

Seasonal Variations in the Vertical Distribution of Benthic Microalgae in the Upper Sediment of the Mdloti Estuary, South Africa¹

Sarasvathi Mundree^a, Renzo Perissinotto^{b*} and Christian Nozais^{b,c}

^a Division of Water, Environment and Forestry Technology, CSIR (KwaZulu-Natal), P.O. Box 17001, Durban 4000, South Africa

^b School of Life and Environmental Sciences, G. Campbell Building, University of Natal, King George V Avenue, Durban 4041, South Africa, e-mail: renzo@biology.und.ac.za

^c Institut des Sciences de la Mer de Rimouski (ISMER), Université du Québec à Rimouski, 310 Allée des Ursulines, Rimouski, Québec, Canada

* Corresponding author

A 12-month survey investigated seasonal variations in the vertical distribution of benthic microalgal biomass in relation to major factors potentially controlling their dynamics in the subtropical temporarily-open Mdloti Estuary, KwaZulu-Natal, South Africa. Benthic microalgal chl-a concentrations in the upper 5 cm of sediment ranged from 259 mg m⁻² to 977 mg m⁻² during the closed phase, and from 6.7 mg m⁻² to 305 mg m⁻² during the open phase. Significant differences were obtained between sampling sites and among seasons. A distinctive trend of increasing chl-a biomass in the deeper layers of the sediment was noted from the upper reaches (head) to the lower reaches (mouth) of the estuary. Chl-a biomass was virtually homogeneously distributed throughout the upper 5 cm of sediment in the lower reaches. Results suggest that benthic microalgal cells not only exhibited diel rhythms of vertical migration but were actively re-suspended into the water-column of the Mdloti Estuary. While a decrease in salinity, temperature and K_d favoured an increase in benthic microalgal chl-a biomass in the upper 5cm sediment, nutrients in the overlying water had no significant impact on the biomass. Results further indicate a physiologically healthy community at all sites during the open phase, as compared to the closed phase of the estuary. During the closed phase, the pheopigment to chl-a ratio indicated an actively growing community in the upper reaches and a “stressed” community in the middle and lower reaches. Thus, the large amounts of “buried” benthic microalgal chl-a biomass found in the upper 5 cm of sediment may represent an important stock of potential primary producers in temporarily-open estuarine systems like the Mdloti.

Keywords: chlorophyll-a; light; microphytobenthos; nutrients; pheopigments, temporarily-open estuary; vertical distribution.

Abbreviations: chl-a, chlorophyll-a; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus.

Introduction

Microphytobenthos, and particularly the benthic diatom component, is closely associated with sediment particles and subjected to the same hydrodynamic forces that act on the surrounding sedimentary environment (Lucas *et al.* 2000). Hence, cycles of re-suspension, deposition and burial of microphytobenthos are caused primarily by turbulent water currents and further influenced by sediment properties or cohesiveness (Mehta 1988), wave action, storm events (Demers *et al.* 1987, de Jonge and van Beusekom 1992, 1995) and bioturbation or biostabilisation by benthic animals (Grant and Daborn 1994, Miller *et al.* 1996). Furthermore, small-scale characteristics of the sedimentary microhabitat, such as grain size, organic content, organic particle size and sediment porosity greatly influence light attenuation below the

interface (Baillie 1987). Measurements on reconstituted and intact sediment have shown that, in general, light penetrates to a depth of 2–3 mm into the substrate (Garcia-Pichel and Bebout 1996, MacIntyre *et al.* 1996). As a result, most benthic microalgae are found in the top few millimetres of sediment (MacIntyre *et al.* 1996). Microalgal cells are, however, also found in substantial numbers down to depths of 10 cm and deeper in the sediment (de Jonge 1992). Although appearing somehow paradoxical, the occurrence of photosynthetic micro-organisms deep in the sediment has been attributed mainly to bioturbation by deposit feeders (Barranguet *et al.* 1997, Lucas and Holligan 1999), migration (MacIntyre *et al.* 1996, Paterson *et al.* 1998) and/or physical hydrodynamic conditions (Pinckney and Zingmark 1993, de Jong and de Jonge 1995).

With particular reference to its occurrence, microphytobenthos may be limited to the upper few millimetres of the oxygenated sediment in low energy,

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organic-rich environments and, conversely, distributed uniformly to depths of tens of centimetres in well-mixed sandy sediments in high energy environments (Fielding *et al.* 1988, MacIntyre *et al.* 1996).

