# Lack of seasonal and geographic variation in mesozooplankton biomass in the Arabian Sea and its structure in the mixed layer

**M. Madhupratap, T. C. Gopalakrishnan*, P. Haridas*, K. K. C. Nair*, P. N. Aravindakshan*, G. Padmavati and Shiney Paul***

National Institute of Oceanography, Dona Paula, Goa 403 004, India
*Regional Center of National Institute of Oceanography, P.B. 1913, Cochin 682 018, India

**Mesozooplankton standing stock, abundance and composition were studied during three seasons (summer, winter and inter-monsoon) from coastal and open ocean waters of the central and eastern Arabian Sea in 1994–95. Concentrations were generally higher in the mixed layer compared to deeper strata. A noteworthy feature was that the standing stocks and abundances did not vary significantly between seasons and areas. Vertical migrations appeared to be in a low key. In all seasons herbivores dominated, followed by carnivores. A few species, common in all seasons, accounted the majority of the population. The 'paradox' of the Arabian Sea, that zooplankton biomass remains more or less invariant, despite seasonally varying primary production regimes, could be explained by a microbial loop.**

PRIMARY productivity and phytoplankton biomass show definite seasonal patterns in the Arabian Sea[1]. They are high during the southwest (summer) monsoon and part of the northeast (winter) monsoon, and are low during the inter-monsoon periods[1,2]. They also show north–south and east–west variability[2] depending on physical events such as upwelling or winter cooling. There are many studies on zooplankton abundances and composition from this region[3], however, relatively few of them concentrate on seasonal cycles[4,5]. Seasonality in zooplankton abundances and composition was addressed as a part of the Indian Joint Global Ocean Flux Study (JGOFS) and sampling was done during three cruises conducted from 12 April to 12 May 1994 (inter-monsoon), 3 February to 4 March 1995 (winter) and 20 July to 12 August 1995 (summer). The stations were positioned to sample the coastal waters along the west coast of India and an open-ocean track along 64° E (Figure 1). A large part of the latter, however, could not be sampled in July–August due to heavy weather.

## Materials and methods

The stations (Figure 1) were occupied for at least 24 h to ensure that sampling of zooplankton was conducted around mid-day and mid-night. Samples were collected with a Multiple Plankton Closing Net (Hyro-Bios, mouth area 0.25 $m^2$, mesh width 200 µm). Five depths were sampled at open-ocean stations: 1000–500 m, 500–300 m, 300-base of thermocline (BT), BT-top of thermocline (TT) and TT-surface (mixed layer). At the coastal stations, the two shallow depth intervals were invariably sampled, deeper sampling depended on the bottom depth (Figure 2). Plankton samples were filtered, drained of excess water on absorbent paper and added to

