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Abundance and productivity of bacterioplankton in relation to seasonal upwelling in the northwest Indian Ocean

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Abstract—The role of bacterioplankton in the Somali Current, the Gulf of Aden and the Red Sea was studied during the SW- (May–August 1992) and NE-monsoon (January–February 1993). The diversity in physical and biological characteristics of the regions and seasons is reflected in a broad range of both phyto- and bacterioplankton production. During the SW-monsoon, the Somali current showed highest bacterial production (up to 849 mgC m^{-2} day^{-1}) in regions with enrichment of the surface waters by upwelling of cold, nutrient-rich, deep water. In contrast, the Gulf of Aden and the Red Sea were most productive during the NE-monsoon (average 225 mgC m^{-2} day^{-1}). Depth profiles of the upper 300 m in general showed a subsurface maximum in bacterial abundance and production at 20–70 m depth. Heterotrophic activity and primary production were closely correlated, indicating the dependence of bacterioplankton on local phytoplankton-derived organic carbon and their ability to adapt quickly to changes in the environment. The bacterial carbon demand in the upper 300 m of the water column was largely supplied by phytoplankton production in the euphotic zone. Bacterial production was 18 ± 7% (average ± S.D.) of primary production. Assuming an assimilation efficiency of 50% for marine bacteria, they consumed up to half of the carbon produced by the phytoplankton. Cycling of carbon within the euphotic zone appears to be achieved by intense grazing by (micro)zooplankton and subsequent remineralization. © 1997 Elsevier Science Ltd

1. INTRODUCTION

Bacterioplankton often constitutes a substantial fraction of the total carbon biomass in the pelagic ecosystem. In oligotrophic waters, the bacterial biomass is commonly 2–3 times larger than the phytoplankton biomass (Cho and Azam, 1990). In the euphotic zone the bacteria play a major role in the recycling of nutrients by remineralization of phytoplankton exudates and dissolved organic matter lost from the grazing chain by inefficient ("sloppy") feeding of mesozooplankton. In its turn the newly formed particulate organic matter (POM) may serve as an additional energy and carbon source for higher trophic levels, e.g. via heterotrophic flagellates to (micro)zooplankton, the so-called "microbial loop" (Williams, 1981; Azam *et al.*, 1983; Sorokin *et al.*, 1985).

Below the euphotic zone the free-living bacteria, and to some extent attached bacteria, have been shown to decompose the sinking organic particles (Cho and Azam, 1988). This results in a decrease in the flux of settling organic matter to the sea floor (de Baar *et al.*, 1989; Karl *et al.*, 1988). The contribution of bacteria to degradation of colloidal organic carbon in aggregates, which are enriched in bacteria (Alldredge and Youngbluth, 1985), and the

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possible sites of intense bacterial exoenzyme activity (Kepkay, 1994), are largely unknown. The opposite pathway, by which dissolved organic matter is taken up by bacteria and transformed to bacterial biomass (as part of the POM-pool), might also occur via rapid abiotic conversion (Alldredge *et al.*, 1993).

The Joint Global Ocean Flux Study (JGOFS) aims to study the flow of carbon through the pelagic system by determining most of the components of the system, known as the core measurements of the JGOFS programme. The role of bacterioplankton in the biogeochemical cycling of carbon in the ocean is estimated from determinations of bacterial abundance and production. Results of earlier programmes as well as JGOFS are available from the main ocean basins: North Atlantic Ocean, Southern Ocean, subarctic and central Pacific Ocean.

The northwestern Indian Ocean, one of the JGOFS process study areas (Smith *et al.*, 1991; SCOR, 1995), is of interest due to its extreme seasonality and extensive oxygen minimum zone. It is characterised by strong seasonal upwelling along the coasts of Somalia, Yemen and Oman, driven by the southwest monsoon from May–September (Schott *et al.*, 1990). Nutrient enrichment in the upper layer of the ocean leads to the observed increase in chlorophyll concentration and phytoplankton productivity during the SW monsoon (Banse, 1987; Owens *et al.*, 1993). In summer the fast Somali current, caused by high average wind velocities, forms a narrow upwelling zone off Somalia with high primary production (Smith and Codispoti, 1980; Hitchcock and Olson, 1992; Brock *et al.*, 1994). In contrast most of the area can be described as oligotrophic during the NE monsoon (January–February). Based on apparent relationships of dissolved organic carbon (DOC) with apparent oxygen utilisation (AOU) and total carbon dioxide, Dileep Kumar *et al.* (1990) have speculated about the role of microbial populations in regulating the carbon and oxygen cycles in the Arabian Sea, but little is known about bacterial variability and their possible role in mineralisation during the different seasons. Despite the scarcity of relevant data from the NW Indian Ocean, Azam *et al.* (1994) state that during the NE-monsoon the Arabian Sea would be fundamentally different from other oligotrophic systems.

Probably the only basin-scale contour sections of bacterial properties in the Indian Ocean have been given by Ducklow (1993). Bacterial abundance and production were reported for the east part ($>60°$E) of the Arabian Sea and the Gulf of Oman measured during an intermonsoon period (September–October 1986). Attention was paid to particle breakdown as carbon supply for bacterial production at greater depth. Despite the use of conservative conversion factors, euphotic zone bacterial production equalled 10 up to 92% of primary production, and deep water production estimates (>100 m) were over 10 times greater than the vertical flux of particulate organic carbon. Ducklow (1993) concluded that the carbon sources usually assumed to support bacterial production (e.g. phytoplankton exudates, particle breakdown) are insufficient to meet the bacterial demand in the NW Indian Ocean. Accumulation of a reservoir of DOC could act as an energy and carbon flux "buffer", moderating the response of bacteria to the extreme cycles of primary production found in the Arabian Sea (Azam *et al.*, 1994). Import of slow-to-degrade DOC could also explain the decoupling between primary production and denitrification found by Naqvi (1994). However, several authors have noted that there is no information on the influences of seasonal variations in phytoplankton dynamics, caused by intense upwelling during the SW-monsoon, on bacterial properties in the NW Indian Ocean (Sorokin *et al.*, 1985; Ducklow, 1993; Naqvi, 1994).

Some information on the role of bacteria in upwelling systems is known for other regions.

In the southern Benguela Current, bacterial biomass was correlated with phytoplankton biomass and production, with initially high biomass of bacteria decreasing with time (Painting *et al.*, 1993). At a nearshore station in the upwelling region off central Chile, net bacterial production varied by about an order of magnitude (0.13–1.40 $\mu gC\ l^{-1}\ h^{-1}$) between newly upwelled and stratified waters and was often a substantial fraction (50%) of primary production (McManus and Peterson, 1988).

In this study the dynamics of bacteria in the Somali Current, Gulf of Aden and Red Sea are described. The aim was to assess the abundance and growth of bacterioplankton during the SW- and NE-monsoon in the upper ocean (0–300 m). Results on bacterial production, measured with [^{3}H]thymidine and [^{3}H]leucine incorporation (Fuhrman and Azam, 1982; Simon and Azam, 1989; Moriarty, 1990), and bacterial numbers and biomass, by epifluorescence microscopy (Hobbie *et al.*, 1977), obtained during three JGOFS cruises of the "Netherlands Indian Ocean Programme 1992–1993" are presented and discussed in relation to phytoplankton primary production (Veldhuis *et al.*, 1997).

2. MATERIALS AND METHODS

Cruise tracks and stations

This study was carried out aboard the R.V. *Tyro* during the Netherlands Indian Ocean Programme 1992–1993 for the project "Monsoons and Pelagic Systems", adopted by the JGOFS Indian Ocean Planning Group as a pilot study for the Arabian Sea Process Study 1994–1996 (SCOR, 1995). The Somali Current, Gulf of Aden and the Red Sea were sampled during three cruises (Fig. 1): at the onset (21 May–12 June 1992) and at the peak (12 July–8 August 1992) of the SW-monsoon and finally during the NE-monsoon (11 January–6 February 1993). A variety of sites were visited in oligotrophic waters (with stratified water column) or in areas with surface water replete with nutrients, supplied by upwelling or strong wind-induced vertical mixing. Underway, XBT measurements were used to obtain temperature profiles along north–south sections through the Somali Basin and sections perpendicular to the coast of Somalia. Continuous vertical profiles of temperature, salinity, oxygen and fluorescence were obtained by CTD rosette sampler during stations lasting 1 or 2 days. At most stations the sampling programme covered most of the JGOFS core measurements. Overviews of sampling efforts and preliminary results are given in the cruise report (Baars, 1994).

Sampling

Discrete water samples were taken with NOEX bottles (10.5-l Technicap) attached to a CTD rosette sampler (Neil Brown CTD during SW-monsoon, Seabird CTD during NE-monsoon). The positions of the stations and some upper layer variables are given in Table 1. One hour before dawn the euphotic zone was sampled for ^{14}C primary production incubations and determination of phytoplankton characteristics (Veldhuis *et al.*, 1997); samples were taken at seven depths corresponding to 53, 48, 25, 11, 5.7, 1.8 and 0.8% of surface irradiation, determined by optical profiles from PAR or Secchi disk casts. The same depths, with three additional depths from below the euphotic zone down to a depth of 300 m, were used for bacterial production incubations and biomass estimates. During the SW-monsoon additional CTD casts in the Somali Current, Gulf of Aden and Red Sea

