THE DYNAMICS OF MICROPHYTOBENTHOS IN THE MDLOTI AND MHLANGA ESTUARIES, KWAZULU-NATAL

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Submitted in partial fulfilment (50% of the degree) of the academic requirements for the degree of Master of Marine and Coastal Management in the School of Life and Environmental Sciences, University of KwaZulu-Natal, Howard College Campus

2004

ABSTRACT

Microphytobenthos (MPB) generally dominates total autotrophic biomass in temporarily open/closed estuaries (TOCEs) of South Africa. A comparative study of MPB biomass was undertaken in two KwaZulu-Natal TOCEs, the Mdloti and the Mhlanga. Both estuaries receive different volumes of treated sewage waters. The Mdloti receives 8 ML.d^{-1}, while the Mhlanga receives 20 ML.d^{-1}, resulting in a capping flow of 0.092 and 0.23 m^3.s^{-1}, respectively. Through these effluents, eutrophication is enhanced and periods of mouth opening are also increased and prolonged, particularly at the Mhlanga. The aim of this study was to investigate fluctuations in MPB biomass in the Mdloti and the Mhlanga systems, with emphasis on freshwater flow and the alternation of closed and open phases. Sediment samples for MPB biomass were collected on a monthly basis, between March 2002 and March 2003, in the lower (mouth), middle, and upper (head) reaches of the two estuaries. MPB biomass ranged from 1.33 to 391 mg chl a m^{-2} and from 1.7 to 313 mg chl a m^{-2} in the Mdloti and the Mhlanga, respectively. A 1-way ANOVA revealed no significant differences in MPB chl a concentrations between the two estuaries for the entire data set ($F_{1,\ 76}$ =1.48, p > 0.05). At the Mdloti, MPB biomass varied considerably, with values ranging from 1.33 to 131 mg chl a m^{-2} during the open phase, and from 18 to 391 mg chl a m^{-2} during the closed phase. A Mann-Whitney U test confirmed the high significance of these differences between open and closed phases (U = 29, p < 0.001). At the Mhlanga, MPB biomass ranged from 7.0 to 313 mg chl a m^{-2} during the open phase, and from 1.7 to 267 mg chl a m^{-2} during the closed phase. Unlike what was observed at the Mdloti, the higher MPB values at the Mhlanga were not always associated with the closed mouth state. In relation to key physico-chemical and biological factors, grazing pressure exerted by the zooplankton community appeared to have played a major role in controlling MPB biomass. Zooplankton biomass was consistently and positively correlated to MPB biomass throughout the study period both at the Mdloti (r = 0.40, p < 0.001) and at the Mhlanga (r = 0.33, p < 0.05). Unlike what was shown in previous studies, light attenuation was not significantly correlated with MPB biomass during the period of the study, either at

the Mdloti or the Mhlanga. These results show that the opening and closing of the mouth play a key role on the MPB biomass of both estuaries. The Mdloti seems to function as a typical TOCE, with prolonged open and closed phases. The Mhlanga, on the other hand, lacks a prolonged closed phase. This, in turn, affects its entire trophic structure and functioning.

DECLARATION

The work described in this dissertation was carried out in the School of Life and Environmental Sciences, University of KwaZulu-Natal, Howard College Campus, from January 2002 to December 2004, under the supervision of Prof. R. Perissinotto and Dr C. Nozais.

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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GENERAL INTRODUCTION

Dynamics of estuarine systems

Estuaries include a wide variety of aquatic coastal systems and range from small bodies of water that are only seasonally connected to the ocean, to large permanently open systems (Day & Yanez-Arancibia 1985). The location of estuaries at the interface between river and sea makes them subject to extreme variability. The influence of the ocean and climate directly affects water levels, circulation patterns, temperature, salinity gradients, nutrient and sediment supply and the state of the mouth of an estuary (Vallino & Hopkinson 1998). Variations in precipitation and drainage from the catchment area also affect temperature, volume as well as nutrient and sediment supply of the riverine input to the estuary (Slinger 1996). Estuaries have been recognised as complex, dynamic systems that are among the most productive on earth. They create more organic matter each year than comparably-sized areas of forest, grassland or agricultural land (Davies & Day 1986), and their well mixed waters provide ideal sites for high rates of photosynthesis and secondary production (Horne & Goldman 1994).

South African estuaries

There are approximately 250 functional estuaries in South Africa (Whitfield 2000), together making up about 70000 ha of one of the country's most productive habitats (Turpie *et al.* 2002). Estuaries are an integral part of the South African coastal landscape. It has been estimated that each year the coastal zone contributes R 168 million to the South African economy. It is therefore critical to ensure that all South African estuaries receive adequate protection and are effectively and sustainably managed (Mander 2001).

South African estuaries differ from their European and American counterparts in that they are generally shallower, narrower, shorter, not always permanently open and subject to erratic flooding (Day 1981). The variability in fluvial inflow and mouth conditions makes a comprehensive definition of South African estuaries cumbersome. Day (1981) considered an estuary to be "a partially enclosed, coastal

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body of water which is either permanently or periodically open to the sea and within which, there is a measurable variation of salinity due to the mixture of the sea water with fresh water derived from land drainage". Whitfield (1992) expanded on the work of Day (1981) to recognise five estuarine types in southern Africa, namely: permanently open estuaries; temporarily open/closed estuaries (TOCEs); estuarine lakes; estuarine bays; and river mouths. The physico-chemical constraints on primary productivity differ dramatically in the two main types of estuaries, namely permanently open and TOCEs (Whitfield 1992).

Permanently open systems exhibit typical estuarine characteristics all year round and are continuously influenced by tidal action e.g. the Mkomazi Estuary in KwaZulu-Natal, which lies south of the city of Durban. The regular inflow of freshwater and seawater that occurs in permanently open estuaries ensure a steady supply of nutrients, and maintain stable and stratified conditions, which are ideal for supporting a large phytoplankton biomass and a well developed pelagic food web (Hilmer & Bate 1990; Allanson & Read 1995; Adams & Bate 1999).

In South Africa, approximately 73% of estuaries do not have a permanently open link to the sea, i.e. they are TOCEs. TOCEs are greatly influenced by river flow, wave conditions and rainfall patterns, all of which are highly seasonal (Schumann et al. 1999). A key feature of TOCEs is their distinctly different open and closed phases. In KwaZulu-Natal, TOCEs are generally closed in winter (May to October) and open in summer (November to April) (Perissinotto et al. 2003). The closed phase is characterised by relatively low freshwater inflow from the catchment area and the absence of tidal influences, ultimately reducing both sediment disturbance and turbidity, and increasing water clarity. As a result of the increased water clarity, a large percentage of surface irradiance is able to reach the sediment, providing a favourable environment for microphytobenthic growth (Wooldridge & McGwynne 1996; Nozais et al. 2001; Perissinotto et al. 2002; Perissinotto et al. 2003). At the onset of the rainy season, the water level inside the estuary may rise suddenly or gradually until it exceeds the height of the sandbar at the mouth (Whitfield 1992). When the height of the water column

exceeds that of the sandbar, breaching occurs, releasing large volumes of water into the ocean. As a result, large areas of substratum, which may have been submerged for long periods and colonised by a rich community of algae and animals, are exposed (Perissinotto *et al.* 2000). This process is often very dramatic in its potential to empty virtually the entire estuary within a time frame of hours to a few days (Begg 1984a; Cooper *et al.* 1999). These systems are generally dominated by submerged macrophytes and microphytobenthos, which are capable of taking advantage of the low turbidity and low current levels, as well as the more stable sediment and salinity environments prevailing in these systems, particularly during the closed phase (Adams & Bate 1999).

The Mdloti and the Mhlanga TOCEs

The Mdloti and the Mhlanga TOCEs are located in close proximity on the KwaZulu-Natal north coast, being approximately 7 km apart (Begg 1978). Earlier assessments of the Mdloti and the Mhlanga estuaries have indicated that neither is in a pristine condition (Whitfield 1995). The Mhlanga, which forms part of a nature reserve controlled by Ezemvelo KZN Wildlife, is classified as being in a relatively 'good' state (Whitfield 2000). The Mdloti is believed to be in a 'fair' condition as a consequence of the estuary being exposed to problems of siltation, pollution and sugar cane encroachment (Whitfield 2000).

The Mdloti is characterized as a well-mixed, shallow estuary (Cooper *et al.* 1993). Most of the sediment entering the estuary is composed of terrestrial mud, silt and sand brought down by the Mdloti River, with minor amounts being derived from marine sediments blown off the beach or washed over the sandbar during storms (Grobbler 1987). The Mdloti experiences problems of sugar cane encroachment, siltation and pollution from sewage works and from the Verulam Township and associated industries, such as the agrochemical factories situated near the Hazelmere Dam (Mundree 2001). A recent development on the north bank has resulted in further degradation of this estuary, with much of its *Barringtonia racemosa* having been destroyed. It is highly probable that this development will impact on the breaching regime of the mouth, resulting in changes in salinity

concentrations in the estuary, thus affecting directly and/or indirectly species composition, nutrient levels, flow patterns and the nursery function of this estuary (KZN Wildlife 2000).

Similar to the Mdloti, the Mhlanga is a relatively shallow estuary. Over the past 50 years, the Mhlanga system has shown little morphological change, thus suggesting that the estuary is in a state of dynamic equilibrium (Cooper 1989). Until the late 80's, the Mhlanga was subjected to a minimal human interference and remained closed to the sea for most of the year due to a low outflow and longshore drift of sand, only opening after heavy rainfall usually in summer (Blaber *et al.* 1984). A large portion of the Mhlanga catchment area is used for the cultivation of sugar cane and is free of industrial development. This is probably due to the estuary forming part of a nature reserve administered by Ezemvelo KZN Wildlife.

Statement of the problem

The question of the quantity and the quality of water that may enter any estuarine system have caused much controversy between ecologists and the Department of Water Affairs and Forestry (DWAF). Estuarine water allocation is now being considered under the National Water Act (No 36 of 1998). This specifies in Section 137 (1) that the Minister of Water Affairs and Forestry must establish national monitoring systems. Section 139 (1) requires the establishment of national information systems, such as a system to monitor the quantity and quality of all water resources. Section 145 (2) goes further, mandating the minister to establish early warning systems for risks posed by various events, including the potential deterioration of water quality. Provision is made in the Act for designating estuaries into Ecological Management Classes that reflect the preferred achievable ecological state. This enables the determination of the amount and quality of freshwater required to sustain an estuary in the defined ecological state (Breen 2001). Estuarine management has now been entrusted to Marine and Coastal Management, Department of Environmental Affairs and Tourism (DEAT) by the Marine Living Resources Act (Act 18 of 1998), and their

water allocation is considered under the new National Water Act. Through the Resource Directed Measures (RDM) process, the latter will ensure a freshwater supply or reserve for estuaries to maintain their ecological functioning. However, the level of the reserve may vary, depending on socio-economic goals, to maintain estuaries in anything from a near pristine state to a satisfactorily – functioning, but altered state (Turpie et al. 2002).

Both the Mdloti and the Mhlanga are subject to various forms of environmental challenge. Presently, the eThekwini Municipality is operating sewage plants that discharge treated sewage effluents into these systems. The Mdloti constantly receives 8 million litres per day (MLd^{-1}) of treated sewage, which is an equivalent to 0.092 m^3 s^{-1} of capping flow (W. Pfaff, eThekwini Municipality, pers. comm.). The Mhlanga, however, constantly receives 20 MLd^{-1} of treated sewage, which is equivalent to 0.23 m^3 s^{-1} of capping flow (W. Pfaff, eThekwini Municipality, pers. comm.). There are plans in place to expand the sewage discharge rate in both estuaries. This would ultimately increase the amount of 'clean waste' discharged into these estuaries. A concern surrounding this activity lies in the fact that increasing flow into these estuaries could greatly reduce or eliminate entirely the period of mouth closure. This would ultimately prevent these systems from functioning as typical TOCEs, with a prolonged closed phase. Simultaneously, nutrient and silt loading into these estuaries will increase. Nutrients will deteriorate further the already eutrophic state of the Mhlanga (Thomas 2003). Due to increased turbidity experienced during the open phase, light availability would decrease. This in turn could have a major impact on the dynamics of primary producers in these TOCEs (Nozais et al. 2001; Nozais et al. 2005).

Objectives of this study

This study forms part of a multi-disciplinary research program endorsed by the Water Research Commission (WRC) to determine the ecological status of the Mdloti and the Mhlanga estuaries. As part of the study, microphytobenthos was considered as a key component of both estuarine systems. The objectives of this study are:

1) to compare the microphytobenthic biomass of the Mdloti and the Mhlanga TOCEs, with emphasis on freshwater inflow, alternation of closed and open phases and key physico-chemical factors;

2) to determine spatial and temporal trends in microphytobenthic biomass within each estuary; and

3) to assess the growth of, and/or grazing pressure on, the microphytobenthic communities of the two estuaries by measuring the ratio of phaeopigments to chl *a*.

A REVIEW OF SOUTH AFRICAN ESTUARINE MICROPHYTOBENTHOS

Introduction

Microphytobenthos (benthic microalgae) refers to microscopic, photosynthetic eukaryotic algae and cyanobacteria that live within the sediment of many different marine and coastal habitats (MacIntyre *et al.* 1996). These habitats include estuaries, sand flats, muddy shores, saltmarshes and bare soft substrate (Admiraal *et al.* 1984; Alongi 1990; Pinckney & Zingmark 1993).

