

## Distribution and vertical dynamics of planktonic communities at Sofala Bank, Mozambique

M.C. Leal<sup>a,\*</sup>, C. Sá<sup>b</sup>, S. Nordez<sup>c</sup>, V. Brotas<sup>b</sup>, J. Paula<sup>a</sup>

<sup>a</sup> Centro de Oceanografia, Laboratório Marítimo da Guia, Faculdade de Ciências da Universidade de Lisboa, Av. N<sup>o</sup> Senhora do Cabo, 939, 2759-374 Cascais, Portugal

<sup>b</sup> Centro de Oceanografia, Instituto de Oceanografia, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

<sup>c</sup> Instituto de Investigação Pesqueira de Moçambique, Av. Mao Tse-Tung No. 389, Maputo, C.P. 4603 Mozambique

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### ABSTRACT

Coastal ecosystem processes are largely influenced by the interaction of different factors operating at various temporal and spatial scales, specifically those responsible for primary production patterns that modulate zooplankton and subsequent trophic levels. Hydrological processes, such as tidal cycles and coastal currents, nutrients availability, phytoplankton groups (studied through algal pigment signatures analysed by HPLC), and zooplankton abundance and distribution were investigated at the Sofala Bank (Mozambique), with special emphasis on their horizontal distribution and vertical dynamics (48 h). Horizontal distribution has shown inshore–offshore gradients in all analysed parameters, as well as inshore waters intrusion probably related to Zambezi River delta runoff. Tidal currents were responsible for major hydrological vertical variations and for horizontal and vertical advection of phytoplankton biomass in the surface and deepest layers, respectively. Nutrient concentrations were typical from oligotrophic regions, and nutrient ratios were strongly influenced by depleted nitrate + nitrite concentrations, indicating low estuarine discharges typical from the dry season. The very low N:P ratio obtained suggests strong nitrogen limitation to phytoplankton communities, supporting the low phytoplankton abundance observed. Both phytoplankton pigments and zooplankton were found mainly near the bottom (40 m depth), despite the latter displayed vertical migrations triggered by light variations. Phytoplankton community was dominated by microflagellates, specifically prymnesiophyceans, and behaved as a whole, except Cyanobacteria that displayed vertical distribution movements different from other phytoplankton groups, being mainly concentrated at mid-water column depths (10–20 m). This investigation enhances physico-chemical phenomena and their importance determining the planktonic communities vertical dynamics at Sofala Bank, a tropical coastal ecosystem of the Western Indian Ocean where planktonic dynamics are still poorly described and understood.

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### 1. Introduction

Coastal shelf waters are ecosystems of great human and ecological interest where complex processes occur. The interaction of physical (e.g. coastal currents, upwelling, tides, and advection), chemical (variable chemical properties including nutrient inputs), and ecological (e.g. biological production and its dynamics, and prey/predator interactions) processes induce high spatial variability on the water column over different time scales (Brunet and Lizon, 2003; Lutjeharms, 2006; Queiroga et al., 2007). This variability determines the abundance and structure of different biological communities present in coastal waters, specifically phyto- and zooplankton as oceanic food chain lower levels. Zooplankton

abundance and distribution is often related to predator/prey interactions, as a prey for both planktivorous fishes and some planktonic larvae, and as consumers of phytoplankton organisms (e.g. González-Gordillo and Rodríguez, 2003; Santos et al., 2006). Therefore, phytoplankton is regulated by zooplankton and fish herbivory, and also by nutrients availability, mainly nitrogen, phosphate, and silica (Vanni, 1987; Svensson and Stenson, 1991; Garnier and Cugier, 2004). The relation between the different nutrient ratios and phytoplankton in coastal systems has been widely studied, and nitrogen generally plays a key role limiting phytoplankton growth, thus strongly determining its community structure and chemotaxonomic pigment composition (Hecky and Kilham, 1988; Tyrrell, 1999).

The present study took place at the Sofala Bank (Mozambique), a wide shallow shelf influenced by the Zambezi River delta and other estuaries, and where important fisheries occur. Besides

\* Corresponding author.

E-mail addresses: [maleal@fc.ul.pt](mailto:maleal@fc.ul.pt), [miguelcleal@gmail.com](mailto:miguelcleal@gmail.com) (M.C. Leal).

important river runoff discharges, strong tidal currents and oceanographic currents from the Mozambique Channel have major effects on hydrological and ecological processes (Ridderinkhof et al., 2001; Lutjeharms, 2006). In spite of the high importance of this coastal ecosystem for Mozambican fisheries and economy, studies from Sofala Bank are very scarce and only cruise and fisheries reports can be found (Bandeira et al., 2002, and references therein). This neritic region has high phytoplankton biomass comparing to the greater part of the Mozambican oligotrophic waters, mainly because of the nutrient input from the Zambezi river runoff, which is closely related to rainfall events (Lutjeharms, 2006). Hence, despite that hydrological and planktonic dynamics of several temperate coastal ecosystems are already studied (e.g. Verity et al., 1993; Balkis, 2003; Sabetta et al., 2008; Silva et al., 2008), Sofala Bank is an excellent case study to understand the nutrients, phytoplankton, and zooplankton dynamics in relation to the physico-chemical environmental variability of a tropical coastal ecosystem from the Western Indian Ocean, where scientific knowledge is very scarce.

Several studies identified tidal energy, light, and diel variations as key factors changing neritic planktonic vertical distribution (Hill, 1991; Queiroga et al., 2007; Brunet et al., 2008). At Sofala Bank, the strong tidal currents and estuarine discharges may strongly determine nutrients availability and water column light penetration due to increased turbidity, thus affecting base processes that modulate planktonic community dynamics. Stratification of the water column, specifically the pycnocline depth and its strength, conditions the effectiveness of primary production magnitude at the surface layer and may act as a barrier to vertical movements of zooplankton (Criales-Hernández et al., 2008). However, due to the strong tidal currents it is probable that vertical mixing locally induces homogenization of the water column. The investigation of tidal and diel variations and other regulating factors is therefore important to understand fundamental ecological processes that act in generating high primary productivity and modulate resources supporting intense local fisheries activity.

The main hypotheses addressed in this study are: (1) the nutrients and planktonic abundance reflect the high productivity that supports intense fisheries in the Sofala Bank, (2) the estuarine discharge affects hydrological properties, nutrient, phytoplankton and zooplankton abundance, and horizontal distribution; (3) the interaction of coastal currents (specifically tides) with estuarine discharge induces a vertical dynamics of water mass physico-chemical properties, nutrient availability, phytopigments composition, and zooplankton vertical distribution. In view of these hypotheses the central objective was to study, by applying an Eulerian approach based on fixed station sampling, the physico-chemical properties and planktonic abundance and vertical dynamics at the Sofala Bank.