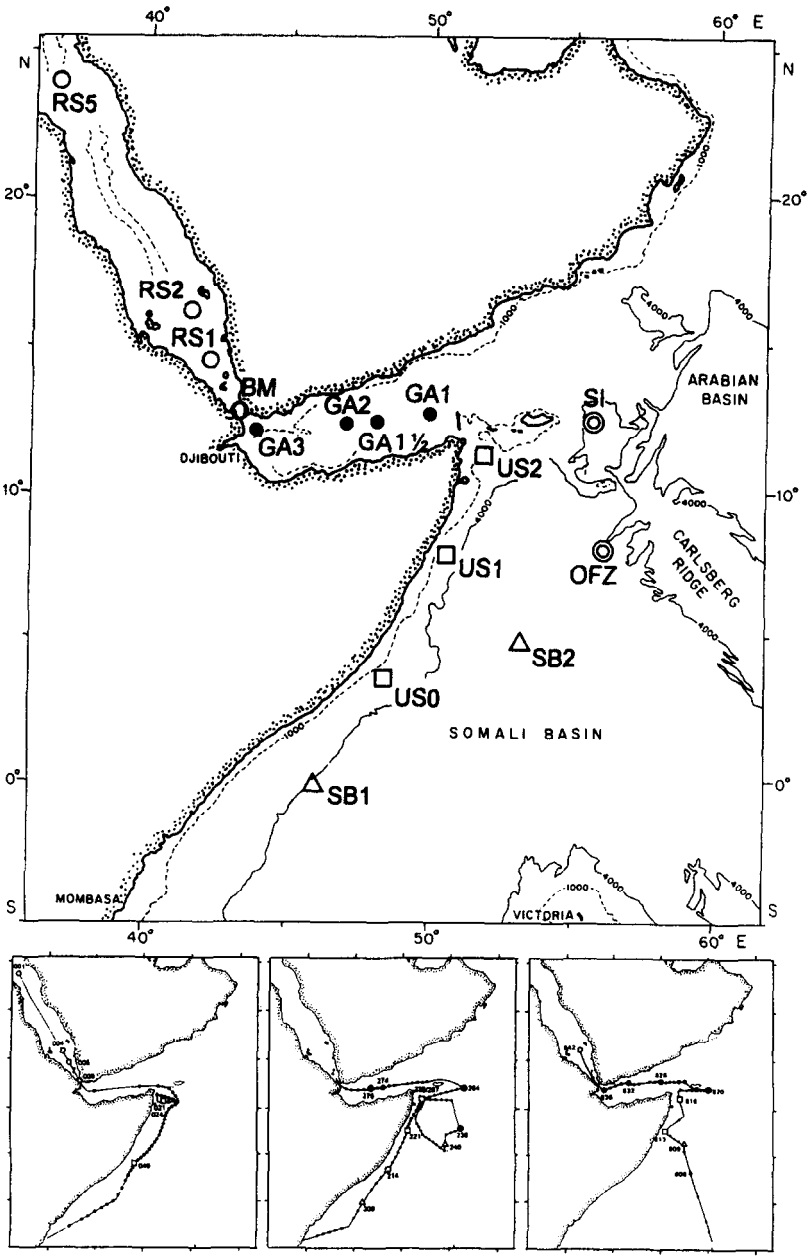

Fig. 1. Chart of the NW Indian Ocean, including the Gulf of Aden and the Red Sea, showing the position of stations (upper panel) and cruise tracks of the three surveys (lower panels) of the project "Monsoons and Pelagic Systems" during the Netherlands Indian Ocean Programme 1992–1993. Station codes involve five regions: Somali Basin Equator (SB); Upwelling Somali Current (US); Somali Basin North consisting of Socotra Island (SI) and Owen Fracture Zone (OFZ); Gulf of Aden (GA); Red Sea (RS) including Bab-el-Mandab (BM).

Table 1. *Sampling dates, station numbers and positions, variables and depths of the mixed layer, depth of pycnocline and euphotic zone (0.5% of surface irradiation)*

Date	Local time (h)	Station code	Station no.	Position N	Position E	Mixed layer Temp (°C)	Mixed layer Nitrate (μM)	Mixed layer Chl *a* (μg.l^{-1})	Mixed layer Depth (m)	Pycnocline (m)	Euphotic zone (m)
Onset SW-monsoon											
23 May 92	14:05	RS5	1	23 38	36 46	25.3	0.04	0.3	44	44	n.d.
27 May 92	05:25	RS2	4	15 47	41 26	30.1	0.00	0.2	10	43	56
28 May 92	05:14	RS1	5	14 50	42 16	30.0	0.05	0.2	12	61	56
29 May 92	05:10	BM	6	12 46	43 14	30.2	0.02	0.2	18	32	56
2 Jun 92	21:48	US2	21	10 45	51 57	26.3	n.d.	**4.7**	24	24	19
4 Jun 92	08:05	US2	24	10 46	51 57	25.8	**3.2**	**0.8**	35	35	31
8 Jun 92	11:40	US0	49	04 00	49 00	26.8	**1.5**	**0.8**	29	29	n.d.
SW-monsoon											
15 Jul 92	04:10	SB1	209	−00 16	45 52	26.5	0.3	0.4	72	98	64
17 Jul 92	04:25	US0	214	03 02	48 11	26.5	n.d.	0.4	48	98	62
17 Jul 92	21:15	US0	214	03 28	48 34	26.4	n.d.	0.4	63	95	62
18 Jul 92	10:00	US0	214	03 48	48 49	26.3	0.7	0.4	64	96	62
19 Jul 92	04:44	US1	221	06 32	49 42	21.3	**8.6**	0.4	16	0	55
22 Jul 92	05:33	US2	230	10 48	52 07	18.7	**17.6**	0.3	64	0	40
26 Jul 92	05:05	OFZ	236	07 52	55 57	25.5	**3.7**	0.4	65	0/168	54
27 Jul 92	04:15	SB2	240	07 02	54 29	25.1	**2.5**	0.4	40	0/168	44
30 Jul 92	07:10	US2	257	10 48	52 00	23.1	**12.1**	**0.7**	31	0	28
1 Aug 92	06:50	SI	264	12 04	56 19	23.2	**8.7**	0.5	31	0/130	23
5 Aug 92	09:23	GA1.5	274	12 19	48 00	30.5	0.0	0.3	77	77	73
6 Aug 92	05:39	GA2	276	12 04	46 43	29.7	0.1	0.2	50	50	73
NE-monsoon											
15 Jan 93	04:02	SB2	809	06 10	52 30	26.8	0.1	0.4	32	36	69
18 Jan 93	04:47	US1	813	07 35	50 33	26.7	0.3	0.3	67	67	56
19 Jan 93	05:31	US1	813	07 55	50 40	26.6	0.3	0.3	75	75	56
21 Jan 93	04:05	US2	818	11 04	52 03	26.0	0.9	0.3	80	83	35
21 Jan 93	19:50	US2	818	11 13	52 01	26.0	1.1	n.d.	62	62	35
25 Jan 93	06:48	SI	820	12 02	54 53	26.0	0.9	0.3	87	87	64
27 Jan 93	05:15	GA1	826	12 45	50 05	25.8	0.4	0.5	93	93	63
30 Jan 93	04:29	GA2	832	12 55	46 39	25.4	1.5	0.5	63	75	41
1 Feb 93	03:55	GA3	836	12 01	43 53	25.8	0.4	0.4	52	127	42
4 Feb 93	04:32	RS2	842	16 00	41 33	25.7	0.7	**1.1**	52	52	35

Bold values represent upwelling sites.

were conducted down to 2000 m (stations US2, GA1.5 and RS5; Fig. 1) for bacterial biomass.

Subsamples from the NOEX bottles were transferred to 250-ml bottles and brought into a lab container for incubation preparation immediately after sampling. Transfer and incubation bottles had been acid washed and rinsed carefully three times with sample water prior to use. From each CTD cast, up to 24 depths were analysed for nutrients (nitrate, nitrite, phosphate, silicate and ammonia) using Technicon autoanalyzers. All hydrographic upcast CTD data, including nutrient and chlorophyll concentrations, are listed in Hiehle and Baars (1994) and are also available on CD-ROM (GOA, 1995).

Bacterial enumeration and biomass

Aliquots of 50 ml were preserved with glutaraldehyde at a final concentration of 1.0% and stored at 5°C. Within a few days, 2–30 ml sample was filtered on to prestained (Sudan black) polycarbonate filters (Poretics, 0.2-μm pore size, 25 mm diameter) and stained for 2 min with Acridine Orange at a final concentration of 0.01%. To facilitate an equal distribution of bacteria, the filter was backed with a cellulose acetate filter (Schleicher and Schuell, 0.45-μm pore size, 25 mm diameter) pre-soaked in filter-sterilised sea water. The filters were mounted on microscopic slides in non-fluorescence immersion oil (Olympus Optical Co., Ltd) and stored frozen. All solutions were preserved with glutaraldehyde and filter-sterilised before use. Blank checks were made regularly to test for particles.

Counting and sizing was performed at 1250× magnification (Leitz Laborlux epifluorescence microscope equipped with a 50-W Hg lamp and filter set for blue and green excitation) using a calibrated ocular grid with cell sizes of 4×4 μm (Hobbie *et al.*, 1977; Lee and Fuhrman, 1987; Fry, 1990). Depending on cell densities, 2–30 ml water of each sample was filtered, resulting in approximately 20 cells per field. Bacteria were counted in 10 different fields, with a minimum of 200 cells. Bacterial cell sizes were estimated and converted to biovolume by treating rods and cocci, respectively, as cylinders and spheres. Cocci were divided into three size classes with volumes of 0.004, 0.034 and 0.27 μm^3 (diameters 0.2, 0.4 and 0.8 μm, respectively) and rods over 15 size classes ranging from 0.025 to 2.0 μm^3 (including cell lengths of 0.8, 1.3, 2.0, 4.0, 6.0, 8.0 and 10.0 μm and different diameters). The relatively large contribution of the big rods to the total biovolume made it necessary to divide them into a large number of size classes to minimise the statistical error. Cell carbon was calculated from biovolume by using a conversion factor of 0.31 pgC μm^{-3} (Fry, 1990).

