JOURNAL OF PLANKTON RESEARCH | VOLUME 23 | NUMBER 10 | PAGES 1121–1136 | 2001

Plankton composition and cycling of carbon during the rainy season in a tropical coastal ecosystem, Zanzibar, Tanzania

CHARLES LUGOMELA, PETRA WALLBERG[1,3] AND TORKEL GISSEL NIELSEN[2]

INSTITUTE OF MARINE SCIENCES, UNIVERSITY OF DAR ES SALAAM, PO BOX 668, ZANZIBAR, TANZANIA, [1]INSTITUTE OF APPLIED ENVIRONMENTAL RESEARCH, STOCKHOLM UNIVERSITY, SE-106 91 STOCKHOLM, SWEDEN AND [2]DEPARTMENT OF MARINE ECOLOGY, NATIONAL ENVIRONMENTAL RESEARCH INSTITUTE, FREDERIKSBORGVEJ 399, DK-4000 ROSKILDE, DENMARK

[3]TO WHOM CORRESPONDENCE SHOULD BE ADDRESSED AT: SWEDISH RADIATION PROTECTION AGENCY, SE-171 16 STOCKHOLM, SWEDEN

Biomass, species composition and production of the planktonic community were investigated during the rainy season in May and June 1999 outside Zanzibar Island, Tanzania. In general, the plankton biomass of different organisms was uniform between depths as well as over time. The integrated water column primary production ranged from 204 to 4142 mg C m^{-2} day^{-1}. Bacterial production varied between 10 and 72 mg C m^{-2} day^{-1}, comprising ~5% of the total bacterial standing stock. The data obtained from these experiments are summarized in a carbon budget. At the most 77% of the total primary production channelled through the heterotrophic flagellates, ciliates and heterotrophic dinoflagellates to higher trophic levels. Of the estimated carbon demand for mesozooplankton, 28% could potentially be met by ciliates and heterotrophic dinoflagellates.

INTRODUCTION

Our knowledge about plankton ecosystems in temperate waters and the role of the microbial food webs has improved considerably over the past decades [e.g. (Sorokin, 1977; Azam *et al.*, 1983)]. In the western Indian Ocean and in tropical ecosystems in general, however, few studies on plankton community structure have been conducted. Along the coast of East Africa, most studies on the plankton community have focused on the taxonomy and biomass determinations of phyto- and zooplankton (Wickstead, 1963; Okera, 1974; Bryceson, 1977; Kitheka *et al.*, 1996; Lugomela, 1996; Paula *et al.*, 1998), and nitrogen fixation by *Trichodesmium* spp. (Bryceson and Fay, 1981; Lyimo, 1995; Kromkamp *et al.*, 1997), and only a few investigations on the microbial food web are available (Goosen *et al.*, 1997; Wallberg *et al.*, 1999; Wallberg and Andersson, 2000).

The hydrography of the western Indian Ocean is strongly influenced by the monsoon trade winds. The northeast (NE) monsoon blows from December to April and is characterized by high temperatures (>30°C), low wind speeds and calm seas. During this period, the East Africa coastal current flows northwards. With the reversal of the wind direction during the south east (SE) monsoon, which persists from June to October, the East Africa coastal current still flows northwards, but with its speed greatly reduced. By contrast, the SE monsoon is cooler (~25°C) with higher wind speeds and rougher seas. Off the East African coast, several observations of elevated chlorophyll (Chl) *a* have been reported during the NE monsoon and during rainfall periods [e.g. (Bryceson, 1977; Kitheka *et al.*, 1996; Kromkamp *et al.*, 1997; Paula *et al.*, 1998)]. Bryceson associated the northern monsoon biomass elevation with a number of meteorological and hydrographic factors (Bryceson, 1977). These include relatively higher exposure to light due to a shallow thermocline, which stabilizes the water column and ensures that phytoplankton remain at optimal growth conditions. The slow East Africa coastal current increases the residence time of the water on the shelf and shallow environments, therefore acquiring neritic characteristics that have been shown to support higher production. Lowered wind speeds during the northern monsoon promote the development of *Trichodesmium* blooms in the area (Bryceson, 1977). The presence of *Trichodesmium* spp. may

© Oxford University Press 2001

also be another important factor leading to a higher Chl *a* concentration due to nitrogen fixation, and subsequent release to the water column of the fixed nitrogen (Glibert and Bronk, 1994). A higher Chl *a* concentration following rainfall has been attributed to increased inorganic nutrient supply as a result of terrestrial run-off (Kitheka *et al.*, 1996; Kromkamp *et al.*, 1997; Paula *et al.*, 1998).

Zanzibar (Unguja) Island is located ~40 miles off the coast of the mainland of Tanzania. The tropical climate has two rainy seasons occurring in March–May (long rainy season) and October–November (short rainy season), with an average annual precipitation of 1100–1500 mm. Tidal currents in this area are of semi-diurnal nature and the water level varies between –0.2 and 4.5 m.

Previous investigations of the plankton community structure off Zanzibar have focused on the microbial food web (Wallberg *et al.*, 1999; Wallberg and Andersson, 2000); here, we also include mesozooplankton and heterotrophic dinoflagellates. The aim of the present paper was to describe the structure of the planktonic food web and to quantify the carbon fluxes within the plankton community during the rainy season.

METHOD

Sampling site

The sampling station off Zanzibar town was visited on 12 occasions between 17 May and 12 June 1999. The maximum depth at the sampling station was 22 m. Water was collected between 10:00 and 12:00 h at five depths (0.5, 2, 5, 10 and 20 m) for measurements of chemical parameters, abundance of plankton organisms and bacterial production (Figure 1). Samples for the estimation of primary production were incubated at seven depths (0.5, 1, 2, 3, 5, 10 and 20 m).

Nutrient analysis

Unfiltered seawater samples (50 ml) were collected for estimation of total nitrogen and phosphorus concentrations.

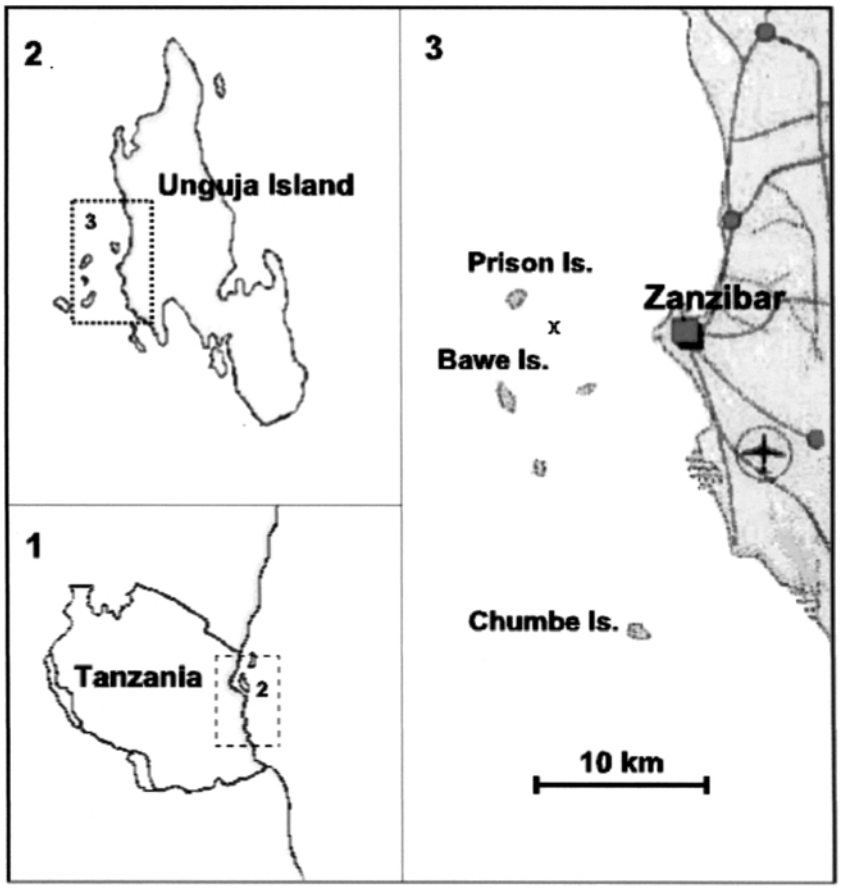


Fig. 1. Map of Tanzania and Zanzibar Island. The sampling station, situated outside Zanzibar town, is marked with ×.

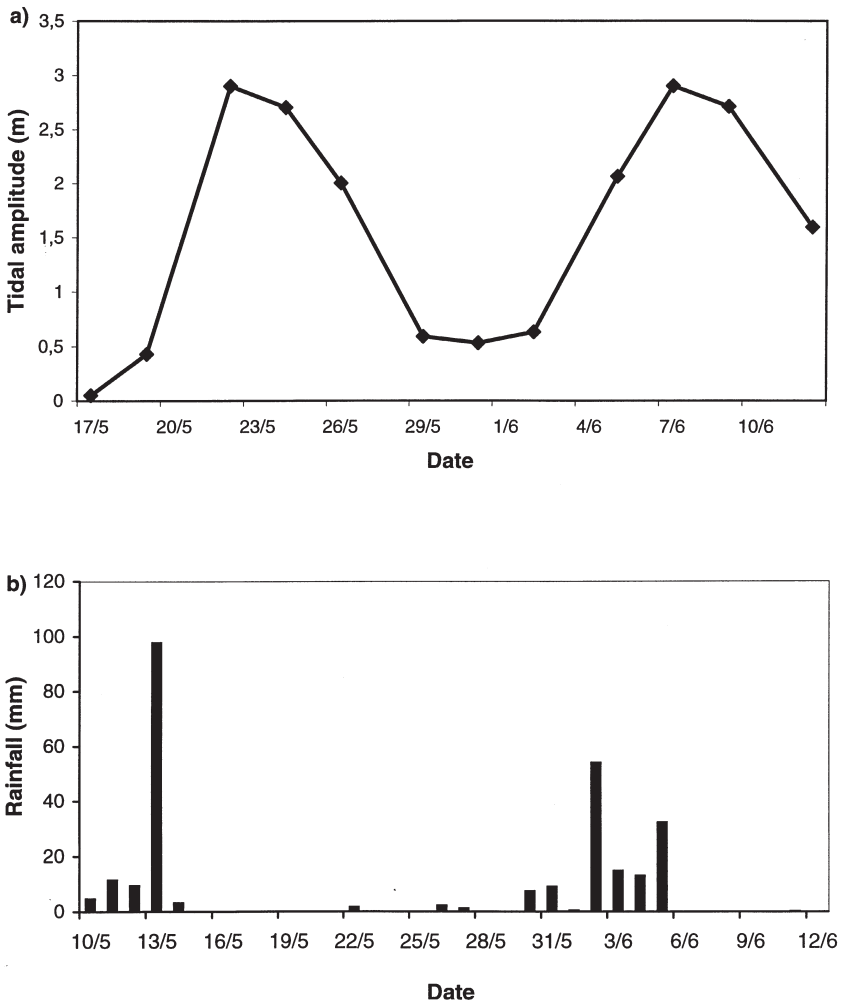


Fig. 2. (**a**) Tidal amplitude at the time of sampling and (**b**) daily rainfall 10 May–12 June 1999 in the Zanzibar area.

