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Relevance of bacterioplankton abundance and production in the oligotrophic equatorial Indian Ocean

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Abstract Bacterioplankton abundance and production, chlorophyll *a* (Chl *a*) concentrations and primary production (PP) were measured from the equatorial Indian Ocean (EIO) during northeast (NEM), southwest (SWM) and spring intermonsoon (SpIM) seasons from 1°N to 5°S along 83°E. The average bacterial abundance was 0.52 ± 0.29, 0.62 ± 0.33 and 0.46 ± 0.19 ($\times 10^8$ cells l^{-1}), respectively during NEM, SWM and SpIM in the top 100 m. In the deep waters (200 m and below), the bacterial counts averaged $\sim 0.35 \pm 0.14 \times 10^8$ cells l^{-1} in SWM and $0.39 \pm 0.16 \times 10^8$ cells l^{-1} in SpIM. The 0–120 m column integrated bacterial production (BP) ranged from 19 to 115 and from 10 to 51 mg C m^{-2} d^{-1} during NEM and SWM, respectively. Compared with many open ocean locations, bacterial abundance and production in this region are lower. The bacterial carbon production, however, is notably higher than that of phytoplankton PP (BP:PP ratio 102% in SWM and 188% in NEM). With perpetually low PP (NEM: 20, SWM: 18 and SpIM: 12 mg C m^{-2} d^{-1}) and Chl *a* concentration (NEM: 16.5, SWM: 15.0 and SpIM: 20.9 mg m^{-2}), the observed bacterial abundance and production are pivotal in the trophodynamics of the EIO. Efficient assimilation and mineralization of available organics by bacteria in the euphotic zone might serve a dual role in the ultra-oligotrophic regions including EIO. Thus, bacteria probably sustain microheterotrophs (micro- and meso-zooplankton) through microbial loop. Further, rapid mineralization by bacteria will make essential nutrients available to autotrophs.

Keywords Heterotrophic bacteria · ^{3}H-thymidine uptake · Chlorophyll *a* · Growth rates · BP:PP ratios · Equatorial Indian Ocean · Ultra-oligotrophy

Uncommon Abbreviations

EIO	Equatorial Indian Ocean
NEM	Northeast monsoon
SWM	Southwest monsoon
SpIM	Spring intermonsoon
TDC	Total direct counts
BP	Bacterial Production
BGR	Bacterial growth rates

Introduction

The distribution of the ubiquitous heterotrophic bacteria in the world oceans is regulated by dissolved organic matter released primarily from phytoplankton exudates and from sloppy feeding of zooplankton (Azam et al. 1983; Fuhrman 1992). Cole et al. (1988)

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suggest that the average bacterial production (BP) in the global oceans is *ca.* 30% of the primary production (PP). However, in some regions heterotrophic bacterial respiration (Del Giorgio et al. 1997) and production (Ameryk et al. 2005) sometimes far exceed the primary photosynthetic production.

Unlike the Atlantic or Pacific Oceans, the Indian Ocean is landlocked in the north and in general, experiences seasonally changing monsoon circulation (Wyrtki 1973). This particular region of equatorial Indian Ocean (EIO) is quite far from coastal influences and, in the absence of equatorial upwelling (Schott et al. 2002), the primary productivity is expectedly low due to nutrient limitation. In general, the biological oceanographic studies in EIO are sparse but for a few earlier reports (Mitzkevich 1974; Sorokin et al. 1985). Further, the intermonsoon phases were poorly covered during the International Indian Ocean Expedition (Krey and Babenard 1976). The JGOFS research has shown that temporal variability exists at least during the intermonsoon phases in the Arabian Sea (Madhupratap et al. 1996; Smith et al. 1998).