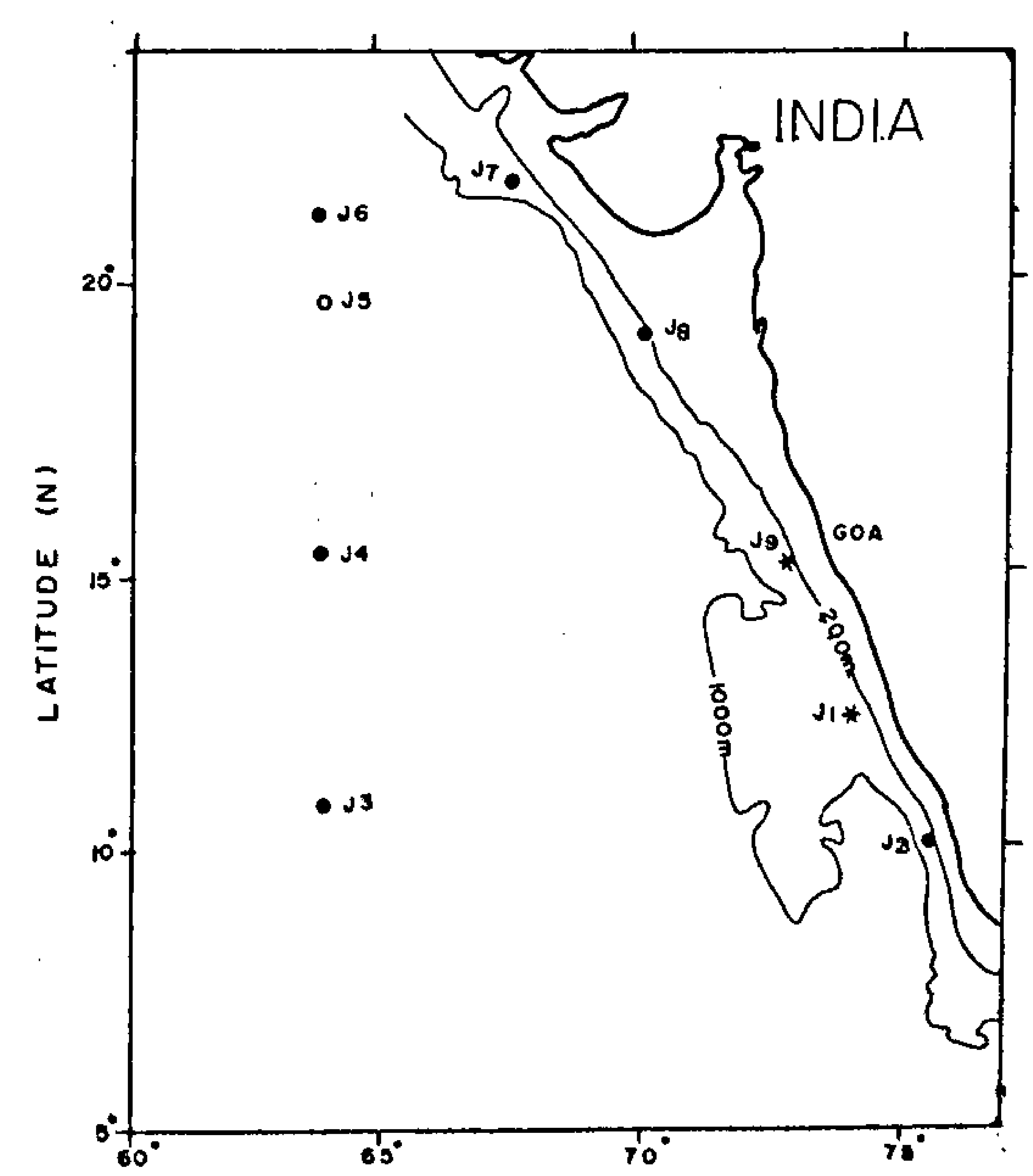


**Figure 1.** Station locations (filled and open circles and stars) during 3 cruises; open circle (J5)- additional station during February–March, 1995; stars (J1, J9)- additional stations during July–August, 1995; J4 to J7 was not occupied in July–August, 1995; J8 was not occupied during April–May, 1994.