Bacterial production

The bacterial production was calculated from [^{3}H]thymidine (TTI) and [^{3}H]leucine (TLI) incorporation rates into the macromolecular fraction extracted with cold trichloroacetic acid (TCA) (Fuhrman and Azam, 1982; Simon and Azam, 1989; Moriarty, 1990). Duplicate or triplicate water samples of 10 ml were incubated for 60 min with [methyl-^{3}H]thymidine (Amersham, 87 Ci $mmol^{-1}$) or L-[4,5-^{3}H]leucine (Amersham, 151 Ci $mmol^{-1}$ diluted 10 times with cold leucine) in 30-ml polycarbonate centrifuge tubes (Nalgene) at *in situ* temperature in the dark. The amounts of tracer added were 10 nM thymidine or 10 nM leucine during the SW-monsoon and 2 nM thymidine or 20 nM leucine during the NE-monsoon, on the basis of test runs described in section 3. Deep samples with low ambient temperature were incubated for 2 h. Incubations were stopped by addition of 600 μl 37% formaldehyde. A prekilled sample was used as a blank. After addition of 550 μl 100% (w/v) ice-cold TCA, the samples were filtered with a Millipore sampling manifold on to 0.2-μm polycarbonate filters (Poretics, 25 mm diameter), rinsed seven times with 2 ml 5% ice-cold TCA and placed in glass vials (Packard) with 10 ml LSC-cocktail (Packard, Filter-count). After 24 h, the samples were radio-assayed in a LKB Rack-Beta liquid scintillation counter.

Radiotracer incorporation rates, expressed as pM h^{-1}, were calculated from the formula:

$$\text{TTI or TLI} = (\text{DPMs} - \text{DPMb})(\text{SV} \times \text{T} \times \text{SA} \times 2.22)^{-1}$$

where: DPMs = disintegrations per minute of the sample on the filter;

DPMb = disintegrations per minute of the blank on the filter; SV = sample volume (l); T = incubation time (h); SA = specific activity of the radiotracer (Ci mol^{-1}).

For comparability in terms of carbon, the corresponding carbon productions were calculated using conversion factors from the literature: 1.1×10^{18} cells mol^{-1} TTI (Riemann *et al.*, 1987; Bjørnsen and Kuparinen, 1991) and 1545 gC mol^{-1} TLI (Simon and Azam, 1989; Moriarty, 1990), assuming no isotope dilution of [^{3}H]leucine. These values are deemed to be lower estimates due to combined theoretical and experimental considerations (Fuhrman and Azam, 1982; Simon and Azam, 1989; Moriarty, 1990). From the number of bacteria dividing per hour (TTI) the carbon production was calculated with 34 fgC $cell^{-1}$ (0.31 pgC.μm^{-3} taken from Fry (1990) and an average cell volume of 0.11 μm^3 obtained in this study). For evaluation of the above conversion factors taken from the literature, these were furthermore determined experimentally during the SW-monsoon (station US2) with the method described by Bjørnsen and Kuparinen (1991). The ensuing conversion factor was calculated to be 2.8×10^{18} cells mol^{-1} TTI. Trapezoid integration was used to calculate integrated values over the depth range from surface to 300 m.

3. RESULTS

Hydrography in the Somali Current, Gulf of Aden and Red Sea

In the Somali Current, upwelling had already started at the beginning of June 1992. Figure 2 gives north–south sections of temperature in the Somali Current based on XBT probe data collected during the onset and peak of the SW-monsoon. At the onset of the SW-monsoon (Fig. 2a) upwelling occurred at 11°N, where the 25°C isotherm approached the surface. An XBT section perpendicular to the coast shows the 25°C isotherm sloping up towards the coast, from 100 m at 53°30′E to 20–40 m at 52°E (Fig. 3). A second upwelling area was encountered at 3–5°N. In the upwelling areas surface temperature was below 26°C, and mean nitrate and chlorophyll concentrations were much higher than offshore. However, patchiness resulted in surface waters high in nutrients and still low in chlorophyll *a*, adjacent to waters with massive phytoplankton blooms. Six weeks later, during the peak of the SW-monsoon, the southern upwelling area had disappeared. Between 0° and 5°N the thermocline was located below 100 m, and to the north the isotherms sloped up to the surface. In a pronounced upwelling area at 7–11°N, the surface temperature dropped below 22°C, with lowest temperature < 18°C and nitrate concentration > 18 μM at 9°N. Perpendicular to the coast the 25°C isotherm sloped up from 100 m in the east and reached the surface at 51°15′E, indicating that upwelling was restricted to a small band along the coast of Somalia (Fig. 3). In the cold, nutrient-rich water of the upwelling area, the chlorophyll concentration was still relatively low in late July, indicating that the phytoplankton stock had just started to develop. Eastward into the "Great Whirl", surface temperature was low and nutrient concentrations were relatively high compared to the equatorial part of the Somali Current. The build-up of large biomass was restricted to eddies near the coast, where chlorophyll concentrations were found as high as 15 mg m^{-3}. The NE-monsoon was much more homogenous but far from oligotrophic, with nitrate concentrations > 0.3 μM at the sea surface. The water column was well mixed down to 100 m, and chlorophyll concentrations were *ca* 0.4 mg m^{-3}.

The Gulf of Aden and the Red Sea had an oligotrophic nature at the end of May 1992, with low nutrient and chlorophyll concentrations in the surface water. Similar conditions

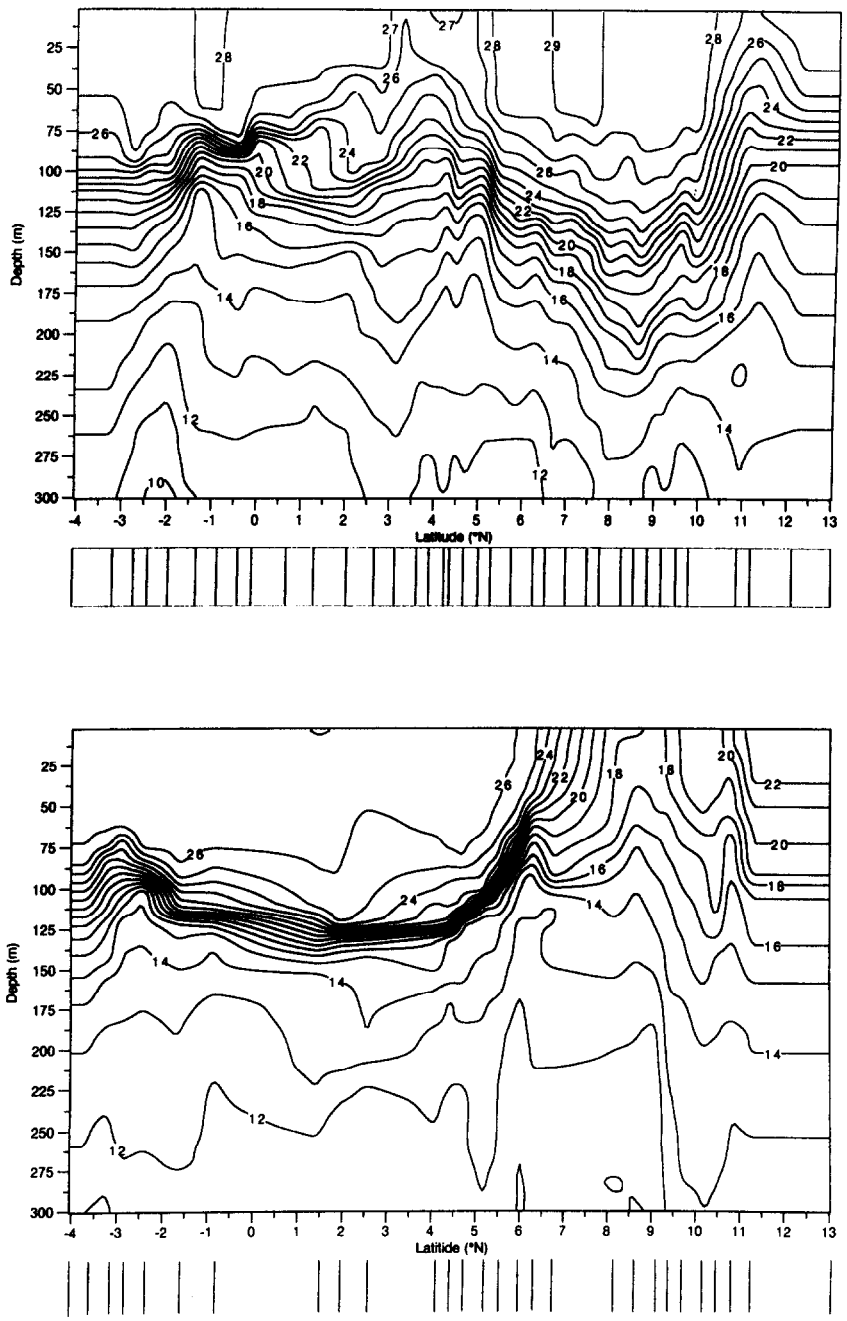

Fig. 2. Contour plot of temperature profiles, obtained by XBT probes, along the north–south section of the Somali Current during the onset (upper panel) and peak (lower panel) of the SW-monsoon, May 31–June 11 and July 12–23, 1992, respectively. Bars below latitude axis indicate XBT

