

**THE ZOOPLANKTON OF TEMPORARILY OPEN/CLOSED  
ESTUARIES: CASE STUDIES OF THE MDLOTI AND THE  
MHLANGA ESTUARIES, KWAZULU-NATAL NORTH COAST**

By

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## ABSTRACT

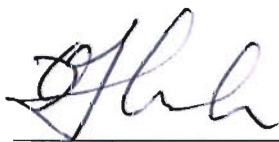
The zooplankton communities of the Mdloti and Mhlanga estuaries were studied over a 13-month period (March 2002-March 2003). Monthly daytime samples were collected from both estuaries at the lower, middle and upper reaches using a WP-2 net and a hyperbenthic sled. Throughout the study period, the Mdloti Estuary experienced nine breachings, while the Mhlanga experienced 16 such events. Significant differences in zooplankton abundance were observed between the two estuaries ( $F_{1,73} = 5.2$ ;  $P < 0.05$ ), with the Mdloti consistently exhibiting higher values than the Mhlanga. No significant differences were, however, observed in zooplankton biomass between the two estuaries ( $U = 634$ ;  $P > 0.05$ ). At the Mdloti, zooplankton abundance ranged from  $20 \text{ ind.m}^{-3}$  to  $5.4 \times 10^6 \text{ ind.m}^{-3}$ , while at the Mhlanga this ranged from  $76 \text{ ind.m}^{-3}$  to  $2.0 \times 10^5 \text{ ind.m}^{-3}$ . Zooplankton biomass ranged from  $0.08 \text{ mg.m}^{-3}$  (DW) to  $2010 \text{ mg.m}^{-3}$  (DW) at the Mdloti, and from  $0.18 \text{ mg.m}^{-3}$  (DW) to  $1210 \text{ mg.m}^{-3}$  (DW) at the Mhlanga. A one-way ANOVA revealed significant differences in zooplankton abundance between the open and the closed phase, both at the Mdloti ( $F_{1,30} = 59$ ;  $P < 0.05$ ) and the Mhlanga ( $F_{1,38} = 7.3$ ;  $P < 0.05$ ), with the closed phase exhibiting consistently higher values than the open. Similarly, biomass was significantly higher during the closed than the open phase, both at the Mdloti ( $U = 16.5$ ;  $P < 0.01$ ) and the Mhlanga ( $U = 88$ ,  $P < 0.01$ ). This pattern may be attributed to the stability achieved by these systems during periods of mouth closure, when the estuaries exhibit less freshwater input and a restricted exchange of water with the sea. At the Mdloti, zooplankton biomass (DW) was positively correlated to both phytoplankton ( $r = 0.36$ ) and microphytobenthos biomass ( $r = 0.41$ ). At the Mhlanga, zooplankton biomass (DW) was only positively correlated to phytoplankton biomass ( $r = 0.45$ ). The most abundant taxa at the Mdloti during the open phase were *Pseudodiaptomus hessei* and copepod nauplii, each contributing 38% and 32% of the total stock, respectively. During the closed phase, however, rotifers were by far the dominant taxon, contributing 82% of the total zooplankton abundance. These were followed by copepod nauplii with 16%. At the Mhlanga, the most abundant groups during the open phase were again the copepod nauplii (89%) and *P. hessei* (7%), while the closed phase was dominated mainly by caridean larvae (39%) and copepod nauplii (26%). The dominance of *P. hessei* during the open phase of both estuaries may be attributed to the pioneering nature of this species. The dominance of rotifers at the Mdloti during the closed phase may have been due to the freshwater conditions that prevailed in this estuary as a result of prolonged mouth closure. The concentration of copepod nauplii increased dramatically 2-4 weeks after major rain events, possibly due to the hatching of dormant eggs in response to freshwater pulses.

**Key words:** zooplankton, microphytobenthos, phytoplankton, hyperbenthic sled

## PREFACE

The work described in this dissertation was carried out in the Biological & Conservation Sciences, University of KwaZulu-Natal, Howard College Campus, from January 2002 to June 2004, 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.



Xolani Christopher Thwala

15 August 2008

Date

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# GENERAL INTRODUCTION

## Statement of the problem

Estuaries form a dominant component of the South African coastal geomorphology (Cooper *et al.* 1999). A total of 258 estuaries are currently found along the South African coastline, with the vast majority (248) situated along the eastern seaboard, while the west coast exhibits only 10 proper estuaries (Perissinotto *et al.* 2004). It is estimated that about 71% of South African estuaries are currently temporarily open/closed estuaries (TOCEs). However, up to date very little information is available about the ecological functioning of these systems (Whitfield 1995, Allanson & Baird 1999).

Generally, South African estuaries are considered to be highly productive ecosystems and are often used as nursery areas by a number of marine fish and crustacean species commonly exploited by man (Whitfield 1994). On a global scale, primary productivity in estuaries is estimated at about  $2000 \text{ g.m}^{-2}.\text{yr}^{-1}$ , while the primary productivity on land and in the marine environment is estimated to be  $730 \text{ g.m}^{-2}.\text{yr}^{-1}$  and  $155 \text{ g.m}^{-2}.\text{yr}^{-1}$ , respectively (Knox 1980 cited in Begg 1984a). Unfortunately, growing human populations coupled with massive industrial developments along the coast have had a negative impact on these highly productive ecosystems. This has led to the increase in scientific interest in the ecological functioning of these systems for management purposes (Whitfield 1995, Allanson & Baird 1999, Nozais *et al.* 2001). However, up to date, most studies have been conducted in the larger permanently open estuaries, while the most abundant TOCEs have received very little attention (Perissinotto *et al.* 2000, Walker *et al.* 2001, Kibirige & Perissinotto 2003).

TOCEs are normally associated with a smaller catchment area ( $<500 \text{ km}^2$ ) and a relatively small tidal prism ( $<1 \times 10^6 \text{ m}^3$ ), compared to their permanently open counterparts (Kennish 1986, Whitfield 1992). During periods of low rainfall, these estuaries are often closed off from the sea by a sand bar that forms at the mouth, as a result of long-shore sediment drift (Cooper *et al.* 1999, Perissinotto *et al.* 2000). Breaching normally occurs following heavy rains and high fresh water runoff (Reddering & Rust 1990), although few cases of spontaneous breaching have also been

observed (D. Stretch, pers. comm.<sup>1</sup>). The latter may occur during the neap low tide, due to very high hydrological gradients (*loc. cit.*). After breaching, water level within the estuary drops rapidly, exposing large substrate areas that have been previously colonised by rich communities of plant and animals (Perissinotto *et al.* 2000, Walker *et al.* 2001). Although the opening and closure of estuarine mouths is a natural phenomenon, retention of water in dams for industrial, agricultural and basic human needs, as well as discharges of treated sewerage to these systems, have led to changes in both frequency and duration of mouth closure (Reddering & Rust 1990).

Generally, TOCEs lack the steady tidal supply of nutrients often observed in their permanently closed counterparts. During the closed phase, the system receives neither tidal nor fluvial nutrient exchange with the sea and the river, respectively (Adams *et al.* 1999), and hence the system depends entirely on nutrients regenerated within the estuary itself (Perissinotto *et al.* 2000). In addition, these systems are much more susceptible to accumulation of pollutants (Begg, 1984b). How all these factors affect the abundance and biomass of zooplankton in TOCEs is still largely unknown. Few studies undertaken in South African TOCEs indicate that major changes in zooplankton standing stock are strongly related to the state of the mouth i.e. open or closed (Perissinotto *et al.* 2000, Kibirige 2002, Kibirige & Perissinotto 2003). These studies also revealed that TOCEs tend to exhibit higher zooplankton abundance and biomass values during the closed phase compared to the open phase (Perissinotto *et al.* 2000, Kibirige 2002, Kibirige & Perissinotto 2003). Zooplankton biomass values recorded in these systems during the closed and open phase are among the highest and lowest ever reported in the literature, respectively (Perissinotto *et al.* 2004). The open phase is characterised by high species diversity, while, on the contrary, the closed phase is often dominated by 3-5 species contributing over 80% of the total abundance (Perissinotto *et al.* 2004). Up to date, however, the underlying environmental factors triggering these major changes in the zooplankton standing stock in TOCEs are still poorly understood.

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<sup>1</sup> Prof. D. Stretch, School of Civil Engineering, University of KwaZulu-Natal, Howard College Campus, Durban 4041, South Africa

components of this research programme include phytoplankton and microphytobenthos. Details of these studies are reported elsewhere (Thomas 2003, Iyer 2005).

### **Objectives of the study**

The aim of this study was to measure the response of the zooplankton communities of the Mdloti and the Mhlanga estuaries to flow variations and the state of the mouth. In addition, the study was also aimed at comparing the zooplankton communities of the two estuaries in relation to their contrasting hydrological characteristics.

For the purpose of this study, the following hypotheses were formulated:

1. As a result of increased freshwater inflow, zooplankton biomass increases as a result of an increase in phytoplankton biomass to attain a maximum after few weeks of mouth closure.
2. As a result of their contrasting hydrological characteristics, the two estuaries exhibit major differences in zooplankton abundance, biomass as well as community structure.
3. Freshwater inflow and salinity dropping to  $<10\text{‰}$  stimulates the hatching of copepod eggs. This is signalled by the appearance of large numbers of copepod nauplii after at least a week of mouth closure.

## Study Area

### Mdloti Estuary

The Mdloti Estuary is situated on the KwaZulu-Natal north coast, between the small townships of Mdloti and La Mercy, approximately 27 km north of Durban, at coordinates 29° 38'S and 31° 08'E (Begg 1978, Grobbler *et al.* 1987). The estuary is accessible from the M4 highway via an off-ramp leading to La Mercy beachfront.

The Mdloti River is approximately 74 km in length, drains a relatively small catchment area of about 550 km<sup>2</sup>, where the mean annual runoff is estimated at  $1.3 \times 10^8$  m<sup>3</sup> (Begg 1978). The estuary occupies a total area of about 13.6 ha and exhibits a relatively broad floodplain (up to 600 m wide) in the lower reaches (Grobbler *et al.* 1987). Originally, the estuary had two main channels but the construction of the M4 highway bridge in 1960, about 500 m above the estuary's mouth, has resulted in the loss of the northern channel, thus confining the flow to the southern channel (Begg 1978, Grobbler *et al.* 1987). The estuary has an axial length of about 1.5 km and a maximum width of 380 m (Begg 1978). Currently the river has only one dam, the Hazelmere Dam, located 20 km above the estuary. The total capacity of this dam is about  $2.4 \times 10^7$  m<sup>3</sup>. Furthermore, the estuary receives about 8-million litres of treated water a day from an upstream sewerage treatment plant (Ethekewini Municipality, pers. comm.).

The southern banks of the lower reaches exhibit dense strands of the so-called "fresh water mangrove" *Barringtonia racemosa*, while the northern banks boast an assortment of vegetation dominated mainly by the swamp reed *Phragmites* sp., although few patches of *B. racemosa* are also visible. The middle and the upper reaches are also dominated by *Phragmites* sp., while small strands of *B. racemosa* can be seen on the northern banks of the upper reaches.

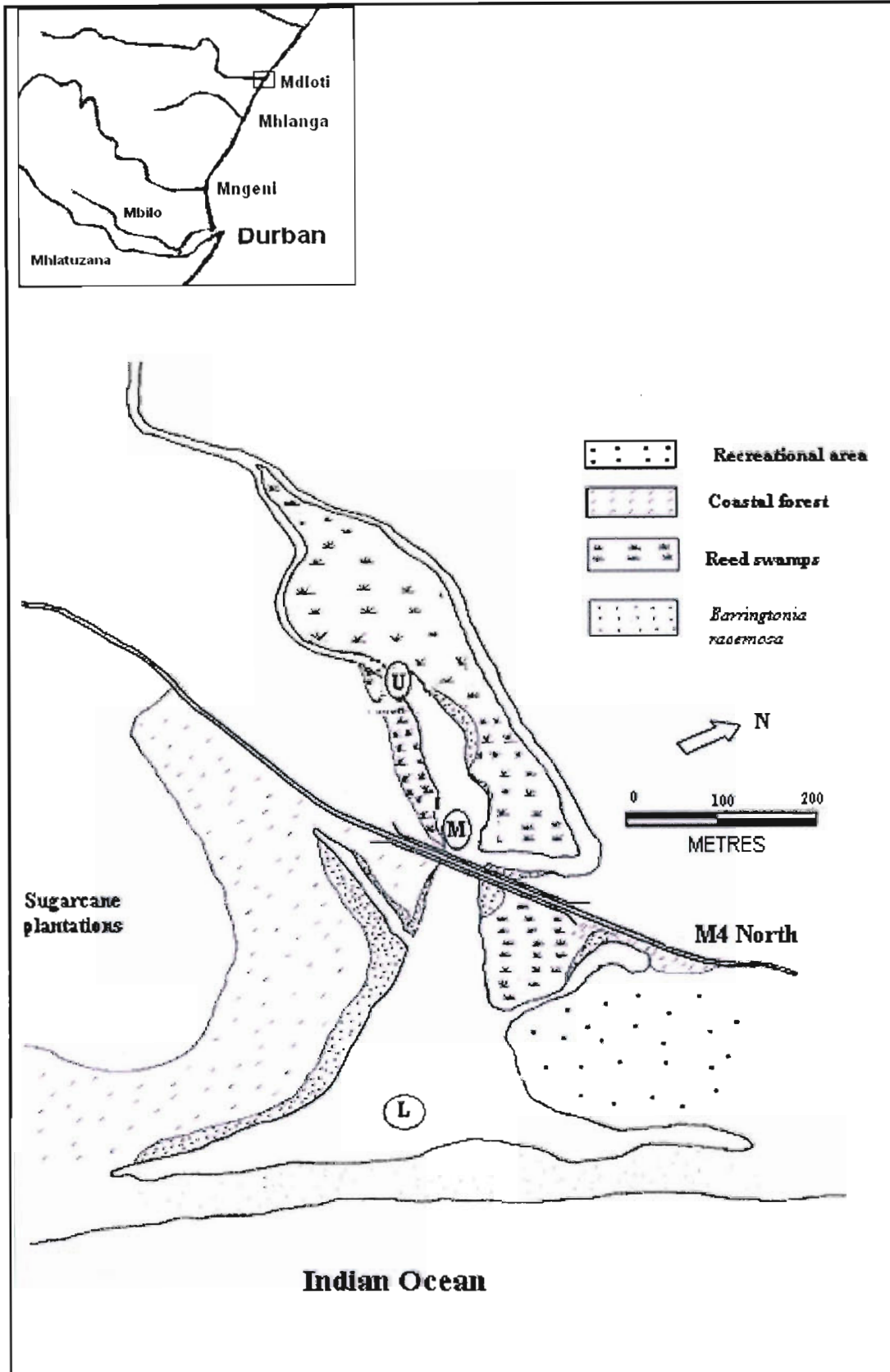
The Ethekewini Municipality recently constructed a recreational facility on the northern banks of the lower reaches of the estuary. This development was conceived despite objections from Ezemvelo KZN Wildlife and other interested parties. Flooding in 2001 resulted in the erosion of a large portion of the facility, including the boat

launching site and a car parking area. As a result of these developments, the Ethekewini Municipality decided to close down the facility in 2002. Most of this facility has been removed during 2004.

Previously, the estuary was used extensively for recreational activities such as swimming, windsurfing, etc. However, the closure of the recreational facility has rendered the estuary inaccessible and hence these activities seem to have ceased. Until recently, the health status of the Mdloti was described as fair<sup>2</sup>, although siltation, pollution and sugarcane encroachment are regarded as serious problems (Whitfield 2000).

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<sup>2</sup> This classification is based on the degree to which human activities have changed the viability of the system. These may be summarised as follows: excellent = negligible impact; good = low impact; fair = moderate impact; poor = high impact.



**Figure 1.** The Mdloti Estuary (29°38'S; 31°08'E) showing the positions of the three sampling stations; L: lower, M: middle & U: upper reaches. (adapted from Begg 1978)

## Mhlanga Estuary

The Mhlanga Estuary is located 20 km north of Durban, near the town of Mhlanga Rocks at co-ordinates (mouth) 29° 42'S and 31°05'E (Cooper 1991). The estuary forms part of the Umhlanga Nature Reserve and is not accessible by road.

