RECOVERY DYNAMICS OF ZOOPLANKTON FOLLOWING A MOUTH-BREACHING EVENT IN THE TEMPORARILY-OPEN MDLOTI ESTUARY.

By:

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As the candidate's supervisor I have approved this dissertation for submission

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I, M. DEALE, declare that

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2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

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ABSTRACT

A high proportion of South Africa's temporarily open/closed estuaries (TOCEs) occur along the coast of KwaZulu-Natal. Mouth breaching events have major impacts on the biological processes of an estuary, resulting in depletion of zooplankton via flushing and sediment scouring. Mouth closure, usually within weeks of a breaching event, initiates a new phase of stable physical conditions, leading to biological recovery. Therefore, the aim of this investigation was: (1) to monitor the recovery of zooplankton abundance and biomass following a breaching event in the Mdloti Estuary; (2) to compare the spatial and temporal patterns in zooplankton distribution in the lower (mouth), middle and upper reaches (head) of the Mdloti Estuary in terms of abundance and biomass just before, during and after a mouth breaching event; and (3) to determine the key environmental variables influencing zooplankton abundance and biomass during such a breaching event. The zooplankton community of the Mdloti Estuary was studied over a 3-month period (27 January to 26 April 2004). The estuary was artificially breached on 12 February 2004, due to a fish kill, and closed again naturally on 18 March 2004. Samples were collected twice a week in the lower, middle and upper reaches using a WP-2 net and an epibenthic sled. Upon breaching, 98% of zooplankton biomass was lost through sediment scouring and flushing. During the open phase, zooplankton biomass showed a temporary recovery, but due to continual sediment scouring and flushing, this was not sustained. One-way ANOVA revealed a significant difference in total zooplankton abundance and biomass between phases ($d.f._{2, 59} = 55.0$; $p < 0.001$; $d.f._{2, 59} = 15.51$; $p < 0.001$). ANCOVA revealed significant differences between zooplankton abundance and biomass ($d.f._{0.05;2,56}=2.97$, $p = 0.05$) at the different estuarine reaches ($d.f._{0.05;2,56}=5.51$, $p < 0.01$) . In both cases, the lower reaches recovered quicker than the middle and upper reaches. Thirty-five taxa were identified during the study, with only 10 contributing more than 1% of the total abundance or biomass. For the overall study, *P. hessei* was the dominant species, accounting for 42% of the total abundance and 58% of the total biomass. *Keratella* sp. 1 accounted for 17% and 11% of the total abundance and total biomass, respectively, while harpacticoid copepodites and *Acartia natalensis* contributed 11% and 10% to the total zooplankton abundance and 3% and 7% to the total zooplankton biomass, respectively. Pre-breaching levels of zooplankton were reached only 9 days after the closure of the mouth, during the recovery phase (mean $1.1 \times 10^5 \pm 6.5 \times 10^4$ SD ind.m^3 and $2.4 \times 10^2 \pm 1.6 \times 10^2$ SD mg.m^3). Zooplankton abundance and biomass reached a peak in the lower reaches after 19 days, in the upper reaches after 28 days and in the middle reaches after 35 days. The zooplankton biomass decreased slightly, but stabilised for the duration of the study. During the study the state of the mouth was primarily responsible for regulating the zooplankton abundance and biomass. However, the zooplankton in the different reaches did not recover in synchrony after mouth re-closure because abiotic factors and food availability were different in the three estuarine reaches.

PREFACE

The work described in this dissertation was carried out in the School of Biological and Conservation Sciences, University of Kwa-Zulu Natal, Westville Campus, from January 2004 to September 2009, under the supervision of Professor Renzo Perissinotto.

This study represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of other authors it is duly acknowledged in the text.

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19 February 2010

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For Tobie

GENERAL INTRODUCTION

A high proportion of the estuaries in South Africa are temporarily open/closed estuaries (TOCEs). These estuaries are closed off from the sea during dry season and under low river flow conditions (Froneman 2003a; Perissinotto *et al*. 2003b). Breaching occurs during periods of high rainfall and freshwater runoff (Nozais *et al*. 2001; Froneman 2003a).

Breaching reduces the biomass of phytoplankton and zooplankton, as well as changing the composition of phytoplankton and the fish fauna (Saad *et al*. 2002; Santangelo *et al*. 2007; Anandraj *et al*. 2008). Other factors such as food availability, changes in salinity, temperature and the trophic state may also change after breaching (Froneman 2003b; Santangelo *et al*. 2007). In TOCEs, zooplankton requires an extended period of mouth closure in order to respond to an increase in microalgal availability and convert it into number and biomass growth (Whitfield 1980; Kibirige & Perissinotto 2003b; Kibirige *et al*. 2006). Zooplankton provides a link between phytoplankton and higher trophic levels, such as fish stocks (Allen *et al*. 1995; Little 2000). Therefore, zooplankton is very important from both an economic and ecological perspective (Harris *et al*. 2000; Little 2000).

Zooplankton studies in the Mdloti Estuary in KwaZulu-Natal are scanty Kibirige *et al*. 2006). No high-resolution studies on the recovery of zooplankton dynamics following a breaching event have ever been done in a TOCE before. This information is an important factor for the effective management of estuaries (Anandraj *et al*. 2008).

The outline of this dissertation is as follows:

Chapter 1 presents a review of existing literature on the breaching dynamics and the biological responses, in particular of zooplankton, of temporarily open/closed estuaries. Natural and artificial breaching is discussed, as well as

the impacts and interferences on TOCEs. The zooplankton in TOCEs is discussed, as well as the factors controlling it.

Chapter 2 is an original study on the recovery dynamics of zooplankton abundance and biomass following a mouth-breaching event in the Mdloti Estuary in KwaZulu-Natal. This is a high-resolution study in order to provide information for the effective management of the Mdloti Estuary and other TOCEs in general.

This study ends with a summary of the findings and recommendations for future research.

1. A REVIEW OF BREACHING DYNAMICS AND BIOLOGICAL RESPONSES IN SOUTH AFRICAN TEMPORARILY OPEN/CLOSED ESTUARIES, WITH EMPHASIS ON ZOOPLANKTON

1.1 South African estuaries

Worldwide the demands of an ever-growing population are placing an increasing pressure on natural resources, especially fresh water. South Africa, a water-scarce country, is no exception (Morant & Quinn 1999). Major inter-basin water transfer schemes have already been implemented to meet the growing requirement for fresh water in a number of provinces, especially Gauteng (Morant & Quinn 1999). As a consequence, the volume of water flowing into estuaries and the intensity of floods have been reduced (Reddering 1988; Allanson & Read 1995; Schumann & Pearce 1997; Snow *et al*. 2000). It is estimated that as little as 8% of the mean annual runoff reaches the coastal zone (Allanson & Baird 1999). Except for the effects in the catchment areas there is also direct pressure on estuaries themselves, mainly because of residential, recreational and industrial developments (Morant & Quinn 1999; Perissinotto *et al*. 2003a; Tracey *et al*. 2006). Due to all these factors, South African estuaries are degrading. All these factors have increased the interest in the ecological functioning of estuaries for managerial purposes (Whitfield 1995; Wooldridge & McGwynee 1996; Allanson & Baird 1999; Allanson & Winter 1999; Morant & Quinn 1999; Snow *et al*. 2000; Nozais *et al*. 2001; Walker *et al*. 2001). Management of estuaries in the past has been mainly undertaken on a piecemeal basis, dependent on and driven by sectorial interests such as fishing, property development etc. (Morant & Quinn 1999).

For management of estuaries, a better understanding of the population dynamics of primary producers and consumers of temporarily open/closed estuaries has been gathered during the last few decades (Blaber *et al*. 1984;

Perissinotto & Wooldridge 1989; Forbes *et al*. 1994; De Villiers *et al*. 1999; Whitfield & Marais 1999; Perissinotto *et al.* 2000; Nozais *et al*. 2001; Kibirige 2002; Perissinotto *et al*. 2002a; Jerling 2003; Kibirige & Perissinotto 2003a; Perissinotto et al. 2003a; Iyer 2004; Thomas 2004; Jerling 2005; Kibirige *et al.* 2006). This has been helpful towards the design and implementation of more holistic management strategies. Information on the recovery of primary and secondary production and biomass after breaching is an important requirement for the effective management of conditions, such as regulation of nutrient influx from sewage plants, eutrophication, monitoring of microalgal growth and artificial breaching (Anandraj *et al*. 2008). Some studies have been undertaken on estuarine zooplankton and phytoplankton dynamics during an annual cycle (Kibirige 2002; Kibirige & Perissinotto 2003a; 2003b; Kibirige *et al.* 2006). Little is still known about the dynamics of the zooplankton community following a mouth breaching event in an estuary. During breaching the zooplankton is flushed out to sea, while juveniles of estuarine-dependent marine fish species are recruited into the estuary (Whitfield 1984; 1992b; Blaber 1997). The dynamics and time-scale of recovery of zooplankton inside the estuary after re-closure is of fundamental importance, as these juvenile fish are all planktivorous.

The recovery of an aquatic ecosystem generally implies a return to the pre-disturbance state, termed an equilibrium state (Picket & Whitefeds 1989) or a nominal state (O'Neill 1999). Ecological resilience is the capacity of an ecosystem to tolerate disturbance without collapsing into a different state that is controlled by a different set of processes (Holling 1973). A resilient ecosystem can withstand disturbance and rebuild itself if necessary. Biological and/or physico-chemical indicators are used to assess the extent of the recovery (Holling 1973). Determining the extent of biological recovery is very complex. The organisms in the ecosystem have to compensate for the disturbance by exhibiting adjusted behavioural and/or physiological mechanisms for survival (Power 1999).

The National Water Act (36) of 1998 recognises two rights. The right to sufficient water to meet basic domestic needs and the right to have the

environment protected for the benefit of present and future generations (Department of Water Affairs and Forestry 1997). Unfortunately, environmental management authorities in South Africa have been slow to accept that estuaries should be given equal priority for water resource allocation. Until a decade ago, the almost universal view has been that water supplied to estuaries is water wasted (Morant & Quinn 1999).

South African estuaries are generally small and microtidal, with the mouth usually constricted or periodically blocked by sandbars (Day 1981a; Reddering & Rust 1990). Often the whole estuary is shallow, however sometimes the supply of sediment is limited, which may result in deep middle and upper reaches (Day 1981a). The eastern coastline of South Africa is particularly endowed with estuaries that comprise a dominant component of its coastal geomorphological landscape (Cooper *et al*. 1999). Most estuaries are drowned river valleys due to eustatic changes in sea level (Day 1981a).

Whitfield (1992a) classified South African estuaries according to the state of the mouth into the following: 1) permanently open estuaries, 2) temporarily open/closed estuaries (TOCEs), 3) river mouths, 4) estuarine lakes and 5) estuarine bays.

Of the 258 estuaries occurring in South Africa, 182 are classified as TOCEs (Whitfield 2000b). That means that around 70% of all estuaries in South Africa are TOCEs, making them important ecosystems for environmental management. Of the five types of estuaries, TOCEs are also the only estuaries to experience regular closure and breaching. Although estuaries occur all along the South African coast, a high proportion of these systems are associated with the steep coastal gradient of the south coast of KwaZulu-Natal. Since estuaries are formed where rivers meet the sea, they are affected by variations in both freshwater and marine conditions (Day 1981a; Harrison 2004). This makes them very sensitive ecosystems.

Estuaries are dynamic, complex ecosystems that exhibit high levels of biological production (Day 1981a; Allanson *et al.* 1999; Baird 1999).

Zooplankton provides a link between phytoplankton production and higher trophic levels, such as commercially exploited fish stocks (Allen *et al.* 1995; Jerling & Wooldridge 1995b; Harris *et al.* 2000; Little 2000). Therefore, zooplankton is indirectly important from an economic and ecological point of view (Jerling & Wooldridge 1995b; Harris *et al.* 2000; Little 2000).

Studies indicate that zooplankton biomass in TOCEs may attain levels equivalent to those found in the most productive permanently open estuaries within the same geographical region (Perissinotto *et al.* 2000; Froneman 2003a) (Table 1.1).

Table 1.1: Standing stock of zooplankton (mg DW m^{-3}) in some South African estuaries. * no data available; POE: permanently open estuary; TOCE: temporarily open-closed estuary; EB: estuarine bay.

Zooplankton standing stock (mg DW m^{-3})				
Estuary	**Description**	**Mean**	**Range**	**Reference**
Great Fish	POE	1597	11681	Grange (1992)
Keiskamma	POE	1627	7497	Allanson & Read (1995)
Kariega	POE	38	108	Grange (1992)
Mbotyi	POE	87	109	Wooldridge (1974)
Mdloti	TOCE	127	2010	Kibirige *et al*. (2006)
Mhlanga	TOCE	52	1210	Kibirige *et al*. (2006)
Mpenjati	TOCE	280	1700	Kibirige (2002)
Msikaba	POE	15	35	Wooldridge (1976)
Nyara	TOCE	*	2030	Perissinotto *et al*. (2000)
Richards Bay	EB	174	344	Grindley & Wooldrige (1974)
Swartskop	POE	17	95	Grindley (1981)

Variations in the zooplankton community structure and biomass in TOCEs have been linked to several factors including mouth condition, salinity, water temperature and food availability (Perissinotto *et al.* 2000; Froneman 2002a; 2003a; 2003b; Kibirige & Perissinotto 2003b; Froneman 2004). These factors will be discussed in more detail throughout this chapter.

1.2 Temporarily Open/Closed Estuaries

TOCEs do not have a permanently open link to the sea, but are normally closed off from it during the dry season (De Villiers *et al*. 1999; Whitfield 2000b; Stretch & Parkinson 2005). Their inlets are unstable due to a combination of energetic wave climate and associated sediment transport, a small tidal prism and low or intermittent river inflows (Stretch & Parkinson 2005). Mouth closure periods may vary naturally from days to months or even years, depending on the climatic conditions, rainfall patterns and outlets (Nozais *et al.* 2005). During the dry season, TOCEs are separated from the sea by an extensive sandbar (Kibirige & Perissinotto 2003a; 2003b; Froneman 2004; Kibirige *et al.* 2006; Anandraj *et al*. 2008).

TOCEs can be perched or non-perched. Perched estuaries have high berms, maintaining water levels above the high tide level of the sea (Cooper 2001; Nozais *et al*. 2005; Stretch & Parkinson 2005). Non-perched estuaries develop behind low-elevation barriers fronted by wide dissipative beach profiles (Cooper 2001). TOCEs in KwaZulu-Natal are generally perched, because of intermediate to reflective beach states. These beach states arise partly due to coarser grain sediment and reduced wave energy (Cooper *et al*. 1999).

1.3 Breaching

1.3.1 Natural Breaching

Following periods of high rainfall and freshwater runoff, the water level in a perched TOCE rises until it exceeds the height of the sandbar. Breaching then occurs, which results in a dramatic decrease in the water level of the estuary. During this phase, river conditions dominate throughout the system (Perissinotto *et al*. 2000; Walker *et al*. 2001; Perissinotto *et al*. 2002a; 2002b; Froneman 2003a). However, a steep beach slope may lead to considerable

wave run-up that in turn may drive a flow into the estuary when it is open (Perissinotto *et al.* 2004).

The breaching process of TOCEs is conceptually similar to the failure of earth-fill dams (Stretch & Parkinson 2005). The process can broadly be considered to comprise of two main phases, namely a breach initiation phase and a breach formation phase (Stretch & Parkinson 2005). During the initiation phase, a channel is scoured on the downstream face of the barrier by the overtopping flow gradually while the upstream crest remains relatively intact, with the upstream water level not changing significantly (Stretch & Parkinson 2005). The breach formation phase starts when the upstream crest of the barrier starts to erode. The volume of water entering the breach channel increases as scouring lowers the upstream crest, in turn increasing the scour rate. The breach channel deepens and widens rapidly. Turbulence and strong velocities at the bottom of the downstream face cause the channel to erode upstream along the base to a pivot point (Stretch & Parkinson 2005). The crest of the breach moves upstream as it erodes. This is because of the sloping face of the barrier, causing the slope of the channel to decrease as the channel bed is eroded. As the breach widens, the upstream water level decreases and the outflow increases (Stretch & Parkinson 2005). The velocity of the water in the channel decreases, the rate of the scouring also decreases, while the breach width attains a maximum value as the breach formation phase ends (Stretch & Parkinson 2005).

The physical impact of breaching can be dramatic, especially in perched estuaries (Stretch & Parkinson 2005). The water level of an estuary may drop very suddenly and the estuary may be emptied within hours (Morant & Quinn 1999; Perissinotto *et al.* 2000). The large outflow that can arise from this sudden breaching of the barrier can scour significant quantities of accumulated sediments from the estuary, changing its morphology by flushing the biota out to sea and exposing large areas of substratum, which had been previously submerged and colonised by a rich community of plants and animals (Morant & Quinn 1999; Perissinotto *et al.* 2000; Stretch & Parkinson 2005).

Breaching also reduces the biomass of the phytoplankton, as well as changing the composition of phytoplankton and the fish fauna (Saad *et al*. 2002; Santangelo *et al*. 2007; Anandraj *et al*. 2008). Other factors such as food availability and quality, competition, predation, changes in salinity, temperature and the trophic state may also change after breaching, influencing the zooplankton community (Froneman 2003b; Santangelo *et al*. 2007).

After breaching, TOCEs seem to experience a period of biological rejuvenation and a period of maximum productivity after re-closure of the mouth (Whitfield 1992a; Nozais *et al.* 2001). The contact between the ocean and the estuary during the open phase is typically associated with the recruitment of marine breeding organisms into the estuarine system. This recruitment increases the zooplankton diversity and results in a change in the zooplankton community structure (Froneman 2003b). The recruitment will also contribute to the build-up of zooplankton biomass during the subsequent closed phase (Froneman 2003b). The recovery of the zooplankton community after a breaching event will also depend on the characteristics of the disturbance, e.g. the frequency and intensity (Santangelo *et al*. 2007).

The salinity increase in oligohaline estuaries after breaching dramatically change the biotic communities, which may then show marine and estuarine characteristics (Saad *et al*. 2002; Kibirige & Perissinotto 2003b). After re-closure the salinity tends to return to its normal oligohaline conditions. This means that the system has to undergo profound alterations, changing from a freshwater community to a transitory marine-estuarine community and then back to a freshwater community (Santangelo *et al*. 2007). The capacity of re-establishing the original oligohaline community, however, is not guaranteed. The system may be colonised by different freshwater species after re-closure (Santangelo *et al*. 2007).

1.3.2 Artificial Breaching

Artificial breaching is a controversial issue. In the past, it used to be common practice to artificially breach closed estuaries when water levels became too high. It was sometimes undertaken to safeguard properties, farmland and other manmade structures built below the normal breaching level of the particular system. Thus, the entire functioning of an ecosystem could be jeopardised by township planning undertaken in ignorance of the natural envelope of variability of an estuary (Morant & Quinn 1999). In other cases artificial breaching was used to flush the system from a build-up of contaminants or sediments (Stretch & Parkinson 2005). Artificial breaching is used as a management tool to address the effects of reduced inflow due to dams upstream. This may be required because reduced inflow can greatly increase the closure periods of TOCEs (Stretch & Parkinson 2005). Another reason for artificial breaching is when the oxygen levels become too low and fish start to die, normally as a result of human interference such as disposal of sewage outlets and other pollutants (Stretch & Parkinson 2005). Figures 1.1 and 1.2 illustrate an artificial breaching at Mdloti Estuary due to a fish kill.

Figure 1.1: Artificial breaching on 11 February 2004 at the Mdloti Estuary due to a fish kill (source: Nicolette Demetriades).

Figure 1.2: Artificial breaching underway on 11 February 2004 at the Mdloti Estuary due to a fish kill (source: Nicolette Demetriades).

Stretch and Parkinson (2005) conducted model experiments to investigate breaching characteristics of perched estuaries as a function of several key parameters. The results were then compared to those obtained from two small, perched TOCEs in KwaZulu-Natal. Even though the laboratory experiments were very simplistic compared to real-life estuaries, these results provided basic information to the scaling of breach characteristics for management applications.