## 2. Methodology

### 2.1. Sampling

The study area was located at the Sofala Bank, in front of the Zambezi river delta. Sampling took place on board the R/V “Dr. Fridtjof Nansen” from the 5th to the 8th December 2007, covering in the first 24 h a total of 11 stations distributed along three transects (Fig. 1), from a bottom depth of 24 to 374 m, and the outermost stations separated by 60 km. Their position was set as to characterize the shelf section where the fixed station sampling was carried out in the following 48-h period. The fixed station was positioned over a bottom depth of 50 m and samples were taken every 2 h.

Current magnitude and direction were measured with a hull-mounted Acoustic Doppler Current Profiler (ADCP) and transparency (m) using a Secchi Disk. At every transect and at the fixed station, CTD profiles were conducted and temperature, salinity, and fluorescence (used as a proxy of chlorophyll *a*) data recorded at every 1 m depth interval. Water samples were taken at five pre-determined depths (5, 10, 20, 30, and 40 m), except for shallower stations, using a rosette equipped with Niskin bottles. Immediately after collection, two replicates of 100 ml were collected and stored frozen for posterior nutrient analysis (nitrate + nitrite, phosphate, and silicate). For HPLC pigment analysis, 2 l of seawater were immediately filtered through glass fibre filters (25 mm Ø and 0.7 µm pore – Whatman GF/F) and filters were kept frozen in the dark for posterior analysis.

Depth-stratified zooplankton samples (0–5, 5–10, 10–20, 20–30, and 30–40 m) were collected with a multinet (Midi model, 0.5 × 0.5 m mouth size, Hydro-bios), 405 µm mesh size, towed at ~2 knots for 2 min, sampling on oblique hauls in each stratum. Flow rate was monitored by a flowmeter mounted in the mouth of the aperture, and each sample represented approximately 40 m<sup>3</sup> of water filtered. A neuston net (0.2 × 1.0 m mouth size) with the same mesh size and a flowmeter mounted was towed horizontally at similar speed and time, sampling the upper 20 cm of the water column. All zooplankton samples were preserved in 4% borax-buffered formaldehyde, prepared with seawater.

### 2.2. Laboratory procedures

All the laboratory procedures were done at the Oceanography Centre of University of Lisbon, Portugal. Colorimetric analyses, with a Tecator FIAStar™ 5000 Analyser, were performed to determine nutrient concentrations. Nitrite (NO<sub>2</sub><sup>-</sup>), nitrate (NO<sub>3</sub><sup>-</sup>), phosphates (PO<sub>4</sub><sup>3-</sup>, hereafter as P), and silicates (Si(OH)<sub>4</sub>, hereafter as Si) were, respectively, determined according to Grasshoff (1976), Bendshneider and Robison (1952), Murphy and Riley (1962), and Fanning and Pilson (1973). Since water properties from this region are typically oligotrophic (Lutjeharms, 2006), the nitrite and nitrate sum was used (NO<sub>2</sub><sup>-</sup> + NO<sub>3</sub><sup>-</sup>, hereafter as N).

The identification and abundance of phytoplankton functional groups can be achieved by high-performance liquid chromatography (HPLC) analytical technique, which is increasingly in use as it is a less time-consuming method in relation to microscopy phytoplankton identification and counting. HPLC quantifies chemotaxonomic pigments allowing to estimate the contribution of phytoplankton groups to chlorophyll *a* (Chl *a*) using photosynthetic marker pigments, such as alloxanthin for cryptophytes, 19'-hexanoyloxyfucoxanthin for prymnesiophytes, and other less-specific biomarkers such as fucoxanthin for diatoms (also present in chrysophytes) and zeaxanthin for cyanobacteria (also present in green algae), among others (Jeffrey et al., 1997). In order to extract photosynthetic pigments, frozen filters were disrupted with 2 ml of 95% cold-buffered methanol (2% ammonium acetate) for 30 min at -20 °C in the dark. Samples were sonicated for 1 min in the beginning of the extraction period and then centrifuged at 4000 rpm for 15 min, at 4 °C. Extracts were filtered (Millipore membrane filters, 0.2 µm) immediately before injection in the HPLC to remove cell and filter debris. Pigment extracts were analysed using a Shimadzu HPLC comprised of a solvent delivery module (IC-10ADVP) with system controller (SCL-10AVP) and a photodiode array (SPD-M10ADVP). The chromatographic separation of pigments was achieved using the method described in Zapata et al. (2000), which uses a monomeric OS C<sub>8</sub> column and a mobile phase constituted by two solutions: methanol:acetonitrile:aqueous pyridine and acetonitrile:acetone; a flow rate of 1 ml min<sup>-1</sup> and a run duration of 40 min. Pigments were identified by comparison of

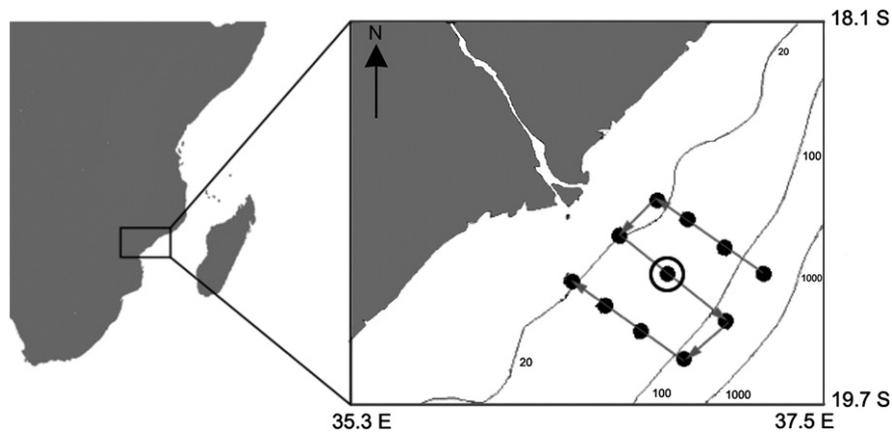


Fig. 1. Sampling stations location. Both transect (●) and fixed stations (○) are presented, and the arrows indicate sampling order.

retention times and absorption spectra with pure crystalline standards.

Biovolume, using sedimentation volumes with a conical jar and 24 h settling time, was measured to assess zooplankton abundance, estimated through planktonic organisms larger than 405  $\mu\text{m}$ . Large gelatinous organisms (e.g. jelly fish) were removed because their significant buoyancy makes the method less precise (Postel et al., 2000).

