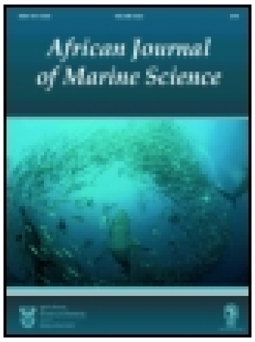

African Journal of Marine Science

ISSN: 1814-232X (Print) 1814-2338 (Online) Journal homepage: http://www.tandfonline.com/loi/tams20

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To cite this article: AK Whitfield , JB Adams , GC Bate , K Bezuidenhout , TG Bornman , PD Cowley , PW Froneman , PT Gama , NC James , B Mackenzie , T Riddin , GC Snow , NA Strydom , S Taljaard , AI Terörde , AK Theron , JK Turpie , L van Niekerk , PD Vorwerk & TH Wooldridge (2008) A multidisciplinary study of a small, temporarily open/closed South African estuary, with particular emphasis on the influence of mouth state on the ecology of the system, African Journal of Marine Science, 30:3, 453-473, DOI: 10.2989/AJMS.2008.30.3.2.636

To link to this article: http://dx.doi.org/10.2989/AJMS.2008.30.3.2.636

African Journal of Marine Science 2008, 30(3): 453–473
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AFRICAN JOURNAL OF
MARINE SCIENCE
ISSN 1814–232X EISSN 1814–2338
doi: 10.2989/AJMS.2008.30.3.2.636

A multidisciplinary study of a small, temporarily open/closed South African estuary, with particular emphasis on the influence of mouth state on the ecology of the system

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Manuscript received April 2008; accepted August 2008

In 2005/2006 a multidisciplinary research programme that included studies on the hydrodynamics, sediment dynamics, macronutrients, microalgae, macrophytes, zoobenthos, hyperbenthos, zooplankton, ichthyoplankton, fish and birds of the temporarily open/closed East Kleinemonde Estuary was conducted. Particular attention was given to the responses of the different ecosystem components to the opening and closing of the estuary mouth and how this is driven by both riverine and marine events. Using a complementary dataset of daily estuary mouth conditions spanning a 14-year period, five distinct phases of the estuary were identified, including closed (average = 90% of the days), outflow (<1%), tidal (9%) and semi-closed (<1%). The open-mouth phase is critical for the movements of a number of estuary-associated fish (e.g. *Rhabdosargus holubi*) and invertebrates (e.g. *Scylla serrata*) between the estuary and sea. The timing of this open phase has a direct influence on the ability of certain estuary-associated fish (e.g. *Lithognathus lithognathus*) and invertebrates (e.g. *Palaemon peringueyi*) to successfully recruit into the system, with a spring opening (October/November) being regarded as optimal for most species. The type of mouth-breaching event and outflow phase is also important in terms of the subsequent salinity regime once the berm barrier forms. A deep mouth breaching following a large river flood tends to result in major tidal inputs of marine water prior to mouth closure and therefore higher salinities (15–25). Conversely, a shallow mouth breaching with reduced tidal exchange during the open phase often leads to a much lower salinity regime at the time of mouth closure (5–15). The biota, especially the submerged macrophytes, respond very differently to the above two scenarios, with *Ruppia cirrhosa* benefiting from the former and *Potamogeton pectinatus* from the latter. River flooding and the associated outflow of large volumes of water through the estuary can result in major declines in zooplankton, zoobenthos, hyperbenthos and fish populations during this phase. However, this resetting of the estuary is necessary because certain marine invertebrate and fish species are dependent on the opening of the estuary mouth in order to facilitate recruitment of larvae and post-larvae into the system from the sea. Slight increases in the numbers of certain piscivorous and resident wading bird species were recorded when the estuary mouth opened, possibly linked to increased feeding opportunities during that phase.

Keywords: East Kleinemonde Estuary, estuarine biota, mouth state, physical conditions, river flow, salinity regime

Introduction

The majority of South African estuaries are isolated from the sea by means of a sand berm for most of the year (Whitfield 1992). Mouth closure normally occurs during periods of low river inflow coupled with high wave conditions in the marine environment that transport sediment along and onto the coast. There are approximately 250 ecologically functional estuaries in South Africa and about 70% are classified as temporarily open/closed estuaries (TOCEs) (Whitfield and Bate 2007). The mouth status of these mostly small systems is primarily regulated by river flow regime, marine sediment supply in the adjacent coastal zone, tidal prism and the local wave climate (Reddering 1988, Cooper 2001).

During 2005/2006 an intensive multidisciplinary research programme was conducted on the East Kleinemonde Estuary as part of a Water Research Commission study on the freshwater requirements of warm-temperate TOCEs (van Niekerk *et al.* 2008a). This review summarises some of the major findings of a number of abiotic and biotic studies that emanated from the programme, which include the following disciplines: hydrodynamics (van Niekerk *et al.* 2008b); sediment dynamics (Theron and Bosman 2008); macronutrients (Taljaard *et al.* 2008, van Niekerk *et al.* 2008b); microalgae (Gama 2008); macrophytes (Riddin and Adams 2008); zoobenthos (Wooldridge and Bezuidenhout 2008); hyperbenthos (Froneman 2008); zooplankton (Froneman 2008); ichthyoplankton and fish (Cowley *et al.* 2008); and birds (Terörde and Turpie 2008). Further details of these studies can be obtained from the appendices in van Niekerk *et al.* (2008a). Additional datasets from reports and publications on the East Kleinemonde Estuary were available for some of the disciplines and were therefore also used in this review. A primary objective of this paper is to synthesise the above information and integrate the findings such that a more holistic understanding of the ecological functioning of the East Kleinemonde Estuary can be achieved.

Study Area

The East Kleinemonde Estuary (33°32′ S; 27°03′ E) is a small system (Figure 1), with a surface area ranging widely from approximately 11.6 ha, immediately after a mouth-breaching event, to 35.7 ha when the water level is high during the closed phase. When the estuary mouth is open, the spring high tide covers an area of approximately 26.6 ha. Similarly, the volume in the estuary varies widely between 16 000 m^3 and 664 000 m^3, depending on the water level and height of the sandbar at the mouth (van Niekerk *et al.* 2008b).

The estuary is approximately 3.7 km in length and 120 m wide in the mouth region. The widest section of 210 m occurs in the lower reaches during the closed phase when low lying salt marsh areas are inundated. Overall, the system is shallow with a water depth varying between approximately 1 m and 2 m in the deeper channel sections. During periods of extended mouth closure the water level can rise to about 2.5 m mean sea level (msl) due to increased berm height at the mouth when extensive back flooding occurs. However, immediately after a mouth-opening event the estuary is very shallow with a maximum depth of approximately 1 m in the main channel.

The catchment of the East Kleinemonde Estuary is estimated to be 43.5 km^2 (Badenhorst 1988), some of which is used for pineapple and cattle farming. The simulated natural mean annual run-off is 2.86×10^6 m^3 (Hughes 2008). The shoreline in the lower reaches has been impacted by residential development.

Summary of Discipline Findings

Estuary hydrodynamics

Between 1993 and 2006, the East Kleinemonde Estuary was predominately closed (90% of the days), but marine overwash events occurred on 16% of those days. Overall, the mouth was open for very limited periods (average of 9% of the days between 1993 and 2006). In 2006, when frequent river flooding occurred, the estuary was open for 33% of the days, which is significantly above the average for open-mouth conditions.

During the period February 2005–October 2006, the water level in the estuary varied between 2.3 m and 0.18 m msl. An analysis of the water level data (note: the water level recorder was only installed in 2004) and continuous mouth observations over the past 14 years shows that the East Kleinemonde Estuary has a tendency to close in the absence of sustained river inflow. Open-mouth events seldom last longer than a few days after river flooding has subsided and in the majority of observed breaching events the system started closing within a few tidal cycles, i.e. the connection to the marine environment is seldom firmly established and is normally only maintained for a few days at a time. This behavioural pattern gives a clear indication that the river baseflow and tidal exchange are insufficient to maintain open-mouth conditions.

A small estuary such as the East Kleinemonde can be very sensitive to the height of the water level behind the berm prior to breaching. Based on a water surface area of c. 35 ha, the estuary would require between 300 000 m^3 and 600 000 m^3 of water to initiate a breach. This translates to an average monthly inflow of about 0.1–0.2 m^3 s^{-1} excluding evaporation and seepage losses. When the water level is high, there is a greater head of water available to scour sediment from the mouth area during a breaching event, thereby increasing the channel dimensions. This in turn can result in an increase in tidal exchange and in maintaining an open mouth, usually for a period of 1–6 days, the duration of which is dependent upon river inflow and sediment deposition within the mouth region. However, sometimes what initially appears to be a sustained open-mouth event for up to 28 days, often consists of a series of rapid breaching and semi-closed events when seawater enters the estuary during the flood tide but is often prevented from flowing out during the ebb tide due to the increased level of the sandbar at the mouth. Breaching of the East Kleinemonde mouth can also occur at a low water level such that very little sediment is scoured from the mouth area, while a shallow stream of estuarine water overtops the berm and flows towards the sea.

The water level before breaching events varied between 0.69 m and 2.31 m msl for the period March 2005–October 2006. High breaching levels usually occur when the mouth has remained closed for an extended period (months), thus allowing the sand berm at the mouth to build up to a level >2.3 m msl. This value of 2.3 m is surprisingly low by comparison with the average of 3.0–3.5 m msl for TOCEs elsewhere along South Africa's coastline (Perissinotto *et al.* 2004) and may be related to regular overwash that removes the berm crest and prevents berm build-up or to localised deflation due

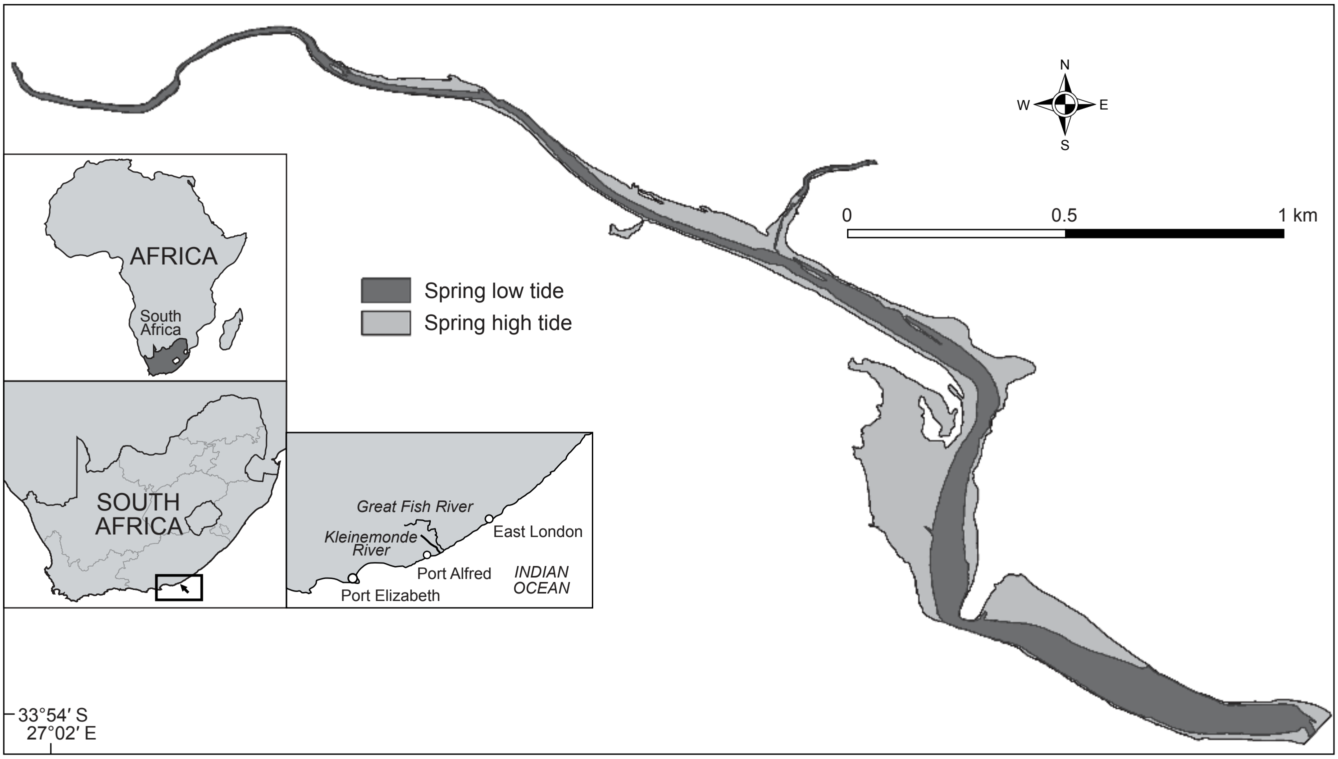


Figure 1: Map of the East Kleinemonde Estuary (arrow indicates its position on the coast) showing the surface water area during spring low and high tides. Water level in the estuary during the closed phase often corresponds to the spring high tide contour (1.3–1.5 m above mean sea level) (after Theron and Bornman 2008)

to wind erosion in the north-eastern corner of the berm. The lower breaching levels are usually related to a brief mouth closure of only a few days before the estuary breaches again as a result of river inflow or marine overwash.