Artificial breaching may have a negative impact on the TOCE by unnaturally changing the frequency, timing and duration of the mouth conditions. This in turn may interfere with the migration patterns of biota between the estuary and the ocean (Perissinotto *et al.* 2004). Artificial breaching will then also have an impact on the salinity, temperature and depth of the estuary, the trophic state, food availability and quality, with all of these factors influencing the zooplankton community (Froneman 2003b; Santangelo *et al*. 2007).

The exact timing and detailed consequences of artificial breaching require an understanding of the processes and its impact on the functioning of estuarine ecosystems (Stretch & Parkinson 2005). There are a number of general recommendations on the methods used for artificially breaching an estuary. Ideally, the water level in the estuary should be as high as possible prior to the breach. This will result in the maximum amount of sediments being flushed out, thus preventing future sediment build-up in the estuary. The estuary should be breached as late in winter and/or spring as possible and, ideally, three to four days before spring tide. The position where the mouth should be breached depends on local conditions. If possible, a deeper and wider channel is better than a small and narrow trench. The actual period of breaching during the tidal cycle is at high tide, or as close after high tide as possible, waves permitting (Van Niekerk *et al.* 2005).

Artificial breaching may have serious long-term impacts on the sediments and the biota of an estuary. When the water level is below the normal breaching levels, it may result in a reduced scour potential. In the long term, this leads to accumulation of sediments in the estuary mouth, thereby compounding the original problem (Morant & Quinn 1999). For instance, between 1948 and 1988 the Klein River Estuary has been breached artificially at least forty times, as a result of previous sand penetration (since 1938) through the mouth to a distance of four kilometers inside the estuary (Waldron 1986; Morant & Quinn 1999). If the scouring potential is reduced by impoundment attenuation, the estuary may open to the sea less frequently, thereby limiting the opportunity for key processes necessary to maintain the estuarine habitat (Morant & Quinn 1999).

1.3.3 Mouth Closure

The development of a sandbar within weeks of mouth breaching is generally due to long shore sand movement in the surf zone and results in the estuary being closed off from the sea again (Perissinotto *et al*. 2000; Kibirige &

Perissinotto 2003a; 2003b; Froneman 2004; Kibirige *et al.* 2006). During this closed phase, seawater inflow is provided by overwash during severe storms and at the peak of spring tides (Perissinotto *et al*. 2000; Walker *et al*. 2001).

The two main water losses from an estuary when the mouth is closed are evaporation and seepage, especially in perched estuaries with narrow sandbars (Perissinotto *et al.* 2004). Seepage losses increase as the water level in the estuary rises, and evaporation losses increase as the surface area increases and water temperature rises. In perched estuaries, the seepage losses tend to dominate evaporation losses (Perissinotto *et al.* 2004) (Figure 1.3).

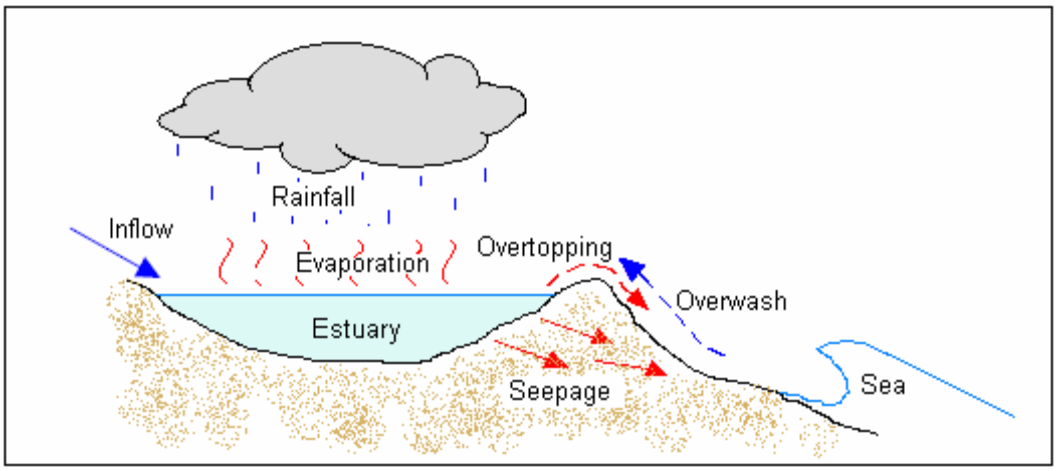


Figure 1.3: Schematic representation of a perched TOCE conceptualised in terms of a dynamic storage system (source: Lawrie 2007).

After mouth closure, the loss of a link to the sea has immediate and profound effects on the physico-chemical nature of the estuarine environment, which translates into equally significant effects on the living organisms in the estuaries (Wooldridge 1994; Bate *et al*. 2002; Forbes & Demetriades 2002).

Mouth closure cuts off all tidal exchange between the estuary and the sea, preventing the development of an intertidal environment. This excludes all organisms dependant on this type of environment as well as any migratory

species to and from such a system (Forbes & Demetriades 2002). A sustained inflow of freshwater into the estuary which is retained by the developing bar at the mouth, results typically in a water level rise, expanding the benthic and water column habitats (Forbes & Demetriades 2002).

After mouth closure, horizontal salinity gradients tend to break down. Some contrast between the mouth and head areas may remain, depending on overtopping and seepage at the bar and the magnitude of freshwater input at the head of the estuary (Forbes & Demetriades 2002).

Oxygen levels in closed systems may decline in bottom water, due to absence of tidal currents, particularly if stratification develops and if there is any organic accumulation on the bottom of the estuary (Forbes & Demetriades 2002).

Zooplankton abundance and biomass in South African TOCEs exhibit marked variations between the open and closed phases (Whitfield 1980; Perissinotto *et al.* 2000; Kibirige & Perissinotto 2003a; 2003b; Froneman 2004; Kibirige *et al.* 2006). A few studies have shown that mouth opening events in TOCEs result in a decrease in plankton biomass in these systems (Perissinotto *et al.* 2000; Kibirige & Perissinotto 2003a; Kibirige *et al.* 2006). The decrease in plankton biomass is due to the outflow of the biomass-rich estuarine waters during mouth opening events into the marine environment (Froneman 2004). On the other hand, when seawater can penetrate the estuary during the open phase, recruitment of marine breeding organisms into the system can occur. Therefore, this recruitment increases the zooplankton taxonomic diversity and changes the zooplankton community structure (Froneman 2004). This recruitment contributes to the build-up of plankton biomass during the subsequent closed phase of the estuary (Froneman 2004).

Along the South African east coast, zooplankton abundance attains its peak during the closed phase, which generally coincides with the winter dry season

(Perissinotto *et al*. 2000; Kibirige 2002; Kibirige & Perissinotto 2003a; 2003b; Perissinotto *et al*. 2004). This could be attributed to the stability of the system, due to reduced freshwater input and restricted access to the sea (Perissinotto *et al.* 2004). As a result, phytoplankton production increases, followed by an increase in zooplankton biomass to a maximum attained some four weeks after mouth closure (Perissinotto *et al.* 2004).

Estuarine biodiversity and the nursery function of estuaries can be maintained only through regular contact with the marine environment (Whitfield 1984). When estuarine mouth conditions are altered through anthropogenic interventions such as water abstractions or impoundments, or through natural causes such as drought, changes occur in the estuarine environment, mostly to the detriment of estuarine biota (Reddering 1988; Whitfield & Bruton 1989). Wooldridge (1991) has indicated that some invertebrate species, such as the mudprawn *Upogebia africana,* may disappear from TOCEs if the open phase is not long enough, due to an obligatory marine phase of development.

Froneman (2002a) suggests that overwash events do not contribute to the build-up of biomass of zooplankton within the estuary. However, post-flexion larvae have been found stranded on a sandbar after overwash (Whitfield 1992b) and juveniles of marine breeding species were present in estuaries that have been separated from the sea for extended periods (Vivier & Cyrus 2001). Overwash events appear to occur far more frequently than breaching events, therefore the surf zone and overwash communities are linked and should not be considered independently of each other (Cowley & Whitfield 2001; Kemp & Froneman 2004). Larvae that manage to enter an estuary via overwashing when this is closed will enter a relatively stable habitat, high in available food resources and not under the influence of tidal currents (Kemp & Froneman 2004).

An extended period of mouth closure is required for zooplankton to respond to an increase in microalgal availability and to convert this into number and biomass growth (Whitfield 1980; Kibirige & Perissinotto 2003b). During a recent study conducted in the Mdloti and Mhlanga estuaries, it was observed

that the Mdloti exhibited prolonged periods of mouth closure, while the Mhlanga had frequent breaching (Kibirige *et al.* 2006). This prolonged closed period most likely allowed the zooplankton community in the Mdloti Estuary to utilise the available food sources in order to build-up a higher biomass, while this was not the case in the Mhlanga Estuary (Kibirige *et al.* 2006). On the other hand, a higher zooplankton taxonomic diversity was found in the Mhlanga than the Mdloti (Kibirige *et al.* 2006). This could be related to the link with the sea that the Mhlanga exhibits during the open estuarine phase (Kibirige *et al.* 2006). Many marine zooplankton groups enter the estuary from the ocean and utilise the local food sources (Kibirige & Perissinotto 2003b).

1.4 Impacts / interferences on TOCEs

TOCEs are much more susceptible to accumulation of pollutants than their permanently open counterparts (Begg 1984). Sewage discharges affect the residence time of water in TOCEs and contribute large amounts of macronutrients to the estuarine water, dramatically impacting the system (Perissinotto *et al.* 2004; Kibirige *et al.* 2006). The Mhlanga Estuary on the east coast of South Africa currently breaches even during periods of low or no rainfall (Kibirige *et al.* 2006), due to a regular sewage discharge of about 0.23 m^3s^{-1} into the estuary (Perissinotto *et al.* 2004). A study conducted thirty years ago showed far fewer breaching events in the Mhlanga Estuary (Whitfield 1980). Thus, the situation of this estuary has changed dramatically and has affected the entire ecosystem functioning, possibly including the food web structure and biodiversity of the estuary (Perissinotto *et al.* 2004).

On the other hand, retention of freshwater by dams for agricultural, industrial and domestic purposes has led to the reduction of the frequency and duration of mouth-opening (Reddering & Rust 1990; Cooper *et al*. 1999). This leads to longer and more frequent closure periods, as well as a decrease in the volume and frequency of estuarine flushing (Begg 1978; Whitfield 1992a; Whitfield & Wooldridge 1994; Wooldridge 1994; Schumann *et al*. 1999; Perissinotto *et al*. 2002a). Due to the long residence time of water and

sediments in estuarine basins, the benthic, pelagic and nekton communities of TOCEs are very vulnerable to environmental degradation, compared to those occurring in permanently open estuaries (Perissinotto *et al.* 2000). Prolonged mouth closure can have a significant impact on an estuarine system. Tides from the sea cease to affect salinity. Larvae from the sea that colonises the TOCE can no longer be recruited and species that return to the sea to breed are prevented from doing so (Branch & Branch 1981). Freshwater deprivation due to dams in the catchment area or droughts may lead to hypersaline conditions in the TOCE, which in turn can result in the loss of major components of the food web (Whitfield & Wooldridge 1994).

Siltation is one of the greatest threats to TOCEs and is primarily a result of intensive agriculture cultivation in their catchments. A small amount of silt is beneficial because it brings fresh organic matter and nutrients for the plankton to utilize, but excessive silt will smother phytoplankton as well as zooplankton in the estuary (Branch & Branch 1981). Furthermore, the silt may increase the turbidity of the waters, which in turn may limit or prevent photosynthesis by the primary consumers (Branch & Branch 1981). The zooplankton will be impacted, because of the lack of food availability and/or changes in food quality.

Urbanisation and tourism bring with them associated infrastructure such as railways, roads, launching ramps, jetties and seawalls. Sometimes this infrastructure is built with little regard to the consequences (Morant & Quinn 1999). Quite often a bridge is built out from each bank on solid embankments. This often cuts across the reed beds or salt marshes of estuaries, radically altering the rate of water-flow (Branch & Branch 1981). The impact may be a reduced scour potential, resulting in the retention of sediment in estuaries and/or a limitation of tidal waters higher up in estuaries (Branch & Branch 1981; Morant & Quinn 1999). Industrial activities e.g. dune mining may interfere with the normal hydrodynamics of estuarine systems (Jerling 2005). Again, this may lead to prolonged mouth closure, impacting on the spatial and temporal variations in abundance and composition of estuarine communities (Jerling 2005).

Whitfield (1995) assessed the conditions of South African estuaries (Table 1.2). It should be noted that a large number of estuaries that are reported in this classification as being in a good or excellent condition are in the former Transkei region and were not considered in previous assessments.

Table 1.2: Conditions of South African estuaries (Whitfield 1995)

Region	Condition			
	Excellent	**Good**	**Fair**	**Poor**
	Estuary in a near pristine state (negligible human impact)	**No major negative anthropogenic influences on either the estuary or the catchment (low impact)**	**Noticeable degree of ecological degradation in the catchment and/or estuary (moderate impact)**	**Major ecological degradation arising from a combination of anthropogenic influences (high impact)**
Cool temperate	1 (10%)	2 (20%)	2 (20%)	5 (50%)
Warm temperate	34 (28%)	52 (43%)	21 (17%)	13 (11%)
Subtropical	39 (33%)	22 (19%)	36 (31%)	20(17%)
Total	74 (30%)	76 (31%)	59 (24%)	38 (15%)

Heydorn (1986) emphasises that the condition of an estuary can change very rapidly as a result of factors such as developments in the immediate environment or at the mouth of the estuary, construction of a major impoundment in the catchment, or an infrequent episodic event like a cyclone. However, Heydorn (1986) also states that the slow degradation of catchments and estuaries can take place as a result of uncoordinated minor developments in its vicinity.

1.5 The Zooplankton of TOCEs

It is estimated that estuarine zooplankton has the potential to replace its numbers about 14 times a year (Branch & Branch 1981). Copepods and mysids mostly dominate the zooplankton abundance and biomass in TOCEs (Wooldridge 1999; Perissinotto *et al.* 2000; Froneman 2002a; 2003b; Kibirige & Perissinotto 2003b; Froneman 2004; Perissinotto *et al.* 2004; Kibirige *et al.* 2006). The copepods *Acartia longipatella* and *A. africana* are most common in

south-west estuaries, while *Pseudodiaptomus stuhlmanni* and *A. natalensis* dominate on the east coast (Grindley 1981; Wooldridge 1999). On the other hand, *Pseudodiaptomus hessei* occurs in virtually all South African estuaries (Wooldridge 1999).

Spatial studies on *P. hessei* in the Kromme, Swartkops and Sundays estuaries have shown that this species responds positively to freshwater pulses and that it is also the first to recolonize the estuary after a flood (Wooldridge & Melville-Smith 1979; Wooldridge & Bailey 1982; Kibirige & Perissinotto 2003b; Froneman 2004). *P. hessei* is considered to be an ubiquitous euryhaline species, thus able to thrive in both freshwater and marine environments (Wooldridge & Bailey 1982; Wooldridge 1999; Froneman 2003b; Jerling 2005). It has been recorded in salinities ranging between 0 and 80 ppt (Grindley 1981). The important contribution of *P. hessei* to the total biomass and abundance in South African estuaries is well established, especially for the closed phase (Blaber *et al.* 1984; Wooldridge 1999; Froneman 2000; 2001; Kibirige & Perissinotto 2003a; 2003b; Jerling 2005; Kibirige *et al*. 2006). The reproduction of *P. hessei* is continuous throughout the year (Hart & Allanson 1975; Jerling & Wooldridge 1991), but winter animals attain a larger mass than summer animals and females are heavier than males (Wooldridge 1999).

Mysids and other macro-zooplankton feed primarily on estuarine copepods, like *A. natalensis* and *P. hessei* (Wooldridge & Bailey 1982; Wooldridge 1999) and are also among the main food sources of estuarine fish (Wooldridge & Bailey 1982; Allen *et al.* 1995; Blaber 1997; Harris *et al.* 2000; Little 2000). During adverse conditions *A. longipatella* can produce resting eggs that accumulate in the sediments. This allows the species to persist in environments that are characterised by extreme variability in physico-chemical variables (Wooldridge 1999). Freshwater inflow, salinity dropping to below 10 ppt and high temperatures are necessary for dormant *A. natalensis* eggs to hatch from the sediment after unfavourable environmental conditions (Marcus 1984; Wooldridge & Callahan 2000; Perissinotto *et al.* 2004). A.

natalensis may also be reintroduced into the system from the sea during the open phase, but has not yet been recorded in the sea (Jerling 2005).

South African estuaries exhibit high abundances of copepods, but relatively low biomass, when compared to mysids. Conversely, mysids have relatively low abundances but account for a high biomass in estuaries (Wooldridge & Bailey 1982). Copepods can contribute more than 95% to the total abundance, while mysid biomass can even at times exceed 90% of the total mesozooplankton dry mass (Wooldridge & Bailey 1982; Wooldridge 1999). The abundance of mysids is often underestimated in research programmes, largely due to inadequate sampling procedures (Wooldridge 1999).

Microzooplankton like rotifers and cyclopoid copepods may dominate zooplankton communities of eutrophic freshwater systems (Bays & Crisman 1983; Santangelo *et al*. 2007). Low salinity and high nutrient levels during the closed phase of the TOCE are considered fundamental for the establishment of these species (Santangelo *et al*. 2007). Most of these species decline in abundance or disappear completely from the estuary after breaching (Jerling 2005).

Cladocerans are recognised as the group least tolerant to salinity increase (Frey 1993; Santangelo *et al*. 2007). Cladocerans are almost absent during brackish and saline conditions in coastal systems in South America (Attayde & Bozelli 1998; Kozlowsky-Suzuki & Bozelli 2004; Santangelo *et al*. 2007) as well as in Australia (Gaughan & Potter 1995) and South Africa (Jerling 2005; Kibirige *et al*. 2006).

Tintinnids and *Oithona* spp. may rapidly recolonise the estuary after breaching (Jerling 2005). These species are particularly abundant in more marine-dominated estuaries (Jerling 2003).

1.6 Factors Controlling Zooplankton in TOCEs

1.6.1 Rainfall

Much of southern Africa receives a low and strongly seasonal rainfall. Rivers may be a trickle for months or even years, and then come down in floods, scouring river banks and beds, gathering large amounts of silt, which are either deposited in the estuary or flushed out to sea (Branch & Branch 1981). This change in water flow is a critical factor affecting estuaries, because it has an impact on the structure and hydrodynamic properties of the water-column and the condition of the estuary's mouth (Cooper 1989; Whitfield 1992a; Schumann *et al*. 1999). The organisms that are not flushed out to sea, or covered by silt, must be able to tolerate the fresh water conditions that replace the brackish water environment (Branch & Branch 1981). The turbidity of floodwaters could also cut the penetration of light, which may limit or prevent photosynthesis (Branch & Branch 1981). Spatial studies in the Kromme and Sundays estuaries have shown that *Pseudodiaptomus hessei* responds positively to freshwater pulses and is also the first to recolonise the estuary after a flood (Wooldridge & Bailey 1982).

1.6.2 Tidal Flows

Axial displacement due to net seaward flow poses a retention problem for the endemic zooplankton community of an estuary. In response, estuarine zooplankton has evolved strategies of avoiding being swept out to sea (Wooldridge 1999). One of the strategies adopted is rhythmic and directed migration in response to the tidal phase or light intensity, providing mechanisms to promote retention in a particular area (Wooldridge 1999). This strategy works best in vertically stratified systems or in well-mixed estuaries, where a current shear still exists due to bottom friction (Schlacher & Wooldridge 1996; Wooldridge 1999). Larger species of zooplankton, like mysids, may also migrate laterally to use the upstream currents on the flood tide or to reduce downstream transport on the ebb tide (Schlacher & Wooldridge 1996; Wooldridge 1999). Different degrees of tidal displacement

for mysids may occur due to differences between sexes and age classes within species, in terms of behavioural adaptation in response to tidal currents (Schlacher & Wooldridge 1996; Wooldridge 1999).