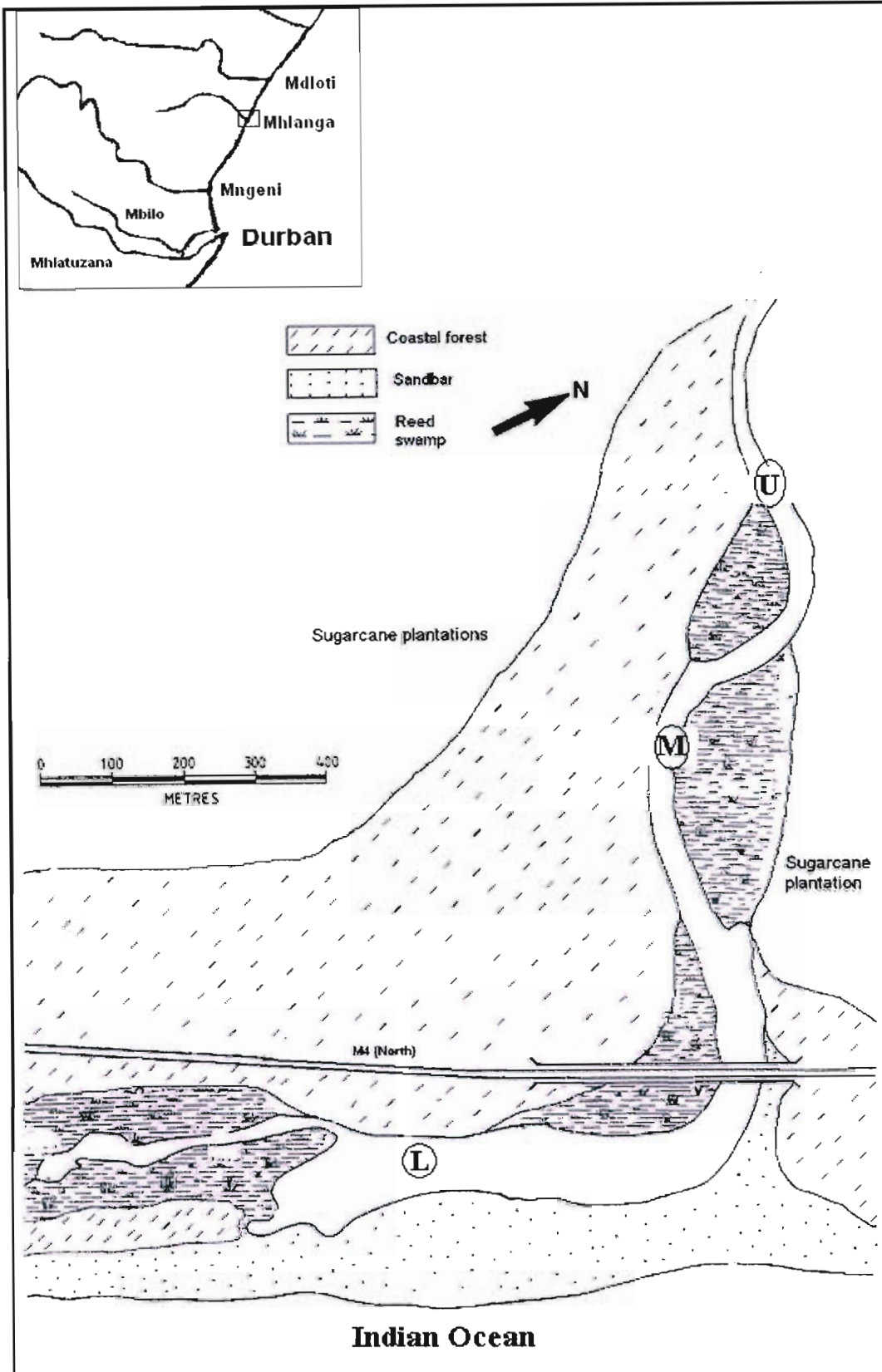
The Mhlanga River is approximately 28 km long and drains a small catchment area of about 118 km<sup>2</sup>, about 1/5 the size of the Mdloti (Begg 1978). Mean annual runoff amounts to  $2.6 \times 10^7$  (Begg 1978, Cooper 1991). The estuary has an axial length of 2.2 km and a maximum width of 100 m (Begg 1978). It is estimated that the estuary receives 20-million litres of treated sewerage water from a treatment plant upstream (Ethekewini Municipality, pers. comm.). Currently no dams are present in the catchment area of the Mhlanga Estuary.

The estuarine flora is dominated by *Phragmites* (see figure 2), believed to play a vital role in trapping sediments that are too fine to settle to the bottom (Cooper 1991). No mangroves are present in this estuary. This can be attributed to low salinities, lack of tidal exchange and large variations in water level following breaching (Cooper 1991).

Since the proclamation of this estuary as a nature reserve, activities such as power boating and bait collection have been prohibited. However, other forms of boating, as well as angling are permitted (Begg 1984). The state of the estuary was recently described by Whitfield (2000) as “good”<sup>3</sup>. No potential threats to the system were identified at that time. However, hypereutrophic conditions were repeatedly encountered during the course of this survey (Thomas 2003).

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<sup>3</sup> Refer to footnotes on page 5.



**Figure 2.** The Mhlanga Estuary ( $29^{\circ} 42'S$ ;  $31^{\circ} 06'E$ ) showing the positions of the three sampling stations; L: lower, M: middle & U: upper reaches. . (Begg 1978)



# THE ZOOPLANKTON OF SOUTH AFRICAN ESTUARIES: A REVIEW

## Composition and structure

South African estuaries are inhabited by a large variety of both holo- and merozooplanktonic organisms. Previous studies in these systems have shown that the endemic holozooplankton component is dominated by a few genera of copepods and mysids (Grindley 1981, Wooldridge 1999). On the west coast of southern Africa, copepod assemblages are often dominated by *Acartia longipatella* and *A. africana*, although *Pseudodiaptomus hessei* and *Oithona plumifera* are often abundant (Grindley 1981). On the south and east coast, copepod assemblages include *A. longipatella*, *A. natalensis*, *Oithonia brevicornis*, *P. hessei* and *P. charteri* (Wooldridge & Melville-Smith 1979, Grindley 1981, Wooldridge & Bailey 1982, Wooldridge 1999).

Although copepods may be numerically dominant over mysids, the latter group is often dominant in terms of biomass. The abundance of mysids is often underestimated in research programmes, largely due to inadequate sampling procedures (Wooldridge 1999). On the south and the east coast of South Africa, mysids are generally represented by *Mesopodopsis africana*, *M. wooldridgei*, *Gastrosaccus brevifissura*, *G. gordonae* and *Rhopalophthalmus terranatalis* (Grindley 1981, Wooldridge & Bailey 1982, Forbes 1989, Wooldridge 1999). Amphipods are normally represented by *Grandidierella lignorum* (Wooldridge 1999). Other taxa such as chaetognaths, ctenophores, amphipods and ciliates may also be common, while euphausiids, foraminiferans, salps and hydroid medusae are scarce (Grindley 1981). In highly perched, river dominated estuaries, such as those on the KwaZulu-Natal north coast, large proportions of polychaetes *Prionospio* spp. and *Ceratoneries keiskama* (Blaber *et al.* 1984), cladocerans *Moina micrura* and *Ceriodaphnia reticulata* (Connell *et al.* 1981), as well as the bivalve *Musculus virgiliae* (Blaber *et al.* 1984), are generally found.

The meroplankton component is normally represented by larval stages of benthic invertebrates. These may include the anomuran mudprawn *Upogebia africana*, the

crabs *Paratyloidiplax edwardsii*, *Hymenosoma orbiculare* and *Sesarma* spp. (Wooldridge 1994). Eggs and larval stages of fish, such as *Gilchristella aestuaria*, are also often common in spring and summer (Wooldridge & Bailey 1982, Harrison & Whitfield 1990).

The spatial distribution and abundance of zooplankton in most estuaries is largely determined by axial and vertical salinity gradients. The lower reaches are often dominated by stenohaline assemblages, which often have a strong affinity with the open sea and are thus unable to withstand major salinity changes (Wooldridge 1999). The incursion of stenohaline species may be evident up to a point, where the salinity falls below 28‰ (Grindley 1981). This group is often characterised by high species diversity (Wooldridge 1999). The upper reaches, where salinity often falls below 4‰, are inhabited by oligohaline or freshwater communities (Grindley 1981, Wooldridge 1999). In terms of biomass, however, these two communities are poorly represented in South African estuaries (Wooldridge 1999). The euryhaline or 'true' estuarine component, on the other hand, is well represented, both in terms of numbers and biomass, in most South African estuaries (*loc. cit.*). This group may include species that are not normally found in freshwater or in the open sea, e.g. *Pseudodiaptomus hessei* (Grindley 1981, Wooldridge 1999).

### **Abundance and biomass**

Temporal trends in zooplankton abundance are often dictated by temperature, although river discharges may modify the effect of spring warming in regions with seasonal rainfall (Wooldridge 1999). Generally, zooplankton abundance and biomass reach their peaks in late spring and summer (Grindley 1981). However, in South African TOCEs, this trend is often disrupted by the opening and closure of the mouth. Recent studies conducted in the Nyara (Perissinotto et al. 2000) and the Mpenjati (Kibirige 2002, Kibirige & Perissinotto 2003) estuaries have shown that these estuaries attain their peak in zooplankton abundance during their closed phase, which often coincide with the winter dry season. The highest biomass values reported from these estuaries are an order of magnitude higher than the average values reported for some of the permanently open estuaries in the Eastern Cape (Wooldridge 1999, Perissinotto *et al.* 2000).

Salinity also plays a very significant role in the abundance and distribution of estuarine zooplankton. Generally, estuaries with well-defined axial salinity gradients attain higher zooplankton abundance and biomass, compared to estuaries exhibiting weak axial salinity gradients (Allanson & Read 1995, Wooldridge 1999). Furthermore, estuaries with strong axial salinity gradients tend to exhibit higher biomass in their middle and upper reaches than in the lower reaches (Grindley 1981).

### **Migratory behaviour**

The net seaward flow of water in permanently open estuaries poses a serious retention problem for estuarine zooplankton. In response, estuarine zooplankton have evolved strategies of avoiding being swept into the sea during the ebb tide or periods of strong fluvial discharge (Wooldridge 1999). Strategies adopted include rhythmic and directed migration in response to tidal phases. Thus, by positioning themselves correctly within the water column, zooplankton can either exploit the prevailing current to transport them to a different location or simply avoid being transported by migrating to the bottom (*loc.cit.*). A study by Schlacher & Wooldridge (1994) on the opossum shrimp *Gastrosaccus brevifissura* has shown that the species avoids seaward flushing through benthic existence during the ebb tide. Tidal transport also appears to play a very significant role in the recruitment and export of neritic and estuarine taxa with obligatory estuarine and marine phases, respectively. In the estuarine mudprawn, *Upogebia africana*, stage 1 larvae are exported on the nocturnal ebb tide, while post-larval stages invade the estuary on the nocturnal flood tide (Wooldridge 1991). The timing of these events often coincides with the crepuscular high water for stage 1 and low water for postlarvae. On the contrary, stage 6 zoeas of the caridean shrimp, *Palaemon peringueyi* invade estuaries on diurnal and nocturnal flood tides, while sub-adults return to the sea on the nocturnal ebb tide (*loc. cit.*). Migratory patterns similar to those displayed by *P. peringueyi* were also observed in megalopae larvae of two species of Atlantic blue crabs, *Callinectes sapidus* and *Uca* sp. (Little & Epifanio 1991).

Beside tidally phased migration, vertical migration in response to changing light intensity has been reported amongst most estuarine zooplankton species (Grindley 1972). Most workers in this field consider diel vertical migration of zooplankton to be strongly associated with predator avoidance behaviour (e.g. Zuret & Suffern 1976,

Iwasa 1982, Jerling & Wooldridge 1992). Studies conducted by Jerling & Wooldridge (1992) on *Pseudodiaptomus hessei*, a species commonly preyed upon by the estuarine clupeid *Gilchristella aestuaria* (Harrison & Whitfield 1990), indicated that this species exhibit strong rhythms of diel vertical migration. Diel vertical migration was more evident in more conspicuous adults and late copepodid stages, with more individuals recorded in the water column after dusk than during the day. On the contrary, the less conspicuous nauplii did not seem to perform any significant vertical migration. Available literature suggests that diel vertical migration of zooplankton is also strongly affected by the lunar cycle, with more animals often recorded in the water column during the new moon compared to the full moon (Gliwicz 1986, Jerling & Wooldridge 1992, Wooldridge 1999). Therefore it appears that the migratory behaviour of estuarine zooplankton is a complex process regulated mainly by tidal, diel and lunar cycles.

## **Grazing**

Although zooplankton species are known to be major consumers of phytoplankton (Webb *et al.* 1987, Cyr & Curtus 1999), there are doubts as to whether the phytoplankton standing stock alone is able to meet the entire energetic needs of zooplankton in TOCEs, particularly during the closed phase. A study conducted on the temporarily open/closed Mpenjati (Kibirige 2002, Kibirige & Perissinotto 2003) shows that during the closed phase autotrophic food consumption by three dominant zooplankton species (*Pseudodiaptomus hessei*, *Gastrosaccus brevifissura* and *Acartia natalensis*) ranged between 34 and 70% of the available phytoplankton biomass. These values are much higher compared to 4-40% recorded from similar studies conducted in South African permanently open estuaries (Grange 1992, Froneman 2000). This reinforces the earlier hypothesis that detritus, particulate organic matter and microphytobenthic algae may play a larger role as alternative food sources for zooplankton than previously believed (Perissinotto *et al.* 2000). This was confirmed by stable isotope analysis using  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Kibirige 2002, Kibirige *et al.* 2002). This study was able to demonstrate that each of the three dominant grazers minimized inter-specific competition by deriving their energetic requirements from a specific and unique food source from the same trophic level (Kibirige 2000, Kibirige & Perissinotto 2003).

# THE ZOOPLANKTON COMMUNITIES OF THE MDLOTI AND THE MHLANGA ESTUARIES

## INTRODUCTION

About 71% of South African estuaries are temporarily open/closed estuaries (TOCEs). However, up to date very little information is available about the ecological functioning of these systems (Whitfield 1995, Allanson & Baird 1999). The few studies conducted on the east coast of South Africa indicate that zooplankton diversity, abundance and biomass in TOCEs are regulated primarily by the state of the mouth, i.e. open or closed (Perissinotto *et al.* 2000, Kibirige & Perissinotto 2003, Perissinotto *et al.* 2004, Perissinotto *et al.* 2003). Following periods of prolonged mouth closure, often coinciding with the winter/spring dry season, most TOCEs generally experience poor species diversity, with the zooplankton assemblages often dominated by 2-5 species contributing up to 80% of the total zooplankton abundance (Perissinotto *et al.* 2000, Perissinotto *et al.* 2004). This is in sharp contrast with what is often reported in their permanently open counterparts, where species richness can be in excess of a hundred species, especially in the mouth area, largely due to the encroachment of marine species (Wooldridge 1999).

During the closed phase, zooplankton assemblages in TOCEs are often dominated by typical estuarine taxa, mostly copepods, mysids and amphipods (Wooldridge 1999). The open phase is generally characterised by the removal of the dominant components of the closed phase and the appearance of freshwater taxa such as chironomid and zygopteran larvae, cladocerans and rotifers (Connell *et al.* 1981, Blaber *et al.* 1984). During the flood tide, the lower reaches may experience the incursion of numerous taxa of marine origin. These may include fish and invertebrate larvae, chaetognaths, gastropod and bivalve veligers as well as barnacle cypris and other taxa (Kibirige 2002). The low zooplankton diversity observed during the closed phase in TOCEs is in sharp contrast with the high biomass often recorded in these systems during this phase (Perissinotto *et al.* 2004). The maximum biomass values recorded in TOCEs during the closed phase may sometimes be up to an order of magnitude higher than the average values reported for some of the permanently open estuaries of the Eastern

Cape (Wooldridge 1999, Perissinotto *et al.* 2000, Kibirige 2002). This may be as a result of growth of populations during the closed phase, without losses associated with tidal flushing. Furthermore, low species diversity observed in TOCEs during the closed phase is considered to be conducive to the build-up of biomass of few species (Grindley 1981). This may explain the high zooplankton biomass often reported in TOCEs during this phase.

Like many other TOCEs on the KwaZulu-Natal coast, the Mdloti and the Mhlanga estuaries have been adversely affected by various human activities. As mentioned earlier, the Mhlanga currently receives about 20-million litres of treated sewerage a day, while the Mdloti receives 8-million litres and exhibits a dam upstream. How these factors impact on the mouth stability, and subsequently on the zooplankton communities of these systems, is still largely unknown. Previous studies by Whitfield (1980) and Blaber *et al.* (1984) provide baseline data with which the current state of these estuaries can be compared.

Due to the diel vertical migratory nature of estuarine zooplankton, sampling in most previous research expeditions was usually carried out at night with a WP2 net. In South Africa, this has proved to be both a logistical and a security problem for researchers. In order to eliminate risks associated with night sampling, epibenthic sleds have recently been used. The epibenthic sled can sample zooplankton a few centimetres above the substratum. The advantage of this device is that it can be operated during the day and still be able to sample diel vertical migrators (R. Perissinotto, pers. comm.<sup>4</sup>)

The aim of this study was to measure the response of the zooplankton communities of the Mdloti and the Mhlanga estuaries to various environmental variables such as salinity, temperature, phytoplankton, microphytobenthic algae and the state of the mouth. In addition, the study is also aimed at comparing the zooplankton communities of the two estuaries in relation to their contrasting hydrological characteristics and to compare their current state with that of 20 years ago.

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## MATERIALS AND METHODS

### Field methods

Zooplankton samples were collected at monthly intervals in the lower, middle and upper reaches of each estuary over a period of 13 months. Sampling commenced in March 2002, and terminated in March 2003. No sampling was done in October at the Mdloti due to the extremely low water level occurring at that time. Sampling was done during the day using a WP-2 net (57 cm diameter, 90- $\mu\text{m}$  mesh) fitted with a General Oceanics flowmeter. The net was attached to a boom extending from the side of a flat bottom boat powered by a 5-hp outboard motor. Throughout the survey the net was towed just below the water surface for approximately five minutes at a speed not exceeding 2 knots. The volume of water filtered through the net was calculated from the equation:

$$V = (F_2 - F_1) \times 0.00675$$

where  $V$  = total volume filtered,  $F_1$  = initial flowmeter reading and  $F_2$  = final reading.