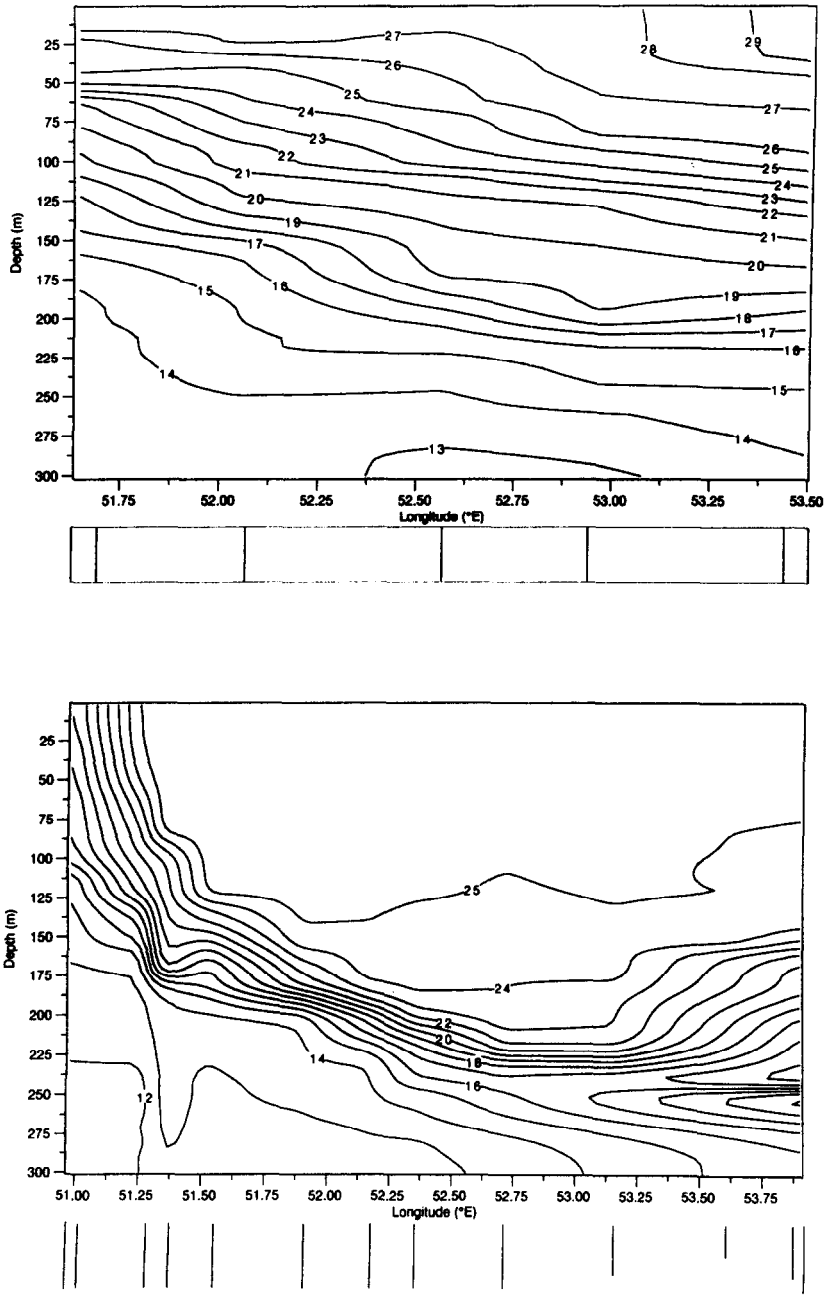

Fig. 3. East–west transect of XBT probes. Upper panel shows data collected in the Somali Current, during the onset of the SW-monsoon (June 1–2, 1992) lower panel during the peak of the SW-monsoon (July 28–29, 1992). Bars below latitude axis indicate XBT positions.

existed in most parts of the Gulf of Aden during the peak of the SW-monsoon, except for a cold water mass south of Strait Bab-el-Mandab, in which chlorophyll *a* increased to about 5 mg m^{-3}. This was derived from upwelling along the coast of Yemen, from which a filament extended south into the Gulf of Aden. Inflow of water from the Gulf of Aden into the Red Sea occurred at intermediate depth during summer, in contrast to surface inflow encountered at the end of May 1992. The NE-monsoon was characterised by a decrease in surface temperature of approximately 5°C, compared with summer, and a deepening of the mixed layer. The resulting entrainment of nutrients favoured an increase in phytoplankton stock in both the Gulf of Aden (0.3–0.6 mg m^{-3}) and the Red Sea (0.5–1.3 mg m^{-3}).

Plankton blooms

During the SW-monsoon, blooms of phytoplankton resulted in high primary production, up to 2.8 gC m^{-2} day^{-1} in the Somali Current (Table 2). In patches with high chlorophyll concentrations the large algae, consisting mainly of diatoms, dominated the phytoplankton composition (Baars *et al.*, 1994). During the onset of the SW-monsoon, such diatom blooms were encountered around 11°N (station US2), but chlorophyll concentrations in this area ranged from 0.2 to 2.7 mg m^{-3}, reflecting the pronounced patchiness. At the peak of the SW-monsoon the upwelling area with cold water along the coast of Somalia (station US2) had relatively low chlorophyll concentrations, but vigorous blooms, with chlorophyll concentrations reaching 15 mg m^{-3}, occurred in eddies near Ras Hafun. Downstream water masses (station OFZ, SI and SB2), although not depleted in nutrients, remained low in chlorophyll *a* (<0.6 mg m^{-3}). During the NE-monsoon, chlorophyll concentrations were *ca* 0.4 mg m^{-3}, and phytoplankton composition was typically dominated by picophytoplankton (up to 80% of total chlorophyll *a* content; Veldhuis *et al.*, 1997). A deep chlorophyll maximum was absent, and mean primary production in the Somali Current was 0.8 gC m^{-2} day^{-1}.

Phytoplankton communities in the Gulf of Aden and the southern Red Sea were dominated by picophytoplankton. Production in the southern Red Sea peaked in a deep chlorophyll maximum at about 50–60 m depth. The Gulf of Aden showed less pronounced subsurface chlorophyll maxima. Both the Gulf of Aden and the Red Sea were most productive during the NE-monsoon (mean primary production 1.5 gC m^{-2} day^{-1} compared to 0.5 gC m^{-2} day^{-1} in the SW-monsoon). Nutrient enrichment favoured phytoplankton blooming consisting mainly of cyanobacteria in the Gulf of Aden and diatoms in the Red Sea (Veldhuis *et al.*, 1997).

Depth variation in bacterial abundance during the SW-monsoon

Examples of vertical profiles of bacterioplankton abundance in the three major areas are given in Fig. 4. High numbers of bacteria were found above the thermocline, but below, numbers rapidly decreased with depth to about 0.3×10^9 cells l^{-1}. The number of bacteria in the upper layer was variable with depth and geographic site but never exceeded 3.0×10^9 cells l^{-1}. Mean mixed layer values, given in Table 3, ranged from 1.0 to 2.5×10^9 cells l^{-1}. With an average of 1.6×10^9 cells l^{-1}, no difference was apparent between oligotrophic stations and stations in the upwelling area. Numerical abundance peaked at most stations at the 20–50 m depth interval, often accompanied by a second maximum at greater depth (50–100 m), and declined exponentially with depth between 50

Table 2. Maximum incorporation rate of [^{3}H]thymidine and [^{3}H]leucine and depth integrated bacterial and primary production in the NW Indian Ocean

		Bacterial production							
		TTI		TLI		Primary production			
Station code	Station no.	(pM h^{-1})	(mgC m^{-2} day^{-1})	(pM h^{-1})	(mgC m^{-2} day^{-1})	(mgC m^{-2} day^{-1})	BP/PP (%)	% chl *a*	%TTI
Somali Basin Equator									
SW-monsoon									
SB1	209	2.2	179			716	25	73	62
US0	214	1.4	100	39.1	118	1149	9	78	70
US0	214	1.9	132	60.7	187				64
US0	214	1.8	142						57
Somali Current									
Onset SW-monsoon									
US2	21	22.7	849			2810	30		34
US2	24	5.2	235			1415	17	65	43
US0	49	2.3	164	49.8					
SW-monsoon									
US1	221	0.8	65			761	9	60	46
US2*		3.5				2800			
US2	230	1.1	110			920	12	49	29
US2	257	2.4	171			1128	15	41	34
NE-monsoon									
US1	813	2.2	139	54.5	148	686	20	60	73
US1	813	1.4	100			461	22	78	66
US2	818	1.2	82	40.3	137	519	16	55	38
US2	818	1.4	73	48.4	106				46
Somali Basin North									
SW-monsoon									
OFZ	236	2.8	223	87.6	348	974	23	41	36
SB2	240	1.6	148			972	15	30	24
SI	264	3.8	202			845	24	24	24
NE-monsoon									
SB2	809	2.9	139	79.0	160	1021	14		80
SI	820	1.6	129			906	14	63	70
Gulf of Aden and Red Sea									
Onset SW-monsoon									
RS5	1	1.1							
RS2	4	1.3	68						52
RS1	5	2.3	163			592	28	52	52
BM	6	1.4	78			514	15	53	72
SW-monsoon									
GA1.5	274	1.2	99						66
GA2	276	0.7	77	29.6	68	501	15	82	49
NE-monsoon									
GA1	826	2.7	263	81.3	340	1619	16	77	55
GA2	832	2.6	184	108.2	299	1221	15	68	46
GA3	836	2.7	227	76.4	285	2203	10	44	43
RS2	842	5.1	224	174.4	320	651	34	65	56

Bacterial production calculated from TTI (conversion factors 1.1×10^{18} cells mol^{-1} and 34 fgC cell^{-1}) integrated to 300 m. See Fig. 1 for sampling sites; [^{3}H]thymidine incorporation; [^{3}H]leucine incorporation; BP/PP, bacterial production (TTI) expressed as percentage of primary production; % chl *a*, percentage of chlorophyll in the euphotic zone; % TTI, percentage of bacterial production (TTI) in the euphotic zone; US2*, surface sample taken from bow inlet.

and 150 m. The lowest bacterial numbers of 1.0×10^9 cells l^{-1} were found in surface water with low temperature and high nutrient concentrations, characteristic for recently upwelled water (station US0, during onset SW-monsoon, and US1). The highest abundance occurred in secondary subsurface maxima at productive stations within the upwelling zone (station US2) and downstream of the upwelling area (OFZ) (see also below paragraph on