### 2.3. Statistical analysis

In order to test for cyclic phenomena in the variation of the different parameters and their co-variations, autocorrelations and linear cross-correlations were performed. Significant autocorrelations with a 2 h lag were analysed considering the 2-h sampling periodicity. Spearman correlation and Student's *t*-test were also applied. The study of phytoplankton community was done through the analysis of chemotaxonomic pigments and their ratios to Chl *a*. Furthermore, the  $F_p$  pigment index (Claustre, 1994) was calculated in order to identify the trophic status of this marine ecosystem. The  $F_p$  pigment index is given by:

$$F_p = \left( \sum \text{fucoxanthin} + \sum \text{peridinin} \right) \times \left( \sum \text{fucoxanthin} + \sum \text{peridinin} + \sum 19'\text{-hexanoyloxyfucoxanthin} + \sum 19'\text{-butanoyloxyfucoxanthin} + \sum \text{zeaxanthin} + \sum \text{chlorophyll } b + \sum \text{alloxanthin} \right)^{-1}$$

All the statistical analyses were carried out using R (R Development Core Team, 2008), while maps for display horizontal distributions were processed using Ocean Data View (Schlitzer, 2008).

## 3. Results

### 3.1. Horizontal distribution patterns

The horizontal variations of hydrological data evidenced the inshore–offshore gradients (Fig. 2A and B). Despite the complex pattern of temperature and salinity distribution, the lowest temperatures were found in the most inshore stations, and generally lower salinities were associated with higher temperatures. However, the water mass closer to the coast showed higher salinity and lower temperature than the central region. Examining the vertical sections of the northern and southern transects (Fig. 3),

a central less saline water mass with higher temperature was observed only at the surface layers, until 20 m depth. The halocline of this structure was noticeable and the vertical temperature profile was stratified along the water column.

Concerning nutrients concentration, P was higher in the northern transect and Si concentration was higher near the coast (Fig. 2C and D), while N was always under method detection limit ( $<0.005 \mu\text{mol l}^{-1}$ ). Shelf vertical cross-sections of P concentration presented no vertical trend, while for S higher concentrations were observed on surface inshore water mass (data not shown). Phytoplankton pigments presented very low concentrations in almost every transect stations, with a distribution pattern similar to fluorescence data, where the southern and closest stations to the coast presented higher biomass signal, with a lowering gradient perpendicular to coast (Fig. 2E), and no different pigment composition at the central region. Vertical sections of the outermost transects displayed different phytoplankton distributions given by fluorescence signal (Fig. 3), with higher biomass on surface water mass nearer to coast on the southern transect, while in the northern transect higher values were obtained near the bottom, where a discontinuity occurs. Zeaxanthin concentration was the only pigment with a different spatial distribution, since higher concentrations were observed in the most northern and offshore stations (Fig. 2F).

Zooplankton total abundance ranged from 0.77 to 7.11  $\text{ml l}^{-1}$  and was generally higher in the northern transect ( $4.52 \pm 2.68 \text{ ml l}^{-1}$ ; average  $\pm$  SD) than in the southern ( $1.90 \pm 0.76 \text{ ml l}^{-1}$ ) or the middle one ( $2.82 \pm 1.66 \text{ ml l}^{-1}$ ), and at the most offshore stations total biovolume was always extremely low ( $0.99 \pm 0.28 \text{ ml l}^{-1}$ ). The majority of night sampled stations (northern transect) presented higher total zooplankton abundances than daylight sampled stations.

### 3.2. Vertical dynamics

Current direction and magnitude measurements were very similar throughout the water column, and the results observed were in accordance with tidal variation (Table 1). Current direction varied mainly between South and West, respectively, during flooding and ebbing tides, and speed was significantly higher during flood tides (*t* value =  $-4.7042$ ,  $p < 0.01$ ), with average current of 252 and 202  $\text{mm s}^{-1}$ , respectively, for flood and ebb tides. Minimum velocity values observed were coincident with predicted tides at Chinde (Fig. 4), near the Zambezi delta, thus showing no significant delay to the study area. Current direction was similar in all sampling depths throughout the 48-h sampling period, and the