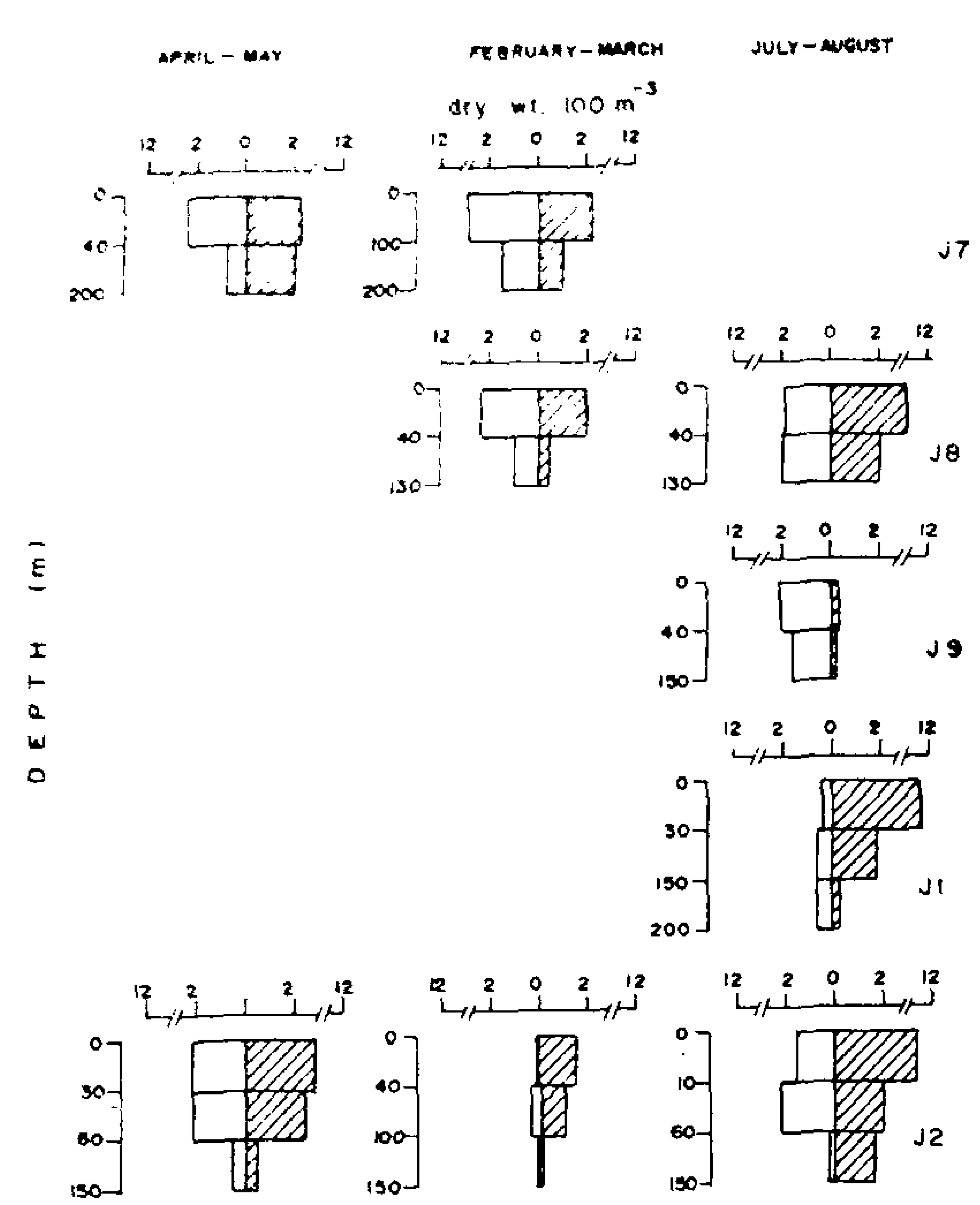


Figure 2. Mesozooplankton biomass (g dry weight 100 m³) at different depth strata at coastal stations during 3 cruises. Station number is shown. Night-shaded.