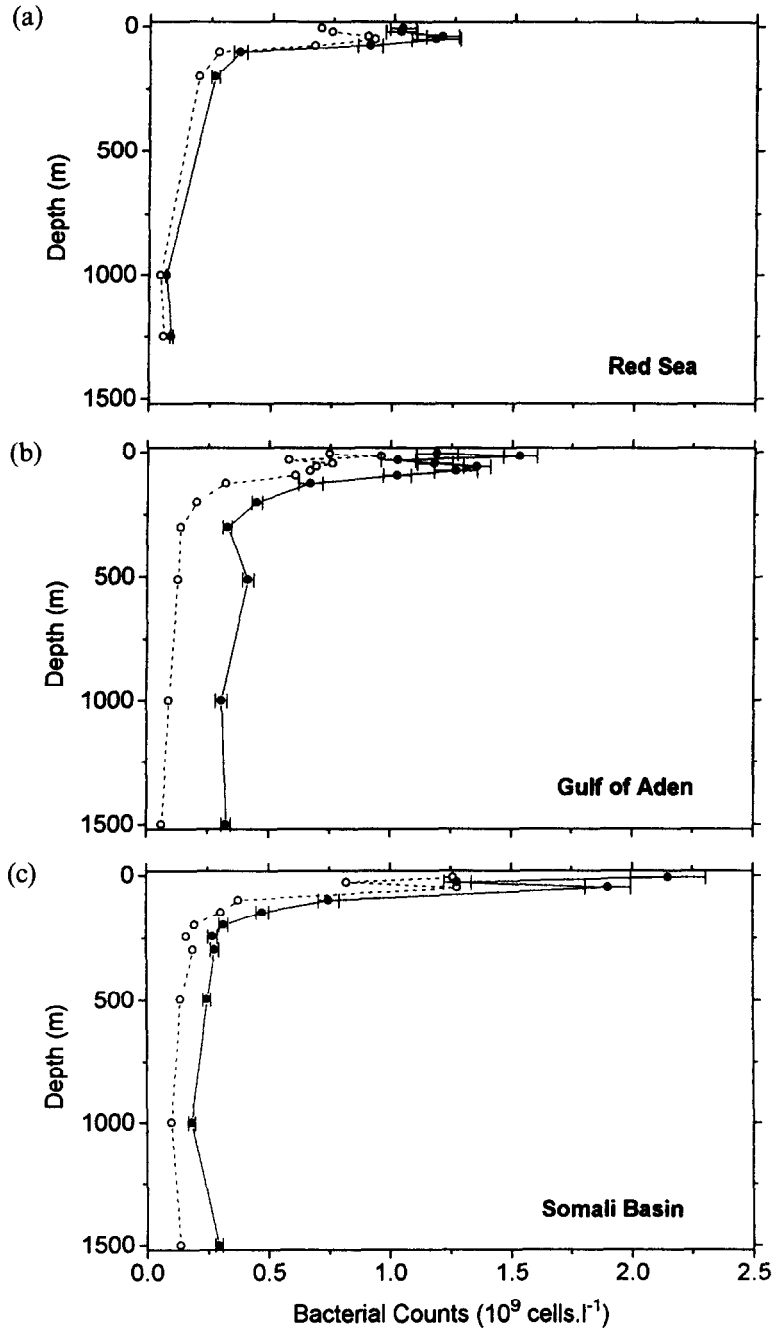

Fig. 4. Vertical profiles of bacterial numbers during the SW-monsoon in (a) Red Sea (station RS5), (b) Gulf of Aden (station GA1.5) and (c) Somali Current (station US2–21). Solid symbols represent total number of bacteria and open symbols the size class consisting of small cocci.

Table 3. *Mean mixed layer values of bacterial counts and biomass during May–August* 1992

Station code	Station no.	Bacterial counts (10^9 cells l^{-1})	Ratio cocci/rods	Bacterial biomass ($\mu g\ C\ l^{-1}$)	Generation time (days)
Oligotrophic					
RS5	1	1.1	2.8	24	25
RS2	4	1.7	2.3	45	39
RS1	5	2.3	4.7	34	29
BM	6	1.6	2.5	28	33
SB1	209	2.5	1.3	66	37
US0	214	1.8	3.3	27	35
GA1.5	274	1.2	1.6	24	35
GA2	276	1.2	2.1	16	53
Mean		**1.7**	**2.6**	**33**	**36**
Upwelling					
US2	21	2.1	1.6	84	3
US2	24	1.7	1.8	55	12
US0	49	1.0	2.3	23	14
US1	221	1.4	2.2	26	42
US2	230	1.5	0.9	45	44
OFZ	236	1.9	1.3	42	34
SB2	240	1.4	1.2	35	42
US2	257	2.1	1.8	46	25
SI	264	1.5	1.6	23	15
Mean		**1.6**	**1.6**	**42**	**26**

Depth of mixed layer given in Table 1.

development of a bloom). In the Red Sea bacterial numbers were low in the northern part (1.1×10^9 cells l^{-1}) but increased towards Bab-el-Mandab (maximum of 2.4×10^9 cells l^{-1} at station RS1). On average 1.2×10^9 cells l^{-1} were found in the euphotic zone of the Gulf of Aden.

Bacterial biomass in the mixed layer, calculated from total cell volume, is given in Table 3. Biomass was slightly higher in the upwelling area compared to the more oligotrophic stations (42 and 33 $\mu gC\ l^{-1}$, respectively). On the basis of cell volumes the bacteria could be divided into two groups, one consisting of very small cocci with weighted average volume of 0.022 μm^3, and a group of much larger rods of 0.19 μm^3. Although small cocci dominated the euphotic zone in number (at all stations ratio cocci/rods > 1; Table 3), their tenfold lower volume resulted in an equal or lower contribution to the total bacterial biomass. Upwelling favoured the contribution of the rods to the total number of bacteria (average ratio 1.6 compared to 2.5 at the oligotrophic stations). At all stations the ratio cocci/rods decreased slightly with depth.

Variation in bacterial production during SW- and NE-monsoon

For each cruise the dependence of radiotracer incorporation on incubation time and radiotracer concentration was tested and the incubation conditions chosen accordingly to ensure complete saturation of the incorporation. For this purpose the incorporation in a sample of the mixed layer was studied as a function of either the thymidine and leucine

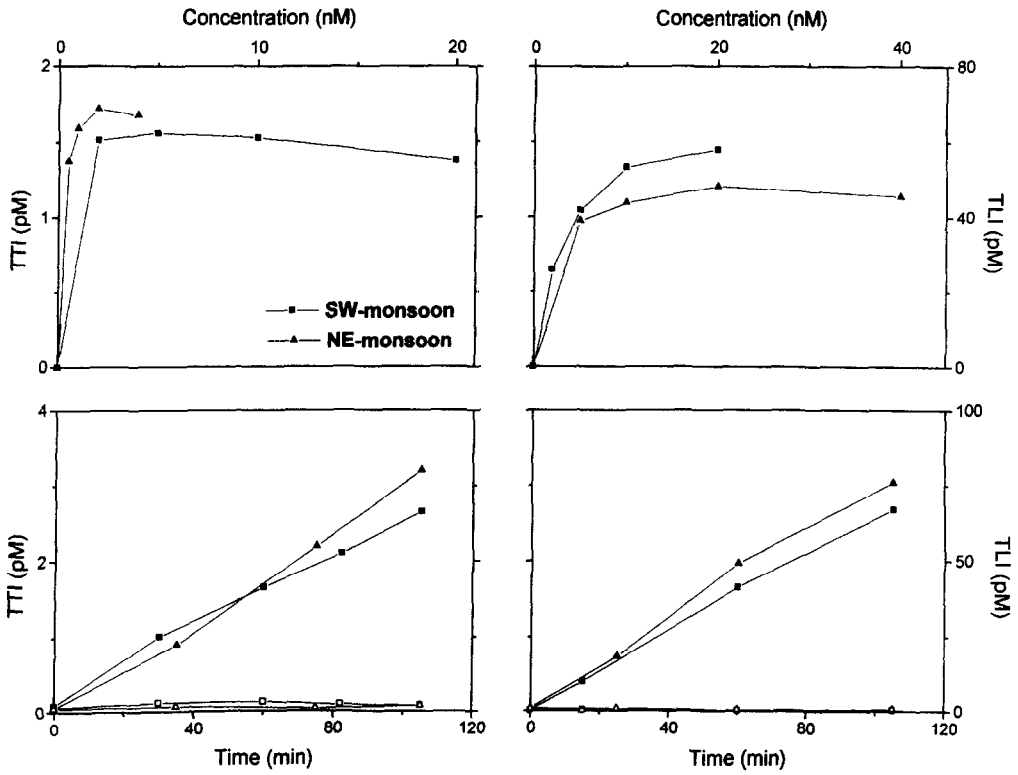

Fig. 5. Dependence of radiotracer incorporation on incubation concentration (upper panel) and incubation time (lower panel) measured as pM of [^{3}H]thymidine (TTI) or [^{3}H]leucine (TLI) incorporated into the macromolecular fraction (cold TCA insoluble material). Duration of incubations in upper panels: 60 min. Conditions in lower panels: 2 and 10 nM [^{3}H]thymidine, 10 and 20 nM [^{3}H]leucine. Squares, SW-monsoon; triangles, NE-monsoon; open symbols, blank controls. Similar results were obtained during the onset of the SW-monsoon.

concentration or incubation time by keeping one of these constant. Results of these tests during the SW- and NE-monsoon are shown in Fig. 5. The incorporation of both tracers versus time was proportional for at least 105 min, indicating that the added tracer concentrations did not change the DNA or protein synthesis rates. Uptake rate saturated at different substrate concentrations, which differed by a factor of 10 (1–2 nM for thymidine and 20 nM for leucine). Subsequently a relatively high concentration of 10 or 20 nM leucine was used for the incubations. On the basis of these tests we implemented the following conditions: during the SW-monsoon, 10 nM thymidine or 10 nM leucine was added for 1 h incubation; during the NE-monsoon, 2 nM thymidine or 20 nM leucine was added for 1 h incubation. Precision of incorporation rates was on average $14 \pm 16\%$ (mean $\pm$ 1 s.d.; $n = 385$).