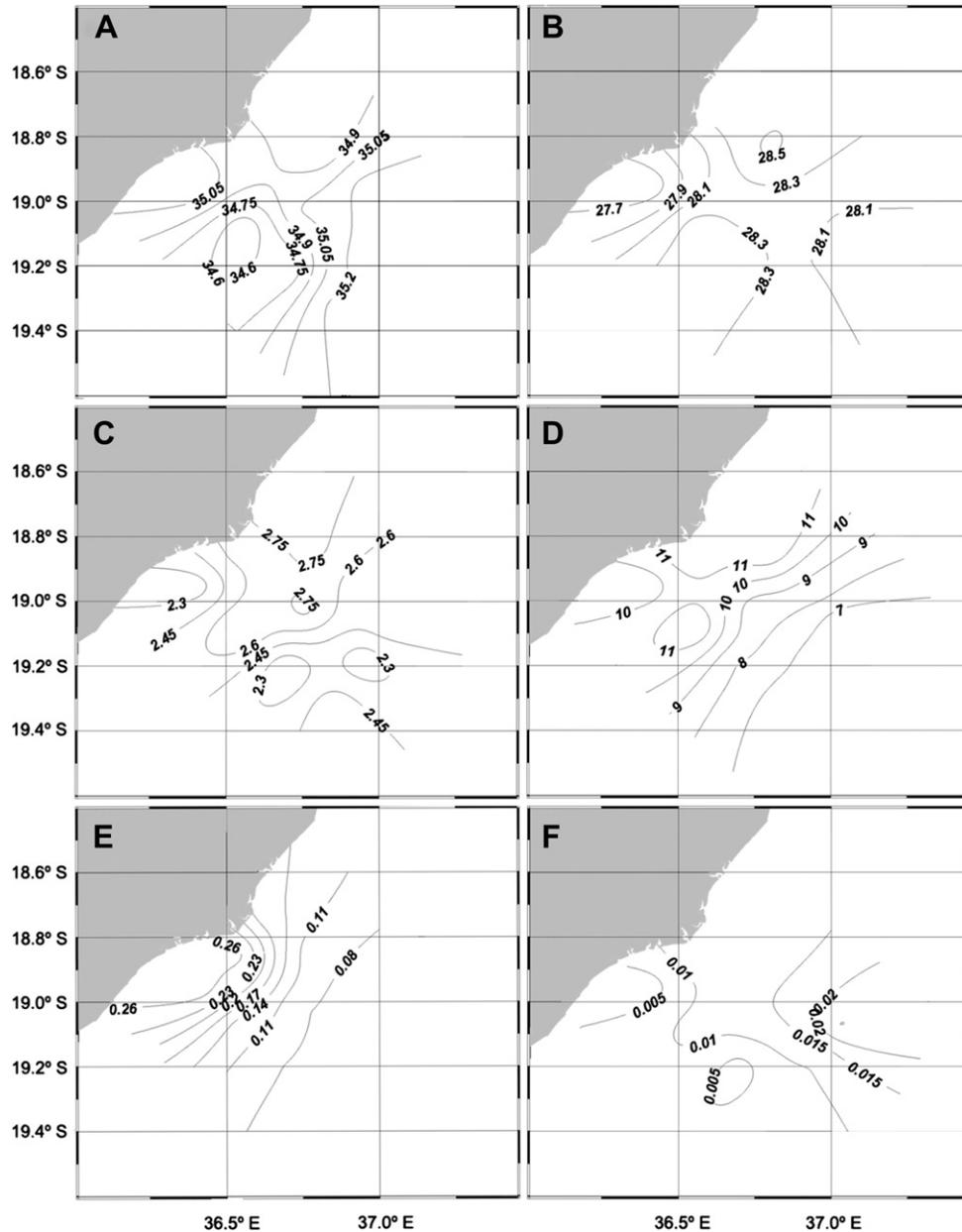


Fig. 2. Surface distribution of salinity (A), temperature (B, °C), phosphates (C,  $\mu\text{mol l}^{-1}$ ), silicates (D,  $\mu\text{mol l}^{-1}$ ), total chlorophyll *a* (E, fluorescence data), and zeaxanthin (F,  $\mu\text{g l}^{-1}$ ).

residual currents were generally over  $150 \text{ mm s}^{-1}$  from South. However, current speed presented vertical variation without apparent consistency, i.e., in some periods higher values were at the 16 m depth, while in others at 25 m. It should be noted that the ADCP only registered below the 16 m depth layer, thus results do not show the water mass behaviour above that depth. Water transparency varied mainly between 10 and 20 m depth, presenting no significant periodicity throughout sampling period.

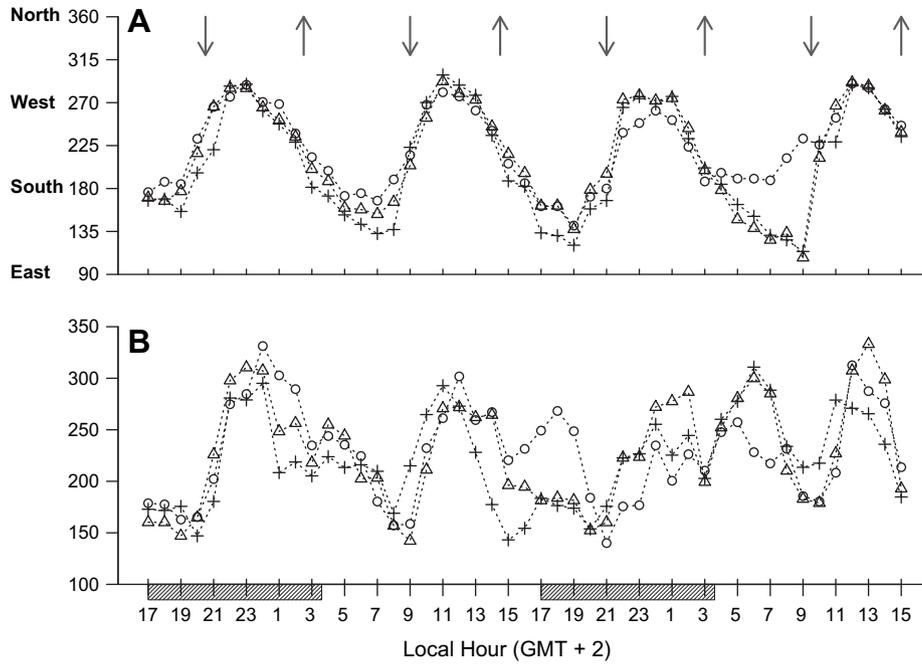
The water column was vertically stratified below the thermocline during the sampling period, as evidenced by temperature data (Fig. 5). Thermocline and halocline depths oscillated between 15 and 20 m for most of the 48-hour cycle, and both temperature and salinity followed the same trend with a 6-h opposed-phase periodicity (Table 1). During the low-tide period, less saline waters and higher temperatures down to greater depths in the water column were generally observed (Fig. 5). Throughout the last period of the 48-h cycle, the physical properties of the water column did not show the same

dynamics, specifically in the end of the second day where an intrusion of less saline waters was observed deeper (around 30 m).

Nutrient concentrations ranged from 0 to  $2.01 \mu\text{mol l}^{-1}$  for N, 1.65 to  $2.94 \mu\text{mol l}^{-1}$  for P, and 4.70 to  $15.70 \mu\text{mol l}^{-1}$  for Si (Fig. 6). N concentration was higher near the bottom during low tides, which is consistent with a significant 6-h opposed-phase periodicity and with the strong correlation found to current direction at the 40 m depth layer (Table 1). Though Si concentration only showed tidal periodicity at shallower depths, it was positively correlated to N and P at 40 m depth (Table 1). Nutrient ratios N:P and N:Si were calculated and ranged both from 0 to 0.90 and 0.15, respectively. These ratios were strongly determined by N concentration that was generally under the method detection limit.

Deep chlorophyll maximum (DCM) was close to the bottom (around 40 m depth) and fluorescence data from 30 and 40 m presented a 6-h opposed-phase periodicity variation (Table 1). HPLC analysis revealed a total of 13 pigments, generally presenting





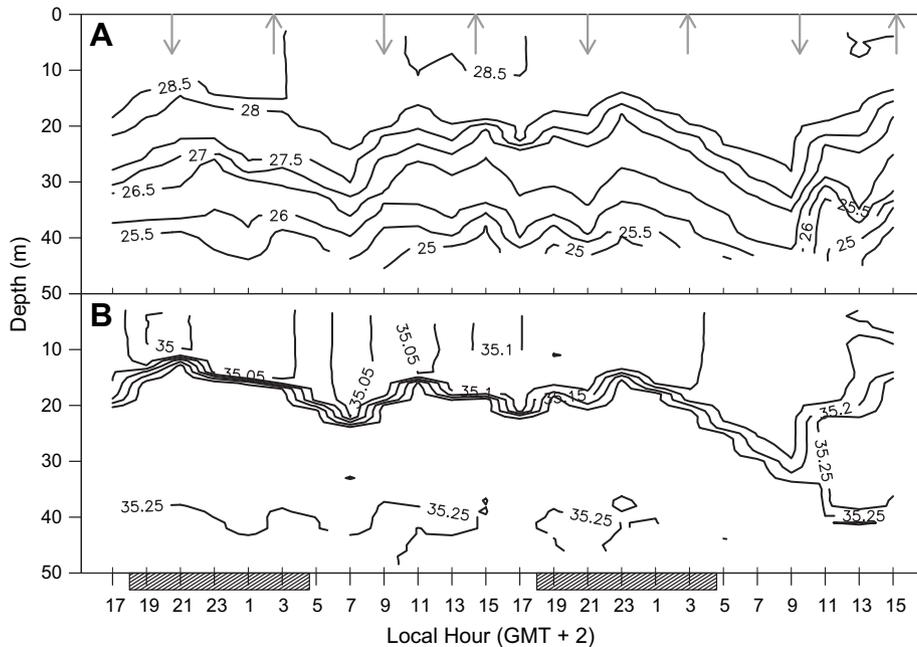
**Fig. 4.** Variation of 1-h average currents direction (A, degrees) and magnitude (B,  $\text{mm s}^{-1}$ ) at several depths ( $\circ$  - 16 m,  $\Delta$  - 25 m, and + - 34 m). Upward and downward arrows indicate predicted high and low tides, respectively; shaded rectangles indicate night periods.