During 2005/2006, mouth closure occurred at water levels varying between 0.54 m and 1.01 m msl. The average water level during that period was estimated to be 0.76 m, indicating that the East Kleinemonde Estuary is only slightly perched when closed. With the exception of the level reached on 18 May 2005 (1.01 m), closure occurred in a narrow 0.3 m band ranging between 0.54 m and 0.88 m. This indicates some consistency in the water level when the mouth closes. The lowest water level reached during the recorded period was 0 m msl in October 2006, after the mouth was scoured deeply following the preceding flood.

The surveys and transects along the crest of the berm barrier provide some data on the mouth channel dimensions, i.e. the width and depth of the outflow channel during open-mouth conditions. Brief descriptions of the mouth channel configuration in conjunction with fixed-point photography provided further information. Estimates based on about 69 *in situ* visual observations from April to November 2006 give an average channel width of only 8 m, with a maximum of about 20 m. The comparative narrowness of the mouth channel is related to the relatively small breaching volume of the estuary, the small catchment, the lack of substantial wave shelter and the abundant supply of marine sediment adjacent to the mouth.

Coastal sediment dynamics

Based on the nature of the surf zone, breaker type and beach slope, conditions at the East Kleinemonde Estuary mouth are usually dissipative to intermediate. However, a reflective beach profile was recorded during April 2006. Mean wave height at the outer breaker zone of the estuary typically ranges between 1 m and 3 m (mostly 1.5–2.5 m), but during rare conditions this can probably range between 0.5 m and 5.5 m. The wave breaker type in the East Kleinemonde surf zone is usually spilling (rolling down gradually from the top), but sometimes becomes plunging, especially during offshore or obliquely offshore wind conditions. A shore-parallel bar and trough system is often observed, but weak rip currents are only occasionally seen in or adjacent to the mouth area.

The aeolian headland-bypass system at Black Rock Point (about 1.5 km south-west of the East Kleinemonde Estuary), together with surf- and swash-zone sediment transport, provides an ample supply of sand to the mouth area from the south-west. The wide sand beach and dunes to the north-east also supply large amounts of sand to the mouth area.

Wave direction near the outer breakpoint off the mouth is mostly close to shore-normal. However, waves breaking with small angles towards the north-west (i.e. up-coast longshore current generated) occur more frequently than waves breaking towards the south-east (i.e. down-coast longshore current). The actual net longshore sediment transport, which is usually up-coast, is also dependent on the amount of sediment available to be transported and is probably much less than the potential transport rate.

The total net rate of possible sedimentation, and even the instantaneous sediment transport rate into the estuary, is orders of magnitude less than the estimated longshore or cross-shore transport rates, which move coastal sediments into the estuary mouth. Even when the longshore transport rate is sometimes zero (0° wave incidence angle), large amounts of marine sediment are usually stirred up by wave action. An ample supply of marine sediment is usually present at the estuary mouth for potential wave and tidal transport into the estuary, thus enabling mouth closure.

The type of wave breaking, the extent of nearshore 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 the estuary mouth. The wave and surf-zone characteristics described above confirm that medium to relatively high wave energy conditions occur relatively close to the estuary mouth, largely during high tide, when the then narrower surf zone includes the steeper part of the beach profile and the water depth increases over the outer sandbar, allowing more wave energy to pass. Sediment loads are entrained by the turbulent wave action and carried into the estuary 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 ebb-tidal and river outflow, a net sediment build-up occurs. If this situation continues for long enough, the mouth closes. Besides river and tidal flow, wave conditions, together with marine sediment availability, play a major role in estuary mouth dynamics and state. Indeed, actual closure of the East Kleinemonde Estuary is often directly correlated with sea storms (high wave events).

The main wind directions are approximately parallel to the coastline, with significantly more wind from the west-south-west sector than from the east-north-east quadrant. The large dune fields in the vicinity of the estuary confirm extensive aeolian activity. From historical aerial photographs and *in situ* observations, it seems that the mouth area is always filled in from the east-south-east due to aeolian and perhaps also wave-driven sediment transport.

Besides being related to wave conditions, sediment characteristics and sometimes also aeolian transport, berm formation and berm barrier dimensions obviously have a direct impact on mouth closure and breaching, overwash into estuaries and seepage (both to and from the sea). Historical aerial photographs show that the berm barrier width is typically in the region of 200 m. Estimates based on the 2006 observations (frequent mouth openings) give an average width of only 70 m, with a maximum width of about 120 m.

Berm height potentially ranges from as low as 0.5 m msl up to a maximum of about 5 m msl, excluding dunes superimposed on top of the berm. From East Kleinemonde Estuary water level recordings it can be derived that during March 2005–November 2006 berm crest elevations ranged from 0.95 m to 2.3 m msl. The observed estimates of berm crest height above water level in the estuary give an average of 0.35 m to a maximum of 1.06 m. The surveyed beach transects and transect along the crest of the berm indicate that on a number of occasions, berm crest elevations typically ranged between about 2–3.5 m msl when the mouth was closed for prolonged periods.

The position of the water line in both the East and West Kleinemonde estuaries, as well as the spring high and low tide line, was mapped on 28 January, 12 April, 10 July, 12 August and 9 September 2006. The mouth of the East Kleinemonde Estuary was closed in April but open in August and September, during which time it migrated towards the west by more than 100 m. There was also a difference in beach width between the April reflective condition (narrower beach) and September dissipative condition (wider beach). The grain size of the reflective beach in April was significantly coarser than the fine sand typical of the dissipative beach recorded at other times during the year.

Estuarine water quality characteristics

Regular salinity measurements were conducted in the East Kleinemonde Estuary during 2006. Salinity data indicated a homogeneous water body, whereas stratification was mostly observed in the upper reaches where freshwater enters the system, but also during the open-mouth phase. The average salinity for the measuring period was 23.3, with a range of 14.5–31.8. During the closed-mouth state the estuary's salinity fluctuated between 15 and 23. Shortly after a breaching event and the dissipation of floodwaters the salinity in the system increased to more than 30 (Figure 2). Because of the small size of the estuary, salinity was very responsive to the tidal cycle during the open state with an average estuary increase of 4 noted on the flood tide.

Marine overwash also contributes to the salinity balance in the East Kleinemonde Estuary. Salinity increases between 0.3 and 3.8 were measured after overwash events. Smaller increases of <1.0 were associated with small overwash events, i.e. those lasting <3 h, whereas larger increases of >2 were measured after significant overwash events lasting >3 h.

Salinity values measured in the East Kleinemonde Estuary during the closed state (18 March 2006) and open state (8–9 September 2006) are presented in Figure 3. On 18 March, when the mouth had been closed for an extended period, the estuary was polyhaline (23–25) showing only a slight horizontal gradient (Figure 3a). However, some rain in the catchment just prior to sampling resulted in a very thin layer (<0.5 m) of mesohaline water in the upper reaches, overlying the more saline bottom water.

Salinity values measured on 8 and 9 September 2006, when the mouth had been open to the sea for some time (Figure 3b), were distinctly different to those observed during the closed state. Not only were there strong horizontal and vertical salinity gradients present when the mouth was open, but there was also a marked difference in salinity profile between low and high tide. The degree to which the salinity profile would differ between high and low tide is, however, dependent on the extent of tidal intrusion, which is determined by the depth of the mouth and volume of river inflow (Snow and Taljaard 2007).

The above salinity observations fit the conceptual model proposed for TOCEs (Snow and Taljaard 2007), where

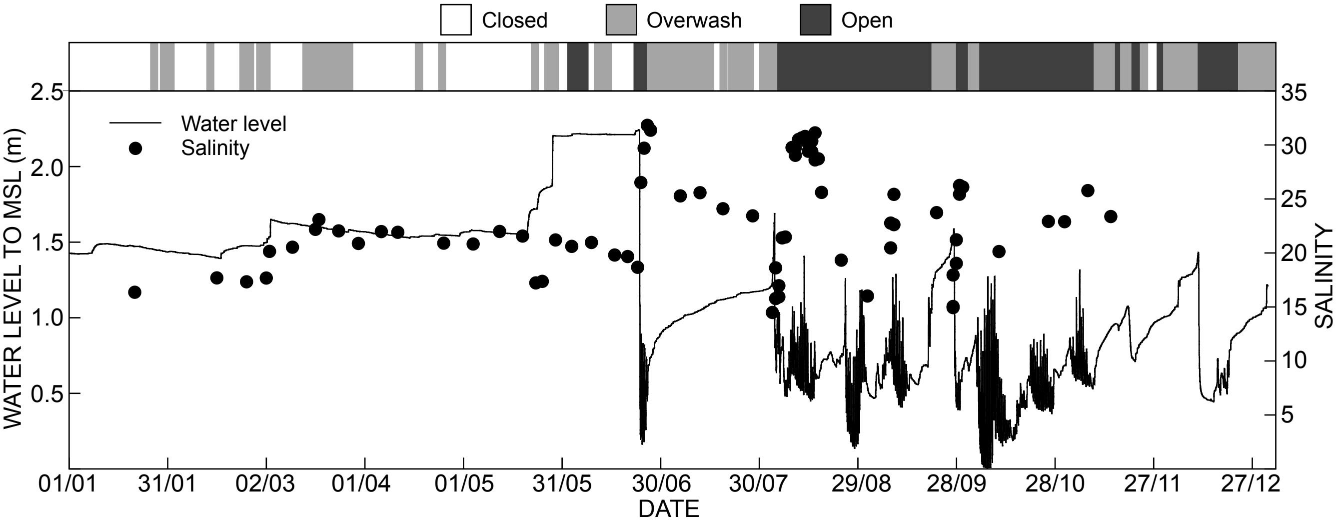


Figure 2: Relationship between salinity and water level in the East Kleinemonde Estuary during 2006 (water level is indicated by the continuous line and salinity by points) (after van Niekerk *et al.* 2008b)

in the closed state these estuaries generally display a homogeneous saline water column, but develop strong longitudinal and sometimes vertical salinity gradients during the open state. The East Kleinemonde Estuary appears to be similar to other Southern and Western Cape estuaries that lie in moderate rainfall areas with medium to high evaporation. These become well-mixed estuarine systems during the closed state and sometimes become more saline if the closed state is prolonged. This is in contrast to the more perched KwaZulu-Natal TOCEs, where the higher wave action causes mouth closure even under increased river inflow associated with the generally higher rainfall of the region. These latter estuarine systems become increasingly fresh during the closed state (Perissinotto *et al.* 2004).

Although there is no seasonality in salinity regime, water temperatures reveal a distinct seasonal pattern. Measurements show that summer temperatures are generally higher (20°–27 °C) than winter temperatures (13°–20 °C). These results also agree with the conceptual model, which proposes that water temperature variations in TOCEs are usually a function of seasonal trends in atmospheric temperature (Snow and Taljaard 2007) and are not linked to sea temperatures as is the case with permanently open estuaries (Read 1983).

East Kleinemonde Estuary water pH did not show any marked variation at different salinity values, along the estuary or between surveys, and ranged between 7.7 and 8.3. These results also agree with the TOCE conceptual model where pH within these systems is expected to range between 7 and 8.5 (Snow and Taljaard 2007).

When the mouth was closed there was a difference in the dissolved oxygen (DO) concentration between surface (<1 m) and bottom (>1 m) water. Results indicated that during the open state when salinity was low as a result of freshwater inflow, the estuary was well oxygenated, with DO levels never declining below 4 mg l^{-1}. During the closed state there was greater variation in DO concentration. Bottom water was well oxygenated with DO concentrations only declining below 2 mg l^{-1} on a few occasions when the mouth had been closed for some time. These measurements fit the TOCE conceptual model and support the hypothesis that DO levels in bottom water, at times, can become hypoxic during the closed phase. Hypoxic to anoxic conditions have been observed in shallow TOCEs such as the Maitland Estuary in the Eastern Cape (Gama *et al.* 2005) and a possible explanation could be that these low-oxygen events are caused by prolonged periods of calm weather when there is no wind-mixing, which generally prevents such conditions from developing in shallow estuaries (Snow and Taljaard 2007).

Turbidity distribution patterns measured in the East Kleinemonde Estuary, in relation to salinity, suggest that there is no clear distinction between turbidity for open or closed states, except that turbidity levels >100 NTU tend to occur during the open state when the river is flooding. The stronger riverine influence and water turbulence during the open state tends to result in a higher turbidity whereas the clear marine water entering the estuary on flood tides tends to have a lower turbidity. In contrast to other physicochemical parameters, these results indicate that there may not always be a marked difference between average turbidity characteristics during open and closed states as hypothesised, although on occasions turbidity levels increased markedly during the river flooding phase.