The presence of large amounts of photosynthetically competent microphytobenthos well below the photic zone in the sediment has been well documented (Light and Beardall 1998, Lucas and Holligan 1999, Lucas *et al.* 2000). Microphytobenthos has the capacity to survive at low irradiance and even in darkness without damage to its photosynthetic capacity (Wulff *et al.* 1997). Thus, buried microphytobenthos likely represents an important source of primary production during sediment re-suspension events (Light and Beardall 1998). Some species can even compensate for the low light levels by resorting temporarily to heterotrophy (Admiraal 1984).

Microphytobenthic chl-a concentrations were detected down to the depth of 5 cm in the permanently-open Swartkops estuary in the Eastern Cape (Adams and Bate 1999), and down to a depth of 30 cm in the Langebaan Lagoon in the Western Cape (Fielding *et al.* 1988). However, no similar studies have been carried out in any of the temporarily-open estuaries in South Africa. River flows and wave conditions are markedly seasonal in the warm temperate and subtropical zones of the South African coastline. Therefore, in summer, temporarily-open estuaries are usually open at times of increased river flow and low wave conditions (or when the intensity and frequency of storms is lower). In winter, with higher wave conditions and a lower average rainfall and runoff occurring, the mouths tend to be closed (Adams and Bate 1999). These estuaries generally exhibit much higher levels of microphytobenthic biomass than their permanently open counterparts (Adams and Bate 1999, Nozais *et al.* 2001). Information on the vertical distribution of microphytobenthos in the sediments is of fundamental importance for the understanding of the trophic functioning of these ecosystems. This study was aimed at investigating the spatial and temporal patterns in the vertical distribution of benthic microalgal biomass (to a depth of 5 cm) in a typically subtropical temporarily-open estuary.

Material and Methods

This study was conducted in the Mdloti Estuary, situated on the KwaZulu-Natal north coast (29°38'S, 31°08'E), 25 km north east of Durban (Fig. 1). Three stations [L: Lower Reaches (mouth); M: Middle Reaches (middle); and U: Upper Reaches (head)] were sampled at regular monthly intervals from May 1999 to April 2000. The estuary remained closed for the first 6 months (May 1999 to October 1999) and then breached in November 1999, remaining open thereafter until the end of the survey (April 2000). The depth of the estuary during sampling varied

from 1.36 to 3.08 m during the closed phase and from 0.3 to 1 m during the open phase.

Microalgal biomass was estimated as chl-a concentration. Samples of the upper 5 cm layer of sediment were collected using an acrylic plastic twin-corer of 20 mm internal diameter, as suggested by Rodriguez (1993) for South African estuaries. All sites sampled were subtidal, and at depths varying with the conditions of the estuary. Following the methodology previously employed by researchers in the area (Nozais *et al.* 2001, Perissinotto *et al.* 2002), 3 replicates of 5 cm corer samples were taken at each station, every month, for a period of one year. These 5 cm sediment corers were cut at 1 cm intervals and each layer was immediately put into 100 ml polyethylene bottle containing 30 ml of 90 % acetone. Pigments were extracted over a period of 24–48 h at 4 °C in the dark. All chl-a concentrations were measured using a 10-AU Turner Designs (USA) fluorometer, fitted with the narrow band, non-acidification system of Welschmeyer (1994). This system allows precise measurements (maximum 10 % error) of chl-a without interference from other photosynthetic pigments or their degradation products. Calibrations were made using pure extracts of chl-a from *Anacystis nidulans* algae (Sigma Products, USA).

The ratio of pheopigments to chl-a concentration was also determined. This ratio gives a general indication of the physiological or grazing state of a microalgal community (Shuman and Lorenzen 1975). High ratio values (range of 0.5 to 1) represent a stressed or declining community, while low ratios (range of 0 to 0.5) indicate an actively growing community relatively free of grazing pressure (Bidigare *et al.* 1986).

Water samples for the determination of DIN (NO_2^- , NO_3^- , and NH_4^+) and DIP (PO_4^{3-}) were collected using a 1000 ml weighted pop-bottle and placed in 500 ml acid pre-washed polyethylene bottles. Nutrient concentrations were later determined using a Technicon Autoanalyzer II system following the methods of Mostert (1983).

