Bacterial abundance and production in the central and eastern Arabian Sea

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Seasonal and spatial variations in bacterial and picoplankton abundances and bacterial production (thymidine incorporation rates) were determined in the water column up to 150 m in several stations in the central and eastern Arabian Sea. Higher bacterial densities of about 1×10^9 cells L^{-1} were observed during the intermonsoon periods of September and April/May compared to the southwest monsoon period of July/August and the winter period of February/March. Although primary production was low during April/May, bacterial production was much higher during this period unlike July/August. It also showed an increase from the northern to the southern Arabian Sea, suggesting the presence of high amounts of dissolved organic carbon in this area. High picoplankton densities, ranging up to 45×10^6 cells L^{-1} were observed during February, particularly in the northern Arabian Sea. Rapid turnover of bacteria during the intermonsoon period of April/May suggests the predominance of a 'microbial loop' in the foodweb and a prevailing source of dissolved organic carbon in the oceanic waters.

THE Arabian Sea is characterized by several unique seasonal and spatial variations in terms of biological, physical and chemical features which would directly influence microbial processes. Enormous amounts of particulate and dissolved organic carbon (POC and DOC) become available to bacteria during the southwest (summer) and northeast (winter) monsoons owing to enhanced primary production[1,2]. Wind-driven upwelling during the southwest monsoon from June to September results in extensive areas of high primary production along the northwestern regions and the south and central west coast of India[1,3–5].

In addition, distinct differences between the northern and southern Arabian Sea will be reflected in the bacterial dynamics. High primary production is sustained in the northern Arabian Sea even after the southwest monsoon owing to cold and dry winds which result in convective mixing[1,3,6]. While primary production decreases towards the south[2], DOC tends to increase from the north to the south. The subsurface waters of the northern Arabian Sea display a pronounced oxygen minimum layer associated with high nitrite maxima. The high-nitrite ridge extends from the continental margin off the north into the relatively oligotrophic central Arabian Sea. Primary production, *per se*, thus appears to be decoupled from microbial processes that lead to denitrification[7].

The months of March to May are periods of low primary production in the Arabian Sea[3] and the possible effects of alternating eutrophy and oligotrophy on bacterial dynamics in the Arabian Sea, suggested by Azam *et al.*[8] would be particularly felt during this season.

A few attempts have been made in recent years to study bacterial activities and picoplankton in the Arabian Sea[9–12]. However, these studies have largely been confined to the monsoon period of July to October and the upwelling areas in the northwest Arabian Sea. Bacterial dynamics during the other seasons and parts of the Arabian Sea still remain poorly investigated.

The present study, as a part of the Joint Global Ocean Flux Studies-India (JGOFS) attempts to address: (1) Bacterial populations and production during the monsoon and intermonsoon periods, (2) Differences between the northern and southern Arabian Sea, and (3) Picoplankton abundance.

Materials and methods

Bacterial abundance

Four cruises were undertaken on board ORV *Sagar Kanya*: (1) Cruise SK #87 during September 1993; (2) SK #91 during April–May 1994 (3) SK #99 during February–March 1995, (4) SK #104 during 4 July–August 1995. Water samples were collected at various depths from different locations (Figure 1) using a CTD rosette sampler. Samples for microbiological studies were drawn from the rosette immediately after samples for dissolved gases were taken. These samples were handled, stored and analysed for bacterial abundances essentially according to the JGOFS protocols[13] except for the addition of 0.22 µm filtered formaldehyde (3.7% final concentration) instead of 10% glutaraldehyde. Acridine orange direct counts (AODC) for bacteria were carried out following Parsons *et al.*[14] and the JGOFS protocols. Up to 25 microscopic fields were counted for bacteria using oil immersion objectives (100 ×) under an Olympus BH2 epifluorescence microscope. Mean cell numbers per field were calculated and the number