Most studies regarding estuarine benthic microalgae have been carried out in the intertidal areas of temperate regions (Admiraal *et al.* 1984; Pinckney & Zingmark 1993; De Jonge & Colijn 1994; Underwood & Chapman 1995; Guarini *et al.* 2002; Mitbavkar & Anil 2002; Underwood 2004). Compared to this extensive volume of work, studies conducted on the standing stock and productivity of microphytobenthos in South African estuarine systems are scarce (Fielding *et al.* 1988; Baird 1999). Microphytobenthic studies are available from only two warm temperate temporarily open/closed estuaries (TOCEs), namely the Groot Brak in the Western Cape (Adams & Bate 1999) and the Nyara in the Eastern Cape (Walker *et al.* 2001). Studies have also been undertaken in subtropical TOCEs, i.e. the Mpenjati (Perissinotto *et al.* 2002), the Mhlabatshane (Watt 1998), the Manzimtoti (Watt 1998), the Mdloti (Blaber *et al.* 1984; Mundree 2001; Nozais *et al.* 2001; Mundree *et al.* 2003; Perissinotto *et al.* 2003), the Tongati (Blaber *et al.* 1984) and the Fafa (Day 1981), which are all located on the KwaZulu-Natal coast.

Distribution

In estuaries, benthic microalgae are generally confined to the uppermost few millimetres of the sediment, due to their dependence on light energy for their growth (Underwood & Chapman 1995). Sedimentary characteristics such as grain size, organic content, and sediment porosity also play an important role in the distribution patterns of benthic microalgae. The trend thus far seems to indicate that in low energy, organic-rich environments microphytobenthos may be limited

to the upper few millimetres of oxygenated soil and, conversely, they are distributed uniformly to depths of 10 cm in the well-mixed sandy sediments found in high energy environments (Fielding *et al.* 1988; MacIntyre *et al.* 1996; Cahoon & Safi 2002). In the upper estuarine reaches, sediment is likely to be muddier than at the lower reaches and generally microphytobenthic biomass is higher in muddy sheltered habitats, as compared to relatively sandy exposed habitats (MacIntyre *et al.* 1996; Adams & Bate 1999; Nozais *et al.* 2001).

Benthic microalgae have also been found in substantial numbers down to depths of 10 cm and more (de Jonge & Colijn 1994; MacIntyre *et al.* 1996; Wulff *et al.* 1997). The occurrence of photosynthetically competent microphytobenthic cells well below the photic zone in the sediment has been well documented (MacIntyre *et al.* 1996; Light & Beardall 1998; Lucas & Holligan 1999) and is related to an array of factors. These include bioturbation by deposit feeders (Miller *et al.* 1996; Barranguet *et al.* 1998; Lucas *et al.* 2000), migration (MacIntyre *et al.* 1996), and/or physical hydrodynamic conditions (Lukatelich & McComb 1986; Reddering & Esterhuysen 1987; Mehta 1988; de Jonge & van Beusekom 1992, 1995). Additionally, some benthic microalgal species can compensate for low light levels by resorting temporarily to heterotrophy (Admiraal 1977, 1984).

Microphytobenthic biomass was observed down to a depth of 5 cm in the permanently open Swartkops Estuary in the Eastern Cape and down to a depth of 30 cm in the Langebaan Lagoon in the Western Cape (Fielding *et al.* 1988; Adams & Bate 1999). Mundree *et al.* (2003) reported substantial numbers of benthic microalgae in the Mdloti TOCE, at depths of up to 5 cm below the sediment surface, which is well below the photic zone. Benthic microalgal occurrence at such depths may represent an important stock of potential primary autotrophs in South African TOCEs.

Composition and abundance

Diatoms, particularly pennate diatoms, are the most common benthic microalgal taxa in most circumstances and are also the most well studied members of the

benthic microalgae (Cahoon 1999). The dominant members of these assemblages have been pennate diatoms, frequently including members of the genera *Amphora*, *Cocconeis*, *Diploneis*, *Navicula* and *Nitzschia*. A variety of centric diatoms are also frequently found in benthic assemblages, including some that are likely to have settled from the plankton and some that are more closely associated with the benthos but are frequently resuspended (Bold & Wynne 1985). Spatial and temporal patterns in composition and abundance of microphytobenthos are largely governed by interactions between light, nutrient availability and grazing pressure (Bianchi & Rice 1988; Posey *et al.* 1995).

In the subtropical Tongati and Mhlanga estuaries, Blaber *et al.* (1984) reported the common presence of unidentified species of the genera *Navicula*, *Nitzchia*, *Synedra*, *Spirulina*, *Oscillatoria* as well as euglenoid flagellates. In a comparative study of the Mhlabatshane and the Manzimtoti estuaries, species composition and dominance were related to water quality (Watt 1998). The nutrient enriched and polluted Manzimtoti sediments contained mainly small species of *Navicula* and *Nitzchia*, while the naturally oligotrophic sediments of the Mhlabatshane were dominated by the diatom genera *Acanthidium* and *Diploneis*. A total of 44 diatom species were identified in the Manzimtoti and 21 in the Mhlabatshane (Watt 1998). A study of the benthic diatom community of the Mdloti TOCE, reported a clear dominance of four genera and 26 species: 13 *Navicula*, 3 *Amphora*, and 2 *Achnanthes* (Mundree 2001). An extensive taxonomic study on the composition of microphytobenthos is currently being carried out at the Mpekweni and Mgwalana TOCEs in the Eastern Cape and at the Manzimtoti Estuary in KwaZulu-Natal by the University of Port Elizabeth as part of a Water Research Commission project (Bate *et al.* 2002). This project aims to evaluate the usefulness of microalgae in the assessment of ecosystem health, by showing associations between estuarine water quality and dominant benthic diatom species.

Biomass and primary production

The chlorophyll a (chl a) concentration of the surface sediment is often used to estimate the biomass of benthic microalgae (Whitney & Darely 1979; MacIntyre *et al.* 1996; Underwood & Kromkamp 1999). Among other techniques, fluorometry enables the measurement of chl a and total pigment concentration through the use of different excitation filters, 436 nm for chl a and 405 nm for phaeopigments. The ratio of phaeopigments to chl a can be used as a diagnostic indicator of the physiological state of the microphytobenthic community (Lucas & Holligan 1999). This ratio has also been used as an indicator of herbivory, with high values (> 0.5) being associated with increased grazing pressure (Shuman & Lorenzen 1975).

In estuarine systems, the determination of microphytobenthic biomass and primary production is an important task as benthic microalgae provide up to a third of the total primary productivity (Admiraal 1984; Pinckney & Zingmark 1993; MacIntyre *et al.* 1996; Miller *et al.* 1996; Underwood & Kromkamp 1999). It is also known that benthic microalgal biomass can equal or exceed that of phytoplankton in shallow ecosystems (Cadée & Hegeman 1974, 1977; Lukatelich & McComb 1986). Bergesch *et al.* (1995) for example, found that the microphytobenthic biomass in the Lagoa dos Patos (southern Brazil) was up to six orders of magnitude higher than that of the phytoplankton.

Microphytobenthos generally dominate the total autotrophic biomass in South African TOCEs (Adams & Bate 1999; Nozais *et al.* 2001; Perissinotto *et al.* 2002; Perissinotto *et al.* 2003). Adams & Bate (1999) have attributed these results to the prevailing conditions in TOCEs, which include low turbidity and current speed, more stable sediment and salinity environment and a large nutrient pool within the substratum, particularly during the closed phase. Perissinotto *et al.* (2002) have suggested that the large concentrations of chl a observed in the sediment during the closed phase might be a result of settled-out phytoplankton. In TOCEs, it is not unusual for the microphytobenthic standing stock to equal or even exceed that of the phytoplankton in the overlying water, often by 1 to 3 orders of magnitude

(Adams & Bate 1999; Perissinotto *et al.* 2000; Nozais *et al.* 2001; Perissinotto *et al.* 2002; Perissinotto *et al.* 2003; Thomas 2003). Benthic microalgal biomass may be less vulnerable than phytoplankton to changes in the physico-chemical and biological variables associated with the alternation of the open and closed phases of TOCEs (Nozais *et al.* 2001). For instance, during the closed phase, which is characterized by low rainfall, low river inflow, increased water clarity and reduced nutrient loading, it would be expected that the more favourable underwater light conditions for photosynthesis would result in an increase in phytoplankton biomass. However, dissolved inorganic nitrogen to phosphate molar ratios (DIN:DIP), well below the Redfield ratio of 16:1 (indicating potential N-limitation of phytoplankton growth) increased the likelihood of nutrient rather than light limitation on phytoplankton growth during the close phase. Conversely, although nutrients are present in high concentrations throughout the open phase, phytoplankton are not capable of attaining maximum biomass levels because increased turbidity in the estuary during this period inhibits primary production. As a consequence of this increased turbidity experienced during the open phase, phytoplankton spend a considerable part of the daytime in the dark, resulting in light limitation, instead of nutrient limitation of phytoplankton growth during this period. (Nozais *et al.* 2001).

The overall variability in sediment chl *a* concentrations in South African and other estuaries, reflects the effects of diverse factors, such as nutrient availability, light flux patterns, substrate characteristics, grazing, and physical disturbance, all of which interact to control benthic microalgal biomass (Slinger 1996; Adams & Bate 1999; Underwood & Kromkamp 1999; Bennett *et al.* 2000; Rusch & Huettel 2000; Sundbäck *et al.* 2000; Thornton *et al.* 2002; Underwood 2002; Kibirige *et al.* 2003; Perissinotto *et al.* 2003).

Light regulation of microphytobenthos is obvious particularly in TOCEs, as a consequence of the two distinctly different open and closed phases (Nozais *et al.* 2001). The closed phase is distinguished by relatively low freshwater inflow from the catchment area and the absence of tidal influences, ultimately reducing both

sediment disturbance and turbidity whilst increasing water clarity (Wooldridge & McGwynne 1996; Nozais *et al.* 2001). Light extinction coefficient, (K_d) generally exhibits very low values (0.4 to 3 m^{-1}) during the closed phase (Perissinotto *et al.* 2003). The low K_d values observed during the closed mouth state reflects the increased water clarity characteristic of this phase, with the only source of turbulence due to the slow inflow of the river (Day 1981). Increased water clarity during the closed phase allows for a greater amount of light to reach the sediment-water interface. During the open phase however, the increase in river runoff and loading of fine sediment, due to an increase in turbidity during this phase inhibits benthic microalgal biomass, with K_d values ranging from 4 to 29 m^{-1} (Nozais *et al.* 2001; Perissinotto *et al.* 2002). Whether such loading has the effect of modifying the sediment composition of the estuary, causing a decrease in benthic biomass is not known and needs to be addressed in future investigations.

Large quantities of nitrogen and phosphorus are gradually being discharged into estuaries, both by riverine and direct anthropogenic inputs, altering the trophic status of these systems. Coupled with tidal flow, this makes the analyses of nutrient effects on benthic biomass complicated. Nutrient loading in TOCEs is controlled predominately by river flow, with increased loading of macronutrients generally occurring during the open phase, a period of increased rainfall (Allanson & Winter 1999; Snow *et al.* 2000a). Knowledge of the dynamics of macronutrients in TOCEs, particularly pore water nutrients, is relatively scarce, since the few studies conducted have focused on water column macronutrients (Nozais *et al.* 2001; Perissinotto *et al.* 2002). The results of these studies are in agreement with those of Gruendling (1971) and Lukatelich & McComb (1986), who found that nutrient concentrations in the water overlying the sediment were not significantly correlated with microphytobenthic biomass, due to the high rate of mineralization within these sediments. While this appears to be true for nutrient-rich muddy estuaries, in many sandy sediments nutrient limitation does seem to occur, with biomass responding positively to nutrient addition (Underwood & Kromkamp 1999).

Benthic microalgae are an important food source in estuarine systems, particularly because they are available throughout the year. Microphytobenthos, in particular, is a preferred food source for deposit-feeding benthic infauna. The resuspension of sediment makes them available to facultative and obligate suspension feeders (Miller *et al.* 1996). Studies in the permanently open Swartkops Estuary and the Swartvlei estuarine lake system, have demonstrated that benthic diatoms are an important food source, especially for mullet (Masson & Marais 1975). In the Mpenjati TOCE, the dominant zooplankton grazers were able to utilise benthic microalgae as an alternative energy source, particularly during periods of low phytoplankton and detritus availability (Kibirige & Perissinotto 2003a/b). Interestingly, this study reported very high levels of microphytobenthic biomass and also found it to be 1 to 2 orders of magnitude higher than vertically integrated phytoplankton biomass (Perissinotto *et al.* 2002). These results suggest that microphytobenthos may be used as an alternative autotrophic food source by the zooplankton grazers in this estuary (Kibirige *et al.* 2003). Studies on grazer-microalgae interactions have in fact stressed the relative importance of benthic microalgae as food source for benthic consumers. The fate of microalgae in estuarine ecosystems and their degree of direct consumption by primary and higher level consumers is thus of fundamental importance to the energy balance of TOCEs.