At each station, a vertical profile of downwelling irradiance (PAR, 400 to 700 nm) was measured with a LI-COR LI-189 underwater quantum sensor (cosine collector). The light attenuation coefficient, K_d , was then determined from these data according to Kirk (1994).

Salinity values were recorded on each occasion using a YSI 6920 Water Logger (USA). Daily precipitation data (mm) were provided by the South African Sugar Association Experiment Station, Durban.

A Kolmogorov-Smirnov non-parametric test (SPSS Statistical package) was done to test for normality and a Cochran Q test was done to test for homoscedasticity of the microphytobenthic chl-a data. The statistical package, Statistica 5.5 (StatSoft Inc.) was then used to analyse and determine any significant spatial or temporal differences in benthic mi-

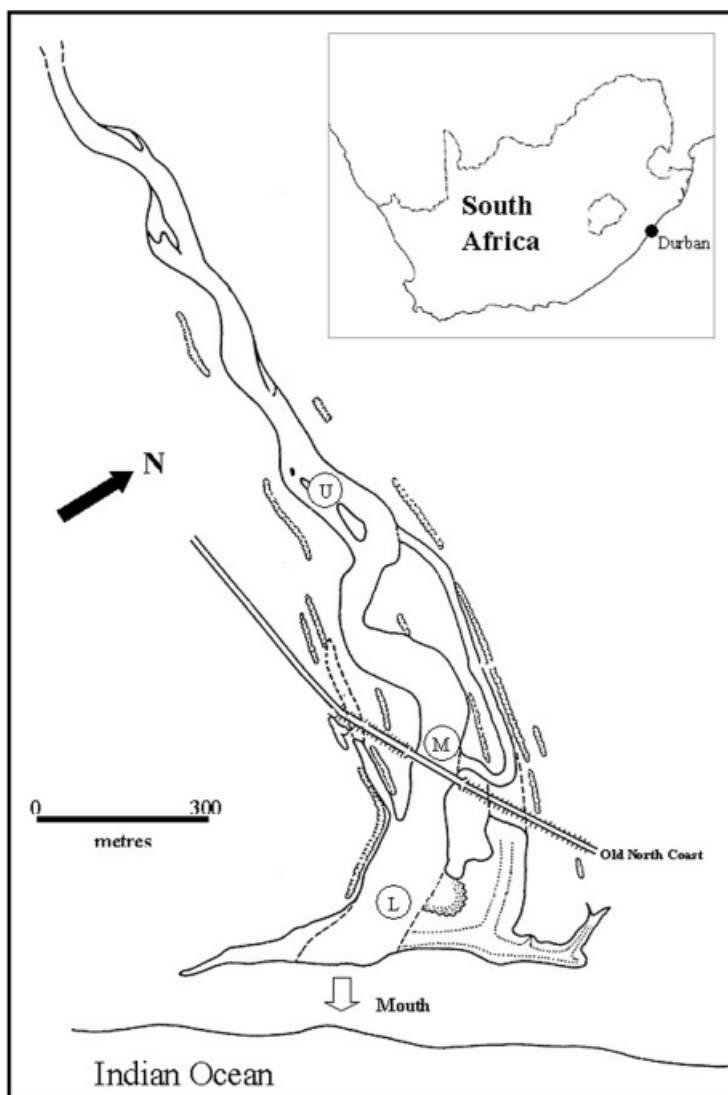


Fig. 1. Map of the Mdloti Estuary with sampling stations. Latitude and longitude at the mouth: 29°38'S, 31°08'E.

croalgal chl-a concentrations in the upper 5 cm sediment. An ANOVA was performed with the chl-a concentrations as the dependent variable. A Tukey HSD post-hoc test was done to test for significant pheopigment to chl-a variations between pairs of sampling sites. Pearson correlations were also calculated to infer relationships between physico-chemical variables and benthic microalgal chl-a concentrations in the upper 5 cm of sediment.

