupeni			4	7	TOCE	0
Zalu				0	TOCE	0
Ngadla				0	TOCE	0
Ku-Mpenzu				0	TOCE	0
Mgwegwe				0	TOCE	0
Mgwetyana				0	TOCE	0

The data in Table 13.1 illustrate the importance of river flow in maintaining an estuary as either a POE or in facilitating the opening of a TOCE. Most of the estuaries that have a high value in the column headed 'Tidal volume x MAR' are POEs. As the value in this column declines there is a tendency for the estuary to become a TOCE. One question that arises from these data is why some estuaries that have a high value in the last column are TOCEs rather than POEs (e.g. Mgeni), and why some estuaries that have a relatively low value are POEs and not TOCEs (e.g. Kariega). The answer lies, inter alia, in the fact that some estuaries (e.g. Mgeni) have dams that have reduced the natural MAR to a point where it is no longer effective in keeping the mouth permanently open, while others (e.g. Kariega) have protected mouths that limit the accumulation of sand in the estuary channel. Other factors that influence the response are: (a) resistance to outflow due to bends, vegetation or shallowness, (b) coastal wave action that causes high volumes of sand to be brought into suspension, (c) the amount of sand available in the adjacent off-shore region and (d) the height of the sand sill in the case of perched estuaries. Well-developed sand sills cause a reduction in the effective tidal amplitude within the estuary and therefore hamper sediment scour from the channel.

In Table 13.1, Column 5 has an apparent anomaly because a tidal amplitude of 1.8m has been applied to all cases in the calculation of the values. The value of 1.8 is likely to be inappropriate for many estuaries, e.g. those systems that have a sill at the mouth will experience a tidal amplitude of < 1.8m and this correction should be applied to each estuary where such a value is known. This obvious error leads on to indicate that other potential errors are present in the determination of whether an estuary will be a TOCE or a POE based almost exclusively on ebb tidal flow. Clearly the answer is one where ebb tidal flow, base flow and a factor of resistance to flow are the operative components in any predictive equation. These factors of resistance will almost certainly include estuary morphology, proximity of the main basin to the sea, bottom roughness, vegetation (submerged and emergent), Man-made structures and cross-sectional area of the outflow channel. These latter factors are measurable but the data for most South African estuaries is largely unknown.

Haines et al. (2006) examined six basic morphometric parameters they considered important. These were area, shape, volume, tidal prism ratio, MAR, catchment load and an entrance closure index. In the case of TOCEs that are closed from the ocean for much of the year, the waterway area is dependent on the water level. The waterway area was assessed from photographs and hence reflects only a snapshot in time. Hence, the waterway area values must be used and interpreted with caution, as realistically they could be both larger or smaller than the values calculated (and at an undefined nominal water level). These authors considered that a variation in waterway area of up to 30% could be expected in some estuaries, as a result of variable water levels. It is clear that South African estuaries should also have these morphometric data collected for important TOCEs.

The data from Table 13.1 were subjected to statistical analysis, which showed that the multiple relationship of catchment MAR and catchment size was the strongest combination and that MAR is probably the single most important variable in determining estuary area. These results are presented in Table 13.2

Table 13.2. Results of regression analyses between catchment size, mean annual run-off (MAR) and estuary size (ha).

Regression	Adjusted R^2	p
Catchment x MAR	0.335	<0.001
Catchment x Estuary area	0.027	<0.05
MAR x Estuary area	0.408	<0.001
Multiple (Catchment x MAR)	0.414	<0.001

The considerations in the latter section of this chapter provide some indication of the management actions that can be taken with regard to TOCEs, to minimise the effects of human reduction of water from rivers and to maximise the effects of remedial actions. An example is that if a manager believes that a mouth should be breached artificially, consideration should be given to the season and the roughness of the sea, the state of the tide (spring or neap), and whether some additional water from an upstream dam can be provided during and after breaching to increase the duration of opening and the scouring of sediment by the out flowing water.

REFERENCES

Begg GW 1978 The estuaries of Natal. *Natal Town and Regional Planning Report* **41** 657 pp.

Bennett BA, Hamman KCD, Branch, GM, and Thorne S 1985 Changes in the fish fauna of the Bot River estuary in relation to opening and closure of the estuary mouth. *Transactions of the Royal Society of South Africa* **45** 449-464.

Chapman V. 1960 Salt Marshes and Salt Deserts of the World. Interscience Publishers, New York. 392 pp.

Chambers PA, Meissner R, Wrona FJ, Rupp H, Guhr H, Seeger J, Culp JM and Brua RB 2006 Changes in nutrient loading in an agricultural watershed and its effects on water quality and stream biota. *Hydrobiologia* **556** 399–415.