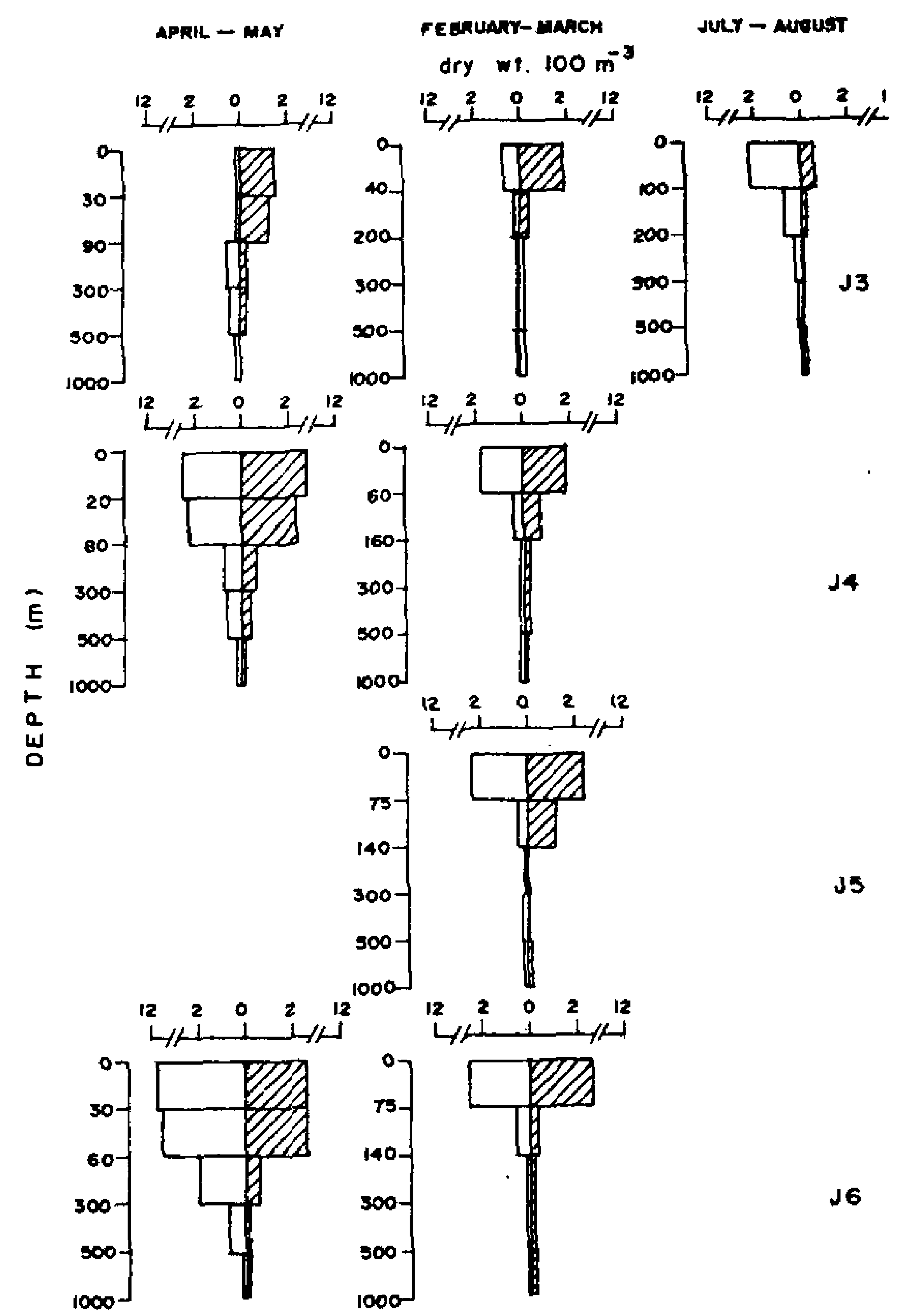


Figure 3. Mesozooplankton biomass (g dry weight 100 m³) at different depth strata at open ocean stations during 3 cruises. Station number is shown. Night-shaded.

known volume of water to estimate biomass. Subsequently, they were preserved in 4% formalin-seawater. A conversion factor of 0.075 g dry weight per 1 ml displacement volume (determined using method described above and without preservation) was used to estimate column and mixed layer standing stocks[6]. Composition of zooplankton from the upper mixed layer, which usually had a higher standing stock, was studied from aliquots. Classification of trophic groups was made according to literature[6–9]. A Wilcoxon rank test was employed to assess significant spatial (coastal vs open ocean) and day-night variations, if any, in biomass in the mixed layer. This was done separately for each season and then combining data from all cruises. The same test was applied to examine significant day–night variations in total counts and composition of trophic groups of zooplankton in the mixed layer.

## Results

Mixed layer was shallow (10–40 m) in April–May and August while it deepened (40–100 m) during February[10]. Zooplankton standing stock did not exhibit any definite spatial or temporal trends (Figures 2, 3; Table 1). Average column standing stocks and the biomass in the mixed layer in coastal and oceanic waters were similar in all three seasons (Table 1, the value for open ocean waters in July–August is based on observation from a single station). The rank test did not show any significant difference ($P > 5\%$) between coastal and oceanic waters within seasons or when all seasons were combined. Biomass decreased drastically with depth, the uppermost two layers sampled accounted for 85 to 95%

Table 1. Average column standing stock of zooplankton (g dry weight m⁻², day and night combined, column depths as in Figures 2 and 3) in coastal and open ocean waters during different seasons. Average zooplankton biomass (g dry weight m⁻²) for mixed layer is given in parentheses

| | April–May | February–March | July–August |
|---|---|---|---|
| Coastal | 3.7±1.7 | 3.1±2.8 | 3.3±0.7 |
| | (1.4±0.7) | (1.6±1.3) | (1.3±0.8) |
| Oceanic | 5.7±2.7 | 3.1±1.4 | 3.3 |
| | (1.5±0.9) | (1.7±1.2) | (1.8) |

**Table 2.** Total number of organisms (per 100 $m^3$, night values) in the mixed layer in coastal and open ocean waters.

| | April–May | February–March | July–August |
|---|---|---|---|
| Coastal | 51370 ± 22140 | 4690 ± 29650 | 61100±50240 |
| Oceanic | 91230±59240 | 81240±32450 | 23450 |

in all seasons. Sharp increases in night-time values in the mixed layer were also not clearly discernible ($P$ > 5%) except in some coastal stations indicating that vertical migration was at a low key.