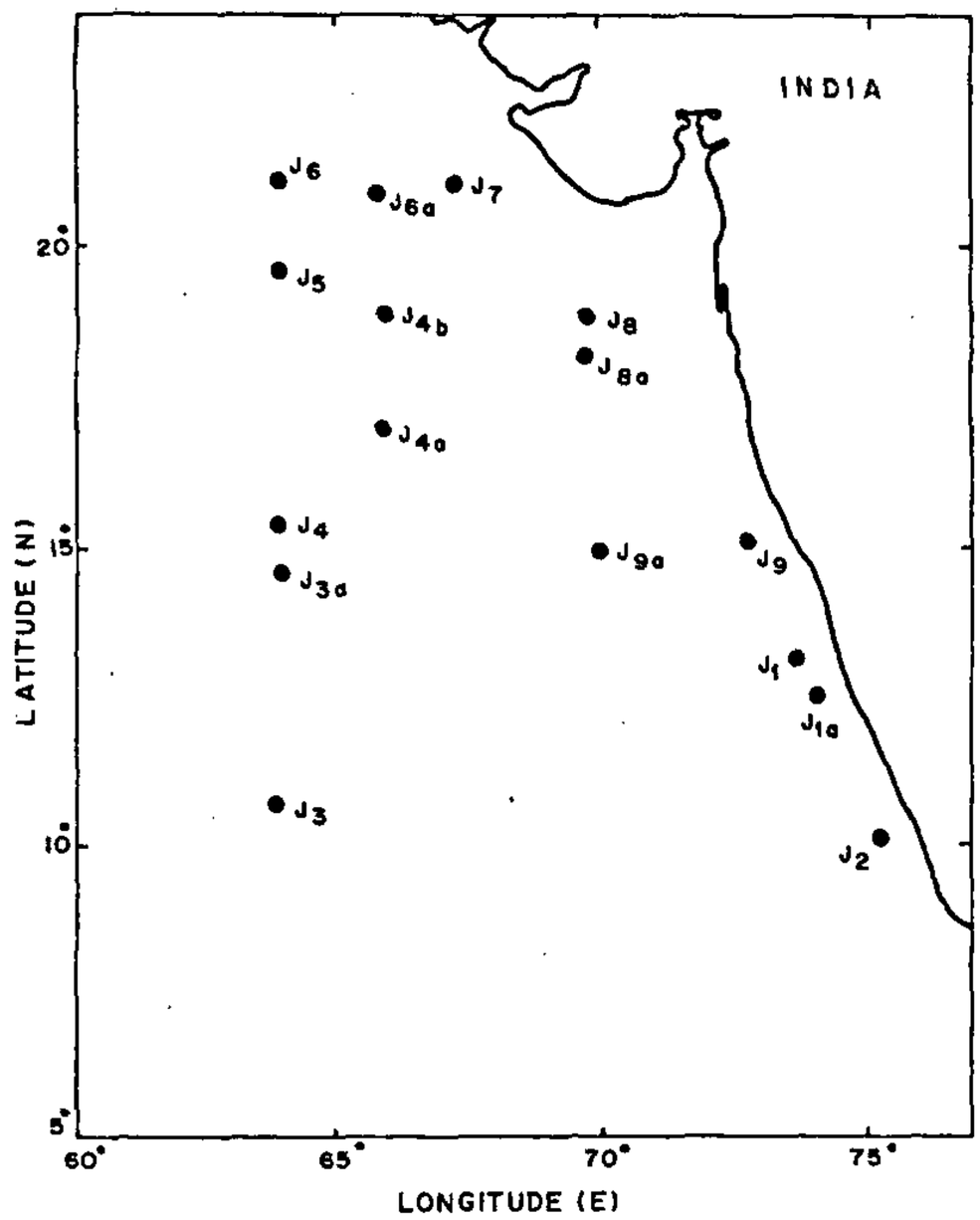

Figure 1. Location of sampling stations.

of bacterial cells L^{-1} determined based on the relationship detailed in Parsons *et al.*[14].

^3H (tritiated) thymidine incorporation rates

Incorporation of ^3H-methyl (tritiated) thymidine (specific activity: 17,000 mCi/mmole; Bhabha Atomic Research Centre, Mumbai) by native bacteria was estimated by the method described in JGOFS protocol[13] during cruises #SK 91 and #SK 104. Seawater samples from various depths, up to 150 m, were collected and analysed. A working solution of 21.25 ml containing 59 nmole of methyl ^3H thymidine was prepared and 100 µl of this solution was added to 27.8 ml of water sample to yield a final concentration of 10 nM thymidine. Samples were incubated for 1 h and the uptake was stopped by adding 37% formaldehyde to yield a final concentration of 3%. The aliquots were immediately filtered over 0.2 µm Millipore filters and cold TCA precipitation and ethanol extraction carried out. Filters were immersed in 3 ml of liquid scintillation cocktail ('Cocktail-W', Spectrochem, Mumbai) and the samples assayed for radioactivity using a Packard 2500 TR liquid scintillation counter.

Bacterial production was estimated using mean oceanic conversion factor values of 2.17×10^{18} cells mol^{-1} thymidine incorporated and by converting the cell abundance to carbon mass using a value of 2×10^{-14} g C per cell[15].

Results

The observations presented in this paper pertain to four different seasons. The summer monsoon period in July/August 1995 was characterized by higher primary production and phytoplankton biomass, especially along the west coast of India (see Bhattathiri *et al.*, this issue). Decay of phytoplankton blooms occurred during September 1993 (SK #87). Primary production and phytoplankton biomass were also quite high in the northern latitudes during the winter month of February 1995 (SK #99). The intermonsoon period in April/May 1994 had the lowest levels of primary production and phytoplankton biomass of all the seasons sampled.