In the ultra-oligotrophic regions such as the EIO, where autotrophic production is poor, heterotrophic bacteria may provide a critical link in the trophodynamics. Bacterial biomass production generates food for phagotrophic heterotrophs through microbial loop and mineralization provides nutrients for autotrophs. Such an importance of heterotrophic prokaryotes in the EIO has not been realized. Rao (1973) and Krey and Babenerd (1976) report the preponderance of meso-zooplankton biomass throughout the year. Information on bacterial abundance and productivity is thus necessary to explain such a perennially high zooplankton biomass in this low chlorophyll region. Bacterial abundance and productivity were studied with an objective to understand their seasonal distribution and to relate to phytoplankton biomass and production.

Materials and methods

Sampling

Water sampling was carried out during the northeast monsoon (NEM, January 29–February 25, 2003) and southwest monsoon (SWM, July 16–August 16, 2003) onboard A. A. Sidorenko and the spring intermonsoon (SpIM, February 26–March 04, 2005) onboard A. Boris Petrov. The water samples were collected using Niskin samplers of 10 l capacity on single hydrocast in the SWM and, single operation of CTD (Conductivity-temperature-depth, Sea-Bird electronics) in the NEM and SpIM at each location. Stations with one degree interval from 1°N to 5°S along 83°E (Fig. 1) were sampled from the top 100 m during NEM and top 1000 m during SWM. In SpIM, samples were collected from upper 1000 m from Equator, 3°S, 4°S and 5°S. Bacterial abundance and chlorophyll *a* (Chl *a*) were measured at all stations whereas BP and in situ incubations for primary productivity from dawn to dusk were done at alternate stations.

Chlorophyll *a*

Chl *a* concentrations were measured fluorometrically (Turner Designs, USA, 10-AU-005-CE) by filtering 1 litre water samples from each depth onto GF/F filters and extracting overnight in 10 ml of 90% acetone at 4°C in refrigerator.

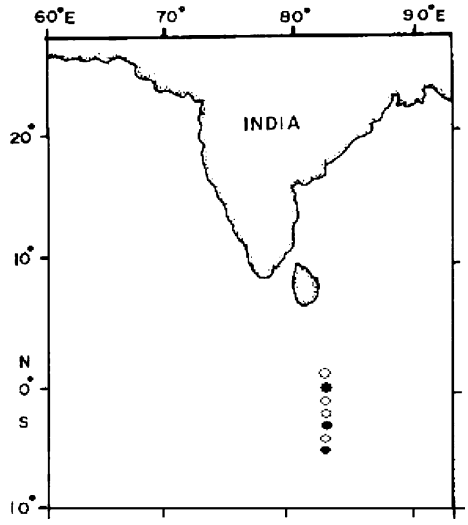

Fig. 1 Study site showing the cruise track and the stations sampled. Stations shown as filled circles were additionally sampled for measuring bacterial and in situ PP. During the SpIM, samples were collected from equator, 3°S, 4°S and 5°S along 83°E from top 1000 m

Primary productivity (PP)

Water samples were collected from the upper 120 m (seven depths viz: surface, 10, 20, 40, 60, 80 and 100 during NEM and, the eighth depth 120 m, during SWM and SpIM) in three 300 ml polycarbonate bottles (Nalgene, Germany) at predawn as per the JGOFS protocols (UNESCO 1994). One ampoule of $NaH^{14}CO_3$ (Board of Radiation and Isotope Technology, Mumbai; Specific activity 185 kBq) was added to each 300 ml bottle (two light and one dark bottles at each depth) and incubated in situ using a mooring system for 12 h from just before sunrise to half-hour past sunset. Aliquots of 100 ml from each bottle were filtered through GF/F filters (47 mm diameter, 0.7 μm pore size, Whatman, USA). The filters were transferred to scintillation vials and exposed overnight to HCl (0.5 N) fumes in a closed container to drive off any inorganic ^{14}C adhering to samples. Five ml liquid scintillation cocktail (Sisco Research Laboratory, Mumbai) was added to each vial and the radioactivity measured in a scintillation counter (Wallac 1409DSA, Perkin Elmer, USA). An internal standard was used for applying appropriate corrections. PP rate was expressed as mg C m^{-3} d^{-1} for discrete depths and, as mg C m^{-2} d^{-1} for column-integrated values for 0–120 m column.