**4. Discussion**

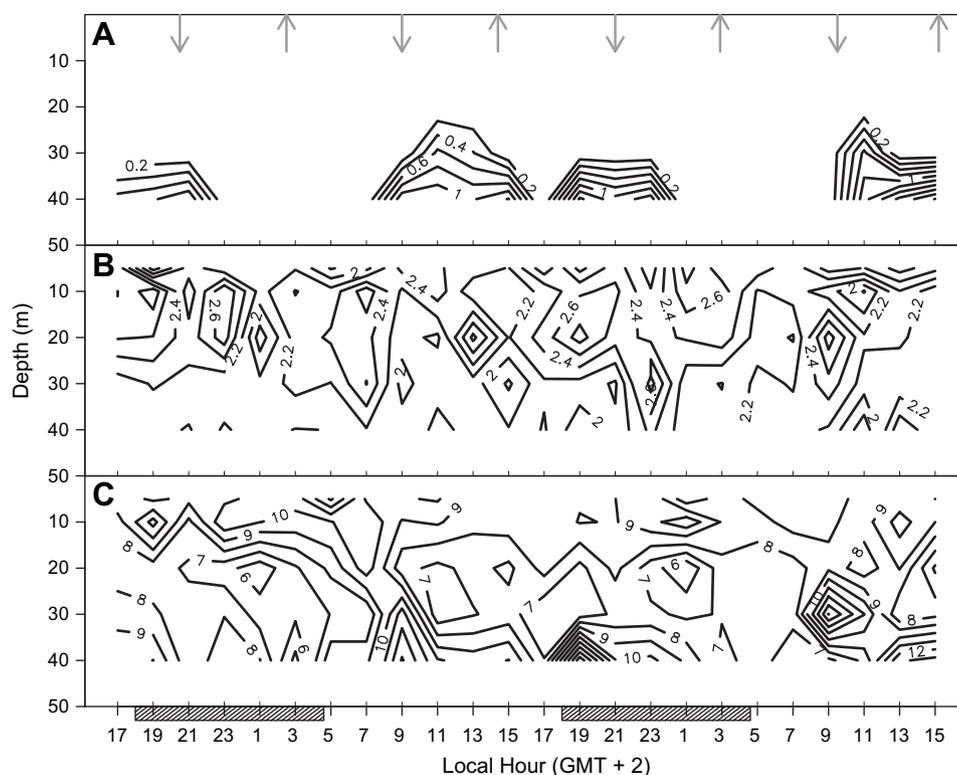
*4.1. Hydrology and nutrients*

The Sofala Bank is a Mozambican wide shelf region with strong tidal currents and great hydrological variability, which is largely determined by the Zambezi delta discharge as well as mesoscale oceanographic features of the Mozambique Channel (Ridderinkhof et al., 2001; Lutjeharms, 2006). Surface distribution of hydrological

parameters, combined with tidal movements during the 48-h period, showed the complexity of this shelf region, and the inshore-offshore gradient revealed the influence of both the Zambezi delta runoff and heterogeneity of oceanographic currents on the mid-continental shelf waters. During the sampling period, the estuarine water intrusion was not significantly affecting this shelf region, since salinity here obtained near the coast was around 35, which is considerably higher than salinity values around 20, as described by Lutjeharms (2006) for the Sofala Bank region during



**Fig. 5.** Temperature (A,  $^{\circ}\text{C}$ ) and salinity (B) variation during 48-h cycle. Upward and downward arrows indicate predicted high and low tides, respectively; shaded rectangles indicate night periods.



**Fig. 6.** Nutrient concentrations ( $\mu\text{mol l}^{-1}$ ) during the 48-h cycle (A – N; B – P; and C – Si). Upward and downward arrows indicate predicted high and low tides, respectively; shaded rectangles indicate night periods.

the wet season. The period from January to March is when higher rainfalls are observed and greater effects of estuarine discharges influence this shelf region, thereby increasing nutrients inputs and decreasing light penetration due to the turbid estuarine plumes dispersal. This study was carried out in December, at the end of dry season in the area, before the beginning of the rainy season. Accordingly, minor estuarine runoff effects were observed, explaining the high salinities and water transparency observed. A surface lens found in the middle part of each transect with different water properties from the inshore and offshore analysed coastal region was evidenced by vertical cross-sections perpendicular to the shore (Fig. 3). The existence of this water mass could be a marker of an earlier estuarine discharge event, because of the distinct lower salinity and its presence only at the surface (<20 m). However, evidence of this particular structure was not reflected in