The highest bacterial densities, ranging from 0.34 to 1.5×10^9 cells L^{-1} were observed at the end of the southwest monsoon (September 1993) at the three stations sampled in the northern Arabian sea along 66°E (Figure 2). Subsurface maxima were evident in all these locations. High bacterial densities were also observed

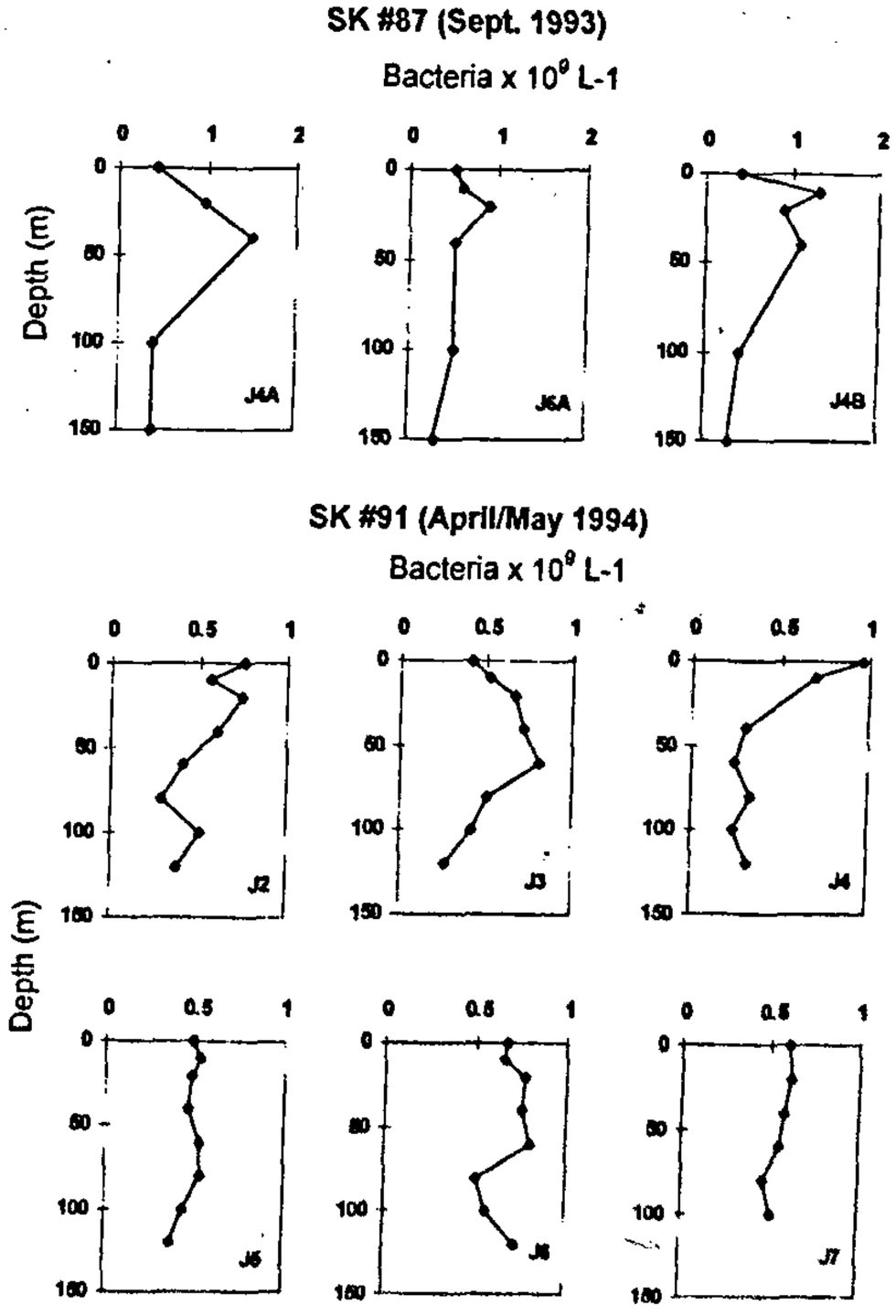

Figure 2. Bacterial abundance during cruises SK #87 (September 1993) and SK #91 (April/May 1994).

in the intermonsoon period of April–May 1994 (Figure 2, range: 0.24–0.96 × 10^9 L^{-1}). However, no sharp subsurface maxima were detected at any of the locations during this period. The coastal stations (for example, J2 and J7) and the offshore stations in the central Arabian Sea (J3 and J4) had similar bacterial abundances. Bacterial numbers were more or less similar from north to south along 64°E (Figure 2). Bacterial densities during the summer monsoon (SK #104) were fairly high, ranging from 0.13 to 0.64 x 10^9 L^{-1} (Figure 3). As in the intermonsoon season, bacterial abundances in coastal stations (J2, J8A and J9) and in the open oceanic stations (J3 and J3A) were similar. These numbers, however, were slightly lower than those observed in September and April. In contrast, bacterial abundance was about an order of magnitude lower (0.05 to 0.09 × 10^9 L^{-1}) during February 1995 in all sampling stations, except the northernmost, coastal station J8 (Figure 4).