Bacterioplankton abundance

For estimation of bacterioplankton total direct counts (TDC), 50 ml aliquots of water samples were fixed with buffered, 0.22 μm prefiltered formaldehyde (final concentration of 2%), stored at 4°C in the dark (Ducklow 1993) and processed within 2–3 weeks after collection. Acridine orange direct counts (AODC) were made following Parsons et al. (1984). Subsamples of 3 ml were stained with acridine orange (final concentration 0.01%) for 2 min, filtered (0.22 μm black Nucleopore filters) and mounted on glass slides using immersion oil (Botzoil, Germany) and observed immediately under 100× objective on an epifluorescence microscope (Olympus BH2, Japan). The blue excitation (450–490 nm) from a mercury lamp, with 510 nm beam splitter and a 520 nm emission filter were used. Bacterial cells in at least 25 microscopic fields were counted and the mean cell number per field was calculated and used for estimating total abundance by using the relationship detailed in Parsons et al. (1984). Bacterial abundances were used to calculate carbon biomass using a conversion factor of 11 fg C $cell^{-1}$ (Garrison et al. 2000).

Bacterial production

BP rates were derived from determination of methyl-^3H-thymidine incorporation rates (TdR; specific activity 18000 mCi $mmole^{-1}$, Bhabha Atomic Research Centre, Mumbai) by the water column bacteria following the method described in JGOFS Protocols (UNESCO 1994) and by Ducklow (1993). Samples were drawn from surface to 100 or 120 m (1, 10, 20, 40, 60, 80, 100 and 120 m) and three replicate subsamples of 20 ml from each depth were transferred to 50 ml polycarbonate tubes. ^3H-thymidine (5.9 nM) was added into these tubes, which were incubated in styroform insulated plastic beakers for 90 min. Ice cubes were added into the water tubs holding samples from depths of 40 m and below so as to mimick the in situ temperature of each sampling depth. The thymidine uptake was stopped by adding 300 μl prefiltered (0.22 μm filter) formaldehyde. Zero time blanks were also run for the samples in order to obtain correction for abiotic/filter adsorption. The samples were filtered through 0.22 μm cellulose acetate filters (25 mm, Millipore India Ltd, Bangalore) and rinsed thrice alternately with 10% (w/v) cold trichloroacetic acid and cold ethanol (96%, v/v). The filters were held individually in moisture free, 8 ml scintillation vials and containing 5 ml scintillation fluid (Cocktail-W, SRL, Mumbai) was added a day prior to radioassaying in a Perkin Elmer Wallac 1409 DSA liquid Scintillation Counter.

Tritiated thymidine incorporated (TdR, pM h^{-1}) was calculated using the formula: TdR = (DPMs–DPMb)/(SA × SV × T × 2.22).

Where, DPMs = disintegrations per minute of the sample on the filter, DPMb = disintegrations per minute (DPM) of the blank on the filter, SA = specific activity (mCi $mmol^{-1}$), SV = Sample volume in litres, T = incubation time in hours.

BP was estimated using a mean oceanic conversion factor of 2.17×10^{18} cells mol^{-1} thymidine incorporated (Ducklow 1993). This conversion factor

appear to hold good for Indian Ocean region (unpublished).

Chl *a*, PP, TDC and BP data were subjected to one-way ANOVA and correlation analysis (Excel).

Results

Hydrography

Figure 2 depicts all hydrographical data. The sea surface temperature (SST) averaged about 28.7°C in the NEM, 28.4°C in the SWM and 29.6°C in the SpIM.

Mixed layer depth (MLD) was ~40 m during all the seasons. Thermocline was evident within the upper 100 m with no variation in temperature, irrespective of the seasons.

Sea surface salinity was lower both during NEM and SpIM (33.6 and 33.63 psu) than that in SWM (34.80 psu). During SWM (range: 34.80–35.05 psu), salinity did not change much with depth unlike in the NEM (range: 33.57–34.65) and SpIM (range: 33.66–35.08 psu).