Vertical profiles of [^{3}H]thymidine incorporation rates (TTI) are given in Fig. 6. They followed the same pattern as the bacterial abundance profiles, with high values in the euphotic zone declining with depth to very low values, characteristically within 100 m. Profiles consisted of a well-defined subsurface maximum at 25–50 m and up to two

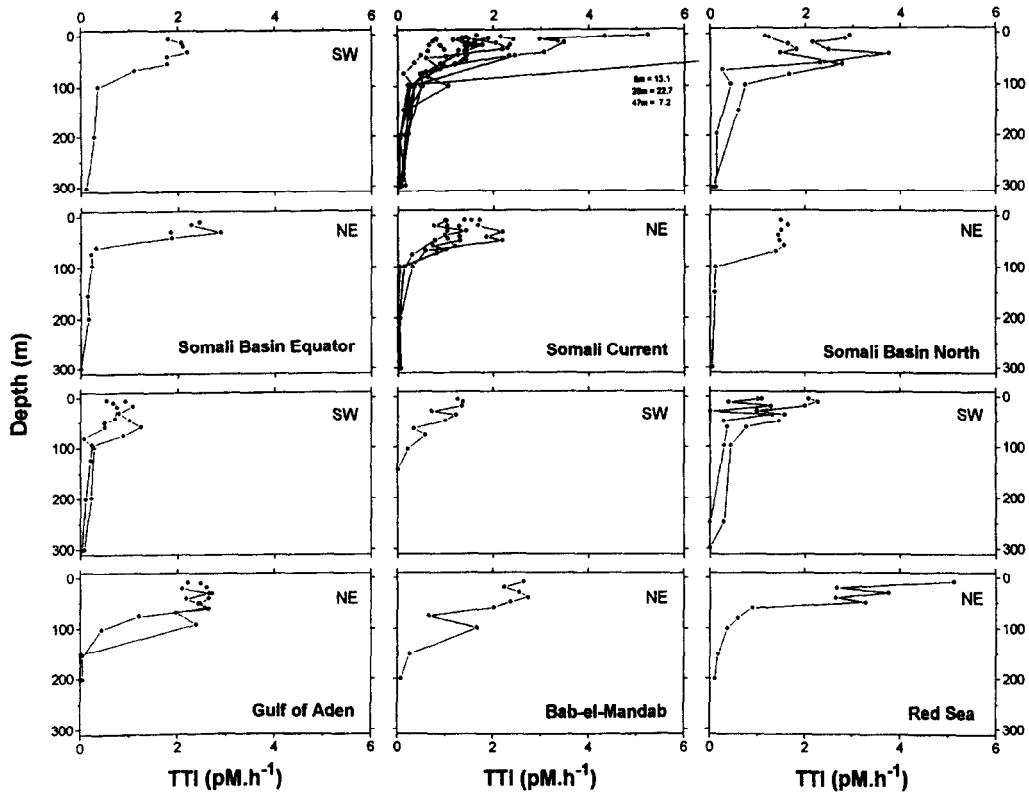

Fig. 6. Composite of vertical depth profiles of [^{3}H]thymidine incorporation rates at stations in the Somali Basin, Gulf of Aden and the Red Sea during the SW-monsoon and NE-monsoon. In the upper panel the stations in the Somali Basin are divided over three regions with different hydrography: Somali Basin Equator; upwelling Somali Current; Somali Basin North. Lower panels shows stations in Gulf of Aden, Bab-el-Mandab and Red Sea.

additional maxima at depths ranging from 50–100 m. During the SW-monsoon, the Somali Current could be divided into three regions: (i) the Somali Basin equator (SB1), (ii) the upwelling area off Somalia (US), with great variability (maximum TTI ranging from 0.8 to 22.7 pM h^{-1}), and (iii) average high rates downstream of the upwelling zone (SI, OFZ). Table 2 summarises maximum and depth-integrated productivity of bacterioplankton measured with TTI and TLI for comparison with primary production (Veldhuis *et al.*, 1997). In contrast to phytoplankton, with productivity limited to the euphotic zone, bacterioplankton production continues at greater depths. In this respect a comparison can be made of the maximum depth at which algae occur with the depth to which bacterial numbers are constant (about 300 m). This is also the depth at which bacterial production reached constant low values. Abundance and production profiles of the bacteria in general showed a subsurface maximum in the upper 100–200 m, declining exponentially below that depth. Therefore the depth of 300 m was considered to be a reliable lower boundary for estimating turnover of organic material within the microbial loop. Below that depth, bacteria are considered to participate in particle breakdown, which is beyond the scope of

this research. Highest TTI in the Somali Current, 4.2–22.7 pM h^{-1} (the two highest production profiles in Fig. 6), were encountered during the onset of the SW-monsoon; 6 weeks later, TTI was less than 3.1 pM h^{-1}. Over the whole area bacterial production ranged from 65 up to 849 mgC m^{-2} day^{-1} (average 215). The variation in productivity reflected the patchiness in this area (see section on hydrography). During the NE-monsoon, all stations in the Somali Current had similar TTI profiles, with subsurface maxima of 1.2–2.2 pM h^{-1}, except for the southernmost station sampled (SB2), where maximum activity was slightly higher (2.9 pM h^{-1}) but restricted to the shallow mixed layer. The bacterial production, ranging from 73–139 mgC m^{-2} day^{-1}, was lower than in the SW-monsoon period, despite the entrainment of nutrients in the wind mixed layer (no oligotrophic situation).

In contrast to the Somali Current, the Gulf of Aden and the Red Sea were much more productive during the NE-monsoon than during the SW-monsoon. During the SW-monsoon, maximum TTI in the Gulf of Aden was 0.7–1.2 pM h^{-1}, resulting in an average bacterial production of 88 mgC m^{-2} day^{-1}. The Red Sea had slightly higher TTI, with pronounced subsurface maxima and a bacterial production of 1.1–2.3 mgC m^{-2} day^{-1}. The NE-monsoon production was higher in both areas, with TTI maxima in the euphotic zone varying by a factor two (ranging from 2.6 to 5.1 pM.h^{-1}) and an average production of 225 mgC m^{-2} day^{-1}.

Bacterioplankton during the development of a bloom

The variability in the upwelling area off Somalia during the SW-monsoon was closely related to the evolution of the developing phytoplankton bloom. In Fig. 7 different stations in this area are ranged in order, representing the evolution of the upwelling: from non-upwelling (US0) through the different stages of the upwelling (US1 and US2) to the area downstream of the upwelling (SI). The initial stage was characterised by a deep mixed layer overlying the distinct thermocline at a depth well below 100 m (similar to the Somali Basin Equator). At the southern border of the upwelling zone (first upwelling station US1), the thermocline reached the surface, introducing high nutrient concentrations (nitrate > 8 μM) in the surface water and diminishing phytoplankton biomass (chlorophyll $a < 0.5$ mg m^{-3}). During upwelling, water low in bacterial numbers is transported to the surface, resulting in very low bacterial production at this station (65 mgC m^{-2} day^{-1}; lowest production encountered in this study). The establishment of a new mixed layer (US2-230) initially reduced the surface temperature to 19°C (accompanied by an increase in nitrate to 18 μM) followed by warming of the surface mixed layer. With the subsequent development of the bloom (chlorophyll $a > 0.5$ mg m^{-3}) the TTI increased from 0.8 to 3.1 pM h^{-1} accompanied by a decrease in nitrate and, in the initial phase, an increase in bacterial numbers and biomass. Only in eddies extending the residence time of the surface water could TTI reach values of 22 pM h^{-1}.

Thymidine versus leucine incorporation

At 12 stations (eight during the NE-monsoon) bacterial production was determined with both [^{3}H]thymidine (TTI) and [^{3}H]leucine incorporation (TLI) rates. TLI showed a close relationship with TTI ($TLI = 32.5 \times TTI + 0.58$; $n = 121$; $p < 0.0005$; Fig. 8). Although small differences between stations existed, no significant differences were found between the

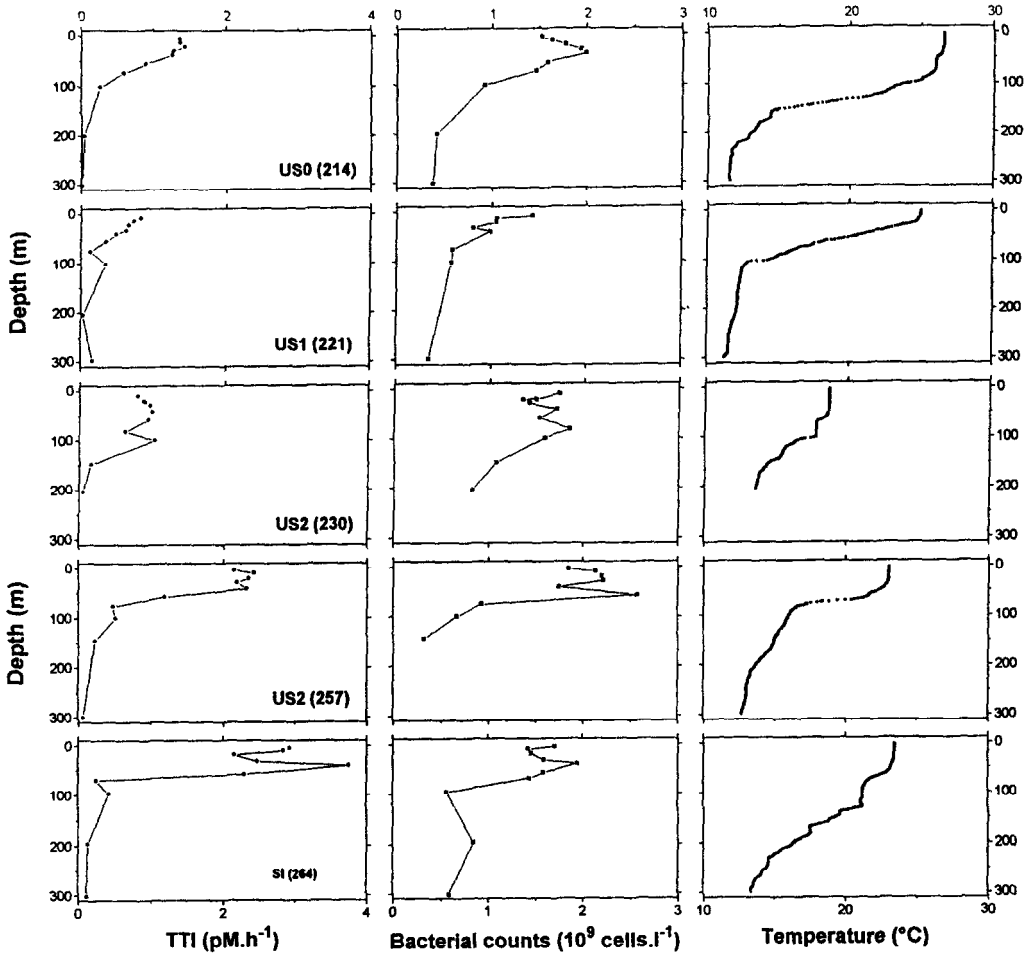

Fig. 7. Vertical profiles of [^{3}H]thymidine incorporation rates (TTI), bacterial total counts and temperature at five stations in the upwelling region of the Somali Current ranging from pre-upwelling (top) to downstream of the upwelling area (bottom).

different regions or seasons. In order to avoid diel variation in productivity and a possible shift between dividing (TTI) and growing (TLI) cells, samples were taken at a fixed time of the day (according to JGOFS protocols sampling was done before sunrise at approximately 04:00 h).