Samples were stored frozen until analysis using an auto-analyser (Lachat Quick Chem 8000).

Particulate organic carbon (POC) and particulate organic nitrogen (PON)

Triplicate samples (400 ml) were pooled from five depths and filtered onto a pre-combusted (450°C for 3 h) GF/F 25 mm glass fibre filter (Whatman). Filters were then dried at 40°C overnight and stored frozen until analysed with a Leco CHN 9000. The carbon content of non-filtered filters was subtracted from the filter samples.

Total organic carbon (TOC)

Triplicate samples (7 ml) were collected at 10 m depth and preserved with 100 µl of 1 M HCl. The samples were stored at 4°C until analysed with a Shimadzu TOC 5000. Estimates of the dissolved organic carbon (DOC) were obtained by subtracting the concentration of POC from the concentration of TOC.

Picoplankton

Sea water (20 ml) was preserved with formaldehyde to a final concentration of 2.5%. For enumeration and size measurement of picocyanobacteria, 10 ml of the preserved sample were filtered onto a 0.6 µm (25 mm) polycarbonate filter (Poretics). For enumeration of heterotrophic bacteria, 1 ml of the preserved sample was stained with DAPI (Porter and Feig, 1980) and filtered onto 0.2 µm (25 mm) black polycarbonate filters (Poretics). Samples were counted in an epifluorescence microscope

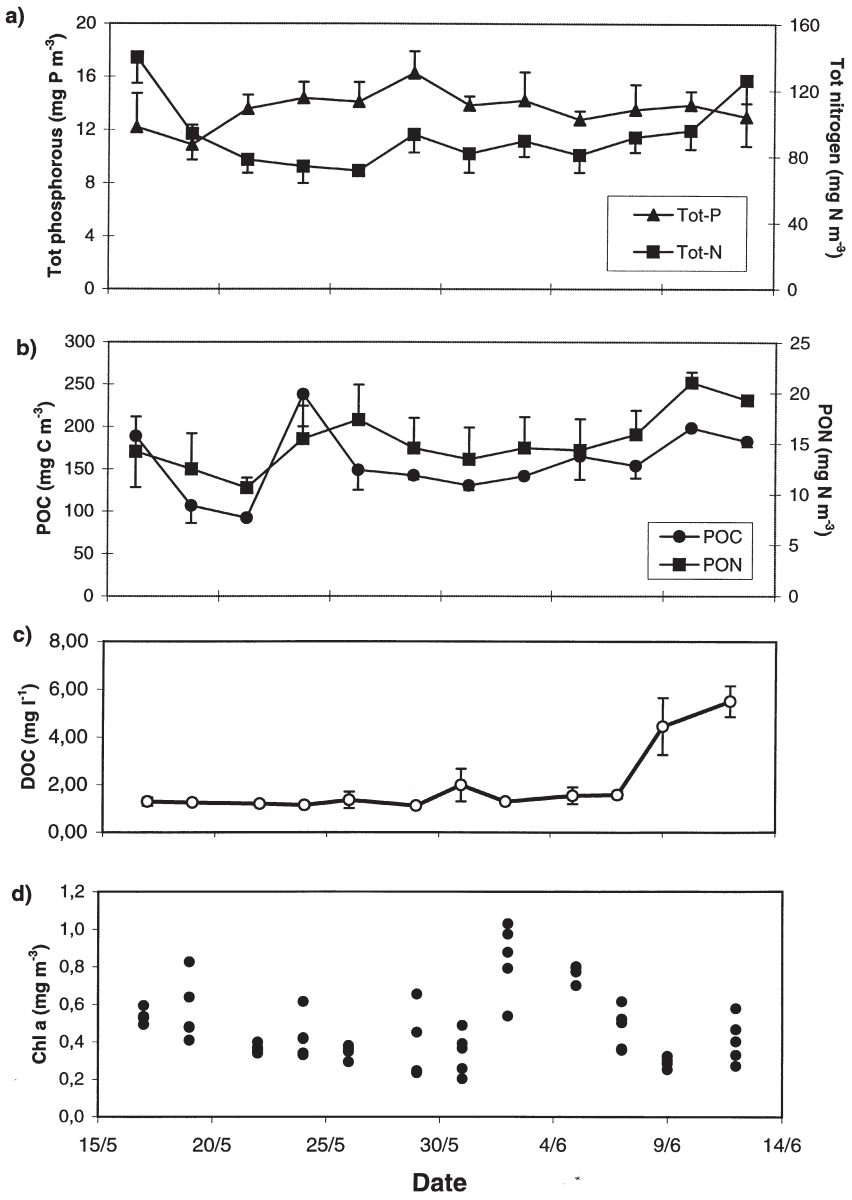


Fig. 3. Average concentration of (**a**) total nitrogen and phosphorus, (**b**) POC and PON, (**c**) DOC and (**d**) Chl *a* over the time course of the study. Total nitrogen and phosphorus are average values of samples collected from five depths. POC, PON and DOC are the average of triplicate seawater samples pooled from five depths.

at ×1200 magnification using UV excitation and a minimum of 300 cells per filter were counted.

Nanoplankton

For enumeration of nanoflagellates, live samples (10 ml) were stained with proflavin, fixed with ice-cold glutaraldehyde and filtered onto 0.8 μm (25 mm) black polycarbonate filters (Haas, 1982). Samples were enumerated in an epifluorescence microscope at ×600 magnification.

Microplankton

For enumeration of ciliates and heterotrophic dinoflagellates, samples of 1 l were preserved in 1% acid Lugol's solution. After 24 h, the fixed samples were concentrated on a 10-μm-mesh net and rinsed into 50 ml containers (Tiselius, 1989). After overnight sedimentation, half of the sedimentation chamber or at least 400 cells (not including the autotrophic *Mesodinium rubra*) were counted in an inverted microscope at ×250 magnification. Identification

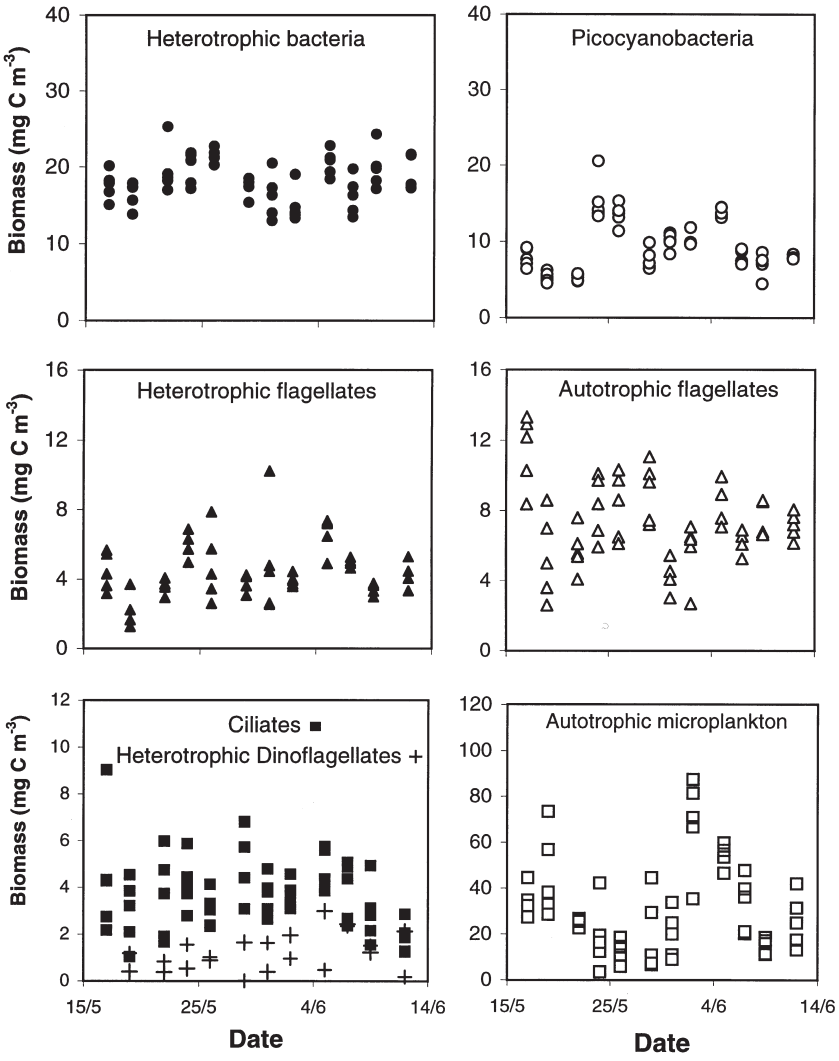


Fig. 4. Biomasses of heterotrophic bacteria, picocyanobacteria, heterotrophic and autotrophic flagellates, ciliates, heterotrophic dinoflagellates and autotrophic microplankton during the sampling period.

of the ciliates to family or genus was based on Montagnes and Lynn (Montagnes and Lynn, 1991) and Marshall (Marshall, 1969). The dinoflagellates were only enumerated in samples from 0.5 and 10 m depth. The dinoflagellates were identified to naked or thecate species according to Dodge (Dodge, 1985) and Thomsen (Thomsen, 1992), and divided into size ranges of 10 μm. Ingestion rate of ciliates was calculated assuming a net growth rate of 1 doubling day^{-1} (Wallberg *et al.*, 1999) and a carbon gross growth efficiency of 30% [e.g. (Fenchel and Finlay, 1983; Andersen and Sørensen, 1986; Wallberg and Andersson, 2000)]. The grazing and production of the heterotrophic dinoflagellates were estimated from general equations in Hansen *et al.* (Hansen *et al.*, 1997); their table 9, assuming maximum clearance rate and that only phytoplankton >10 μm and ciliates were available as food for the dinoflagellates. The grazing and production rates were converted to the *in situ* temperature by using a Q_{10} of 2.8 (Hansen *et al.*, 1997). Growth rates were estimated by assuming 33% efficiency (Hansen *et al.*, 1997). For abundance estimates of phytoplankton >10 μm in size, 100 ml of sea water were preserved with 1% acid Lugol's solution and concentrated in an Utermöhl sedimentation chamber (Utermöhl, 1931). After overnight sedimentation, two diagonals of the sedimentation chamber were counted in an inverted microscope at ×250 magnification.