Inorganic nutrient characteristics (nitrogen, phosphorous and silica) in the East Kleinemonde Estuary largely fit within the TOCE conceptual model. During the river outflow and tidal phase, nutrient concentrations in these smaller systems are mainly influenced by the concentrations in the inflowing river and seawater, whereas the distribution of nutrients within the estuary is a function of mixing between the different water sources. Results from the East Kleinemonde also indicated that after prolonged mouth closure, water column inorganic nutrients (nitrogen and phosphorous) become depleted. This finding is also in agreement with the TOCE model that during prolonged periods of mouth closure, water column nutrients become

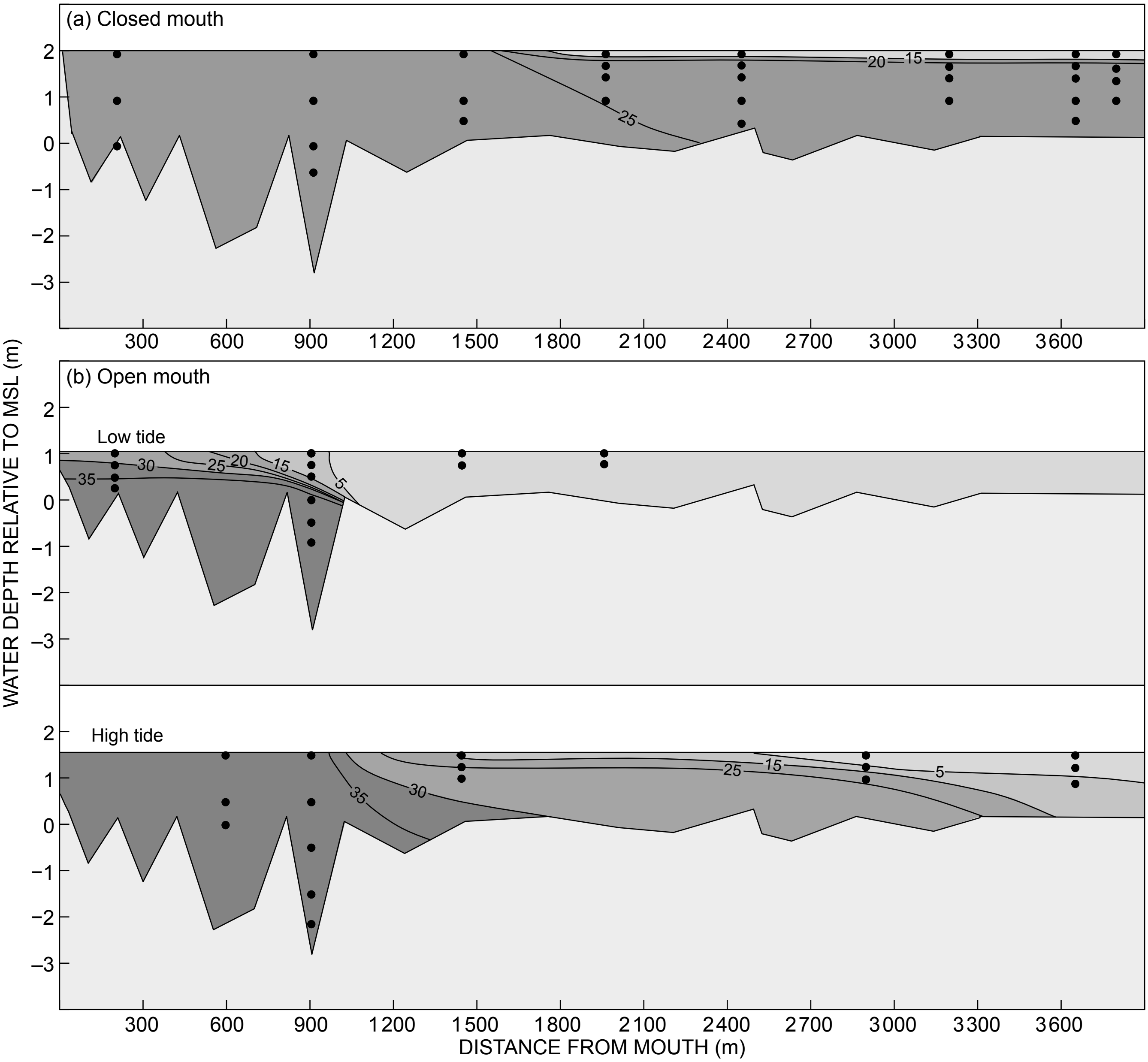


Figure 3: Salinity profile measured in (a) the closed East Kleinemonde Estuary on 18 March 2006 and (b) the open East Kleinemonde Estuary on 8 September 2006 (low tide) and 9 September 2006 (high tide) (after Taljaard *et al.* 2008)

depleted, probably because there is no significant *in situ* regeneration of inorganic nutrients into the water column (Snow and Taljaard 2007).

The duration and extent of connection between estuaries and the sea greatly influences inorganic nutrient concentrations within the estuary. The inflow of marine water over a closed estuary sandbar might increase certain nutrient levels within the system through re-suspension of sediments if they contain a large nutrient pool (Perissinotto *et al.* 2000). An increase in nutrient concentrations during a barrier overwash phase was reported in the temporarily closed Kasouga Estuary in the Eastern Cape (Froneman 2004). However, the contribution of marine overwash nutrients into the nearby East Kleinemonde Estuary during the closed phase is unknown (Vorwerk 2007).

Outflow of nutrient-rich riverine and estuarine waters following a TOCE opening event will tend to promote phytoplankton growth in the nearshore marine environment, particularly as several studies have demonstrated that the marine waters along the south-eastern coastline of southern Africa are nutrient poor (van Ballegooyen *et al.* 2007). Although the ‘outwelling’ of riverine and estuarine water is significant when these systems are breached, Vorwerk (2006) showed that nutrient seepage through the East Kleinemonde Estuary berm also appears to promote the development of phytoplankton in the marine zone, as evidenced by elevated chlorophyll *a* levels adjacent to the closed estuary mouth (Vorwerk 2007).

Phytoplankton

As with most Eastern Cape TOCEs, water column microalgal chlorophyll *a* concentrations in the East Kleinemonde are typically low (mostly <15 µg l^{-1}). Monthly phytoplankton chlorophyll *a* concentrations exhibited high spatial and temporal variability. There were no significant differences between chlorophyll *a* concentrations in surface and bottom waters. There were also no consistent trends in chlorophyll *a* biomass along the length of the estuary.

The water column phytoplankton chlorophyll *a* response after the mouth breached on the 23 June 2006 was variable, with mean weekly concentrations increasing following the decline recorded during the outflow phase (Figure 4). In terms of size structure, the pico- (1.2–2.7 µm), nano- (2.7–20 µm) and microphytoplankton (>20 µm) size classes were equally represented throughout the water column one week after the mouth opened. This suggests that all size classes were equally susceptible to the strong river outflow following mouth breaching. Studies on the Kasouga Estuary (Froneman 2002a) have also demonstrated that phytoplankton stocks decline during the TOCE outflow phase.

As river flow declined over the four weeks after the 23 June breach, coupled with an increase in the mixing of seawater and freshwater, there was a gradual community recovery with the nano- and picophytoplankton showing the greatest response by contributing 67% and 27% respectively to total chlorophyll *a*. The highest phytoplankton chlorophyll *a* biomass levels during the study period were recorded five weeks following the opening of the mouth (Figure 4). This increase may also be indicative of the time required by phytoplankton to re-establish after a mouth-breaching event by rapidly exploiting the newly available mineral nutrients. From these data, it seems that a minimum of 5–6 weeks is necessary to establish maximum phytoplankton biomass after a significant breach of the mouth. This observation is in line with what has been reported regarding the post-mouth-breaching period required to produce maximum phytoplankton chlorophyll *a* biomass in TOCEs on the Eastern Cape coast.

Although there was vertical salinity stratification in the water column during the open-mouth phase, phytoplankton chlorophyll *a* biomass did not appear to be affected and showed no vertical stratification, although there were higher concentrations of chlorophyll *a* at the surface in the middle reaches of the estuary. The phytoplankton community composition during March 2006 was composed mainly (62%) of diatoms, with cryptophytes and dinoflagellates constituting the second and third highest contributions with 15% and 13% respectively. By September 2006, the community composition had shifted and dinoflagellates and cryptophytes were more abundant.

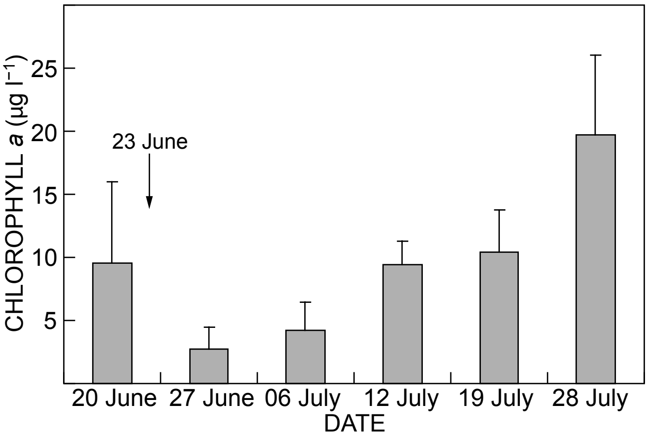


Figure 4: Mean weekly phytoplankton chlorophyll *a* concentrations sampled over six weeks (20 June–28 July 2006). Arrow shows the date when the mouth opened. Vertical bars denote +SE (after Gama 2008)

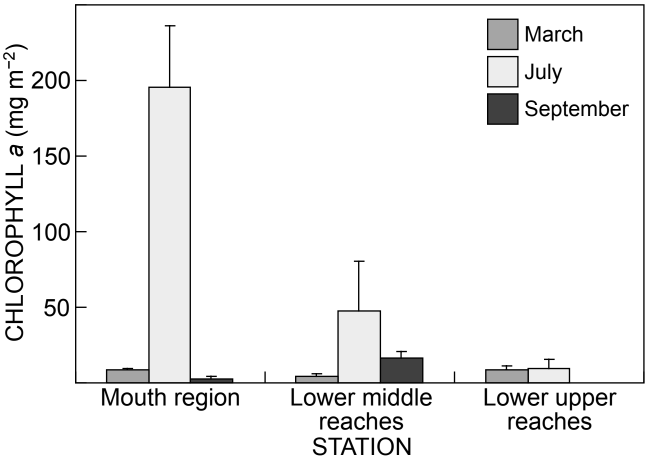


Figure 5: Mean microphytobenthic chlorophyll *a* concentrations recorded in March, July and September 2006 from three sites along the East Kleinemonde Estuary. Mouth conditions at the time of sampling were March = closed, July and September = open (vertical bars denote +1SE) (after Gama 2008)

Microphytobenthos

One week after mouth breaching on 23 June 2006, microphytobenthic chlorophyll *a* concentrations had increased considerably over the concentrations measured in March 2006 under closed-mouth conditions, especially in the mouth area. There were significant differences between March and July 2006 microphytobenthos chlorophyll *a* concentrations in the lower (mouth region) and higher reaches of the estuary ($p < 0.001$). There was also a more distinct spatial distribution pattern during July 2006 compared to the March and September surveys (Figure 5) when chlorophyll *a* concentrations were more evenly distributed. Following the June mouth-opening event, the estuary experienced intermittent opening and closing of the mouth. This series of breaching events resulted in a depleted microphytobenthic community, as documented in the September 2006 survey when microphytobenthos chlorophyll *a* biomass had declined to levels observed prior to the initial mouth breaching (Figure 5).

Under closed-mouth conditions, groundwater seepage areas were generally associated with dense communities of microphytobenthos that are important in the biogeochemical cycling of minerals. Samples collected in March 2006, when the mouth was closed, indicated a benthic microalgal community composed mainly of bacillariophytes, chlorophytes and mats of cyanobacteria with a proportional representation of 75%, 15% and 10% respectively.

Macrophytes

The macrophyte community structure and composition in the East Kleinemonde Estuary (Figure 6) is influenced by freshwater inflow, tidal exchange, salinity, water level fluctuations and sediment dynamics. The response of aquatic macrophytes within temporarily open/closed estuaries is event-driven, especially river flooding and the opening and closing of the estuary mouth. Biomass loss can either be partial or complete as a result of physical removal by floods, or a die-back in response to desiccation due to a prolonged low water level following mouth breaching. The ability to colonise available space and re-establish after a disturbance is essential for the long-term persistence of communities and this recovery depends on the availability of propagules and the seed bank. There is a low species richness of macrophytes in TOCEs, which means that species lost due to changing physico-chemical conditions often results in reduced habitat diversity.