Thymidine incorporation rates were measured during the intermonsoon (SK #91) and the summer monsoon (SK #104) cruises (Figures 5 and 6). During the former, higher uptake rates, up to 25 to 50 pmol L^{-1} h^{-1}, were observed in the southern coastal station J1 and the southern offshore stations, J3 and J4, all below the latitude of 15°N. Many of the stations showed higher rates at about 40–60 m depths. Uptake rates during summer monsoon ranged from 0.2 to 3 pmol L^{-1} h^{-1}, about an order of magnitude lower than those observed in the intermonsoon (Figure 6). The highest uptake rate during this season occurred in the southern coastal station J1A. Bacterial production increased with depth in all the stations except J1A.

Bacterial production (BP) exceeded primary production (PP) throughout the 120 m water column in 3 out of the 4 stations during intermonsoon (Figure 7). PP in the upper 50 m at some of these stations was only about 2% of the BP. In contrast, PP during the summer monsoon far exceeded the BP till a depth of 40 m (Figure 7), BP contributing only ca. 10% of the PP.

High picoplankton abundance, with a maximum of up to ca. 60 × 10^6 cells L^{-1} was observed in the northern stations during February/March 1995, compared to ca. 10 × 10^6 cells L^{-1} in the more southern, oceanic stations (Figure 8). Picoplankton densities were similar to these oceanic waters during summer monsoon. However, the southernmost coastal station J2 harboured high numbers of picoplankton similar to coastal stations during February/March 1995 (Figure 8).

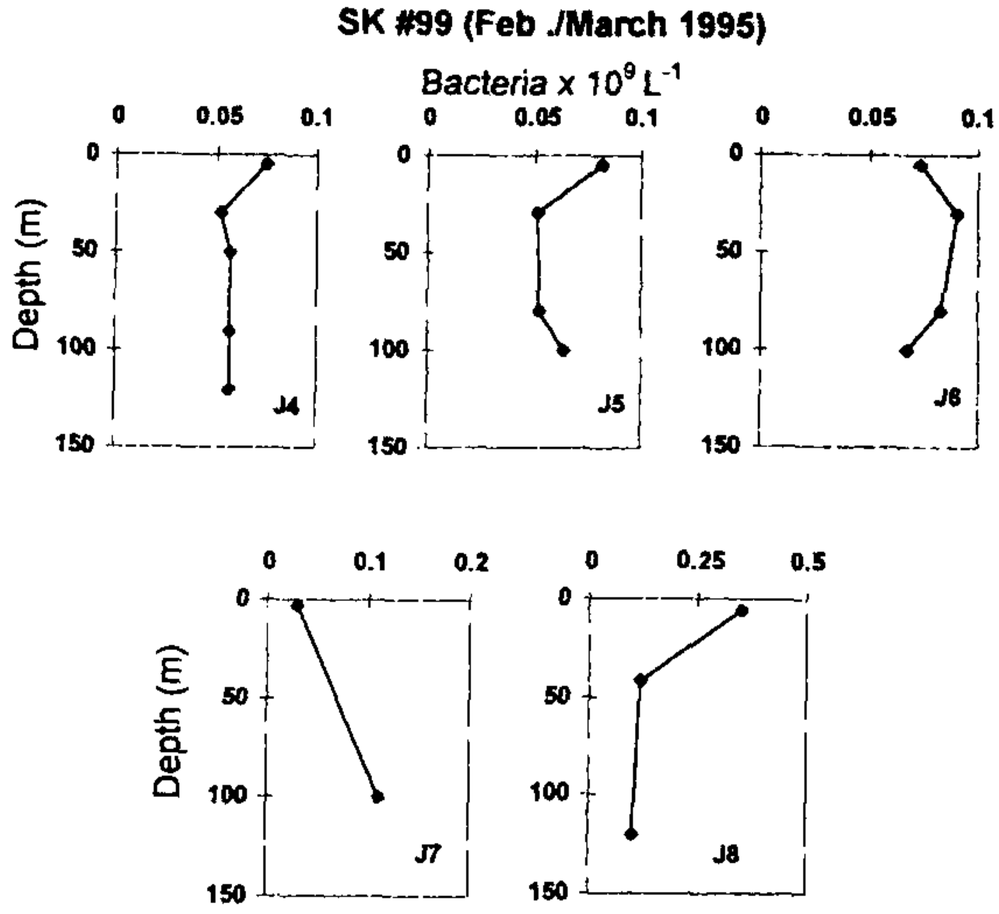

Figure 4. Bacterial abundance during cruise SK #99 in February/March 1995.