Mesozooplankton

On each sampling occasion, replicate samples for mesozooplankton were taken by integrated net hauls from the

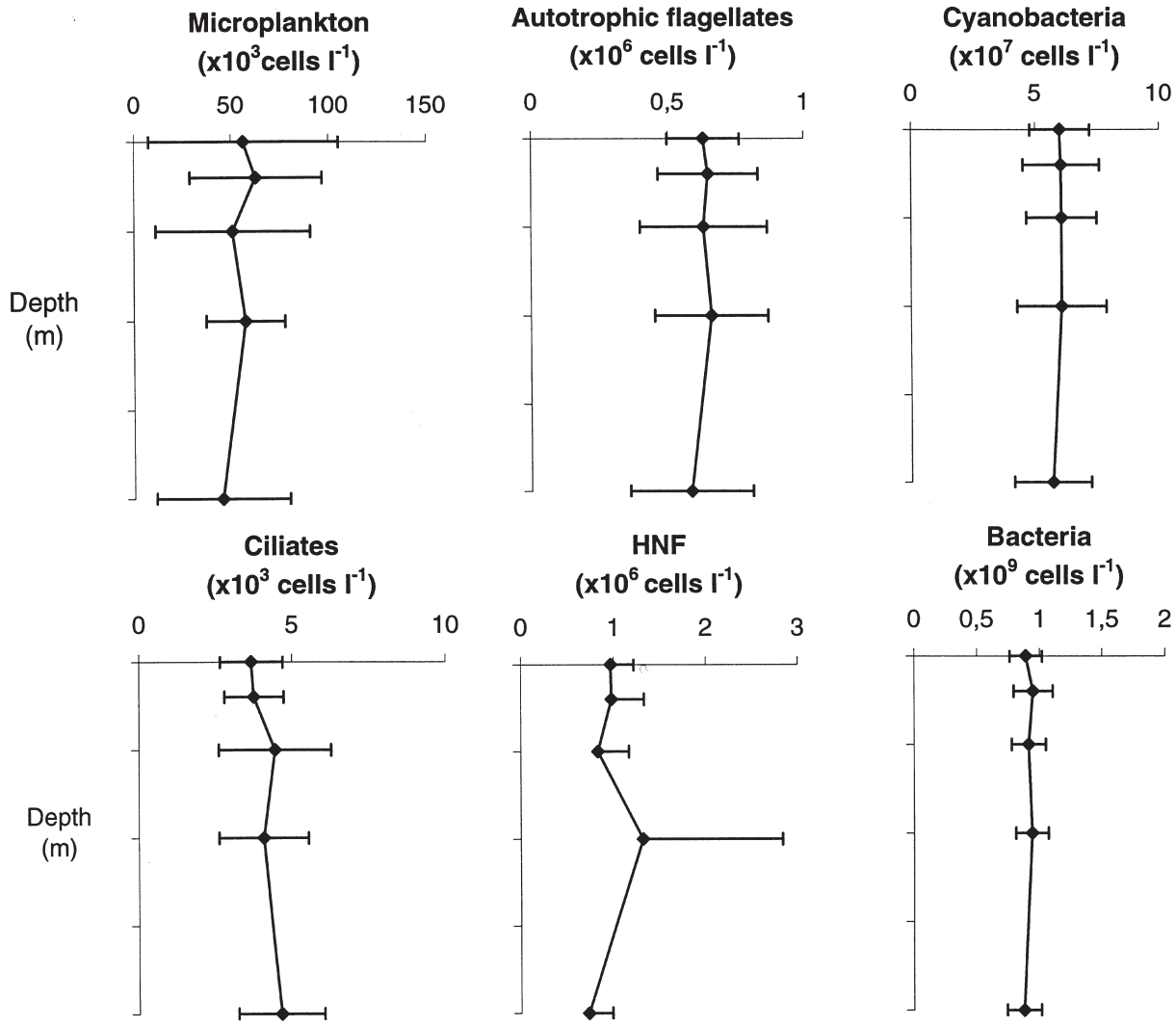


Fig. 5. Vertical profiles of the abundance of heterotrophic bacteria, picocyanobacteria, heterotrophic and autotrophic flagellates, ciliates and autotrophic microplankton during the sampling period. Error bars show the SD.

bottom of the water column to the surface (0–18 m), using a modified WP-2 net equipped with a 50-μm-mesh net. Immediately after arrival on deck, the cod-end sample was fixed in buffered formaldehyde (5% final concentration) for later microscopic analysis of the copepod biomass and community speciation. The formaldehyde-fixed samples were sorted and identified. The harpacticoids and cyclopoids were identified to genus. In the case of calanoids, 15% were identified to genus and the rest were measured for length and pooled as unidentified calanoid copepods. With the exception of nauplii and harpacticoid copepods, where total length was measured, each remaining group was enumerated and the cephalothorax length was measured. The size estimates were converted to carbon biomass using the length–weight regressions in Berggreen *et al.* (Berggreen *et al.*, 1988), Satapoomin (Satapoomin, 1999), Sabatini and Kiørboe (Sabatini and Kiørboe, 1994) and Hopcroft *et al.* (Hopcroft *et al.*, 1998). The production of the copepod community (*I*) was estimated assuming temperature-

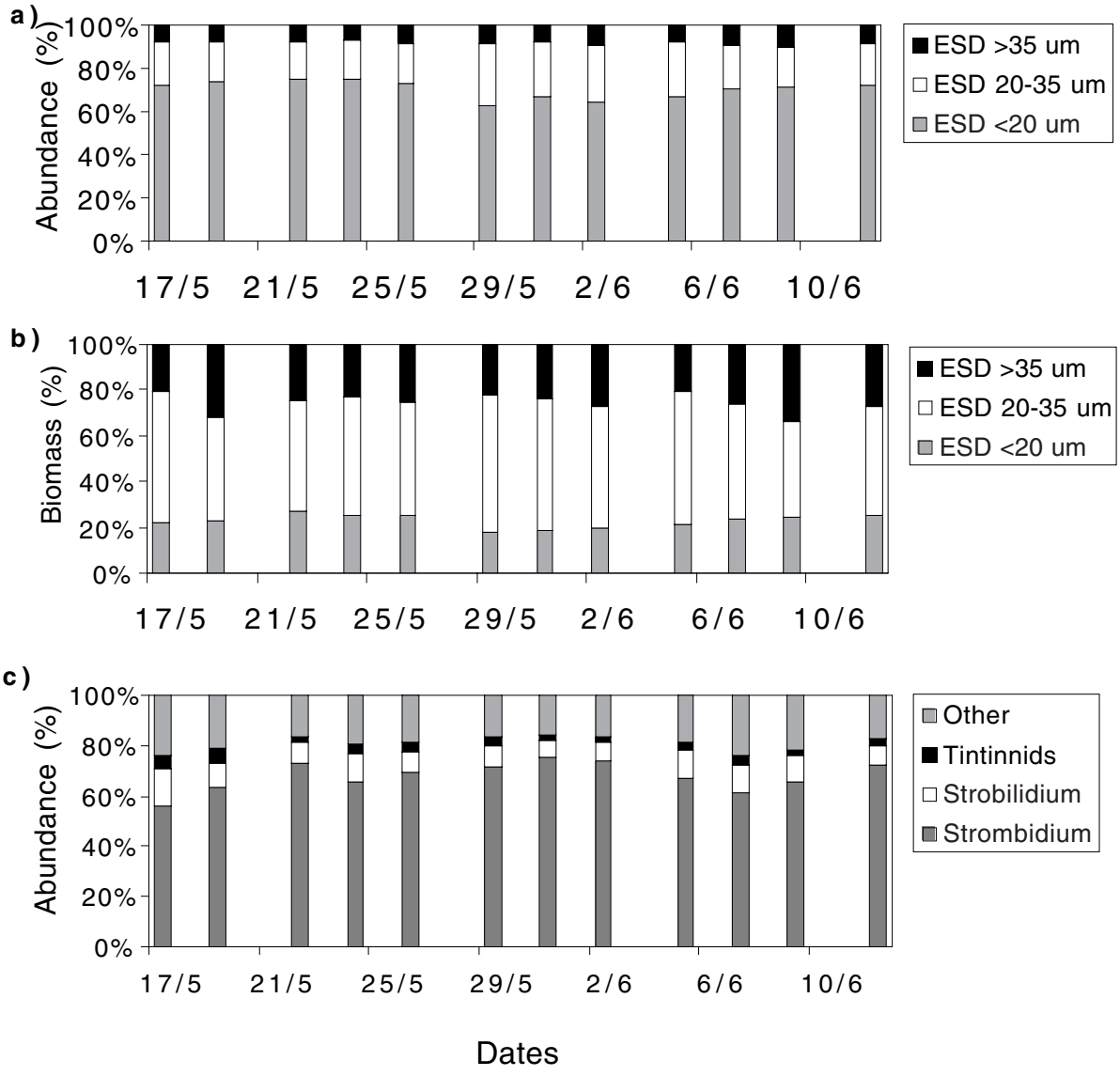


Fig. 6. Relative (**a**) ambundance, (**b**) biomasses of different size fractions of ciliates and (**c**) the composition of the ciliate community during the sampling period.

dependent production, following the equation $P = B \times 0.045e^{0.111T}$ (Huntley and Lopez, 1992), where P is production, B is the standing stock and T is the average temperature of the water column. Consumption was calculated from production, assuming a 33% growth efficiency: $I = 3 \times P$ (Peterson, 1988).