The total number of organisms (night-time values; Table 2) also did not vary much within coastal and oceanic waters in the mixed layer except in August. Neither the total number of organisms nor trophic groups registered significant night-time increase in the mixed layer. Surprisingly, higher numbers were present in open waters compared to coastal waters during inter-monsoon and winter periods.

Copepods dominated (Table 3), contributing 50 to 88% of the numbers in coastal areas and 77 to 87% in the open ocean. Other dominant groups were Chaetognatha and Tunicata. Herbivores dominated in both areas in all seasons, but appreciable number of carnivores was also present (Table 4). Among copepods, a few herbivorous families, viz. Paracalanidae, Eucalanidae, Calanidae and Clausocalanidae were dominant, accounting for more than 50% of total copepods in all seasons and both areas in the mixed layer (Table 5). These are generally small (< 2 mm, except some species of *Eucalanus*) filter feeding forms. Dominant repre-

**Table 3.** Relative abundances of major zooplankton groups in the mixed layer (day and night combined, values as a percentage of individuals 100 $m^3$) in coastal and open ocean waters (latter in parentheses)

| Group | April-May | February-March | July-August |
|---|---|---|---|
| Hydromedusae* | 0.6 (0.1) | 0.3 (0.4) | 0.002 (-) |
| Siphonophora* | 2. 2 (0.3) | 0.9 (0.9) | 0.04 (0.3) |
| Ctenophora* | 0.1 (-) | - (-) | - (-) |
| Polychaeta* | 1. 2 (0.1) | 0.3 (0.4) | 0.1 (0.3) |
| Cladocera | 0.3 (0.1) | - (-) | 0.6 (-) |
| Ostracoda | 0.5 (2. 2) | 0.5 (1.5) | 0.6 (2.1) |
| Amphipoda* | 0.7 (0.9) | 0.8 (0.7) | 0.2 (0.7) |
| Copepoda | 50 (87.3) | 79 (82) | 88 (77) |
| Sergestidae | 0.2 (0.7) | 0.9 (0.3) | 1.1 (2. 3) |
| Euphausiacea | 0.4 (0.1) | 0.4 (0.6) | 0.2 (1.3) |
| Heteropoda* | 0.5 (0.2) | 0.2 (0.2) | 0.1 (-) |
| Pteropoda | 2.1 (0.1) | 0.1 (0.1) | 0.6 (0.1) |
| Chaetognatha* | 18 (3.0) | 10 (4.9) | 3.1 (7.1) |
| Salps | 0.5 (0.1) | 0.1 (0.6) | 0.3 (-) |
| Dolioids | 0.1 (0.2) | 0.2 (0.6) | 0.2 (0.7) |
| Copelata | 15 (3.9) | 4.5 (5.8) | 0.4 (0.2) |
| Fish eggs | 0.3 (0.3) | 0.1 (0.2) | 1.8 (4.4) |
| Fish larvae* | 0.5 (0.1) | 0.2 (0.1) | 0.4 (0.3) |
| Decapod larvae | 3.5 (0.3) | 0.8 (0.2) | 1.5 (2.0) |

- Indicates absence

*Groups considered as carnivores in Table 3. The trophic status of copepods was classified according to genera, see text.

**Table 4.** Percentage of abundances of different trophic groups of zooplankton in the mixed layer (day and night combined) in coastal and open ocean waters (latter in parentheses)

| Group | April–May | February–March | July–August |
|---|---|---|---|
| Herbivores | 57 | 53 | 66 |
| | (57) | (54) | (69 |
| Carnivores | 33 | 43 | 25 |
| | (35) | (41) | (21) |
| Omnivores | 10 | 4 | 9 |
| | (8) | (5) | (10) |

sentatives from these families were *Acrocalanus* spp., *Paracalanus* spp., *Eucalanus attenuatus*, *E. mucronatus*, *E. subcrassus*, *Cosmocalanus darwini*, *Undinula vulgaris*, *Canthocalanus pauper* and *Clausocalanus* spp. Common carnivorous copepods were the calanoid *Euchaeta* (*rimana*), the cycloipoid *Oithona* spp. and the poecilostomatoids *Oncaea* spp. and *Corycaeus* spp.