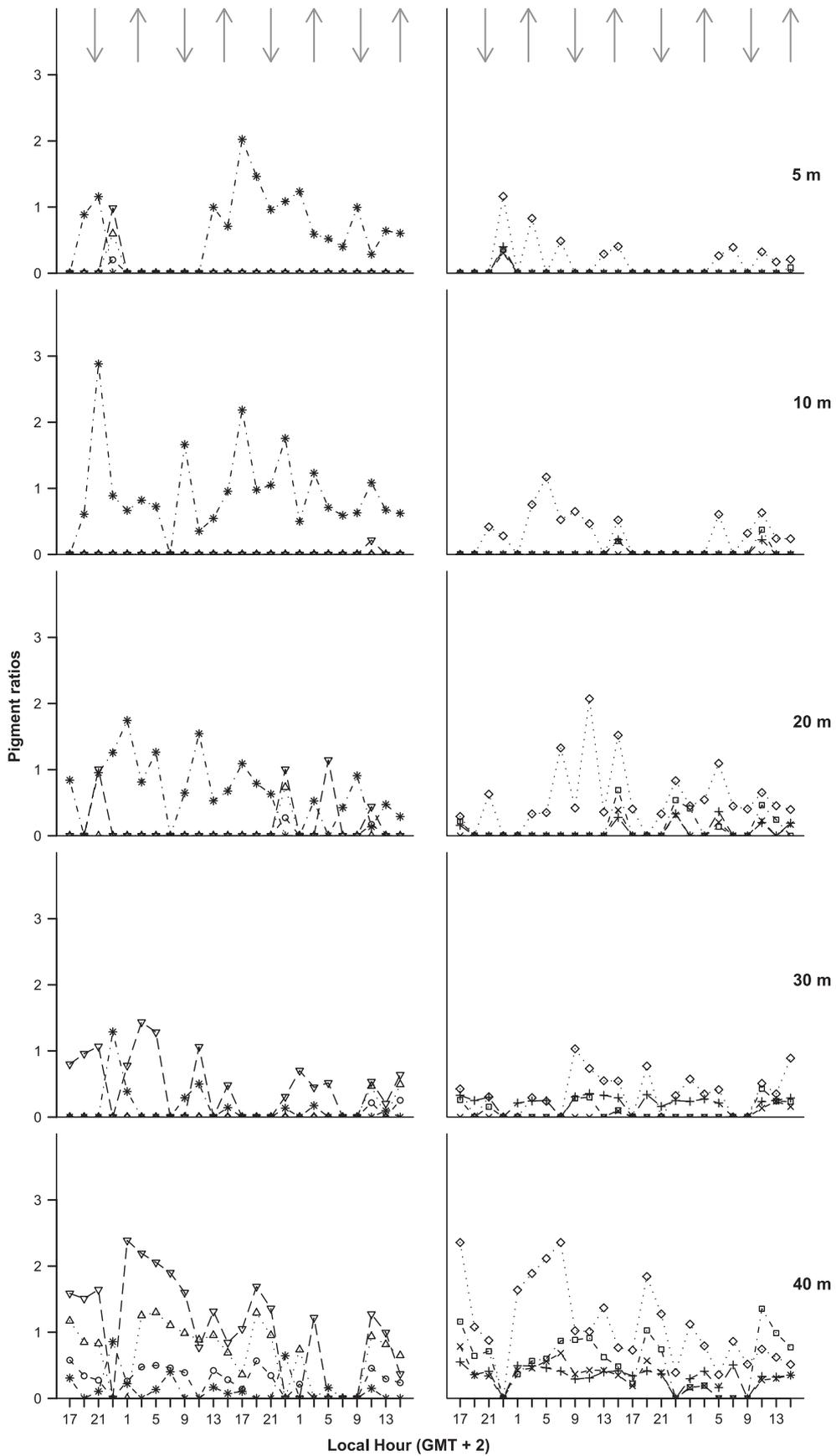
nutrient concentrations, and only Si concentrations evidenced a gradient perpendicular to shore.

Diel hydrological variations also showed a degree of river influence through lower salinity in the upper water column layers, modulated by tidal currents as well as other oceanographic currents. The lower salinity values observed until greater depths at the end of the sampling period (Fig. 5) could be explained by vertical mixing phenomena, since during that period the tidal currents were slightly different for the analysed depths, and the surface water mass seemed to be homogenised down to greater depths. Tidal currents also affected nutrient dynamics, observed by N and Si concentrations periodicity at certain depths. These trends were probably associated with sediment resuspension, and not to estuarine intrusion, as a source of nutrient loadings, since none of the nutrient periodicities were detected near the surface, where

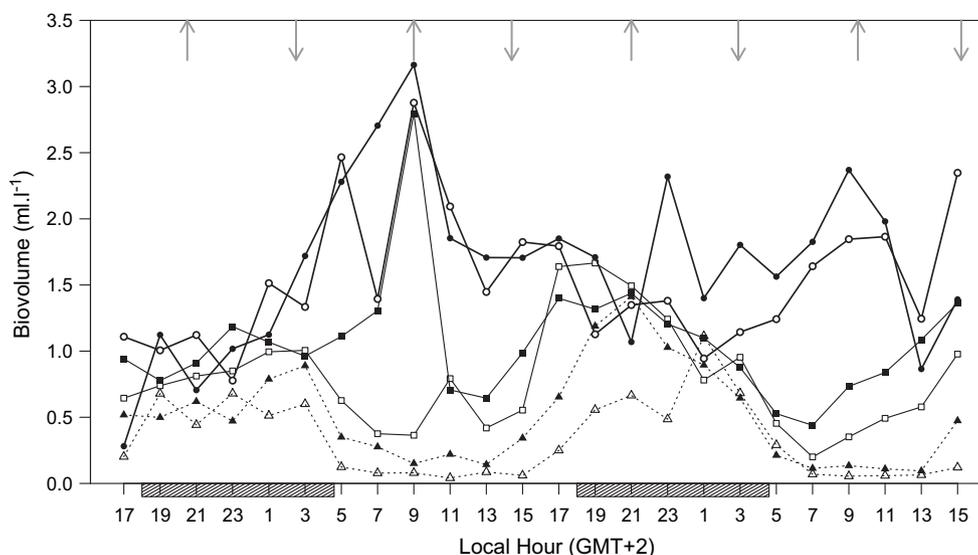
**Table 2**

HPLC pigment mean concentrations ( $\mu\text{g l}^{-1}$ ) at 40 m depth and their associated phytoplankton classes (Jeffrey et al., 1997).

Pigments	Concentration (min–max)	%	Occurrence
Chlorophyll <i>a</i>	0.080 (0.013–0.189)	41	A proxy of total algae biomass
Chlorophyll <i>c1, c2</i>	0.024 (0.000–0.071)	12.3	Diatoms, prymnesiophytes, crysophytes, and dinoflagellates
Chlorophyll <i>c3</i>	0.062 (0.000–0.145)	31.8	Crysophytes and prymnesiophytes
Chlorophyll <i>b</i>	0.029 (0.000–0.079)	14.9	Chlorophytes, euglenophytes, and prasinophytes
Total chlorophylls	0.195 (0.013–0.484)	100	
Fucoxanthin	0.054 (0.000–0.210)	27.1	Diatoms, prymnesiophytes, and crysophytes
Peridinin	0.003 (0.000–0.143)	1.5	Dinoflagellates
Diadinoxanthin	0.008 (0.000–0.021)	4.0	Diatoms, prymnesiophytes, crysophytes, and dinoflagellates
19'-Hexanoyloxyfucoxanthin	0.086 (0.000–0.154)	43.2	Prymnesiophytes
Alloxanthin	0.001 (0.000–0.002)	0.5	Cryptophytes
Prasinoloxanthin	0.012 (0.000–0.028)	6.0	Prasinophytes
Zeaxanthin	0.007 (0.000–0.023)	3.5	Cyanobacteria and chlorophytes
19'-Butanoyloxyfucoxanthin	0.028 (0.000–0.066)	14.1	Crysophytes and prymnesiophytes
Total carotenoids	0.199 (0.000–0.647)	100	
Phaeophorbide <i>a</i>	0.091 (0.000–0.197)		Zooplankton grazing



**Fig. 7.** Pigment ratios during the 48-h cycle (left graphic:  $\Delta$  - chlorophyll c3,  $\circ$  - chlorophyll c1 + c2, \* - zeaxanthin  $\nabla$  - pheophorbide a; right graphic:  $\diamond$  - 19'-hex-anoyloxyfucoxanthin, + - chlorophyll b,  $\times$  - 19'-butanoyloxyfucoxanthin, and  $\square$  - fucoxanthin). Upward and downward arrows indicate predicted high and low tides, respectively; shaded rectangles indicate night periods.