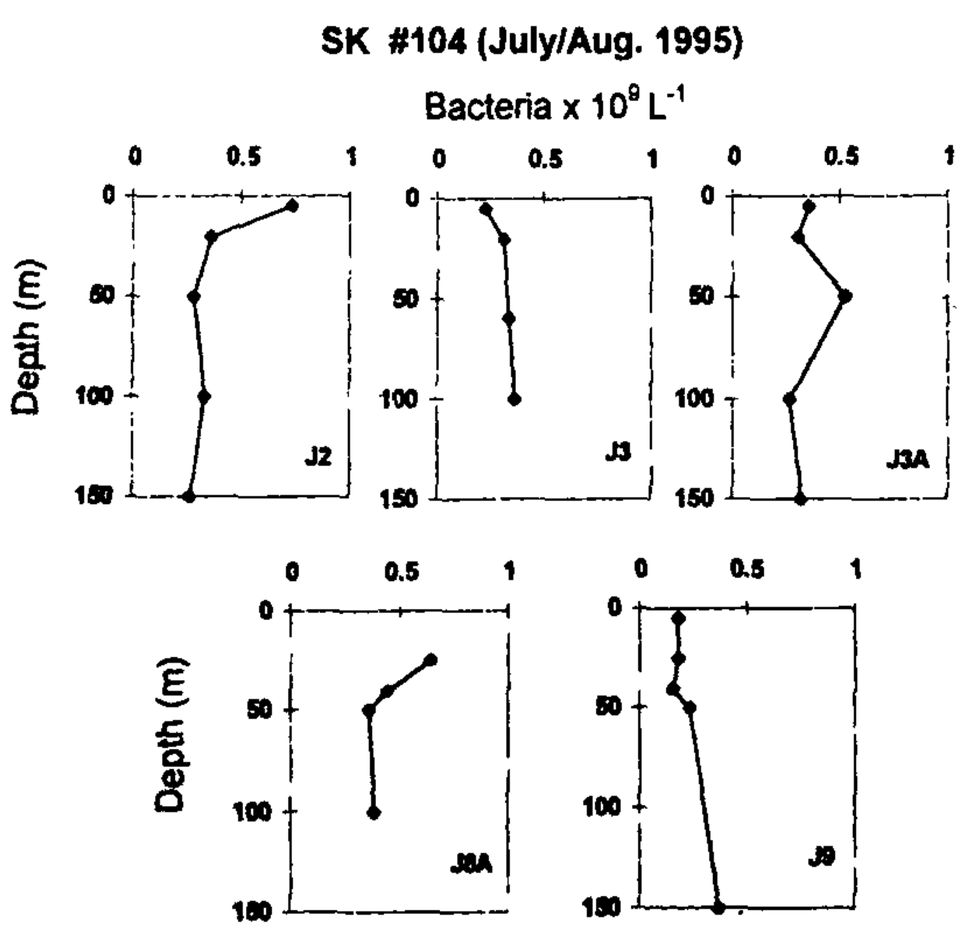

Figure 3. Bacterial abundance during cruise SK #104 in July/August 1995.