The compositon of copepods was quite similar in the coastal and open ocean waters except that species like *Acartia amboinensis*, *Calocalanus pavo*, *C. plumulosus*, *Temora turbinata*, *Centropages alcocki*, *C. furcatus* and *Labidocera* spp. were more or less restricted to coastal areas. Few others such as *Pleuromamma indica*, *Lucicutia flavicornis* and *Acartia negligens* were ubiquitous albeit occurring in low numbers.

## Discussion

The striking feature with regard to zooplankton standing stock and abundances was a general lack of seasonal and spatial variations. Another noteworthy feature was the maintenance of high biomass offshore in the mixed layer comparable to the coastal stations. Zooplankton standing stocks were highest in the mixed layer and sometimes to the base of the thermocline (Figures 2, 3). Sharp decrease in biomass with depth has been described from many areas[6]. Although the oxygen minimum layer (<10 µM, ca. 150–1000 m) in the Arabian Sea might affect distributions, the present study shows that standing stocks start decreasing at shallower depths. Relatively higher zooplankton counts at coastal stations in summer probably resulted from increase in phytoplankton biomass through coastal upwelling (*vide infra*). Although there was some shift in the percentage of abundance of some copepod families, particularly during summer (Table 5), the overall species composition remained more or less the same. Absence of vertical migration by a large number of dominant epipelagic copepods has been reported earlier[6]. However, possible zonal migrations[9] would not be detected with the present sampling strategy.

International Indian Ocean Expedition (IIOE) data[11] from the Arabian Sea show much lesser displacement volumes from open waters (ca. 10–40 ml 200 $m^3$ from the upper 200 m) compared to present observations (usually about 20–90 ml 100 $m^3$ from the mixed layer). IIOE also shows some decrease in biomass from summer to winter in the western Arabian Sea although for open waters the variations were less pronounced. One reason for the lower biomass obtained may be the larger mesh size used during IIOE (300 µm) which might not have effectively sampled the smaller, dominant forms mentioned earlier. A second reason may be that while mixed layer had maximum standing stock, the conversion factor used for IIOE data is for the upper 200 m which also included deeper strata with lower biomass.

A fairly high proportion of carnivores (Table 3) in the zooplankton composition of the Arabian Sea has been reported earlier and this seems to be a persistant situation[4,6,12,13]. Longhurst and Pauly[9] noted that the biomass of predators is about twice that of herbivores and detritivores in the tropics compared to colder oceans. It would be of future interest to study how the classical concept of a time-lag between the development of herbivores to carnivores apply to the tropics.

The general lack of seasonality in mesozooplankton standing stocks in the Arabian Sea despite seasonally varying plant biomass has been noticed in some recent studies[4,14–16]. Seasonal and spatial variations were observed in most of the other biological parameters measured along with the present data set. This Arabian Sea paradox of maintenance of high zooplankton biomass can be plausibly explained through the following scenario. It was observed that in February–March, nutrient availability in the euphotic zone was substantial[17] in the northern coastal and oceanic waters (north of 15°N) due to winter cooling and convective mixing. This led to an increase in primary production, chlorophyll *a* phytoplankton and picoplankton cell counts during this season (up to 800 mg C $m^{-2}$ $d^{-1}$, 34 mg $m^{-2}$, 1320 × $10^2$ $l^{-1}$ and 45 × $10^6$ $l^{-1}$ respectively)[2,18,19]. A similar feature was observed in August along southwest coast of India (up to 1070 mg C $m^{-2}$ $d^{-1}$, 87 mg $m^{-2}$, 155 × $10^2$ $l^{-1}$ and 50 × $10^6$ $l^{-1}$ respectively); during this period the nutrients were supplied through coastal upwelling. But, during inter-monsoon the entire study area became oligotrophic (values were up to a maximum of 310 mg C $m^{-2}$ $d^{-1}$, 16 mg $m^{-2}$ and 93 × $10^2$ $l^{-1}$, picoplankton was not counted).