Chlorophyll *a*

Duplicate samples of 2 l of sea water were filtered onto 0.45 μm (47 mm) Millipore membrane filters and extracted in 90% acetone overnight at 4°C, and measured using a Shimadzu 1201 spectrophotometer according to Parsons *et al.* (Parsons *et al.*, 1984).

Biomass estimations

The sizes of cyanobacteria (≥15 cells per sample), flagellates (≥50 cells per sample) and ciliates were measured under the microscope using an ocular micrometer. The carbon content of pico- and nanoplankton was calculated according to Verity *et al.* (Verity *et al.*, 1992): $\log_{10} C = -0.363 + 0.863 (\log BV)$, where BV is biovolume in μm^3 $cell^{-1}$ and the carbon content (C) is given in pg C $cell^{-1}$.

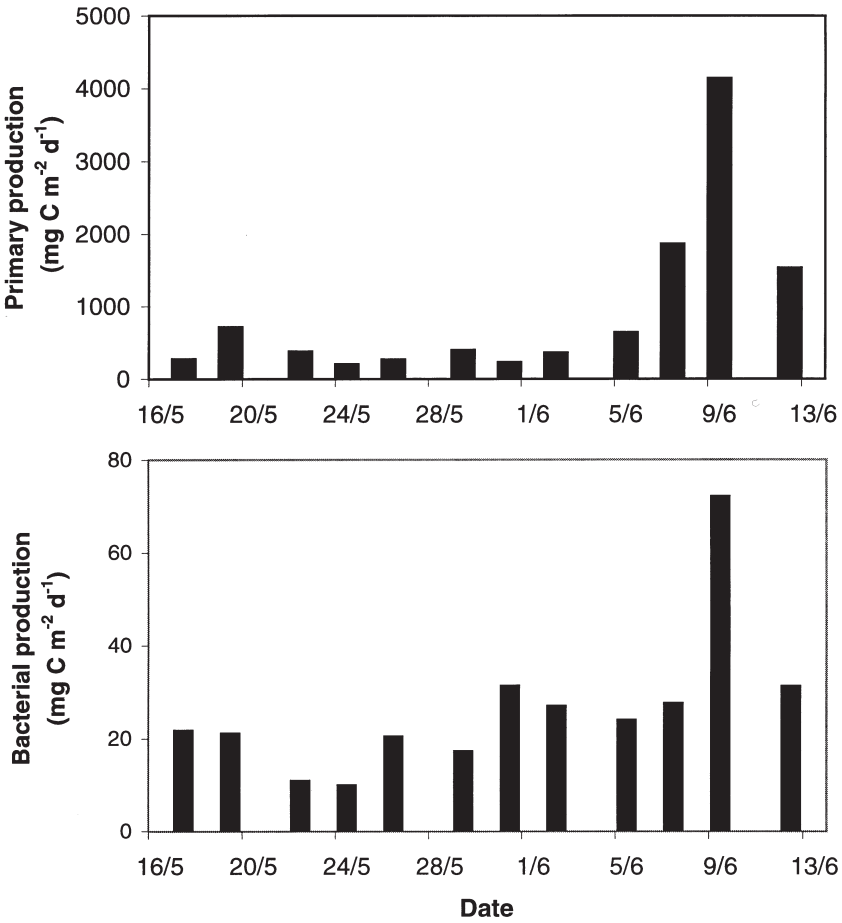


Fig. 7. Integrated water column bacterial and primary production during the sampling period.

The carbon content of bacteria and ciliates was calculated using a conversion factor of 20 fg C cell^{-1} (Lee and Fuhrman, 1987) and 0.19 pg C μm^{-3} (Putt and Stoecker, 1989), respectively. The carbon content of the heterotrophic dinoflagellates was calculated from the carbon to volume relationship established by Menden-Deuer and Lessard (Menden-Deuer and Lessard, 2000). Phytoplankton biomass was converted from Chl *a* using a conversion factor of 100 (Hewes *et al.*, 1990; Buck *et al.*, 1996; Verity *et al.*, 1996; Wallberg and Andersson, 2000), and the carbon biomass of phytoplankton >10 μm was calculated by subtracting the biomass of cyanobacteria and autotrophic flagellates.

Primary production

Sea water (30 ml) was poured into polycarbonate bottles (Nalgene) and 8 μCi of sodium [^{14}C]bicarbonate (52 mCi mmol^{-1}) were added to each bottle. Light and dark bottles were incubated from noon until sunset. After incubation, subsamples (5 ml) were poured into scintillation vials, acidified with 300 μl of 6 M HCl and purged for 40 min with air. Size-fractionated subsamples of 7 ml were filtered through 0.2, 2, 10 and 100 μm filters from the fourth day of the study. In addition, phytoplankton exudate was measured by collecting 5 ml of the 0.2 μm filtrate and thereafter treated as above. Filtrations were carried out in parallel in order to minimize breakage of cells, which is more likely to occur when water is passed through multiple filters. Scintillation fluid Optiphase Hisafe 3 (Wallac) was added to the samples, followed by counting on a Beckman LS1801 scintillation counter using a quench-correcting program. The total dissolved inorganic carbon concentration in the water was calculated from pH and salinity measurements (Parsons *et al.*, 1984), and the net primary production was calculated assuming 5% isotope discrimination. The coefficient of variation between replicates was ≤10%. As post-fractionation

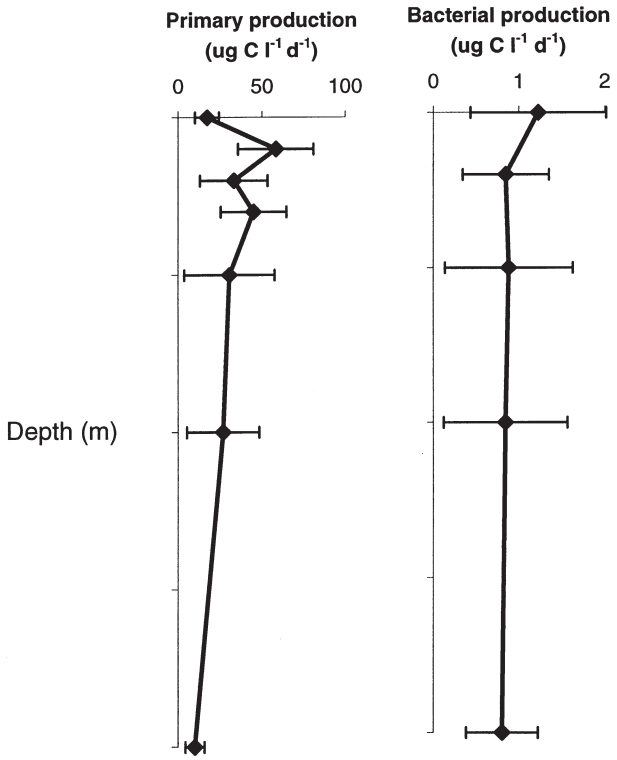


Fig. 8. Vertical profiles of bacterial and primary production measured during the sampling period. Error bars show the SD.

underestimates growth compared with unfiltered samples (Larsson and Hagström, 1982), the growth rates in size fractions were recalculated in proportion to unfiltered samples.

Bacterial production

Triplicate samples and blanks were incubated using the tritiated thymidine method as modified by Smith and Azam (Smith and Azam, 1992). Tritiated thymidine (83 Ci mmol^{-1}; Amersham) was added to a final concentration of 20 nM, which was at the level of saturation. A conversion factor of 1.3×10^{18} cells produced per mol thymidine incorporated was used (Wallberg *et al.*, 1999). Production, in terms of carbon biomass, was calculated using a conversion factor of 20 fg C cell^{-1} (Lee and Fuhrman, 1987). Bacterial production was assumed to be constant over a 24 h period and carbon gross growth efficiency to be 50% (Ducklow and Carlson, 1992).

RESULTS

Hydrography and nutrients

In 1999, the long rains started in March and continued up to June with monthly precipitation of 204, 316, 186 and 162 mm in March, April, May and June, respectively (Directorate of Meteorology, Zanzibar). The daily rainfall over the sampling period ranged from 0 to 54.1 mm day^{-1} (Figure 2). Higher rainfall was recorded 4 days before the start and towards the end of the sampling period. The temperature (27 ± 1°C) and the salinity (35) were homogeneous throughout the water column. The tidal amplitude varied between 0 and 3 m (Figure 2). On average, the concentration of total nitrogen was 93 ± 20 μg l^{-1} and total phosphorus was 14 ± 1 μg l^{-1} (Figure 3). The coefficient of variation between different depths was ≤20%, with the exception of the last day, when it was 32% for the concentration of total nitrogen. The concentration of DOC ranged between 1100 and 5500 μg C l^{-1} (average 2000 μg C l^{-1}), with the highest concentrations measured on the two last days of the sampling period. The concentration of POC and PON was 157 ± 40 and 15 ± 3 μg l^{-1}, respectively.