1.6.3 Salinity

Horizontal and vertical salinity gradients are sometimes present in TOCEs during the open, tidal phase. The horizontal salinity gradients tend to break down once marine influence is cut off and are usually replaced by mesohaline (5 – 18 ppt) and oligohaline (0.5 – 5 ppt) conditions during the closed phase (Begg 1984; Whitfield 1992a; Forbes & Demetriades 2002; Perissinotto *et al.* 2002a). An oligohaline or freshwater-associated community may occur in the upper reaches of the estuary, while a stenohaline assemblage may be present in the lower reaches. However, in terms of biomass, stenohaline and oligohaline communities are not well represented in South African estuaries (Wooldridge 1999). Salinity levels in TOCEs in KwaZulu-Natal do not often exceed 10-20 ppt, even in the lower reaches during the open phase (Nozais *et al.* 2005). These estuaries differ from the warm temperature estuaries found along the south-eastern region of South Africa, which experience substantial intrusions of sea water, both via tidal action at high tide during the open phase and overwash during the closed phase (Nozais *et al*. 2005). Whitfield and Bruton (1989) reported a case study in the Seekoei River with hypersaline conditions of 98 ppt. It followed the complete extraction of river flow for agricultural purposes. Such hypersaline conditions resulted in the loss of a high proportion of aquatic biota. Table 1.3 shows the different levels of salinity stratification normally observed in estuaries (Livingston 2003).

Table 1.3: Various levels of salinity stratification occurring in estuarine waters (Source: Livingston 2003)

Level of salinity stratification	If difference in top and bottom salinity is:
Highly stratified	> 10 ppt
Partially stratified, strong	< 10 ppt and > 5 ppt
Partially stratified, weak	< 5 ppt and > 2 ppt
Vertically homogeneous	< 2 ppt

South African estuaries usually show a greater salinity than temperature variation (Schumann *et al.* 1999). Due to this, salinity is generally the key abiotic variable regulating the spatial structure of estuarine plankton communities (Day 1981b; Tett 1987; Schumann *et al.* 1999; Wooldridge 1999; Jerling 2005). TOCEs generally exhibit lower salinities, a more stratified water column and estuarine and freshwater taxa dominance during the closed phase (Perissinotto *et al.* 2003b).

Axial and vertical salinity gradients largely determine the spatial distribution and abundance of zooplankton in most TOCEs (Wooldridge 1999). Generally, estuaries with a well-defined axial salinity gradient will attain a higher phytoplankton and zooplankton abundance and biomass than estuaries with a weaker axial salinity gradient (Allanson & Read 1995; Schlacher & Wooldridge 1996; Wooldridge 1999). The lower reaches of an estuary, where generally the salinity does not fall below 28 ppt, are commonly occupied by crustaceans. However, the number of species becomes reduced further up an estuary (Grindley 1981; Wooldridge 1999).

Vertical migration in estuarine zooplankton is also influenced by reduced salinity (Grindley 1964). Low salinity water inhibit many zooplankton species from migrating to the surface layers during time of floods, thus preventing them being washed out to sea. This has great significance, because it enhances the survival and recovery rates of populations after flooding (Grindley 1964).

Few freshwater species will tolerate even very low salinities, so that fresh water plankton normally plays very little part in estuaries (Day 1981b; Wooldridge 1999). In the upper reaches, the plankton community may include characteristic estuarine species not normally found in the open sea or the fresh waters of rivers (Day 1981b). This estuarine community can become well established in terms of numbers and biomass above the general volume of mixed estuarine water that reaches the inlet area around low tide (Wooldridge 1999).

A number of TOCEs in South Africa are characterised by the absence of a horizontal gradient in water temperature and salinity (Walker *et al*. 2001; Froneman 2002b; 2003b). There are several factors contributing to the absence of these gradients. One factor is a small catchment size (usually less than 50 km^2) which results in sporadic freshwater inflow into the estuary. Other factors contributing are shallow depth of the estuary, generally less than 1.5 m, and strong coastal winds responsible for horizontal and vertical mixing of the water column (Froneman 2002a; 2002b; 2004). Peaks in the biomass of dominant zooplankton and freshwater pulses have been linked in a number of permanently open estuaries in southern Africa (Wooldridge 1999).

1.6.4 Temperature

Heat distribution in estuaries is primarily a function of climate, depth of the estuary, solar radiation and the effect of stream inflow and tidal exchange (Day 1981b). TOCEs exhibit a smaller range in temperature than their permanently open counterparts in the same climatic region, as they have a slower freshwater inflow and are isolated from the sea most of the time (Perissinotto *et al.* 2002a). Water temperature in TOCEs is primarily dependent on river water temperature, since the main input of water is through river flow (Gama *et al*. 2005). However, cooler marine waters are introduced to the estuary during the open phase, resulting in vertical and horizontal stratification in temperature (Gama *et al*. 2005). On the other hand, wind action and new fresh or marine water inflow can homogenise the whole water column in a short time (Gama *et al*. 2005). In some estuaries water temperature is one of the most important driving factors of the phytoplankton/zooplankton system as well as the seasonal cycle in ecosystems (Scheffer 2004). Some organisms (e.g. Cladocerans) can produce dormant structures and the timing of production and emergence usually depends on temperature (Scheffer 2004). However, zooplankton biomass in KwaZulu-Natal estuaries is normally at a maximum in winter due to the closed state of the mouth (Kibirige 2002; Kibirige & Perissinotto 2003b; Kibirige *et al*. 2006). This may indicate that temperature does not play a

significant role in KwaZulu-Natal estuaries, but the zooplankton abundance and biomass is rather influenced by the state of the mouth.

1.6.5 Dissolved Oxygen (DO)

Dissolved oxygen is a fundamental requirement for all oxygen-consuming species. Most estuarine biota can tolerate short exposures to low dissolved oxygen without showing any negative effects (EPA 1998). However, fauna and flora exposure to moderate hypoxia (DO < 5 mg/L) for prolonged periods may be severely affected. Some aquatic fauna may avoid water with low dissolved oxygen, resulting in increased predation and decreased movements into certain feeding areas and spawning habitats (EPA 1998).

Oxygen is required to decompose dead algae, decreasing available dissolved oxygen for aquatic life. The rate of decomposition increases with increasing temperature, thus reducing the concentration of available dissolved oxygen (EPA 1998). Vertical stratification prevents reoxygenation of bottom waters, impacting on the bottom-dwelling organisms (EPA 1998). Temperature and salinity play an important role in the amount of oxygen available to estuarine biota. The dissolved oxygen content decreases with an increase in water temperature and salinity (EPA 1998). Reoxygenation may occur due to increased flows, turbulence in the water due to wind and photosynthetic O_2-byproduct (EPA 1998).

Extended periods of freshwater conditions may lead to the growth of substantial beds of freshwater macrophytes (Jerling 2005). These plants may cause a layer of decaying material to form on the bottom of the estuary, leading to lower oxygen levels. It may also reduce the phytoplankton biomass in the water column, impacting on the zooplankton community, especially the filter feeders (Jerling 2005).

1.6.6 Nutrients

Temporarily open/closed estuaries are much more susceptible to accumulation of pollutants than permanently open estuaries (Begg 1984;

Whitfield 1992a; Perissinotto *et al*. 2000). A reduction in river water and increased human activity in catchments has resulted in a marked increase in nutrients, particularly dissolved inorganic nitrogen and phosphorus (Snow *et al.* 2000). Siltation is also one of the greatest threats to estuaries, primarily as a result of intensive sugarcane cultivation in the catchment areas (Morant & Quinn, 1999).

All biota need small amounts of nutrients, like nitrogen and phosphorus, in order to grow and reproduce. However, an excess of nutrients can lead to eutrophication, where algal blooms rob other organisms of light and oxygen (EPA 1998).

Nutrients can originate at point sources or non-point sources (EPA 1998). Point sources are normally highly localised spots, like sewage treatment facilities and other industries (EPA 1998). Non-point sources are normally more diffuse regions such as farmlands, leaking septic systems and the atmosphere (EPA 1998).

Nitrogen can occur in estuaries as organic or inorganic nitrogen. According to the Department of Water Affairs and Forestry (1996), eutrophic conditions are often related to inorganic nitrogen concentrations of 2.5 to 10 µM and above, provided that other environmental conditions are favourable.

Phosphorous is actively utilised because it is essential for growth in all organisms (Department of Water Affairs and Forestry 1996). However, phosphorous levels may be elevated due to domestic and industrial wastewater effluents and storm water runoff (Department of Water Affairs and Forestry 1996). Inorganic phosphorous levels between 25 and 250 µM are generally associated with eutrophic conditions (Department of Water Affairs and Forestry 1996).

Changes in the contribution of nitrogen and phosphorous in estuaries can change the composition of the estuarine biota (Livingston 2001). This is an important factor to consider when evaluating natural eutrophication processes

and hypereutrophication (Livingston 2001). The residence time of water in the estuary is also an important factor in terms of biota utilising nutrients. Phytoplankton can not trap all available nutrients during short retention times, because they are washed out to sea during open mouth conditions (Bate & Adams 2000).

Heavy rainfall and an increase in river flow can not only result in decreased water clarity and euphotic depth, but could also increase the nutrient loading to the system (Nozais *et al.* 2001). A study conducted in a TOCE indicates that, after increased eutrophication, large species may replace smaller ones (Gliwicz 1969). The total zooplankton biomass appears to increase with increased eutrophication, while the micro-zooplankton assemblage shows no changes (Pace 1986). However, eutrophication on a long-term basis can cause a decline in meso-, macrozooplankton and fish populations (Cloern 2001; Kibirige *et al*. 2006).

Froneman (2004) found a positive correlation between total chl-*a* concentration and zooplankton biomass, which suggests that the increase in zooplankton biomass following freshwater inflow can be attributed to greater food availability.

Small estuaries generally fluctuate between extremes and may lack the buffering capacity observed in larger volume estuaries. This can be seen in the relative stability in the zooplankton community throughout the year in the larger estuaries, compared to the aperiodic boosts in growth followed by periods of low activity observed in some TOCEs (Perissinotto *et al.* 2000).

1.7 Summary

Estuaries are dynamic, complex ecosystems that exhibit high levels of biological production (Day 1981a; Allanson *et al.* 1999; Baird 1999). Unnatural changes in freshwater flow e.g. extraction upstream and artificial breaching may have a negative impact by changing the frequency, timing and duration of mouth conditions (Perissinotto *et al.* 2004). In turn, this will interfere with

the migration patterns of the biota between the estuary and the sea, changing the ecological functioning of the estuary (Perissinotto *et al.* 2004). In order to predict the changes in the ecological status of the estuary, the effects of such changes need to be determined (Perissinotto *et al.* 2004). Artificial breaching will play a more important role in the future due to increasing human impact on estuaries and their catchment areas. Further research still needs to be conducted to fully understand the timing and impact of artificial breaching on the functioning of TOCEs for future management purposes.

Zooplankton abundance and biomass in South African TOCEs exhibit marked variations between the open and closed phases. Breaching events normally culminate in a decrease in zooplankton biomass and abundance, due to the outflow of the biomass-rich estuarine waters into the sea. The state of the mouth is thus the primary influence on zooplankton abundance and biomass in the estuary. In turn, the state of the mouth influences environmental parameters, like salinity, temperature, DO and nutrient availability, also influencing the zooplankton abundance and biomass in estuaries. After mouth closure, the zooplankton normally stabilises, possibly due to the stabilization of the estuarine system.

2. RECOVERY DYNAMICS OF ZOOPLANKTON FOLLOWING A MOUTH-BREACHING EVENT IN THE TEMPORARILY-OPEN MDLOTI ESTUARY

2.1 Introduction

Of the 258 estuaries occurring along the South African coastline, around 70% can be classified as temporarily open/closed estuaries (Whitfield 1992a; 1995; Perissinotto *et al*. 2000; Froneman 2003a). During the dry season and under low river flow conditions, these estuaries are separated from the sea by a sandbar that forms at the mouth (Perissinotto *et al*. 2000; Nozais *et al*. 2001; Froneman 2003a; Perissinotto *et al*. 2003b; Nozais *et al.* 2005). Following periods of high rainfall and freshwater runoff, the volume in the estuary rises until it exceeds the height of the sandbar (Whitfield 1992a; Perissinotto *et al*. 2000; Nozais *et al*. 2001; Froneman 2003a; Perissinotto *et al.* 2003b; Nozais *et al*. 2005). Breaching then occurs and the water level drops dramatically, often exposing large areas of substratum (Perissinotto *et al*. 2000; Nozais *et al*. 2001; Froneman 2003a; Perissinotto *et al.* 2003a; Nozais *et al*. 2005). River conditions dominate the estuary during this phase (Perissinotto *et al*. 2000; Nozais *et al*. 2001; Walker *et al*. 2001; Froneman 2002a; Perissinotto *et al*. 2002b; Froneman 2003a; Perissinotto *et al*. 2003a; Nozais *et al*. 2005). Due to long shore sand movement in the surf zone, a sandbar develops within weeks of breaching, resulting in the estuary being closed off from the sea again (Perissinotto *et al*. 2000; Nozais *et al*. 2001; Froneman 2003a; Perissinotto *et al*. 2003a; Nozais *et al*. 2005). The re-closure of the estuary initiates a new phase of relatively stable physical conditions in the estuary and an associated biological recovery (Anandraj *et al*. 2008).

Zooplankton is an integral part of estuarine ecosystems, providing a link between phytoplankton production and higher trophic levels, such as commercially exploited fish stocks (Allen *et al*. 1995; Blaber 1997; Harris *et al*.

2000; Little 2000). Therefore, zooplankton is very important from both an economic and ecological perspective (Harris *et al*. 2000; Little 2000). A number of zooplankton studies have been conducted in permanently open estuaries throughout South Africa, but only a few studies have been conducted in South African TOCEs. (Reddering & Rust 1990; Whitfield 1992a; Perissinotto *et al*. 2000; Whitfield 2000a; Nozais *et al*. 2001; Kibirige & Perissinotto 2003a; Kibirige *et al*. 2006).

In TOCEs, zooplankton requires an extended period of mouth closure in order to respond to an increase in microalgal availability and convert it into number and biomass growth (Whitfield 1980; Kibirige & Perissinotto 2003b; Kibirige *et al*. 2006). Perissinotto *et al*. (2004) found that the highest recorded zooplankton abundance and biomass for the study period occurred 22 days after mouth closure. However, in the study done by Perissinotto *et al*. (2004), the sampling frequency was monthly, so not sufficiently high to detect neither the precise timing of the recovery nor the short-term dynamics associated with it. In particular, it may be possible that the zooplankton abundance and biomass peak earlier than three weeks. Not only the state of the mouth but other abiotic factors such as freshwater inflow, salinity, temperature, dissolved oxygen and nutrients also play a major role in zooplankton abundance and biomass recovery. As these factors may differ in different regions within an estuary, zooplankton recovery may not be in synchrony between the regions (Froneman 2000; 2004; Kibirige *et al*. 2006; Anandraj *et al*. 2008).

The fish communities of the Mdloti Estuary in KwaZulu-Natal have been investigated previously (Blaber *et al*. 1984; Harrison & Whitfield 1990), and yet zooplankton studies in this system remain scanty (Kibirige *et al*. 2006). The few studies conducted in the Mdloti Estuary so far have shown that zooplankton abundance and biomass exhibit marked variations between the closed and open phase, as well as between day time and night time (Whitfield 1980; Perissinotto *et al*. 2000; Nozais *et al*. 2001; Perissinotto *et al*. 2004; Kibirige *et al*. 2006).

Perissinotto *et al*. (2004) found that zooplankton biomass in the Mdloti Estuary increases to a maximum four weeks after mouth closure. This is in response to an increase in phytoplankton biomass due to increased freshwater flow.

No high-resolution studies on the recovery dynamics of zooplankton following a breaching event have ever been done in the Mdloti, or any other TOCE. Information on the recovery of zooplankton abundance and biomass following a breaching event is an important factor for the effective management of estuarine conditions, such as artificial breaching, monitoring and regulation of nutrient influx from sewage plants and eutrophication (Anandraj *et al*. 2008).

In order to provide a better understanding of the recovery dynamics of zooplankton following a mouth breaching event in a TOCE, a study was conducted in the Mdloti Estuary.

The objectives of this study were:

1. To monitor the recovery of zooplankton abundance and biomass following a breaching event in the Mdloti Estuary.
2. To compare the spatial and temporal patterns of zooplankton distribution in the lower (mouth), middle and upper (head) of the Mdloti Estuary in terms of abundance and biomass just before, during and after a mouth breaching event.
3. To determine the key environmental parameters influencing zooplankton abundance and biomass during such a breaching event.

The following hypotheses were formulated:

1. After closure, zooplankton abundance and biomass start to increase and attain a maximum after a month following mouth closure (cf. Perissinotto *et al*. 2004).
2. The zooplankton community in the three estuarine reaches does not recover in synchrony after breaching (cf. Froneman 2000; 2004; Kibirige *et al*. 2006; Anandraj *et al*. 2008).

2.2 Materials & Methods

2.2.1 Study Area

The Mdloti Estuary is a perched temporarily open/closed estuary situated on the KwaZulu-Natal north coast, between the townships of La Mercy and Umdloti, approximately 27 km north of Durban (Figure 2.1). The co-ordinates at the mouth are 29 38'S and 31 08'E (Begg 1978; Grobbler *et al*. 1987).

The Mdloti River is about 74 km in length. It has a relatively small catchment area of about 550 km^2, but a broad floodplain of up to 600 m wide in its lower reaches (Begg 1978; Grobbler *et al*. 1987; De Villiers & Maharaj 1994). The estuary is shallow and under the influence of a subtropical climate (De Villiers & Maharaj 1994). The deepest point in the estuary during this study was 2.1 m on 15 April 2004. The annual runoff is estimated at 1 x 10^8 m^3 (De Villiers & Maharaj 1994). Originally, the estuary had two main channels but since the construction of the N2 national road bridge in 1960, about 500 m above the estuary's mouth, flow has been confined to one channel (Begg 1978; Grobbler *et al*. 1987). The Hazelmere Dam is located 20 km above the estuary in the Mdloti River. The estuary receives about 8 ML of treated water per day from an upstream sewerage treatment plant, which is equivalent to a capping flow of 0.092 $m^3.s^{-1}$ (Kibirige *et al*. 2006). Evaporation losses from the system, when it is full and the maximum water level is exposed, is approximately 0.02 $m^3.s^{-1}$ or 5% of the maximum seepage (Perissinotto *et al.* 2004). The Health Index of the estuary has been estimated as fair (Whitfield 2000a; Turpie 2004).

The northern banks of the lower reaches have an assortment of vegetation, dominated by the swamp reed *Phragmites* sp., with a few patches of the so-called fresh water mangrove, *Barringtonia racemosa*. The southern banks have dense strands of *B. racemosa*. The middle and upper reaches are also dominated by *Phragmites* sp., with small strands of *B. racemosa* present on the northern banks of the upper reaches (Kibirige *et al*. 2006).