The importance of benthic microalgae in shallow estuarine systems as carbon fixers, oxygen producers and food source for grazers, makes them key components of the estuarine biota. There is therefore an urgent need to quantify microphytobenthic productivity and biomass particularly in TOCEs, where the periodic closure from the sea and flushing of water out of the estuary is likely to have implications for the trophic functioning of the entire estuarine ecosystem, as well for the management of these systems.

THE DYNAMICS OF MICROPHYTOBENTHOS IN THE MDLOTI AND MHLANGA ESTUARIES, KWAZULU-NATAL

Introduction

Microphytobenthic communities are important autotrophic components of estuarine systems. This is primarily due to their role in the trophodynamics of estuarine foodwebs, not only as a carbon source, but also as an important component of nutrient cycles as well as a sediment stabilizer via the secretion of exopolymers (Delgado *et al.* 1991; Rizzo *et al.* 1992; MacIntyre *et al.* 1996; Miller *et al.* 1996; Underwood *et al.* 2004). In these ways, microphytobenthos exert their effect over a range of different scales going from the thin sediment layer, where they are active, to the scale of whole estuaries, where they are able to influence the morphology of the coast.

Temporarily open/closed estuaries (TOCEs) are a typical and dominant feature on the South African coastline (Whitfield 1992; Cooper *et al.* 1999). Most information regarding TOCEs deal with taxonomic, recruitment and stock assessment studies of macro-organisms, essentially for economic and conservation interests (Begg 1978; 1984a/b; Day 1981; de Villiers *et al.* 1999). Recently, there has been a shift towards understanding the trophic functioning of these particular systems. Preliminary investigations have shed some light on the dynamics of phytoplankton, microphytobenthos, zooplankton and meiofauna inhabiting these systems (Campbell *et al.* 1991; Nozais *et al.* 2001; Kibirige *et al.* 2003; Kibirige & Perissinotto 2003a/b; Mundree *et al.* 2003; Perissinotto *et al.* 2003; Perissinotto *et al.* 2004; Nozais *et al.* 2005).

In particular, it has been shown that in South African estuaries microphytobenthic biomass is higher in TOCEs, than their permanently open counterparts (Adams & Bate 1999; Snow *et al.* 2000a/b). A general trend in TOCEs, seem to suggest an association of high microphytobenthic biomass with the closed phase of the estuary (Adams & Bate 1999; Perissinotto *et al.* 2003). Microphytobenthos are capable of taking advantage of favourable environmental conditions, which

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prevail in TOCEs, particularly during the closed phase. These include low turbidity and current speed, a more stable sediment and salinity environment, as well as a larger nutrient pool within the substratum (Adams & Bate 1999; Schumann et al. 1999; Perissinotto et al. 2003). A decline in microphytobenthic biomass is generally observed during the open phase. This is likely due to the high turbidity and frequent flushing/scouring that occurs, particularly at the onset of the open phase. In TOCEs, it is not unusual for the microphytobenthic standing stock to equal that of the vertically integrated phytoplankton biomass in the overlying water, often actually exceeding it by 1-3 orders of magnitude (Nozais et al. 2001; Perissinotto et al. 2002; Thomas et al. 2003).

The Mdloti and the Mhlanga are both TOCEs situated in close proximity to each other. With a catchment area of 560 km^2 (Grobbler 1987), the Mdloti is about five times larger than the Mhlanga (118 km^2, Cooper 1991). There are no dams present in the catchment of the Mhlanga. At the Mdloti, the Hazelmere Dam is located approximately 20 km upstream from its mouth (Begg 1978). Presently, the eThekwini Municipality is running sewage plants, which discharge a total of 28 MLd^{-1} treated sewage effluents into these systems (W. Pfaff, eThekwini Municipality, pers. comm.). The much smaller Mhlanga receives three times more sewage effluent (20 MLd^{-1}), than the Mdloti (8 MLd^{-1}). This increases the natural flow of the two estuaries by 0.23 m^3 s^{-1} and 0.092 m^3 s^{-1}, respectively (W. Pfaff, eThekwini Municipality, pers. comm.). Due to development pressures in their catchments, it is expected that the sewage discharge rate at both estuaries will increase drastically in the future. The anticipated increased nutrient loading will impact on the dynamics of primary producers in these systems, which in turn will affect their trophic functioning (Nozais et al. 2001). Additionally, the effects of increased inflow could be detrimental to the overall status of estuarine functioning, preventing these systems from functioning as typical TOCEs, with a prolonged closed phase.

This study forms part of a multi-disciplinary research program endorsed by the Water Research Commission (WRC) to determine the ecological status of the

Mdloti and the Mhlanga estuaries. The overall aim of this study is to expand on current information regarding benthic microalgal biomass in TOCEs, in order to contribute to our understanding of the ecological functioning of these peculiar systems. The specific purposes of this study were to: 1) to compare the microphytobenthic biomass of the Mdloti and the Mhlanga TOCEs with emphasis on freshwater inflow, alternation of closed and open phases and key physico-chemical factors; 2) to determine spatial and temporal trends in microphytobenthic biomass within each estuary; and 3) to assess the growth of, and/or grazing pressure on, the microphytobenthic communities of the two estuaries by measuring the ratio of phaeopigments to chl *a*.

Materials and methods

Study areas

This study was conducted in the Mdloti (29°38'S, 31°08'E) and the Mhlanga (29°42'S, 31°06'E) subtropical TOCEs (Fig. 1). At each estuary, three stations were sampled at regular monthly intervals, from March 2002 to March 2003. These included the lower reaches (mouth), on the seaward boundary, the middle reaches, approximately mid-way of the estuary and upper reaches (head), at the river boundary. Survey dates were predetermined to coincide with the middle of a neap tidal cycle, in order to minimize tidal effects during the open phase.

Physico-chemical variables

Vertical profiles of depth (m), salinity (psu) and temperature (°C), were measured using a YSI 6920 Water Logger. Instrument calibration was checked prior to each survey. On each occasion and at each station, a vertical profile of downwelling irradiance (PAR, 400 to 700 nm) was measured with a manufacturer's calibrated LI-COR LI-189 underwater spherical quantum sensor. Light levels were measured every 50 cm down to the bottom. The diffusive attenuation coefficient, K_d (m^{-1}), an inherent optical property of the water, was then estimated using the relation: $K_d = -\ln(Iz_2 / Iz_1) / Z_2 - Z_1$, where Iz_2 = irradiance (μmol m^{-2} s^{-1}) at depth Z_2 (m), Iz_1 = irradiance at depth Z_1 ($Z_2 > Z_1$, i.e. z increases positively downwards) (Kirk 1983).
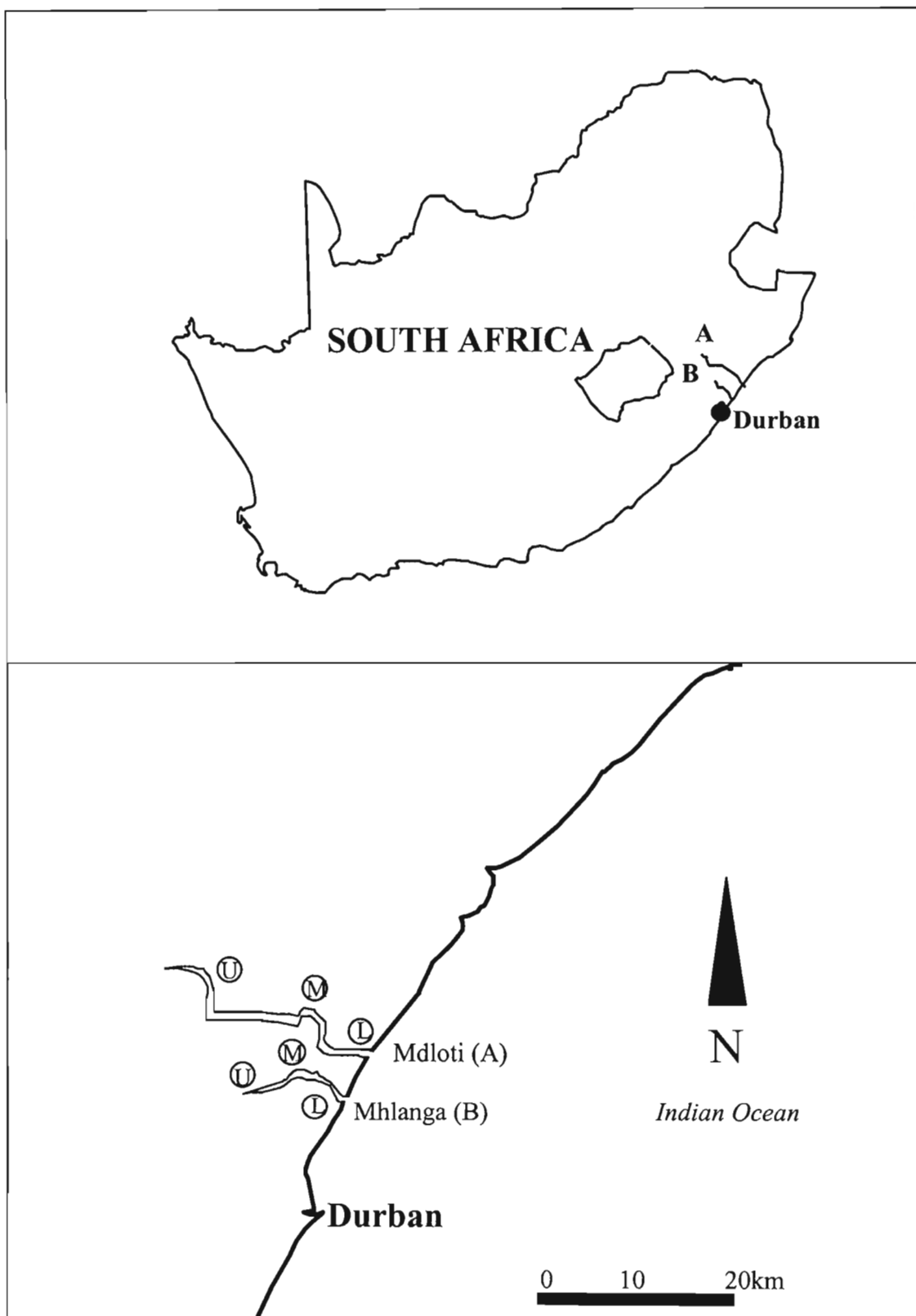
Figure 1. Location of the Mdloti (A) and Mhlanga (B) estuaries showing the positions of the sampling stations. L: lower, M: middle & U: upper reaches.

Daily precipitation data (mm) were provided by the South African Sugar Association Experiment Station, Mount Edgecombe. Ezemvelo KZN Wildlife and independent residents in the area provided daily observations on the state of the mouth. Pore water samples for the measurement of dissolved inorganic nitrogen, DIN (nitrate + ammonium), and dissolved inorganic phosphorus, DIP (orthophosphate), were collected using a hand operated vacuum pump extractor connected to a stainless steel closed pipe inserted into the sediment (5-10 cm below the sediment-water interface). At the lower tip of the pipe, tiny holes were drilled, in order to ensure the inward flow of pore water, while minimising the passage of fine sand and silt particles. Pore water samples were then placed in 500 ml acid pre-washed polyethylene bottles. Concentrations of pore water DIN and DIP were determined by the Analytical Laboratory of the CSIR- Durban, using a Technicon Autoanalyzer II system and following the methods of Mostert (1983).

DIN:DIP molar ratios were used to test for potential limiting effects of nutrients on microalgal biomass (Howarth 1988). DIN:DIP molar ratios below the critical value 16: 1 are indicative of a potential limiting effect of nitrogen on microalgal growth, while values above this critical value are suggestive of a potential phosphorus limitation of microalgal growth in estuarine waters.

Microphytobenthic biomass

Sediment samples for the determination of microphytobenthic chlorophyll *a* (chl *a*) and phaeopigment were collected on a monthly basis between March 2002 and March 2003. In accordance with the methodology previously employed by researchers in the area (Perissinotto *et al.* 2000; Nozais *et al.* 2001; Perissinotto *et al.* 2002), triplicate core samples were taken on each occasion and at each station. The upper 1 cm of the sediment was collected using a Perspex twin-corer of 20 mm internal diameter, and placed into a 100 ml polyethylene bottle with 30 ml of 90% acetone for 24-48 hours to enable the extraction of pigments, following the recommendations of Rodriguez (1993) for South African estuaries. After extraction, fluorescence readings were taken using a Turner Designs 10-AU Fluorometer fitted with the narrow band, non-acidification system of

Welschmeyer (1994). This system allows for precise measurements (max 10% error) of chl *a* without interference from other photosynthetic pigments or their degradation products (Welschmeyer 1994). Calibrations were made at regular intervals of 2 months, using 10-AU Solid Secondary Standards. To obtain chl *a* and phaeopigment concentrations in the sediment, the fluorescence readings were converted using the following equation:

$$[\text{mg chl } a \text{ m}^{-2}] = \frac{\text{fluorescence reading}}{1000} \times \frac{\text{Volume acetone (ml)}}{\text{Core area (m}^2)} \times \text{dilution factor}$$

The ratio of phaeopigments to sediment chl *a* concentration was also determined. This ratio gives a general indication of the physiological or grazing state of a microalgal community (Shuman & Lorenzen 1975). High ratios (0.5-1) represent a stressed or declining community, while low values (0-0.5) indicate an actively growing community relatively free of grazing pressure (Bidigare *et al.* 1986; Light & Beardall 1998; Brotas & Plunte-Cuny 2003).