Plankton biomass

In general, the biomass of the plankton groups showed a low variation between depths as well as over time (Figures 4 and 5). The abundance of heterotrophic bacteria varied between 0.7 and 1.3×10^9 cells l^{-1}, and showed a weak correlation with the tidal amplitude (r^2 = 0.38, $P < 0.05$, Statistica 5.0; Figure 5). The variation in bacterial abundance between different depths on the same sampling occasion was <20%. The abundance of heterotrophic nanoflagellates (HNF) varied between 0.2 and 1.6 $\times 10^6$ cells l^{-1}, except on 31 May, when it was 6×10^6 cells l^{-1} at 10 m depth. The higher abundance of HNF coincided with higher heterotrophic bacterial abundance and an increase in bacterial production by a factor of 2–4 compared with the abundance and production at the 5 and 20 m depths.

The abundance of ciliates varied between 1.4 and 8.8 $\times 10^3$ (average 4.1×10^3) cells l^{-1} (Figure 5). The dominant group was Strombidiidae (*Laboea*, *Strombidium* and *Tontonia*) and the suborders Strobilidina and Tintinnina (Figure 6). Abundances of the tintinnids varied between 40 and 345 cells l^{-1}. Abundant tintinnid species included *Tintinnopsis* spp., *Climacocylis* sp., *Cordonellopsis ecaudata*, *Cordonellopsis contracta*, *Protorhabdonella curta*, *Dadayiella ganymedes*, *Epiplocyloides brandti*, *Amphorides minor*, *Amphorides quadrilineata*, *Amphorellopsis acuta*, *Eutintinnus* spp. and *Salpingella* spp. The smallest sized ciliates with an equivalent spherical diameter (ESD) of <20 μm dominated the

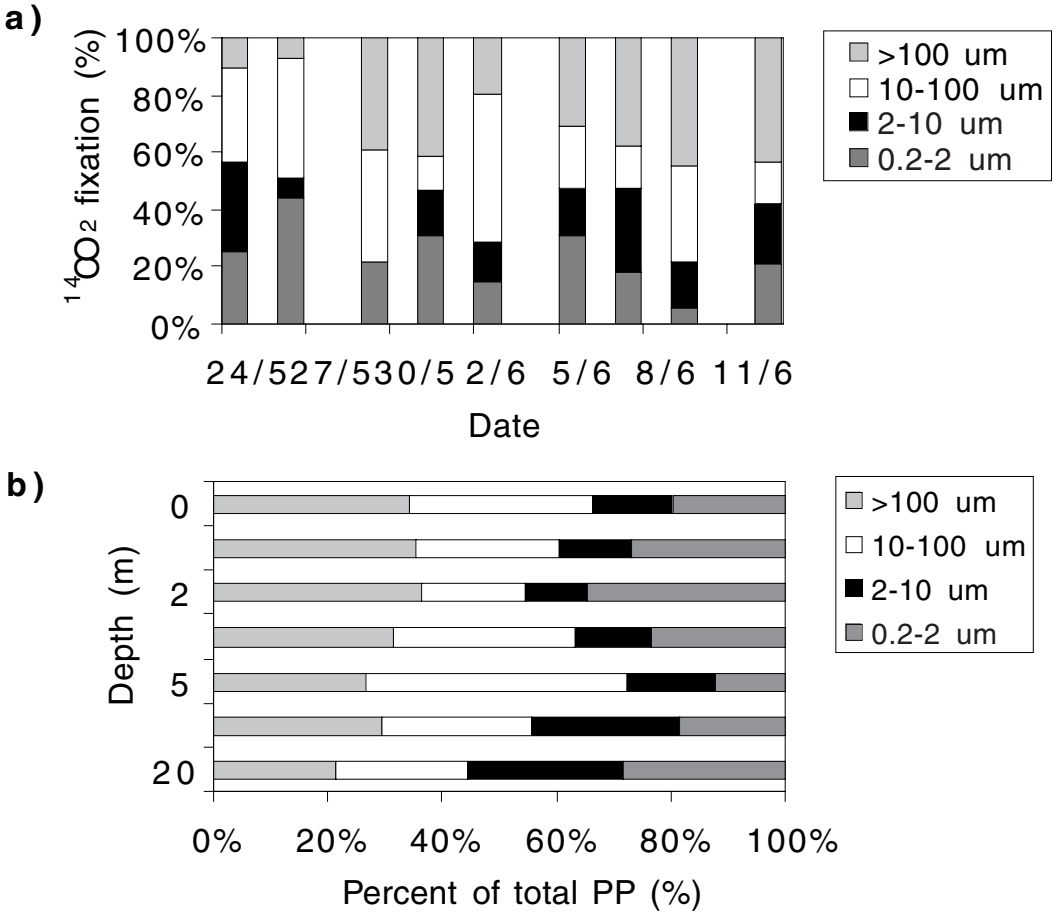


Fig. 9. Size-fractionated primary production (**a**) on each sampling occasion and (**b**) at each depth over the sampling period.

abundance and contributed 70% of the total ciliate community (Figure 6). However, in terms of biomass, ciliates with ESD between 20 and 35 μm contributed most, and accounted for 50% of the total biomass.

The abundance of heterotrophic dinoflagellates varied between 0.4 and 6.5 × 10^3 (average 2.5 × 10^3) cells l^{-1}. Naked gymnodinoid dinoflagellates (20–25 μm ESD) dominated the heterotrophic dinoflagellate community in terms of abundance and biomass. Of the heterotrophic dinoflagellates, *Gyrodinium spiral*e was the most abundant species. The average biomasses of the naked and thecate groups of dinoflagellates were 0.71 ± 0.1 and 0.53 ± 0.1 μg C l^{-1}, respectively. The average cell volume of the thecate group, the naked group and *Gyrodinium spirale* was 10 600 ± 1700, 1500 ± 500 and 7000 ± 600 μm^3, respectively.

Within the autotrophic plankton community, the abundance of picocyanobacteria varied between 3 and 11 × 10^7 cells l^{-1}, and the biomass accounted for half of that of heterotrophic bacteria (9.3 ± 3.4 and 18.3 ± 2.8 mg C m^{-3}, respectively; Figures 4 and 5). The abundance of autotrophic flagellates varied between 0.2 and 1.1 × 10^6 cells l^{-1}, and was on average lower than that of HNF (0.6 ± 0.2 × 10^6 and 0.9 ± 0.3 × 10^6 cells l^{-1}, respectively; Figure 5). However, due to a larger cell size, the biomass of autotrophic flagellates was on average 40% higher than that of HNF (7.3 ± 2.4 and 4.4 ± 1.6 mg C m^{-3}, respectively; Figure 4). Between depths, the microphytoplankton abundance varied on average between 4.6 and 6.3 × 10^4 cells l^{-1}. The highest abundance of microphytoplankton occurred at 2 m depth (Figure 5). Chlorophyll *a* concentrations ranged between 0.3 and 0.8 μg Chl *a* m^{-3} (Figure 3). The phytoplankton community was dominated by diatoms of the genus *Chaetoceros* spp., *Rhizosolenia* spp., *Bacteriastrum* spp., *Thalassiothrix* spp. *Leptocylindrus* spp. and *Pseudonitszchia* spp. Common autotrophic dinoflagellates were *Ceratium* spp., *Protoperidinium* spp. and *Prorocentrum* spp. The abundance of the filamentous cyanobacterium *Trichodesmium* spp. varied between 0 and 5180 filaments l^{-1} (average 150 filaments l^{-1}).

Bacterial and primary production

The integrated bacterial production ranged from 10 to 72 mg C m^{-2} day^{-1}, with the highest production measured on 9 June (Figure 7). On average, the bacterial carbon production amounted to 5 ± 4% of the bacterial carbon standing stock. Primary production was relatively low at the surface, possibly due to photoinhibition. It increased at 1–3 m depths, followed by a decrease with depth from 5 down to 20 m (Figure 8). Integrated primary production ranged from 204 to 4142 mg C m^{-2} day^{-1}, and the highest primary production coincided with the highest value for bacterial production (Figure 7). Integrated bacterial production amounted on average to 5 ± 4% of the integrated primary production. On average, the >100 and 10–100 μm phytoplankton size fractions contributed ~30% each to the total CO_2 fixation, while the 2.0–10 and 0.2–2.0 μm fractions contributed ~20% (Figure 9). However, the contribution of the >100 μm fraction tended to decrease with depth in favour of the <10 μm fractions. On average, the dissolved fraction contributed ~25% of the total primary production.

Mesozooplankton

The diversity of the copepod community was high. The calanoid copepods (*Acrocalanus gibber*, *Eucalanus* spp., *Temora stilifera*, *Temora turbida*, *Centrophages furcata*, *Acartia* spp.) dominated the copepod community. On average, the calanoid copepods contributed 75% of the biomass, followed by cyclopoid (*Oithona*, *Oncaea* and *Cryceaus*, 18%) and harpacticoid copepods (*Microsetella*, *Macrosetella* and *Euterpina*, 7%; Figure 10). Copepod nauplii contributed a significant fraction of the copepod biomass: 29.4 ± 2.9%. The only important non-copepod group was the appendicularians, who contributed 13 ± 2% of the mesozooplankton biomass. The biomass of mesozooplankton varied between 3 and 10 mg C m^{-3}. Since the temperature was constant throughout the investigation and copepod consumption is estimated from biomass, consumption mirrors biomass succession.

Carbon budget

To evaluate the importance of the different compartments in the pelagic food web, a carbon budget was established based on the average values for the whole investigation (Table I; Figure 11). At the most 77% of the total primary production, channelled through the HNF, ciliate and heterotrophic dinoflagellate communities. For the HNF, the amount of carbon available for consumption (i.e. the production of picocyanobacteria and heterotrophic bacteria) did not balance the estimated carbon demand. The production of picocyanobacteria and heterotrophic bacteria combined accounted for 43% of the estimated HNF carbon demand, of which 37% could potentially be met by picocyanobacteria. In contrast, the amount of carbon available for consumption by ciliates (i.e. the production of HNF and autotrophic flagellates) balanced the estimated carbon demand. The total carbon resource is, however, twice as high as the estimated carbon demand for mesozooplankton. Excluding the production of phytoplankton >100 μm as a potential prey balances the budget for mesozooplankton. Of the estimated carbon demand for mesozooplankton, 28% could potentially be met by ciliates and heterotrophic dinoflagellates.