Populations of two groups of organisms, viz. bacteria and microzooplankton, however, showed increased abundances during inter-monsoon compared to the other two periods. Highest bacterial counts were 0.09, 0.6 and 2.2 × $10^9$ $l^{-1}$ for the winter, summer and inter-monsoon

Table 5. Percentage of abundance of orders and families of copepods (day and night combined) in the mixed layer in coastal oceanic waters (latter in paranthesis)

| Family | April–May | February–March | July–August |
|---|---|---|---|
| **Order Calanoida** | | | |
| Calanidae | 22 (25.4) | 4 (6.3) | 10.3 (61) |
| Eucalanidae | 5 (0.5) | 6.3 (6.9) | 14 (4) |
| Paracalanidae | 17.5 (21.6) | 18 (26.8) | 24 (11) |
| Calocalanidae | 2.5 (0.1) | 1.2 (0.8) | 0.1 (0.1) |
| Clausocalanidae | 8 (9) | 6.8 (15.7) | 9 (4) |
| Aetideidae | 0.4 (0.1) | 0.1 (0.1) | 5 (0) |
| Euchaetidae | 8.4 (12.7) | 12.7 (8) | 4 (8.6) |
| Scolecitrichidae | 0.5 (0.1) | 0.8 (0.3) | 0.2 (0.1) |
| Temoridae | 1.8 (0.1) | 0.6 (0.1) | 2 (0.1) |
| Metridinidae | 5.7 (0.3) | 1.1 (0.5) | 1 (2.6) |
| Centropagidae | 1.9 (0.1) | 0.2 (0.1) | 2 (0) |
| Lucicutiidae | 1 (0.2) | 0.6 (0.3) | 1 (0.2) |
| Heterorhabdidae | 0.1 (0) | 0 (0.1) | 0.3 (0) |
| Augaptilidae | 0.4 (0) | 0 (0.1) | 0.2 (00) |
| Candaciidae | 1 (0.4) | 0.8 (0.1) | 0.3 (0.5) |
| Pontellidae | 3.3 (0.1) | 0.4 (0.4) | 0.2 (2) |
| Acartiidae | 1.5 (0.1) | 1.2 (0.7) | 4 (1) |
| **Order Mormonilloida** | 0 (0) | 0 (0.1) | 0.2 (0) |
| **Order Cyclopoida** | 3 (0.6) | 12.6 (8) | 9 (1.6) |
| **Order Poecilostomatoida** | 16 (28.5) | 32 (23.7) | 13 (3) |
| **Order Harpacticoida** | 0 (0) | 0.6 (0.9) | 0.2 (0.2) |

respectively[19]. These were 56, 139 and 188 × $10^3$ $m^{-2}$ for microzooplankton[20]. It could be envisaged that this happened along with a build-up of dissolved organic carbon pool as the winter bloom became senescent and by the microbial loop.

As mentioned earlier, the herbivorous component of the zooplankton consisted mostly of fine filter feeding copepods and tunicates. It is now established that these organisms are capable of feeding on small organisms such as microzooplankton and even bacteria[21,22]. It would seem that in the Arabian Sea the herbivorous mesozooplankton are able to sustain the biomass during a lean phytoplankton period through a partial switch over from feeding on phytoplankton to the microbial loop. A high zooplanton biomass would in turn support the bacterial population through its metabolic by-products[23]. Such adaptations may not be a dominant feature in high latitude food chains since both phytoplankton and zooplankton increase during/after the spring bloom. Zooplankton populations are low during winter in these latitudes as most of them produce resting eggs to survive this season[24]. The high zooplankton biomass in the Arabian Sea also apparently sustains a large biomass of mesopelagic myctophid fishes (100 million tons $yr^{-1}$ in northwestern Arabian Sea)[25] which migrate to the surface at night to feed exclusively on zooplankton.