Phytoplankton biomass

Water samples for phytoplankton chl *a* determination were collected 10 cm below the surface and 30 cm above the bottom, using a 500 ml polyethylene bottle and a 1000 ml weighted pop-bottle respectively (see Thomas 2003 for further details).

Zooplankton biomass

Daytime midwater and suprabenthic samples were collected at the same time and stations as the microphytobenthic samples, using a WP-2 (90 µm mesh) and a hyperbenthic sled (200 µm mesh), respectively. Samples collected were fixed in 5% formalin for laboratory analysis. Biomass was estimated by measuring the dry weight of half of each zooplankton samples, after removal of detrital particles under a dissecting microscope (see Thwala 2004 for further details).

Data analysis

Prior to analysis, data normality was assessed using the Kolmogorov-Smirnov goodness of fit test. When required, data were $\log_{10}$-transformed to comply with

the assumptions of the various parametric tests employed. Temporal and spatial variations in phyisco-chemical variables at each estuary were determined using a 1-way ANOVA. An ANOVA was also performed to compare microphytobenthic chl a concentrations between the two estuaries. Differences in microphytobenthic chl a concentrations between the open and closed phases and between the different reaches of each estuary were examined using a 2-way ANOVA. Where significant differences were detected, a Tukey HSD *post-hoc* test was applied to determine the extent of the variation. Mann-Whitney U-tests were performed to investigate potential differences in physical chemical and biological variables between estuaries and within each estuary, during the open and closed phase. This was done using the statistical package Statistica 5.5 (StatSoft Inc). Spearman and partial rank correlation analyses were also performed using the SPSS 9.0 Statistical package. Statistical tests and analysis were selected and performed following Zar (1999).

Results

Physico-chemical environment

An unusual erratic rainfall pattern occurred during the study period (Fig. 2). The total rainfall for the year amounted to 938 mm, with an unusual peak in winter (291 mm), a steady decline in spring (160 mm), a sudden increase in summer (228 mm) and again a decrease in autumn (174 mm). The highest amount of rain fell in July 2002 (205 mm), accounting for approximately 21% of the total. The lowest figures were recorded in May 2002 (6.3 mm), June 2002 (22 mm) and February 2003 (18 mm). The state of the mouth of both estuaries was affected by this unseasonal rainfall pattern. The Mdloti and the Mhlanga experienced prolonged periods of open phase during the winter and unusual closed phases during part of the summer. The Mhlanga breached at regular (quasi-periodic) intervals, and remained closed for only short periods each time. While the Mhlanga was closed 49% and open or partly open for 51% of the time, the Mdloti was closed 57% of the time and open or partly open 43% (excluding missing data) (Fig. 3A/B).
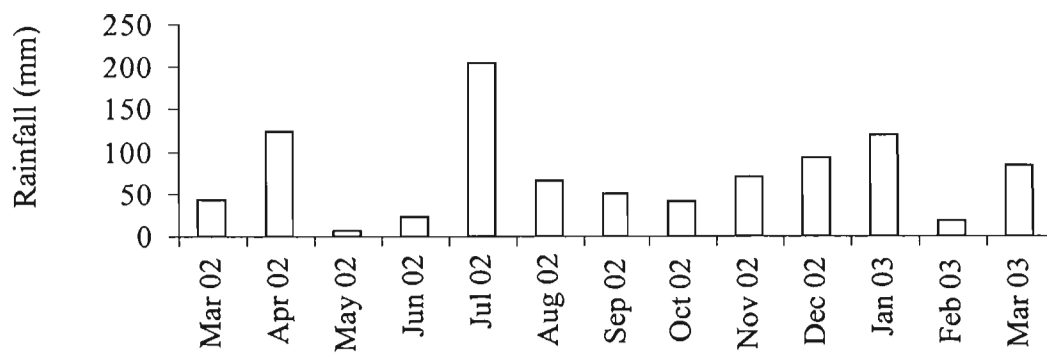
Figure 2.   Monthly rainfall data (mm) for the Mdloti and the Mhlanga estuaries
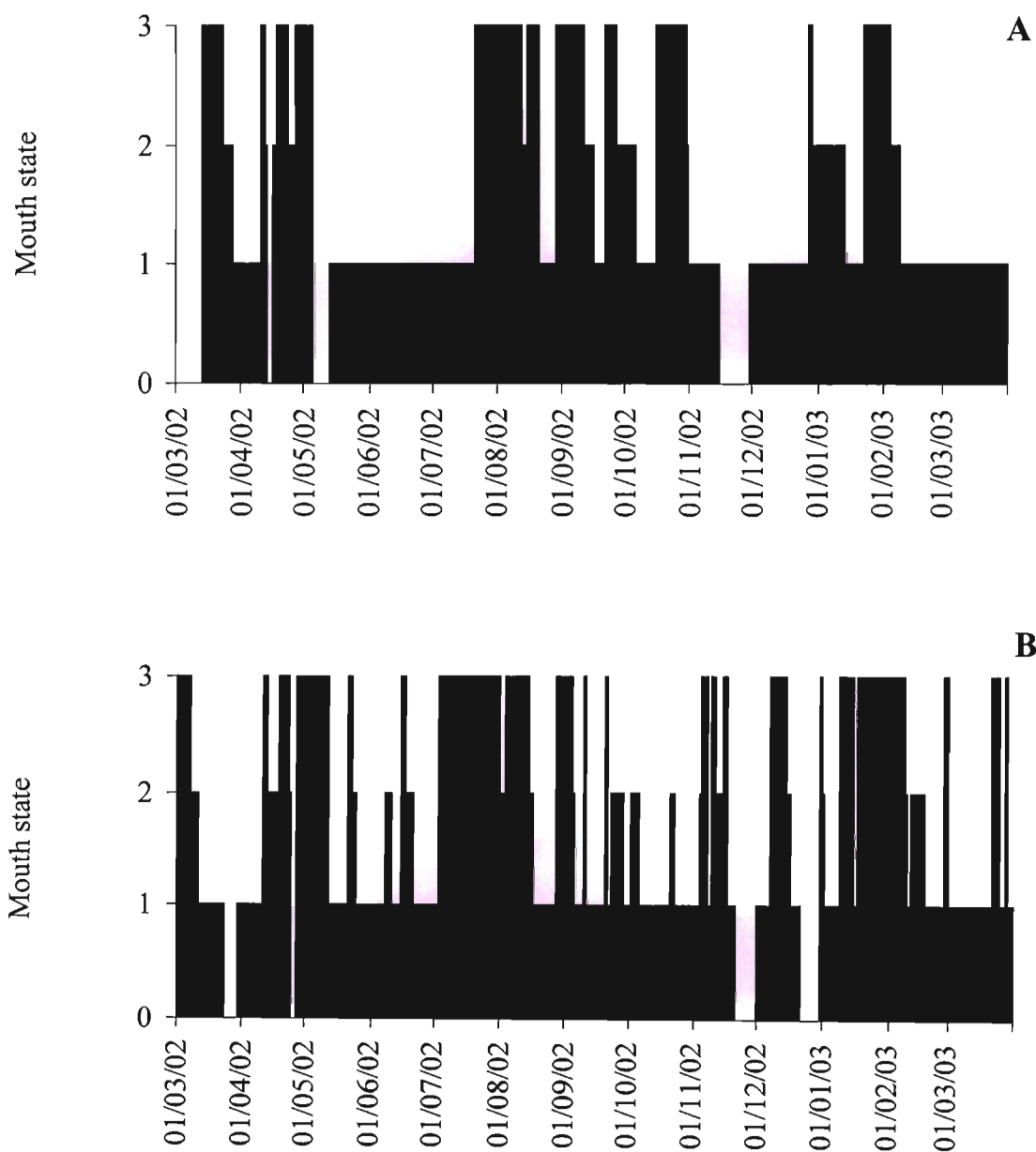during the period of the study (March 2002 to March 2003).

Figure 3.   Mouth conditions at the Mdloti (A) and the Mhlanga (B) during the
period of study. 0 = no data, 1 = closed, 2 = partly open, 3 = open.

The average depth of the water column ranged from 0.15 to 3.0 m at the Mdloti (Fig. 4) and from 0.1 to 2.3 m at the Mhlanga (Fig. 5). Water depth exhibited significantly temporal variations at both the Mdloti ($F_{12, 26}$ = 8.58, p < 0.0001) and the Mhlanga ($F_{12, 26}$ = 3.96, p < 0.05) estuaries. Significant differences between estuarine phases were observed in both the Mdloti (U = 6.51, p < 0.0001) and the Mhlanga (U = 73.51, p < 0.05). Depth generally increased during the closed phase and decreased during the open phase. Spatial variations in water depth were insignificant at the Mdloti ($F_{2, 36}$ = 2.04, p > 0.05) but significant at the Mhlanga ($F_{2, 36}$ = 3.43, p < 0.05), particularly between its middle and upper reaches (p < 0.05) (Tukey HSD, Zar 1999).

Temperature at the sediment–water interface ranged from 14.5 to 29.5 °C at the Mdloti and from 17.4 to 30 °C at the Mhlanga. Temporal variations in temperature at the sediment–water interface were observed at both the Mdloti ($F_{12, 26}$ = 4.90, p < 0.0001) and the Mhlanga ($F_{12, 26}$ = 12.05, p < 0.0001) estuaries. Neither estuary exhibited significant differences in temperature at the sediment-water interface, either spatially or between estuarine phases.

Salinity at the sediment-water interface ranged from 0.10 to 24 at the Mdloti (Fig. 6) and from 0.1 to 28 at the Mhlanga (Fig. 7). Salinity at the sediment–water interface exhibited significant temporal variations both at the Mdloti ($F_{12, 26}$ = 4.88, p < 0.001) and the Mhlanga ($F_{12, 26}$ = 4.31, p < 0.001). Significant differences in salinity at the sediment-water interface, between estuarine phases were observed only at the Mhlanga (U = 98.5, p < 0.05). No significant spatial variations in salinity at the sediment-water interface were observed at either estuary.
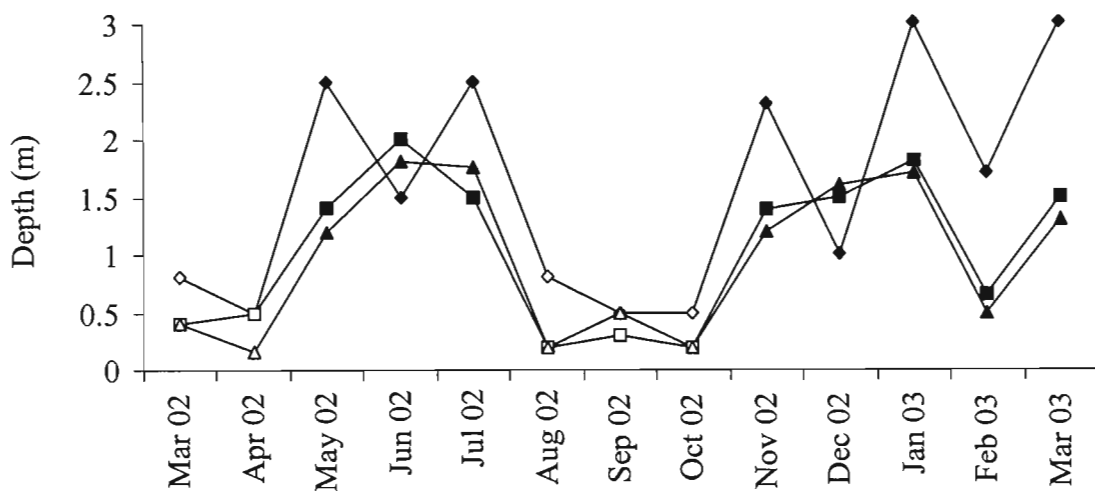
Figure 4.   Temporal variations in depth (m) at the lower (◊: open phase; ♦:
closed phase), middle (□: open phase; ■: closed phase) and upper
reaches (Δ: open phase; ▲: closed phase) of the Mdloti Estuary.

Figure 5.   Temporal variations in depth (m) at the lower (◊: open phase; ♦:
closed phase), middle (□: open phase; ■: closed phase) and upper
reaches (Δ: open phase; ▲: closed phase) of the Mhlanga Estuary.

Figure 6. Temporal variations in salinity (‰) at the lower (◊: open phase; ♦: closed phase), middle (□: open phase; ■: closed phase) and upper reaches (Δ: open phase; ▲: closed phase) of the Mdloti Estuary.

Figure 7. Temporal variations in salinity (‰) at the lower (◊: open phase; ♦: closed phase), middle (□: open phase; ■: closed phase) and upper reaches (Δ: open phase; ▲: closed phase) of the Mhlanga Estuary.