DISCUSSION

In the near coastal areas, rainfall influences the nutrient input through drainage from land, which in turn influences the structure and productivity of the plankton community. Fertilizing of coastal plankton productivity by rainfall has previously been documented from the area (Wallberg *et al.*, 1999) and in adjacent areas off East Africa (Bryceson, 1977; Kitheka *et al.*, 1996; Kromkamp *et al.*, 1997; Paula *et al.*, 1998). Wallberg *et al.* showed that during the rainy season the turnover rate within the microbial loop increased rather than the biomass, illustrating tight couplings between different trophic compartments (Wallberg *et al.*, 1999). It is possible that the phytoplankton and bacterial activity was stimulated following a few days with rainfall, which may also explain the increase in the concentration of DOC at the end of the sampling period. In contrast, the concentrations of total nitrogen and phosphorus did not follow the same trend. However, the sampling site was located in an open area with mixed water due to a northward current and tides, which resulted in sampling of different water masses over time.

The estimated biomasses and fluxes of carbon in the plankton community are within the range previously reported in this area during the rainy season (Wallberg *et al.*, 1999; Wallberg and Andersson, 2000). Our estimates of the biomass of heterotrophic bacteria and HNF were, however, slightly higher than those reported by Goosen *et al.* (Goosen *et al.*, 1997), ranging between 0.8 and 5.9 × 10^5 cells ml^{-1} and 20 and 736 cells ml^{-1}, respectively, in the adjacent areas off the Kenyan coast. The Chl *a* concentration was within the range previously reported by Bryceson (Bryceson, 1977), ranging between 0.04 and 1.4 mg m^{-3}. The integrated primary production values are similar to those of Ryther *et al.*, who measured primary production around the Dar es Salaam area and reported values ranging between 0.26 and 0.5 g C m^{-2} day^{-1} (Ryther *et al.*, 1996). The composition of phytoplankton was similar to observations by Bryceson

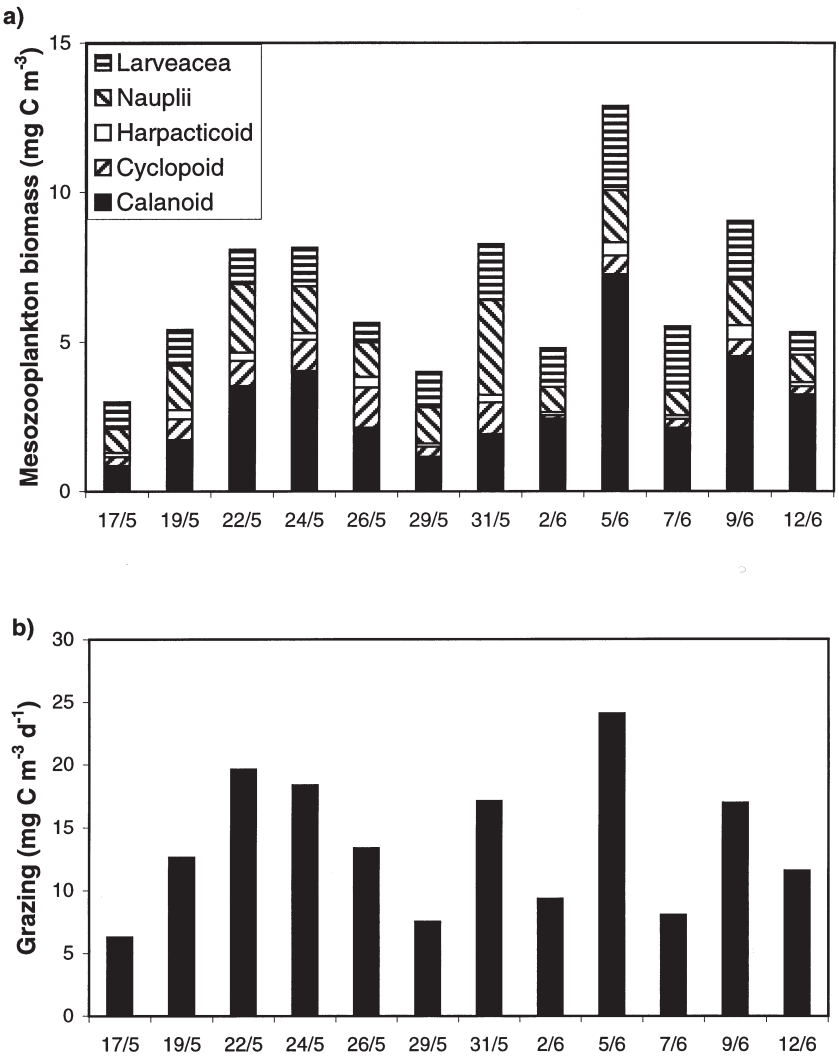


Fig. 10. (**a**) Biomass and (**b**) grazing by mesozooplankton during the sampling period.

(Bryceson, 1977) and Lugomela (Lugomela, 1996). Both observed blooms of *Trichodesmium* spp. in March and April, followed by a mixture of diatoms dominated by *Chaetoceros* and *Rhizosolenia* spp. in May–July.

The planktonic cyanobacteria *Trichodesmium* spp. were abundant throughout the investigation, although the Utermöhl (Utermöhl, 1931) settling method may underestimate the biomass. *Trichodesmium* spp. have gas vacuoles used for buoyancy regulation (Walsby, 1978); hence, colonies may have remained suspended in the sedimentation chamber, leading to underestimation of the abundance (Chang, 2000). *Trichodesmium* is considered to be the major diazotrophic organism in the tropical and sub-tropical pelagic ecosystems (Capone *et al.*, 1997). The nitrogen-fixing ability of *Trichodesmium* may influence new production. For instance, experiments by Bryceson and Fay using ^{15}N incorporation showed uptake of the isotope by *Trichodesmium* colonies and subsequent transfer of the fixed ^{15}N to the bacterial and phytoplankton populations (Bryceson and Fay, 1981). This observation supports the contention that *Trichodesmium* enhances overall phytoplankton by increasing the availability of assimilable new nitrogen in the surface oceans. Furthermore, Glibert and Bronk demonstrated that ~50% of the nitrogen fixed by *Trichodesmium* is released as dissolved organic nitrogen (DON) (Glibert and Bronk, 1994). This DON release is likely to stimulate microbial activity and phytoplankton primary production.

The results from the carbon budget show that the amount of carbon available for consumption by HNF (i.e. production of heterotrophic bacteria and cyanobacteria) did not balance their estimated carbon demand. One possible explanation is the use of an excessive growth rate for

Table I: Summary of data for the flow of carbon within the microbial food web

Organism	Standing stock (mg C m^{-3})	Specific growth rate (day^{-1})	Net production (mg C m^{-3} day^{-1})	Carbon consumption (mg C m^{-3} day^{-1})
Autotrophic				
Cyanobacteria	9.3 ± 3.4	0.7	6.5 ± 3.7	
Nanoplankton	7.3 ± 2.4	1.1	8.0 ± 8.7	
Microplankton				
10–100 μm	31.1 ± 19.8		10.2 ± 12.3	
>100 μm			15.0 ± 18.8	
Exudates			6.5 ± 9.2	
Heterotrophic				
Bacteria	18.3 ± 2.8	0.05	1.0 ± 0.6	2.0 ± 1.2
Nanoflagellates	4.4 ± 1.6	1.2 ± 0.6[a]	5.3 ± 2.6	17.6 ± 8.8
Ciliates	3.7 ± 1.5	0.9 ± 0.4[a]	3.3 ± 1.9	11.1 ± 6.2
Heterotrophic dinoflagellates	1.2 ± 0.8	0.5 ± 0.1	0.6 ± 0.3	1.8 ± 1.0
Mesozooplankton	5.2 ± 0.7	0.9 ± 0.0	4.6 ± 0.5	13.7 ± 1.6

The gross growth efficiency was assumed to be 30% for HNF and ciliates, and 50% for bacteria. The generation time for the ciliates was assumed to be 24 h (Wallberg *et al.*, 1999). The production and consumption of heterotrophic dinoflagellates were estimated from equations in Hansen *et al.* (Hansen *et al.*, 1997). The production of mesozooplankton was calculated according to Huntley and Lopez (Huntley and Lopez, 1992), and consumption according to Peterson (Peterson, 1988). The values are given with the SD.
[a]Data from Wallberg *et al.* (Wallberg *et al.*, 1999).

HNF. The growth rate used originates from two rainy seasons when the growth rate for HNF had a mean value of 1.2 ± 0.6 day^{-1} (Wallberg *et al.*, 1999). Assuming an HNF growth rate of 0.6 day^{-1}, which is in the lower range, gives a carbon demand of 8.8 mg C m^{-3} day^{-1}, which is close to the estimated carbon production for picoplankton (7.5 mg C m^{-3} day^{-1}). For the nanoflagellates (i.e. both heterotrophic and autotrophic), this would in turn yield a total carbon production of 10.7 mg C m^{-3} day^{-1}, which would still balance the estimated carbon demand for ciliates (11.1 ± 6.2 mg C m^{-3} day^{-1}). Another factor that may contribute to the imbalance between the carbon available for consumption by HNF and carbon demand is that the diel production of heterotrophic bacteria is underestimated. The production of heterotrophic bacteria was extrapolated over 24 h and was estimated to contribute only 13% of the total production of the picoplankton (0.2–2 μm). As the rate of primary production increases during the day and, hence, the production of phytoplankton exudate, bacterial production generally shows a diel variation (Hagström *et al.*, 1988; Wallberg and Andersson, 2000). Results from experiments conducted in the same area suggest that the diel variation in bacterial production is higher during the rainy season compared with the dry season (Wallberg and Andersson, 2000).