Results

Spatio-temporal distribution

A Kolmogorov-Smirnov non-parametric test revealed that microphytobenthic chl-a data were not normal at $p < 0.05$ and therefore were \log_{10} transformed. A Cochran's Q test indicated no significant differences between variances at $p < 0.001$, thus homoscedasticity and normality of the transformed

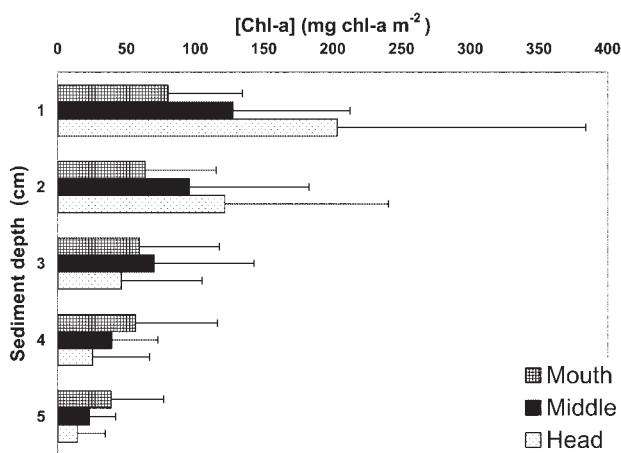


Fig. 2. Annual average depth distribution of benthic microalgal chl-a concentration (mean + SD) in the upper 5 cm of sediment in the lower reaches (mouth), middle reaches (middle) and upper reaches (head) of the Mdloti Estuary (May 1999 to April 2000).