In order to sample diel vertical migrators, a 200- $\mu\text{m}$  semicircular hyperbenthic sled with a mouth radius of 0.2 m was also used. The sledge was pulled over a pre-determined distance of 50 m. The volume of water filtered by the sled was calculated using the equation:

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

where  $V$  = volume filtered,  $d$  = distance travelled by the sled and  $r$  = sled's mouth radius. All samples collected were preserved in 5% formalin solution, buffered with hexamine, for later laboratory analysis.

Vertical salinity and temperature profiles were measured using a YSI 6920 data logger. Samples for phytoplankton and microphytobenthic algae were also collected and analysed by other workers, as part of this multidisciplinary research programme. Full details of the protocols and the results of these analyses are reported elsewhere (Thomas 2003, Iyer 2005.). Daily rainfall data was provided by the South African

Sugar Association's Experimental Station and Durban International Airport. The state of the mouth of both estuaries was monitored on a daily basis by rangers of Ezemvelo KZN Wildlife and residents in the area.

### **Laboratory methods**

Zooplankton samples were firstly suspended in 200 ml to 10 l of water, depending on their concentration. Three 20 ml sub-samples for identification and enumeration were drawn from each sample after vigorous stirring to avoid sedimentation (Perissinotto & Wooldridge 1989). Identification and counting was done under a dissecting microscope at 10 to 40x magnification. A minimum of 100 individual zooplankton organisms were counted in each subsample. Zooplankton counts were standardised to numbers of individuals per cubic meter ( $\text{ind.m}^{-3}$ ). Total dry weight was obtained from half of each sample, after removing detritus material under a dissecting microscope and drying it at 60 °C for 24 hours in a laboratory oven. Dry weights for each dominant zooplankton taxa were obtained by drying subsets ranging from 20 to 800 individuals, depending on their size. The total biomass of a species within a given sample was then determined by multiplying the average weight of an individual with its abundance within that sample. Dry weight was standardised to milligrams per cubic meters ( $\text{mg.m}^{-3}$ ).

### **Statistical analysis**

In order to equalise variance and normalise distribution, all data used in the analysis of variance (ANOVA) was  $\log(x + 1)$  transformed. A one-way ANOVA was applied to the abundance data in order to test for spatial and temporal differences (separately) and also for differences between the two estuaries. A similar approach was used to test for differences between the open and the closed phase of each estuary. In addition, a Mann-Whitney  $U$  test was applied to untransformed biomass data to test for spatial and temporal differences (separately), and also for differences between the open and the closed phases of each estuary. The same technique was also used to test for differences between the two estuaries.

A Spearman's rank correlation was applied to the untransformed data to determine the correlation between zooplankton biomass and environmental variables, such as



temperature, salinity, rainfall as well as phytoplankton and microphytobenthic algal biomass. All tests were performed using the STATISTICA computer program (StatSoft Inc).

Spatial and temporal distributions of zooplankton were analysed using the cluster and multidimensional scaling (MDS) method of the PRIMER statistical program (Clarke & Warwick 1994). Cluster and MDS similarities between taxa were computed on  $\log(x+1)$  transformed data. The hierarchical clustering was based on rank order of similarities (Clarke & Warwick 1994).

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

$$H' = -\sum [(n_i/N) \cdot \ln(n_i/N)]$$

where  $H'$  is the Shannon-Wiener diversity index;  $n_i$  is the population size of species  $i$  and  $N$  is the population size of all species combined. A one-way ANOVA was used (separately) to test for differences between the diversity indexes of the two estuaries and for differences between the open and closed phase of each estuary.

## RESULTS

### **Environmental variables**

Rainfall patterns observed during the sampling period were very unusual. Higher precipitation was recorded in winter than in summer. The highest rainfall, of about 200 mm, was recorded in July 2002. This accounted for 24% of the total annual precipitation of 805 mm. The second highest rainfalls were recorded in April 2002 (124 mm) and in January 2003 (119 mm). The lowest figures were recorded in May 2002 (63 mm) and June 2003 (21.6 mm), as well as in February 2003 (18.1 mm). The unusual rainfall pattern resulted in both estuaries experiencing prolonged periods of open phase in winter and unusual closure during part of the summer. In total, the Mdloti Estuary experienced nine breaching events, while the Mhlanga experienced 16. At the Mdloti, a total of five sampling sessions coincided with the open phase, while eight coincided with the closed phase. At the Mhlanga, seven sampling sessions coincided with the open phases and six with the closed phase.

Spatio-temporal variations in temperature and salinity recorded at the Mdloti and the Mhlanga during the survey are presented in Figures 3 and 4 respectively. At the Mdloti, temperatures ranged from a minimum of 15.5 to a maximum of 29.6 °C, while at the Mhlanga the range was between 14.8 and 28.3°C. No marked vertical temperature stratification was observed in either system. Salinity values recorded at the Mdloti ranged from 0.1‰ to 23.9‰, with the lower reaches generally exhibiting higher salinity values than the middle and the upper reaches. Vertical salinity stratification was more pronounced in the middle and the upper reaches, with the bottom waters showing consistently higher values than surface waters. Little vertical salinity stratification was observed in the lower reaches (Figure 3). The Mhlanga Estuary exhibited salinity values ranging from 0.1‰ to 28.3‰, with the lower reaches showing consistently higher values than the rest of the estuary. Vertical salinity stratification was evident at all stations. Surface salinity values were consistently lower than bottom values throughout the estuary (Figure 4).

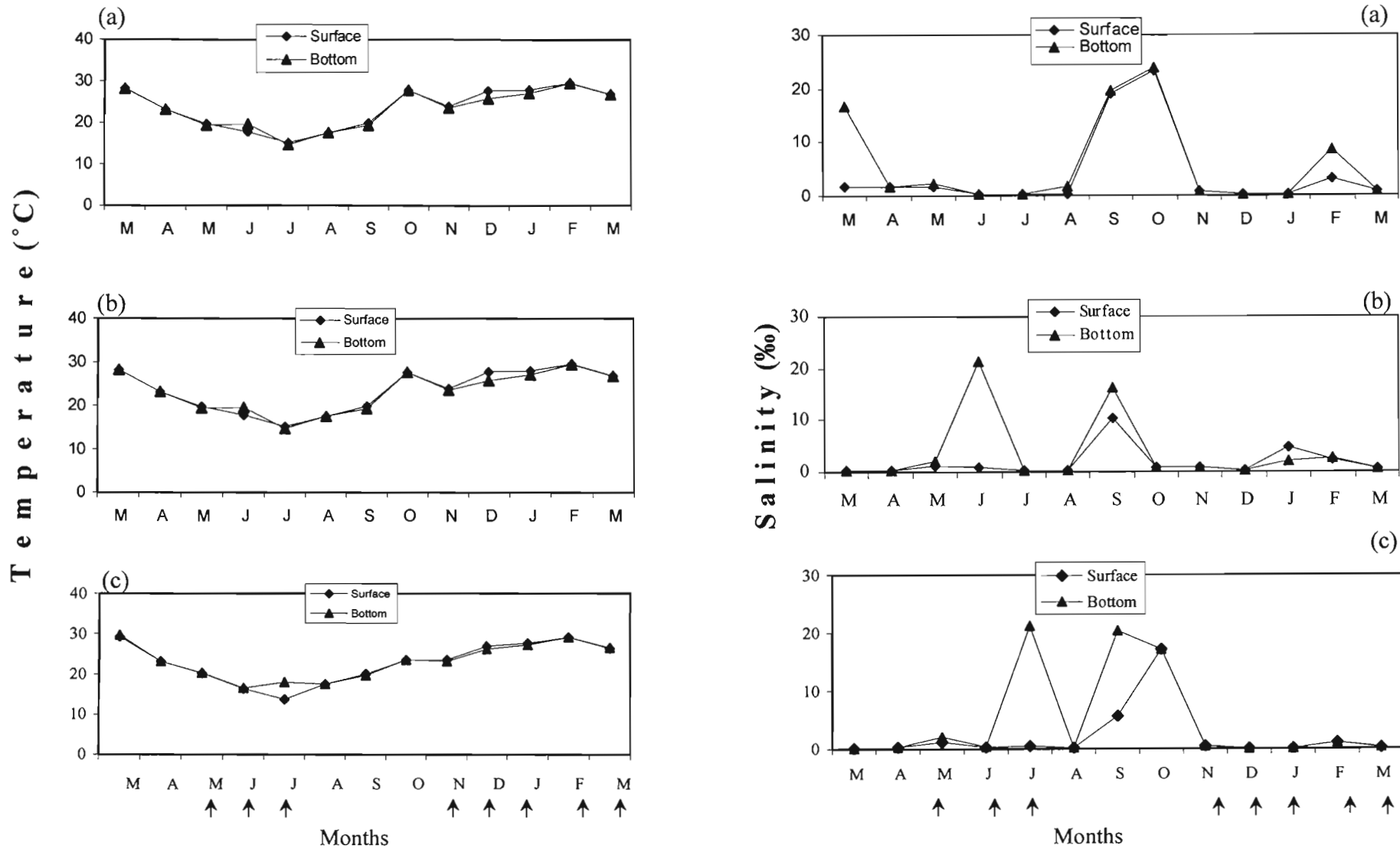


Figure 3. Spatio-temporal variations in temperature and salinity at the Mdloti Estuary during the survey period: (a) lower, (b) middle and (c) upper reaches.

↑ = Closed phase.

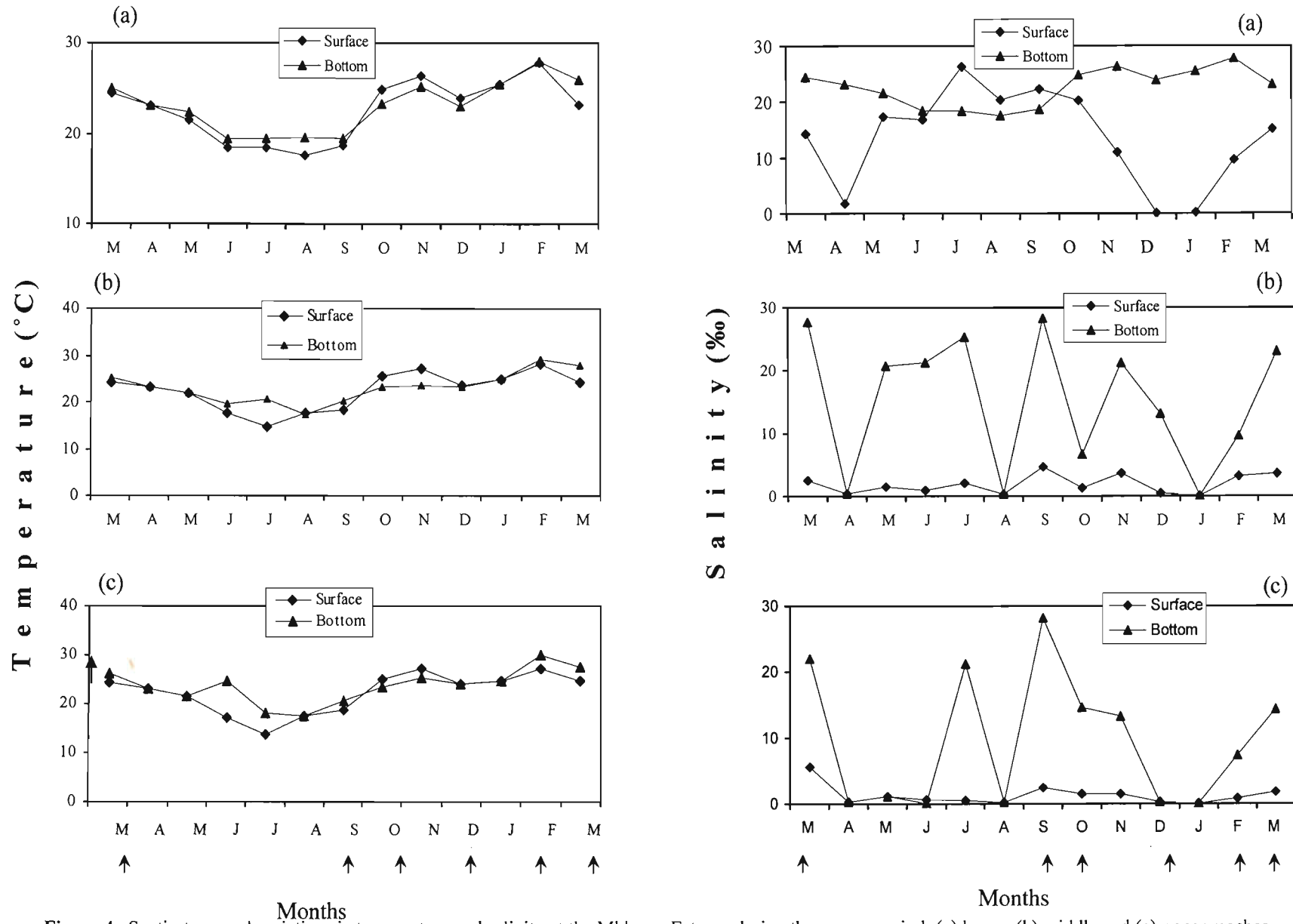


Figure 4. Spatio-temporal variations in temperature and salinity at the Mhlanga Estuary during the survey period: (a) lower, (b) middle and (c) upper reaches.

↑ = Closed phase.

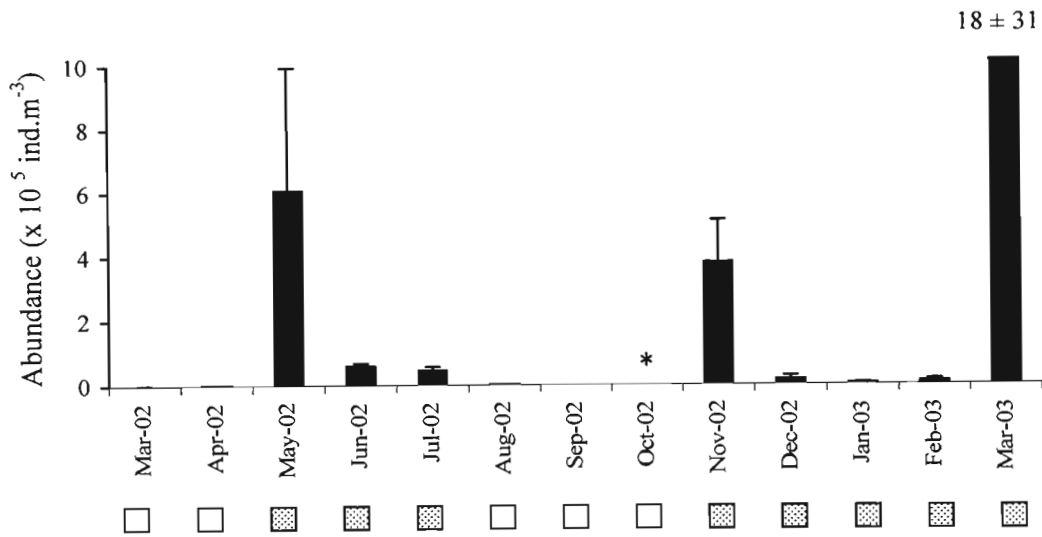
### **Trophic environment**

Phytoplankton and microphytobenthic algal biomass (as chlorophyll-a content, chl-a) varied significantly between the open and the closed phase in both estuaries. Full details of these results can be obtained elsewhere (Thomas 2003, Iyer 2005). In summary, at the Mdloti, phytoplankton chl-a content ranged from 2.15 to 11.7 mg.m<sup>-3</sup> (mean 4.89 ± 3.94 SD mg.m<sup>-3</sup>) during the open phase, while during the closed phase the range was 6.2 - 72.1 mg.m<sup>-3</sup> (mean 27.9 ± 22.2 SD mg.m<sup>-3</sup>). At the Mhlanga, phytoplankton chl-a content varied from 1.47 to 23 mg.m<sup>-3</sup> (mean 7.05 ± 8.2 SD mg.m<sup>-3</sup>) during the open phase, and from 2.8 to 145 mg.m<sup>-3</sup> (mean 42.7 ± 58.6 SD mg.m<sup>-3</sup>) during the closed phase. Similarly, the microphytobenthic chl-a content at Mdloti varied from a minimum of 8.73 mg.m<sup>-2</sup> to a maximum of 44.67 mg.m<sup>-2</sup> (mean 19.9 ± 15.0 SD mg.m<sup>-2</sup>) during the open phase, and from 57.6 to 206 mg.m<sup>-2</sup> (mean 109 ± 56.2 SD mg.m<sup>-2</sup>) during the closed phase. At the Mhlanga, microphytobenthic chl-a ranged from 15.7 to 194 mg.m<sup>-2</sup> (mean 77.6 ± 70.2 SD mg.m<sup>-2</sup>) during the open phase, and from 34.3 to 191 mg.m<sup>-2</sup> (mean 104 ± 58.3 SD mg.m<sup>-2</sup>) during the closed phase.