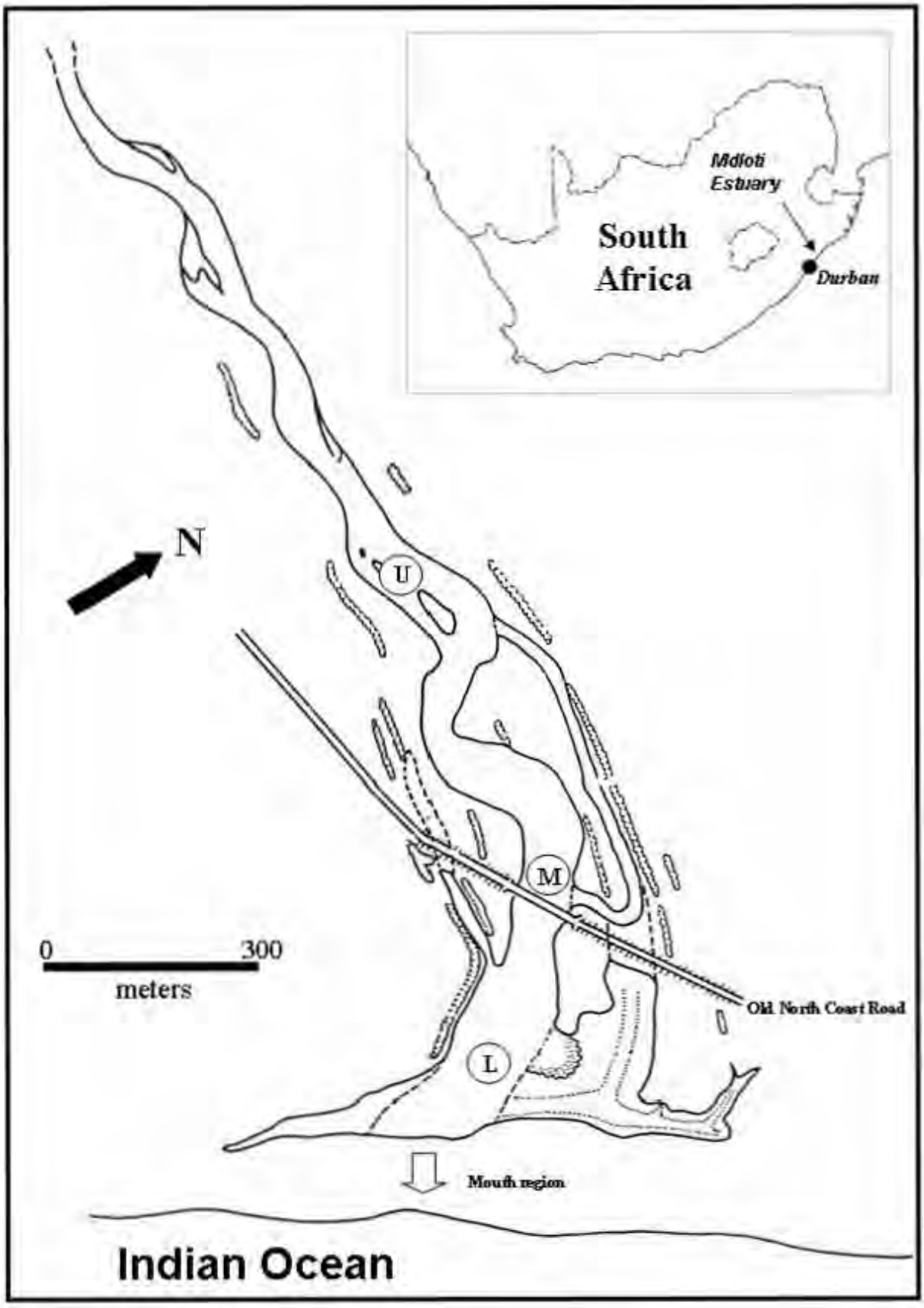


Figure 2.1: Map of the Mdloti Estuary (29 38'S; 31 08'E), showing the positions of the three sampling stations; L: Lower, M: Middle, U: Upper reaches (Source: Kibirige *et al.* 2006).

The Mdloti Estuary was artificially breached on 11 February 2004 due to a fish kill. During the phase prior to the breaching, 189 mm of rain was recorded in the area. During the open phase, which lasted until 18 March 2004, 153 mm of rain were recorded, while only 31 mm were recorded during the recovery phase up to the end of the survey, on 26 April 2004. The highest rainfall recordings in one day were on 23 January 2004 and 29 January 2004, with 71 and 70 mm, respectively.

After the initial breach, the mouth closed partially on 1 March 2004, but breached again on 3 March 2004. It stayed open until 18 March 2004, when eventually it closed completely for the remainder of the survey. Because the mouth of the estuary only closed partially the first time, this was still considered as part of the open phase. Therefore, there were three phases during the study, namely a closed phase prior to breaching, an open phase after breaching and then finally a recovery phase, after mouth re-closure.

In this study, the recovery phase will be defines as the period coinciding with re-closure of the estuary's mouth and during which the zooplankton biomass increases to reach pre-breaching levels (Anandraj *et al*. 2008)

2.2.2 Field methods

Sampling commenced on 27 January 2004 and terminated on 26 April 2004. Samples were collected twice a week at three sites in the estuary, namely lower (near the mouth), middle and upper reaches (at the head of the estuary). Only one station per site was used, due to the small size of the estuary. One sample per site was collected prior to the breaching of the estuary. During the open phase, there were eight sampling occasions prior to mouth closure and then eleven sampling occasions during the recovery phase.

Trophic and environmental parameters measured during the study included temperature, salinity, dissolved oxygen (DO), pH, dissolved inorganic

nutrients (DIN and DIP), as well as phytoplankton and microphytobenthic biomass.

On each occasion, one sample for phytoplankton biomass analysis was collected at the sub-surface (ca. 5 cm below the surface) and another in near-bottom waters (ca. 20 cm above the sediment) of each station, using a 500 ml acid pre-washed polyethylene bottle and a 1000 ml weighted pop-bottle, respectively. Water-column samples (200 ml) were sequentially size-fractionated into microphytoplankton (> 20µm), nanophytoplankton (2 – 20 µm) and picophytoplankton (< 2µm), using a 20 µm Nitex filter, a 2 µm Millipore filter and a GF/F Advantec filter, respectively. The filters were then placed in 10 ml of 90% acetone for the extraction of pigments (Nozais *et al*. 2001; Perissinotto *et al*. 2002b). Size-fractionated phytoplankton biomass was determined during the open and recovery phases only.

A 20 mm diameter Perspex twin-corer was used to determine microphytobenthic chl-*a*. Three core samples were taken on each occasion at each sampling point. The top 10 mm of the sediment were cut and placed in 30 ml of 90% acetone for the extraction of pigments (Nozais *et al*. 2001; Perissinotto *et al*. 2002b; Anandraj *et al*. 2008).

Two zooplankton samples were collected on each occasion at each sampling point. Sampling was done during daytime using a 90- m WP-2 net fitted with a General Oceanics flowmeter (Tranter & Fraser 1968). The net was attached to a boom extending from the side of a flat bottom boat powered by a 5-hp outboard motor and towed for five minutes at a speed less than 2 knots, keeping the upper part of the net 5-10 cm below the surface (Kibirige *et al.* 2006). The mesh size used in this study is suitable for the qualitative collection of copepods and other micro- and mesozooplankton (Jerling & Wooldridge 1991; 1992; Perissinotto *et al*. 2000). A 200 *µ*m semicircular epibenthic sled with a mouth radius of 0.2 m was used to account for diel vertical migration (Kibirige *et al.* 2006). The sled was pulled over a distance of

50 m. The volume filtered by the sled was calculated using the following equation:

$$V = d \frac{(\pi r^2)}{2}$$

Where *V* is the volume filtered, *d* is the distance traveled by the sled and *r* is the mouth radius of the sled.

All samples were preserved in 5% formalin solution, buffered with hexamine, for laboratory analysis.

One vertical profile of salinity, temperature, dissolved oxygen (DO) and pH were taken at 10 cm intervals at each sampling point on each occasion using an YSI 6920 multi-probe data logger. One water sample for nutrient analysis were collected from midwater at each sampling point on each occasion using a 500 ml acid pre-washed polyethylene bottle. DIN and DIP concentrations were determined by using a Technicon Autoanalyzer II system by the Analytic Laboratory of the CSIR-Environmentek in Durban. The methods of Mostert (1983) were used. The depth of the estuary was measured using a pre-marked rope with a weight on the end. Daily rainfall data were provided by the South African Sugar Association's Experimental Station, as well as Durban International Airport. The state of the mouth was closely monitored by rangers of Ezemvelo KZN Wildlife, residents in the area and the sampling team. It was described as closed if little or no water crossed the sandbar from the sea at high tide (Blaber *et al.* 1984).

2.2.3 Laboratory methods

Phytoplankton and benthic microalgal pigments were all extracted in 90 % acetone over 24-48 h, at 4ºC in the dark. Chl-*a* and phaeopigment concentrations of phytoplankton and benthic microalgae were estimated using a 10-AU Turner Designs fluorometer, fitted with the narrow band, non-

acidification system (Welschmeyer 1994; Nozais *et al.* 2001). Vertically-integrated water-column chl-*a* concentrations were calculated for each station by averaging the surface and bottom chl-*a* values and multiplying the average by total water depth.

Zooplankton samples were suspended in water, the lowest concentration in 250 ml and higher concentrations in up to 5 L of water. After vigorous stirring to avoid settlement, a 20 ml sub-sample was drawn for identification and enumeration (Perissinotto & Wooldridge 1989). A dissecting microscope was used for this purpose, using 10x to 40x magnification. The zooplankton counts were standardized to number of individuals per cubic meter ($ind.m^{-3}$). The total dry mass of each sample was obtained by drying half of the sample at 60ºC for 24 hours in a laboratory oven. The dry mass for each dominant taxon was obtained by drying subsets of individuals. The total biomass of each taxon within a given sample was then calculated by multiplying the average mass of an individual with its abundance within that particular sample. The dry mass was standardised to milligrams per cubic meter ($mg.m^{-3}$).

Only one sub-sample per sample was drawn for identification and enumeration. This is consistent with other studies and is based on the low coefficient of variation (CV < 10%) that is generally obtained between subsamples drawn from the same sample using the procedure indicated above (Campbell *et al*. 1991; Forbes *et al*. 1994).

2.2.4 Statistical analysis

For some of the statistical analysis, the one sample prior to breaching was ignored, so that a clear open and recovery phase could be shown for the duration of the study.

The zooplankton abundance was calculated by averaging the data from the WP-2 net and the epibenthic sled to determine individuals per cubic meter.

Prior to analysis, all values were $\log_{10}$ (x+1)-transformed to normalise the data.

Student's *t*-tests were used to test for differences in total zooplankton abundance and biomass between estuarine phases (open and recovery) for each station (upper, middle and lower) separately. All the data were pooled in one open and one closed set. To establish whether zooplankton at the three stations recovered in synchrony or not after breaching, a one-way analysis of covariance (ANCOVA) was used to test for potential differences between the slopes of the regression lines of zooplankton versus time at the different stations (McDonald 2009). A one-way analysis of variance (ANOVA) without replication was used to test for differences in zooplankton abundance and biomass between estuarine phases (open and recovery) and stations (upper, middle and lower) and the interaction effect (ZAR 1999).

Zooplankton diversity indexes were calculated using the Shannon-Wiener equation (Shannon 1948):

$$H' = - \sum [(ni/N).\ln(ni/N)]$$

where H' = Shannon-Wiener diversity index, ni = population size of taxon i and N = the population size of all taxa combined.

A correlation analysis (Pearson *r*) was performed on all environmental data to identify any potential relationship between these and zooplankton abundance/ biomass.

A correlation-based principal component analysis (PCA) was also used to identify those environmental factors that may have played the most significant role in the variability observed in the zooplankton abundance / biomass of the three stations.

The SAS JMP version 7.0 statistical software package was used for all statistical analysis (JMP, Version 7. SAS Institute Inc., Cary, NC, 1989-2007).

2.3 Results

2.3.1 Environmental variables

The maximum water depth in the estuary prior to breaching was 2.4 m, recorded in the lower reaches (Figure 2.2). After breaching, the estuary's depth dropped to about 0.1 m in the upper reaches, 0.2 m in the middle reaches and 1 m in the lower reaches. After mouth re-closure, the estuary gradually became deeper and by the end of the study the maximum water depth was 1.7 m in the lower reaches and about 0.9 m in the middle and upper reaches.

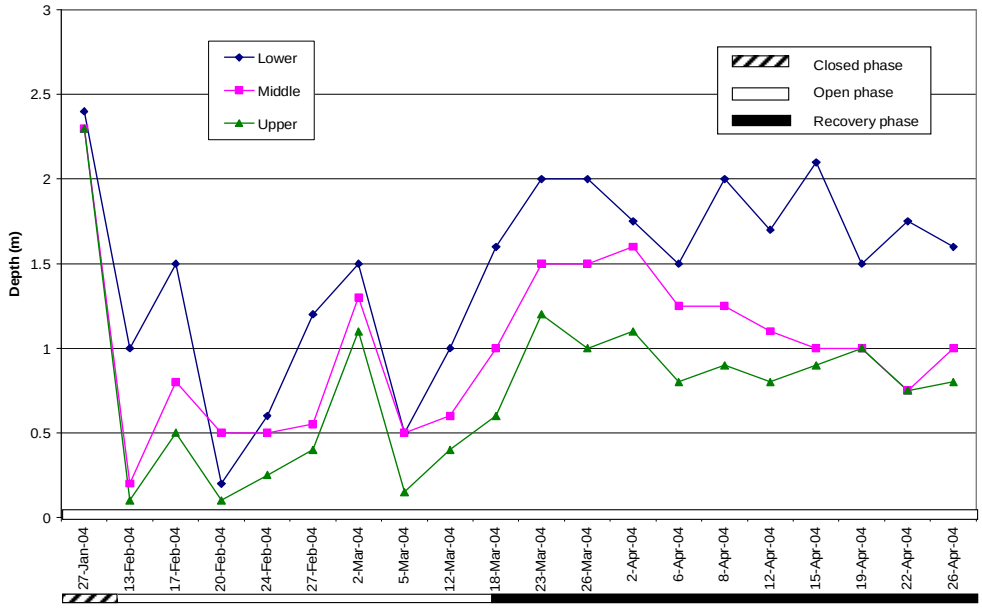


Figure 2.2: Depth of the Mdloti Estuary during the sampling period.

The water temperature ranged from a minimum of 22.5°C to a maximum of 32.2°C in the lower reaches, 22.3°C to 33.4°C in the middle reaches and 21.1°C to 31.4°C in the upper reaches (Figure 2.3). No marked vertical temperature stratification was observed in either region of the estuary.

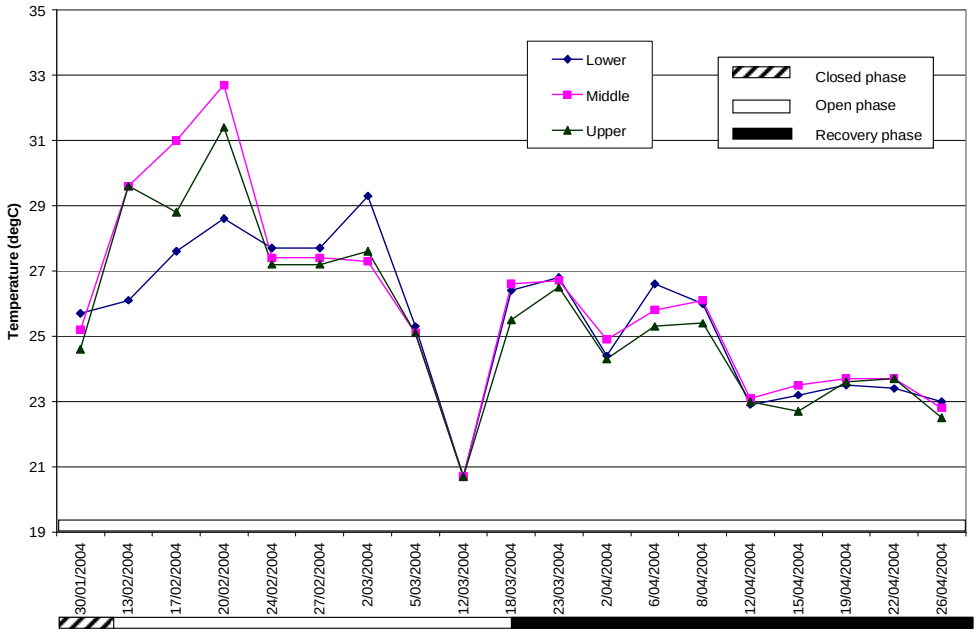


Figure 2.3: Water temperature in the Mdloti Estuary during the sampling period.

Prior to breaching, salinity was 0.9 ppt throughout the estuary. Salinity values fluctuated over time at all three stations during the open phase, varying from 0.9 ppt to 30.9 ppt in the lower reaches, 0.8 ppt to 30.2 ppt in the middle reaches and 0.9 ppt to 16.4 ppt in upper reaches. Some stratification was observed during the open phase, especially in the lower reaches, where the bottom water exhibited at times higher values than those observed in surface waters. The salinity values for the recovery phase were more constant and ranged from 1.1 ppt to 10.2 ppt in the lower reaches, 1.1 ppt to 1.8 ppt in the middle reaches and 0.9 ppt to 1.2 ppt in the upper reaches. No marked stratification in salinity was observed during the recovery phase (Figure 2.4).

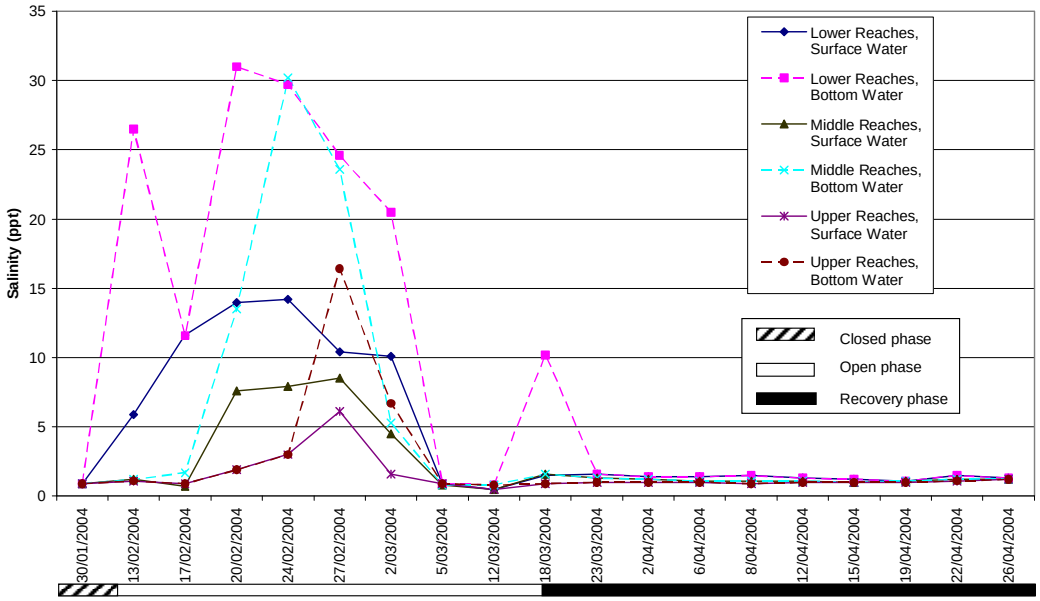


Figure 2.4: Salinity recorded at the lower, middle and upper reaches of the Mdloti Estuary during the sampling period.

The mean measured water column DIP concentrations were plotted against time, as illustrated in Figure 2.5. The samples were collected at the sub-surface (ca. 5 cm below the surface). DIP tends to decrease during the open phase and increase during the closed phase. The maximum DIP concentration was 130 µM (in the upper reaches during the closed phase) and the minimum concentration was 1 µM (in the lower and middle reaches during the open phase). DIP concentrations varied during the open phase, but were consistently higher during the closed phase for all the stations.