Submerged macrophytes were extensive during the 1990s and early 2000s (14.5 ha), primarily as a result of stable water level conditions following prolonged mouth closure (maximum of two years closure in the late 1990s). The dominant submerged macrophyte was usually *Ruppia cirrhosa*, but as salinity decreased with continual freshwater inflow, *Potamogeton pectinatus* expanded into the upper and middle reaches of the estuary and gradually replaced *R. cirrhosa*. When the mouth opened in August 2001, large beds of *P. pectinatus* were present within the system whereas *R. cirrhosa* was very limited in its distribution. Partial drainage of the estuary and limited tidal exchange meant that salinity remained relatively low, conditions that were favourable to the continued proliferation of *P. pectinatus* when the mouth closed. In May 2003, a major flood resulted in significant scouring of sediments from the estuary mouth region and caused exceptionally low water levels for the duration of the open phase. Desiccation of the marginal *P. pectinatus* beds during the open phase and the prevalence of salinity >15 following mouth closure prevented

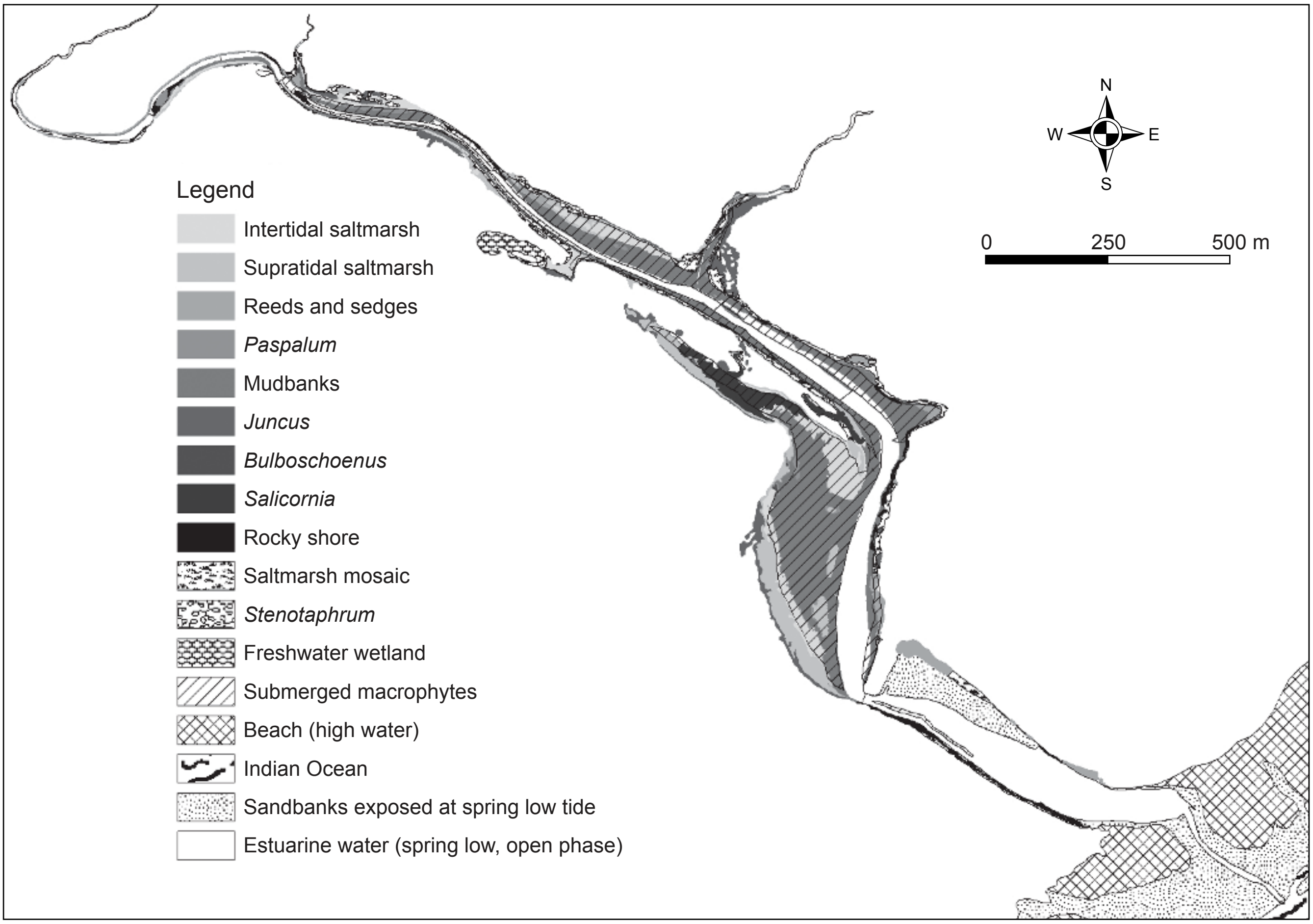


Figure 6: Vegetation map of the East Kleinemonde Estuary under 2006 open-mouth conditions (after Riddin and Adams 2008). There were no submerged macrophytes during 2006 but the areas of previous colonisation are shown

recovery of *P. pectinatus* in the subsequent closed phase. Re-establishment of *R. cirrhosa* beds within the estuary during the closed phase may have been hampered by depleted seed banks following the May 2003 flood and/or fluctuating water levels between 2004 and 2006, which may have prevented germination requirements from being met. These plants grow and expand in cover when the mouth is closed and water levels are >1.5 m msl for more than two months. Because of the increase in open-mouth conditions in 2006 (33% of the year), which also resulted in widely fluctuating water levels, submerged macrophyte cover was 4.5% of optimal (Figure 6, Table 1).

When the mouth opened, the exposed habits were rapidly colonised by the salt marsh succulent *Sarcocornia perennis*, which germinated from a large seed bank (mean = 7 929 seeds m^{-2}). Seedlings emerged three days after the mouth breached and germinated intermittently thereafter. These plants are, however, sensitive to prolonged inundation (>3 months) following mouth closure and following death the habitat is once again colonised by submerged macrophytes. Under higher, stable water levels *R. cirrhosa* can complete its life cycle within 8–12 weeks (Adams and Bate 1994, Gesti *et al.* 2005). Rapid breaching and semi-closed events and associated water level changes in 2006 in the East Kleinemonde Estuary prevented the recovery of submerged macrophytes and expansion of salt marsh beds. Although macrophytes in temporarily open/closed estuaries are resilient and have large seed banks to colonise available habitat when conditions are favourable, frequent mouth opening and closing can result in exposed bare mudbanks (Table 1).

Changes in the distribution and abundance of emergent macrophytes has also been recorded in recent decades, primarily as a result of altered sedimentary processes and freshwater run-off associated with road and urban developments in the lower reaches of the estuary. Construction of the R72 bridge over the East Kleinemonde Estuary in the early 1960s resulted in localised sedimentation downstream of the bridge on the east bank where *Phragmites australis* growth has been encouraged. Similarly, since the 1990s *P. australis* beds have expanded along the eastern shore of the lower reaches, most likely on account of increased fertiliser and freshwater run-off from the urban lawns adjacent to the littoral zone.

Zoobenthos

Temporarily open/closed estuaries such as the East Kleinemonde tend to support fewer zoobenthic species compared with permanently open estuaries that experience a strong marine influence. In all, 30 macrobenthic invertebrate species were recorded from the East Kleinemonde, similar to the number of species (21–29) recorded by Teske and Wooldridge (2001) in other Eastern Cape TOCEs. Permanently open estuaries with a strong marine influence tend to have between 42 and 61 species, whereas those permanently open system with a strong freshwater influence have fewer taxa (23–32 species). Although fewer species are usually present in TOCEs, the density of benthic invertebrates is usually higher compared with permanently open systems (Teske and Wooldridge 2001).

Temporal and spatial variation in the horizontal salinity gradient, mouth state and sediment type all influence estuarine benthic community composition and structure. Salinity variation and sediment characteristics are considered to be the most important abiotic regulatory factors (e.g. de Villiers *et al.* 1999), although their relative influence is variable over time and space. In Eastern Cape estuaries, salinity is more important as a regulatory factor at the extremes of the horizontal salinity gradient. The degree of marine dominance affects species assemblages in the lower estuary, whereas at the head, freshwater inflow

Table 1: Area cover for each of the habitat types in the East Kleinemonde Estuary during 2006 (after Riddin and Adams 2008)

Estuarine vegetation type	Cover (ha)	Comments
Intertidal saltmarsh	2.45	*Sarcocornia perennis* dominant
Supratidal saltmarsh	2.77	*Sporobolus virginicus* and *Sarcocornia pillansii* dominant, *Limonium scabrum* also present
Saltmarsh mosaic	1.78	Mixture of *Juncus* spp., *Sarcocornia* spp., *Triglochin striata, Samolus porosus, Sporobolus virginicus*, *Bassia diffusa* and other sedges
Sarcocornia	1.02	*Sarcocornia* sp. dominant. May become bare during exposed periods or submerged during closed-mouth phases
Paspalum	0.57	Wetland grass growing in the water, prefer closed and stable water levels
Juncus	1.81	*Juncus kraussii* dominant but also *Juncus acutus*
Reeds and sedges	1.01	*Phragmites australis* dominant
Exposed mudbanks	9.83	Mudbanks exposed during spring low tide (open phase). These mudbanks had very limited vegetation growth during 2006, but may be colonised by *Sarcocornia* spp. during the open phase and submerged macrophytes during extended closed periods
Estuarine water area	12.69	Measured during spring low tide (open phase). Includes side channels and streams influenced by tidal exchange
Sandbank seaward of the bridge	1.78	Only large sandbank occurs seaward of the bridge. Mapped during spring low tide (open phase)
Total	35.71	
Potential submerged macrophytes	14.5	*Ruppia cirrhosa* and *Potamogeton pectinatus* were virtually absent in 2006 due to events described in the text

influences assemblages in this low salinity zone (Teske and Wooldridge 2003). Both these community types were absent from the East Kleinemonde Estuary during the present study, probably due to the mesohaline or polyhaline conditions prevailing during both the open- and closed-mouth state.

True estuarine or euryhaline species characterised the benthic invertebrate assemblage at all East Kleinemonde stations. Within this assemblage, similarity analysis showed a significant difference between the mouth region and all other sites for all sampling trips. The composition and structure of the community in the mouth region also remained relatively stable, with no significant statistical evidence for any substructures during the visits in 2006. These results reflect zoobenthic community resilience, despite major changes in the state of the mouth and salinity shifts over the sampling period.

Biotic variability increased at subtidal sites above the mouth station, particularly during the open phase. In March and July 2006, the zoobenthic community above the road bridge was relatively homogeneous with no significant differences between them (Figure 7). After the mouth had remained open for about one month, the community developed very different substructures in September 2006 at the two upper sites (Figure 7). This was in response to the environmental changes brought about by persistent riverine input and the draining of the estuary after mouth opening. The estuary mouth remained mostly open for another month and data suggest that a distinct upper estuarine community had developed relative to that in the middle and lower reaches. This was due to a persistent inflow of freshwater that also helped maintain the open-mouth condition over the two months.

During the tidal phase, much of the intertidal and supratidal areas that are inundated during the closed phase are unavailable for colonisation by the full range of zoobenthic invertebrates. At higher taxonomic levels, amphipods, tanaeids, isopods and polychaetes were the most abundant groups in the benthic community (Figure 7). Amphipods generally were dominant at all sites, making up a larger proportion of the benthic community after mouth opening. This was not as a consequence of an increase in amphipod abundance, because total abundance was approximately 45 000 individuals m^{-2} (closed, March 2006), 13 500 individuals m^{-2} (recently closed, July 2006) and 24 500 individuals m^{-2} (open, September 2006), but rather as a result of proportionally lower numbers of other invertebrate groups. When all groups are combined, the highest total abundance occurred in March 2006 (c. 144 000 individuals m^{-2}), which coincided with the closed phase.

Euryhaline conditions and a weak horizontal salinity gradient persisted during the study period and no marine-associated assemblage developed, even towards the end of the open-mouth phase. Instead, the community was composed of mostly endemic estuarine species that have low species richness, high resilience to environmental fluctuations and are structured mainly by sediment characteristics (Teske and Wooldridge 2001, 2003). A sand-associated invertebrate fauna characterised the assemblage in the mouth region of the East Kleinemonde Estuary, whereas further upstream, a fauna typical of muddy substrata persisted.

Low species richness within in the estuary is also influenced by specific life-history requirements. The mudprawn *Upogebia africana*, for example, is probably excluded from the benthic community since it requires a prolonged open phase (>3 months) in order to complete its life cycle (Wooldridge 1999). Other examples of taxa that are rare or absent from the East Kleinemonde Estuary due to the lack of a permanently open mouth include numerous crab species (Hill 1975, Pereyra Lago 1993, Papadopoulos *et al.* 2002). In contrast to the scarcity of the above taxa, the sand prawn *Callianassa kraussi* does not require a marine larval phase and the density and biomass of this species in the East Kleinemonde Estuary has been estimated at 37–44 individuals m^{-2} and 8–10 t wet mass for the entire estuary (AIT, unpublished data).