During the Mdloti open phase, the light attenuation coefficient (K_d) ranged from 0.08 to 4 m^{-1}. During the closed phase of the estuary, K_d values ranged from 1.1 to 3.4 m^{-1} (Fig. 8). At the Mdloti, K_d values did not exhibit significant differences temporally, spatially or between estuarine phases. During the Mhlanga open phase, K_d values ranged from 0.21 to 14 m^{-1}, while during its closed phase, these ranged from 0.70 to 2.7 m^{-1} (Fig. 9). At the Mhlanga, K_d differed significantly temporally ($F_{12, 26} = 2.28$, $p < 0.05$) and between the open and closed phase ($U = 114$, $p < 0.05$), but not spatially.
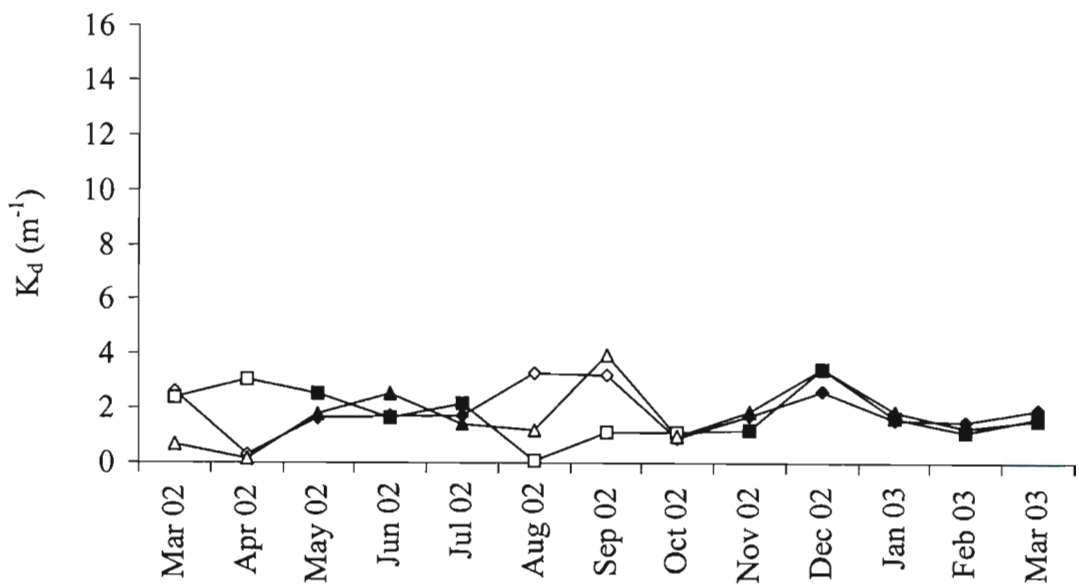
Figure 8.   Temporal variations in the coefficient of light extinction, K_d at the lower ($\lozenge$: open phase; $\blacklozenge$: closed phase), middle ($\square$: open phase; $\blacksquare$: closed phase) and upper reaches ($\triangle$: open phase; $\blacktriangle$: closed phase) of the Mdloti Estuary.
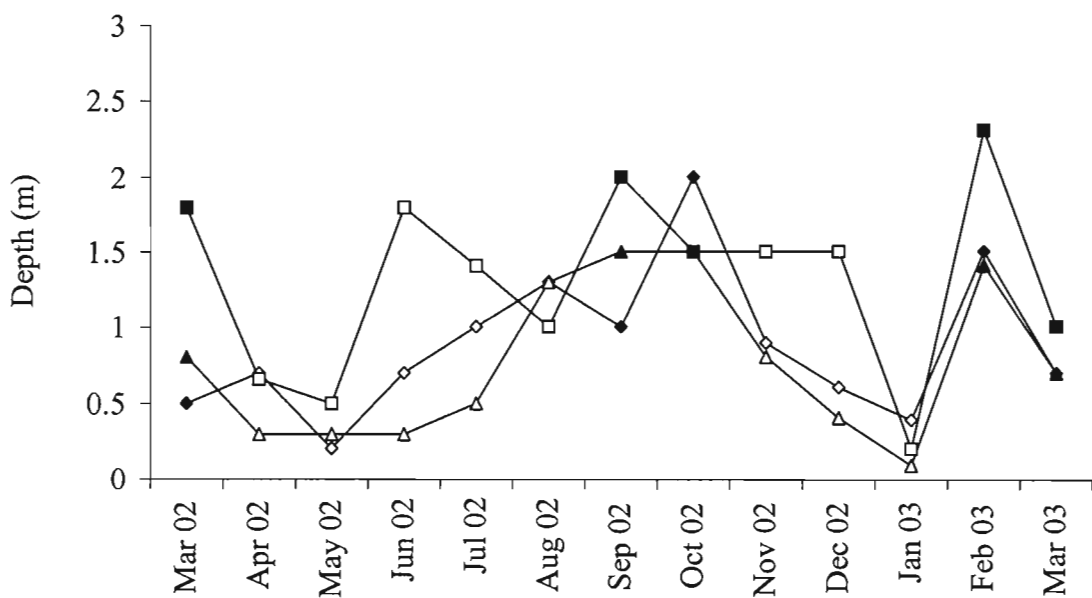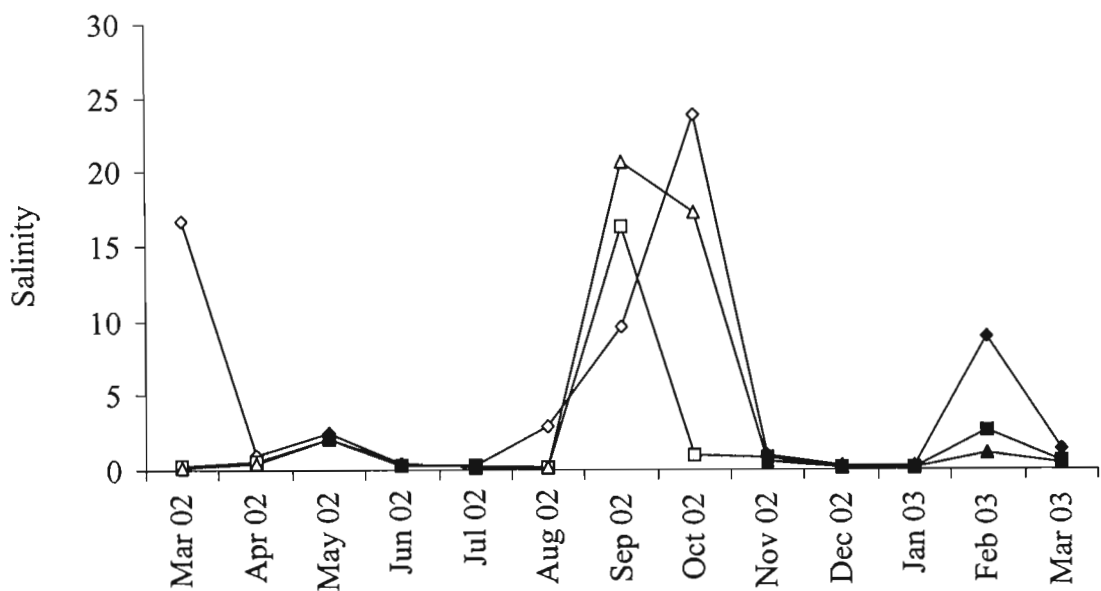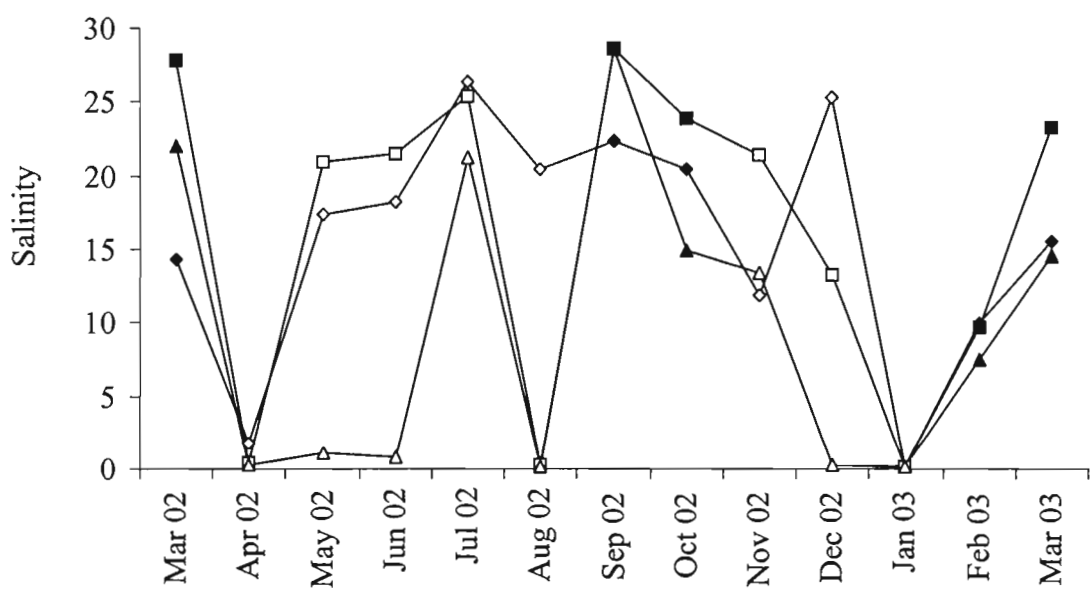
25
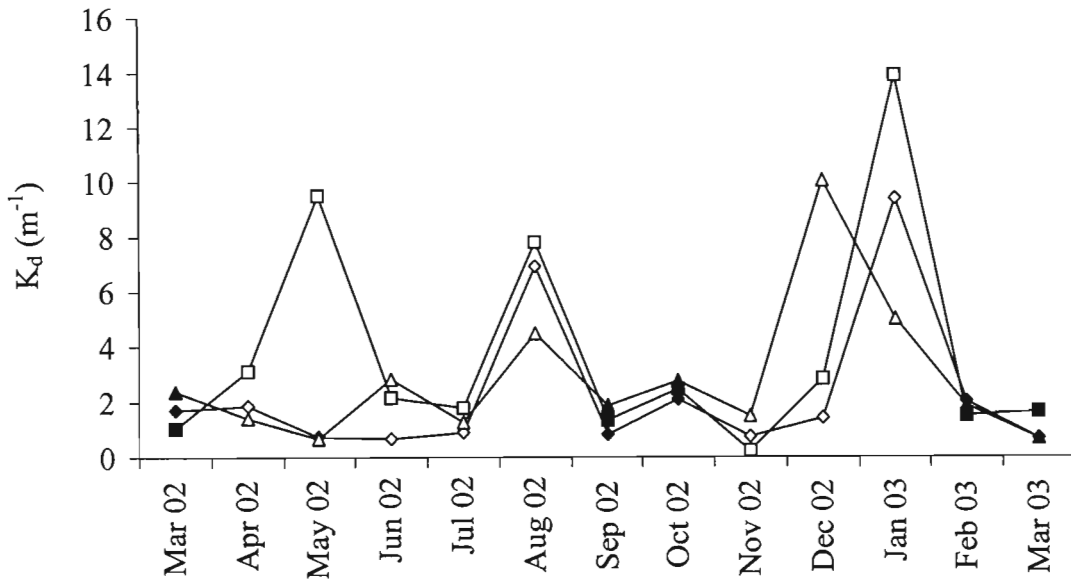
Figure 9. Temporal variations in the coefficient of light extinction, K_d at the lower (◊: open phase; ♦: closed phase), middle (□: open phase; ■: closed phase) and upper reaches (Δ: open phase; ▲: closed phase) of the Mhlanga Estuary.

At the Mdloti, the dissolved inorganic nitrogen (DIN: nitrate + ammonium) content of pore water ranged from 5.4 to 310 μM during the open phase and from 1.5 to 98 μM during its closed phase (Fig. 10A). Pore water DIN concentrations exhibited significant variations temporally ($F_{12, 26}$ = 2.76, p < 0.05), but not spatially ($F_{2, 36}$ = 0.62, p > 0.05) or between estuarine phases (U= 96.5 p > 0.05). At the Mhlanga, the DIN content of pore water ranged from 12 to 218 μM during the open phase and from 5.3 to 212 μM during its closed phase (Fig. 11A). Pore water DIN concentrations did not exhibit significant variations temporally ($F_{12, 26}$ = 1.28, p > 0.05) or between the open and closed phases (U= 140; p > 0.05). However, significant spatial variations were observed ($F_{2, 36}$ = 4.10, p < 0.05). A *post-hoc* test (Tukey HSD, Zar 1999) revealed significant differences in pore water DIN between lower and upper reaches (p < 0.05). Pore water DIN also varied significantly between the two estuaries ($F_{1, 76}$ = 14.1, p < 0.001), particularly during their closed phase (U = 9.2, p < 0.05).

Dissolved inorganic phosphorous (DIP: orthophosphate) in pore water ranged from 0.13 to 3.3 µM during the Mdloti open phase and from 0.10 to 17.3 µM during its closed phase (Fig. 10B). Here, pore water DIP concentrations differed significantly temporally ($F_{12, 26}$ = 3.31, p < 0.01), but not spatially ($F_{2, 36}$ = 0.11, p = 0.89) or between estuarine phases (U = 151, p > 0.05). At the Mhlanga, pore water DIP concentrations varied between 0.70 and 45.1 µM during the open phase and between 1.4 and 41.3 µM during the closed phase (Fig. 11B). At the Mhlanga, pore water DIP did not differ significantly either temporally ($F_{12, 26}$ = 1.49, p > 0.05), spatially ($F_{2, 36}$ = 2.93, p > 0.05) or between estuarine phases (U = 168, p > 0.05). Pore water DIP differed significantly between the two estuaries during the survey period ($F_{1, 76}$ = 71.2, p < 0.0001). These differences were also significant when comparing their open (U = 28.5, p < 0.0001) and closed phases (U = 48, p < 0.0001).