Depending on the factor used as specific growth rate for HNF, picocyanobacteria could contribute between 37 and 74% of the estimated HNF carbon demand. Previous studies in the same area suggested that picocyanobacteria may contribute between 8 and 33% of the carbon demand for HNF during the rainy season (Wallberg *et al.*, 1999; Wallberg and Andersson, 2000). Similarly, off the Kenyan coast, Goosen *et al.* reported that grazing by HNF exceeded the production of heterotrophic bacteria and suggested that picocyanobacteria may be an alternative carbon source (Goosen *et al.*, 1997). Also, in the Mediterranean Sea, Hagström *et al.* estimated that picocyanobacteria contributed 57% of the HNF carbon demand (Hagström *et al.*, 1988), and in the Arabian Sea, Reckermann and Veldhuis estimated that HNF could satisfy their carbon demand exclusively from picophytoplankton (Reckermann and Veldhuis, 1997). The larger size of picocyanobacteria compared with heterotrophic bacteria suggests that cyanobacteria are selectively grazed upon by HNF (Andersson *et al.*, 1986).

Protozooplankton (ciliates and heterotrophic dinoflagellates) and copepods contribute equally to the heterotrophic biomass (on average 4.9 and 5.2 mg C m^{-3}, respectively), which illustrates the importance of the microbial food web in carbon cycling. Assuming that the potential prey for mesozooplankton consisted of protozooplankton and phytoplankton (10–100 μm), production

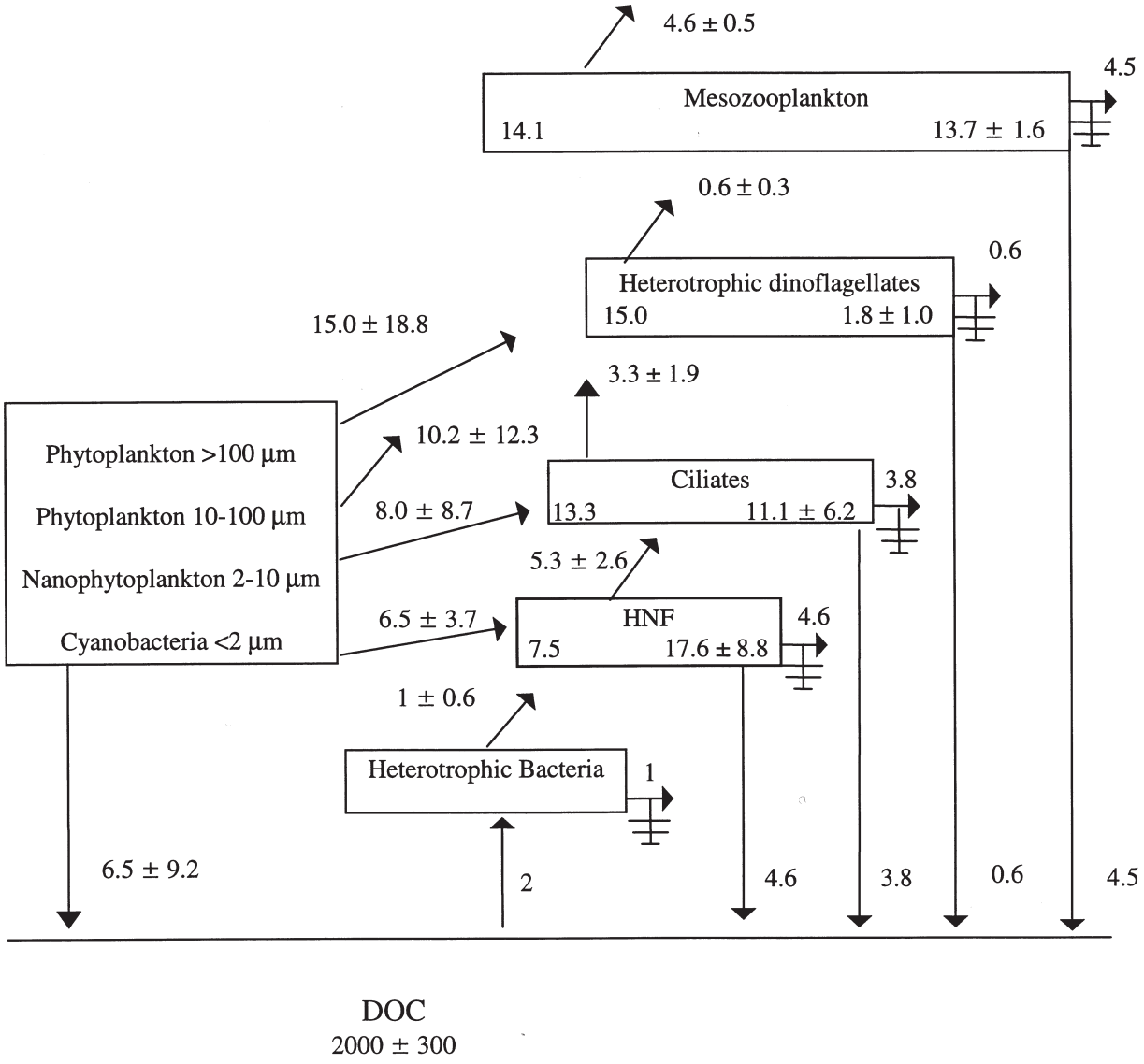


Fig. 11. Budgets for the flow of carbon during the rainy season investigated in the present study. In the figure, the inward- and outward-going arrows represent the consumption, production and respiration (mg C m^{-3} day^{-1}). In the boxes, the number to the right represents the carbon demand estimated from the production rates obtained, and the number to the left represents the net production of the assumed prey.

balances their estimated carbon demand (14.1 and 13.7 mg C m^{-3} day^{-1}, respectively). Including the production of phytoplankton >100 µm in size as a potential prey for mesozooplankton gives a carbon resource (29.1 mg C m^{-3} day^{-1}) twice as high as their demand. Phytoplankton >100 µm consisted mainly of chain- and colony-forming species, such as *Chaetocerous*, *Bacteriastrum* and *Trichodesmium* species. Harpacticoid copepods that can potentially exploit phytoplankton >100 µm constituted ~7% of the mesozooplankton biomass. For instance, harpacticoid copepods, such as *Macrosetella*, *Miracia* and *Oculosetella* spp., have been observed to feed on *Trichodesmium* colonies (O'Neil and Roman, 1992, 1994).

The present carbon budget is, however, a simplification of much more complex interactions. For instance, copepod nauplii formed a substantial biomass component of the zooplankton community. The significance of nauplii in secondary production was recently emphasized by e.g. Roff *et al.* (Roff *et al.*, 1995) and Hopcroft and Roff (Hopcroft and Roff, 1998). The authors suggest that

copepod nauplii are an important link between the classical and microbial food webs because of their small size, abundance and ability to feed on pico-sized particles, which are generally unavailable to the later copepodites and adults. In the present investigation, the role of nauplii and Appendicularia is probably underestimated since their grazing and production are estimated from a general equation of temperature-dependent growth (Huntley and Lopez, 1992) not taking species or developmental stages into consideration.

The budget suggests that as much as 77% of the primary production could be channelled through the heterotrophic organisms and that the protozooplankton community could potentially contribute 28% of the carbon available for consumption by larger predators. This illustrates the importance of the microbial food web as a link for the transfer of carbon fixed by small autotrophs to mesozooplankton. Previous studies conducted in the same area have shown that, during the dry season, when nutrients are more limited, the phytoplankton community becomes dominated by smaller cells (Wallberg *et al.*, 1999; Wallberg and Andersson, 2000). As the production and biomass within the autotrophic plankton community decrease during the dry season, the significance of the heterotrophic community for the carbon cycle increases.

This is the first *in situ* study of the carbon flow through the planktonic community in the tropical western Indian Ocean. The result emphasizes the role played by the microbial food web compared with the classical grazing food chain. Further studies of the plankton community structure are needed in order to fully understand temporally and spatially the variability in the regulation of the pelagic production and carbon cycling of this tropical ecosystem.

ACKNOWLEDGEMENTS

We thank Karin Karlsson and Muhiddini Abdallah for technical assistance during sampling, Anders Sjösten for the nutrient analysis and help with the POC and TOC analysis, Khodeeyoe Pornchai and Birgit Søborg for identification and enumeration of mesozooplankton and heterotrophic dinoflagellates, respectively, and Directorate of Meteorology, Zanzibar, for the rainfall data. The use of laboratory facilities at the Institute of Marine Sciences, Zanzibar, is gratefully acknowledged. This work was supported by grants from the Swedish International Development Cooperation/Department for Research Cooperation (SIDA/SAREC) and from Danish Research Council contract No. 9801391 (to T. G. N.).

REFERENCES

Andersen, P. and Sørensen, H. M. (1986) Population dynamics and trophic coupling in pelagic microorganisms in eutrophic coastal waters. *Mar. Ecol. Prog. Ser.*, **33**, 99–109.

Andersson, A., Larsson, U. and Hagström, Å. (1986) Size-selective grazing by microflagellates on pelagic bacteria. *Mar. Ecol. Prog. Ser.*, **33**, 51–57.

Azam, F., Fenchel, T., Field, J. G., Grey, J. S., Meyer-Reil, L. A. and Thingstad, F. (1983) The ecological role of water-column microbes. *Mar. Ecol. Prog. Ser.*, **10**, 257–263.

Berggreen, U., Hansen, B. and Kiørboe, T. (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for the determination of copepod production. *Mar. Biol.*, **99**, 341–352.

Bryceson, I. (1977) An ecological study of phytoplankton of the coastal waters of Dar es Salaam. PhD Thesis, University of Dar es Salaam, Dar es Salaam, Zanzibar.

Bryceson, I. and Fay, P. (1981) Nitrogen fixation in *Oscillatoria* (*Trichodesmium*) *erythraea* in relation to bundle formation and trichome differentiation. *Mar. Biol.*, **61**, 159–166.

Buck, K. R., Chavez, F. P. and Campbell, L. (1996) Basin-wide distributions of living carbon components and the inverted trophic pyramid of the central gyre of the North Atlantic Ocean, summer 1993. *Aquat. Microb. Ecol.*, **10**, 283–298.

Capone, D. G., Zehr, J. P., Paerl, H. W., Bergman, B. and Carpenter, E. J. (1997) *Trichodesmium*, a globally significant marine cyanobacterium. *Science*, **276**, 1221–1229.