Although the macrobenthic fauna in the East Kleinemonde Estuary demonstrated spatial and temporal shifts in community structure over the study period, an underlying basic pattern persisted throughout 2006. This would suggest that different estuarine types support stable zoobenthic assemblages relatively unique to each type, a concept

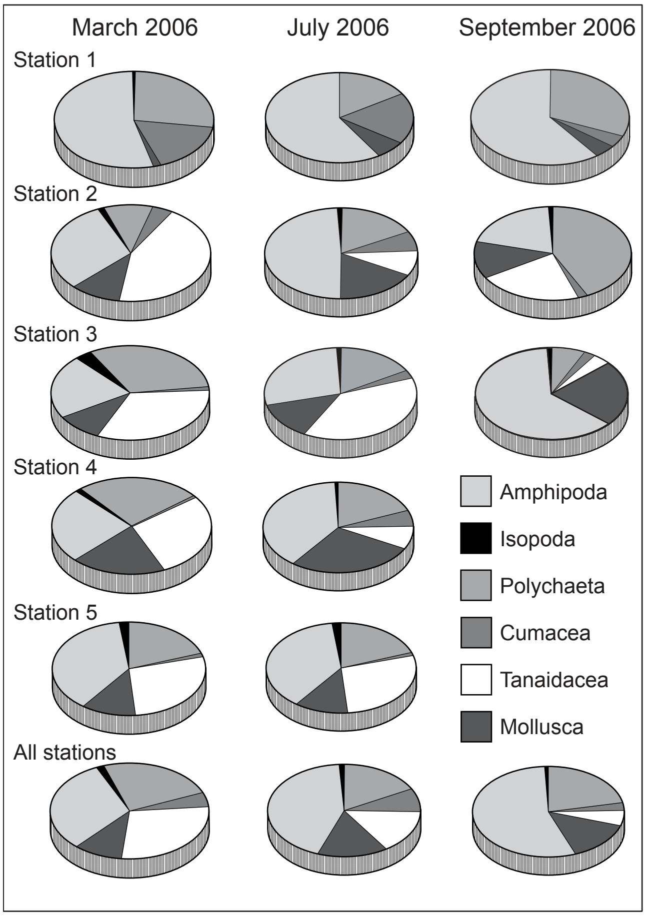


Figure 7: Proportion of the six most important zoobenthic invertebrate groups in the East Kleinemonde Estuary (after Wooldridge and Bezuidenhout 2008). Station 1 is situated in the mouth region, Stations 2 and 3 in the lower reaches, Station 4 in the middle reaches and Station 5 in the upper reaches of the estuary. The mouth was closed in March 2006, recently closed after a brief opening (3–4 days) a month before in July 2006 and open in September 2006 when only three sites were sampled

already described by Teske and Wooldridge (2001).

Hyperbenthos

The caridean shrimp *Palaemon peringueyi* has been identified as the dominant component of the hyperbenthos in both permanently open and temporarily open/closed southern African estuaries (Emmerson 1986, de Villiers *et al.* 1999, Bernard and Froneman 2005). Recent studies in Eastern Cape TOCEs indicate that recruitment of juvenile *P. peringueyi* into these estuaries occurs mainly during breaching events and that the overwash of marine water into closed estuaries fulfils only a minor role in the recruitment process.

The demographics of *P. peringueyi* in the East Kleinemonde Estuary exhibited a distinct spatial and temporal pattern. From a spatial perspective, the highest abundance and biomass of this species occurred in the lower or middle reaches, with the lowest values consistently recorded in the upper reaches. In terms of temporal distribution, the population was dominated by adults in the first seven months of the survey, comprising 72–87% of all shrimps counted. The breaching event in August 2006 was associated with a loss of mainly adults to the sea. During October and November 2006 recruitment of *P. peringueyi* occurred (Figure 8) and juveniles accounted for between 68% and 73% of all specimens collected during this period.

The breaching of the mouth in late August 2006 was associated with a large decrease in the total abundance and biomass of the *P. peringueyi* within the estuary (Figure 8). The observed trend may be linked to the outflow of estuarine water, together with adult *P. peringueyi*, into the marine environment (Froneman 2004). The decline in water level during the open phase would also have been associated with a loss of habitat, mainly submerged littoral vegetation, a favoured habitat of *P. peringueyi* (Emmerson 1986).

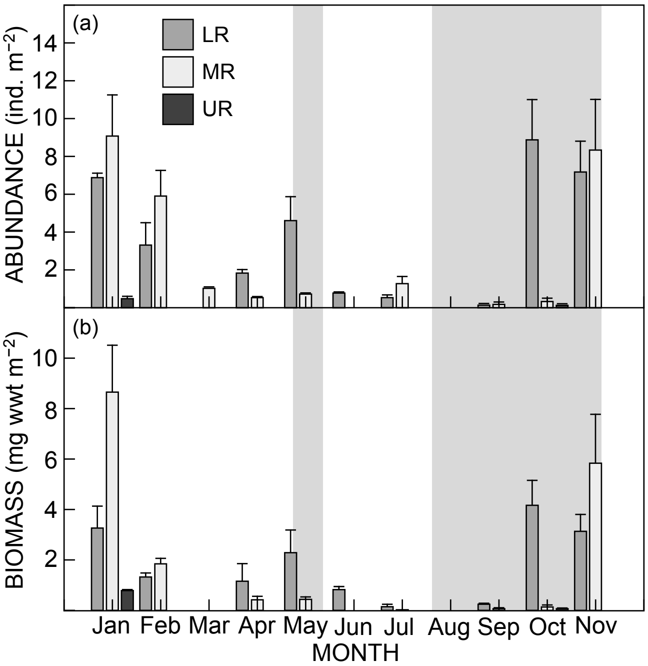


Figure 8: Spatial and temporal pattern in the total abundance and biomass (wet weight) of the hyperbenthic caridean shrimp *Palaemon peringueyi* in the temporarily open/closed East Kleinemonde Estuary during 2006 (after Froneman 2008). The shaded background indicates when the estuary was open (LR = lower reaches, MR = middle reaches, UR = upper reaches)

Recent studies conducted within TOCEs in the Eastern Cape have demonstrated that breaching events coincide with the recruitment of juvenile *P. peringueyi* into these systems (Bernard and Froneman 2005, Froneman 2006). The breaching event in August 2006 was, however, not associated with a major recruitment of *P. peringueyi* into the estuary. A peak in the recruitment of *P. peringueyi* into permanently open estuaries occurs mainly during summer (Emmerson 1986). The open-mouth phase in August would therefore have coincided with a period when the shrimp is reproductively less active. It is noteworthy that the numerical dominance of juveniles observed in October and November 2006 suggests that recruitment of juvenile *P. peringueyi* into the estuary had occurred in spring.

The estimates of total abundance and biomass of *P. peringueyi* during this study (0–9 individuals m^{-2} and 0–5.84 mg wet mass m^{-2}) are substantially lower than those recorded in permanently open estuaries within the same biogeographic region. For example, in the Swartkops and Kromme estuaries (Eastern Cape), *P. peringueyi* attained abundance levels of 200–400 individuals m^{-2} with a biomass equivalent to between 3 g and 6 g dry mass m^{-2} (de Villiers *et al.* 1999). It is worth noting, however, that the estimates of the shrimp abundance and biomass within the East Kleinemonde Estuary are within the range reported for other TOCEs in the region (Bernard and Froneman 2005, Froneman 2006).

Zooplankton

A number of studies have described TOCE zooplankton community structure in the warm-temperate region of South Africa (e.g. Froneman 2002a, 2002b, Perissinotto *et al.* 2000). Among the zooplankton, copepods of the genera *Pseudodiaptomus* and *Acartia* dominate the community numerically and by biomass (Perissinotto *et al.* 2000, Froneman 2002a, 2004).

The mean total zooplankton abundance and biomass in the East Kleinemonde Estuary during the day ranged from 958 individuals m^{-3} to 4 678 individuals m^{-3} and from 9 mg dry mass m^{-3} to 16 mg dry mass m^{-3} respectively. During the night, total zooplankton abundances in the surface layers varied from 3 018 individuals m^{-3} to 18 116 individuals m^{-3} whereas the biomass ranged from 19 mg dry mass m^{-3} to 41 mg dry mass m^{-3}. The estimates of total zooplankton abundance and biomass are within the range reported for other warm-temperate TOCEs (Froneman 2002a, 2004).

The major breaching event in August 2006 was associated with a decline in the total zooplankton abundance and biomass within the estuary, as well as a change in species composition (Table 2). These observations are consistent with the published literature and can be related to the export of the biomass-rich estuarine waters into the marine environment and the movement of marine species into the

Table 2: The average abundances of the five most numerically dominant zooplankton species in the East Kleinemonde Estuary during 2006, divided into two groups according to hierarchical cluster analysis (after Froneman 2008)

Group 1 (before major mouth breaching)		Group 2 (after major mouth breaching)	
Species	Average abundance (ind. m^{-3})	Species	Average abundance (ind. m^{-3})
Pseudodiaptomus hessei	4 316	*P. hessei*	1 116
Acartia longipatella	314	*A. longipatella*	113
Nauplii	397	*Oithona plumifera*	87
Oithona nana	172	*Palaemon peringueyi*	12
Halicyclops sp.	68	*Calanus agulhensis*	8

open estuary (Froneman 2004).

Results of the numerical analyses also indicate that mouth phase plays a critical role in determining the zooplankton species composition within the East Kleinemonde Estuary. In the absence of any direct link to the marine environment, the zooplankton community was overwhelmingly dominated by typical estuarine copepod species of the genera *Pseudodiaptomus*, *Acartia* and *Halicyclops*, which collectively contributed >86% of all the zooplankton counted (Table 2).

The establishment of a link to the marine environment following breaching of the estuary in August 2006 coincided with a decline in the estuarine copepod species and an increased contribution of marine breeding zooplankton taxa to the system (Table 2). However, the absence of any distinct change in the zooplankton community structure following the breaching event in June 2006 suggests that the influence of these events on the zooplankton community structure is variable. The absence of any major response to the June 2006 breaching is probably related to both the magnitude of the breaching event and the availability of recruits within the surf-zone adjacent to the estuary (Froneman 2002a, Kemp and Froneman 2004). A minor flushing event following mouth breaching is likely to retain a higher proportion of estuarine zooplankton within the system than a major flushing event.

Vorwerk (2006) showed that nutrient seepage through the East Kleinemonde Estuary berm appears to promote the development of phytoplankton in the marine zone, as evidenced by elevated chlorophyll *a* levels adjacent to the closed estuary mouth (Vorwerk 2007). The increase in marine zooplankton biomass and density adjacent to the East Kleinemonde mouth may have been linked to the above increased phytoplankton availability (Vorwerk 2007).

Fish

The larval, juvenile and adult fish associated with the East Kleinemonde Estuary have been well studied over the past decade. Research includes descriptions of the fish community (Cowley and Whitfield 2001a, Strydom *et al.* 2003, Vorwerk *et al.* 2003), quantification of fish population sizes (Cowley and Whitfield 2001b), fish biomass and production estimates (Cowley and Whitfield 2002), composition of larvae in the marine environment adjacent to the estuary mouth (Cowley *et al.* 2001), and estuary recruitment strategies by marine-spawning species (Bell *et al.* 2001).

A comparison of larval fish community structure and abundance in the East Kleinemonde Estuary between 1998/1999 and 2005/2006 was undertaken. No mouth-opening events were recorded during the earlier sampling period. However, an estuary opening was documented in the summer of 2005. Mean larval fish density in the water column (1 621 individuals 100 m^{-3}) for the 1998/1999 dataset was significantly higher ($p < 0.05$) than the mean density (570 individuals 100 m^{-3}) for the 2005/2006 study. However, closer examination of the densities of estuary-resident and estuary-associated marine species showed that contrasting mouth conditions affected these groups differently. Density of estuary-resident species was significantly higher ($p < 0.001$) during the closed phase and the density of estuary-associated marine species peaked during the sampling year characterised by an opening event, although this latter increase in mean density was not statistically significant.

Catches of postflexion larvae and early juveniles of estuary-associated marine species were high along the margins of the estuary during the open-mouth phase sampled in 2005. High abundance of young fish was directly attributed to the open-mouth phase coinciding with peak fish breeding and recruitment to estuaries along the warm-temperate coast. This highlights the importance of timing in estuary opening events for larval and early juvenile fish utilising estuaries as nurseries. During spring, the region receives the second of the typical bimodal rainfall peaks which facilitates estuary opening events along the coast.

Numerous researchers (e.g. Bell *et al.* 2001, Vorwerk *et al.* 2003) have suggested that the timing, duration and frequency of the open-mouth phase plays an important role in determining juvenile and adult fish species composition, diversity and seasonality within TOCEs. The East Kleinemonde study provided an opportunity to test the hypothesis that long-term changes in TOCE fish communities reflect the period that these estuaries were isolated from the sea, because the current study was able to combine a long-term dataset of seine-net fish catches with a matching long-term dataset of estuary mouth state.