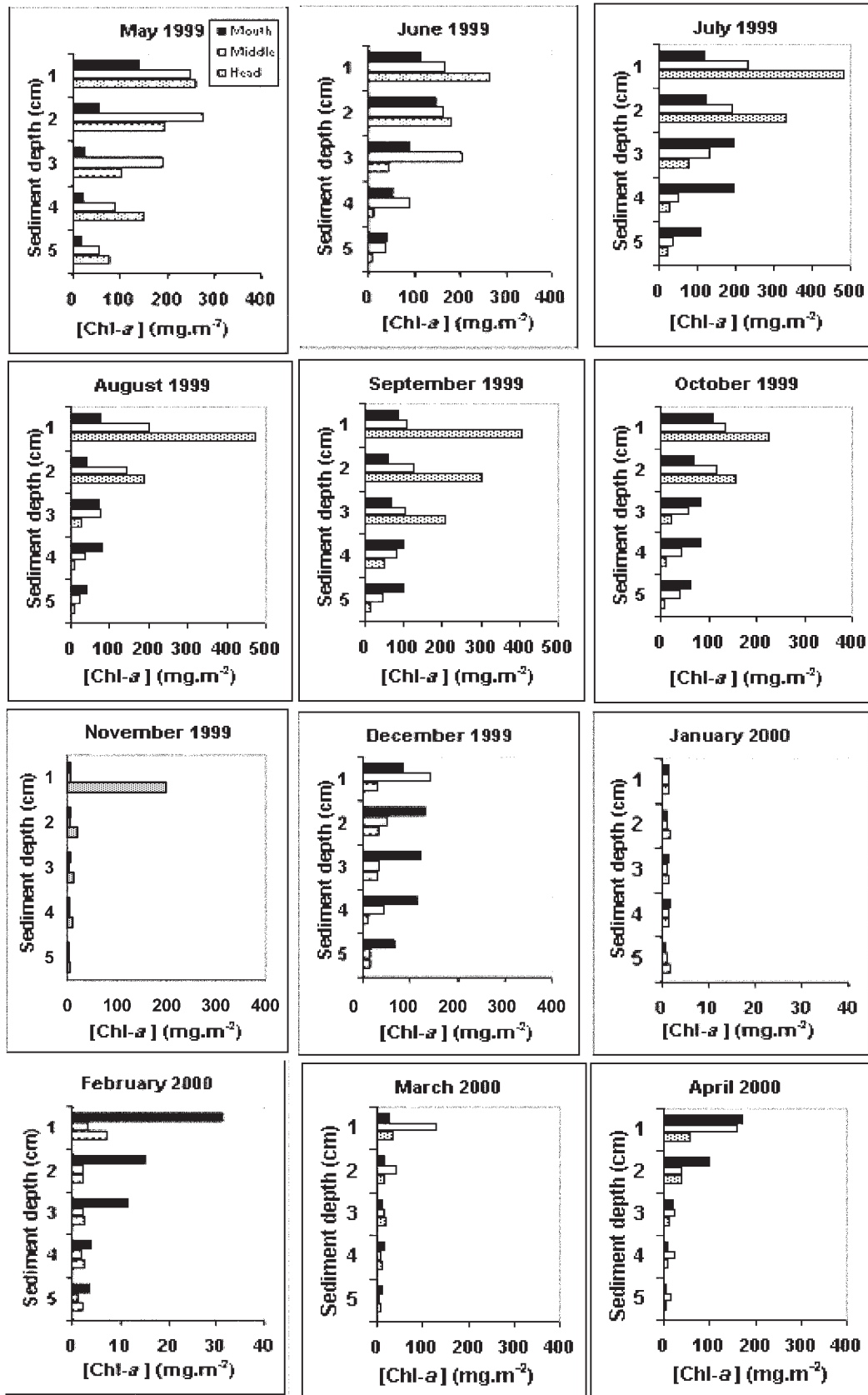


Fig. 3. Monthly depth distribution of benthic microalgal biomass in the upper 5 cm of sediment in the lower reaches (mouth), middle reaches (middle) and upper reaches (head) of the Mdloti Estuary (May 1999 to April 2000).

data were achieved. A 2-way mixed model ANOVA revealed significant interaction between sampling sites and season ($F_{6,524} = 2.7$, $p < 0.05$, $MS_{\text{error}} = 0.4$).

The annual average chl-a biomass was homogeneously distributed throughout the upper 5 cm of sediment at the lower reaches, as compared to the decreasing chl-a biomass at the middle and upper reaches (Fig. 2). Figure 3, however indicates that such a trend may change by month. A 2-way ANOVA revealed significant variations with depth in the upper 3 cm of sediment benthic microalgal chl-a in the different reaches ($F_{2,315} = 7.7$, $p < 0.001$, $MS_{\text{error}} = 0.6$), but there was no significant effect of reach ($F_{2,315} = 1.7$, $p > 0.05$, $MS_{\text{error}} = 0.6$). A depth distribution of chl-a concentration, as percentage of the total, indicated that on average 80 % of chl-a biomass was found in the upper 3 cm at the head, but in the upper 4 cm in the middle reaches and at the mouth of the estuary.

In terms of absolute concentration, benthic microalgal chl-a in the upper 5 cm of sediment ranged from 259 mg m^{-2} (mouth, May 1999) to 977 mg m^{-2} (head, September 1999) during the closed phase. However, much lower values were observed during the open phase: from 6.7 (mouth and middle reaches, January 2000) to 305 mg m^{-2} (mouth, April 2000) (Table I, Fig. 3).

Pheopigment to chl-a ratio

Analysis of the Mdloti data for the benthic microalgal community in the upper 5 cm of sediment, indicated a ratio ranging from 0.2 to 0.79 for the sampling period May 1999 to April 2000 (Fig. 4). A 2-way ANOVA revealed a significant interaction between the sampling sites and the estuarine phases ($F_{2,30} = 3.6$, $p < 0.05$, $MS_{\text{error}} = 0.4$). A Tukey HSD post-hoc test further revealed that significant variations were between the lower and upper reaches and between the middle and upper reaches. The ratio for the

Table I. Total chl-a concentration (mg m^{-2}) with standard errors for the upper 5 cm of sediment in the lower reaches (mouth), middle reaches (middle) and upper reaches (head) of the Mdloti Estuary (May 1999 to April 2000).

| | Mouth | Middle | Head |
|----------------|----------|------------|-------------|
| May 1999 | 259±22.8 | 861±43 | 785±32.9 |
| June 1999 | 449±19.6 | 661±30.4 | 508±51.4 |
| July 1999 | 742±18.9 | 640±37.8 | 939±92.9 |
| August 1999 | 308±8.7 | 475±33.9 | 705±90.2 |
| September 1999 | 412±7.8 | 461±14.1 | 977±74.6 |
| October 1999 | 410±7.7 | 391±19.5 | 420±44.6 |
| November 1999 | 21±0.5 | 18.5±0.6 | 243±37.6 |
| December 1999 | 517±12.3 | 287±22.1 | 117±4.3 |
| January 2000 | 6.8±0.2 | 6.66±0.1 | 7.5±0.2 |
| February 2000 | 65±5.1 | 10.4±0.4 | 16.4±1 |
| March 2000 | 79±2.4 | 196±23.4 | 87±4.4 |
| April 2000 | 305±32.8 | 257±27.4 | 118±0.9 |
| Mean + STD | 297.8±65 | 355.4±80.3 | 410.3±118.6 |