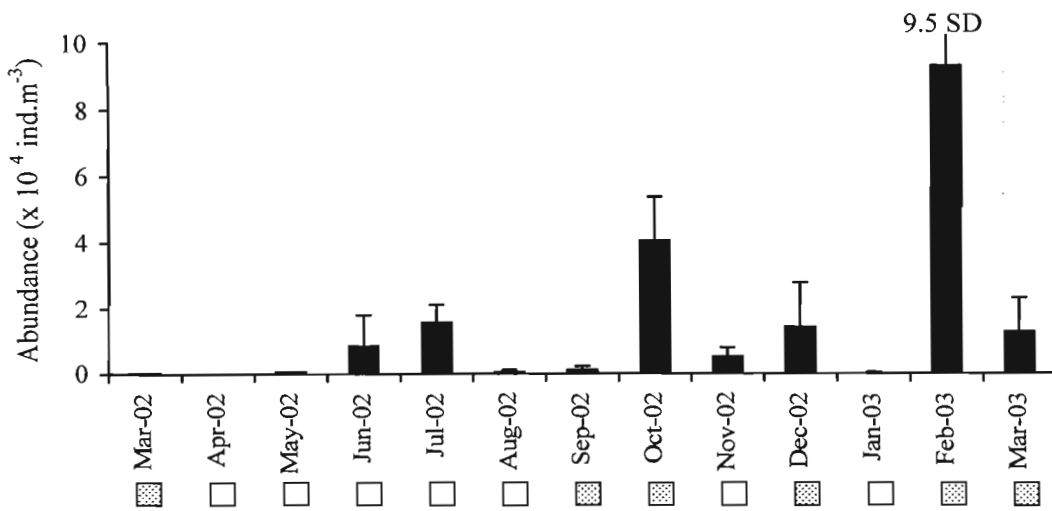
### **Zooplankton abundance and biomass**

Throughout the study, zooplankton abundance varied greatly between the two estuaries (Figures 5a & 5b) as well as between the open and closed phases of each system. No significant differences in zooplankton abundance were, however, observed between stations at either the Mdloti ( $F_{2, 33} = 0.16$ ;  $P > 0.05$ ) or the Mhlanga ( $F_{2, 37} = 0.01$ ;  $P > 0.05$ ). Overall, a one-way ANOVA revealed significant differences in zooplankton abundance between the two estuaries ( $F_{1, 73} = 5.2$ ;  $P < 0.05$ ), with the Mdloti showing consistently higher values than the Mhlanga. Significant differences in zooplankton abundance were also detected between the open and the closed phase, both at the Mdloti ( $F_{1, 30} = 59$ ;  $P < 0.05$ ) and the Mhlanga ( $F_{1, 37} = 7.3$ ;  $P < 0.05$ ), with the closed phase exhibiting consistently higher values than the open. At the Mdloti, zooplankton abundance ranged from  $2.0 \times 10^1$  to  $1.5 \times 10^3$  ind.m<sup>-3</sup> (mean  $6.3 \times 10^2 \pm 4.9 \times 10^2$  SD ind.m<sup>-3</sup>) during the open phase, while during the closed phase it ranged from  $3.0 \times 10^3$  to  $5.4 \times 10^6$  ind.m<sup>-3</sup> (mean  $3.7 \times 10^5 \pm 1.1 \times 10^6$  SD ind.m<sup>-3</sup>). Zooplankton abundance at the Mhlanga ranged from  $7.6 \times 10^1$  to  $2.0 \times 10^4$  ind.m<sup>-3</sup> (mean  $4.5 \times 10^3 \pm 6.7 \times 10^3$  SD ind.m<sup>-3</sup>) during the open phase, and from  $2.1 \times 10^2$  to  $2.0 \times 10^5$  ind.m<sup>-3</sup> (mean  $2.7 \times 10^4 \pm 4.7 \times 10^4$  SD ind.m<sup>-3</sup>) during the closed phase.

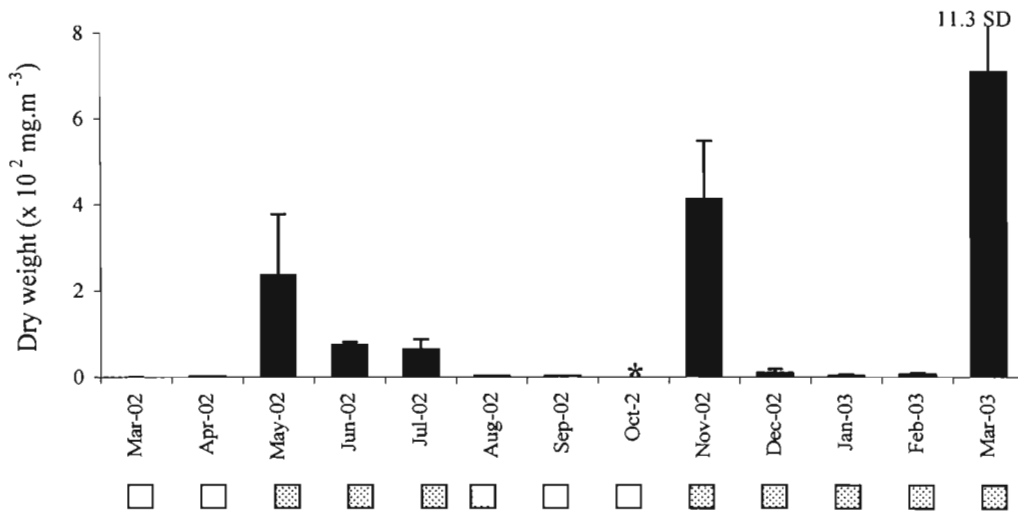
Similarly, zooplankton biomass varied greatly between the open and closed phase both at the Mdloti and the Mhlanga (Figures 6 a & b). A Mann-Whitney  $U$  test revealed significant differences in zooplankton biomass between the open and the closed phase, both at the Mdloti ( $U= 16.5$ ;  $P<0.01$ ) and the Mhlanga ( $U= 88$ ;  $P<0.01$ ), with the closed phase consistently exhibiting higher values than the open phase. However, no significant differences were observed in zooplankton biomass between the two estuaries ( $U = 634$ ;  $P>0.05$ ). At the Mdloti, zooplankton biomass ranged from 0.08 to 4.1  $\text{mg.m}^{-3}$  (mean  $1.7 \pm 1.2$  SD  $\text{mg.m}^{-3}$ ) during the open phase and from 0.99 to 2010  $\text{mg.m}^{-3}$  (mean  $189 \pm 415$  SD  $\text{mg.m}^{-3}$ ) during the closed phase. Zooplankton biomass at the Mhlanga varied from 0.18 to 25.3  $\text{mg.m}^{-3}$  (mean  $7.6 \pm 8.0$  SD  $\text{mg.m}^{-3}$ ) during the open phase, while during the closed phase it ranged from 0.12 to 1210  $\text{mg.m}^{-3}$  (mean  $103 \pm 279$  SD  $\text{mg.m}^{-3}$ ).



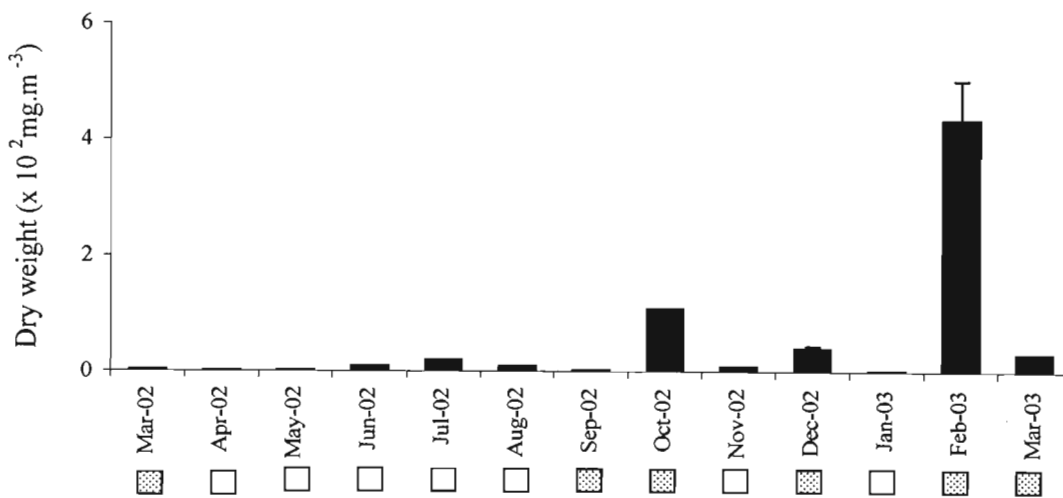
**Figure 5a.** Total zooplankton abundance (mean  $\pm$  SD) at the Mdloti Estuary during the study period (March 2002 - March 2003); \*: no data:  $\square$  Open phase,  $\blacksquare$  closed phase



**Figure 5b.** Total zooplankton abundance (mean  $\pm$  SD) at the Mhlanga Estuary during the study period (March 2002 - March 2003).  $\square$  Open phase,  $\blacksquare$  closed phase



**Figure 6a.** Total zooplankton biomass (mean  $\pm$  SD) at the Mdloti Estuary during the study period (March 2002 - March 2003); open phase; closed phase; \*: no data.



**Figure 6b.** Total zooplankton biomass (mean  $\pm$  SD) at the Mhlanga Estuary during the study period (March 2002 - March 2003); open phase; closed phase.



The results of Spearman rank order correlation (Table 1) showed that total zooplankton biomass at the Mdloti was positively correlated to both microphytobenthic algae ( $r = 0.41$ ;  $P < 0.05$ ) and phytoplankton biomass ( $r = 0.36$ ;  $P < 0.05$ ). There was also a significant inverse correlation with rainfall ( $r = -0.58$ ;  $P < 0.01$ ). No significant correlations were observed between total zooplankton biomass and other variables, such as salinity ( $r = 0.04$ ;  $P > 0.05$ ) and temperature ( $r = -0.29$ ;  $P > 0.05$ ). At the Mhlanga, total zooplankton biomass was positively correlated to phytoplankton biomass ( $r = 0.45$ ;  $P < 0.01$ ), but no significant correlations were observed with other biological and environmental variables (Table 2).

**Table 1.** Results of the Spearman rank correlation analysis between zooplankton biomass (including dominant groups) and environmental variables at the Mdloti Estuary;  $n = 36$ ; \*:  $P < 0.05$ ; \*\*:  $P < 0.01$ .

Variable	Total biomass	<i>P. hessei</i>	Copepod nauplii	Rotifers	Brachyuran larvae
	<i>r</i>	<i>r</i>	<i>r</i>	<i>r</i>	<i>r</i>
Temperature	-0.29	-0.56**	0.14	0.21	-0.11
Salinity	0.04	0.21	-0.27	-0.11	-0.37*
Rainfall	-0.58**	-0.53**	-0.27	-0.2	-0.25
Microphytobenthos biomass	0.41*	0.07	0.49**	0.41	0.4*
Phytoplankton biomass	0.36*	0.12	0.2	0.76**	0.16

**Table 2.** Results of the Spearman rank correlation analysis between zooplankton biomass (including dominant groups) and environmental variables at the Mhlanga Estuary.  $n = 39$ ; \*:  $P < 0.05$ ; \*\*:  $P < 0.01$

Variable	Total biomass	<i>P. hessei</i>	Copepod nauplii	Rotifers	Brachyuran larvae
	<i>r</i>	<i>r</i>	<i>r</i>	<i>r</i>	<i>r</i>
Temperature	0.23	0.07	0.15	0.37*	0.47**
Salinity	0.14	0.23	0.25	0.28	0.26
Rainfall	-0.3	-0.2	-0.51**	-0.12	-0.16
Microphytobenthos biomass	0.3	0.02	0.4**	0.13	0.22
Phytoplankton biomass	0.45**	0.36	0.06	0.16	0.43**

## Community structure

### *Mdloti Estuary*

A total of 25 taxa were recorded at the Mdloti during the open phase, but only 11 of them contributed >1% of the total abundance (Table 3). During the closed phase, the number of taxonomic groups recorded in this estuary dropped to 23, with only three groups contributing >1% of the total zooplankton abundance (Table 4). The zooplankton community was dominated by the calanoid copepod, *Pseudodiaptomus hessei*, an unidentified species of rotifer and a cladoceran, *Ceriodaphnia* sp. (Figures 7 a-c). Combined, these three taxa accounted for 51% and 83.4 % of the total zooplankton abundance during the open and closed phases, respectively. The single most important abundant species during the open phase was *P. hessei*, accounting for up to 39% and 56.1% of the total zooplankton abundance and biomass, respectively. Rotifers were the single most important contributor during the closed phase, accounting for up to 82 % of the total zooplankton abundance. The biomass plots of the dominant taxa are presented in figures 8 a-c.

Spearman rank correlation coefficients between the biomass of the dominant taxa and environmental variables at the Mdloti are presented in Table 1. The biomass of *P. hessei* was inversely correlated to temperature ( $r = -0.56$ ;  $P < 0.01$ ), and rainfall ( $r = -0.53$ ;  $P < 0.01$ ). The biomass of copepod nauplii was only positively correlated to microphytobenthos biomass ( $r = 0.49$ ;  $P < 0.01$ ), while the biomass of rotifers was correlated to phytoplankton biomass ( $r = 0.76$ ;  $P < 0.01$ ). Brachyuran larvae biomass was inversely correlated to salinity ( $r = -0.37$ ;  $P < 0.05$ ) and positively correlated to microphytobenthos biomass ( $r = 0.4$ ;  $P < 0.05$ ).

Dendograms of the hierarchical cluster analysis, at the arbitrary similarity level of 50%, show that only three groups can be identified at the Mdloti (Figure 9). The two-dimensional MDS plots for the entire sampling period exhibited stress levels of 0.12. Generally, stress levels between 0.1 and 0.2 provide a potentially useful two-dimensional representation (Clarke & Warwick 1994). In addition, the dendrogram groups matched well the MDS plots, thus providing confidence in the two-dimensional representation of the MDS plots (Clarke & Warwick 1994).

Of the main zooplankton categories identified by the cluster and multidimensional scaling analysis (Figure 9), the largest group consists of taxa that were present almost throughout the sampling period (group 3). These include *P. hessei*, *Ceriodaphnia* sp., *Chydorus* sp., ostracods, harpacticoids, cyclopoids, rotifers, brachyuran larvae, caridean larvae, chironomid larvae and copepod nauplii. The second largest group consists of opportunistic taxa that did not display any particular spatial or temporal trend throughout the sampling period (group 2). The latter includes *Ceratonereis keiskama*, *Prionospio* sp., zygopteran larvae and few unidentified polychaete species. The last group (group 1) consists of taxa that appeared only during the early stages of the sampling period and then disappeared throughout the later part of the survey. Members of this group include *Acartia natalensis* and fish larvae.

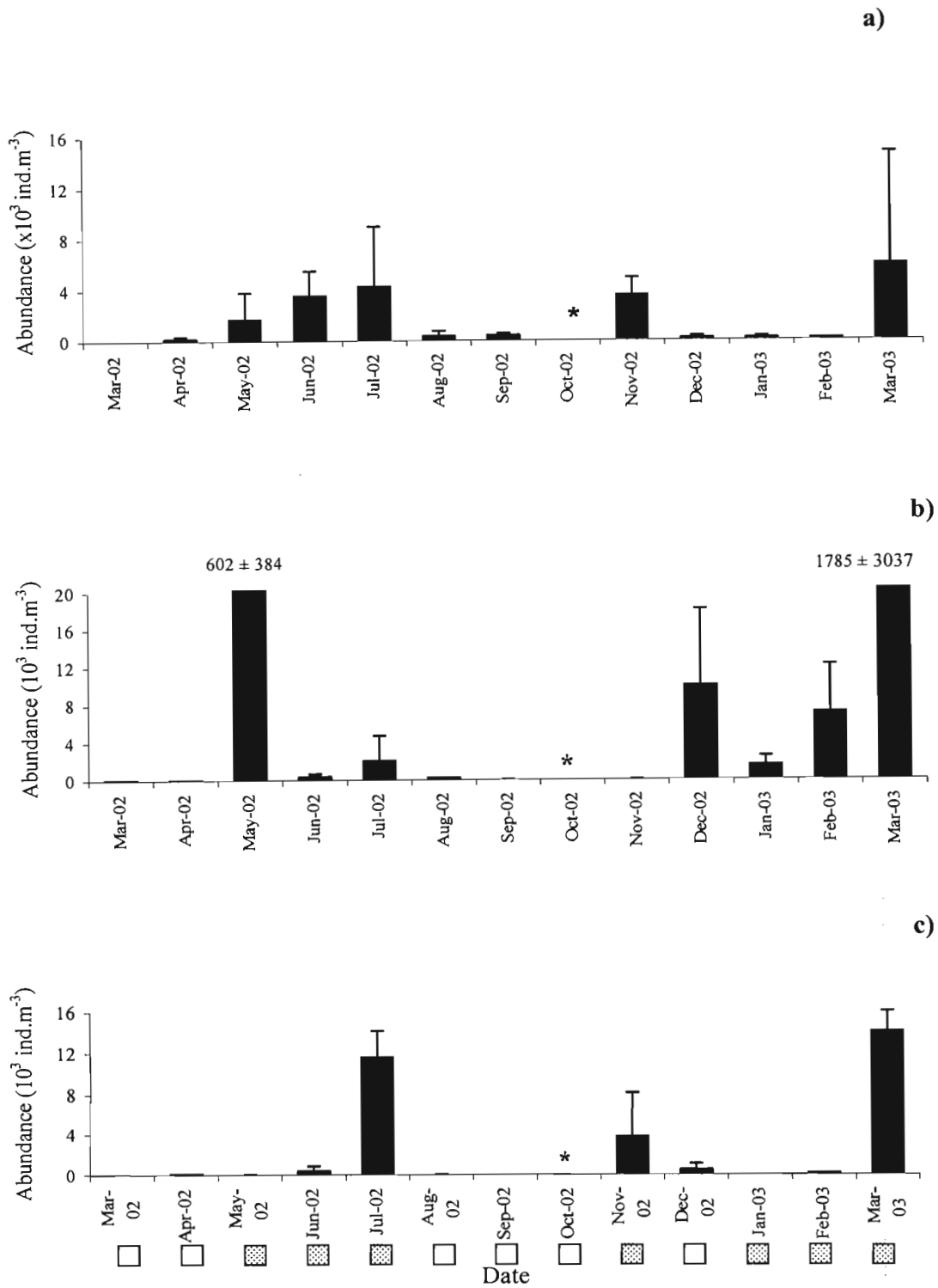
The Shannon-Wiener diversity indexes ( $H'$ ) of zooplankton species for each sampling station are presented in Figure 10. A one-way ANOVA revealed significant differences in diversity indexes between the open and closed phases ( $F_{1, 35} = 22.7$ ;  $P < 0.05$ ), with the open phase exhibiting consistently higher values than the closed phase. No significant differences were observed between stations (one-way ANOVA,  $F_{2, 35} = 0.2$ ;  $P > 0.05$ ). Diversity indexes ranged from 0.1 to 2 during the open phase, while during the closed phase they ranged from 0.03 to 1.