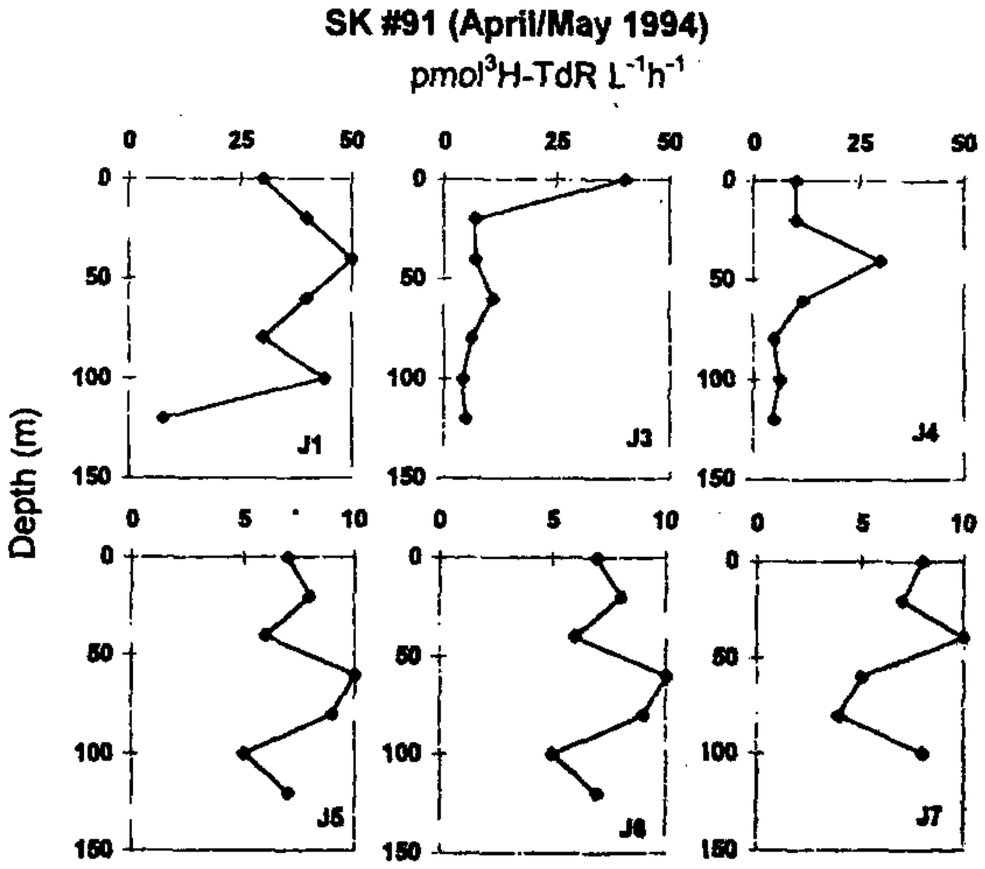

Figure 5. Thymidine incorporation rates during cruise SK #91 in April/May 1994.

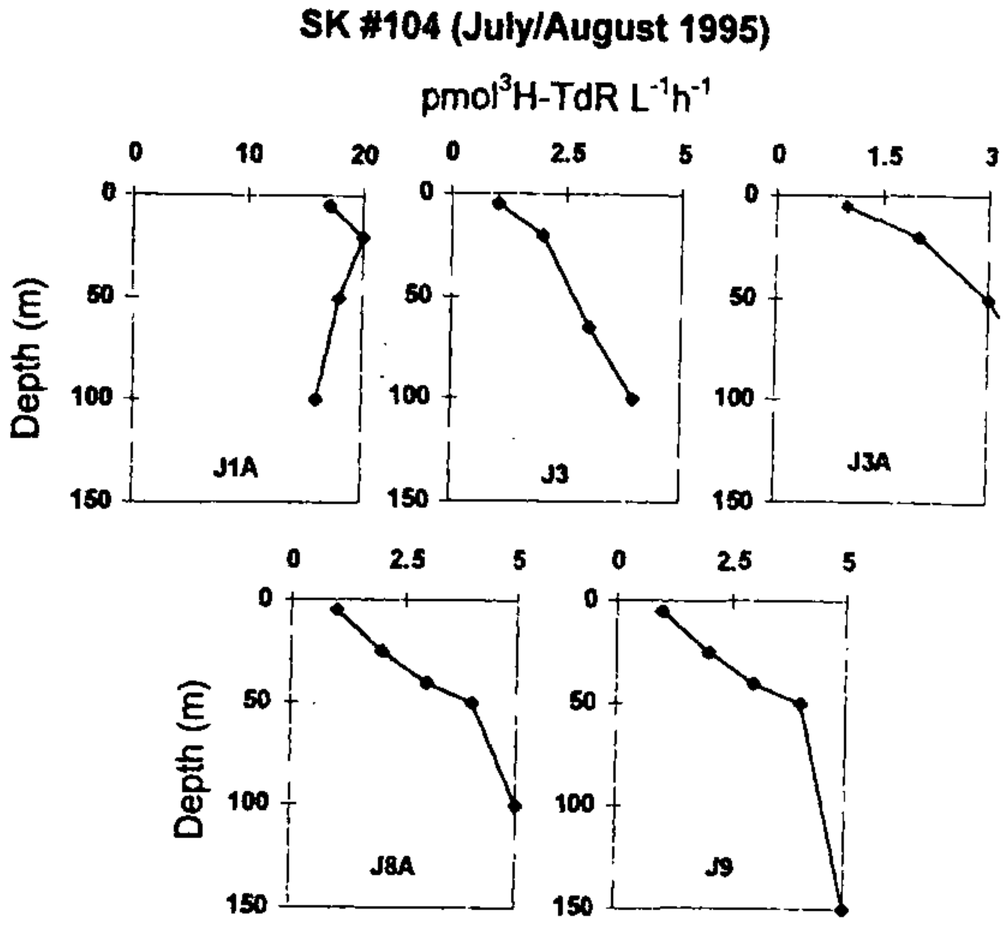

Figure 6. Thymidine incorporation rates during cruise SK #104 in July/August 1995.

Discussion

Peak bacterial abundances were not related to seasons of high primary productivity during the summer or winter monsoons. Thus, the highest bacterial densities were observed at the end of the southwest monsoon in September (Figure 2). Although only three stations at the northern Arabian Sea were sampled during this period, the high bacterial densities observed during this period are probably typical of this season. The values measured in this study are similar to those reported by Ducklow[9] (>1 × 10^9 L^{-1}) for the Northern Arabian Sea and the Gulf of Oman during September 1994. Likewise, although a pronounced enhancement of primary production and phytoplankton biomass and high picoplankton abundance with a distinct north to south gradient occurred along 64°E as a result of winter cooling and convectional mixing[5] (Figure 8), bacterial densities were not related to such high primary production and were the lowest during this season for the Arabian Sea.