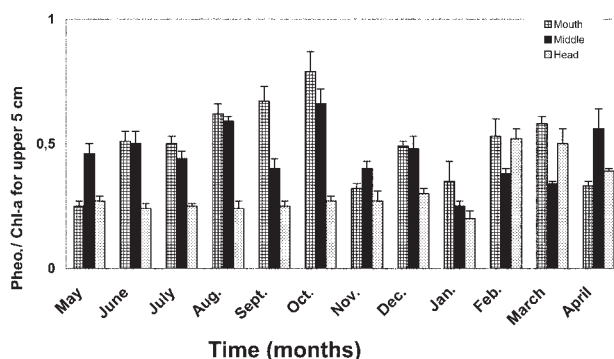


Fig. 4. Ratio of pheopigment to chl-a concentration for the upper 5 cm of sediment in the lower reaches (mouth), middle reaches (middle) and upper reaches (head) of the Mdloti Estuary (May 1999 to April 2000). Bars represent standard errors.

closed phase suggests an actively growing community at the head (0.24–0.27), a somewhat “stressed” community in the middle reaches (0.4–0.66), and a community at the mouth that appears to be getting progressively “stressed” (0.25–0.79). In contrast, the ratio for the open phase suggests a physiologically healthy community throughout the estuary, with ratios ranging from 0.32 to 0.58 (mouth); 0.25–0.56 (middle reaches) and 0.2–0.52 (head).

Physico-chemical analysis

During the period of the survey, DIN concentrations in the Mdloti Estuary differed significantly among estuarine phases ($F_{1,24} = 7.3$, $p < 0.01$, $MS_{\text{error}} = 0.5$). Conversely, DIP concentrations exhibited no such temporal trend. DIN and DIP concentrations varied between 0.5–14.0 and 0.6–6.0 μM during the closed phase and between 7–204 and 0.3–6 μM during the open phase, respectively (Nozais *et al.* 2001).

K_d values differed significantly among estuarine phases ($F_{1,24} = 10.18$, $p < 0.001$, $MS_{\text{error}} = 0.4$) with values ranging from 0.94–2.95 m^{-1} during the closed phase and from 8.14–28.9 m^{-1} during the open phase. The average salinity ranged between 0.13–0.28 PSU during the closed phase, and between 0.7–4.88 PSU during the open phase. Salinity levels were largest at the lower reaches, between 1.1 to 9.6 PSU compared to the middle, 0.5–3.7 PSU, and the upper reaches, 0.4–2.1 PSU. Rainfall was significantly seasonal ($F_{3,24} = 14.74$, $p < 0.001$, $MS_{\text{error}} = 0.5$) being low in winter (23 mm), with a rapid increase in spring (177 mm), a peak in summer (270 mm) and a sharp drop in autumn (49 mm). Sampling took place during a dry-wet cycle, with such values being regarded as average for this area.

Correlation analysis

The benthic microalgal chl-a biomass in the upper 5 cm sediment was found to have a significant posi-

Table II. Correlation coefficients between chl-a concentration in the upper 5 cm of sediment and chl-a concentration in the upper 1 cm of sediment and the physico-chemical variables.

| Variable | Chl-a in upper 5 cm sediment |
|------------------------------|------------------------------|
| Chl-a in upper 1 cm sediment | 0.85* |
| Phytoplankton | 0.35* |
| K_d | -0.60* |
| Temperature | -0.70* |
| Salinity | -0.39* |
| DIN (bottom) | -0.16 |
| DIP (bottom) | -0.05 |

Number of observations: $n = 36$. * Significant at the $p < 0.05$ level.

tive correlation with the benthic microalgal chl-a biomass in the upper 1 cm sediment (Table II), suggesting the possibility of diel rhythms of vertical migration in the benthic microalgal community of the Mdloti Estuary. The re-suspension of benthic microalgae into the water-column may explain the positive correlation observed between benthic microalgal chl-a biomass in the upper 5 cm sediment and phytoplankton biomass (Table II).

Correlation analysis also suggests that a decrease in salinity, temperature and K_d is significantly related to an increase in the benthic microalgal chl-a biomass in the upper 5 cm of sediment. The increase in K_d during the open phase appeared to significantly limit benthic microalgae during this period. No significant correlation was noted, however, between the nutrient concentrations in the overlying water and the benthic microalgal chl-a biomass in the upper 5 cm sediment (Table II). This suggests that under conditions of low nutrient availability in the water column, benthic microalgae may survive by using the relatively high nutrient concentrations in the pore water of sediments (Meyercordt and Meyer-Reil 1999).