The dissolved oxygen (DO) in the surface varied from 182 μM in the NEM to 203 μM in the SWM and 200 μM in the SpIM. The oxycline occurred in the top 200 m. Below 200 m, the decline in DO was gradual until 1000 m. Oxygen minimum zone (OMZ) was not very marked as the DO values were mostly above 50 μM.

Chlorophyll *a* and PP

Chl *a* profiles are from averages of all sampled stations whereas PP from stations at the Equator, 3°S and 5°S). Surface Chl *a* (Fig. 3a) varied from 0.07 mg m^{-3} (range, 0.05–0.08 mg m^{-3}) in NEM to 0.06 mg m^{-3} (range, 0–0.19 mg m^{-3}) in SWM and 0.08 mg m^{-3} (range, 0.07–0.09 mg m^{-3}) in SpIM. Subsurface chlrophyl *a* maxima (SCM) were observed during all three seasons at a depth of 60–80 m. Surface PP (Fig. 3b) averaged to a highest of 1.22 mg C m^{-3} d^{-1} in NEM (range, 0.47–2.14 mg C m^{-3} d^{-1}) followed by 0.42 mg C m^{-3} d^{-1} in SWM (range, 0.1–0.73 mg C m^{-3} d^{-1}) and 0.23 mg C m^{-3} d^{-1} in SpIM (range, 0.1–0.49 mg C m^{-3} d^{-1}). Below 10 m, the rate did not vary much till 120 m in all the three seasons as the euphotic depths are deeper than 120 m in the EIO (Krey and Babenerd 1976).

Bacterial abundance

During NEM, the TDC varied between 0.17 and 2.18 ($\times 10^8$ cells l^{-1}; Fig. 4) with an overall seasonal average of $0.52 \pm 0.29 \times 10^8$ cells l^{-1}. The surface counts increased from 1°N (0.55×10^8 cells l^{-1}; station

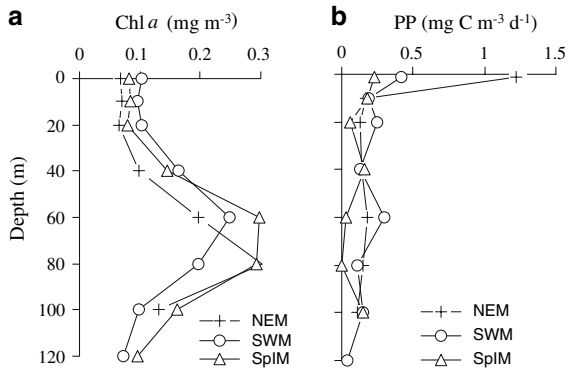

Fig. 3 Vertical profiles of mean values of (**a**) chl *a* and (**b**) PP in the upper 120 m from all the sampled locations during each season

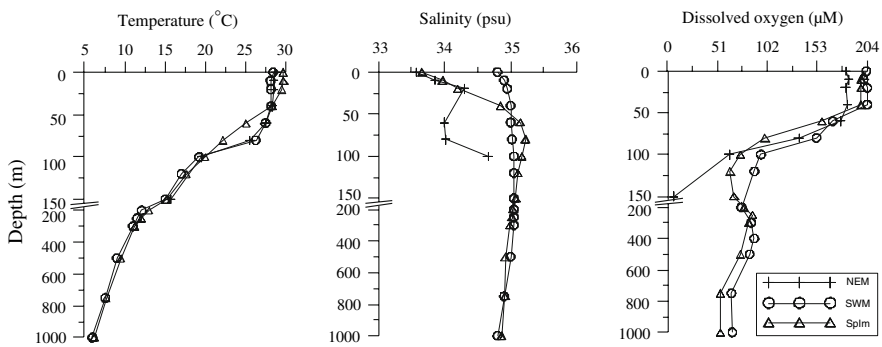

Fig. 2 Vertical profiles of (**a**) temperature, (**b**) salinity and (**c**) dissolved oxygen for the upper 1000 m during NEM, SWM and SpIM