At the Mdloti, the DIN:DIP ratio ranged from 8 to 490 during the open phase and from 5 to 299 during the closed phase (Fig. 10C). At the Mhlanga, the DIN:DIP ratio varied between 1.9 and 104 during the open phase and between 0.17 and 71 during the closed phase (Fig. 11C).

Figure 10. Temporal variations in pore water A: dissolved inorganic nitrogen (DIN = nitrate + ammonium); B: dissolved inorganic phosphorous (DIP: orthophosphate) and C: DIN:DIP ratios in the Mdloti Estuary. The DIN:DIP Redfield ratio of 16:1 is indicated by the dash line. Symbols as in previous figures.
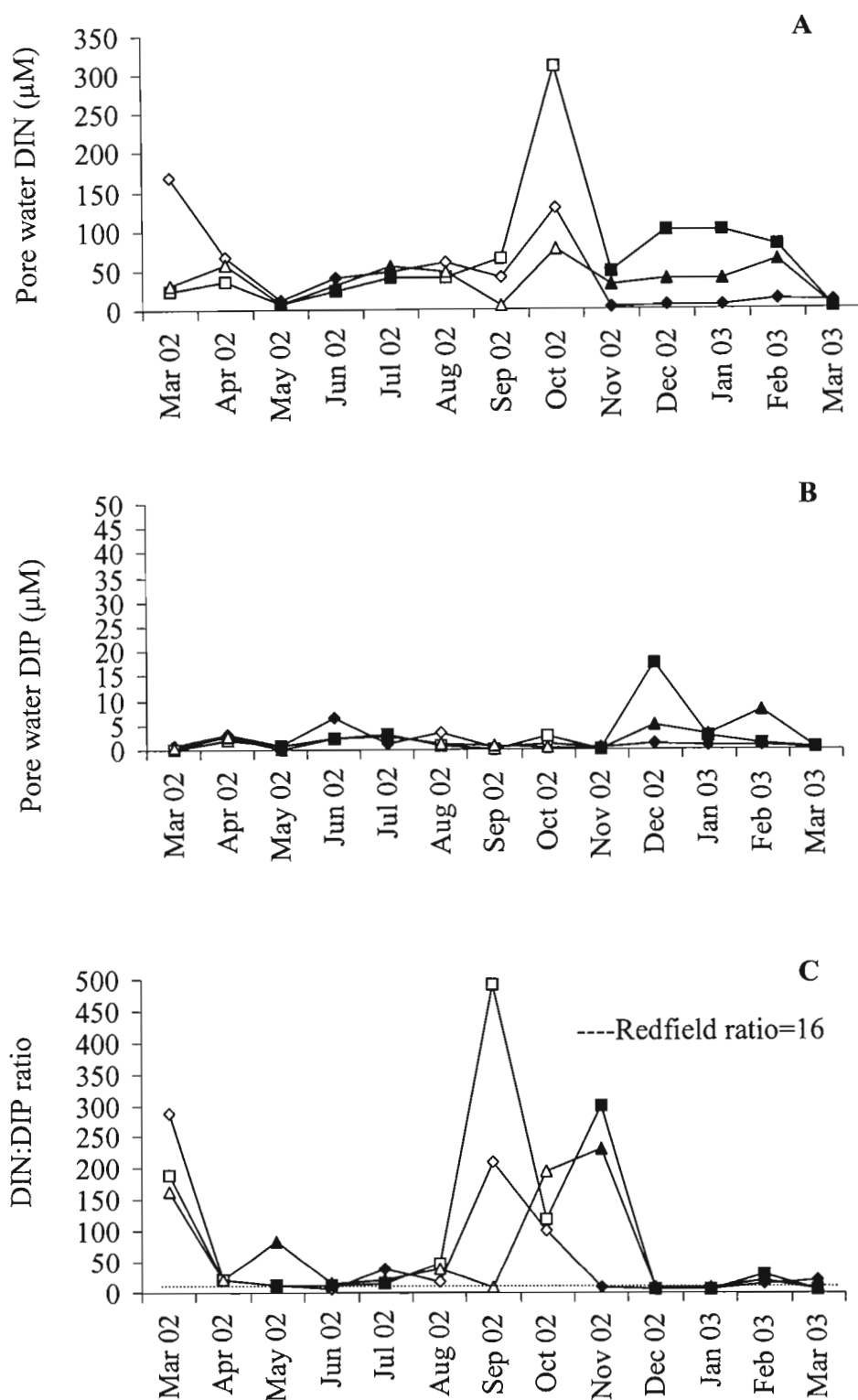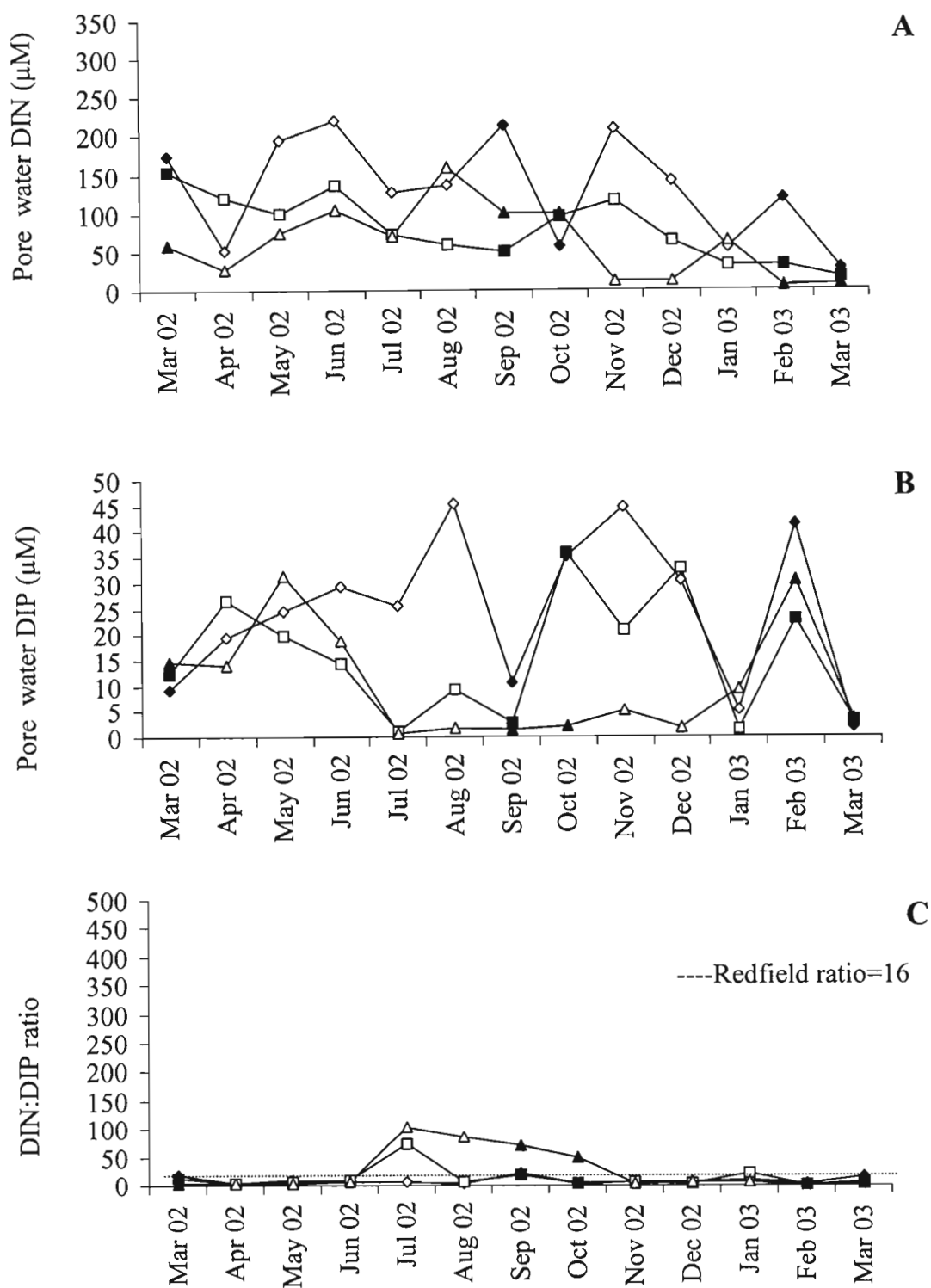
Figure 11. Temporal variations in pore water A: dissolved inorganic nitrogen (DIN = nitrate + ammonium); B: dissolved inorganic phosphorous (DIP: orthophosphate) and C: DIN:DIP ratios in the Mhlanga Estuary. The DIN:DIP Redfield ratio of 16:1 is indicated by the dash line. Symbols as in previous figures.

Microalgal biomass

At the Mdloti, microphytobenthic chl *a* concentrations varied considerably, from 1.33 mg chl *a* m^{-2} (lower reaches, September 2002) to 131 mg chl *a* m^{-2} (upper reaches, September 2002) during the open phase, and from 18 mg chl *a* m^{-2} (lower reaches, February 2003) to 391 mg chl *a* m^{-2} (upper reaches, December 2002) during the closed phase (Fig. 12). At the Mhlanga, microphytobenthic chl *a* concentrations ranged from 7.0 mg chl *a* m^{-2} (lower reaches, December 2002) to 313 mg chl *a* m^{-2} (lower reaches, June 2002) during the open phase, and from 1.7 mg chl *a* m^{-2} (lower reaches, September 2002) to 267 mg chl *a* m^{-2} (middle reaches, February 2003) during the closed phase (Fig. 13).

Along the Mdloti, the mean microphytobenthic biomass was lowest in the lower reaches (43.8 mg chl *a* m^{-2} ± 66.3 SD) and highest in the upper reaches of the estuary (96.1 mg chl *a* m^{-2} ± 114 SD). The middle reaches exhibited a mean microphytobenthic biomass of 84 ± 73 (SD) mg chl *a* m^{-2}. Similarly, at the Mhlanga, mean microphytobenthic biomass was lowest in the lower reaches of the estuary, with 68.1 ± 93.9 (SD) mg chl *a* m^{-2}. The highest, was observed in the middle reaches with 105 ± 114 (SD) mg chl *a* m^{-2}, while the upper reaches exhibited a mean microphytobenthic biomass of 96.4 ± 86 (SD) mg chl *a* m^{-2}.

A 1-way ANOVA revealed no significant differences in microphytobenthic chl *a* concentrations between the two estuaries ($F_{1, 76}$ =1.48, p > 0.05). However, when separated into open and closed phases, differences in microphytobenthic chl *a* concentrations were significant between the estuaries during their open phase (U = 64, p < 0.05), but not during their closed phase (U = 155, p > 0.05). At the Mdloti, microphytobenthic biomass differed significantly between the open and closed phases (U = 29, p < 0.001). However, at the Mhlanga, this was not the case. A 2-way ANOVA, performed on log_{10}-transformed chl *a* values, revealed significant variations between the open and closed phase (F = 160, p < 0.0001) as well as between reaches (F = 17.8, p < 0.0001) at the Mdloti. At the Mhlanga, however, a significant interaction between the open and closed phase and reaches (F = 3.18, p < 0.05), as well as significant variations between reaches (F = 5.91, p

< 0.05), were observed. A *post-hoc* test (Tukey HSD, Zar 1984) revealed significant differences between lower and upper reaches (p < 0.001) as well as between lower and middle reaches (p < 0.001), both at the Mdloti and the Mhlanga. Throughout this study, sediment chl *a* concentrations were consistently higher than the vertically integrated water column chl *a* concentrations (phytoplankton), by an order of magnitude at the Mdloti and by 1-2 orders of magnitude at the Mhlanga (Thomas 2003).

The ratio of phaeopigments to chl *a* was used to obtain a general indication of the "physiological" state of, or alternatively of the grazing pressure on, the microphytobenthic community of the two estuaries. The ratio for the entire data set ranged from 0.40 to 0.73 at the Mdloti (Fig. 14), and from 0.43 to 0.70 at the Mhlanga (Fig. 15). At the Mdloti, the ratio varied between 0.43 and 0.73 during the open phase and between 0.40 and 0.65 during the closed phase. At the Mhlanga, the ratio varied between 0.50 and 0.70 during the open phase and between 0.43 and 0.70 during the closed phase. Temporal differences were observed only at the Mdloti ($F_{12,\ 26}$ = 2.40, p < 0.05). Neither estuary exhibited any significant differences between reaches or between estuarine phases.