Discussion and Conclusion

Sediment chl-a contents are usually reported as rather constant throughout the year, with no clear pattern of seasonal variations (Varela and Penas 1985, Goto *et al.* 2000). The Mdloti Estuary exhibited significant temporal variations in its benthic microalgal standing stock in the upper 5 cm of sediment, with the highest biomass observed during the closed phase and lowest during the open phase (Fig. 3). Studies have shown that the vertical distribution of benthic microalgal chl-a in the sedimentary microhabitat (both spatially and temporally) is influenced not only by the environmental variables and sedimentary characteristics to which they are subjected, but also by their vertical migration behaviour and liv-

ing forms within the benthic microalgal community itself (Sun *et al.* 1991, Lucas and Holligan 1999).

The small scale characteristics of the sedimentary microhabitat, such as grain size, organic content and sediment porosity are known to influence greatly the depth to which light penetrates into the sediment (Baillie 1987, MacIntyre *et al.* 1996). In the Mdloti, significant spatial variations of microalgal biomass (upper 3 cm) were noted, with the highest biomass observed in the upper reaches and the lowest in the lower and middle reaches (Table I, Fig. 3). In sandy sediments (e.g. Mdloti mouth), light may penetrate down to approximately 4 mm and be further enhanced by scattering, while in more silty sediments (e.g. middle and upper Mdloti reaches) the photic zone is often much thinner (Lassen *et al.* 1992, Kuhn *et al.* 1994). A depth distribution of benthic microalgal chl-a concentration in the Mdloti, as percentage of the total, indicated that 80% of benthic microalgal biomass was found in the upper 3 cm at the head, and in the upper 4 cm in the middle reaches and at the mouth. The paradoxical presence of large amounts of buried benthic microalgae, at depths well below the maximum potential depth of light penetration, appears to be a common feature in estuarine systems and has been well documented (Light and Beardall 1998, Lucas and Holligan 1999, Lucas *et al.* 2000). Such benthic microalgae, found at depths well below the sediment photic zone, constitute an important stock of potential primary producers, since they have been reported to resume promptly their photosynthetic activity when exposed to light (Lucas and Holligan 1999, Lucas *et al.* 2000).

Benthic microalgae are known to move towards the surface of the sediment when the latter is exposed to high light or low tide and descend into deeper layers to avoid transport due to re-suspension by advancing tides, or to reduce predation by surface deposit feeders (Round 1979, MacIntyre *et al.* 1996). Such diel rhythms of vertical migration may explain the strong positive correlation found in the Mdloti between chl-a concentration in the upper 5 cm of sediment and that of the upper 1 cm (Table II).

In the Mdloti, the sediment at the mouth is largely composed of beach sand of marine origin, while the occurrence of more silty sediment at the head is probably the result of the dramatic increase in silt loading into the estuary, arising from soil erosion as a consequence of the development and agricultural activities (KZN-Wildlife Report 2000). The annual average benthic microalgal chl-a concentration found in the upper 2 cm layer at the head (325 mg m^{-2}) was comparable to the annual average chl-a found in the upper 4 cm layer of the middle reaches and in the upper 5 cm layer at the mouth (Fig. 2). Similar results were reported by Adams and Bate (1999) and Lucas *et al.* (2000). These authors found that silty sediments contain up to 5–25 times more chl-a in their surface layer than sandy sediments. Sandy sediments have

also been reported to have vertically-homogenous chl-a distribution and can undergo bed load transport up to several centimetres depth (Lucas *et al.* 2000). In this context, the mouth and middle reaches of the Mdloti Estuary appeared to have greater homogenous depth distribution of chl-a biomass in the upper 5 cm of sediment than the head of the estuary (Fig. 2).

The vertical distribution of benthic microalgal chl-a biomass in the sediment has also been associated with the degree of shelter or physical disturbance (de Jong and de Jonge 1995). Relatively exposed sites (such as the mouth and the middle reaches of the Mdloti) exhibit a gradual decrease or almost uniform distribution of chl-a with depth, as a result of both the sediment and the chl-a being continuously reworked and exported over a greater depth (de Jong and de Jonge 1995). In the Mdloti Estuary, the mouth, in particular, was exposed to a great deal of physical disturbance during the transition from the closed to the open phase of the estuary. In contrast, sheltered sites (such as the Mdloti head) exhibit a steep decrease in chl-a biomass with sediment depth, because tidal currents and waves exert very little disturbance on the uppermost sediment layer (Fielding *et al.* 1988, de Jong and de Jonge 1995). The head of the Mdloti Estuary is generally well sheltered from wind by vegetation throughout the year and salinity changes were negligible, indicating that tides had no likely effect. Thus, the distinctive trend observed from the head to the mouth in the Mdloti Estuary, of increasing benthic microalgal chl-a in the deeper layers of the sediment (Fig. 2), may be ascribed to the different sedimentary and hydrodynamic characteristics prevailing in the different reaches of the estuary.