4. DISCUSSION

Monsoons, upwelling and blooms in the NW Indian Ocean

From infrared satellite images, it is clear that the northward propagation of the southern upwelling wedge, encountered at 4°N in May 1992, took place earlier in the year than the event reported by Evans and Brown (1981). By the time of the second visit to the area, 6 weeks later, the southern wedge had moved north, coinciding with the large upwelling area

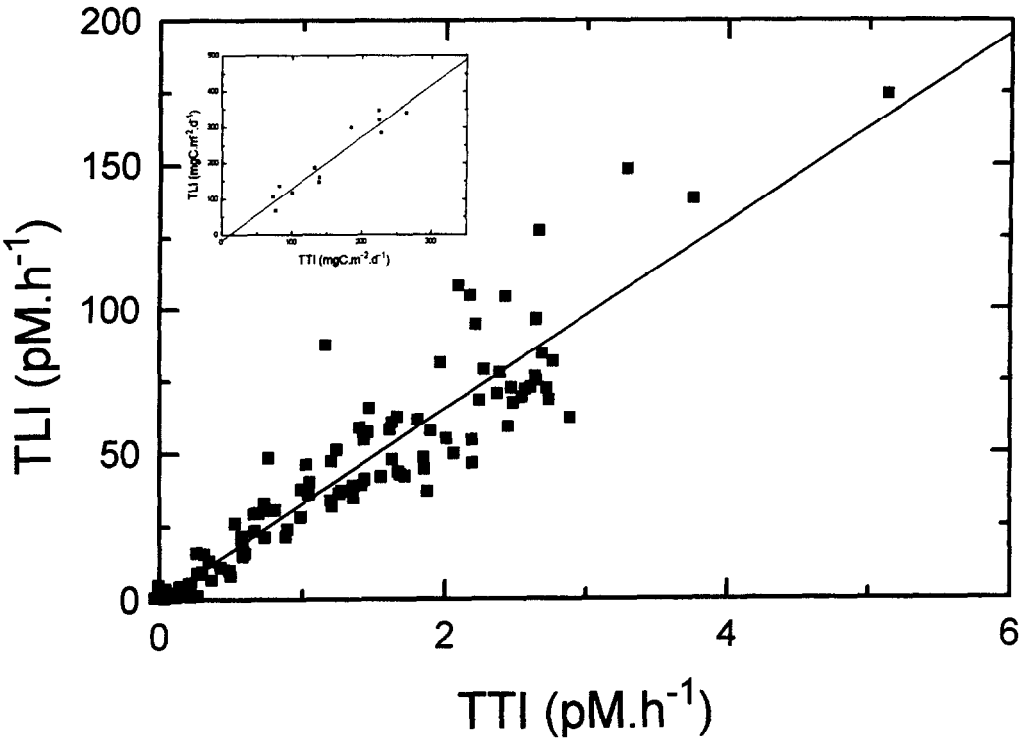

Fig. 8. Relationship of [^{3}H]thymidine (TTI) with [^{3}H]leucine (TLI) incorporation rates in the NW Indian Ocean. Data expressed as pM h^{-1} of 121 individual samples of all depths at all stations reported in this study. Inset shows data integrated to 300 m expressed as mgC m^{-2} day^{-1}, calculated from incorporation rates by using a conversion factor of 1.1×10^{18} cells mol^{-1} TTI, 34 fgC $cell^{-1}$ and 1545 gC mol^{-1} TLI.

called the "Great Whirl". High mean wind force drove the freshly upwelled water northward, diluting the starting phytoplankton bloom over a vast area. The complex structure of eddies was divided in two main directions, one bending off the Somali coast at 8°N eastwards into the Great Whirl (Schott *et al.*, 1990), and the other northeast towards Socotra Island (Baars *et al.*, 1994). Low chlorophyll concentrations in the cold upwelling area indicated that the phytoplankton stock had just started to increase. Although downstream water masses had higher biomass the strong wind mixed up to 75% of the chlorophyll *a* down the euphotic zone, thereby reducing primary production in this area (Table 2). Eddies might have extended the residence time of water upwelled near the coast, resulting in massive blooms adjacent to freshly upwelled water (Baars *et al.*, 1994). This leads to the pronounced patchiness in the Somali current during the SW-monsoon.

During the NE-monsoon, the Somali Current, although lower in production compared to the SW-monsoon period, was far from oligotrophic. Baars *et al.* (1994) suggest that nutrient enrichment of the surface layers was wind-induced. Based on weather reports the average wind force in January 1993 was considered to be above normal, reducing the extremities between the two monsoonal seasons in the NW Indian Ocean. The seasonality in the Gulf of Aden and the Red Sea appears to be reversed compared to the Somali Current; that is, rich in winter and oligotrophic during the SW-monsoon.

Changes in the bacterioplankton community

Despite the different types of surface waters and primary productivities encountered in this study, there was a strikingly small difference in spatial bacterioplankton abundance during the SW-monsoon (Table 3). Bacterial numbers in the mixed layer ranged from 1.0–2.5 × 10^9 cells l^{-1}, which is consistent with earlier data from the Indian Ocean collected during an intermonsoon period (Ducklow, 1993) and slightly higher compared to colder regions (Southern Ocean; Kuparinen and Bjørnsen, 1992). It appears that bacterial numbers remain rather constant, irrespective of the season (SW-monsoon versus intermonsoon). In the region with active upwelling (station US1), bacterial numbers in the mixed layer were lowest (*ca* 1.0 × 10^9 cells l^{-1}), which is in agreement with the low numbers present in deep water that have been transported to the surface by upwelling. Highest numbers were found in surface water during phytoplankton blooms and at depths of 100–150 m downstream of the actual upwelling area in matured water (Stations SI, OFZ). In contrast the dynamics of bacterioplankton in an upwelling plume in the southern Benguela (Painting *et al.*, 1993) showed a much higher increase in number (and biomass) up to 10 × 10^9 cells l^{-1} in the bloom area, decreasing downstream. Grazing possibly plays a major role in controlling the standing stock of bacteria. After an initial increase in bacterial number related to an increase in phytoplankton biomass and subsequent release of phytoplankton exudates, the numbers of heterotrophic nanoflagellates, feeding on picoautotrophs and bacteria, would increase, thus preventing further increase in bacterial numbers. Microzooplankton was dominated by very small flagellates, which were responsible for the high turnover of picoautotroph carbon (Reckermann and Veldhuis, in press). This negative feedback mechanism ensures the stability of the "regenerating system" or "microbial network" (Smetacek *et al.*, 1990).

In a microcosm simulation, Painting *et al.* (1989) followed the development and interactions of natural phytoplankton and microbial communities during the growth and decay of a phytoplankton bloom. Bacterial numbers were low in recently upwelled water and increased during phytoplankton growth, as in our observations. The community was dominated (both in numbers and biomass) by large cocci and small rods during phytoplankton growth, and by small cocci (numbers) and large rods (biomass) during phytoplankton decay. In contrast our study shows only a minor shift in the cocci/rods relationship during upwelling (Table 3). Over the whole region large rods dominated the entire water column in biomass, and small cocci dominated the surface waters in number.

Euphotic zone carbon fluxes

Bacterial production integrated to 300 m ranged from 65–849 mgC m^{-2} day^{-1} (Table 2), with maximum values in the upwelling area (station US2). Levels outside the upwelling area (average 135 mgC m^{-2} day^{-1}) are comparable with previous estimates from oceanic regions calculated with the same conversion factors (Kuparinen and Bjørnsen, 1992: 40–230 mgC m^{-2} day^{-1}; 0–150 m range) but are considerably lower than those reported from the Indian Ocean during September 1986 (Ducklow, 1993: 117–574 mgC m^{-2} day^{-1}; 0–100 m range). The latter discrepancy is even more striking when it is considered that a much lower conversion factor was used in the study of Ducklow (1993). For the sake of comparison the values of Ducklow (1993) were recalculated using our conversion factors and integration to 300 m, resulting in bacterial production ranging from 384 to 1696 mgC m^{-2} day^{-1}.

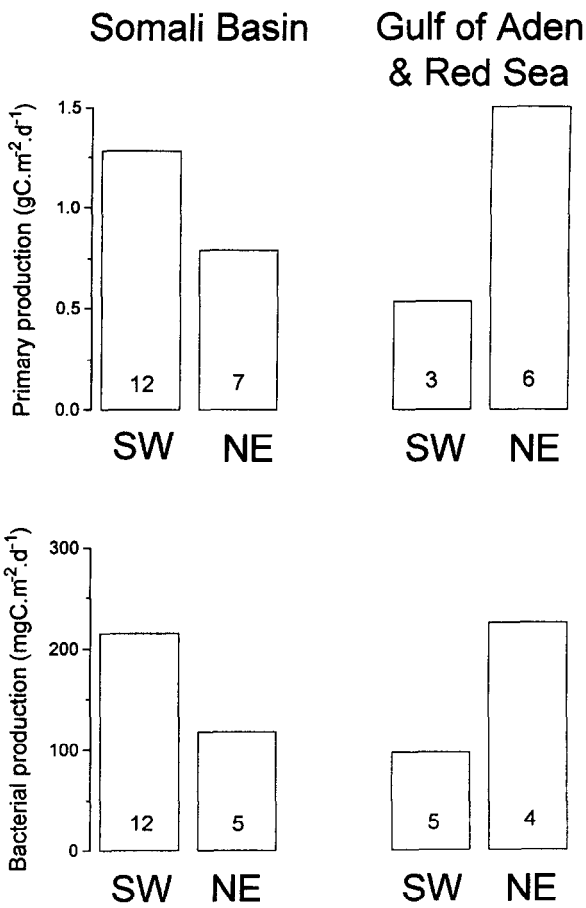

Fig. 9. Seasonal variation between SW- and NE-monsoon in primary production (gC m^{-2} day^{-1}) and (b) bacterial production (mgC m^{-2} day^{-1}) in two regions of the NW Indian Ocean. Number of stations averaged for each region indicated inside the columns. Bacterial production integrated to 300 m and calculated with 1.1×10^{18} cells mol^{-1} TTI and 34 fgC $cell^{-1}$. For the 21 individual stations, the overall relationship of depth integrated productivity is: $BP = 0.15 \times PP - 32.5$ ($r = 0.8$).