**Fig. 8.** Zooplankton abundance ( $\text{ml l}^{-1}$ ) at sampled strata ( $\Delta$  – neuston,  $\blacktriangle$  – 0–5 m,  $\circ$  – 5–10 m,  $\bullet$  – 10–20 m,  $\square$  – 20–30 m, and  $\blacksquare$  – 30–40 m) during the 48-h cycle. Upward and downward arrows indicate predicted high and low tides, respectively; shaded rectangles indicate night periods.

less dense estuarine waters were present. Nitrogen source is typically from river effluents (Verity et al., 1993; Wawrik et al., 2004), however, the N distribution here observed suggests vertical resuspension as its source ascribable to tidal energy, which could also explain the correlation amongst nutrients concentrations at 40 m depth.

Nutrient concentrations obtained were typically from oligotrophic waters (Kromkamp et al., 1997; Tyrrell, 1999; Giraud et al., 2008), and the extremely low concentrations of N in relation to P and Si should be carefully discussed. During the 48-h cycle, P concentration was on average  $2.253 \mu\text{mol l}^{-1}$ , which is high when compared to other coastal zones studies (e.g. Balkis, 2003; Wawrik et al., 2004; Sabetta et al., 2008) though comparable to other Western Indian Ocean studies (e.g. Paula et al., 1998; Lugomela et al., 2001). Regarding Si, average concentration was  $8.857 \mu\text{mol l}^{-1}$ , considerably higher than P or N, in accordance with other studies at the Western Indian Ocean (Paula et al., 1998; Barlow et al., 2007, 2008). The unusual N:P and N:Si ratios observed were strongly determined by the extremely low N concentrations. Several studies have also found such low ratios. Wawrik et al. (2004) studied the nutrient dynamic in the Mississippi River plume and obtained nutrient ratios of N:P  $\sim 2$  and N:Si  $\sim 0.2$  at non-plume stations, while Burford et al. (1995) obtained N:P ratios generally less than 4, ranging from 0.1 to 20, in the Gulf of Carpentaria (Australia). For the Western Indian Ocean, in particular, Kitheka et al. (1996), reporting results on nutrient dynamics at the Kenya coast, observed mean N:P ratios  $\sim 1$  during the flood tide. Mengesha et al. (1999) also observed very low N concentrations ranging from  $<0.1$  to  $0.41 \mu\text{mol l}^{-1}$ , even lower concentrations than observed in this study. These authors identified ammonia as the major inorganic nitrogenous nutrient, representing on average 72% of the total dissolved inorganic nitrogen concentrations. In the present study ammonia concentration was not measured, however, it is unlikely that if this component was taken into account the N:P ratio would change significantly. For N at oligotrophic waters, Lalli and Parsons (1997) indicated values of  $0.01$ – $0.1 \mu\text{M}$  as constants of semi-saturation. Therefore, as discussed by several authors (Burford et al., 1995; Tyrrell, 1999; Balkis, 2003; Wawrik et al., 2004; Howarth and Marino, 2006), the limiting role of N during this study seems to be clear, thus influencing phytoplankton abundance and composition.

#### 4.2. Phytoplankton

Sofala Bank is known as one of the most productive shelf regions of Mozambique (Lutjeharms, 2006; Barlow et al., 2008), however, the horizontal distribution of Chl *a* revealed very low phytoplankton biomass, apart from the nearer to coast area where the effects of river runoff nutrient loadings undergo first. Currents describe south-western directions throughout the tidal wave rotation, therefore, the estuarine plume was most likely moving southwards, and the major estuarine effluents were enhancing phytoplankton biomass at this southern nearer to coast area. This hypothesis is confirmed by vertical cross-section of the southern transect, where phytoplankton biomass was higher at the surface waters nearer to shore. On the other hand, the vertical profiles of northern stations display higher phytoplankton biomass near the bottom, where a discontinuity occurs. This bottom discontinuity probably promotes the resuspension of sediment ascribed to tidal direction and magnitude variation, supporting nutrients availability that enhanced phytoplankton biomass.

Apart from the distance to shore and the associated environmental gradients, phytoplankton communities' structure and abundance are also determined by hydrological vertical variations (Balkis, 2003; Barlow et al., 2007; Sabetta et al., 2008). During the 48-h cycle the majority of phytoplankton biomass was near the bottom, probably because of nutrient availability and high light penetration, as DCM was always below the pycnocline depth. Nutrient availability often determines primary production vertical patterns and phytoplankton communities' structure and abundance (Verity et al., 1993; Bouman et al., 2003). The higher planktonic concentrations observed near the 30 and 40 m layers are explained by the availability of N near the bottom and its role limiting phytoplankton biomass. As regards to light penetration, the exposure to high light radiation induces photodamaging and physiological stress in phytoplankton cells, even though some photoprotective pigments can be present (Brunet et al., 2008). Therefore, phytoplankton depth regulation will depend upon nutrients availability and light penetration, leading to a better exploration of the ecosystem resources by phytoplankton cells. Moreover, biological responses to environmental conditions seem to be simultaneously depending on the group and size of the phytoplankton species (Brunet and Lizon, 2003).

Microflagellated phytoplankton cells (e.g. prymnesiophytes) were the most abundant group observed at Sofala Bank, which is in agreement with Claustre (1994), Cortés et al. (2001), and Dandonneau et al. (2006), among others, who pointed out prochlorophytes and small flagellates to be most adapted to survive in impoverished oligotrophic environments. The pigment ratios  $> 1$  obtained indicate pigment concentrations higher than Chl *a*, which is in accordance to other phytoplankton communities from distinct oligotrophic environments (e.g. North Atlantic and Mediterranean Sea), where phytoplanktonic cells contain more accessory pigments than Chl *a* (Claustre, 1994). The trophic status here identified by nutrients composition is in accordance to the  $F_p$  pigment index calculated. The 0.16 mean pigment index obtained agrees with the results from the North Atlantic ( $0.06 \pm 0.01$ ) and Mediterranean ( $0.18 \pm 0.01$ ) oligotrophic regions (Claustre, 1994), where picoplankton and nanoplankton are dominant. Contrasting  $F_p$  pigment index results similar to 0.80 were obtained for meso- and eutrophic regions where microplankton (e.g. diatoms and dinoflagellates) is dominant (Claustre, 1994).