Correlation analysis

Results of Spearman rank correlation analysis on the Mhlanga data set show a significant relationship between total microphytobenthic biomass, pore DIN concentration (r = -0.43, p < 0.01) and temperature (r = 0.42, p < 0.01). The Mdloti data set shows, however, significant correlations between microphytobenthic biomass and salinity (r = -0.40, p < 0.01). Positive correlations between microphytobenthic biomass and zooplankton biomass occurred both at the Mdloti (r = 0.40, p < 0.001) and at the Mhlanga (r = 0.33, p < 0.05) (Table 1). Considering separately the two phases of each estuary, i.e. open and closed, more significant correlations were obtained (Table 2). In particular, during the Mhlanga closed phase microphytobenthic biomass was inversely correlated with pore DIN concentration (r = -0.69, p < 0.01) and salinity (r = -0.52, p < 0.05), and positively correlated with K_d (r = 0.58, p < 0.05) and temperature (r = 0.60, p < 0.05).

During the Mdloti closed phase, microphytobenthic biomass was significantly correlated with rainfall ($r = 0.52$, $p < 0.01$), pore DIP concentrations ($r = 0.49$, $p < 0.05$) and salinity ($r = -0.69$, $p < 0.05$). On the other hand, no significant correlations were obtained for the open phase either at the Mhlanga or the Mdloti.
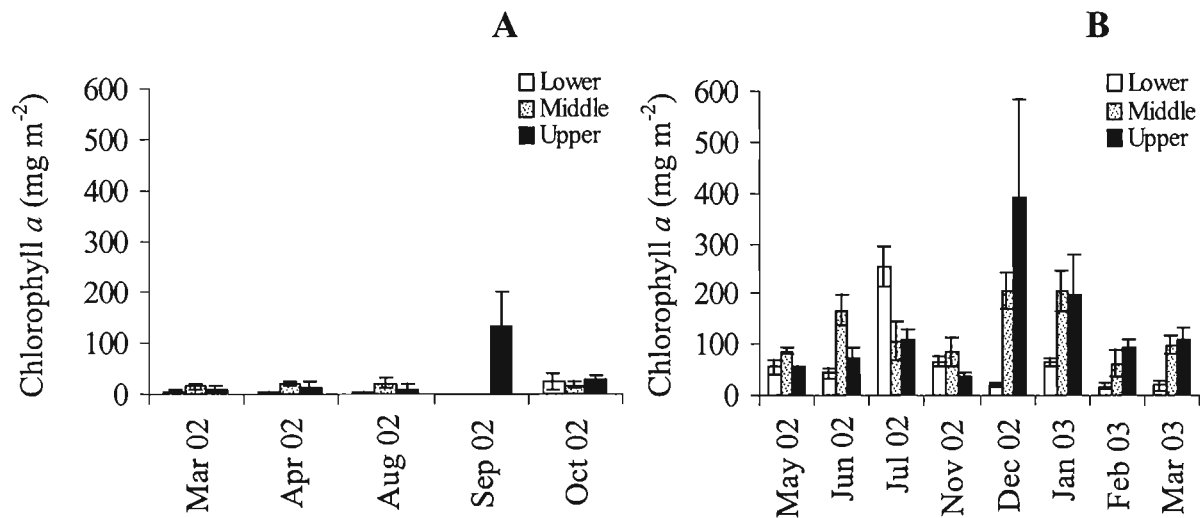
Figure 12. Temporal and spatial distribution of microphytobenthic biomass (mean ± SD) in the Mdloti Estuary during: A) open; and B) closed phase.

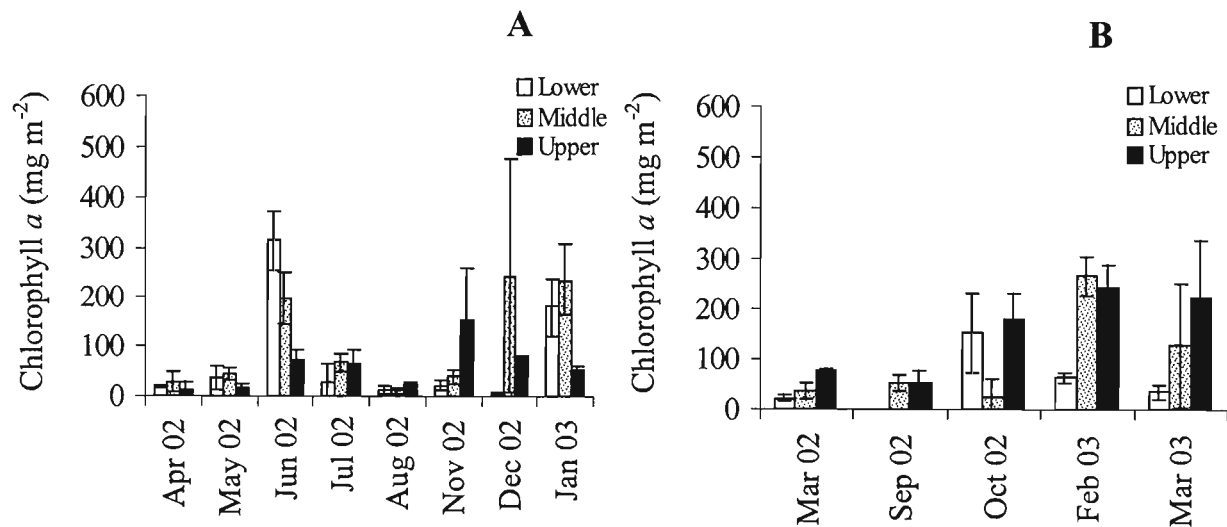Figure 13. Temporal and spatial distribution of microphytobenthic biomass (mean ± SD) in the Mhlanga Estuary during the open (A) and closed (B) phase.
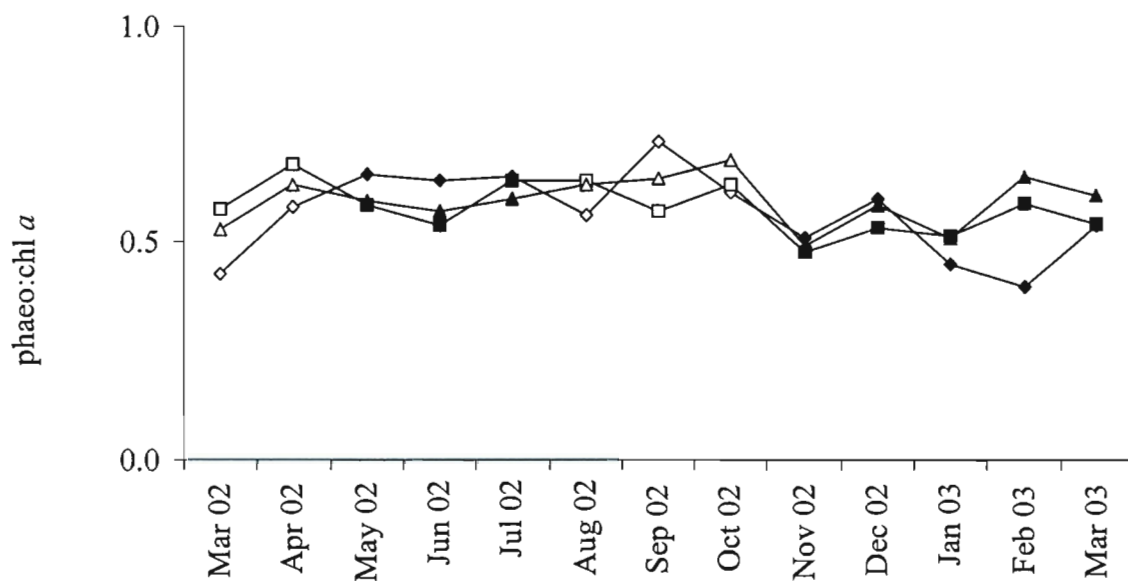
Figure 14. Ratio of phaeopigment to chl *a* concentration for the Mdloti Estuary (March 2002 to March 2003). Symbols as in previous figures.
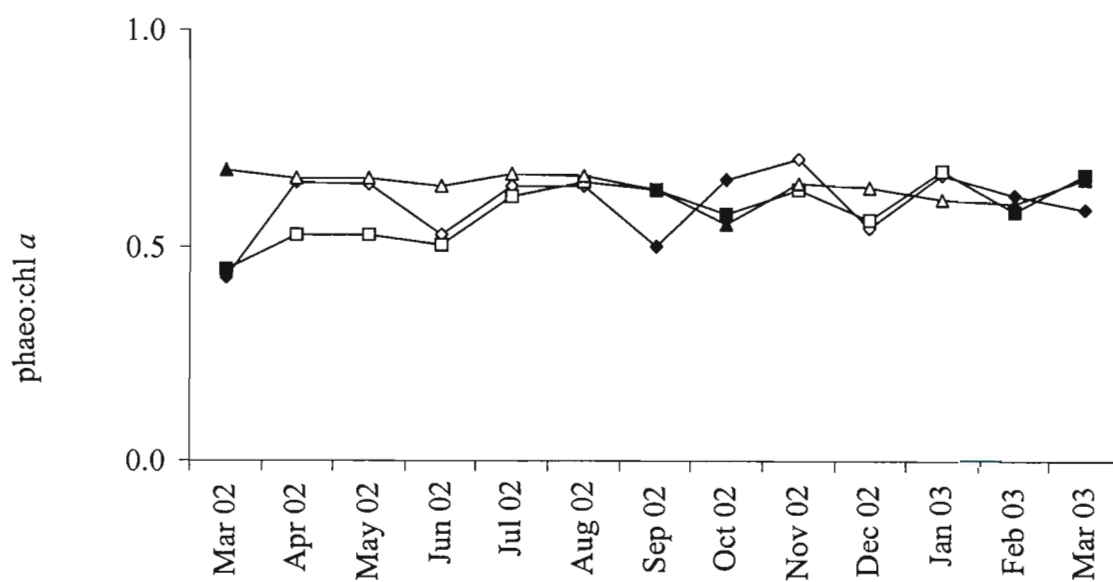
Figure 15. Ratio of phaeopigment to chl *a* concentration for the Mhlanga Estuary (March 2002 to March 2003). Symbols as in previous figures.

Table 1. Rank correlation coefficients and partial rank correlation coefficients (in parentheses) between physico-chemical and biological variables and sediment chl *a* biomass in the Mdloti and the Mhlanga estuaries with pooled open and closed phases (March 2002 to March 2003). Number of observations, n = 39. Significant at *0.05, **0.01 and ***0.001 level

	Sediment chl *a*	
Variable	**Mdloti Estuary**	**Mhlanga Estuary**
Rainfall	0.21 (0.11)	-0.13 (0.23)
K_d	0.24 (0.31)	0.29 (0.17)
Temperature	0.09 (0.40)	0.42** (0.25)
Salinity	-0.41** (0.07)	-0.09 (-0.04)
Porewater DIN	-0.21 (0.10)	-0.43** (-0.09)
Porewater DIP	0.31 (0.01)	-0.17 (0.004)
Water column DIN	-0.41* (-0.21)	-0.04 (-0.11)
Water column DIP	-0.04 (0.27)	0.12 (-0.01)
Phytoplankton biomass	0.06 (-0.07)	0.24 (0.08)
Zooplankton biomass	0.40** (-0.52*)	0.33* (-0.21)

Table 2. Rank correlation coefficients and partial rank correlation coefficients (in parentheses) between physico-chemical and biological variables and sediment chl *a* biomass in the Mdloti and the Mhlanga estuaries during their separate open and closed phases (March 2002 to March 2003). Significant at: *0.05, **0.01 and ***0.001 level

	Sediment chl *a*			
	Mdloti Estuary		**Mhlanga Estuary**	
Variable	**Open phase**	**Closed phase**	**Open phase**	**Closed phase**
Rain	-0.31 (0)	0.52** (-0.10)	0 (-0.39)	-0.32 (-0.51)
K_d	-0.11 (0)	0.08 (-0.12)	0.26 (-0.11)	0.58* (-0.37)
Temperature	0.01 (0)	-0.09 (0.43)	0.20 (0.21)	0.60* (0.64)
Salinity	0.15 (0)	-0.69** (-0.23)	-0.04 (0.16)	-0.52* (-0.41)
Porewater DIN	-0.16 (0)	0.38 (0.52)	-0.20 (-0.12)	-0.69** (-0.47)
Porewater DIP	0.06 (0)	0.37 (-0.02)	-0.33 (-0.29)	0.12 (-0.52)
Water column DIN	0.01 (0)	0.28 (0.02)	0.13 (0.15)	-0.34 (0.36)
Water column DIP	0.28 (0)	0.48* (0.50)	0.14 (-0.42)	-0.15 (0.60)
Phytoplankton biomass	0.43 (0)	0.03 (-0.07)	0.02 (-0.18)	0.45 (-0.39)
Zooplankton biomass	-0.44 (0)	-0.24 (0.11)	0.10 (0.21)	0.44 (0.13)

Discussion

During this study, microphytobenthic biomass differed significantly between the open and closed phases ($U = 29$, $p < 0.001$), only at the Mdloti. In TOCEs, major changes in microphytobenthic biomass are in fact strongly related to the alternation of open and closed phase of the mouth (Adams & Bate 1999; Perissinotto et al. 2003). In agreement with previous studies in the area (Nozais et al. 2001; Perissinotto et al. 2002; Perissinotto et al. 2003), the higher microphytobenthic biomass values in this estuary generally coincided with the closed phase (18 to 391 mg chl a m^{-2}), while the lowest biomass values typically occurred during the open phase (1.33 to 131 mg chl a m^{-2}) (Fig. 12).