Cowley PD, Whitfield AK and Bell KNI 2001 The surf zone ichthyoplankton adjacent to an intermittently open estuary, with evidence of recruitment during marine overwash events. *Estuarine and Coastal Shelf Science* **52** 339-348.

De Decker HP and Bally R 1985 The benthic macrofauna of the Bot River estuary, South Africa with a note on its meiofauna. *Transactions of the Royal Society of South Africa.* **45** 379-396.

Department of Water Affairs and Forestry (DWAF) 2002 Rapid determination of the Resource Directed Measures of the Mdloti Estuary (including preliminary estimates of capping flows for the Mdloti and Mhlanga estuaries. Final Draft Report submitted to the Directorate Resource Directed Measures, February 2002. Pretoria: Department of Water Affairs and Forestry.

Department of Water Affairs and Forestry (DWAF) 2003a Determination of the Preliminary Ecological Reserve on a Rapid Level for Mhlanga Estuary. Final Report submitted to Directorate Resource Directed Measures, July 2003. Pretoria: Department of Water Affairs and Forestry.

Department of Water Affairs and Forestry (DWAF) 2003b Determination of the Preliminary Ecological Reserve on a Rapid Level for the Tsitsikamma Estuary (Including a desktop assessment on other estuaries in K80 tertiary catchment). Final Report submitted to Directorate Resource Directed Measures, March 2003.

Department of Water Affairs and Forestry (DWAF) 2003c Determination of the Preliminary Ecological Reserve on a Rapid Level for the Orange River Estuary. Final Draft Report. Prepared for The Department of Water Affairs and Forestry, (Republic of South Africa) and The Department of Water Affairs (Namibia). Pretoria: Department of Water Affairs and Forestry.

Department of Water Affairs and Forestry (DWAF) 2004a Thukela Water Project Decision Support Phase. Reserve Determination Model. Volume 1 Appendices to Thukela Estuarine Flow Requirements. PBV000-00-10307. Pretoria: Directorate of National Water Resource Planning.

Department of Water Affairs and Forestry (DWAF) 2004b Preliminary Determination of the Ecological Reserve on a Rapid Level for the St Lucia Estuary. Final Draft Report. Prepared for the Department Water Affairs and Forestry and Department Environmental Affairs and Tourism. Pretoria, South Africa.

Department of Water Affairs and Forestry (DWAF) 2004c Water resource protection and assessment policy implementation process. Resource directed measures for protection of water resource: Methodology for the Determination of the Ecological Water Requirements for Estuaries. Version 2, Pretoria: Department of Water Affairs. Available online at http://www-dwaf.pwv.gov.za/idwaf/Documents/Policies/WRPP/

Froneman PW 2002a Response of the plankton to three different hydrological phases of the temporarily open/closed Kasouga Estuary, South Africa. *Estuarine, Coastal and Shelf Science* **55** 535-546.

Froneman PW 2002b Trophic cascading in an oligotrophic temperate etuary, South Africa. *Journal of Plankton Research* **24** 807-816.

Froneman PW 2004 Zooplankton community structure and biomass in a southern Africa temporarily open/closed estuary. *Estuarine, Coastal and Shelf Science* **60** 125-132.

Fuggle RF and Rabie MA 1992 Environmental Management in South Africa. Juta and Co. Cape Town. 823 pp.

Haines PE, Tomlinson RB and Thom BG 2006 Morphometric assessment of intermittently open/closed coastal lagoons in New South Wales, Australia. *Estuarine, Coastal and Shelf Science* **67** 321-332.

Hay D, Huizinga P and Mitchell S 2005 Managing Sedimentary Process in South African Estuaries: A Guide. *WRC Report* **TT 241/04**. ISBN 1-77005-272-0. Water Research Commission, Pretoria.

Huizinga P, Van Niekerk L and Withers A1997 Klein River Estuary: The effects of high water levels during mouth breaching in 1996. *CSIR Report ENV/S* **97016**. Stellenbosch: CSIR.

Huizinga P and van Niekerk L 1998 Klein River Estuary: The effects of high water levels during mouth breaching in 1997. *CSIR Report ENV/S* **98031**. Stellenbosch: CSIR

Huizinga P and Van Niekerk L 1999 Klein River Estuary: The effects of mouth breaching in 1998. *CSIR Report ENV/S* **99014**. Stellenbosch: CSIR.

Humphries P, Potter IC and Loneragan NR (1992) The fish community in the shallows of a temperate Australian estuary: Relationships with the aquatic macrophyte Ruppia megacarps and environmental variables. *Estuarine, Coastal and Shelf Science* **34** 325-346.