In a typical temporarily-open estuary, like the Mdloti, the closed phase is characterised by low river flow and the absence of tidal influence, which minimise both sediment disturbance and turbidity while increasing water clarity (Wooldridge and McGwynne 1996, Nozais *et al.* 2001). The dominance of such favourable light conditions in the Mdloti (K_d between 0.94 and 2.95 m^{-1} , euphotic depth between 1.7 and 4.9 m), increased the availability of light at the sediment surface and its penetration into deeper layers. Hence, the total benthic microalgal chl-a biomass for the upper 5 cm layer was observed to be higher during the closed phase than during the open phase (Table I). The open phase was characterised by a dramatic reduction in benthic microalgal chl-a biomass in the upper 5 cm, as the breaching of the estuary's mouth (in November 1999) led to the subsequent scouring of the sediment and to an increase in fine sediment and heavy silt loading in the estuary. The primary effect of the re-suspension of fine sediments is that the photic zone becomes thinner, as turbidity in the overlying water increases (Wulff *et al.* 1997). Hence, the significantly negative correlation between K_d and the chl-a biomass in the sediment (Table II)

may suggest that the benthic microalgae in the upper 5 cm sediment were most probably limited by light during the open phase. The same pattern was observed for the upper 1 cm layer (Nozais *et al.* 2001).

The ratio of pheopigments to chl-a, however, indicates that although light was limiting during the open phase, the benthic microalgal community was in a relatively "good" physiological state throughout the sampling period (Fig. 4). Such result may be ascribed to the fact that the benthic microalgae of the Mdloti always experienced the theoretical minimum light intensity of 0.1 % of surface incident flux, which is required to support growth (Falkowski 1988).

The significantly positive correlation found between the chl-a concentration in the upper 5 cm of sediment and the phytoplankton at the bottom of the water-column (Nozais *et al.* 2001) may suggest that benthic microalgal cells have been re-suspended into the water-column by tidal currents during the open phase, and by wind-driven mixing effect during the closed phase. Re-suspension of benthic microalgae and their presence and importance as temporary members of the phytoplankton is a well-known phenomenon with benthic microalgae contributing up to 60 % of the total water-column biomass (de Jonge and van Beusekom 1992, Lucas *et al.* 2000).

Redistribution of benthic microalgal biomass can also be caused by biological stress exerted by macrofauna and meiofauna through grazing, filter feeding and bioturbation of the sediment, which makes it more erodible (Fielding *et al.* 1988, Miller *et al.* 1996, Lucas *et al.* 2000). In the Mdloti, a large number of burrowing sand prawns (*Callinassa kraussi*) have been reported to inhabit areas adjacent to the sandbar during the closed phase and they are known to cause considerable mixing of sediment with their burrowing activity (Grobblet *et al.* 1987). They may, therefore, play a role in redistributing the benthic microalgal chl-a into the deeper layers of the sediment at the mouth. The ratio of pheopigments to chl-a further indicates that the benthic microalgal community was under increasing physiological stress or grazing pressure during the closed phase, as compared to the open phase (Fig. 4).

Substantial increases in benthic microalgal biomass during the open phase (Table I, Fig. 3), suggest that although the biomass may decline temporarily during the transition from the closed to the open phase, in-situ growth and advective transport of "buried" benthic microalgae may be sufficient to re-supply the community within a relatively short period of time (Ray 1989, Lucas *et al.* 2000).

In conclusion, the large amounts of "buried" benthic microalgal chl-a biomass (down to 5 cm of sediment depth) are important seeding stocks of potential primary producers in temporarily-open estuarine systems, such as the Mdloti. This inherent capacity to adapt to the environmental extremes of temporarily-open systems is further reflected in the ability of

benthic microalgae to effectively utilise the optimal conditions of irradiance, sediment stability and remineralization within the sediment, to attain maximum growth during the closed phase.

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