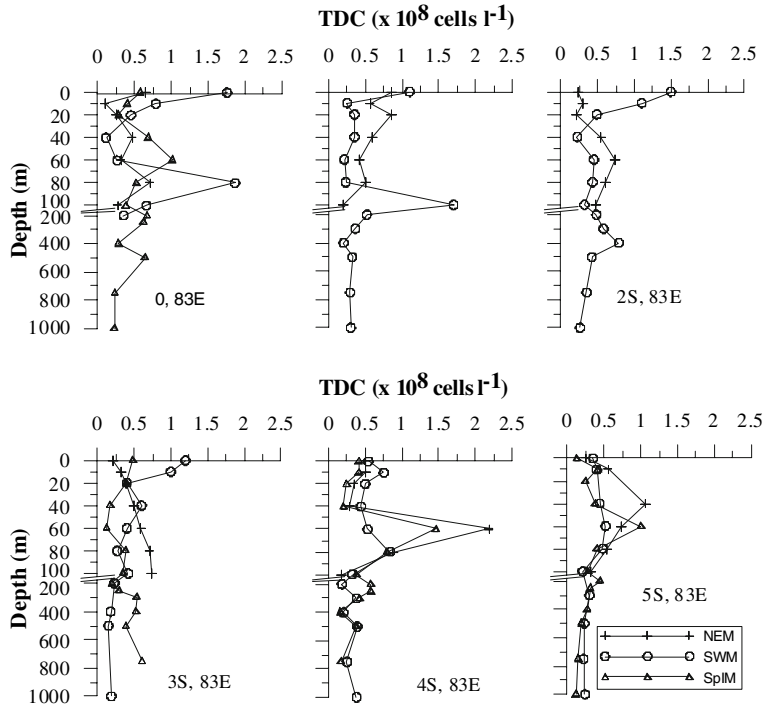

Fig. 4 Vertical profiles of bacterial abundance (TDC, number $\times 10^8$ cells l^{-1}) from top 1000 m of the EIO during NEM, SWM and SpIM

not shown in figure) to 1°S (0.85×10^8 cells l^{-1}) and, in general, decreased thereafter (0.25×10^8 cells l^{-1} at 5°S). The abundance showed subsurface peaks that generally coincided with SCM but did not vary significantly with depth.

During the SWM, the bacterial numbers in the surface ranged from 0.35 to 1.76 ($\times 10^8$ cells l^{-1}). The counts were high in the surface at the Equator and decreased towards 5°S. They showed subsurface maxima at around 80 m roughly coinciding with the SCM at many stations and decreased rapidly with depth ($F_{13,59}$:2.6 > F_{critical}: 1.9, $p < 0.05$). The abundance during this season in the top 100 m ranged from 0.11 to 1.87 ($\times 10^8$ cells l^{-1}) with an average of $0.62 \pm 0.33 \times 10^8$ cells l^{-1}. Between 120 and 1000 m, the range was from 0.19 to 0.79 ($\times 10^8$) cells l^{-1} with an average of $0.35 \pm 0.14 \times 10^8$ cells l^{-1}.

During SpIM, the bacterial numbers in the surface ranged from 0.13 to 0.58 ($\times 10^8$ cells l^{-1}). As also observed during SWM, the counts were high in the surface at the Equator and decreased towards 5°S. Bacterial numbers showed subsurface maxima ~80 m similar to that of chlorophyll maxima, and decreased with increase in depth ($F_{14,\ 44}$: 2.7 > F_{critical}: 1.9, $p < 0.05$). The abundance in the top 100 m ranged from 0.30 to 0.56 ($\times 10^8$) cells l^{-1} with an average of $0.46 \pm 0.19 \times 10^8$ cells l^{-1}. In the 120–1000 m depth, they ranged from 0.34 to 0.48 ($\times 10^8$) cells l^{-1}, with an average of $0.39 \pm 0.16 \times 10^8$ cells l^{-1}.