Bacterial abundance increased substantially by April/May at all stations sampled (Figure 2). This period is generally known to be a season of low primary productivity and oligotrophic conditions in the Arabian Sea[3,16]. Increase in bacterial abundance during the two intermonsoon periods in September and April/May might be related to a decay of the earlier phytoplankton blooms, increasing phytoplankton exudation and particle breakdown at the end of the season[9]. Our observations during April/May suggest that bacteria during this season responded to the phytoplankton blooms of February/March only after a pronounced lag period[15]. In the equatorial Pacific, Kirchman *et al.*[17] observed a lack of covariance and an uncoupling between primary and bacterial productions over a similar time scale of about 1–2 months. Azam *et al.*[8] suggested that following a phytoplankton bloom, labile DOC would be rapidly utilized by bacteria, while the slow-to-degrade DOC would

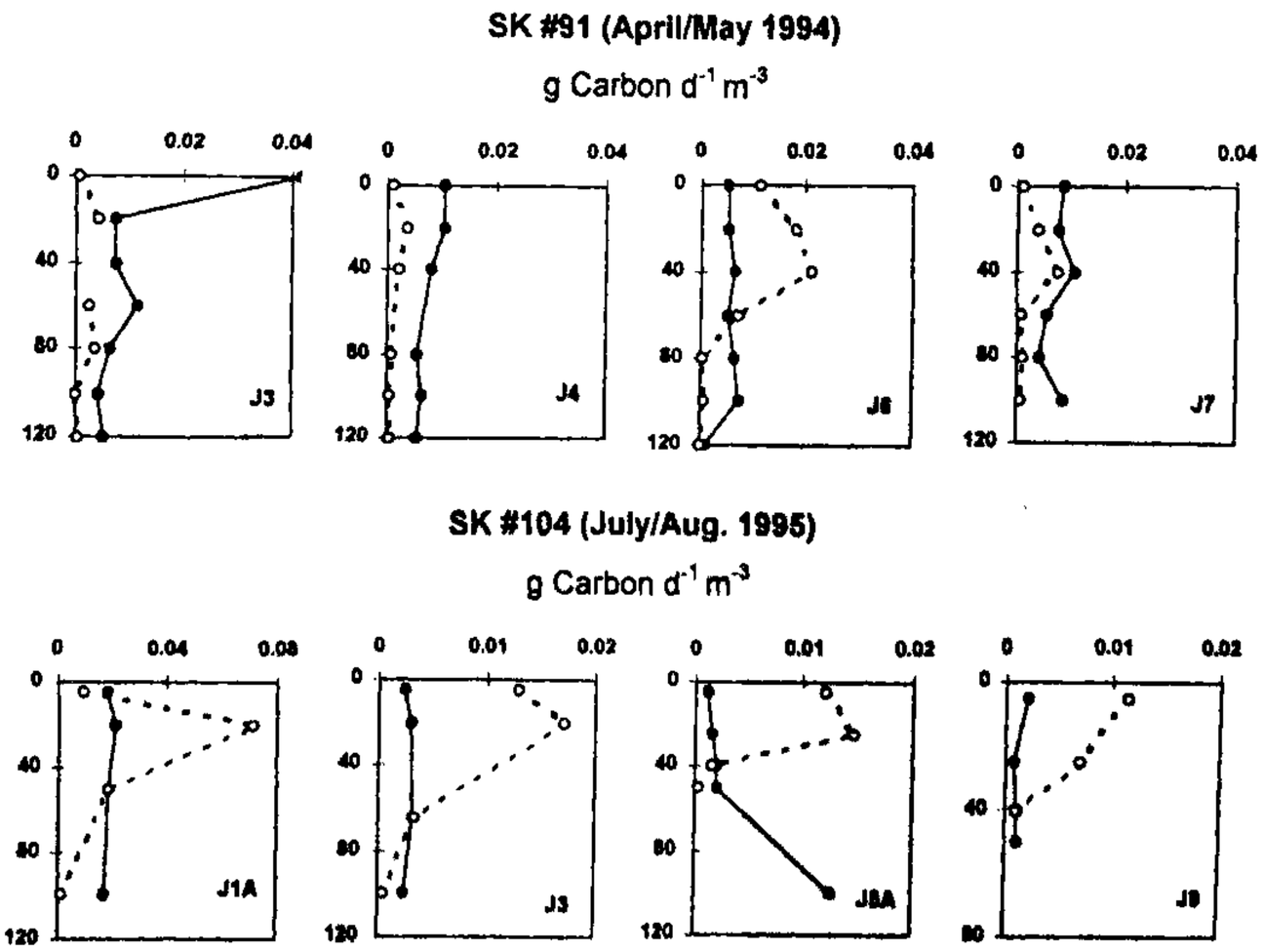

Figure 7. Bacterial (continuous lines) and primary (stippled lines) production during cruises SK #91 in April/May 1994 and SK #104 in July/August 1995.