1. Yentsch, C. S. and Phinney, D. A., in *Oceanography of the Indian Ocean* (ed. Desai, B.N.), Oxford & IBH, New Delhi, 1992, pp. 57–66.
2. Bhattathiri, P. M. A., Pant, A., Sawant, S., Gauns, M. U., Matondkar, S.G.P., and Mohanraju, R., *Curr. Sci.*, 1996, **71**, this issue.
3. Madhupratap, M. and Parulekar, A. H., in *Monsoonal Biogeochemistry* (ed. Ittekot, V. and Nair, R. R.) Universitat Hamburg, Hamburg, 1993, pp. 51–72.
4. Madupratap, M., Haridas P., Ramaiah, N. and Achuthankutty, C. T., in *Oceanography of the Indian Ocean* (ed. Desai, B.N.) Oxford & IBH, New Delhi, 1992, pp. 99–112.

5. Menon, M. D. and George, K. C., Proceedings of the Symposium Warm Water Plankton, Spl Pub., National Institute of Oceanography, Goa, 1977, pp. 205–213.
6. Madhupratap, M. and Haridas, P., *J. Plankton Res.*, 1990, **12**, 305–321.
7. Timonin, A. G., *Mar. Biol.*, 1971, **9**, 281–289.
8. Longhurst, A. R. and Williams R., *J. Plankton Res.*, 1979, **1**, 1–28.
9. Longhurst, A. R. and Pauly, D., *Ecology of Tropical Oceans*, Academic Press, San Diego, 1987, p. 407.
10. Prasanna Kumar, S. and Prasad, T. G., *Curr. Sci.*, 1996, **71**, this issue.
11. *International Indian Ocean Expedition Plankton Atlas*, Indian Ocean Biological Centre, vol. 1, Fasc. 1, 1968, p. 18.
12. Madhupratap, M. and Haridas P., *Oceanol. Acta*, 1986, **9**, 105–117.
13. Madhupratap M., Nair S. R. S., Haridas P. and Padmavati, G., *J. Coastal Res.*, 1990, **6**, 413–426.
14. Smith, S. L., Banse, K., Cochran, J. K., Codispoti, L. A., Ducklow, H. W., Luther, M. E., Olson, D. B., Peterson, W. T., Prell, W. L., Surrgi, N., Swallow, J. C. and Wishner, K., *US JGOFS: Arabian Sea Process Study*, Planning Rep. No. 13, Woods Hole Oceanographic Institution, Woods Hole, 1991, p. 164.
15. Baars, M. A., Bakker, K. M. J., de Bruin, T. F., van Couwelaar, M., Hiehle, M. A., Karaaij, G. W., Oostrehuis, S. S., Schalk, P. H., Sprong, I., Veldhuis, M. J. W., Wiebinga, C.J. and Witte, J. I. J., in *Monsoons and Pelagic Systems* (ed. Baars, M.A.), National Museum of Natural History, Leiden, 1994, pp. 13–34.
16. van Couwelaar M. and Schalk, P. H., Arabian Sea Workshop, Texel, The Netherlands, 13–16 Feb. 1995, Abstracts, p.23
17. De Sousa, S., Kumar, M. D., Sardesai, S., Sarma, V. V. S. S. and Shirodkar, P. V., *Curr. Sci.*, 1996, **71**, this issue.
18. Surekha, S. and Madhupratap M., *Curr. Sci.*, 1996, **71**, this issue.
19. Ramaiah, N., Raghukumar, S. and Gauns, M., *Curr. Sci.*, 1996, **71**, this issue.
20. Gauns, M., Mohanraju, R. and Madhupratap, M., *Curr. Sci.*, 1996, **71**, this issue.
21. Christoffersen, K., Riemann, B., Hansen, L. R., Klysner, A. and Sorensen, H. B., *Microb. Ecol.*, 1990, **20**, 253–272.
22. Painting, S. J., Moloney, C. L. and Lucas, M. I., *Mar. Ecol. Prog. Ser.*, 1993, **100**, 55–69.
23. Jumars, P. A., Penry, D. C., Baross, J. A., Perry, M. J. and Frost, B. W., *Deep-Sea Res.*, 1989, **36**, 483–495.
24. Madhupratap, M., Nehring, S. and Lenz, J., *Mar. Biol.*, 1996, **125**, 77–87.
25. Gjosaeter, J., *Deep-Sea Res.*, 1984, **31**, 1019–1035.

ACKNOWLEDGEMENTS. This work was carried out as a part of the JGOFS (India) programme under a grant from the Department of Ocean Devolopment, New Delhi. We thank Profs. Karl Banse and B. Zeitzschel for their constructive criticisms. This is NIO contribution no. 2508.