The timing of mouth opening has a significant effect on marine species composition in the East Kleinemonde Estuary, with multi-dimensional scaling (MDS) grouping years into two distinct clusters. More fish species were recorded during years that followed spring (September–November) mouth-opening events than in years following no mouth-opening events in spring. Mean annual catch per unit effort for species that recruit predominantly in spring were higher in years where the mouth did open in spring. Species that are known to recruit during both overwash and open-mouth conditions were consistently recorded each year, irrespective of a spring opening (James *et al.* 2007a, 2008).

Two different periods of stability were identified in the East Kleinemonde Estuary, viz. 1995–2000 and 2001–2005. During the latter period, a higher value for Kendall's coefficient of stability (*W*) was recorded and there was also an increase in interannual community stability and seriation from the 'other' years to the 'spring' years. These results suggest that optimum mouth opening for marine fish recruitment is during spring (September–November) in TOCEs from the Eastern Cape Province and that the predominance of spring opening events between 2001 and 2005 probably allowed for the regular recruitment of a wide variety of marine species into the estuary (James *et al.* 2008).

Individual fish species populations in the East Kleinemonde Estuary were dynamic, as the abundance of all species varied markedly between years. For example, maximum abundance for the marine migrant *Rhabdosargus holubi* (264 fish haul^{-1} in 2003) and estuarine resident *Gilchristella aestuaria* (1 662 fish haul^{-1} in 2005) was several times greater than in the years of least abundance (21 fish haul^{-1} for *R. holubi* in 2001 and 97 fish haul^{-1} for *G. aestuaria* in 1996). This was because the recruitment strengths of juvenile cohorts varied between years, and the years when recruitment was greatest varied between the different species (James *et al.* 2007a).

Similarly, Cowley and Whitfield (2001b) found that overall populations of marine migrant species associated with the East Kleinemonde Estuary are characterised by a high degree of interannual variability. For example, the total population size of all marine fish in the estuary increased by almost eightfold from a mark-recapture experiment conducted between October 1994 and December 1994 (~18 000 individuals) to a mark-recapture experiment conducted between October 1995 and February 1996 (~133 000 individuals). The large interannual variability was attributed to both abiotic (estuary mouth state) and biotic conditions such as spawning success and larval survival in the marine environment (James *et al.* 2008).

In the East Kleinemonde Estuary, the timing of mouth-opening events (abiotic factors) and life-history characteristics of the fish (biotic factors) together influenced species composition and abundance (Figures 9 and 10). Species with extended breeding seasons that recruit during overwash and open-mouth conditions, or breed within the estuary, dominated catches numerically. In contrast, species with restricted spawning seasons, most of which only recruit into estuaries during open-mouth conditions, were usually found in lower numbers within the system (James *et al.* 2007a, 2008).

Cowley and Whitfield (2001a) also found that mouth state is important for the reproductive success of estuarine-spawning species within the East Kleinemonde. Reproductive activity is halted during low water level conditions following a mouth-opening event. On the other hand, closed-mouth conditions result in more stable physical conditions, elevated water levels and habitat inundation, and increased food availability which in turn results in greater breeding success. Submerged macrophyte beds, which expand during extended closed-mouth phases, are an important habitat for the estuarine pipefish *Syngnathus watermeyeri*, a species that disappeared from the estuary when submerged macrophytes were absent between 2004 and 2007.

Analysis of the long-term seine-net (5 mm mesh size) dataset suggests that interannual changes in the abundance of certain estuarine-spawning species were related to rainfall and thus river pulses. The filter-feeding *G. aestuaria* is the most abundant species in the East Kleinemonde Estuary and forms an important link in the food chain of South African estuaries because it is preyed upon by various predatory fish. However, major flooding of TOCEs usually results in a temporary decrease in the abundance of this species due to the flushing of eggs and larvae out to sea (James *et al.* 2007b) and the loss of zooplanktonic food resources to the same event.

Timing and duration of mouth-opening events can also influence the breeding and recruitment success of the freshwater cichlid *Oreochromis mossambicus*. In 2004, the East Kleinemonde mouth opened in late December, thus allowing successful breeding, whereas in 2005 the mouth opened during November before the breeding cycle could be completed. Recruitment success was consequently very poor in 2005/2006 (Ellender *et al*. 2008).

Birds

The mean number of birds recorded per count at the East Kleinemonde Estuary during 2005/2006 was 63, and there was no significant difference between summer and winter mean abundances. Although there was a significant difference between the mean number of birds recorded during open- and closed-mouth phases, these differences were not significant for all groups of birds (Table 3). In addition, the proportion between the different groups of birds remained similar between the open- and closed-mouth phases (Figure 11).

Three species, grey heron *Ardea cinerea*, pied kingfisher *Ceryle rudis* and reed cormorant *Phalacrocorax africanus*, were encountered during more than 75% of all counts, and were classified as regulars. Eight species were encountered frequently, nine species occasionally and a further 27 species rarely. The three most frequent species were also the most abundant, with *P. africanus* having the highest mean number of individuals per count. Of the 20 most abundant species only three can be regarded as full-time residents. Other breeding species, such as great egret *Egretta alba* and *A. cinerea*, which are present year round, often fly elsewhere to feed, mostly to the adjacent larger West Kleinemonde Estuary. *P. africanus*, African spoonbill *Platalea alba*, little egret *Egretta garzetta*, among others, use the estuary mainly for feeding and roosting, but breed elsewhere.

Piscivorous birds dominated the avifauna of the East Kleinemonde Estuary, making up 70% of all recorded individuals. Invertebrate feeding waders formed the second most numerous component (24%). Waterfowl were particularly scarce in the estuary, making up only 6% of all recorded individuals. In summer, the piscivorous component was dominated by wading piscivores. The percentage of pursuit-swimming piscivores (cormorants, grebes, darters) increased considerably from summer (17.3%) to winter

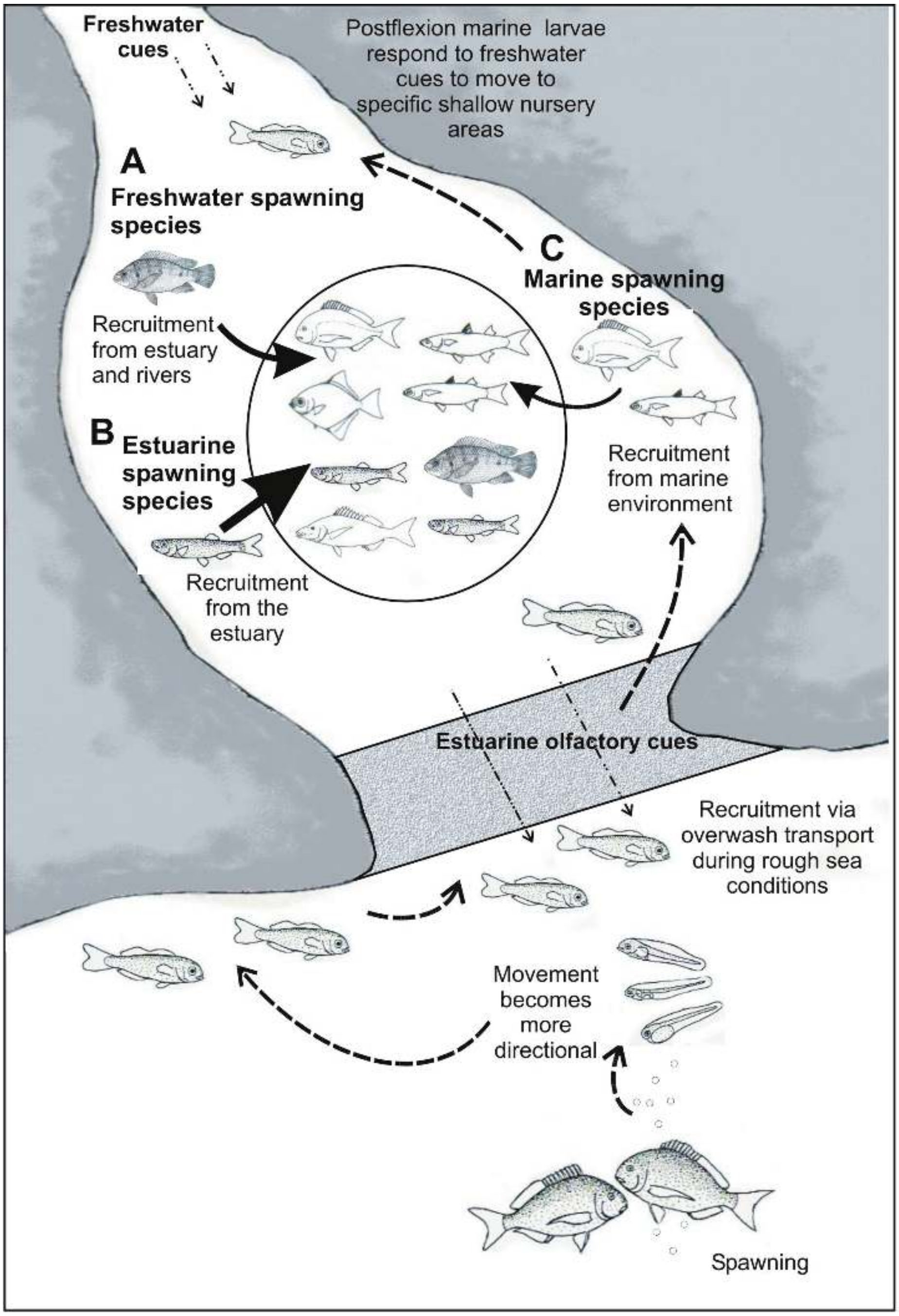


Figure 9: Major contributors to fish community structure in the East Kleinemonde Estuary during a prolonged closed phase. The movement of estuary-associated marine fish larvae from marine spawning grounds into the estuary is also shown (after Cowley *et al.* 2008)

CLOSED-MOUTH CONDITIONS

Community structure determined by the recruitment of (A) freshwater, (B) estuarine and (C) marine spawning species

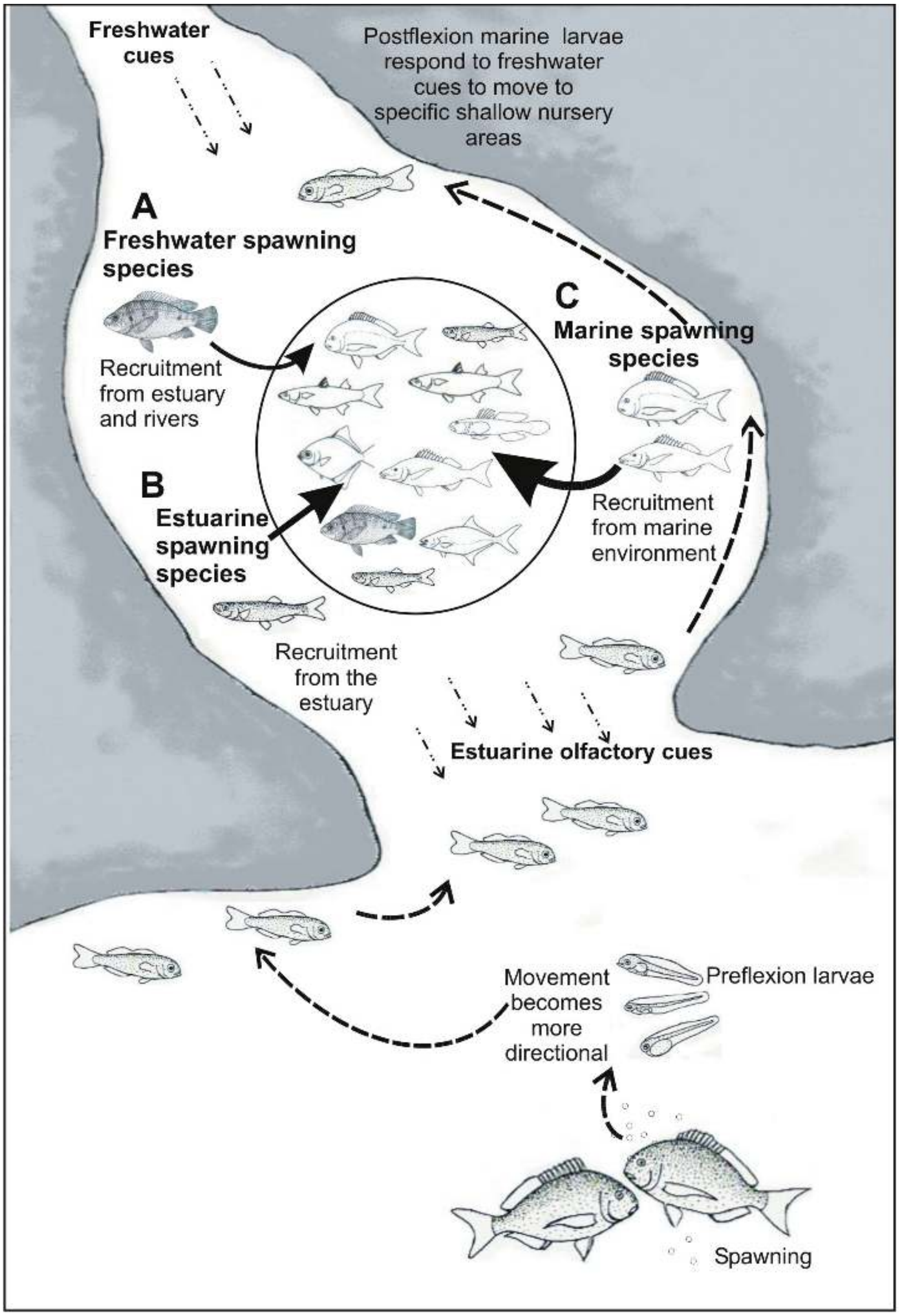
(A) Closed conditions result in the inundation of marginal vegetation, stable water levels and an absence of water currents, thus providing favourable conditions for breeding of *Oreochromis mossambicus* and enhanced recruitment.