Bacterial production

Thymidine incorporation rate by bacteria ranged from 0.007 to 3.12 pM h^{-1} during the SWM. Consequently, the BP ranged from 0.004 to 1.79 mg C m^{-3} d^{-1} (Fig. 5) with an average of 0.35 ± 0.50 mg C m^{-3} d^{-1} in the 0–120 m. Similarly, the estimated BP during the NEM was in the range of 0.04–4.70 mg

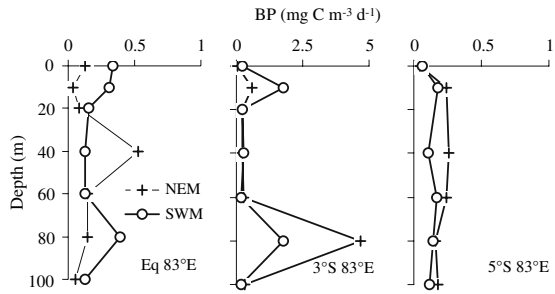

Fig. 5 BP in the top 100 m in the EIO during SWM and NEM monsoon seasons. For reasons not explainable, the observed BP was quite high at 3°S

C m^{-3} d^{-1} with a mean production rate of 0.43 ± 1.01 mg C m^{-3} d^{-1}.

Column (0–120 m) integrated values of different parameters

Integrated chlorophyll concentration (Fig. 6 a) ranged from 14 to 20 mg m^{-2} (average of 16.6 ± 2.2 mg m^{-2}) during the NEM, 7.4–20 mg m^{-2} (average of 15 ± 4.8 mg m^{-2}) in the SWM and 16–25 mg m^{-2} (average of 21 ± 4.6 mg m^{-2}) in SpIM. The annual mean Chl *a* biomass was 18 ± 3 mg m^{-2}.

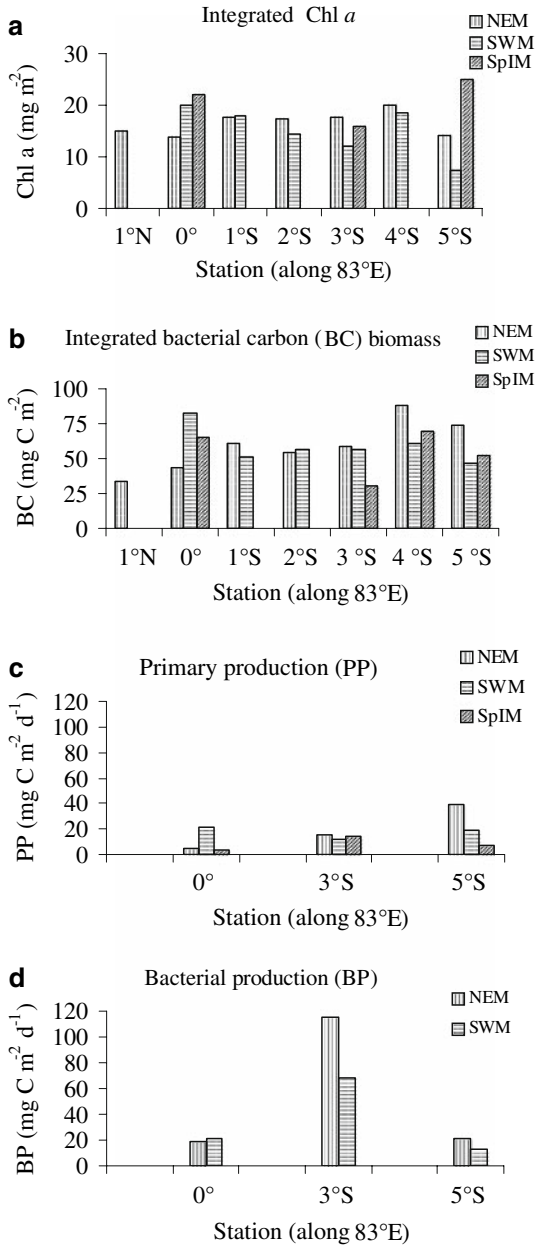

Fig. 6 Column integrated Chl *a* (**a**), BC (**b**) PP (**c**) and BP (**d**) in the top 100 m in the EIO during NEM, SWM and SpIM