Lukey JR, Booth AJ and Froneman PW 2006 Fish population size and movement patterns in a small intermittently open South African estuary. *Estuarine, Coastal and Shelf Science* **67** 10-20.

Martin-Smith K M (1993) Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology* **174** 243-260.

Morant P and Quinn N 1999 Influence of man and management of South African estuaries. In Allanson, BR and Baird, D (eds.) *Estuaries of South Africa* **289-321**. Cambridge: Cambridge University Press.

Naidoo G and Naicker K 1992 Seed germination in coastal halophytes *Triglochin bulbosa* and *Triglochin striata*. *Aquatic Botany* **42** 217-229.

O’Callaghan M 1990 Salt marshes along the Cape Coast. In: Ecology and Conservation of Wetlands in South Africa. *CSIR Occasional Report* No. **28**.

O'Neill 1972 Alkali Bulrush seed germination and culture. *Journal of Wildlife Management* **36** 649-652.

Paterson, KJ, Schreider M, and Zimmerman KD 2003 Effect of catchment disturbance on seston quality and quantity in Brisbane Water, NSW. *Estuarine, Coastal and Shelf Science* **56** 355-368

Perissinotto R., Blair, A., Connell, A., Demetriades, N.T., Forbes, A.T. Harrison, T.H., Lyer, K., Joubert, M., Kibirige, I., Mundree, S., Simpson, H., Stretch, D., Thomas, C., Thwala, X., Zietsman, I. (2004). *Contribution to information required for the implementation of Resource Directed Measures for estuaries (Volume 2). Responses of the biological communities to flow variation and mouth state in two KwaZulu-Natal temporarily open/closed estuaries.* Water Research Commission Report No. 1247/2/04.

Petr T. 2000. Interactions between fish and aquatic macrophytes in inland waters. A review. *FAO Fisheries Technical Paper*. No. 396. Rome, FAO. 185p.

Piehler MF, Twomey, LJ, Hall, NS, Paerl, HW 2004 Impacts of inorganic nutrient enrichment on phytoplankton community structure and function in Pamlico Sound, NC, USA. *Estuarine, Coastal and Shelf Science* **61** 197-209.

Riddin T (Personal communication. Department of Botany, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa).

Snow GC, Adams JB and Bate GC 2000 Effect of river flow on estuarine microalgal biomass and distribution. *Estuarine, Coastal and Shelf Science* **51** 255-266.

Snow GC, Bate GC and Adams JB 2000 The effect of a single artificial freshwater release into the Kromme Estuary. 2: Microalgal response. *Water SA* **26** 301-310.

Soo Park G and HG Marshall 2000 Estuarine relationships between zooplankton community structure and trophic gradients. *Journal of Plankton Research* **22** 121-135.

Steinke TD 1972 Further observations on the distribution of mangroves in the Eastern Cape Province. *South African Journal of Botany* **38**165-178.

Strydom NA 2003 Occurrence of larval and early juvenile fishes in the surf zone adjacent to two intermittently open estuaries, South Africa. *Environmental Biology of Fishes* **66** 349-359.

Strydom NA, Whitfield A. and Wooldridge TH 2003 The role of estuarine type in characterising early stage fish assemblages in warm temperate estuaries, South Africa. *African Zoology* **38** (1) 29-43.

Taljaard S, van Niekerk L, Huizinga P and Joubert W 2003 Resource Monitoring Procedures for Estuaries. For application in the Ecological Reserve Determination and Implementation Process. *Water Research Commission Report* No. **1308/1/03**. Pretoria.

Ungar IA 1962 Influence of salinity on seed germination in succulent halophytes. *Ecology* **55**199-201.

Ungar IA 1978 Halophyte seed germination *Botanical Review* **44** 233-264.

Van Niekerk L and Taljaard S (2003) A framework for effective cooperative governance of South African estuaries. *Water Reseach Commission. CSIR Report ENV-S-C* **2003-077**

Van Niekerk L Van der Merwe JH and Huizinga P 2005 The hydrodynamics of the Bot River estuary revisited. *Water SA* **31**(1): 73-86.

Wessels N 1997 Aspects of the ecology and conservation of swamp forests in South Africa. PhD Thesis, Port Elizabeth Technicon, Port Elizabeth.

Whitfield AK 1998 Biology and ecology of fishes in southern African estuaries. Ichthyological *Monographs of the J.L.B. Smith Institute of Ichthyology* **2** 223 pp.

Whitfield AK 2000 Available Scientific Information on Individual South African Estuarine Systems. *Water Research Commission Report* No. **577/3/00**. Pretoria.

WRC, 2004. The WRC… the visible difference. Knowledge Review 2004/5. Water Research Commission. 311 pp.