**Table 3.** Numerical composition (mean ind.m<sup>-3</sup> ± SD) of the zooplankton community of the Mdloti Estuary during the open phase.

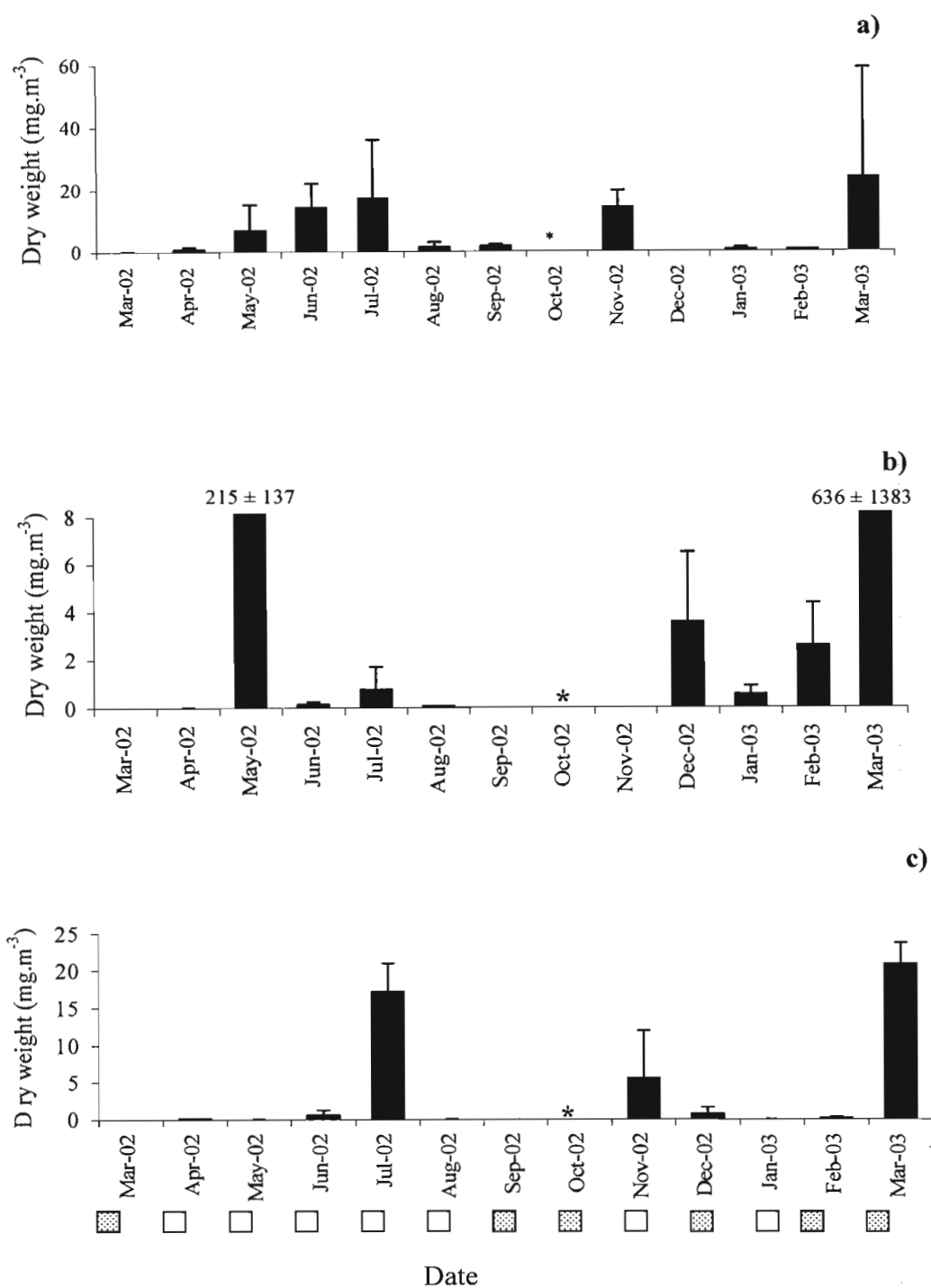
TAXA	Sled		WP2		Total (Sled + WP2)	
	Mean ± SD	% Contribution	Mean ± SD	% Contribution	Mean ± SD	% Contribution
<b>Hydrozoa</b>						
<i>Hydra</i> sp?	0.03 ± 0.09	0.02	0.00 ± 0.00	0.00	0.03 ± 0.09	<0.01
<b>Annelida</b>						
<i>Ceratonereis keiskama</i>	0.21 ± 0.57	0.19	2.98 ± 5.28	0.57	3.19 ± 5.61	0.51
Prionospio sp.	0.93 ± 2.63	0.84	7.05 ± 15.7	1.36	7.98 ± 18.97	1.27
Other polychaetes (4 sp)	0.93 ± 1.85	0.01	1.29 ± 4.45	0.25	2.21 ± 5.19	0.35
Unidentified Oligochaete	0.00 ± 0.00	0.00	0.07 ± 0.24	0.01	0.07 ± 0.24	0.01
<b>Cladocera</b>						
Ceriodaphnia sp	6.37 ± 15.89	5.78	16.3 ± 28.8	3.14	22.7 ± 42.34	3.60
Chydorus sp.	2.12 ± 3.37	1.93	19.7 ± 24.4	3.80	21.82 ± 26.66	3.47
<b>Copepoda</b>						
Copepod nauplii	0.00 ± 0.00	0	200 ± 284	38.50	200 ± 297	31.70
Cyclopoids	10.1 ± 21.4	9.16	15.9 ± 23	3.05	26 ± 41.5	4.12
Harpacticoids	0.00 ± 0.00	0.00	8.14 ± 9.17	1.57	8.14 ± 9.58	1.29
<i>Oithonia</i> sp.	0.96 ± 3.21	0.87	0.00 ± 0.00	0.00	0.96 ± 3.21	0.15
<i>Pseudodiaptomus hessei</i>	70.1 ± 213	63.57	172 ± 183	33.10	242 ± 262	38.50
<b>Mysidacea</b>						
<i>Mesopodopsis africana</i>	0.05 ± 0.12	0.05	0.00 ± 0.00	0.00	0.05 ± 0.12	0.01
<b>Decapoda</b>						
Brachyuran larvae	0.27 ± 0.68	0.24	1.01 ± 2.04	0.19	1.28 ± 2.46	0.20
Caridean larvae	5.65 ± 8.59	5.13	10.4 ± 14.3	2.01	16.1 ± 22.51	2.55
<b>Insecta</b>						
Chironomid larvae	0.29 ± 0.66	0.26	4.18 ± 5.67	0.80	4.48 ± 5.89	0.71
Zygoteran larvae	0.05 ± 0.18	0.05	2.43 ± 5.3	0.47	2.49 ± 5.64	0.39
<b>Pisces</b>						
Fish eggs	2.06 ± 6.17	1.87	0.00 ± 0.00	0.00	2.06 ± 6.17	0.33
Fish larvae	0.05 ± 0.12	0.05	0.00 ± 0.00	0.00	0.05 ± 0.12	0.00
<b>Other taxa</b>						
Nematodes	0.00 ± 0.00	0.00	1.97 ± 3.9	0.25	1.97 ± 4.07	0.31
Ostracods	10.1 ± 21.4	9.16	0.09 ± 0.3	0.02	10.19 ± 21.36	1.62
Rotifers	0.00 ± 0.00	0	56.1 ± 85.8	10.80	56.1 ± 85.8	9.00
<b>Totals</b>	<b>110 ± 221</b>	<b>100</b>	<b>520 ± 390</b>	<b>100</b>	<b>630 ± 491</b>	<b>100</b>

**Table 4.** Numerical composition (mean ind/m<sup>-3</sup> ± SD) of the zooplankton community of the Mdloti Estuary during the closed phase.

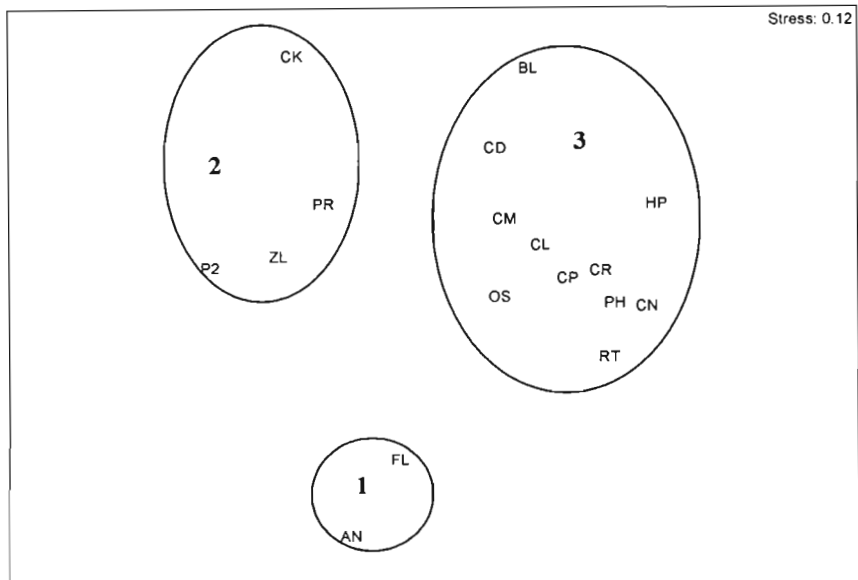
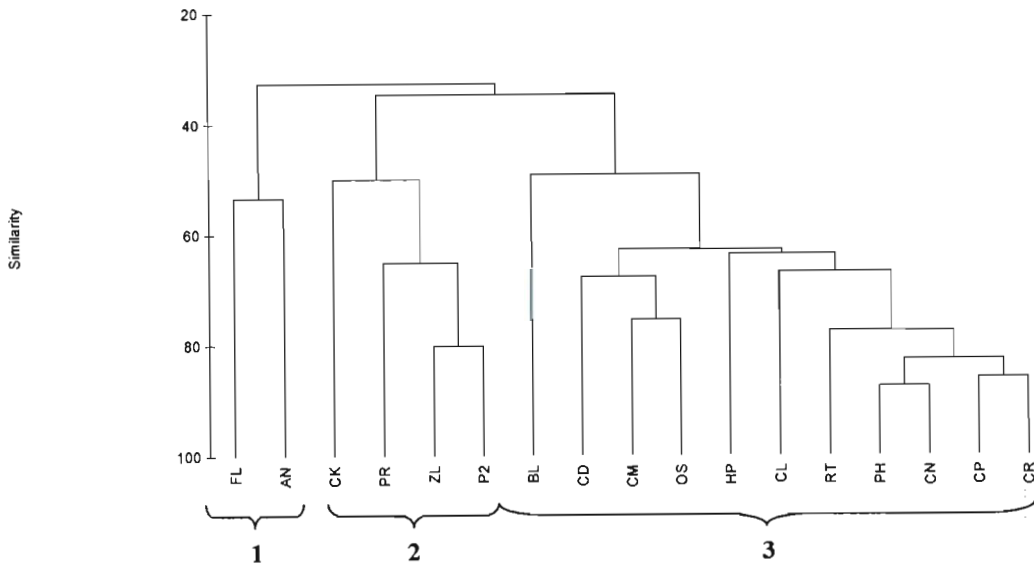
TAXA	Sled		WP2		Total (Sled + WP2 )	
	Mean ± SD	% Contribution	Mean ± SD	% Contribution	Mean ± SD	% Contribution
<b>Hydrozoa</b>						
<i>Hydra</i> sp (?)	18.7 ± 91	0.45	0.00 ± 0.00	0.00	18.7 ± 91	0.01
<b>Annelida</b>						
<i>Ceratonereis keiskama</i>	0.06 ± 0.23	<0.01	0.07 ± 0.34	<0.01	0.13 ± 0.4	<0.01
Other polychaetes (2 sp.)	6.6 ± 40	0.15	0.06 ± 0.27	<0.01	6.38 ± 30.3	<0.01
<i>Prionospio</i> sp.	2.15 ± 8.56	0.05	1.32 ± 5.05	<0.01	3.38 ± 9.49	<0.01
<b>Cladocera</b>						
<i>Ceriodaphnia</i> sp	1515 ± 2399	34.91	2342 ± 3609	0.64	3794 ± 5682	1.03
<i>Chydorus</i> sp.	0.32 ± 155	0.01	11.9 ± 30.8	<0.01	12.2 ± 31.1	<0.01
<b>Copepoda</b>						
<i>Acartia natalensis</i>	440 ± 1166	10.15	6.71 ± 19.6	<0.01	447 ± 1142	0.12
Copepod nauplii	0.00 ± 0.00	0.00	60133 ± 128315	16.51	60133 ± 128315	16.32
Cyclopoids	18.72 ± 35.1	0.42	131 ± 241	0.04	147 ± 237	0.04
Harpacticoids	1.45 ± 4.37	0.03	204 ± 831	0.06	206 ± 831	0.06
<i>Pseudodiaptomus hessei</i>	2278 ± 3444	52.50	247 ± 541	0.07	2429 ± 3740	0.66
<b>Amphipoda</b>						
<i>Grandidierella lignorum</i>	2.92 ± 7.35	0.07	0.00 ± 0.00	0.00	2.92 ± 35	<0.01
<b>Mysidacea</b>						
<i>Mesopodopsis africana</i>	0.11 ± 0.44	<0.01	0.00 ± 0.00	0.00	0.1 ± 0.43	<0.01
<b>Decapoda</b>						
Brachyuran larvae	2.57 ± 58.46	0.06	5.71 ± 28	<0.01	8.17 ± 28.3	<0.01
Caridean larvae	24.37 ± 58.46	0.56	16.4 ± 33.7	<0.01	40 ± 81.1	0.01
<b>Insecta</b>						
Chironomid larvae	0.97 ± 2.36	0.02	13.7 ± 22	<0.01	14.6 ± 22.1	<0.01
Zygoteran larvae	0.13 ± 0.48	<0.01	1.9 ± 7.5	<0.01	2.03 ± 7.49	<0.01
<b>Pisces</b>						
Fish eggs	0.04 ± 0.2	<0.01	0.00 ± 0.00	0.00	0.04 ± 0.2	<0.01
Fish larvae	7.69 ± 22.4	0.18	0.37 ± 1.5	<0.01	8.06 ± 21.9	<0.01
<b>Other taxa</b>						
Nematodes	0.03 ± 0.13	<0.01	0.00 ± 0.00	0.00	0.03 ± 0.13	<0.01
Ostracods	18.7 ± 35.1	0.43	3.13 ± 9.95	<0.01	21.8 ± 34.5	0.01
Rotifers	0.00 ± 0.00	0.00	3011192 ± 1088129	82.70	301192 ± 1088129	81.7
<b>Totals</b>	<b>4339 ± 4824</b>	<b>100</b>	<b>364311 ± 20764776</b>	<b>100</b>	<b>368469 ± 1090128</b>	<b>100</b>



**Figure 7.** Abundance (mean  $\pm$  SD) of the three dominant taxa at the Mdloti Estuary during the study period (March 2002-March 2003): (a) *P. hessei*, (b) rotifers (c) *Ceriodaphnia* sp. Note that in May 2002 rotifer abundance was an order of magnitude higher than the average, while in March 2003 this was two orders of magnitude higher than average. □ Open phase    ▨ closed phase    \*: no data



**Figure 8.** Biomass of the three dominant taxa (mean  $\pm$  SD) at the Mdloti Estuary during the study period: (a) *P. hessei*, (b) rotifers and (c) *Ceriodaphnia* sp. Note that in May 2002 and March 2003 rotifer biomass was an order of magnitude higher than average.  $\square$  Open phase;  $\square$  closed phase  
\*: no data