The bacterial carbon biomass (BC, Fig. 6b) derived from the total counts ranged from 34 to 88 mg C m^{-2} (59 ± 18 mg C m^{-2}), 47–82 mg C m^{-2} (59 ± 12.4 mg C m^{-2}) and from 28 to 66 mg C m^{-2} (54 ± 17.3 mg C m^{-2}), respectively during NEM, SWM and SpIM. The annual mean BC biomass was 56 ± 3 mg C m^{-2}. The BC biomass increased southwards with a maximum at 4°S during NEM and SpIM, which was unlike the observations during the SWM where maximum abundance was observed at the Equator.

The PP (Fig. 6c) ranged from 5 to 40 mg C m^{-2} d^{-1} (20 ± 18 mg C m^{-2} d^{-1}) in NEM, 11–22 mg C m^{-2} d^{-1} (17 ± 5.4 mg C m^{-2} d^{-1}) in SWM and 4–14 mg C m^{-2} d^{-1} (8 ± 5 mg C m^{-2} d^{-1}) in SpIM. The annual mean PP was 15 ± 6 mg C m^{-2} d^{-1}. The BP (Fig. 6d) during NEM, ranged from 19.2 to 115.3 mg C m^{-2} d^{-1} (average of 52 ± 55 mg C m^{-2} d^{-1}). During SWM, it ranged from 13.5 to 68.3 mg C m^{-2} d^{-1} (average of 34 ± 29.7 mg C m^{-2} d^{-1}). BP was not measured during SpIM. Therefore, the mean BP for the two seasons was 43 ± 12 mg C m^{-2} d^{-1}.

BP:PP ratios and Bacterial growth rates (BGR)

The BP:PP ratios ranged from 34 to 345% (average, 188%) during NEM and from 40 to 137% (average, 102%) during SWM. BGR calculated (using BP divided by bacterial abundance) ranged from 0.17 to 1.33 d^{-1} (mean = 0.61 d^{-1}) in NEM. The doubling time ranged from 0.75 to 5.8 days (average of 1.64 days). During SWM, BGR ranged from 0.18 to 0.74 d^{-1} (mean = 0.36 d^{-1}) and the doubling time varied from 1.36 to 5.58 days (mean = 2.74 days). The highest BP:PP ratios, BP rates and fastest turnover times occurred at 3°S in both the seasons.

Statistical analyses

Since the *F*-values (one-way ANOVA) were lower than the $F_{critical}$, no significant ($p > 0.05$) spatio-temporal variation in Chl *a*, PP, TDC and BP was

discernible. However, significant correlation was observed between TDC and Chl *a* during NEM ($r = 0.44$, $n = 48$, $p < 0.05$) and, SpIM ($r = 0.57$, $n = 24$, $p < 0.05$) but not in SWM ($p > 0.05$).

Discussion

Spatio-temporal variations in bacterial abundance and BP, as well as Chl *a* concentrations and PP were not pronounced. Overall, the bacterial counts in the top 100 m (average: 0.53×10^8 cells l^{-1}) were lower than those in the northwestern (1.6×10^9 cells l^{-1}; Wiebinga et al. 1997) or northeastern (1.9×10^9 cells l^{-1}; Gauns et al. 2005) Indian Ocean. However, they were comparable with those from the central Indian Ocean (Sorokin et al. 1985). Also, the deep water counts from 200 to 1000 m (0.37×10^8 cells l^{-1}) agreed well with the observations of Hansell and Ducklow (2003) and Koppelmann et al. (2005) in the open waters of the Arabian Sea. Further, similar to the results of Mitzkevich and Kriss (1975) from the southern Indian Ocean, bacterial counts were higher, coinciding with the subsurface chlorophyll maxima. Similar to bacterial abundance, BP (0.003–4.7 mg C m^{-3} d^{-1}) was also lower than in the Arabian Sea (Ducklow 1993; Ramaiah et al. 1996).