(B) Recruitment of estuarine spawning species is greater during the closed phase as eggs and larvae are retained in the estuary, conditions are physically more stable, and marginal vegetation is inundated. River flow leading to the mouth opening may also enhance populations through nutrient input.

(C) The recruitment of marine spawning species is lower when the mouth is closed (particularly during spring). Species such as *Rhabdosargus holubi* and various mullet are able to recruit via overwash transport but other species such as *Lithognathus lithognathus* and *Pomadasys commersonnii* are unable to recruit, resulting in lower marine species richness and a less stable marine fish community.

(27.5%), mostly due to cormorants that arrive in winter to utilise the estuary for foraging.

The estuary mouth was open to the sea mainly in the winter months of the study period, with only six out of 21 bird counts conducted in summer taking place during the open phase. Therefore, a comparison between open and closed conditions is largely a within-winter issue. There was a significant increase in the mean number of aerial diving piscivores, wading piscivores and resident waders from closed- to open-mouth conditions (Table 3). In the case of small TOCEs such as the East Kleinemonde, it appears that water level is a major factor determining avifaunal abundance, because it affects habitat availability (e.g. shallow areas for wading) and food availability directly or indirectly (e.g. by affecting the availability of submerged macrophyte beds suitable for certain fish species). However, there was no noteworthy change in overall longitudinal distribution of birds between open- and closed-mouth phases.



OPEN-MOUTH CONDITIONS

Community structure determined by the recruitment of (A) freshwater, (B) estuarine and (C) marine spawning species

(A) Spawning and nest building by *Oreochromis mossambicus* is disrupted when the mouth opens during peak breeding season, resulting in a decrease in recruitment.

(B) During periods of high river flow, eggs and larvae of estuarine spawning species may be swept out to sea, resulting in a decrease in recruitment.

(C) The recruitment of marine spawning species is enhanced when the mouth is open (particularly during spring), thus leading to higher species richness of marine spawning species and a more stable marine fish community.

Figure 10: Major contributors to fish community structure in the East Kleinemonde Estuary during/following an open-mouth phase. The movement of estuary-associated marine fish larvae from marine spawning grounds into the estuary is also shown (after Cowley *et al.* 2008)

Synthesis of Estuary Phases

The ecological functioning of the East Kleinemonde Estuary is driven primarily by physico-chemical parameters that can vary considerably over both spatial and temporal scales. Estuary mouth phase, a critical driver for all the biotic components within the system, has been documented daily for more than a decade and there are five recognisable hydrodynamic states within the system, one of which (marine overwash) occurs as an event during the closed phase (Figure 12).

The phases described below represent a synthesis of information gleaned from the individual discipline studies described above and represent current understanding of the overall functioning of the East Kleinemonde Estuary. They differ from the TOCE model proposed by Snow and Taljaard (2007), which identified only three phases, namely open, semi-open and closed. Although these phases are broadly valid for the East Kleinemonde Estuary, the open phase is further divided into an outflow phase, which is distinct from the tidal phase (see below).

Table 3: Mean, standard deviation (SD) and range in numbers of individuals of different groups of birds recorded per count during the study period under open- and closed-estuary mouth conditions

Group	Closed (n = 51)			Open (n = 21)			Significance
	Mean	SD	Range	Mean	SD	Range	(p)
Aerial-diving piscivores	10.1	4.6	1–19	12.9	5.3	4–25	< 0.05
Pursuit-swimming piscivores	12.9	13.4	0–66	16.1	17.9	2–75	ns
Wading piscivores	16.0	14.4	1–60	23.1	10.4	6–48	< 0.01
Resident waders	8.3	9.1	0–50	13.6	6.7	2–27	< 0.01
Migratory waders	4.8	10.0	0–50	4.5	8.6	0–40	ns
Herbivores	3.5	5.3	0–24	3.1	2.5	0–9	ns

ns = Not significant

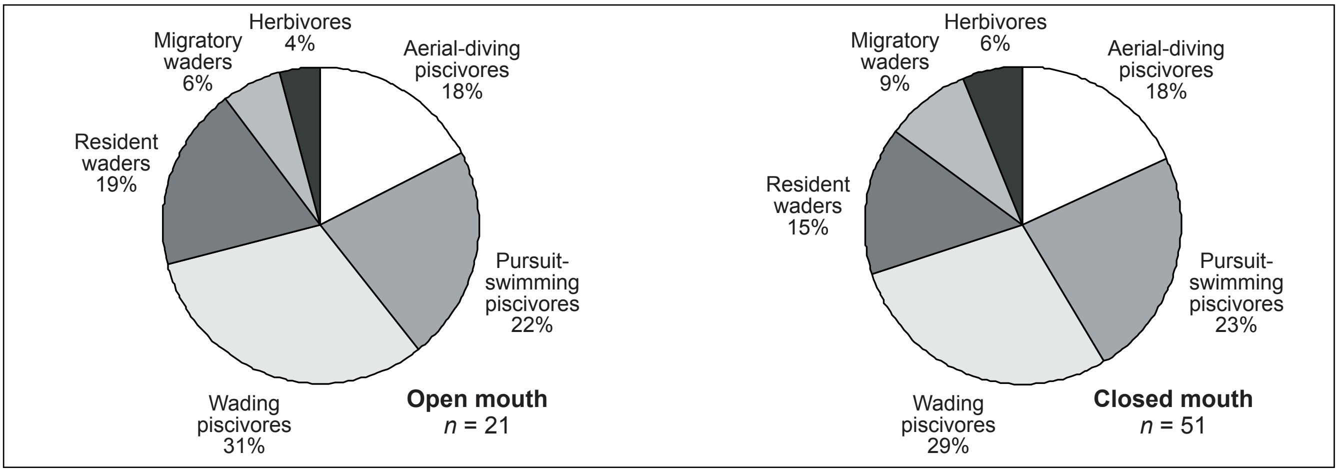


Figure 11: Community composition of the avifauna at the East Kleinemonde Estuary during open and closed estuary mouth conditions (after Terörde and Turpie 2008)

Closed phase

This occurs when a well-developed sandbar is formed at the mouth and this state is dominant for much of the year (average = 90% of the time over 14 years). During this phase, river flow is usually minimal (average monthly inflow volume $<0.3 \times 10^6$ m^3) and often ceases altogether (van Niekerk *et al.* 2008a). Seepage of estuarine water through the sandbar at the mouth occurs when the water level in the estuary exceeds that in the sea (Figure 12a). This seepage rate increases as the estuary becomes more 'perched' and, together with evaporation, tends to prevent the estuary from overtopping the bar under river base flow conditions (<0.01 m^3 s^{-1}).

Average salinity within the estuary tends to range between 15 and 30, depending on the prevailing salinity regime at the time of mouth closure. Generally, there is little or no major vertical or longitudinal salinity difference within the estuary, and salinity tends to decline as the berm barrier builds up and the volume of estuarine water increases due to freshwater inflow. Seepage of estuarine water through the sandbar into the sea also results in the loss of salts from the system, but compensation for this loss is provided by marine overwash events.

Inorganic nutrient levels within the estuary indicate that after prolonged closure, water column nitrogen and phosphorous largely become depleted, probably because there is no significant *in situ* regeneration of inorganic nutrients into the water column (Snow and Taljaard 2007). Water turbidity tends to remain low during the closed phase, provided there is no significant riverine input during that period.

The absence of strong water currents and clear conditions during the closed phase favour the development of extensive littoral aquatic macrophyte beds, especially *R. cirrhosa*. This aquatic plant extends from the upper to the lower reaches and is gradually replaced by another aquatic macrophyte, *P. pectinatus*, if salinity within the estuary falls below 15 for an extended period (>6 months). Phytoplankton stocks, as indicated by chlorophyll *a* levels, during the closed phase range between 5 µg l^{-1} and 20 µg l^{-1}, depending on water column nutrient availability (Gama 2008). Some of these estuarine nutrients seep through the berm where they support elevated phytoplankton stocks in the sea adjacent to the estuary (Vorwerk 2006).

Zooplankton stocks reach peak abundance and biomass during the closed phase and the community is dominated by the calanoid copepod *P. hessei*, which had an average density during this phase of >4 000 individuals m^{-3} (Froneman 2008). Elevated chlorophyll *a* levels in the nearshore marine zone, probably driven by estuarine water seepage through the berm, support higher zooplankton stocks in the sea adjacent to the estuary (Vorwerk 2006).

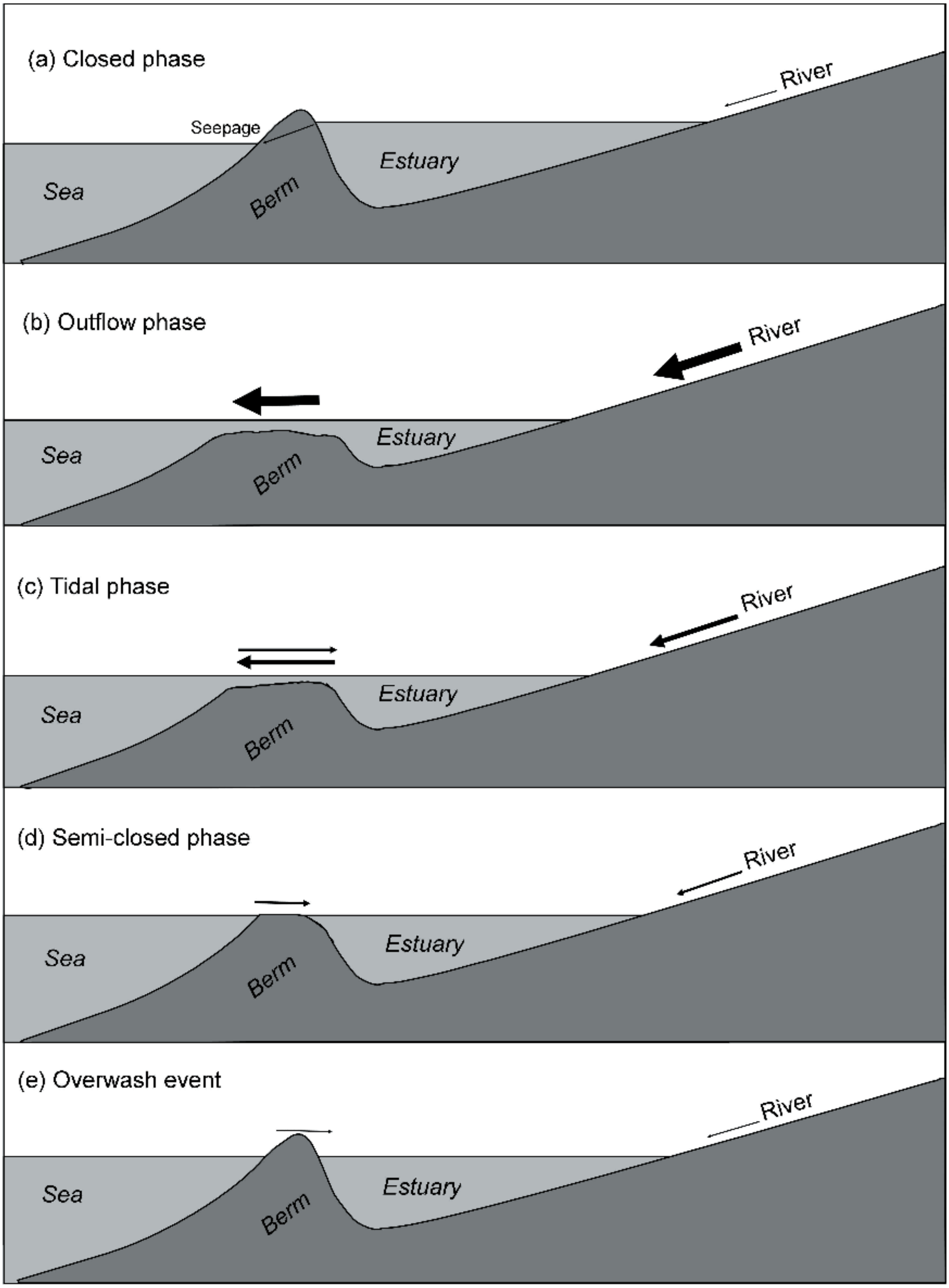


Figure 12: Diagrammatic representation of the major hydrodynamic phases and events in the East Kleinemonde Estuary

The hyperbenthos is dominated by the caridean shrimp *P. peringueyi*, which also reaches peak abundance (c. 9 individuals m^{-2}) and biomass (c. 9 mg wet mass m^{-2}) during the closed phase (Froneman 2008). In terms of biomass, the zoobenthos is dominated by the macruran prawn *C. kraussi*, which has densities of 37–44 individuals m^{-2} or 29–35 g wet mass m^{-2} (AIT, unpublished data). This species is most abundant in the lower reaches of the estuary and is little affected by mouth phase. Overall zoobenthic community stability is greatest during the closed phase (Wooldridge and Bezuidenhout 2008) when maximum habitat availability is also present, especially for epibenthic invertebrate species that are able to expand their distribution into flooded marginal areas.