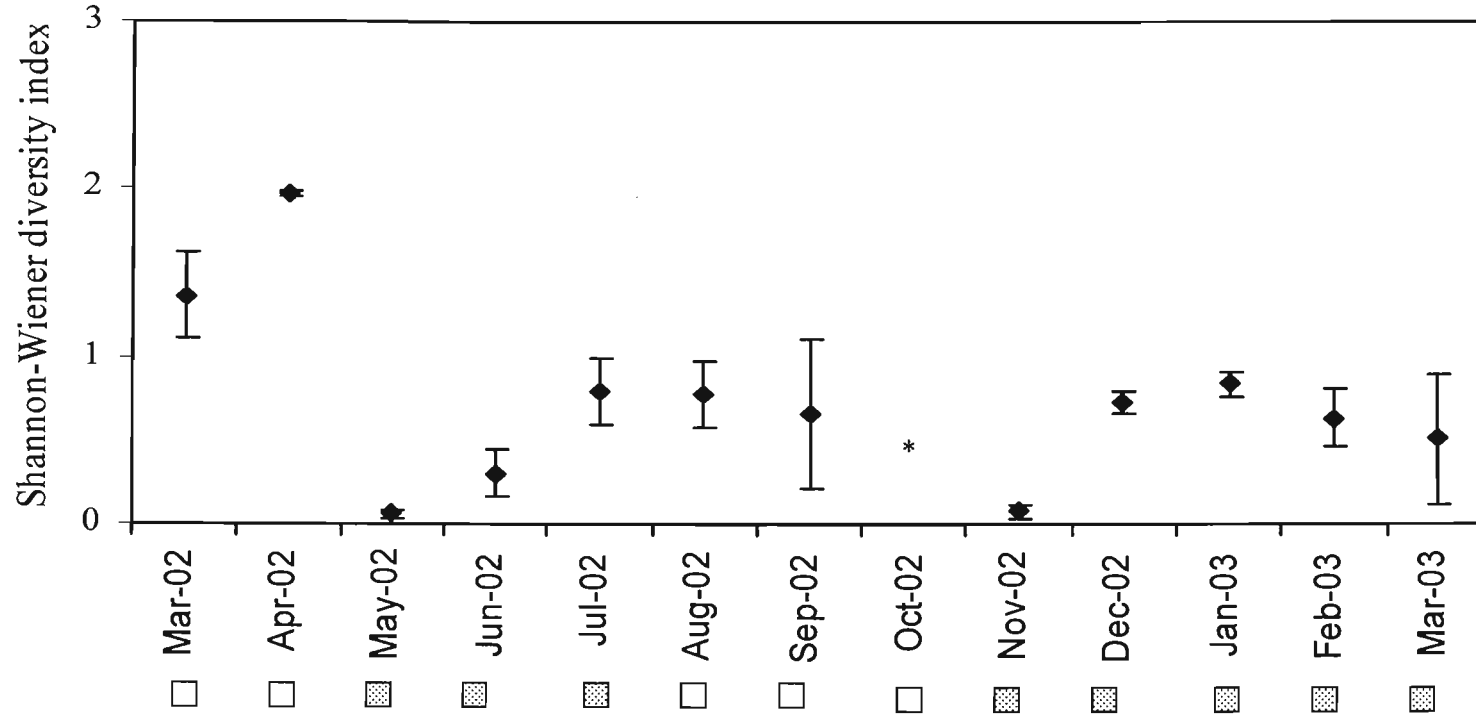


**Figure 9.** Results of cluster and corresponding MDS analysis of the zooplankton community structure of the Mdloti Estuary (refer to Table 5 for codes used).



**Table 5.** Codes used for cluster and MDS analysis at the Mdloti

<b>Taxon</b>	<b>Codes</b>
<i>Acartia natalensis</i>	AN
Brachyuran larvae	BL
Caridean larvae	CL
<i>Ceratonereis keiskama</i>	CK
<i>Ceriodaphnia</i> sp.	CR
Chaetognaths	CH
Chironomid larvae	CM
<i>Chydorus</i> sp.	CD
Copepod nauplii	CN
Cyclopoids	CP
Euphausiids	EP
Fish eggs	FE
Fish larvae	FL
Gastropod veligers	GV
<i>Grandidierella lignorum</i>	GL
Hirudineans	HR
<i>Hydra</i> sp.(?)	HY
<i>Mesopodopsis africana</i>	MA
Mites	MC
Nematodes	NM
<i>Oithona</i> sp.	OT
Oligochaetes	OL
Ostracods	OS
Polychaete II	P2
Polychaete I	P1
Polychaete IV	P4
Polychaete VI	P6
<i>Prionospio</i> sp.	PR
<i>Pseudodiaptomus hessei</i>	PH
Rotifers	RT
Zygoteran larvae	ZL



**Figure 10.** Shannon-Wiener diversity indexes (mean  $\pm$  SD) for the zooplankton community of the Mdloti Estuary during the study period; \*: no data.

□ Open phase ;    ▨ closed phase

### *Mhlanga Estuary*

A total of 31 taxa were recorded at the Mhlanga during the open phase. However, only three of these contributed >1% to the total abundance (Table 6). The copepod nauplii were the single most abundant group during this phase, contributing up to 89% of the total zooplankton abundance. The three other dominant taxa were *P. hessei*, unidentified cyclopoids and harpacticoids, each contributing 6.5%, 2% and 0.4% of the total zooplankton abundance, respectively. During the closed phase, 25 taxa were recorded at the Mhlanga, with only four groups contributing >1% of the total zooplankton abundance (Table 7). The three dominant taxa during the closed phase were *P. hessei*, rotifers, and brachyuran larvae, contributing 15%, 18% and 39% of the total zooplankton abundance, respectively. Copepod nauplii were also abundant, contributing 26% of the total zooplankton abundance. Abundance and biomass plots for the three most dominant taxa are presented in Figures 11 and 12, respectively.

Spearman rank correlation coefficients between the biomass of the dominant taxa and environmental variables are presented in Table 2. *P. hessei* exhibited no significant correlation with any environmental parameters. Copepod nauplii biomass was positively correlated to microphytobenthic algae ( $r = 0.4$ ,  $P < 0.01$ ), but exhibited an inverse correlation with rainfall ( $r = -0.51$ ;  $P < 0.01$ ). Rotifers were positively correlated to temperature only ( $r = 0.37$ ;  $P < 0.05$ ), while brachyuran larvae were positively correlated to both temperature ( $r = 0.47$ ;  $P < 0.01$ ) and phytoplankton biomass ( $r = 0.43$ ;  $P < 0.01$ ).

Dendograms of the hierarchical cluster analysis at the arbitrary similarity level of 50% show that up to five groups can be identified at the Mhlanga (Figure 13). The two-dimensional MDS plots exhibited stress levels of 0.2 for the entire sampling period, thus providing a potentially useful two-dimensional representation (Clarke & Warwick 1994). In addition, the dendogram groups matched well the MDS plots, thus providing confidence in the two-dimensional representation of the MDS plots (Clarke & Warwick 1994).

Of the five groups identified by cluster and MDS analysis, group 1 was more abundant during the closed phase and was represented by *Mesopodopsis africana* and

*Prionospio* sp. Group 2 was well represented during the summer months. This group included *Ceratonereis keiskama* and *Grandidierella lignorum*. The largest group (group 4) consisted of typically estuarine taxa that were present almost throughout the sampling period. This group was represented by *P. hessei*, caridean larvae, copepod nauplii, rotifers, fish larvae, cyclopoids and brachyuran larvae. The second largest group (group 3) showed no particular spatial and/or temporal trends and was represented by *Acartia natalensis*, zygopteran larvae, nematodes, ostracods, and chironomid larvae. The last group (group 5) consisted of typically freshwater taxa that were well represented during the closed phase. This group included *Ceriodaphnia* sp, *Chydorus* sp. and unidentified harpacticoids.

Shannon-Wiener diversity indexes ( $H'$ ) of zooplankton species for each sampling station at the Mhlanga are presented in Figure 14. No significant differences were observed in zooplankton diversity indexes between open and closed phases (one-way ANOVA,  $F_{1,38} = 0.07$ ;  $P > 0.05$ ) and between sampling stations (one-way ANOVA,  $F_{2,38} = 0.24$ ;  $P > 0.05$ ). Diversity indexes ranged from 0.5 to 2.2 during the open phase, while during the closed phase they ranged from 0.2 to 1.9.

#### ***Copepod nauplii – rainfall relationship***

The copepod nauplii were numerically abundant in both estuaries. Their abundance fluctuated drastically throughout the sampling period, with high numbers often recorded shortly after 2-4 weeks of major rainfall (Figures 15a & 15b).

**Table 6.** Numerical composition (mean ind.m<sup>-3</sup> ± SD) of the zooplankton community of the Mhlanga Estuary during the open phase.

Taxa	Sled (200 µm)		WP2 (90 µm)		Total (WP2 + Sled)	
	Mean ± SD	%Contribution	Mean ± SD	%Contribution	Mean ± SD	%Contribution
<b>Annelida</b>						
<i>Ceratonereis keiskama</i>	0.02 ± 0.08	<0.01	13.0 ± 26.5	0.06	13.0 ± 26.5	0.05
Hirudineans	0.21 ± 0.90	<0.01	0.00 ± 0.00	0.00	0.21 ± 0.90	<0.01
Oligochaeta	2.49 ± 10.6	0.06	6.29 ± 17.39	0.03	8.74 ± 19.5	0.03
Other polychaetes (3 sp.)	0.78 ± 2.22	0.02	0.04 ± 0.12	<0.01	0.82 ± 2.32	<0.01
<i>Prionospio</i> sp.	20.1 ± 74.7	0.47	0.00 ± 0.00	0.00	20.1 ± 74.7	0.08
<b>Cladocera</b>						
<i>Ceriodaphnia</i> sp.	1.12 ± 2.27	0.03	0.04 ± 0.18	<0.01	1.17 ± 2.7	<0.01
<i>Chydorus</i> sp.	0.12 ± 0.29	<0.01	5.63 ± 18.3	0.02	5.75 ± 18.4	0.02
<b>Copepoda</b>						
<i>Acartia natalensis</i>	1.13 ± 2.84	0.03	0.03 ± 0.13	<0.01	1.16 ± 2.95	<0.01
Copepod nauplii	0.00 ± 0.00	0.00	6944 ± 9836	30.8	6944 ± 9836	25.90
Cyclopods	7.37 ± 13.8	0.17	151 ± 356	0.67	159 ± 355	0.59
<i>Pseudodiaptomus hessei</i>	4141 ± 7252	97.40	39.5 ± 118	0.18	4180 ± 7338	15.60
<b>Amphipoda</b>						
<i>Grandidierella lignorum</i>	1.08 ± 3.27	0.03	8.38 ± 33.1	0.04	9.46 ± 36.0	0.04
<b>Mysidacea</b>						
<i>Mesodopsis africana</i>	3.77 ± 12.97	0.09	0.00 ± 0.00	0.00	3.77 ± 13.0	0.01
<b>Decapoda</b>						
Branchyuran larvae	42.4 ± 87.3	1.00	10357 ± 43314	46	10399 ± 43364	38.80
Caridean larvae	17.0 ± 26.1	0.40	109 ± 263	0.48	125 ± 271	0.47
<b>Insecta</b>						
Chironomid larvae	0.00 ± 0.00	0.00	4.96 ± 6.93	0.02	4.96 ± 6.93	0.02
Zygoteran larvae	0.52 ± 1.59	0.01	18.8 ± 48.0	0.08	19.4 ± 49.4	0.07
<b>Pisces</b>						
Fish larvae	8.55 ± 17.1	0.20	34.1 ± 50.4	0.15	42.7 ± 51.1	0.05
Fish eggs	0.71 ± 2.03	0.02	0.03 ± 0.14	<0.01	0.74 ± 2.02	<0.01
<b>Other taxa</b>						
Chaetognaths	0.23 ± 0.98	0.01	0.00 ± 0.00	0.00	0.23 ± 0.98	<0.01
Rotifers	0.00 ± 0.00	0.00	4824 ± 11971	21.4	4824 ± 11971	18.01
Nematodes	0.72 ± 2.03	0.02	1.52 ± 3.82	0.01	2.24 ± 4.14	0.01
Ostracods	2.64 ± 4.42	0.06	0.62 ± 1.43	<0.01	3.26 ± 4.38	0.01
<b>Total</b>	<b>4252 ± 7236</b>	<b>100</b>	<b>22538 ± 46058</b>	<b>100.00</b>	<b>16019 ± 17174</b>	<b>100</b>

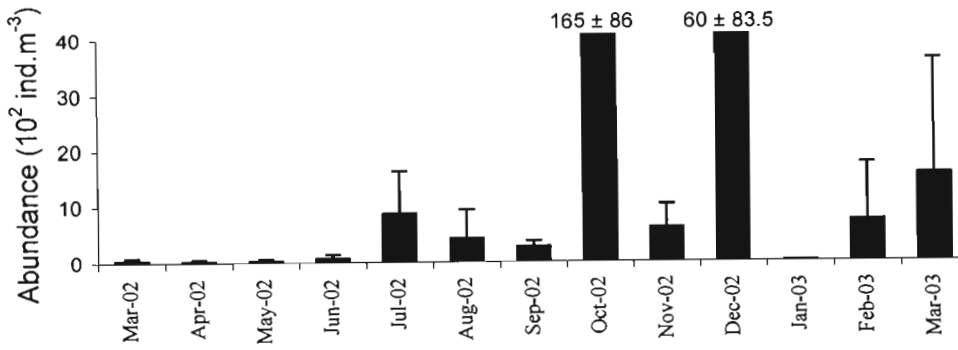
**Table 7** Numerical composition (mean ind/m<sup>3</sup> ± SD) of the zooplankton community of the Mhlanga Estuary during the closed phase.

Taxonomic groups	Sled (200 µm)		WP2 (90 µm)		Total (WP2 + Sled)	
	Mean ± SD	%Contribution	Mean ± SD	%Contribution	Mean ± SD	%Contribution
<b>Hydrozoa</b>						
<i>Hydra</i> sp. (?)	0.06 ± 0.22	0.03	0.00 ± 0.00	0.00	0.06 ± 0.22	<0.01
<b>Annelida</b>						
Oligochaeta	0.00 ± 0.00	0.00	0.79 ± 2.65	0.02	0.79 ± 2.65	0.02
Hirudinea	0.11 ± 0.49	0.05	0.91 ± 3.59	0.02	1.02 ± 3.6	0.02
<i>Ceratonereis keiskama</i>	0.31 ± 0.72	0.14	0.00 ± 0.00	0.00	0.31 ± 0.72	0.01
<i>Prionospio</i> sp.	0.2 ± 0.47	0.02	0.00 ± 0.00	0.00	0.2 ± 0.47	<0.01
<b>Cladocera</b>						
<i>Ceriodaphna</i> sp.	6.84 ± 8.58	2.97	2.81 ± 8.96	0.07	9.65 ± 13.5	0.22
<i>Chydorus</i> sp.	1.15 ± 2.6	0.5	6.84 ± 19.1	0.16	8.0 ± 18.9	0.18
<b>Copepoda</b>						
<i>Acartia natalensis</i>	0.20 ± 0.37	0.09	2.91 ± 12.7	0.07	3.11 ± 13.0	0.07
Copepod nauplii	0.00 ± 0.00	0.00	3953 ± 65016	94	3953 ± 6516	88.70
Cyclopods	5.64 ± 7.74	2.45	81.7 ± 146	1.93	87.4 ± 145	2.00
Harpacticoids	0.00 ± 0.00	0.00	18.5 ± 35.0	0.44	18.5 ± 35.0	0.42
<i>Oithonia</i> sp.	0.05 ± 0.21	0.02	0.00 ± 0.00	0.00	0.05 ± 0.21	<0.01
<i>Pseudodiaptomus hessei</i>	199 ± 417	86.10	100 ± 217	2.15	299 ± 458	6.50
<b>Amphipoda</b>						
<i>Grandidierella lignorum</i>	0.00 ± 0.00	0.00	5.83 ± 21.8	0.14	5.83 ± 21.8	0.13
<b>Mysidacea</b>						
<i>Mesodopsis africana</i>	0.02 ± 0.07	0.01	0.00 ± 0.00	0.00	0.02 ± 0.07	<0.01
<b>Decapoda</b>						
Branchyuran larvae	0.05 ± 0.21	0.02	5.59 ± 22.9	0.13	5.64 ± 22.9	0.13
Mud prawns	0.00 ± 0.00	0.00	0.01 ± 0.04	<0.01	0.01 ± 0.04	<0.01
Caridean larvae	3.79 ± 6.49	1.64	7.21 ± 14.3	0.17	11 ± 20.3	0.25
<b>Insecta</b>						
Chironomid larvae	0.9 ± 3.69	0.41	7.62 ± 30.3	0.18	8.52 ± 30.4	0.19
Zygoteran larvae	0.05 ± 0.15	0.02	1.67 ± 4.44	0.04	1.72 ± 4.5	0.04
<b>Pisces</b>						
Fish larvae	1.27 ± 4.66	0.55	0.6 ± 2.22	0.01	1.87 ± 5.12	0.04
Fish eggs	0.2 ± 0.72	0.09	0.33 ± 1.42	0.01	0.53 ± 1.55	0.01

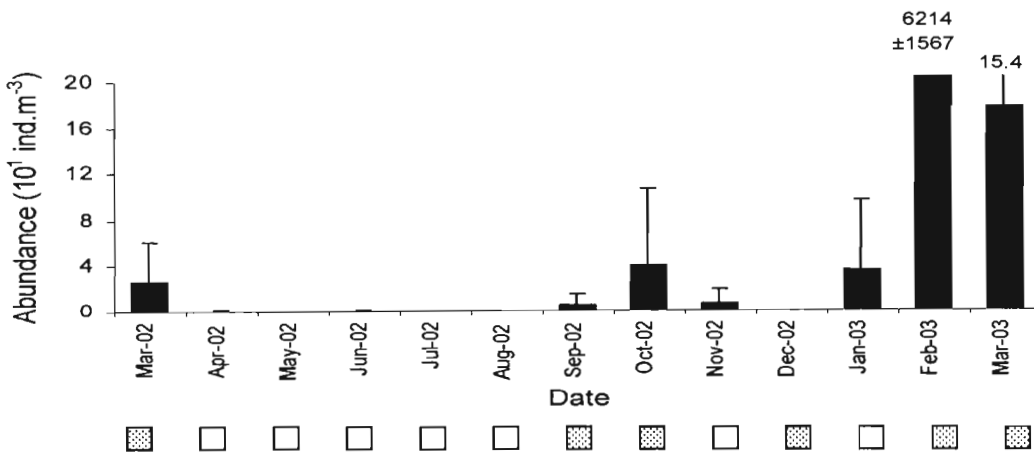
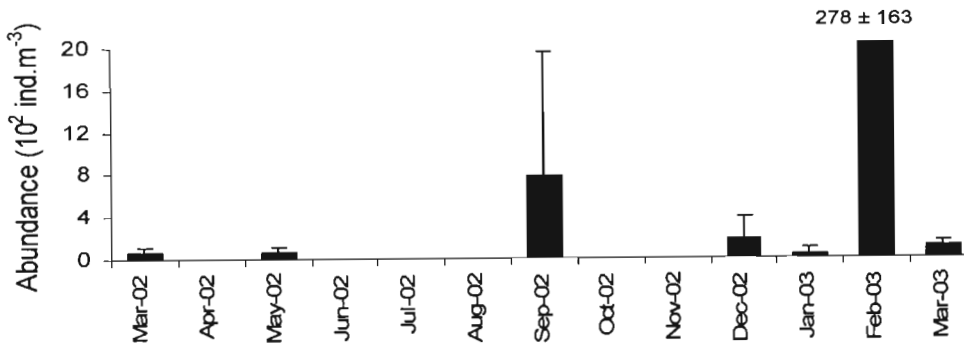
Table 7. Continues. . . .