Typical of TOCEs, the Mdloti experienced prolonged periods of mouth closure, with a maximum duration of sixty-nine consecutive days of mouth closure and only nine breaching events (Fig. 3A). Compared to the 1999-2000 period, a distinct seasonal rainfall pattern was not observed during this study (see Nozais et al. 2001 for further details). In addition, total rainfall recorded for the duration of this study was much lower than that reported by Nozais et al. (2001) (Fig. 2). The reduced freshwater inflow into this estuary may partly be attributed to the Hazelmere Dam being located in its relatively large catchment area. Furthermore, the low rainfall regime observed during this survey also contributed to the reduction in the volume of freshwater inflow into this estuary, which resulted in the prolonged periods of mouth closure (Fig. 3A).

Light and nutrients are the most important proximal factors that influence microalgal production, and therefore biomass accumulations (Droop et al. 1982; Perissinotto et al. 2003). In this study, the light extinction coefficient, K_d, exhibited very low values (1.1 to 3.4 m^{-1}) during the Mdloti closed phase (Fig. 8), increasing the availability of light and its penetration into deeper layers. The dominance of such favourable light conditions may have contributed to the high microalgal biomass observed during the closed phase of this estuary. The K_d values reported in this study are consistent with those reported for the closed phase in other TOCEs (Perissinotto et al. 2003). The closed phase was also

characterised by lower pore water nutrient values than that of the open phase. In particular, pore water DIN values were approximately 3 times lower during the Mdloti closed phase, as opposed to its open phase. Microphytobenthic biomass was consistently high during the closed phase, a period of decreased nutrient loading. Correlation analysis did not show any significant relationship between microphytobenthic biomass and pore water nutrients for the duration of this study (Table 1), irrespective of the open/closed phase (Table 2). Growth of shallow water microphytobenthos, like those found in the Mdloti, are generally not limited by inorganic nutrients, due to the high rates of remineralization that occurs within the sediment (Sundbäck et al. 1996). Indeed, the closed phase of the Mdloti was characterised by low river flow, reduced turbidity and increased water clarity, and thus provided a favourable environment for elevated microphytobenthic biomass.

Microphytobenthic biomass in the Mdloti was often higher in the upper reaches (96 mg chl a m^{-2} ± 114 SD), closest to the freshwater input, than in the lower (44 mg chl a m^{-2} ± 66 SD) or middle reaches (84 mg chl a m^{-2} ± 73 SD). The upper reaches of the Mdloti are typically sheltered by vegetation and sugar cane plantations, while the mouth region of the estuary is relatively unsheltered and exposed to a great deal of physical disturbance (Mundree 2001). Also, in the upper estuarine reaches sediment is likely more muddy than in the lower reaches (Adams & Bate 1999), and generally microphytobenthic biomass is higher in muddy sheltered habitats, as compared to relatively sandy exposed habitats (MacIntyre et al. 1996).

In contrast to previous findings in other TOCEs, no significant differences were observed in microphytobenthic biomass between the open and the closed phase at the Mhlanga (U = 148, p > 0.05). Unlike typical TOCEs, the higher biomass values at the Mhlanga were not always associated with the closed mouth state. In fact, the highest microphytobenthic biomass values observed at the Mhlanga, of 313 mg chl a m^{-2}, was recorded in June 2002, during an extended period (approximately 7 days) of a partly open mouth condition. High biomass levels during the open phase may be related to two factors: decreased scouring

efficiency due to frequent breaching (Reddering & Esterhuysen 1987, Cooper *et al.* 1999); and steady supply of high nutrient levels due to the discharge of treated sewage waters into the estuary. The first factor would ensure that substantial amounts of microphytobenthic biomass are still present during and after each breaching event (Fig. 13), while the second factor would contribute to a rapid growth response of microalgae following the disturbance (Underwood 2004, Guarini *et al.* 2004).

During the study period, pore water (Fig. 10 & 11) and water column nutrient concentrations (DIN and DIP) were often higher (2-5 times) at the Mhlanga than at the Mdloti (Perissinotto *et al.* 2004). The high nutrient values observed at the Mhlanga can be explained in terms of the large volume of treated sewage effluent received by this estuary on a daily basis. The Mhlanga receives 20 MLd^{-1} resulting in a capping flow of 0.23 m^3.s^{-1} (W. Pfaff, eThekwini Municipality, pers. comm.). Through this capping flow, eutrophication is enhanced at the Mhlanga and periods of mouth opening are also increased and prolonged (Thomas 2003; Perissinotto *et al.* 2004).

Although rainfall was low throughout the study period, thirteen breaching events were recorded at the Mhlanga (Fig. 3B). This is possibly due to the large volume of sewage effluent received by this estuary, which never experienced extended closure of more than fifteen consecutive days. Thus, it is clear that the natural cycles of mouth opening and closure of the Mhlanga is being altered by the high capping flow from the sewage treatment works (Perissinotto *et al.* 2004). Unlike the Mdloti, which seems to be significantly impacted by the prevailing drought conditions in the region, the Mhlanga seems to be responding strongly to the discharge of treated water effluents into its upper reaches. It was initially expected that the drought conditions observed in this region would result in a reduction in the frequency and duration of mouth opening, especially in the much smaller Mhlanga. However, the opposite was actually the case as a result of this steady capping flow.

During the closed phase of the Mhlanga, microphytobenthic biomass was significantly correlated to light ($r = 0.58$, $p < 0.05$) and temperature ($r = 0.60$, $p < 0.05$) (Table 2). Specific adaptations of microphytobenthos to light and temperature have often been suggested in correlative field studies (Cadee & Hegeman 1974; Rasmussen et al. 1983; Blanchard et al. 1996; Barranguet et al. 1998; Underwood & Kromkamp 1999). However, during the Mhlanga open phase, microphytobenthic biomass was not significantly correlated with any physico-chemical factors.

Remarkable differences were observed in the dynamics of the two estuaries. The Mdloti experienced periods of prolonged mouth closure, whereas the Mhlanga experienced frequent breaching. These differences were reflected in the phytoplankton and zooplankton stocks, which differed significantly between the two estuaries (Thomas 2003; Thwala 2004). Contrary to these findings, microphytobenthic biomass did not exhibit significant differences between the two estuaries (1-way ANOVA, $p > 0.05$). A possible reason for this may be found in the rapid recovery ability that microphytobenthic communities exhibit in response to both physical and chemical disturbances. Recent studies suggest that the recovery time scale of microphytobenthos exposed to physico-chemical disturbances may be extremely short (Underwood 2004). This is consistent with model results of tidally-induced disturbance on microphytobenthos, which shows that even during the intertidal short time-scales, microphytobenthic communities exhibit great resilience (Guarini et al. 2004). Results from this study show that at the Mhlanga the microphytobenthic community was able to attain biomass levels equal to those exhibited prior to breaching, within periods of only 5-10 days after breaching with the mouth still open (Figs. 3B & 13).

The ratio of phaeopigment:chl a gives a general indication of the physiological or grazing state of a microalgal community (Shuman & Lorenzen 1975). The ratios observed in our study indicated stressed/declining (>0.5) microphytobenthic populations in both estuaries, irrespective of their open or closed phase (Fig. 14 & 15). Exceptions to this at the Mdloti were the lower reaches during March 2002

(0.43), January 2003 (0.45) and February 2003 (0.40). At the Mhlanga, there was only one exception, the middle reaches in March 2002 (0.45). Benthic microalgae grow rapidly, having the potential to double their standing stock in days. They respond quickly to changes in the environment and thus are potential useful indicators of ecosystem health (Watt 1998; Bate *et al.* 2002).

Grazing pressure exerted on microphytobenthos by the zooplankton community may also have influenced the ratio of phaeopigment to chl *a*. Indeed, correlation analysis showed that microphytobenthic biomass was positively and significantly correlated with zooplankton biomass, both at the Mdloti (r = 0.46, p < 0.01) and the Mhlanga (r = 0.55, p < 0.05) (Table 1). This suggests that microphytobenthos are likely to represent an important food source to these primary consumers (Kibirige & Perissinotto 2003a/b; Kibirige *et al.* 2003). Preliminary studies in TOCEs suggest that these systems may at times exhibit very low phytoplankton biomass in conjunction with high zooplankton standing stocks (Perissinotto *et al.* 2000; Kibirige & Perissinotto 2003a/b). In the Mpenjati TOCE, the dominant zooplankton grazers, such as the mysid *Gastrosaccus brevifissura* and the copepod, *Pseudodiaptomus hessei* and *Acartia natalensis*, were able to utilise benthic microalgae as an alternative energy source to phytoplankton and detritus (Kibirige & Perissinotto 2003). Since *G. brevifissura* and *P. hessei* live in close association with the sediment, at least during the daytime, it seems reasonable that substantial proportions of the microphytobenthos may be used as an alternative autotrophic food source by the mysids and copepods in this and similar estuaries (Kibirige *et al.* 2003). Benthic meiofauna has an even higher potential to affect the phaeopigment:chl *a* ratio through its grazing on benthic microalgae (Miller *et al.* 1996). Presently, however, information regarding the potential grazing impact of the benthic meiofauna on microphytobenthos in TOCEs is extremely scarce (e.g. Nozais *et al.* 2005).

In a typical TOCE, like the Mdloti, microphytobenthic biomass is clearly associated with the alternation of open/closed phases (Nozais *et al.* 2001; Perissinotto *et al.* 2002; Mundree *et al.* 2003). In such systems, it is not unusual

for microphytobenthic biomass to increase during the closed phase and decline during the open phase. The Mhlanga system on the other hand, seems to lack a prolonged period of mouth closure, which is a distinct characteristic of TOCEs, and therefore did not exhibit any significant differences in microphytobenthic biomass between the open and the closed phase. Also, the Mhlanga appears much more complicated than the Mdloti, primarily because it is experiencing very frequent breaching, to the point that the whole system has become disturbed. The vigilant management and monitoring of the volume and quality of sewage effluent discharged into both these estuaries are crucial to ensure the ecological integrity of both systems. In this respect, a rehabilitation programme is urgently required for the Mhlanga.

GENERAL CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

Approximately 73% of estuaries in South Africa lack a permanently open link to the sea, that is, they are temporarily open/closed estuaries (TOCEs). The open and closed phase of TOCEs governs the water exchange between the sea and the estuary, as well as biological exchanges between the two systems. Thus, the influence of flow on the open/closed state of an estuary is a critical factor in determining reserve estuarine water requirements, as regulated by the South African National Water Act of 1998, where the aim is to maintain estuarine ecological functioning, while also meeting other demands on the water resources.

From the results of this study, it is clear that the daily discharge of exceedingly high volumes of treated sewage effluent, 20 MLd^{-1} with a capping flow of 0.23 m^3.s^{-1}, have impacted negatively on the mouth breaching regime of the Mhlanga. This estuary experienced regular and frequent breaching, with periods of mouth closure never exceeding more than fifteen consecutive days. Thus, for the duration of this study, the Mhlanga appeared to be functioning more like a permanently open estuary than a TOCE, as it lacked a period of prolonged mouth closure. Also, due to the extremely high nutrient input from the treated sewage effluent, eutrophication in this estuary was also enhanced. Consequently, microphytobenthic biomass in this estuary did not differ significantly between the open and the closed phases. A possible explanation for this is that, decreased scouring efficiency due to frequent breaching allowed substantial amounts of microphytobenthic biomass to be present during and after each breaching event (Reddering & Esterhuysen 1987, Cooper *et al.* 1999). Additionally, the steady supply of high nutrient levels due to the discharge of treated sewage waters into the estuary contributed to a rapid growth response of microalgae following the disturbance (Underwood 2004, Guarini *et al.* 2004). The response of benthic microalgae to the increased flow and nutrient addition from the sewage works demonstrate that the Mhlanga is on a trajectory of drastic change. Accordingly, the eThekwini Municipality has recently commissioned an Environmental Impact

Assessment for the proposed diversion of effluent from this estuary. It is anticipated that the diversion of treated sewage effluents from the Mhlanga will result in this estuary returning to its pristine state.

Comparatively, the Mdloti had a much lower nutrient input (8 MLd^{-1}) and capping flow (0.092m^3.s^{-1}) than that of the Mhlanga. Unlike the Mhlanga, the duration and frequency of the open and closed phases of the Mdloti were not significantly impacted by the increased inflow from the sewage effluent. As a result, the Mdloti seems to function as a typical TOCE, with prolonged open and closed phases. In this estuary, microphytobenthic biomass was clearly associated with the alternation of the open and closed phases. Similar to studies conducted in other TOCEs, peaks in microphytobenthic biomass coincided with the closed phase, while low values generally occurred during the open phase.

In order to facilitate the management of these estuaries in a sustainable manner, a taxonomic study on the dominant microphytobenthic assemblages of both systems is warranted. It is envisaged that such information could serve as useful indicators of water quality in both these systems. Additionally, future studies need to investigate the levels of nutrient addition that TOCEs can hold, without compromising their ecological functioning. Furthermore, it is also important to determine the dynamics of sediment bacteria in TOCEs, in order to elucidate the role of bacteria in the nutrient recycling of these systems.

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