The East Kleinemonde Estuary fish community benefits directly from the greater habitat availability and food resources during the closed phase. Although certain marine species may decline in abundance under prolonged closed-mouth conditions due to predation and the lack of new recruits, the dominant estuarine-resident species *G. aestuaria* breeds during this phase and attains maximal abundance and biomass (Strydom *et al.* 2003). Although the actual numbers of marine species may decline during the closed phase, growth of these fish ensures that the overall ichthyofaunal biomass actually increases (Cowley and Whitfield 2002).

The abundance of wading, swimming and diving piscivorous birds in the East Kleinemonde Estuary during the closed phase is lower than that recorded during the open phase (Terörde and Turpie 2008). A lower abundance of these birds during the closed phase may be related to the deeper, more difficult fishing conditions and the increased littoral refuge areas for fish.

Overwash events

Marine overwash during the closed phase can be classified into two types, small and large events. Small overwash events last <3 h and are usually associated only with a specific high tide. Large overwash events last >3 h and are primarily driven by stormy seas and high waves that are not restricted to the high tide cycle. Over a 14-year period, small overwash events occurred on 14% of the days and large overwash events on 2% of the days. Limited increases in salinity (0.3–3.8) were recorded in the lower reaches of the East Kleinemonde Estuary after an overwash event, with greater increases being associated with large overwash events (van Niekerk *et al.* 2008b).

Overwash events introduce seawater and associated biota into the estuary. Froneman (2002a, 2004) investigated the effects of overwash on the zooplankton community of 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 these events generally coincides with the recruitment of marine-breeding invertebrate species into the estuary, which contributes to increased diversity of zooplankton within these temporarily closed systems. Altogether, 16 species of macrozooplankton were recorded recruiting into the East Kleinemonde during overwash events, with three species, *P. 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 overwash events that shifted the species composition within that system.

Although phytoplankton and zooplankton tend to be carried passively into the East Kleinemonde Estuary with overwashing waves, it would appear that fish larvae actively utilise these events to enter the system (Bell *et al.* 2001, Cowley *et al.* 2001). Kemp and Froneman (2004) indicated that during seven different overwash events, the minimum and maximum number of fish recruits estimated to enter the East Kleinemonde Estuary during a 1 h period were 8 000 and 33 500 individuals respectively. Similarly, Cowley *et al.* (2001) suggested that in the same estuary, the highest densities of fish larvae of specific species were associated with overwash events rather than the open-mouth phase. In addition, under certain conditions, large fish may attempt to move across the berm barrier if the overwashing waves are deep enough.

Outflow phase

Breaching of the sandbar at the mouth by overtopping can occur at any time of the year and is usually initiated by river flooding when the water level in the closed estuary is already high (1.5–2.5 m msl). Two types of outflow phases have been recorded, the most common being a complete breaching of the berm. The other is a partial breaching of the sandbar such that a sustained low volume of water leaves the estuary and flows into the sea.

Sometimes mouth breaching can be precipitated by both river inflow and a major marine overwash event, which also tends to flatten the berm and thus facilitate an outflow channel once the overwash subsides. The duration of the outflow phase is usually very short (<2 days), primarily due to the small size of the East Kleinemonde River catchment (43.5 ha) and the limited volume of the estuary (maximum = 664 000 m^3).

At the commencement of the outflow phase, salinity in the lower reaches is likely to be similar to that recorded in the estuary prior to mouth breaching. The inflow of river floodwaters into the upper reaches will result in a rapid decline in salinity within this zone, spreading downstream as estuarine water is replaced by river water. Freshwater conditions are likely to prevail once all the estuarine water has flowed out to sea and the system then becomes temporarily dominated by the river, especially in terms of water column nutrients, temperature and turbidity. Episodic river floods with a frequency >1:20 years are likely to cause major scouring of estuarine sediments, especially from the lower reaches.

The strong water currents during the outflow phase tend to remove large amounts of submerged macrophytic material from the estuary and episodic flooding may even remove seed banks of species such as *R. cirrhosa*. This aquatic plant failed to recover following the May 2003 episodic flood, possibly due to the loss of much of the seed bank during the outflow phase. Open-mouth conditions and fluctuating water levels thereafter would have also prevented re-establishment. Phytoplankton stocks, as indicated by chlorophyll *a* levels during the outflow phase, decline below 5 µg l^{-1} and are probably derived primarily from river phytoplankton being washed into the estuary but also from suspended microphytobenthos.

Zooplankton abundance undergoes a major decline during the outflow phase as floodwater sweeps through the estuary and out to sea (Perissinotto *et al.* 2000). Adult hyperbenthic invertebrates that are ready for the marine phase of their life cycle (e.g. *P. peringueyi*, *S. serrata* and penaeid prawns) will leave the estuary with the floodwater. In contrast, large infaunal invertebrates such as *C. kraussi* that do not have a marine phase in their life cycle will be relatively unaffected by the outflow phase as their burrow systems are more than 50 cm deep. Epibenthic invertebrates such as the amphipods *Corophium triaenonyx* and *Grandidierella* spp. will be impacted both by the sudden salinity decline and the strong water currents associated with the river flood (Read and Whitfield 1989).

The outflow phase is perhaps the most stressful period in the existence of almost all estuary-associated fish species in the East Kleinemonde. Adult marine fish that have been trapped in the estuary during the closed phase actively seek out the newly breached channel through the sand berm and many juvenile marine fish take temporary refuge in the sea during the peak of the flood. Although small estuarine-resident species such as *G. aestuaria* will attempt to remain within the estuary during the outflow phase, many individuals will be lost to sea, especially eggs and larvae of these taxa (Strydom *et al.* 2002).

Little information is available on the behaviour of estuary-associated birds during the outflow phase in the East Kleinemonde, but a study by Heÿl and Currie (1985) in the Bot Estuary recorded changes in the occurrence and mortalities of red-knobbed coot *Fulica cristata* associated with the outflow phase. No bird mortalities associated with outflowing floodwaters were recorded at the East Kleinemonde Estuary, but this could be related to the absence of coot from this particular system. Feeding opportunities for piscivorous birds do arise from the rapid changes in the physico-chemical environment and fish becoming trapped in aquatic macrophyte beds or receding pools of water.

Tidal phase

In the case of a partial breaching of the berm, which occurs between zero and 2% of the time, no tidal regime is established because the base of the outflow channel is normally above the high tide level. When there is a complete breaching of the berm, a tidal regime within the estuary becomes established once the flood has dissipated. The duration of each tidal phase is variable (1–28 days) and is linked to river flow and the build-up of the sandbar at the mouth. A river flow in excess of 0.08 m^3 s^{-1} is usually sufficient to keep the mouth open (van Niekerk *et al.* 2008a). On average, the tidal phase is in place for about 8% of the year in the case of the East Kleinemonde Estuary. The range, however, is large and was 0% in 1999 and 32% in 2006 (PDC unpublished data). Episodic flooding (>1:20 year floods) results in major sediment scour from the estuary, especially in the subtidal and intertidal lower reaches, and this leads to very low tides during the open phase until such time as the berm begins to form.

With the establishment of a tidal regime, salinity in the lower and middle reaches increases rapidly and eventually extends into the upper reaches as well. Salinity will tend to be highest over the spring tidal cycle and lowest during the neap tidal cycle. There will also be large differences in salinity concentration and distribution between high and low tides each day (Taljaard *et al.* 2008). As the river flow declines so a more uniform vertical and horizontal salinity distribution within the system becomes established. In the case of a partial breaching of the berm, the loss of estuarine water from the mouth region and its replacement with river water results in lower salinity within the estuary under this regime.

The exposure and desiccation of littoral macrophyte beds during the tidal phase, especially in the lower and middle reaches, can have a significant effect on the rate of recovery of these plant beds when the mouth closes and the water level rises. A prolonged tidal phase will result in the death of aquatic macrophytes that are located above the high tide level and therefore prevent their vegetative recovery in these areas. The effect of exposure of *R. maritima* and *P. pectinatus* seeds to desiccation is unknown.

The longer residence time of estuarine waters during the tidal phase compared to the outflow phase, together with inorganic nutrients provided by the river and sea, will allow phytoplankton stocks to recover. Chlorophyll *a* levels in the water column during the tidal phase increase to 5–10 μg l^{-1} and are probably prevented from rising further due to tidal replacement of most of the water column each day. In addition, the volume of nutrients being supplied to the estuary by the river following the cessation of the flood will be reduced, and marine nutrient levels along this section of the Eastern Cape coast are naturally low (Vorwerk 2006).

Zooplankton abundance undergoes a major change compared with the closed phase, with estuarine species recovering from losses experienced during the outflow phase and marine species being introduced into the estuary from the sea (Froneman 2008). Larvae and post-larvae of hyperbenthic invertebrates such as *P. peringueyi*, *S. serrata* and penaeid prawns will enter the estuary during the tidal phase and colonise suitable habitats. Zoobenthic invertebrates in the upper reaches will undergo a community composition shift if the estuary remains in this phase for an extended period (>1 month).

The tidal phase is an optimum period for the recruitment of estuary-associated marine fish species into the system. The exact species composition of the new fish assemblage will be determined by season, duration of the open-mouth conditions and the cohort strength of potential recruits from sea. Certain estuarine-resident fish species that have a marine larval phase will spawn during the tidal phase but no information is available on the breeding success of these taxa from the East Kleinemonde Estuary. Piscivorous bird activity is linked to the increased vulnerability of fish because of the absence of extensive aquatic macrophyte refuge areas and the shallowness of the estuary, particularly at low tide.

Semi-closed phase

As the berm height increases, only water near the peak high tide level enters the estuary and ebb tidal flow is effectively prevented (van Niekerk *et al.* 2008b). Therefore, nutrients and planktonic biota contained in the seawater entering the estuary during this phase are effectively trapped within the system. Eventually, the stage is reached in which only water from the spring high tide enters the estuary, in the form of a series of small overwash waves. Once no further water enters the estuary, on either neap or spring tide, the estuary is deemed to have entered the closed phase.

In the case of a full breaching open phase, the average salinity within the estuary during the semi-closed phase is usually polyhaline (18–29.9), especially in the lower reaches where the highest salinity occurs. The longer the duration of the closing phase the more seawater is able to enter the system, and the higher the overall starting salinity for the closed phase.

In the case of a partial berm breaching open phase, the resultant lowered salinity during the closing phase is favourable for those estuarine biota that favour oligohaline (0–4.9) or mesohaline (5–17.9) conditions. The rapid spread of *P. pectinatus* during 2001 and 2002 was due to the lowered estuarine salinity (<10) following partial breaching events in those years. Similarly, low salinity (<5) arising from the above scenario, in combination with a sudden lowering of water temperature, can result in fish kills of marine species within the estuary (as occurred in May 2000).

Future Studies

Current research on the East Kleinemonde Estuary has exposed the connectivity between catchment, estuarine and marine processes. Although understanding of the importance of these processes has been improved as a result of the research reviewed here, considerable gaps still exist, especially in terms of a quantified approach to the flow of organic and inorganic material within and between systems.

There is much circumstantial evidence to suggest that Eastern Cape TOCEs make a large contribution to the productivity of the nearshore marine environment. However, further detailed studies are required to quantify the contributions of individual TOCEs such as the East Kleinemonde to the overall coastal ecosystem, especially in terms of inorganic nutrients, organics and biota. There is also an urgent need to assess the impact of changing catchment run-off scenarios on these small systems, brought about by increasing coastal and catchment developments, as well as climate change.

Acknowledgements — We thank the Water Research Commission for funding this study (Project K5/1581) and our respective institutions for providing logistical and infrastructural support to undertake the work. The comments of two anonymous referees are gratefully acknowledged.

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