Taxa	Sled (200 $\mu\text{m}$ )		WP2 (90 $\mu\text{m}$ )		Total (WP2 + Sled)	
	Mean $\pm$ SD	%Contribution	Mean $\pm$ SD	%Contribution	Mean $\pm$ SD	%Contribution
<b>Other taxa</b>						
Chaetognaths	0.00 $\pm$ 0.00	0.00	0.31 $\pm$ 1.23	0.01	0.31 $\pm$ 1.23	0.01
Euphausiids	0.3 $\pm$ 1.39	0.13	0.00 $\pm$ 0.00	0.00	0.3 $\pm$ 1.39	0.01
Gastropod viligers	0.00 $\pm$ 0.00	0.00	6.32 $\pm$ 29	0.15	6.32 $\pm$ 29.0	0.14
Nematodes	0.29 $\pm$ 0.77	0.12	10.2 $\pm$ 14.5	0.24	10.49 $\pm$ 14.7	0.23
Ostracods	0.67 $\pm$ 1.07	0.29	1.59 $\pm$ 4.89	0.04	2.26 $\pm$ 5.35	0.05
Rotifers	0.00 $\pm$ 0.00	0.00	14.8 $\pm$ 34.1	0.35	14.8 $\pm$ 34.1	0.30
<b>Total</b>	<b>4252 <math>\pm</math> 7236</b>	<b>100</b>	<b>4225 <math>\pm</math> 6468</b>	<b>100</b>	<b>4456 <math>\pm</math> 6652</b>	<b>100</b>

a)



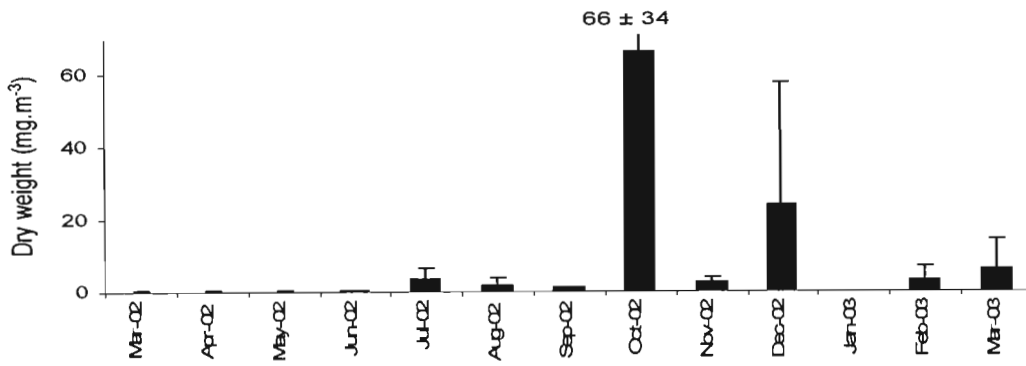
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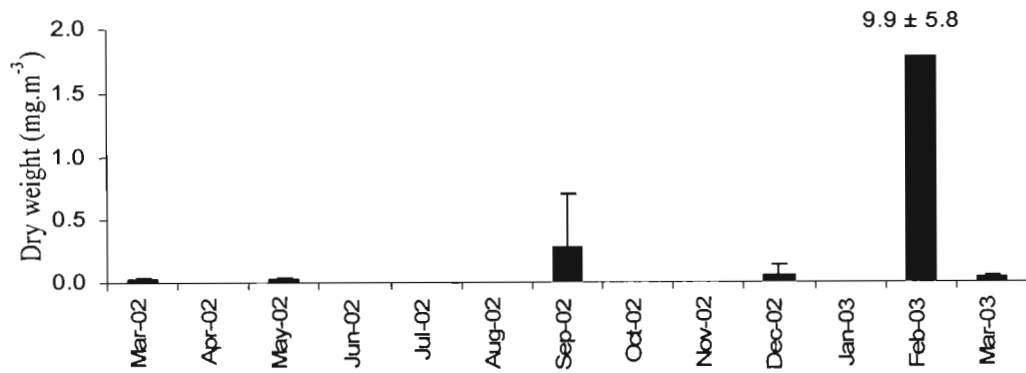
**Figure 11.** Abundance of the three dominant taxa (mean  $\pm$  SD) at the Mhlanga Estuary during the survey period (March 2002 to March 2003): (a) *Pseudodiaptomus hessei*, (b) rotifers and (c) brachyuran larvae. Note that the rotifers and brachyuran larvae were an order of magnitude more abundant in February 2003 than during the rest of the sampling period.  $\square$  Open phase;  $\square$  closed phase



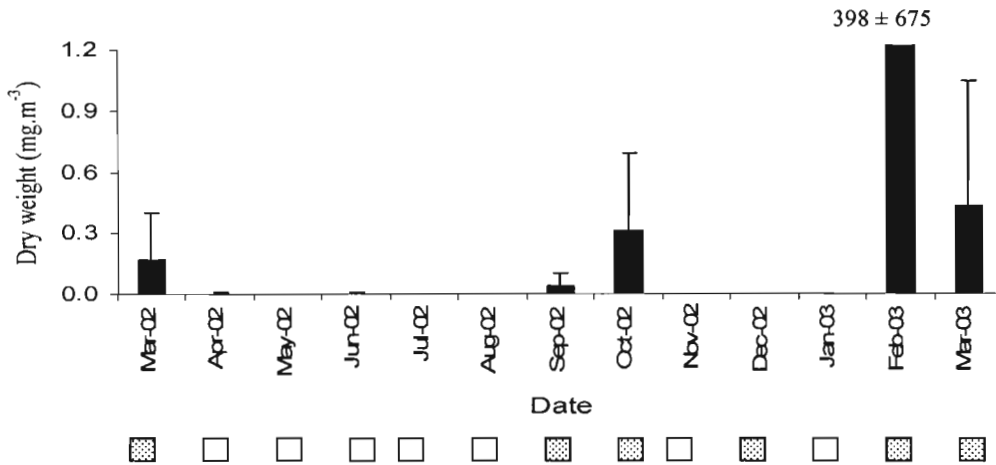
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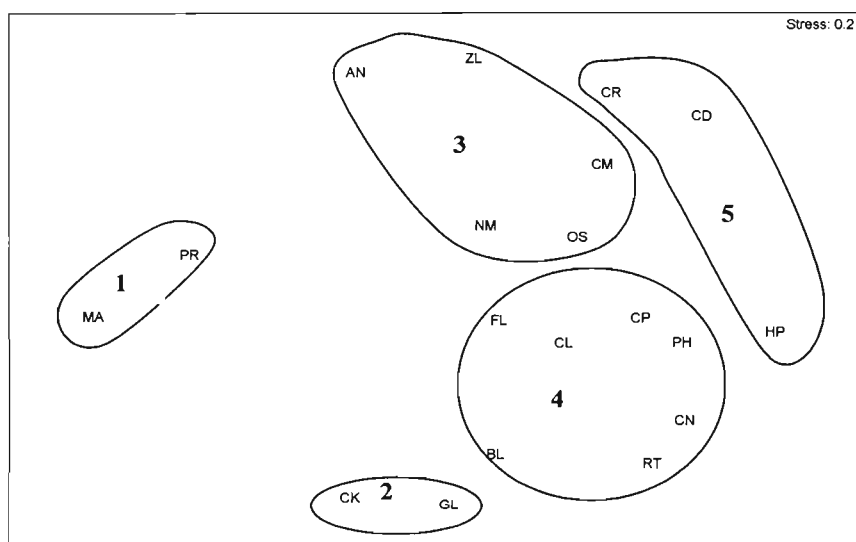
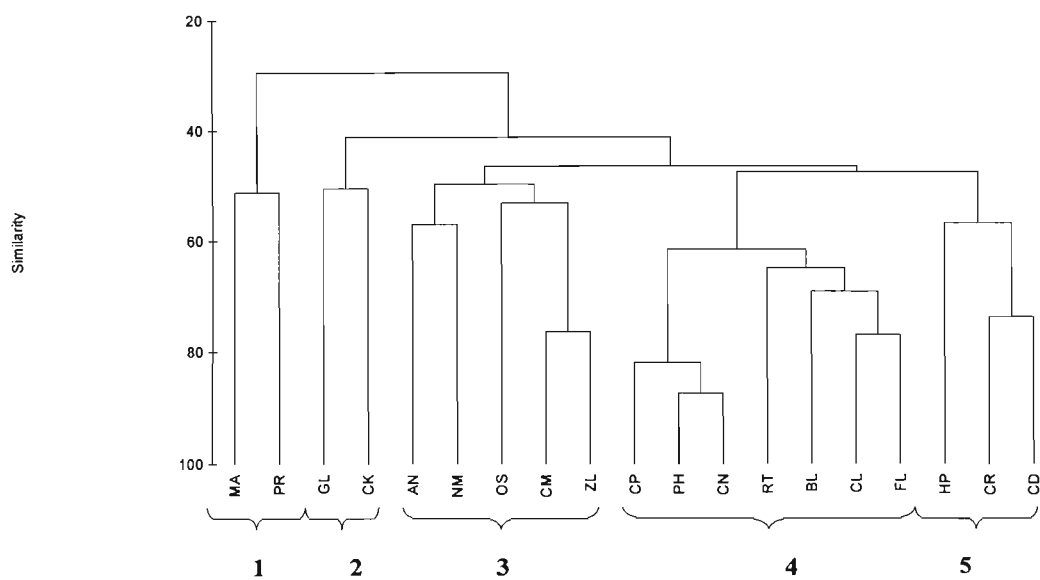
b)



c)



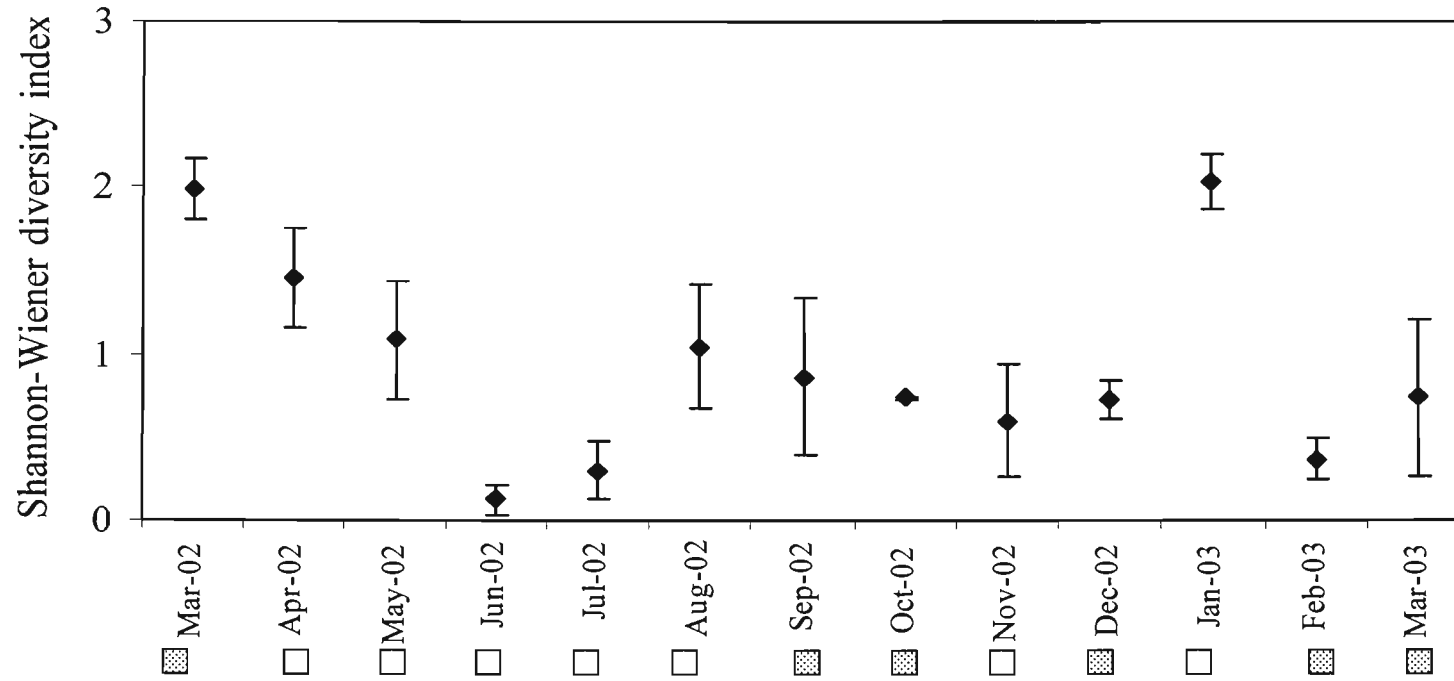
**Figure 12.** Biomass of the three most abundant taxa (mean  $\pm$  SD) at the Mhlanga Estuary during the survey period: (a): *Pseudodiaptomus hessei*, (b): rotifers and (c): brachyuran larvae. Note that the biomass of rotifers was two orders of magnitude higher in February 2003 compared to the rest of the sampling period.  $\square$  Open phase;  $\boxtimes$  closed phase.



**Figure 13.** Results of cluster and corresponding MDS plots of the zooplankton community structure of the Mhlanga Estuary (refer to Table 8 for codes used).

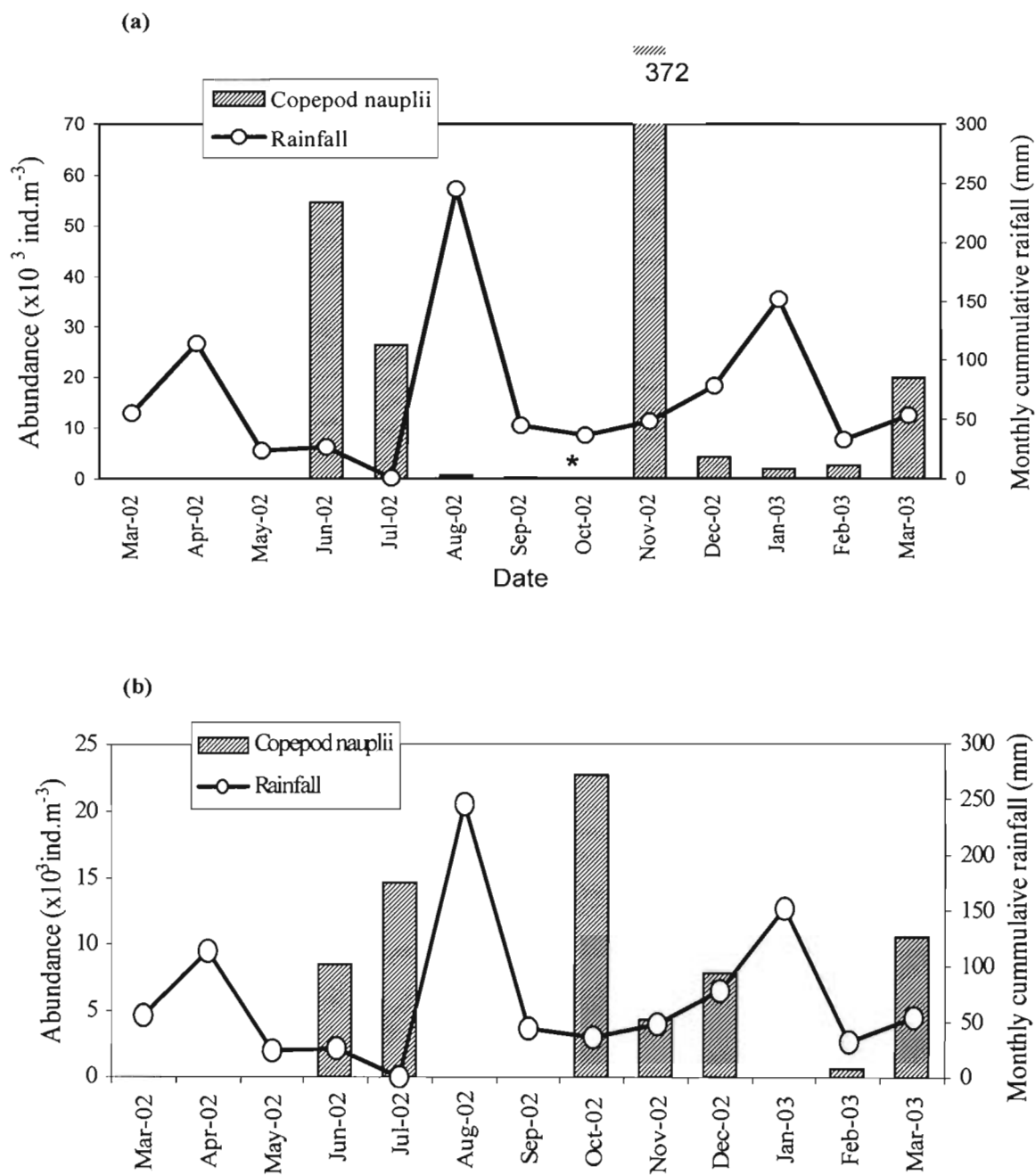
**Table 8.** Codes used for the cluster and MDS analysis at the Mhlanga Estuary.