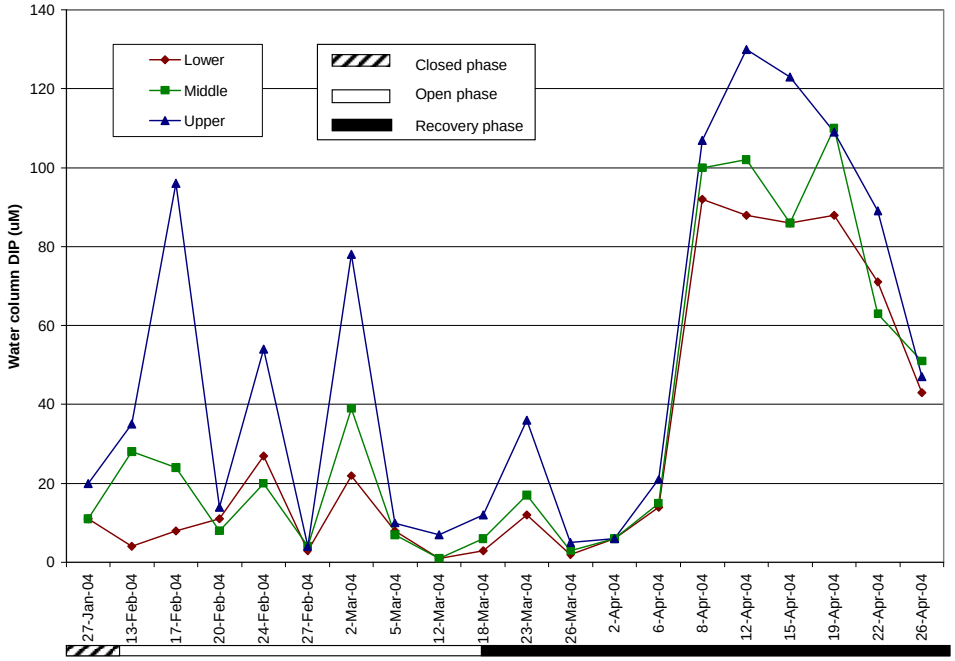


Figure 2.5: DIP concentrations recorded at the lower, middle and upper reaches of the Mdloti Estuary during the sampling period.

Figure 2.6 illustrates measured water column DIN concentrations during the study period. The DIN concentrations increased slightly after the breaching event (from <1 µM to 30 µM), but increase significantly towards the end of the open phase (maximum was 390 µM in the upper reaches). However, it dropped again to the pre-breaching levels within two weeks.

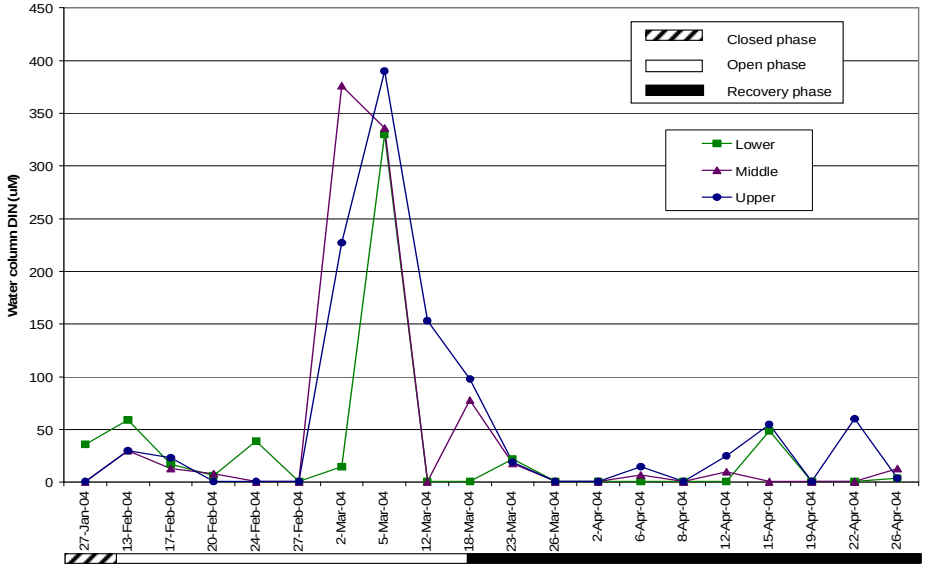


Figure 2.6: DIN concentrations recorded at the lower, middle and upper reaches of the Mdloti Estuary during the sampling period.

Prior to breaching, phytoplankton biomass (chl-*a*) was 115 ± 10 (mean ± SD), 181 ± 0.4 mg.m^{-3} and 106 ± 0 mg.m^{-3} in the lower, middle and upper reaches, respectively (Figure 2.7). During the open phase, average phytoplankton biomass ranged from 3.2 ± 0 mg.m^{-3} to 88 ± 0 mg.m^{-3} in the lower reaches, 1.4 ± 0 mg.m^{-3} to 60 ± 17 mg.m^{-3} in the middle reaches, and 0.7 ± 0 mg.m^{-3} to 79 ± 6 mg.m^{-3} in the upper reaches of the estuary. The nanophytoplankton fraction dominated phytoplankton biomass (85%) during this period. The average phytoplankton biomass during the recovery phase ranged from 15.8 ± 4 mg.m^{-3} to 131 ± 3 mg.m^{-3} in the lower reaches, 39.1 ± 5 mg.m^{-3} to 93 ± 9 mg.m^{-3} in the middle reaches, and 10.4 ± 9 mg.m^{-3} to 111 ± 126 mg.m^{-3} in the upper reaches. Once again phytoplankton was dominated by the nano size-class, which accounted for 62% of the total chl-*a* biomass in the estuary.

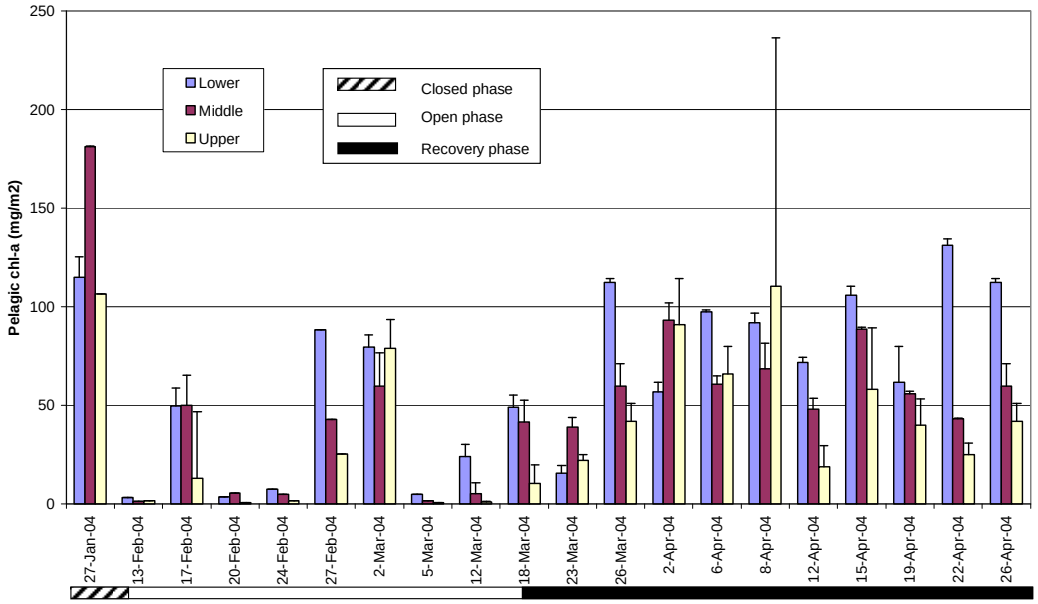


Figure 2.7: Phytoplankton concentrations recorded at the lower, middle and upper reaches of the Mdloti Estuary during the sampling period.

The benthic chl-*a* concentrations prior to breaching were 109 ± 28 (mean ± SD), 42 ± 8, 57 ± 17 mg.m^{-3} in the lower, middle and upper reaches, respectively (Figure 2.8). Benthic chl-*a* concentrations during the open phase ranged from 0.9 ± 0.5 mg.m^{-3} to 302 ± 18 mg.m^{-3} in the lower reaches, 1 ± 1 mg.m^{-3} to 130 ± 88 mg.m^{-3} in the middle reaches and 0.8 ± 0.6 mg.m^{-3} to 82 ± 13 mg.m^{-3} in the upper reaches. During the recovery phase, benthic chl-*a*

concentrations ranged from 78 ± 14 mg.m^{-3} to 291 ± 86 mg.m^{-3}, 81 ± 29 mg.m^{-3} to 355 ± 221 mg.m^{-3} and 15 ± 3 mg.m^{-3} to 415 ± 53 mg.m^{-3} in the lower, middle and upper reaches, respectively. Both highest and lowest mean benthic microalgal biomass values were observed in the upper reaches, the highest during the recovery phase and the lowest during the open phase.

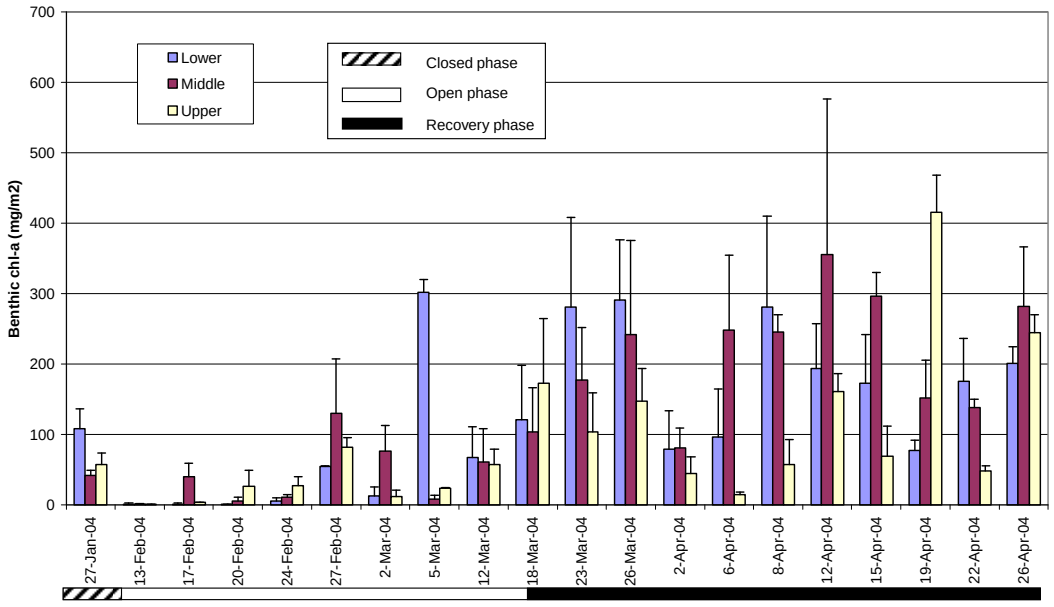


Figure 2.8: Microphytobenthos concentrations recorded at the lower, middle and upper reaches of the Mdloti Estuary during the sampling period.

More information on the phytoplankton and microphytobenthos dynamics in the Mdloti Estuary during this study period can be obtained from Anandraj *et al*. (2008).

2.3.2 Zooplankton composition

The first sampling within this study was done on 27 January 2004, before the estuary was artificially breached on 11 February 2004. A total of 19 zooplankton taxa were identified throughout the estuary prior to mouth breaching (Table 2.1). Thirteen taxa were identified in the lower reaches, with only 5 taxa contributing more than 1% to the total abundance. In the middle reaches, 16 taxa were identified, with only 5 taxa contributing more than 1%

to the total abundance. The upper reaches exhibited 9 of the 13 taxa identified, contributing more than 1% to the total abundance.

Even though 96% of biomass loss was experienced after mouth breaching, a total of 17 taxa were identified throughout the estuary during the first sampling occasion after mouth breaching, with 14 taxa in the lower reaches, 8 taxa in the middle reaches and 6 taxa in the upper reaches. A total of 27 different taxa were identified during the open phase of the study, with 11 taxa contributing more than 1% of the total abundance in the lower reaches, 13 taxa in the middle reaches and 10 taxa in the upper reaches (Table 2.2).

During the open phase, the zooplankton community was dominated by *Keratella* sp. 1, harpacticoid copepodites and *Acartia natalensis*, especially in the lower and middle reaches. Combined, these three taxa accounted for 63% of the abundance in the lower reaches, 65% in the middle reaches and 60% in the upper reaches. *Cyclocypris* sp. 1 was among the dominant taxa during the open phase in the upper reaches, contributing 16%.

The most abundant taxon at all three reaches during the open phase was *Keratella* sp. 1, contributing 31% in the lower, 45% in the middle and 50% in the upper reaches. Even though *Keratella* sp. 1 was the most abundant taxon during the open phase, it was *Gastrosaccus brevifissura* that generally contributed most to total biomass, with 66% in the lower, 75% in the middle and 23% in the upper reaches.

After mouth re-closure, 28 taxa were identified within the estuary, with 8 taxa contributing more than 1% of the zooplankton abundance in the lower and middle reaches, respectively, and 9 taxa in the upper reaches (Table 2.3). However, 2 taxa, namely *Candona* sp. and *Daphnia pulex* only occurred during the recovery phase. A number of taxa showed an increase in abundance after mouth re-closure, namely *Keratella* sp. 1, all copepodites, *Cyclocypris* sp. 1, *Oithona* sp., *Ceriodaphnia* sp., *A. natalensis* and *Chydorus sphaericus*.

During the recovery phase, *Keratella* sp. 1 contributed 21% of the total abundance in the lower, 12% in the middle and 10% in the upper reaches (Table 2.3). Even though the percentage contribution was lower during the recovery phase, their abundances were much higher during the recovery phase than during the open phase (mean: 135345 ± 106970 SD ind.m^{-3} versus 1933 ± 2707 SD ind.m^{-3}) (Tables 2.2 and 2.3).

During the recovery phase, the zooplankton community was dominated by *Pseudodiaptomus hessei*, *Keratella* sp. 1 and harpacticoid copepodites. Combined, these three taxa accounted for 70% of abundance in the lower, 67% in the middle and 78% in the upper reaches. The single most abundant taxon during the recovery phase was *P. hessei* in all three reaches, accounting for 38% of the total zooplankton abundance in the lower, 45% in the middle and 59% in the upper reaches (Table 2.3). *P. hessei* contribution to zooplankton biomass for the same period was 30% in the lower, 37% in the middle and 49% in upper reaches.

The copepod component contributed 73% (copepodites 17%, adults 56%) of the total zooplankton abundance in the lower reaches and 83% in the other two reaches (nauplii 0.01%, copepodites 17%, adults 66%) (Tables 2.2 and 2.4). The contribution of the copepod component to the total zooplankton biomass was very similar, with 72% in the lower reaches (copepodites 5.5%, adults 66.5%), 81% in the middle reaches (copepodites 5.4%, adults 75.6%) and 82% in the upper reaches (copepodites 4.8%, adults 77.2%) (Tables 2.3 and 2.5). The highest copepod contribution for all reaches was during the recovery phase.

For the overall study, *P. hessei* was the dominant species, accounting for 42% of the total abundance and 58% of the total biomass. *Keratella* sp. 1 accounted for 17% and 11% of the total abundance and total biomass, respectively, while harpacticoid copepodites and *A. natalensis* contributed 11% and 10% to the total zooplankton abundance and 3% and 7% to the total zooplankton biomass, respectively (Tables 2.2, 2.3, 2.4 and 2.5).

Table 2.1: Zooplankton abundance and composition (mean) during the closed phase of the Mdloti Estuary (27 Jan 2004) (taxa listed in phylogenetic order).

	Lower		Middle		Upper	
Taxa	**Mean**	**% contribution**	**Mean**	**% contribution**	**Mean**	**% contribution**
Tintinnids	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
***Brachionus* sp. 1**	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
***Brachionus* sp. 2**	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
***Gastropus* sp.**	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
***Keratella* sp. 1**	**98646**	**87.84**	**10945**	**83.21**	**6296**	**43.34**
***Keratella* sp. 2**	**0**	**0.00**	**16**	**0.12**	**228**	**1.57**
***Rotatoria* sp.**	**149**	**0.13**	**90**	**0.68**	**416**	**2.86**
***Testudinella* sp.**	**0**	**0.00**	**0**	**0.00**	**2624**	**18.06**
Polychaete larvae	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
***Candona* sp.**	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
***Cyclocypris* sp. 1**	**679**	**0.60**	**315**	**2.39**	**2876**	**19.8**
***Cyclocypris* sp. 2**	**149**	**0.13**	**0**	**0.00**	**0**	**0.00**
***Cyclocypris* sp. 3**	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
Copepod nauplii	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
Calanoid copepodites	**5184**	**4.62**	**610**	**4.64**	**702**	**4.83**
Cyclopoid copepodites	**1650**	**1.47**	**40**	**0.30**	**22**	**0.15**
Harpacticoid copepodites	**1535**	**1.36**	**223**	**1.70**	**397**	**2.73**
Acartia natalensis	**1721**	**1.54**	**160**	**1.21**	**536**	**3.69**
***Oithona* spp.**	**525**	**0.47**	**11**	**0.08**	**0**	**0.00**
Pseudodiaptomus hessei	**380**	**0.34**	**63**	**0.48**	**38**	**0.26**
***Ceriodaphnia* sp.**	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
Chydoridae cladoceran	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
Chydorus sphaericus	**158**	**0.14**	**36**	**0.27**	**266**	**1.83**
Daphnia pulex	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
Gastrosaccus brevifissurra	**454**	**0.40**	**82**	**0.62**	**0**	**0.00**
Dipteran larvae 1	**157**	**0.14**	**27**	**0.21**	**10**	**0.07**
Dipteran larvae 2	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
Ephemeropteran larvae	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
Hemipteran larvae	**0**	**0.00**	**36**	**0.27**	**0**	**0.00**
Mosquito larvae	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
Tyrophagus putrescentiae	**0**	**0.00**	**0**	**0.00**	**2**	**<0.01**
Fish eggs	**0**	**0.00**	**0**	**0.00**	**0**	**0.00**
Fish larvae	**0**	**0.00**	**11**	**0.08**	**0**	**0.00**
Unidentified eggs	**6**	**<0.01**	**89**	**0.68**	**0**	**0.00**
Total	**112301**	**100**	**13154**	**100**	**14527**	**100**

Table 2.2: Zooplankton abundance and composition (mean ± SD) during the open phase of the Mdloti Estuary (13 Feb 2004 to 12 Mar 2004) (taxa listed in phylogenetic order).

	Lower		Middle		Upper	
Taxa	**Mean ± SD**	**% contribution**	**Mean ± SD**	**% contribution**	**Mean ± SD**	**% contribution**
Tintinnids	1 ± 2.8	0.02	0 ± 0	0.00	0 ± 0	0.00
***Brachionus* sp. 1**	0 ± 0	0.00	421 ± 1190.8	8.51	0 ± 0	0.00
***Brachionus* sp. 2**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
***Gastropus* sp.**	0.8 ± 2.1	0.01	0 ± 0	0.00	0 ± 0	0.00
***Keratella* sp. 1**	1932.6 ± 2707.2	31.13	2245 ± 3336.7	45.40	1952.5 ± 2993.4	50.02
***Keratella* sp. 2**	8.9 ± 17.4	0.14	15.9 ± 44.9	0.32	35.6 ± 42.5	0.91
***Rotatoria* sp.**	16.4 ± 20.1	0.26	70.5 ± 136.9	1.43	155.5 ± 332.9	3.98
***Testudinella* sp.**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Polychaete larvae	16.9 ± 34	0.27	12.1 ± 24.7	0.25	5.4 ± 8.0	0.14
***Candona* sp.**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
***Cyclocypris* sp. 1**	352.3 ± 196.6	5.67	249.1 ± 202.9	5.04	621 ± 1015.4	15.91
***Cyclocypris* sp. 2**	41.4 ± 66.7	0.67	35.9 ± 76.4	0.72	13.3 ± 12.5	0.34
***Cyclocypris* sp. 3**	0.5 ± 1.4	<0.01	6.5 ± 14.2	0.13	2.4 ± 6.7	0.06
Copepod nauplii	1.4 ± 3.5	0.02	1.0 ± 2.8	0.02	0 ± 0	0.00
Calanoid copepodites	103 ± 88.5	1.64	57.5 ± 93.2	1.12	40 ± 61.9	0.88
Cyclopoid copepodites	274.5 ± 255.1	4.37	214.4 ± 359.5	4.16	218.5 ± 372.4	5.71
Harpacticoid copepodites	908.9 ± 843.4	14.71	464.6 ± 774.3	9.07	241.1 ± 409.7	6.21
Acartia natalensis	1047 ± 1186.5	16.86	500 ± 774.4	10.11	161.9 ± 203.1	4.15
***Oithona* spp.**	310.4 ± 505.4	5.00	232.6 ± 406.5	4.70	145 ± 241.1	3.71
Pseudodiaptomus hessei	61 ± 51.0	0.98	61.8 ± 80.5	1.25	99.6 ± 154.0	2.25
***Ceriodaphnia* sp.**	114.1 ± 181.2	1.84	53.9 ± 145.6	1.09	22.1 ± 30.1	0.57
Chydoridae cladoceran	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Chydorus sphaericus	642.9 ± 1031.6	10.35	121.9 ± 187.9	2.46	48 ± 55.8	1.23
Daphnia pulex	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Gastrosaccus brevifissurra	110 ± 133.5	1.77	136.5 ± 327.6	2.76	15.3 ± 42.3	0.39
Dipteran larvae 1	9.5 ± 19	0.15	4.5 ± 7.2	0.09	106.5 ± 168.2	2.73
Dipteran larvae 2	0.1 ± 0.4	<0.01	0 ± 0	0.00	0 ± 0	0.00
Ephemeropteran larvae	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Hemipteran larvae	17.1 ± 27.4	0.28	15.3 ± 38.9	0.31	2.5 ± 7.1	0.06
Mosquito larvae	5.5 ± 14	0.09	3 ± 8.5	0.06	3.0 ± 5.7	0.08
Tyrophagus putrescentiae	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Fish eggs	18.6 ± 29.8	0.30	2.8 ± 7.8	0.06	0 ± 0	0.00
Fish larvae	27.8 ± 46.5	0.45	8.6 ± 15.7	0.17	1.3 ± 3.5	0.03
Unidentified eggs	186 ± 434.2	3.00	10.8 ± 29.2	0.22	13 ± 28.0	0.33
Total	6208.4 ± 3522.8	100	4984.5 ± 4473.0	100	3903.4 ± 4986.1	100

Table 2.3: Zooplankton abundance and composition (mean ± SD) during the recovery phase of the Mdloti Estuary (18 Mar 2004 to 24 Apr 2004) (taxa listed in phylogenetic order).