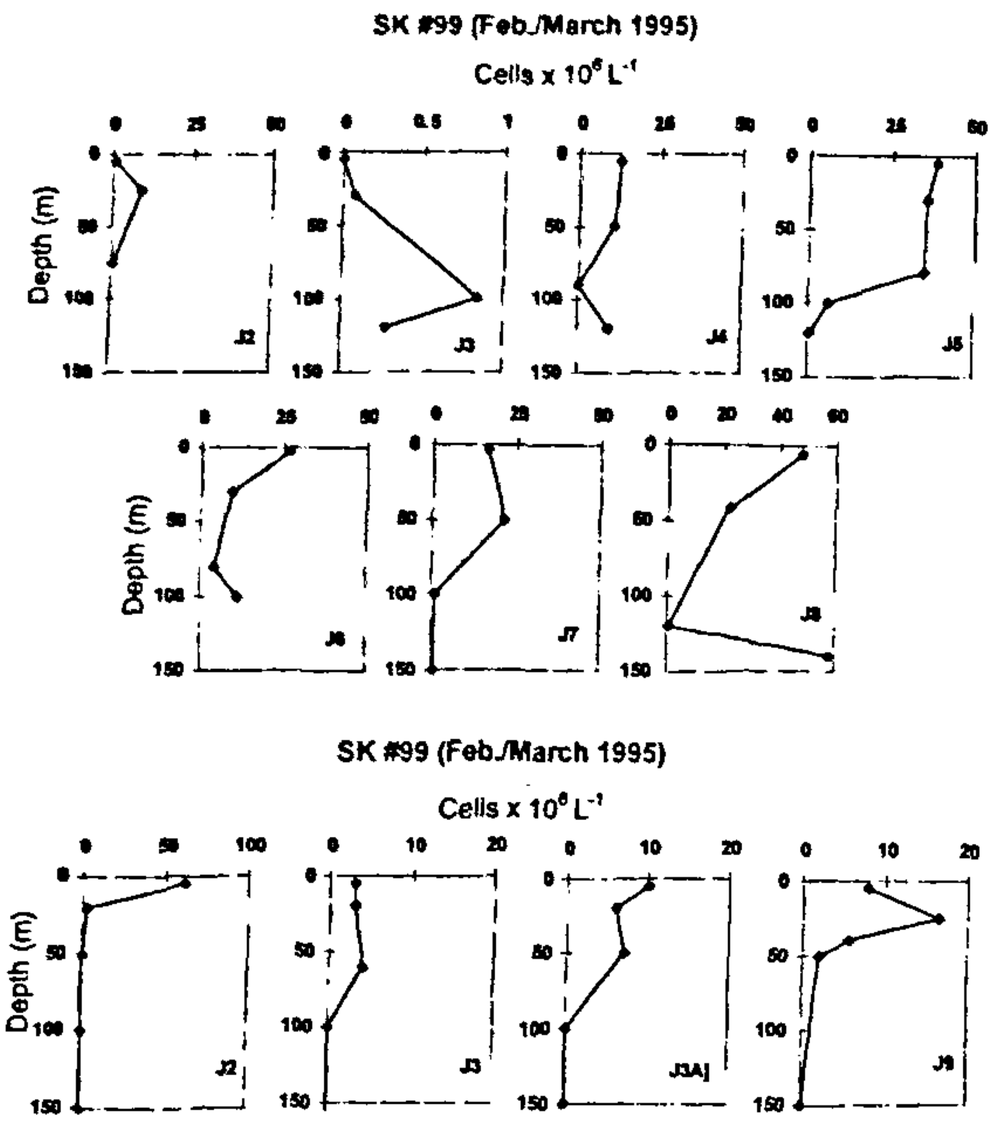

Figure 8. Picoplankton abundance during cruises SK #99 in February 1995 and SK #104 in July/August 1995.

sustain bacteria during oligotrophic conditions.

Bacterial production also was much higher during April/May than during July/August. Although bacterial production is normally about 20% of the primary production, values up to 80% of the primary production have been recorded in equatorial Pacific[17]. Our observations indicate that biological production during the premonsoon period of April/May was dominated by bacteria, phytoplankton production often accounting for only about 2% of the BP (Figure 7). This is in contrast to the summer monsoon period, when bacterial production was lower and comprised only about 18% of the phytoplankton production. It is not yet clear from our studies as to why bacterial production increased towards the south during April/May. Chandralata Raghukumar (pers. commun.) observed patches of *Trichodesmium* (red tide) blooms in some stations in this area. It is likely that a vigorous red tide bloom preceding our observations provided DOC to promote bacterial dynamics during this season. Such *Trichodesmium* blooms are common in March–April in the Arabian Sea[18].

Our observations might help to provide an explanation to the zooplankton paradox of the Arabian Sea[19]. Zooplankton biomass remains more or less constant throughout the year in the Arabian Sea despite variations in primary productivity leading to the suggestion that secondary production in the Arabian Sea might be sustained through the 'microbial loop'[20] during 'lean' seasons. The rapid bacterial turnover in April/May is an evidence that flagellate and ciliate grazing during this period might be intense and further sustain the zooplankton[21].

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