Chang, J. (2000) Precision of different methods used for estimating the abundance of the nitrogen-fixing marine cyanobacterium, *Trichodesmium* Ehrenberg. *J. Exp. Mar. Biol. Ecol.*, **245**, 215–224.

Dodge, J. D. (1985) *Marine Dinoflagellates of the British Isles*. Her Majesty's Stationery Office, London.

Ducklow, H. W. and Carlson, C. A. (1992) Oceanic bacterial production. *Adv. Microb. Ecol.*, **12,** 113–181.

Fenchel, T. and Finlay, B. J. (1983) Respiration rates in heterotrophic free-living protozoa. *Microb. Ecol.*, **9**, 99–122.

Glibert, P. M. and Bronk, D. A. (1994) Release of dissolved organic nitrogen by marine diazotrophic cyanobacteria, *Trichodesmium* spp. *Appl. Environ. Microbiol.*, **60**, 3996–4000.

Goosen, N. K., Riswijk, P. V., De Bie, M., Peene, J. and Kromkamp, J. (1997) Bacterioplankton abundance and production and nanozooplankton abundance in Kenyan coastal waters (Western Indian Ocean). *Deep-Sea Res.*, **44**, 1235–1250.

Haas, L. W. (1982) Improved epifluorescence microscopy for observing planktonic micro-organisms. *Ann. Inst. Oceanogr.*, **58(Suppl.)**, 261–266.

Hagström, Å., Azam, F., Andersson, A., Wikner, J. and Rassoulzadegan, F. (1988) Microbial loop in an oligotrophic pelagic marine ecosystem: possible role of cyanobacteria and nanoflagellates in the organic fluxes. *Mar. Ecol. Prog. Ser.*, **49**, 171–178.

Hansen, P. J., Hansen, B. and Bjørnsen, P. K. (1997) Zooplankton grazing and growth: scaling within the 2 μm–2000 μm body size range. *Limnol. Oceanogr.*, **42**, 687–704.

Hewes, C. D., Sakshaug, E., Reid, F. M. H. and Holm-Hansen, O. (1990) Microbial autotrophic and hetetrotrophic eucaryotes in Antarctic waters: relationships between biomass and chlorophyll, adenosine triphosphate and particulate organic carbon. *Mar. Ecol. Prog. Ser.*, **63**, 27–35.

Hopcroft, R. R. and Roff, J. C. (1998) Zooplankton growth rates: the influence of female size and resources on egg production of tropical marine copepods. *Mar. Biol.*, **132**, 79–86.

Hopcroft, R. R., Roff, J. C. and Bouman A. A. (1998) Zooplankton growth rates: the larvaceans *Appendicularia*, *Fritillaria* and *Oikopleura* in tropical waters. *J. Plankton Res.*, **20**, 539–555.

Huntley, M. E. and Lopez, M. D. G. (1992) Temperature dependent production of marine copepods: a global synthesis. *Am. Nat.*, **140**, 201–242.

Kitheka, J. U., Ohowa, B. O., Mwashote, B. M., Shimbira, W. S., Mwaluma, J. M. and Kazungu, J. M. (1996) Water circulation, water column nutrients and plankton productivity in a well-flushed tropical bay in Kenya. *J. Sea Res.*, **35**, 257–268.

Kromkamp, J., De Bie, M., Goosen, N., Peene, J., Van Rijswijk, P., Sankie, J. and Duineveld, G. C. A. (1997) Primary production by phytoplankton along the Kenyan coast during the SE monsoon and November intermonsoon 1992, and the occurrence of *Trichodesmium*. *Deep-Sea Res.*, **44**, 1195–1212.

Larsson, L. and Hagström, Å. (1982) Fractionated phytoplankton primary production, exudate release and bacterial production in a Baltic eutrophication gradient. *Mar Biol.*, **67**, 57–70.

Lee, S. and Fuhrman, J. A. (1987) Relationship between biovolume and biomass of naturally derived marine bacterioplankton. *Appl. Environ. Microbiol.*, **33**, 1225–1228.

Lugomela, C. (1996) Studies of phytoplankton in the near shore waters of Zanzibar. MSc Thesis, University of Dar es Salaam, Dar es Salaam, Zanzibar.

Lyimo, T. J. (1995) Role played by phytoplanktonic cyanobacteria with an emphasis on *Trichodesmium* species in increasing nitrogen levels in the near shore waters of Tanzania. MSc Thesis, University of Dar es Salaam, Dar es Salaam, Zanzibar.

Marshall, S. M. (1969) Protozoa. Order Tintinnida. *Cons. Int. Explor. Mer Fiches Ident. Zooplankton*, *Fiche*, pp. 117–124.

Menden-Deuer, S. and Lessard, E. J. (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnol. Oceanogr.*, **45**, 569–579.

Montagnes, D. J. S. and Lynn, D. H. (1991) Taxonomy of choreotrichs, the major marine planktonic ciliates, with emphasis on the aloricate forms. *Mar. Microb. Food Webs*, **5**, 59–74.

Okera, W. (1974) The zooplankton of the inshore waters of Dar es Salaam (Tanzania, S. E. Africa) with observations on the reaction to artificial light. *Mar. Biol.*, **26**, 13–25.

O'Neil, J. M. and Roman, M. R. (1992) Grazers and associated organisms of *Trichodesmium*. In Carpenter, E. J., Capone, D. G. and Rueter, J. (eds), *Marine Pelagic Cyanobacteria: Trichodesmium and Other Diazotrophs*. Kluwer Academic Press, Dordrecht pp. 61–73.

O'Neil, J. M. and Roman, M. R. (1994) Ingestion of the cyanobacterium *Trichodesmium* spp. by the pelagic harpacticoid copepods *Macrosetella*, *Miracia* and *Oculosetella*. *Hydrobiologia*, **292**, 235–240.

Parsons, R., Maita, Y. and Lalli, C. M. (1984) *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Oxford, pp. 14–17, 141–149.

Paula, J., Pinto, I., Guembe, I., Monteiro, S., Gove, D. and Guerreiro, J. (1998) Seasonal cycle of planktonic communities at Inhaca Island, southern Mozambique. *J. Plankton Res.*, **20**, 2165–2178.

Peterson, W. T. (1988) Rates of egg production by the copepod *Calanus marshallae* in the laboratory and the sea off Oregon. *Mar. Ecol. Prog. Ser.*, **47**, 229–237.

Porter, K. G. and Feig, Y. (1980) The use of DAPI for identifying and counting aquatic microflora. *Limnol. Oceanogr.*, **25**, 943–948.

Putt, M. and Stoecker, D. K. (1989) An experimentally determined carbon–volume ratio for marine oligotrichous ciliates from estuarine and coastal waters. *Limnol. Oceanogr.*, **34**, 1097–1103.

Reckermann, M. and Veldhuis, M. J. W. (1997) Trophic interactions between picophytoplankton and micro- and nanozooplankton in the western Arabian Sea during the NE monsoon 1993. *Aquat. Microb. Ecol.*, **12**, 263–273.

Roff, J. C., Turner, J. T., Webber, M. K. and Hopcroft, R. R. (1995) Bacterivory by tropical copepod nauplii: extent and possible significance. *Aquat. Microb. Ecol.*, **9**, 165–175.

Ryther, J. H., Hall, J. R., Bakun, A. K. and Jones, M. M. (1966) Primary organic production in relation to chemistry and hydrography of the western Indian Ocean. *Limnol. Oceanogr.*, **11**, 371–380.

Sabatini, M. and Kiørboe, T. (1994) Egg production, growth and development of the cyclopoid copepod *Oithona similis*. *J. Plankton Res.*, **16**, 1329–1351.

Satapoomin, S. (1999) Carbon content of some common tropical Andaman Sea copepods. *J. Plankton Res.*, **21**, 2117–2123.

Smith, D. C. and Azam, F. (1992) A simple economical method for measuring bacterial protein synthesis rates in seawater using ^{3}H-leucine. *Mar. Microb. Food Webs*, **6**, 107–114.

Sorokin, Y. I. (1977) The heterotrophic phase of plankton succession in the Japan Sea. *Mar. Biol.*, **41**, 107–117.

Thomsen, H. A. (1992) Plankton i de indre danske farvande. Miljøstyrelsen no 11 (in Danish).

Tiselius, P. (1989) Contribution of aloricate ciliates to the diet of *Acartia clausi* and *Centropages hamatus* in coastal waters. *Mar. Ecol. Prog. Ser.*, **56**, 49–56.

Utermöhl, H. (1931) Nue wege in der quantitaiven erfssung de planktos. *Verh. Int. Ver. Limnol.*, **5**, 1–38.

Verity, P. G., Robertson, C. Y., Tonzo, C. R., Andrews, M. G., Nelson, J. R. and Sieracki, M. E. (1992) Relationships between cell volume and the carbon and nitrogen content of marine photosynthetic nanoplankton. *Limnol. Oceanogr.*, **37**, 1434–1446.

Verity, P. G., Beatty, T. M. and Williams, S. C. (1996) Visualizing and quantification of plankton and detritus using digital confocal microscope. *Aquat. Microb. Ecol.*, **10**, 55–67.

Wallberg, P. and Andersson, A. (2000) Transport of carbon and a polychlorinated biphenyl through the microbial food web in a tropical coastal ecosystem. *Environ. Toxicol. Chem.*, **19**, 827–835.

Wallberg, P., Jonsson, P. R. and Johnstone, R. (1999) Abundance, biomass and growth rates of pelagic microorganisms in a tropical coastal ecosystem. *Aquat. Microb. Ecol.*, **18**, 175–185.

Walsby, A. E. (1978) The properties and buoyancy providing role of gas vacuoles in *Trichodesmium* Ehrenberg. *Br. Phycol. J.*, **13**, 103–116.

Wickstead, J. H. (1963) Estimates of total zooplankton in the Zanzibar area of the Indian Ocean with a comparison of the results with two different nets. *Proc. Zool. Soc. Lond.*, **141**, 577–608.

Received on October 8, 2000; accepted on May 10, 2001