	Lower		Middle		Upper	
Taxa	**Mean ± SD**	**% contribution**	**Mean ± SD**	**% contribution**	**Mean ± SD**	**% contribution**
Tintinnids	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
***Brachionus* sp. 1**	0 ± 0	0.00	134.4 ± 445.6	0.03	0 ± 0	0.00
***Brachionus* sp. 2**	307.3 ± 1019.1	0.05	717.6 ± 2380.1	0.14	0 ± 0	0.00
***Gastropus* sp.**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
***Keratella* sp. 1**	135345.1 ± 106969.8	21.04	58658.3 ± 63674.1	11.80	19441 ± 22656.3	9.97
***Keratella* sp. 2**	0 ± 0	0.00	375.8 ± 1023.7	0.08	72.9 ± 135.9	0.04
***Rotatoria* sp.**	0 ± 0	0.00	64.1 ± 152.0	0.01	54.3 ± 134.1	0.03
***Testudinella* sp.**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Polychaete larvae	0 ± 0	0.00	3.6 ± 12.1	<0.01	8.7 ± 24.1	<0.01
***Candona* sp.**	1477.5 ± 3385.0	0.23	3286.4 ± 9277.9	0.66	207.5 ± 419.0	0.11
***Cyclocypris* sp. 1**	2.2 ± 7.2	<0.01	8.7 ± 28.9	<0.01	53.2 ± 91.4	0.03
***Cyclocypris* sp. 2**	101.3 ± 249.4	0.02	1237.5 ± 2139.0	0.25	5.8 ± 19.3	<0.01
***Cyclocypris* sp. 3**	23594.5 ± 20046.5	3.67	22653.5 ± 27163.6	4.54	15294.3 ± 24601.1	7.87
Copepod nauplii	1989.1 ± 3295.2	0.31	1959.2 ± 1614.3	0.39	2087.2 ± 1452.1	1.07
Calanoid copepodites	13969.5 ± 17565.8	2.17	10205.4 ± 13541.6	2.05	2429.4 ± 3908.0	1.22
Cyclopoid copepodites	27910.3 ± 319138.7	4.34	11899.1 ± 12812.0	2.39	3618.3 ± 6196.6	1.86
Harpacticoid copepodites	74771.2 ± 71249.6	11.62	56011.2 ± 58106.8	11.29	17005.6 ± 27394.4	8.72
Acartia natalensis	62615 ± 60330.2	9.73	56795.5 ± 4333.7	11.43	13250.8 ± 33817.8	6.80
***Oithona* spp.**	58004.2 ± 68530.5	9.02	48687.5 ± 53377.3	9.80	5962.5 ± 12264.6	3.06
Pseudodiaptomus hessei	241549.3 ± 279490.9	37.55	221956.3 ± 196139.7	44.65	114806 ± 158404.4	58.87
***Ceriodaphnia* sp.**	184.9 ± 308.3	0.03	156.3 ± 476.9	0.03	0 ± 0	0.00
Chydoridae cladoceran	0 ± 0	0.00	0 ± 0	0.00	3.6 ± 12.1	<0.01
Chydorus sphaericus	0.9 ± 3.0	<0.01	24.7 ± 55.1	<0.01	11.3 ± 37.4	<0.01
Daphnia pulex	665.9 ± 1161.1	0.10	376.4 ± 709.5	0.08	231.5 ± 534.5	0.12
Gastrosaccus brevifissurra	91.5 ± 147.7	0.01	39.9 ± 73.1	<0.01	12.8 ± 27.3	0.01
Dipteran larvae 1	14.8 ± 33.9	<0.01	139.2 ± 327.1	0.03	80 ± 134.8	0.04
Dipteran larvae 2	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Ephemeropteran larvae	0.1 ± 0.3	<0.01	6.9 ± 18.3	<0.01	4 ± 10.0	<0.01
Hemipteran larvae	0.1 ± 0.3	<0.01	0 ± 0	0.00	0 ± 0	0.00
Mosquito larvae	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Tyrophagus putrescentiae	0 ± 0	0.00	6 ± 19.9	<0.01	0 ± 0	0.00
Fish eggs	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Fish larvae	25.3 ± 71.6	<0.01	4.3 ± 14.2	<0.01	0 ± 0	0.00
Unidentified eggs	584.3 ± 1152.8	0.09	1643.8 ± 2554.9	0.33	370 ± 754.3	0.19
Total	643204.1 ± 462602.0	100	497051.5 ± 324999.7	100	195007.1 ± 244044.1	100

Table 2.4: Zooplankton biomass and composition (mean ± SD) during the open phase of the Mdloti Estuary (13 Feb 2004 to 12 Mar 2004) (taxa listed in phylogenetic order).

	Lower	Middle		Upper		
Taxa	**Mean ± SD**	**% contribution**	**Mean ± SD**	**% contribution**	**Mean ± SD**	**% contribution**
Tintinnids	0.002 ± 0.004	<0.01	0 ± 0	0.00	0 ± 0	0.00
***Brachionus* sp. 1**	0 ± 0	0.00	0.8 ± 2.4	2.16	0 ± 0	0.00
***Brachionus* sp. 2**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
***Gastropus* sp.**	0.002 ± 0.004	<0.01	0 ± 0	0.00	0 ± 0	0.00
***Keratella* sp. 1**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
***Keratella* sp. 2**	0.02 ± 0.04	0.05	0.03 ± 0.09	0.08	0.07 ± 0.09	0.50
***Rotatoria* sp.**	0.03 ± 0.03	0.07	0.1 ± 0.2	0.27	0.2 ± 0.5	1.63
***Testudinella* sp.**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Polychaete larvae	0.2 ± 0.4	0.51	0.1 ± 0.3	0.34	0.06 ± 0.09	0.40
***Candona* sp.**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
***Cyclocypris* sp. 1**	0.1 ± 0.2	0.29	0.1 ± 0.2	0.23	0.03 ± 0.03	0.23
***Cyclocypris* sp. 2**	0.001 ± 0.004	<0.01	0.02 ± 0.04	0.04	0.006 ± 0.01	0.04
***Cyclocypris* sp. 3**	0.2 ± 0.2	0.70	0.2 ± 0.3	0.49	0.2 ± 0.3	1.27
Copepod nauplii	0.9 ± 0.5	2.48	0.6 ± 0.5	1.60	1.6 ± 2.5	10.83
Calanoid copepodites	0.1 ± 0.1	0.26	0.1 ± 0.1	0.13	0.04 ± 0.06	0.23
Cyclopoid copepodites	1.0 ± 1.5	2.71	0.2± 0.3	0.47	0.07 ± 0.08	0.50
***H*arpacticoid copepodites**	0.8 ± 0.8	2.30	0.4 ± 0.7	1.07	0.2 ± 0.4	1.63
Acartia natalensis	2.3 ± 2.6	6.48	1.1 ± 1.7	2.83	0.4 ± 0.4	2.48
***Oithona* spp.**	0.7 ± 1.1	1.92	0.5 ± 0.9	1.32	0.3 ± 0.5	2.22
Pseudodiaptomus hessei	0.09 ± 0.08	0.26	0.09 ± 0.12	0.24	0.15 ± 0.23	1.04
***Ceriodaphnia* sp.**	0.5 ± 0.7	1.28	0.22 ± 0.58	0.55	0.09 ± 0.12	0.62
Chydoridae cladoceran	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Chydorus sphaericus	0.003 ± 0.008	<0.01	0.002 ± 0.006	<0.01	0 ± 0	0.00
Daphnia pulex	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Gastrosaccus brevifissurra	23.7 ± 28.7	66.48	29.3 ± 70.4	75.45	3.3 ± 9.1	22.86
Dipteran larvae 1	0.3 ± 0.6	0.91	0.15 ± 0.25	0.39	3.6 ± 5.7	25.24
Dipteran larvae 2	0.004 ± 0.012	0.01	0 ± 0	0.00	0 ± 0	0.00
Ephemeropteran larvae	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Hemipteran larvae	0.1 ± 0.2	0.31	0.1 ± 0.2	0.25	0.02 ± 0.04	0.11
Mosquito larvae	0.2 ± 0.5	0.54	0.1 ± 0.3	0.27	0.1 ± 0.2	0.73
Tyrophagus putrescentiae	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Fish eggs	0.03 ± 0.04	0.08	0.004 ± 0.011	0.01	0 ± 0	0.00
Fish larvae	0.2 ± 0.4	0.70	0.08 ± 0.14	0.20	0.01 ± 0.03	0.07
Unidentified eggs	0.3 ± 0.7	0.78	0.016 ± 0.044	0.04	0.02 ± 0.04	0.14
Total	35.57 ± 33.36	100	38.90 ± 70.97	100	14.3 ± 17.2	100

Table 2.5: Zooplankton biomass and composition (mean ± SD) during the recovery phase of the Mdloti Estuary (18 Mar 2004 to 24 Apr 2004) (taxa listed in phylogenetic order).

	Lower		Middle		Upper	
Taxa	**Mean ± SD**	**% contribution**	**Mean ± SD**	**% contribution**	**Mean ± SD**	**% contribution**
Tintinnids	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
***Brachionus* sp. 1**	0 ± 0	0.00	0.3 ± 0.9	0.03	0 ± 0	0.00
***Brachionus* sp. 2**	0.6 ± 2.0	0.05	1.4 ± 4.8	0.16	0 ± 0	0.00
***Gastropus* sp.**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
***Keratella* sp. 1**	270.7 ± 213.9	22.44	117.3 ± 127.3	13.17	38.9 ± 45.3	11.15
***Keratella* sp. 2**	0 ± 0	0.00	0.8 ± 2.0	0.08	0.15 ± 0.27	0.04
***Rotatoria* sp.**	0 ± 0	0.00	0.1 ± 0.2	0.01	0.08 ± 0.20	0.02
***Testudinella* sp.**	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Polychaete larvae	0 ± 0	0.00	0.04 ± 0.13	<0.01	0.09 ± 0.26	0.03
***Candona* sp.**	3.7 ± 8.5	0.31	8.2 ± 23.2	0.92	0.5 ± 1.0	0.15
***Cyclocypris* sp. 1**	0.005 ± 0.018	<0.01	0.02 ± 0.07	<0.01	0.13 ± 0.23	0.04
***Cyclocypris* sp. 2**	0.3 ± 0.6	0.01	3.1 ± 5.3	0.35	0.01 ± 0.05	<0.01
***Cyclocypris* sp. 3**	21.2 ± 18.0	2.20	20.4 ± 24.4	2.50	13.8 ± 22.1	3.50
Copepod nauplii	5.0 ± 8.2	0.27	4.9 ± 4.0	0.55	5.2 ± 3.6	1.50
Calanoid copepodites	12.6 ± 15.8	1.69	9.2 ± 12.2	1.75	2.2 ± 3.5	1.64
Cyclopoid copepodites	41.9 ± 58.7	3.47	17.8 ± 19.2	2.00	5.4 ± 9.3	1.56
Harpacticoid copepodites	67.3 ± 64.1	4.49	50.4 ± 52.3	4.73	15.3 ± 24.7	3.82
Acartia natalensis	137.8 ± 132.7	11.42	125.0 ± 95.3	14.03	29.2 ± 74.4	8.36
***Oithona* spp.**	127.6 ± 150.8	10.58	107.1 ± 117.4	12.02	13.1 ± 27.0	3.76
Pseudodiaptomus hessei	362.3 ± 419.2	30.04	332.9 ± 294.3	37.37	172.2 ± 237.6	49.39
***Ceriodaphnia* sp.**	0.7 ± 1.2	0.06	0.63 ± 1.9	0.07	0 ± 0	0.00
Chydoridae cladoceran	0 ± 0	0.00	0 ± 0	0.00	0.008 ± 0.027	<0.01
Chydorus sphaericus	0.002 ± 0.007	<0.01	0.05 ± 0.12	<0.01	0.02 ± 0.08	<0.01
Daphnia pulex	133.2 ± 232.2	11.04	75.3 ± 141.9	8.45	46.3 ± 106.9	13.28
Gastrosaccus brevifissurra	19.7 ± 31.8	1.63	8.6 ± 15.7	0.96	2.8 ± 5.9	0.79
Dipteran larvae 1	0.5 ± 1.2	0.04	4.7 ± 11.1	0.53	2.7 ± 4.6	0.78
Dipteran larvae 2	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Ephemeropteran larvae	0.001 ± 0.003	<0.01	0.07 ± 0.18	<0.01	0.04 ± 0.10	<0.01
Hemipteran larvae	0.001 ± 0.002	<0.01	0 ± 0	0.00	0 ± 0	0.00
Mosquito larvae	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Tyrophagus putrescentiae	0 ± 0	0.00	0.06 ± 0.22	<0.01	0 ± 0	0.00
Fish eggs	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00
Fish larvae	0.3 ± 0.6	0.02	0.04 ± 0.13	<0.01	0 ± 0	0.00
Unidentified eggs	0.9 ± 1.7	0.07	2.5 ± 3.8	0.28	0.6 ± 1.1	0. 16
Total	1206.08 ± 826.52	100	890.87 ± 568.49	100	348.7 ± 442.1	100

2.3.3 Zooplankton abundance and biomass

Prior to breaching, the total zooplankton abundance was 1.12 x 10^5 ind.m^{-3} in the lower reaches, 1.32 x 10^4 ind.m^{-3} in the middle reaches and 1.45 x 10^4 ind.m^{-3} in the upper reaches. The zooplankton abundance decreased drastically when the estuary breached, dropping to 1.6 x 10^3 ind.m^{-3}, 5.8 x 10^2 ind.m^{-3} and 1.7 x 10^2 ind.m^{-3} in the lower, middle and upper, respectively. This amounted to a 98% loss in total zooplankton abundance (Figures 2.9). For the duration of the open phase, zooplankton abundance ranged from 1.4 x 10^2 ind.m^{-3} (upper reaches) to 1.6 x 10^4 ind.m^{-3} (upper reaches) with a mean value of 5.3 x 10^3 ± 4.5 x 10^3 ind.m^{-3} SD (Figure 2.9).

A one-way ANOVA revealed significant differences between phases ($d.f._{2, 59}$ = 55.0; p < 0.001), with the recovery phase showing consistently higher values than the open and closed phases.

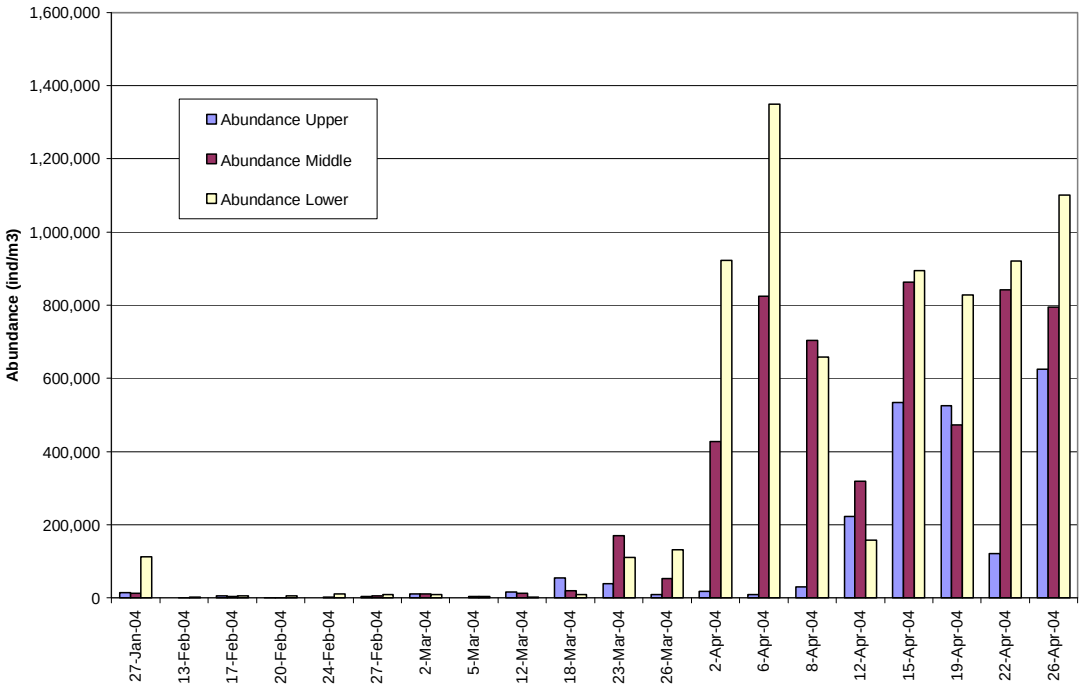


Figure 2.9: Zooplankton abundance obtained at each station at the Mdloti Estuary during the sampling period.

Before breaching, zooplankton biomass was 318 mg.m^{-3}, 43.9 mg.m^{-3} and 29.4 mg.m^{-3} for the lower, middle and upper reaches, respectively. The day after breaching, the biomass dropped dramatically to 12.9, 1.97 and 0.3 mg.m^{-3} at the three stations, experiencing a 96% loss in total zooplankton biomass (Figure 2.10). Within five days after breaching, a rapid temporary build-up of zooplankton biomass was evident, with the lower, middle and upper reaches attaining 18.4, 10.2 and 11.8 mg.m^{-3} respectively. For the duration of the open phase, biomass ranged from 0.3 mg.m^{-3} (upper reaches) to 211 mg.m^{-3} (middle reaches), with a mean value of 30.1 mg.m^{-3} ± 45.7 SD.

One-way ANOVA results for zooplankton biomass showed significant differences between the phases ($d.f._{2, 59}$ = 15.51; p < 0.001), with the recovery phase showing higher values than the other phases.