From the literature, it is clear that heterotrophic bacteria in oligotrophic regions are efficient in the turnover of organic matter derived primarily from phytoplankton (Nagata 2000). The PP in the 0–120 m that ranged between 0.003 and 1.22 mg Cm^{-3} d^{-1} is much lower than that in the northwestern Indian Ocean (Bhattathiri et al. 1996, 3.8–35.8 mg C m^{-3} d^{-1} during NEM, 9.4–49.9 mg C m^{-3} d^{-1} during SWM) or the Bay of Bengal (0.03–16 mg C m^{-3} d^{-1}; Madhupratap et al. 2003). This reaffirms the ultra-oligotrophic nature of this region. Thus, the formation of DOM must be in the lower range of ~10–50% of PP as suggested by Azam et al. (1983). Further, as Kirchman et al. (1993) suggest, bacteria appear to efficiently utilize the available organic matter at higher temperatures, prevalent perennially in the surface layers of the EIO. Bacterial growth rates (average, 0.6; range 0.17–1.33 d^{-1} and average doubling time 1.6 days; range 0.75–5.8 days) in EIO, though higher than those from sub-artic Pacific (Kirchman et al. 1993), are comparable with those observed in northeast Atlantic (Ducklow et al. 1993) and equatorial Pacific (Kirchman et al 1995). Consequently, rapid turnover of dissolved organic carbon by heterotrophic bacteria (Kirchman et al.1991) would result in an increased mineralization rate (Azam and Hodson 1977), which then will facilitate autotrophic production in the EIO.

Further, as Cole et al. (1988) suggested, heterotrophic bacteria by serving as food to both micro- and meso-zooplankton sustain their biomass in the EIO. In the 1970s, Rao (1973) and Krey and Babenerd (1976) reported meso-zooplankton biomass (in the range of 0.1–20 ml: averaging 10 ml 100 m^{-3} (displacement volume); and recently recorded values of 0.7–4.5 ml 100 m^{-3}, data courtesy M. Gauns). Such reported biomass would be difficult to be sustained by low Chl *a* and PP observed from the EIO region. It is in this context that heterotrophic bacteria with rapid growth rates are important in operating the microbial loop. Although there are no studies yet on the micro-zooplankton (heterotrophic organisms in the size range of 20–200 μm) from the EIO, it is presumed that they feed on heterotrophic bacteria and are in turn consumed by meso-zooplankton as reported from other oceanic regions (Landry et al. 1998). This has been also reported in the periods of low chlorophyll especially from the Arabian Sea (Gauns et al. 1996; Madhupratap et al. 1996; Ramaiah et al. 2005).

The DOM released from grazing by the micro- and meso-zooplankton could be partly responsible for the high BP:PP ratios exceeding 100% in the EIO as also suggested by Ducklow (1993) and Burkill et al. (1993). Nagata (2000) points out that BP in the euphotic zone is sustained by the flux of fresh DOM released through physiological and trophodynamic processes. Goosen et al. (1997) also attributed BP:PP ratios of over 100% to high grazing rates by heterotrophic flagellates in the western Indian Ocean. However, in most open ocean locations studied under the JGOFS, the BP was seldom greater than 20% of PP (Ducklow 1999). In the Antarctic, BP seldom exceeded 5% of the PP (Bird and Karl 1999). In the Atlantic, BP ranged between 1 and 14% (Zubkov et al. 2001; Hoppe et al. 2002) with north of 30°N exceeding 40% whereas in the equatorial Pacific, ratios ranging from 12 to >30% have been reported (Kirchman et al. 1995). Thus, the BP:PP ratios reported by us from the Indian Ocean are unique.

From the lack of marked seasonal differences in bacterial abundance in the ultra-oligotrophic EIO,

plus shorter doubling times and high BP:PP ratios, it is inferred that heterotrophic bacteria rapidly recycle the labile DOM produced in situ, which explains their abundance. Thus our results highlight the much greater importance of heterotrophic BP in the overall biological productivity in the EIO.

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