The majority of detected pigments displayed similar vertical movements in accordance with tidal variation and presented higher concentrations near the bottom. Despite that tidal energy was a key factor determining water mass physico-chemical properties variation, the majority of phytoplankton groups temporal variation revealed strong correlations to N, and diatoms also to Si. Low diatoms abundance was probably related to the high temperatures registered, which limits their growth (Verity et al., 1993; Bouman et al., 2003; Barlow et al., 2008), while peridinin-containing dinoflagellates were probably limited by these oligotrophic waters.

Zeaxanthin presence is normally associated with Chlorophytes and Cyanobacteria, however, since in this study there were no correlations between zeaxanthin and chlorophyll *b* (marker pigment of Chlorophytes), and divinyl chlorophyll *a* was below detection limits, which is also in accordance with Barlow et al. (2008) for inshore stations at Delagoa Bight (Mozambique), zeaxanthin here detected was attributed to Cyanobacteria, also assumed in other Western Indian Ocean studies (e.g. Barlow et al., 2007, 2008). Thereby, zeaxanthin horizontal distribution here observed is in accordance to the preference for offshore waters also detected in other Cyanobacteria studies (Hajdu et al., 2007; Barlow et al., 2008). Concerning vertical dynamics, Cyanobacteria were the only analysed group that seemed to have its maximum abundance at surface layers above thermocline depth, where turbulence phenomena are less intense, which is in accordance with other studies describing shallower distribution patterns of Cyanobacteria, specifically the ubiquitous *Synechococcus* sp. throughout world oceans (Glover et al., 1988; Goericke et al., 2000; Brunet et al., 2008). Cyanobacteria variation periodicity at 20 m depth was probably related to the water mass cyclical movements, as seen by salinity and temperature variations at the same depth.

The determination of the vertical distribution and the migration patterns of Cyanobacteria and other phytoplankton groups are easily biased by sampling errors due to horizontal advection of the water mass, disruption of vertical structures by wind and patchiness, which, together with the accumulation of phytoplankton groups in relatively thin layers, makes it difficult to resolve the real vertical distribution (Hajdu et al., 2007). Some pigments registered different and amply distributions along the 48-h cycle. Their presence at surface layers, specifically those detected at 5 m depth, could be related to horizontal transport from water mass nearer shore and not to phytoplankton vertical movements. The advection of water mass occurs during the low tides when water movements are transversal, i.e., inshore–offshore, contributing to the exportation of biomass from the coast. Therefore, less-saline surface waters

transport allochthonous biomass from coastal waters where the Chl *a* concentration is higher, suggesting an enhancement of the system productivity ascribable to tidal energy (Brunet and Lizon, 2003).

#### 4.3. Zooplankton

Zooplankton biovolume measurements gave rough estimations of zooplankton abundance with no detailed information concerning zooplankton groups, however, they showed the trend of the community as a whole. Zooplankton horizontal distribution was greater at the northern stations, where estuarine influence and phytoplankton biomass were concomitantly lower, as it probably suffered high grazing pressure. However, transect stations where zooplankton abundance was higher were sampled during night, therefore giving a biased view of zooplankton distribution.

During the 48-h sampling, zooplankton abundance was higher at the upper strata during night and at deeper strata during day. These results are in accordance with the typical diel vertical migration (DVM) behaviour where light variation plays a key role. However, the deeper affinity of zooplankton here verified could also be related to deeper DCM, since most of the zooplankton organisms are herbivorous. Zooplankton higher densities were often at layers deeper than 20 m, and there were no greater shallower abundances during the night, which might be related to energy acquisition and phytoplankton deeper affinity, and to the avoidance of unnecessary risks related to energy expenditure and predation threat (Zaret and Suffern, 1976; Lampert, 1989). The absence of significant correlations of zooplankton to any hydrobiological parameter could be explained by different feeding activity periodicities, linked to the different species diversity and/or developmental stages (Daro, 1985). Pheophorbide *a* has been considered a proxy of zooplankton grazing (Barlow et al., 1993; Brotas and Plante-Cuny, 1998), and its concentration at shallower levels here observed during night periods could be associated with zooplankton DVM. Pheophorbide *a* higher concentration at 40 m depth could also be related to grazing as well to sediment resuspension and phytoplankton degradation products, thus it was not possible to determine their source and the real impact of zooplankton on phytoplankton community structure and abundance.

#### 5. Conclusion

Low phytoplankton biomass and nutrient concentrations here obtained are in accordance with typical oligotrophic regions, yet a productive shelf region such as the Sofala Bank should have rich nutrient loadings and high phytoplankton biomass to support the strong fisheries levels that characterize the area. These unexpected strong oligotrophic features were probably related to low precipitation levels prior to and during the sampling period, therefore conditioned by low estuarine discharges and associated low nutrient inputs. Even though nutrients flux from the Zambezi delta may be significantly subsequent to rain, concentrations in coastal waters could also remain low due to mixing of different water masses from the estuarine effluents and shelf waters (Verity et al., 1993).

Nutrient dynamics observed here was strongly determined by low N concentration. Even though data collected and incomplete existent knowledge about Sofala Bank are clearly insufficient to a full comprehension of the abnormal nutrient ratios obtained, it was possible to conclude that phytoplankton biomass was strongly limited by N availability, which together with tidal variations were important driving factors modulating this ecosystem vertical dynamics. Phytoplankton abundance and community structure, given by chemotaxonomic pigments, was dominated by

prymnesiophyceans and other microflagellates, and vertical distribution changes on pigments concentration were quite probably associated with water mass advection, which is an important process to enhance offshore system productivity. Despite the horizontal hydrological processes influencing phytoplankton, the highest pigment concentrations were observed near the bottom layers (30 and 40 m) and not at the surface layers. This phytoplankton deeper affinity was quite probably influencing zooplankton vertical movements, since most of the zooplankton organisms are herbivorous and no greater shallow abundances during night were observed. However, it still remains to be answered why some zooplankton organisms were migrating if their food was on the bottom layers.

Few worldwide coastal studies are aimed to vertical dynamics of planktonic communities, from hydrological processes and nutrients that modulate production processes to phyto- and zooplankton. The present study contributes therefore to vertical dynamics knowledge on planktonic ecosystems, specifically for tropical ecosystems where these processes are still poorly understood. However, to achieve a better understanding, further studies should aim to seasonal variations. Special attention should be given to nutrient dynamics in tropical ecosystems, in order to understand the biogeochemical cycles occurring at tropical coastal regions.

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