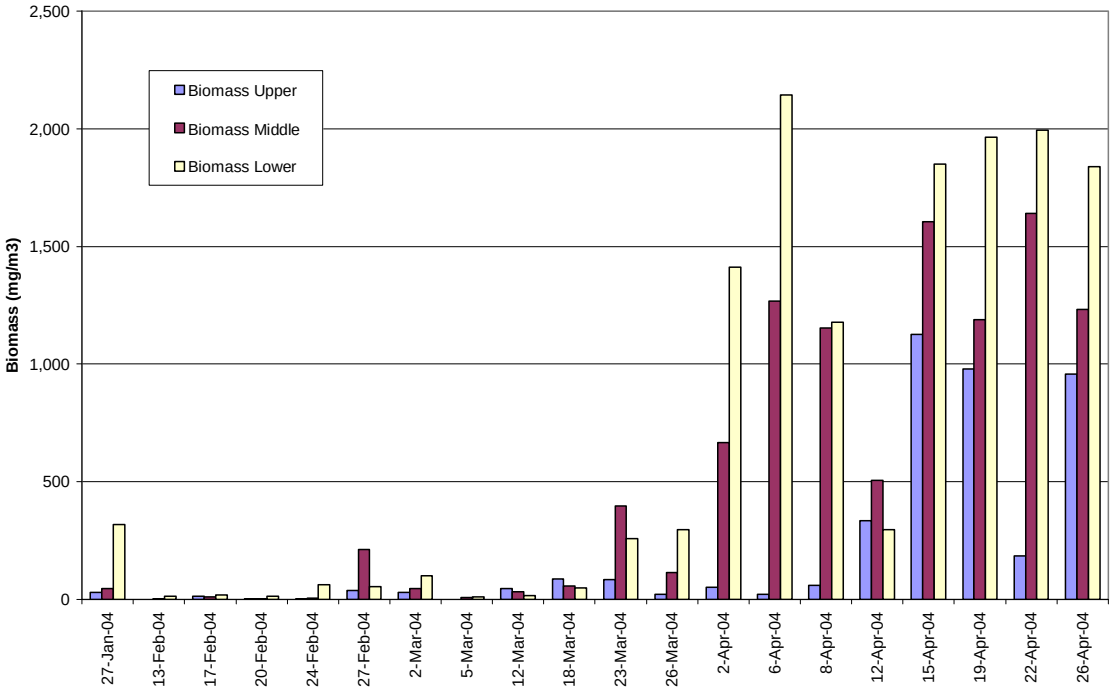


Figure 2.10: Zooplankton biomass obtained at each station at the Mdloti Estuary during the sampling period.

At the time of mouth re-closure, zooplankton abundance increased three fold in the lower reaches, nearly doubled in the middle reaches and increased nearly four times in the upper reaches from the levels observed four days earlier. Six days later, zooplankton abundance increased nearly twelve fold in

the lower reaches (from 8.7 x 10^3 ind.m^{-3} to 1.1 x 10^5 ind.m^{-3}), nearly nine fold in the middle reaches (from 1.9 x 10^4 ind.m^{-3} to 1.7 x 10^5 ind.m^{-3}), but decreased in the upper reaches (from 5.5 x 10^4 ind.m^{-3} to 3.9 x 10^4 ind.m^{-3}).

Zooplankton abundance in the lower reaches increased over time, reaching a peak nineteen days after mouth re-closure (1.3 x 10^6 ind.m^{-3}), but later decreased again settling at around 9.0 x 10^5 ind.m^{-3} for the rest of the study period. Zooplankton abundance in the middle reaches fluctuated between 1.9 x 10^4 ind.m^{-3} and 8.4 x 10^5 ind.m^{-3} for the duration of the study, not stabilising or peaking at any stage. In the upper reaches, zooplankton abundance first decreased to 8.7 x 10^3 ind.m^{-3} and then increased to 6.2 x 10^5 ind.m^{-3} towards the end of the study.

At the time of mouth re-closure, zooplankton biomass had doubled at each station from its previous levels, four days earlier. Six days after mouth re-closure, zooplankton biomass increased nearly five-fold in the lower reaches, (from 47.7 mg.m^{-3} to 257 mg.m^{-3}) and seven-fold in the middle reaches (from 56.2 mg.m^{-3} to 406 mg.m^{-3}), but remained virtually the same in the upper reaches (from 87.3 mg.m^{-3} to 88.7 mg.m^{-3}).

Zooplankton biomass reached a peak in the lower reaches 19 days after mouth re-closure (4.36 g.m^{-3}), dropping again during the following week, just to pick up and stabilise at around 2.3 g.m^{-3} (Figure 2.10). The middle reaches also experienced a biomass peak after 19 days (2.9 g.m^{-3}). Twenty-one days after mouth re-closure, the middle reaches exhibited slightly higher zooplankton biomass than the lower reaches (2.2 g.m^{-3} versus 1.8 g.m^{-3}), before a drop occurred 4 days later (835 mg.m^{-3}). It then stabilised at around 2 x 10^3 mg.m^{-3} for the duration of the study, never reaching the same biomass levels as those recorded in the lower reaches again. The upper reaches, however, exhibited much higher biomass levels during the recovery phase than the other two reaches (87 mg.m^{-3} versus 48 mg.m^{-3} and 56 mg.m^{-3}). Eight days after mouth re-closure, biomass in the upper reaches dropped to only 21 mg.m^{-3}, but increased to 109 mg.m^{-3} 21 days after mouth re-closure. A week later, the biomass recorded in the upper reaches was 2.28 g.m^{-3},

before dropping again to 317 mg.m^{-3}. At the end of the study, the biomass in the upper reaches was 1.5 g.m^{-3}.

ANCOVA revealed significant differences between zooplankton abundance (d.f.$_{0.05;2,56}$=*5.51, p* < 0.01) and biomass (d.f.$_{0.05;2,56}$=*2.97, p* = 0.05) at the three different reaches. In both cases, the lower reaches recovered quicker than the middle and upper reaches.

T-tests conducted revealed a number of significant differences. Total zooplankton biomass in the lower reaches showed a significant difference between the open and the recovery phase (*t* = 3.6; *p* < 0.001). Total zooplankton biomass in the middle and upper reaches also showed a significant difference between the open and the recovery phase (middle: *t* = 4.1; *p* < 0.001; upper: *t* = 2.1; *p* < 0.05). Total zooplankton abundance showed a significant difference between open and recover phase in the lower reaches (*t* = 7.2; *p* < 0.001), as well as in the middle and the upper reaches (middle: *t* = 8.1; *p* < 0.001; upper: *t* = 4.9; *p* < 0.001). The dominant species, *P. hessei*, also showed a significant difference between the open and the recovery phase throughout the estuary (lower: *t* = 5.2; *p* < 0.001; middle: *t* = 6.7; *p* < 0.001; upper: *t* = 5.0, *p* < 0.001).

For the lower reaches, Pearson correlation analysis of total zooplankton abundance and biomass showed significant correlations with temperature, salinity, DIP and phytoplankton, but not with the other physico-chemical parameters measured during the study (Table 2.6). The dominant taxon, *P. hessei*, was not correlated to any parameter, while the other three taxa where all positively correlated to DIP and phytoplankton. *Keratella* sp. 1 was also positively correlated to depth and salinity, *Acartia natalensis* to temperature, while the harpacticoid copepodites were negatively correlated to temperature and salinity.

Table 2.6: Results of the Pearson correlation analysis between: (a) zooplankton abundance; and (b) biomass in the lower reaches (including dominant groups) and environmental variables; *p<0.05; ** p<0.01.

(a)

Variable	Total Abundance *r*	*P. hessei* *r*	*Keratella* sp. 1 *r*	Harpacticoid copepodites *r*	*A. natalensis* *r*
Depth	0.63	0.53	0.76*	0.23	0.39
Temperature	-0.24*	-0.35	-0.28	-0.04**	-0.28*
Dissolved O_2	0.009	0.04	0.03	-0.06	-0.07
pH	0.34	0.26	0.22	-0.90	0.31
Salinity	-0.44*	-0.43	-0.53*	-0.28*	-0.38
DIN	-0.39	-0.45	-0.20	-0.22	-0.46
DIP	0.64*	0.62	0.59**	0.18*	0.59*
Phytoplankton	0.67**	0.62	0.67*	0.42**	0.56*
Microphytobenthos	0.61	0.53	0.66	0.32	0.48

(b)

Variable	Total Biomass *r*	*P. hessei* *r*	*Keratella* sp. 1 *r*	Harpacticoid copepodites *r*	*A. natalensis* *r*
Depth	0.67	0.48	0.72*	0.41**	0.42
Temperature	-0.26*	-0.39	-0.26	-0.28	-0.34*
Dissolved O_2	-0.04	0.03	0.02	-0.06	-0.06
pH	0.34	0.26	0.25	0.15	0.29
Salinity	-0.38*	-0.41	-0.52*	-0.39*	-0.37
DIN	-0.43	-0.46	-0.22	-0.35	-0.49
DIP	0.62*	0.61	0.65**	0.39**	0.58*
Phytoplankton	0.72*	0.59	0.64*	0.58**	0.58*
Microphytobenthos	0.57	0.49	0.61	0.48	0.48

For the middle reaches, total zooplankton abundance and biomass again showed a significant correlation with temperature, salinity, DIP, and microphytobenthos (Table 2.7). *P. hessei* showed a negative correlation with salinity, but a positive correlation with microphytobenthos. The other taxa again showed a significant correlation with temperature, DIP and microphytobenthos.

Table 2.7: Results of the Pearson correlation analysis between: (a) zooplankton abundance; and (b) biomass in the middle reaches (including dominant groups) and environmental variables; *p<0.05; ** p<0.01.

(a)

Variable	Total Abundance *r*	*P. hessei* *r*	*Keratella* sp. 1 *r*	Harpacticoid copepodites *r*	*A. natalensis* *r*
Depth	0.56	0.43	0.64	0.58	0.49
Temperature	-0.45*	-0.37	-0.35**	-0.48	-0.43**
Dissolved O_2	-0.005	0.17	-0.07	0.007	0.01
pH	0.06	0.27	-0.15	0.03	0.15
Salinity	-0.29*	-0.27*	0.05	-0.12	0.002*
DIN	-0.34	-0.47	-0.41	-0.40	-0.53
DIP	0.49**	0.45	0.49*	0.33*	0.36**
Phytoplankton	0.68	0.60	0.78	0.78	0.71
Microphytobenthos	0.86**	0.74**	0.80*	0.93*	0.88**

(b)

Variable	Total Biomass *r*	*P. hessei* *r*	*Keratella* sp. 1 *r*	Harpacticoid copepodites *r*	*A. natalensis* *r*
Depth	0.52	0.39	0.61	0.34	0.35
Temperature	-0.39*	-0.37	-0.40	-0.49**	-0.48**
Dissolved O_2	-0.03	0.07	-0.04	0.02	0.07
pH	0.12	0.31	-0.16	0.23	0.29
Salinity	-0.23*	-0.33*	-0.19	-0.28	-0.25*
DIN	-0.39	-0.40	-0.31	-0.39	-0.44
DIP	0.45**	0.55	0.56*	0.52*	0.51**
Phytoplankton	0.71	0.54	0.71	0.55	0.55
Microphytobenthos	0.87**	0.70**	0.79*	0.75*	0.78**

The zooplankton abundance and biomass in the upper reaches of the estuary showed very similar results to the zooplankton abundance and biomass in the middle reaches, with a significant correlation to temperature, DIP and microphytobenthos (Table 2.8). However, no significant correlation was found for salinity. *P. hessei* showed a negative correlation with temperature and a positive correlation with DIP and microphytobenthos. The other three dominant taxa showed a significant correlation with microphytobenthos, while *Keratella* sp. 1 and the harpacticoid copepodites showed a negative correlation with temperature, with *Keratella* sp. 1 also showing a positive correlation with DIP.

Table 2.8: Results of the Pearson correlation analysis between: (a) zooplankton abundance; and (b) biomass in the upper reaches (including dominant groups) and environmental variables; *p<0.05; ** p<0.01.

(a)

Variable	Total Abundance *r*	*P. hessei* *r*	*Keratella* sp. 1 *r*	Harpacticoid copepodites *r*	*A. natalensis* *r*
Depth	0.63	0.49	0.67	0.58	0.64
Temperature	-0.62*	-0.61*	-0.57*	-0.60*	-0.51
Dissolved O_2	0.27	0.27	0.34	0.38	0.08
pH	0.24	0.20	0.15	0.41	0.24
Salinity	-0.29	-0.41	-0.20	-0.16	-0.14
DIN	-0.007	0.02	0.10	-0.04	-0.09
DIP	0.42*	0.52*	0.42*	0.25	0.34
Phytoplankton	0.64	0.60	0.59	0.60	0.64
Microphytobenthos	0.69**	0.55*	0.62**	0.76*	0.72*

(b)

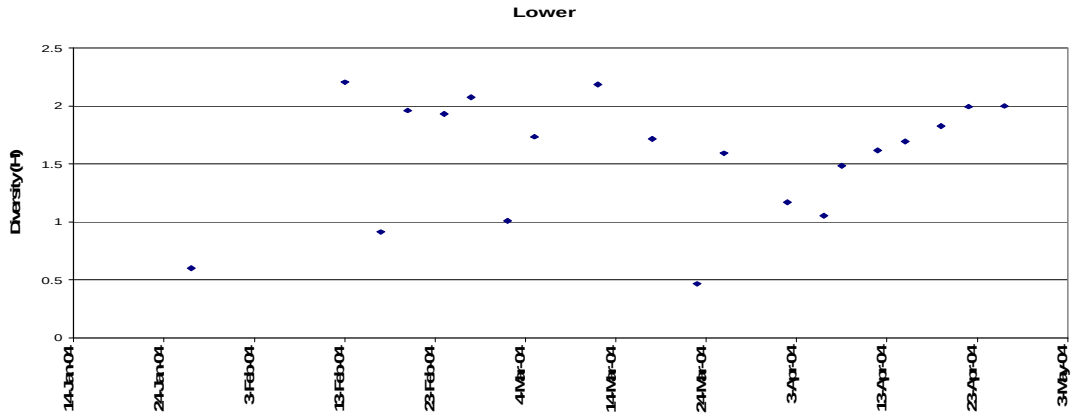
Variable	Total Biomass *r*	*P. hessei* *r*	*Keratella* sp. 1 *r*	Harpacticoid copepodites *r*	*A. natalensis* *r*
Depth	0.56	0.35	0.58	0.29	0.33
Temperature	-0.64**	-0.60**	-0.62*	-0.62*	-0.51
Dissolved O_2	0.29	0.35	0.40	0.33	0.27
pH	0.27	0.30	0.15	0.34	0.38
Salinity	-0.25	-0.34	-0.17	-0.21	-0.10
DIN	-0.03	-0.06	0.17	0.003	-0.08
DIP	0.43**	0.58**	0.51*	0.47	0.38
Phytoplankton	0.63	0.49	0.47	0.33	0.33
Microphytobenthos	0.69**	0.53**	0.59**	0.67**	0.65*

2.3.4 Zooplankton community structure

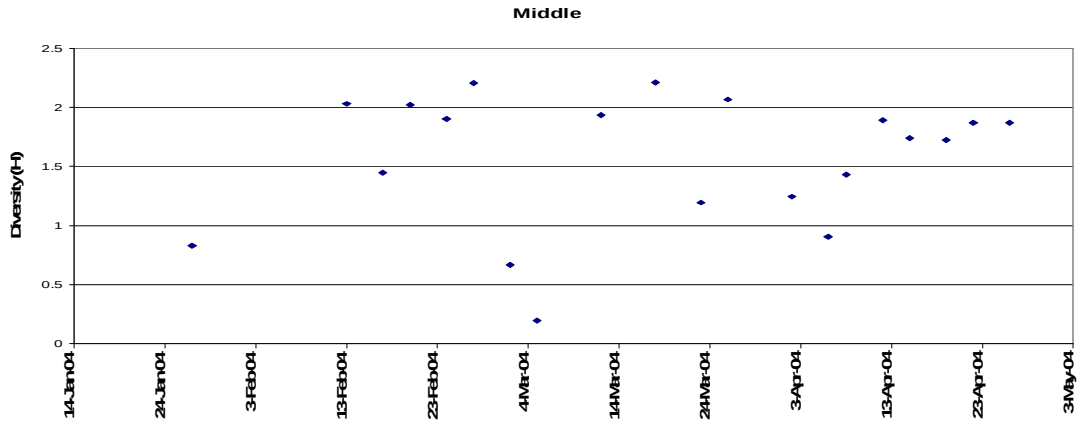
A total of 35 zooplankton taxa were recorded during the entire study period. A total of 19 taxa were identified prior to breaching, while 27 taxa were recorded during the open phase and 28 taxa during the recovery phase.

Shannon-Wiener diversity indexes (*H'*) of the untransformed means of zooplankton abundance ranged from 0.47 to 2.21 for the lower reaches, 0.67 to 2.21 for the middle reaches and 0.57 to 2.52 for the upper reaches (Figure 2.11).

(a)



(b)



(c)

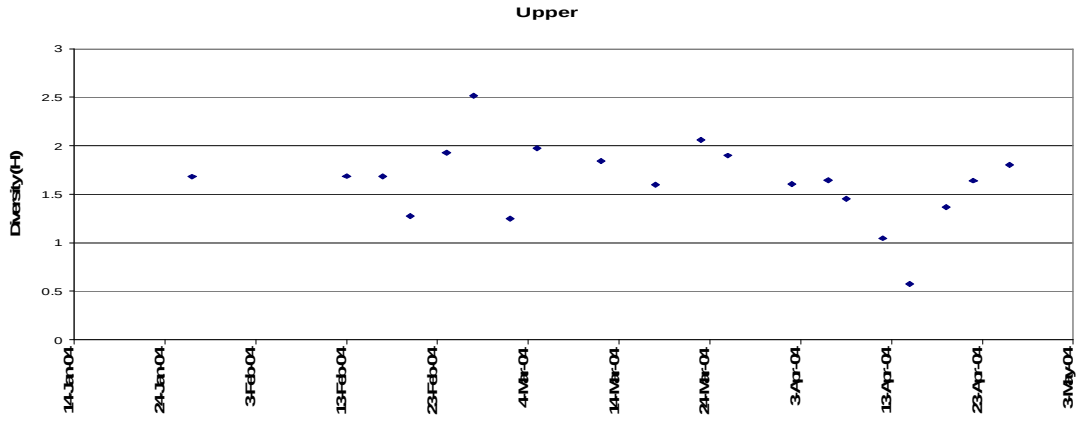


Figure 2.11: Shannon-Wiener diversity indices for the zooplankton community of: (a) the lower reaches; (b) the middle reaches; and (c) the upper reaches of the Mdloti Estuary during the study period.

Using the mean values over time of the environmental variables for the lower, middle and upper reaches, a PCA ordination was performed to summarise the contribution of the most important factors to zooplankton variance (Figure 2.12).