Seasonal variation in phyto- and bacterioplankton production in two regions of the NW Indian Ocean (based on geographical and hydrological features) are given in Fig. 9. Differences in bacterial production were of the same magnitude as differences in primary production, and average values show clear seasonal changes between the SW- and NE-monsoon. In the Somali Current, productivity was significantly higher during the SW monsoon, in contrast to the Gulf of Aden and the Red Sea, where higher productivity occurred during the NE-monsoon. The high variation in the upwelling area indicates the patchiness of phytoplankton in this region. In response to increased primary production, the growth rate of bacterioplankton in the mixed layer increased dramatically, with cells doubling approximately every 1–10 days, in contrast to an average generation time of 30 days outside the upwelling area (Table 3; generation time calculated from TTI). This is in

Table 4. *Comparison between primary (PP) and bacterial production (BP) in the Somali Current, Gulf of Aden and the Red Sea*

	SW-monsoon				NE-monsoon		
	PP ($gC\ m^{-2}\ day^{-1}$)	BP/PP (%)	Number of stations		PP ($gC\ m^{-2}\ day^{-1}$)	BP/PP (%)	Number of stations
Oligotrophic	0.7 (0.5–1.1)	18 (9–28)	5	Somali Basin	0.7 (0.4–1.0)	15 (14–22)	5
Upwelling	1.2 (0.7–2.8)	18 (9–30)	8	Gulf of Aden and Red Sea	1.4 (0.6–2.2)	19 (10–34)	4

Conversion factors: 1.1×10^{18} cells mol^{-1} and 34 fgC $cell^{-1}$. Bacterial production integrated to 300 m and expressed as percentage of PP. Ranges given in parentheses.

good agreement with the range from 2 to 31 days reported for the euphotic zone of the Gulf Stream front regions (Børsheim, 1990).

Bacterial production estimates equalled 9–34% of primary production (Table 2), a production percentage commonly found in colder regions (Kuparinen and Bjørnsen, 1992; Sullivan *et al.*, 1990). Bacterioplankton in temperate marine ecosystems is considered to remineralize a higher fraction of the carbon fixed by photosynthesis. In a review of bacterial production in fresh and saltwater ecosystems, Cole *et al.* (1988) reported an average bacterial production of 30%. During the SW-monsoon, we found an average of 18% at upwelling stations as well as at oligotrophic stations, and 15 and 19% were encountered during the NE-monsoon at oligotrophic and wintermixing stations, respectively (Table 4). Open ocean values ranging from 30 to 92% have been reported during an intermonsoon period in the Indian Ocean making use of very low conversion factors (Ducklow, 1993). To facilitate evaluation of our results with those reported by Ducklow (1993), we give a recalculation of his values in Table 5, making use of our conversion factors of 1.1×10^{18} cells mol^{-1} TTI and 34 fgC $cell^{-1}$ and integration to 300 m (the southernmost station with extreme high bacterial production compared to primary production has been omitted). High primary production (> 1.4 gC $m^{-2}\ day^{-1}$) near the coast of Oman indicates that upwelling was still going on in September 1986. Therefore we made a subdivision between oligotrophic and upwelling stations, with mean bacterial production of 122% and 36–90%, respectively. Such high values, almost an order of magnitude higher than ours, are

Table 5. *Comparison between primary (PP) and bacterial production (BP) in the Arabian Sea, Sept–Oct* 1986 *(data taken from Ducklow,* 1993*)*

	Intermonsoon			Recalculation BP/PP (%)	Remarks
	PP ($gC\ m^{-2}\ day^{-1}$)	BP/PP (%)	Number of stations		
Oligotrophic	0.4 (0.3–0.5)	34 (30–42)	3	122	Darwin St. 3,5,7
Upwelling	2.0 (1.4–2.7)	16 (10–22)	2	36–90	Darwin St. 14, 16

For comparison bacterial production, recalculated from [^{3}H]thymidine incorporation rates (conversion factors: 1.1×10^{18} cells mol^{-1} and 34 fgC $cell^{-1}$), was integrated to 300 m (see section 4). Ranges given in parentheses.

considered to occur during non steady-state intervals of biomass decomposition; if true, they would require a dramatic reconsideration of carbon mass-balance fluxes unless revaluation of the applied methods is also taken into consideration.

Despite the apparent lack of knowledge about bacterioplankton dynamics and their role in remineralisation of organically bound nutrients, the assumption that 80–90% of primary production is recycled within the euphotic zone has been widely used in the literature. Notably, some recent reports (Bjørnsen, 1986; Bjørnsen and Kuparinen, 1991) of bacterioplankton growth efficiency yield considerably lower efficiencies than the 50% generally assumed. Bacterioplankton production estimates should therefore be more than doubled to obtain the gross bacterial uptake. For example taking 50% as an upper limit, we found 18–68% uptake of the primary production. At lower efficiency of conversion (e.g. ~30%), bacterial consumption will equal the primary production. Using the data of Ducklow (1993), this would result in a carbon demand that exceeds the input by local primary production. In our study, no evidence was found for sustained high bacterial production during the NE-monsoon fuelled by a reservoir of organic material accumulated during the SW-monsoon. Thus the area studied appears not to be fundamentally different from other oligotrophic systems, this in contrast to the suggestion by Azam *et al.* (1994). Nevertheless this might be the case for the NE Arabian Sea, which is characterised by an extensive oxygen minimum zone where uncoupling between primary production and denitrification has been reported (Naqvi, 1994). The proper estimate of conversion factors remains a matter of general concern. Otherwise the high bacterial versus primary productivity reported by Ducklow (1993) appears to be the exception rather than the rule (Børsheim, 1990; Kuparinen and Bjørnsen, 1992; this study).

Additional information on the dynamics of the bacterioplankton community can be obtained by the comparison of TTI and TLI. The growth of the cell is roughly proportional to TLI, whereas the synthesis of DNA in preparation for cell division is proportional to TTI. Thus the ratio TLI/TTI of a community is indicative for the ratio of growth rate versus division rate. The calculation of protein synthesis per new cell (TLI [gC l^{-1}]/TTI [cells l^{-1}] × average cell mass [pgC $cell^{-1}$]; Simon and Azam, 1989) yields average growth stage of dividing bacteria and can be used to indicate whether smaller or larger than average size bacteria are responsible for growth. The outcome will be linearly dependent on the conversion factors used for calculating bacterial production from thymidine and leucine incorporation, as discussed extensively in the literature. The conversion factor of 2.8×10^{18} cells mol^{-1} obtained in this study during the SW-monsoon fell well within the range reported by others (Table 6). We report bacterial productions calculated from TTI with a conservative conversion factor of 1.1×10^{18} cells mol^{-1} (Riemann *et al.*, 1987; Bjørnsen and Kuparinen, 1991) which agrees well with the theoretical value reported by Fuhrman and Azam (1980). Notwithstanding the uncertainties in conversion factors used here, the bacteria actively in the process of cell division appear to be mostly in the larger size class. The close correlation between TTI and TLI found in this study (Fig. 8) is indicative for a balanced growth of bacteria with only minor variation of division versus growth in the region studied. In conclusion no indication of uncoupled DNA and protein synthesis could be found. In this study saturation of incorporation was checked during both monsoons (Fig. 5) and the radiotracer concentrations adjusted accordingly, resulting in a higher leucine concentration (20 nM) than generally used. As already recognised by others (Bjørnsen and Kuparinen, 1991), this implies that average growth rates based on TLI may previously have underestimated bacterial production due to undersaturation of protein synthesis. This

Table 6. Conversion factors for calculating bacterial cell production from [^{3}H]thymidine incorporation rates ($\times 10^{18}$ cells mol^{-1})

Value	Range	*N*	Reference	Location
	0.2–1.3		Fuhrman and Azam (1980)	Theoretical
1.7		2	Fuhrman and Azam (1982)	Nearshore
2.4		4	Fuhrman and Azam (1982)	Offshore
4	2–6	27	Ducklow and Hill (1985)	NW Atlantic
1.1	0.5–5.8	66	Riemann *et al.* (1987)	Coastal marine
1.1	0.65–3.18	6	Bjørnsen and Kuparinen (1991)	Southern Ocean
1.74		18	Kirchman (1992)	Subarctic Pacific
1.0 and 2.3		2	Li *et al.* (1993)	North Atlantic
2.8		1	Wiebinga *et al.* (this study)	NW Indian Ocean
Studies with conversion factors taken from literature				
2			SCOR (1990: p. 55)	N Atlantic
4			Børsheim (1990)	NW Atlantic
1.18			Ducklow (1993)	NW Indian Ocean
2.15			Kirchman *et al.* (1995)	Equatorial Pacific
1.1			Wiebinga *et al.* (this study)	NW Indian Ocean

might explain the wide range of published conversion factors (i.e. gC mol^{-1} leucine for the TLI method) in the literature. The higher incorporation rate of radiotracer in protein and the higher specific activity of [^{3}H]leucine allow the use of diluted tracer, thereby increasing precision compared to TTI.

Grazing might be an important factor controlling both the phyto- and bacterioplankton standing stocks. The time lag between a starting bloom and the subsequent increased growth of grazers might determine the dynamics of different components of the biota at different stages of the developing bloom. Although a wide variety of water masses, each with their specific factors influencing growth of plankton (e.g. nutrient input, wind stress), were encountered in this study (seasonal and spatial variation included), a well balanced and closely correlated growth of the total plankton community appears to occur. The fate of bacterial production is still unknown, and insights into grazing by (micro)zooplankton appear of crucial importance in understanding the dynamics of phyto- and bacterioplankton and the cycling of carbon in the open ocean.

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