<b>Taxa</b>	<b>Codes</b>
<i>Acartia natalensis</i>	AN
Brachyuran larvae	BL
Caridean larvae	CL
<i>Ceratonereis keiskama</i>	CK
<i>Ceriodaphnia</i> sp.	CR
Chaetognaths	CH
Chironomid larvae	CM
<i>Chydorus</i> sp.	CD
Copepod nauplii	CN
Cyclopoids	CP
Euphausiids	EP
Fish eggs	FE
Fish larvae	FL
Gastropod veligers	GV
<i>Grandidierella lignorum</i>	GL
Hirudineans	HR
Hydra (sp.)?	HY
<i>Mesopodopsis africana</i>	MA
Mites	MC
Nematodes	NM
<i>Oithona</i> sp.	OT
Oligochaetes	OL
Ostracods	OS
Polychaete II	P2
Polychaete I	P1
Polychaete IV	P4
Polychaete VI	P6
<i>Prionospio</i> sp.	PR
<i>Pseudodiaptomus hessei</i>	PH
Rotifers	RT
Zygoteran larvae	ZL



**Figure 14.** Shannon-Wiener diversity indexes (mean  $\pm$  SD) for the zooplankton community of the Mhlanga Estuary during the study period;

□ open phase;    ▨ closed phase.



**Figure 15.** Temporal variation in the abundance of copepod nauplii and rainfall at (a) the Mdloti and (b) the Mhlanga estuaries during the study period; \*:no data.

## DISCUSSION

The Mdloti and the Mhlanga estuaries have experienced major changes over the past 20 years, both in terms of their flow dynamics and the frequency of breaching events. In an earlier study conducted on the Mhlanga Estuary, it was reported that this system experienced prolonged periods of mouth closure (Whitfield 1980). This is typical of a system with a small catchment area. A similar study conducted at the Mdloti (Blaber *et al.* 1984) indicated that although this system also experienced periods of mouth closure, it breached more frequently than the Mhlanga. Again, this is what one would expect as the Mdloti exhibits a catchment area five times the size of the Mhlanga. During the current study, however, the Mhlanga experienced more breaching events than the Mdloti. This can be attributed to the large volume of water currently discharged into the Mhlanga. The Mdloti, on the other hand, receives less treated sewerage and has a dam upstream. The lower frequency of breaching events experienced by the Mdloti has resulted in the estuary exhibiting relatively lower salinity values than the Mhlanga. Furthermore, the Mdloti also exhibited weaker axial and vertical salinity gradients than the Mhlanga. Both these disparities may have important implications for the zooplankton in these systems.

In terms of zooplankton abundance and biomass, both estuaries exhibited higher values during the closed, compared to the open phase. The highest abundance value of  $\sim 2 \times 10^6 \text{ ind.m}^{-3}$ , which corresponded to a biomass of  $704 \text{ mg.m}^{-3}$ , was recorded at the Mdloti, following 44 days of mouth closure in March 2003. Similarly, the Mhlanga exhibited a maximum abundance value of  $9.2 \times 10^4 \text{ ind.m}^{-3}$ , and a maximum biomass of  $430 \text{ mg.m}^{-3}$ , following 11 days of mouth closure in February 2003. This pattern may be attributed to the stability achieved by these systems during periods of mouth closure, when the estuaries exhibit less freshwater input and a restricted exchange of water with the sea. Furthermore, high levels of phytoplankton and microphytobenthic algae were recorded during the closed phase (Thomas 2003, Iyer 2005), thus providing optimal trophic conditions for zooplankton growth during this phase. This view is further supported by the positive correlation observed between the zooplankton biomass and both phytoplankton and microphytobenthic algal biomass. These findings confirm the validity of the first hypothesis, as stated in the “General Introduction” on page 3, and are also consistent with observations made in other TOCEs, such as Nyara (Perissinotto *et al.* 2000) and Mpenjati (Kibirige 2002, Kibirige & Perissinotto 2003).

The average zooplankton abundance value of  $2.5 \times 10^5 \text{ ind.m}^{-3}$  recorded at the Mdloti during the survey was 17 times higher than the value of  $1.5 \times 10^4 \text{ ind.m}^{-3}$  recorded at the Mhlanga. Similarly, the average zooplankton biomass value of  $127 \text{ mg.m}^{-3}$  calculated for the entire survey at the Mdloti was more than two times higher than the  $52 \text{ mg.m}^{-3}$  recorded at the Mhlanga. The lower zooplankton abundance and biomass values recorded at the Mhlanga, relative to the Mdloti, may be attributed to the shorter residence time of water at the Mhlanga, as a result of the estuary breaching more often than the Mdloti. This may not have allowed the build-up of zooplankton biomass (Perissinotto *et al.* 2000). These findings are also consistent with the second hypothesis stated in page 3.

The maximum values of  $\sim 1.2 \text{ g.m}^{-3}$  and  $\sim 2 \text{ g.m}^{-3}$  (DW) recorded during the closed phase at the Mhlanga and the Mdloti, respectively, compare well with the values of  $\sim 2 \text{ g.m}^{-3}$  (DW) recorded at Nyara (Perissinotto *et al.* 2000, Perissinotto *et al.* 2003) and  $\sim 1.7 \text{ g.m}^{-3}$  (DW) recorded at Mpenjati (Kibirige 2002). However, the average value of  $\sim 0.05 \text{ g.m}^{-3}$  (DW) calculated for the entire survey at the Mhlanga is an order of magnitude lower than the value of  $0.5 \text{ g.m}^{-3}$  (DW) reported from the Mpenjati Estuary (Kibirige 2000, Kibirige & Perissinotto 2003) and also three times lower than the value of  $\sim 0.15 \text{ g.m}^{-3}$  (DW) reported from the Nyara Estuary (Perissinotto *et al.* 2000, Perissinotto *et al.* 2003). This may also be attributed to the higher frequency of breaching of the Mhlanga compared to both Mpenjati and Nyara. On the contrary, the average value of  $\sim 0.13 \text{ g.m}^{-3}$  (DW) recorded at the Mdloti compares well with the value reported for the Nyara (Perissinotto *et al.* 2000, Perissinotto *et al.* 2003), but is four times lower than that reported from the Mpenjati (Kibirige 2002).

The maximum zooplankton biomass values recorded at the Mhlanga and the Mdloti estuaries compare well with the average values reported from some of their permanently open counterparts (Table 9). This suggests that these estuaries are able to build-up a large biomass during their closed phase. However, this is often followed by a period of depression during the open phase (Whitfield 1980, Perissinotto *et al.* 2003). Although very few studies have been conducted on South African TOCEs, available information suggests that zooplankton biomass in these systems range 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.* 2004). During the closed phase, TOCEs are known to exhibit average zooplankton biomass values higher than the values reported for some permanently open estuaries (Wooldridge 1999, Perissinotto *et al.* 2000).

**Table 9.** Standing stock of zooplankton ( $\text{mg DW}\cdot\text{m}^{-3}$ ) in some South African estuaries. \* no data available; POE: Permanently open estuary; TOCE: Temporarily open/close estuary; EB: Estuarine Bay.

<b>Zooplankton standing stock (<math>\text{mg}\cdot\text{m}^{-3}</math> DW)</b>				
<b>Estuary</b>	<b>Description</b>	<b>Average</b>	<b>Maximum</b>	<b>Reference</b>
Great Fish	POE	1597	11681	Grange 1992
Keiskamma	POE	1627	7497	Allanson & Read 1995
Richards Bay	EB	174	344	Grindley & Wooldridge 1974
Swartskops	POE	17	95	Grindley 1981
Msikaba	POE	15	35	Wooldridge 1976
Mbotyi	POE	87	109	Wooldridge 1974
Kerieka	POE	38	108	Grange 1992
Nyara	TOCE	*	2030	Perissinotto et al. 2000
Mpenjati	TOCE	280	1700	Kibirige 2000
Mhlanga	TOCE	52	1210	Current study
Mdloti	TOCE	127	2010	Current study

Both the Mdloti and the Mhlanga exhibited slightly higher numbers of taxa during their open phase than the closed phase, possibly due to the incursion of marine and freshwater taxa during the open phase. However, no significant differences in Shannon-Wiener diversity indexes ( $H'$ ) were observed between the open and the closed phase at the Mhlanga ( $F_{2, 38} = 0.24$ ;  $P > 0.05$ ). Again this can be attributed to the Mhlanga breaching more often, thus not allowing enough time for major changes in the zooplankton community structure to occur. The Mdloti, on the other hand, exhibited significant differences in Shannon-Wiener diversity indexes between the two phases, with the open phase consistently exhibiting higher values than the closed phase. Unlike the Mhlanga, the Mdloti experienced prolonged periods of mouth closure, which enabled changes in the zooplankton community structure to occur.

Differences in zooplankton community structure between the two estuaries were further confirmed by the results of the cluster and multidimensional analysis. Results of this analysis revealed that the zooplankton community of the Mdloti can be divided into three groups (at 50% similarity), while up to five groups were identified at the Mhlanga. The fewer groups recorded at the Mdloti may be attributed to slightly lower species diversity observed in this system, as a result of its stability due to fewer breaching events. The Mhlanga breached more frequently and thus exhibited slightly higher species diversity than the Mdloti. This explains the higher number of groups identified by the cluster and multidimensional analysis in this estuary. Again, these findings are consistent with the second hypothesis formulated on page 3 of the “General Introduction.”



At the Mdloti, the closed phase was marked by the clear dominance of rotifers, which contributed 82% of the total zooplankton abundance. Rotifers reached their peak in March 2003, numbering over  $1.8 \times 10^6$  ind.m<sup>-3</sup>. This phenomenon may be attributed to the prevalence of freshwater conditions in the estuary at that time during the closed phase. This may have been optimal for the proliferation of this group. Similarly, another freshwater taxon, *Ceriodaphnia* sp., exhibited a drastic increase in abundance, from an average of 22 ind.m<sup>-3</sup> during the open phase to an average of 3794 ind.m<sup>-3</sup> during the closed phase. This taxon reached its peak of 15310 ind.m<sup>-3</sup> in March 2003, following 44 days of mouth closure. The proliferation of freshwater taxa during periods of prolonged mouth closure has been previously reported by other workers (e.g. Jerling & Cyrus 1999). In their study conducted at the Nhlabane Lake, Jerling & Cyrus (1999) reported that the zooplankton community structure of this system showed a gradual shift from typically estuarine to freshwater-dominated, after periods of prolonged mouth closure. In addition, at the Mdloti, the Spearman correlation revealed a strong positive correlation between the biomass of rotifers and phytoplankton chl-a ( $r = 0.76$ ;  $P < 0.01$ ). This suggests that the large blooms of rotifers observed during the closed phase may have been triggered by the high phytoplankton biomass observed during this phase (Thomas 2003). Although rotifers were abundant at the Mhlanga during the closed phase, their densities did not reach the bloom proportions observed at the Mdloti. The short duration of the closed phase, and the conditions resulting from this, may not have been conducive to the formation of massive blooms of this taxon at the Mhlanga.

The community structures of these estuaries have changed significantly over the past twenty years. Studies conducted by Blaber *et al.* (1984) at the Mdloti indicated that the zooplankton communities at that time were dominated mainly by chironomid larvae, macruran larvae, *Musculus virgiliae* larvae and *P. hessei*. During this survey, however, the zooplankton communities were dominated by rotifers, cladocerans and *P. hessei*. Similarly, earlier studies conducted at the Mhlanga indicated that the community structure of this system was dominated mainly by *P. hessei* (Whitfield 1980). The results of the current study at the same estuary show that although *P. hessei* is still the dominant species, other taxa such as rotifers and brachyuran larvae are now also abundant. These changes in community structure may have been triggered by the changes in the flow dynamics and trophic conditions that have occurred in each estuary.

Copepod nauplii were also among the most abundant groups both at the Mdloti and the Mhlanga. Their abundance and biomass fluctuated greatly with respect to rainfall throughout the survey (Figures 15a & 15b). Although copepod nauplii were negatively correlated to rainfall, they often

appeared in large numbers about two to four weeks after major rainfall events. This may be attributed to the hatching of resting eggs in response to freshwater pulses (Marcus 1984). The apparent 2-4 week delay in the appearance of copepod nauplii, as opposed to the one week stated in the third hypothesis (see "General Introduction", page 3), may be attributed to inadequate sampling frequency. The hypothesis may be better tested by designing a higher sampling frequency protocol. Nevertheless, the findings obtained so far are consistent with the hypothesis.

## CONCLUSION AND SUGGESTIONS FOR FUTURE RESEARCH

Estuaries are amongst the most productive yet highly sensitive ecosystems in the world. They are increasingly subjected to highly destructive human activities. Retention and abstraction of water for industrial as well as domestic use remains one of the most serious threats to these ecosystems. Although the closure of most TOCEs is considered to be a natural phenomenon, the above-mentioned human activities have had an impact on both the duration and frequency of mouth closure. For example, the results of this study revealed that despite the Mhlanga having a catchment area five times smaller than that of the Mdloti, it experienced more breaching events than the Mdloti. This may be attributed to the huge volume of treated sewerage (20 million litres a day) discharged into this system. The Mdloti, on the other hand, receives significantly less treated sewerage than the Mhlanga (8-million litres a day). The presence of a dam in the catchment area of the Mdloti further reduces the freshwater input into this estuary, thus increasing the frequency and duration of mouth closure. Therefore the Mdloti Estuary functions as a true TOCE, while the Mhlanga currently behaves more like a semi-permanently open estuary.

The major differences in the hydrological features exhibited by these estuaries were also reflected in terms of their zooplankton abundance and community structure. This study revealed that the longer residence time of water at the Mdloti was conducive to the build-up of large densities of zooplankton. At the Mhlanga, where the residence time of water was much shorter, zooplankton abundance and biomass were significantly lower compared to the Mdloti. Both estuaries, however, exhibited higher zooplankton abundances and biomass during the closed phase than the open phase. The community structure exhibited by these estuaries was also substantially different. The Mdloti was dominated by typically freshwater taxa, such as the rotifers and *Ceriodaphnia* sp. The rotifers appeared to be in their bloom phase in March 2003, reaching densities of up to 1.8 million ind.m<sup>-3</sup>, after 44 days of mouth closure. On the contrary, the Mhlanga was dominated by typical estuarine taxa, such as *Pseudodiaptomus hessei* and brachyuran larvae.

It appears that both estuaries have been affected by human activities in one way or the other and this was manifested in the frequency of mouth breaching and the structure of their biological communities. TOCEs are important nursery areas for marine fish and a number of invertebrates. The disruption of the natural cycle of opening and closure of these systems may have an adverse impact on the life cycles of marine species with an obligatory estuarine phase. Prolonged periods of mouth closure during the wrong season, for example, may affect the recruitment of larvae into the system, while frequent breaching of the mouth may result in the premature release of juveniles. Clearly, estuaries require management practices based on sound scientific understanding of their hydrological and biological processes. Unfortunately, in South Africa previous environmental legislation made little provisions for the proper management of estuaries. However, recent developments, especially the White Paper for Sustainable Coastal Development (2000) and the Coastal Management Bill (2004), make provisions for sustainable utilization and protection of estuaries. Whether these provisions will translate into proper estuarine management strategies still remains to be seen.

Up to date, studies on zooplankton dynamics have focused mainly on their abundance and biomass in relation to physico-chemical variables, both on a temporal and spatial scale, with relatively little emphasis placed on biological factors such as food availability and predation. In addition, very little (if any) advances have been made towards formulating mathematical models to describe and predict zooplankton dynamics in relation to their controlling factors in South African estuaries. Furthermore, very little information is available on the response of zooplankton communities to anthropogenic activities such as the impoundment of rivers, water extraction and discharge of treated sewerage water into estuaries. Based on these shortcomings outlined above, one can summarise the research needs in this field as follows:-

1. Development of mathematical models to describe and predict zooplankton dynamics in South African estuaries.
2. Investigation of zooplankton community structure in response to eutrophication and other anthropogenic effects on estuarine systems.

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