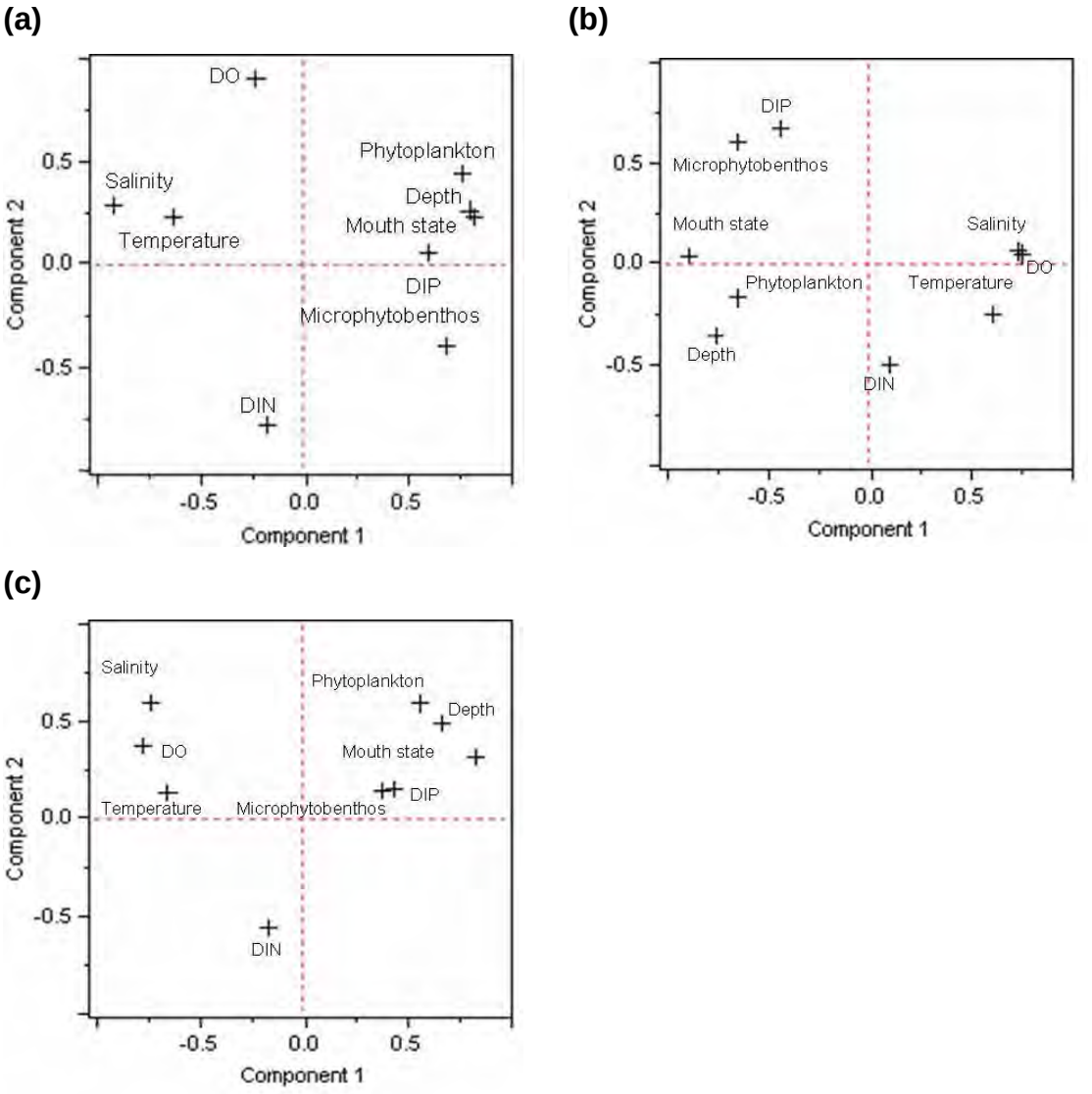


Figure 2.12: Principal components ordination of environmental and biological parameters for: (a) lower reaches (b) middle reaches and (c) upper reaches of the Mdloti Estuary during the study period. (DIN: dissolved inorganic nitrogen; DIP: dissolved inorganic phosphorus; DO: dissolved oxygen).

In the lower reaches, three components accounted for 77.6% of the variance. Component I represented 24.9% of the variance and included dissolved oxygen (DO) and DIN. Component II represented 41.7% of the variance and

included the state of the mouth, depth, salinity, phytoplankton and microphytobenthos biomass. The third component represented 11% of the variance and included DIP and temperature.

In the middle reaches, the three components accounted for 69% of the total variance. Component I represented 39.7% of the variance and included the state of the mouth, depth, temperature, salinity and phytoplankton biomass. Component II represented 16.8% of the variance and was associated with DO, while Component III represented 12.5% of the variance and included DIN, DIP and microphytobenthos biomass.

In the upper reaches, the three components accounted for 72.9% of the total zooplankton variance. Component I represented 11.7% of the variance and was associated with depth, DO, the state of the mouth and phytoplankton biomass. Component II represented 50.2% of the variance and included temperature and salinity. Component III represented 11% of the variance and included DIN, DIP and microphytobenthos biomass.

2.4 Discussion

The Mdloti Estuary was artificially breached on 11 Feb 2004 due to a fish kill. The breaching event had a severe impact on the zooplankton community, with 98% of its abundance / biomass being washed out to sea. A number of studies in TOCEs have shown that breaching events culminate in a decrease in zooplankton biomass and abundance (Perissinotto *et al.* 2000; Kibirige & Perissinotto 2003a; 2003b; Kibirige *et al.* 2006). The decrease can be attributed to the outflow of zooplankton-rich water from the estuary into the ocean. Therefore, the sharp decrease in zooplankton abundance and biomass observed in the Mdloti Estuary after the breaching event is not unexpected (Figures 2.9 and 2.10).

For the duration of the study, the mean zooplankton abundance value of 3.6 x 10^5 ± 4.6 x 10^5 ind.m^{-3} SD recorded in the lower reaches was 1.3 times higher that the value of 2.7 x 10^5 ± 3.5 x 10^5 ind.m^{-3} observed in the middle reaches

and 3.3 times higher than that of the upper reaches, with 1.1 x 10^5 ± 2.0 x 10^5 ind.m^{-3}. Similarly, the mean zooplankton biomass of 1.0 x 10^3 ± 1.3 x 10^3 mg.m^{-3} for the lower reaches was 1.3 times higher that the biomass of 8.1 x 10^2 ± 1.0 x 10^3 mg.m^{-3} for the middle reaches and 2.9 times higher than the upper reaches with 3.6 x 10^2 ± 6.8 x 10^2 mg.m^{-3}. During the open phase, seawater penetrated the estuary, bringing marine breeding organisms into the estuary. This increased the zooplankton taxonomic diversity and led to a change in the zooplankton community structure, especially in the lower reaches. This is in agreement with results obtained in other studies (Kibirige & Perissinotto 2003b; Froneman 2004; Kibirige *et al.* 2006).

Before mouth breaching, 19 zooplankton taxa were identified in the entire estuary. After mouth breaching, 27 taxa were identified, possibly due to the incursion of marine taxa. Two taxa were recorded during the closed phase, but disappeared during the open phase. On the other hand, 12 taxa not present during the closed phase were recorded during the open phase. However, the total zooplankton abundance and biomass during the open phase were much lower than during the closed phase for all three stations (Figures 2.10 and 2.11). The zooplankton abundance during the open phase was marked by a clear dominance of *Acartia natalensis*, harpacticoid copepodites, *Keratella* sp. 1 and *Cyclocypris* sp. 1 at all three stations. Even though *Gastrosaccus brevifissura* was not dominant in numbers, it dominated the zooplankton biomass during the open phase. This is in accordance with previous findings by Jerling and Wooldridge (1995a) and shows that mysids may dominate zooplankton in terms of biomass, even though their abundance may be low.

It has been suggested that zooplankton requires an extended period of mouth closure in order to respond to an increase in microalgal availability and convert this into number and biomass growth (Whitfield 1980; Kibirige & Perissinotto 2003b; Kibirige *et al*. 2006). Re-closure of the Mdloti mouth prevented further losses of zooplankton through flushing and stabilising of the estuary, thereby promoting zooplankton biomass accumulation. A rapid accumulation of zooplankton abundance and biomass was evident

immediately after mouth closure. Pre-breaching levels were exceeded only nine days after mouth closure. Therefore, the state of the mouth is the primary factor responsible for regulating the recovery of zooplankton abundance and biomass in the Mdloti. The timing of the recovery was shorter than expected, indicating the impact of the state of the mouth on the zooplankton community.

Zooplankton abundance and biomass continued to increase, especially in the lower reaches, reaching a peak after 19 days. The zooplankton abundance and biomass in the upper reaches peaked after 28 days and in the middle reaches after 35 days. This supports the first hypotheses that zooplankton abundance and biomass will attain maximum levels after a month. It also supports the second hypothesis that the zooplankton community in the three estuarine reaches does not recover in synchrony after breaching. Thus, even though the state of the mouth is the primary factor controlling zooplankton abundance and biomass, other factors such as salinity, temperature, depth and food availability also play an important role.

The zooplankton biomass decreased slightly after reaching a peak, but basically stabilised for the duration of the study. The slight decrease might be attributed to a decline in primary production due to a reduced nutrient availability (Han & Furuya 2000; Anandraj *et al.* 2008). The mean zooplankton biomass levels in the lower reaches during the recovery phase was still 5.6 times higher than prior to breaching, 32 times higher in the middle reaches and 22 times higher in the upper reaches. When comparing the three reaches during the recovery phase, the mean zooplankton biomass of $1.8 \times 10^3 \pm 1.3 \times 10^3$ $mg.m^{-3}$ for the lower reaches was 1.3 times higher that the biomass of $1.4 \times 10^3 \pm 9.6 \times 10^2$ $mg.m^{-3}$ for the middle reaches and 2.8 times higher than the upper reaches with $6.4 \times 10^2 \pm 8.2 \times 10^2$ $mg.m^{-3}$. The stabilisation phase may also be attributed to the stability achieved by the estuarine system upon re-closure, because of restricted exchange of water with the sea and less freshwater input. This observation is consistent with results obtained from studies conducted in other TOCEs, such as the Mpenjati (Kibirige 2002; Kibirige & Perissinotto 2003b), Nyara (Perissinotto *et al.* 2000), Mhlanga (Kibirige *et al.* 2006), as well as previous studies in the Mdloti (Kibirige *et al.*

2006; Anandraj *et al.* 2008). In fact, a study conducted by Kibirige and Perissinotto (2003b) at the Mpenjati concluded that the state of the mouth is the main factor controlling zooplankton abundance and biomass. Similar observations have also been made elsewhere in the world (Monbet 1992; Calbet *et al.* 2000; Gotsis-Skretas *et al.* 2000; Christian & Thomas 2003). Other studies have also shown that periods of prolonged mouth closure can lead to proliferation of freshwater taxa (Jerling & Cyrus 1999; Kibirige *et al.* 2006). Jerling and Cyrus (1999) reported that, after prolonged mouth closure, the zooplankton community structure in the Nhlabane Lake showed a gradual shift from estuarine to freshwater-dominated taxa.

The maximum values of ~2.1 $g.m^{-3}$ and ~1.6 $g.m^{-3}$ (DW) recorded in the lower and middle reaches, respectively, during the recovery phase compare well with the value of ~2 $g.m^{-3}$ (DW) recorded at the Mdloti during a previous study (Kibirige *et al.* 2006). It also compares well with the value of ~1.7 $g.m^{-3}$ (DW) recorded at the Mpenjati (Kibirige 2002) and ~2 $g.m^{-3}$ (DW) recorded in the Nyara Estuary (Perissinotto *et al.* 2000; Perissinotto *et al.* 2003b). Similarly, the maximum value of ~1.1 $g.m^{-3}$ (DW) recorded in the upper reaches compares well with the value of ~1.2 $g.m^{-3}$ (DW) recorded at the Mhlanga (Kibirige *et al.* 2006).

The maximum zooplankton biomass value recorded at the Mdloti Estuary compares well with the values reported from other estuaries throughout South Africa, even highly productive permanently open estuaries (see Table 1.1). This supports the conclusion of Whitfield (1980) and Perissinotto *et al.* (2003b) that estuaries are able to build up a large zooplankton biomass during their closed phase. This is then often followed by periods of depression during the open phase. Available information suggests that zooplankton biomass in temporarily open/closed estuarine systems varies from the highest ever reported in the literature during the closed phase, to the lowest during the open phase (Perissinotto *et al.* 2000; Kibirige 2002; Perissinotto *et al*. 2003b). The mean value of ~0.7 ± 0.3 $g.m^{-3}$ obtained for the duration of the study period was 9 - 24 times higher than the mean values reported by Wooldridge

(1999) for the most (~0.08 g DW m^{-3}) and the least (~0.03 g DW m^{-3}) productive permanently open South African estuaries.

From the Principal Components Analysis it can be concluded that the major variations in zooplankton abundance and biomass are mainly controlled by the state of the mouth and also depth, temperature, salinity and nutrients (DIN and DIP). This supports the hypothesis that the state of the mouth may largely determine the nutrient enrichment and also the zooplankton dynamics of TOCEs (Cloern 2001; Kibirige & Perissinotto 2003b; Kibirige *et al*. 2006). The different weighting of variables in the three reaches suggests a varied influence of environmental parameters on zooplankton abundance and biomass (Anandraj *et al*. 2008).

Dernie *et al*. (2003) suggest that physical and biological recovery rates are mediated by a combination of physical, chemical and biological factors that differ in their relative importance in different habitats. As recorded in previous studies, the main controlling factors of zooplankton abundance and biomass are the state of the mouth (Wooldridge 1994; Bate *et al*. 2002; Forbes & Demetriades 2002; Kibirige & Perissinotto 2003b), salinity (Day 1981b; Tett 1987; Schumann *et al*. 1999; Wooldridge 1999; Jerling 2005), nutrients (Cloern 2001; Kibirige & Perissinotto 2003b; Kibirige *et al*. 2006) and food availability (Kibirige *et al*. 2006; Anandraj *et al*. 2008). As these factors will vary in the different reaches, it is not surprising that the zooplankton in the three reaches does not recover in synchrony after mouth closure.

The nutrient values obtained during this study are in the range of what was previously reported for the Mdloti Estuary (Nozais *et al*. 2001; Kibirige *et al*. 2006). When the total zooplankton biomass and the dominant species were correlated with DIN, DIP and chl-*a*, most of the correlations were not significant. This may suggest that the Mdloti Estuary is oligotrophic or only slightly eutrophic (Park & Marshall 2000). This observation is in agreement with a previous study conducted in the same estuary (Kibirige *et al.* 2006). As discussed in Section 1.6.6, the Department of Water Affairs and Forestry (1996) states that DIN concentrations of 2.5 µM to 10 µM and above indicate

eutrophic conditions. At the maximum, the measured DIN concentration exceeded that value 39 times.

Kibirige *et al.* (2006) reported that rotifers in the Mdloti Estuary had a strong positive correlation with phytoplankton chl-*a* (r = 0.76; p < 0.01). This suggested that the peak of rotifers may have been triggered by the high phytoplankton biomass observed. Results of the Pearson correlation obtained in this study indicated a significant correlation between zooplankton abundance / biomass, and phytoplankton chl-*a* in the lower reaches. However, in the middle and upper reaches zooplankton showed a significant correlation with microphytobenthic, rather than phytoplankton biomass.

The importance of the phytoplankton / microphytobenthic biomass throughout the estuary is highlighted in the numerous significant correlations between total zooplankton abundance / biomass and chl-*a* (Tables 2.6, 2.7 and 2.8). During the study, the water column was mainly dominated by nanophytoplankton (2-10 *µ*m in size), an ideal food source for mesozooplankton (Kibirige *et al.* 2003). The role played by this specific cell size of phytoplankton, as a major food source for zooplankton, has also been observed in other temperate coastal environments (Miller *et al.* 1991; Dittel *et al.* 2000; Gotsis-Skretas *et al.* 2000; Mousseau *et al.* 2001).

The recovery phase of the Mdloti Estuary was marked by a clear dominance of *Pseudodiaptomus hessei*, harpacticoid copepodites and *Keratella* sp. 1 at all three stations. *Keratella* sp. 1 contributed 38% of the total zooplankton abundance during the open phase, but only 16% during the recovery phase. However, the abundance of *Keratella* sp. 1 during the open phase was much lower than during the recovery phase (open: $4.9 \times 10^4 \pm 2.9 \times 10^3$ ind.m^3 ; recovery: $2.3 \times 10^6 \pm 8.6 \times 10^4$ ind.m^3). This might indicate that, even though the freshwater taxon *Keratella* sp. 1 can survive the estuarine conditions prevailing during the open phase, it will actually thrive in the estuary only once the recovery phase has started.

The important contribution of the copepod *P. hessei* to the total abundance and biomass in South African estuaries is well established (Wooldridge 1999; Perissinotto *et al.* 2000; Froneman 2002a; 2003a; 2003b; Kibirige & Perissinotto 2003b; Froneman 2004; Perissinotto *et al*. 2004; Kibirige *et al.* 2006). As previously stated, *P. hessei* is able to thrive in both marine and freshwater environments and is the first to recolonize an estuary after a flood (Wooldridge & Melville-Smith 1979; Wooldridge & Bailey 1982; Wooldridge 1999; Kibirige & Perissinotto 2003b). Therefore, the high contribution of *P. hessei* to the total zooplankton abundance and biomass observed in this study, especially during the recovery phase, is not surprising.

The copepod, *Acartia natalensis* sp., was also very abundant in this study, especially during the recovery phase. Therefore, it is not surprising to have observed copepodites in such large numbers during the study (Tables 2.2 and 2.3) (Marcus 1984). It is well known that copepods generally dominate zooplankton abundance and biomass in TOCEs (Wooldridge 1999; Perissinotto *et al.* 2000; Froneman 2002a; 2003b; Kibirige & Perissinotto 2003b; Froneman 2004; Perissinotto *et al.* 2004; Kibirige *et al.* 2006).

When mysids are scarce in samples, their virtual absence can be explained either through inadequate sampling procedures (Wooldridge 1999) or the high predation impact of large numbers of zooplanktivorous fish in the system (Froneman 2004).

Over the past twenty-five years the community structure of the Mdloti has changed significantly. Blaber *et al.* (1984) indicated that the zooplankton community at that time was dominated mainly by chironomid larvae, macruran larvae, the mussel *Musculus virgiliae* and the calanoid copepod *P. hessei*. More recently, Kibirige *et al.* (2006) indicated that the dominant taxa were rotifers, cladocerans and *P. hessei*. During this study the dominant taxa were *P. hessei*, *Keratella* sp. 1, harpacticoid copepodites and *A. natalensis*.

The changes in community structure from 1984 to date may have been triggered by changes in hydrodynamics that have occurred within the estuary,

mainly as a result of human interference (Nixon 1995; Blaber 1997; Park & Marshall 2000; Cloern 2001; Kibirige *et al*. 2006). Effluents that flow into estuaries can cause a difference in mean flow rate, impacting on the frequency of breaching events. This will likely affect the variations in zooplankton abundance / biomass and composition (Kibirige *et al*. 2006).

Apart from the impact on flow rate, sewage effluents can also impact on the nutrient loading (eutrophication) of an estuary. Zooplankton diversity, abundance and biomass of an estuary may increase or decrease with an increase in eutrophication (Gliwicz 1969; Gannon & Stemberger 1978; Bays & Crisman 1983; Pace 1986; Bays & Crisman 1989; Park & Marshall 2000; Kibirige *et al*. 2006).

During this study, the state of the mouth was primarily responsible for regulating the zooplankton biomass within the Mdloti Estuary. However, the zooplankton in the different reaches did not recover in synchrony after mouth re-closure because abiotic factors and food availability were different in the three estuarine reaches.

CONCLUSION AND SUGGESTIONS FOR FURTHER RESEARCH

The objectives of this study were to measure the response of the zooplankton community to a mouth breaching event, to compare the spatial and temporal patterns of zooplankton distribution in the three reaches in terms of biomass and abundance just before, during and after a mouth breaching event and to identify the impact of key physical and chemical factors on the distribution patterns of zooplankton during such a breaching event.

During breaching, 98% of the estuarine zooplankton abundance and biomass were washed out to sea. More taxa were recorded during the open phase than prior to breaching, possibly due to the incursion of marine and freshwater taxa. Throughout the study, the lower reaches consistently showed the highest zooplankton abundance and biomass, compared to the other two reaches. The recovery of estuarine zooplankton abundance and biomass following the breaching event seemed to be primarily influenced by the state of the mouth, which in turn would have affected the environmental parameters. Temperature, salinity, nutrient availability and chl-*a* concentrations stimulated zooplankton abundance and biomass during the open phase, but continuous flushing precluded the build-up of zooplankton biomass. After mouth re-closure, the zooplankton stabilised for the duration of the study period, probably due to the stabilization of the estuarine system itself.

TOCEs play an important role for the survival of a number of invertebrates and in the life cycle of estuarine-dependent marine fish as nursery areas. The disruption of the natural cycle of breaching may have a severe impact on the estuarine community. Management practices with sound scientific understanding of the hydrological and biological processes are required to manage estuaries and conserve them for future generations. However, the monitoring of the recovery of a TOCE is complex, because indicators such as

zooplankton biomass, primary production and the state of the mouth might not necessarily recover in synchrony.

Artificial breaching can never replace natural breaching and further research still needs to be conducted to fully understand the impact of artificial breaching on TOCEs. A study is recommended where daily primary production samples and zooplankton samples are taken for a longer period to further expand current knowledge about the food-web dynamics. This information could also then be used to investigate the responses of the communities of primary producers and zooplankton consumers to eutrophication and other anthropogenic effects in estuarine systems.

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