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# Mesozooplankton biomass, composition and distribution in the Arabian Sea during the Fall Intermonsoon: implications of oxygen gradients

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## Abstract

Mesozooplankton biomass and distribution of calanoid copepods were studied for the upper 500 m between 3 and 21°N along an open-ocean transect in the Arabian Sea during the Fall Intermonsoon (September–October 1992, 1993). The region studied has strong gradients in the oxygen minimum zone (OMZ), being acutely deficient in oxygen in the north and with increasing concentrations towards the south. In the upper layers, mesozooplankton biomass was higher in the northern latitudes, above the thermocline, apparently avoiding the OMZ. In the deeper strata, relatively higher biomass was observed in the more oxygenated southern latitudes. Highest mesozooplankton biomass in open waters of the Arabian Sea was observed during the intermonsoon seasons. Calanoid copepods occurred at all depths, and surface-living species did not undertake conspicuous diel migrations, even when they occurred in the deeper waters of the more southern latitudes. A few species belonging to the families Metridinidae and Augaptilidae appeared to be characteristic of the poorly oxygenated mid-depths of the more northern latitudes. Seasonal variations in the composition of the copepod community were negligible. The evolution of the OMZ in the Arabian Sea and its implications are discussed. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

The Arabian Sea is one of the most productive region of the world's ocean (Ryther et al., 1966). Recent findings show that its open waters sustain high primary productivity (ca.  $> 0.5 \text{ g m}^{-2} \text{ d}^{-1}$ )

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almost throughout the year. This takes place through open-ocean upwelling and lateral advection in summer (Bauer et al., 1991; Kumar et al., unpublished manuscript) and convective mixing due to surface cooling in winter (Banse and McClain, 1986; Madhupratap et al., 1996a); in summer increased primary productivity is generally confined to the north of 10°N, and in winter to the north of 15°N (Krey and Babenerd, 1976; Brock et al., 1991; Banse, 1994). During summer, the eastern Arabian Sea shows low production except for a narrow upwelling belt along the south-western coast of India. High surface productivity leads to considerable flux of organic particles to deep water (Nair et al., 1989; Hakke et al., 1993) and high rates of oxygen consumption. High oxygen utilisation rates combined with the low oxygen content of waters entering the Arabian Sea from the east (Swallow, 1984) generates a thick (ca. 150–1000 m) oxygen-deficient/minimum zone (OMZ, oxygen content  $< 5 \mu\text{mol kg}^{-1}$ , Naqvi, 1991, 1994). The core of this OMZ occurs at about 200–500 m depth.

In the Arabian Sea, the OMZ is more pronounced in the central northern areas and acute oxygen deficiency is experienced in coastal waters only during summer upwelling (Naqvi, pers. comm). Thus, spatial variations in the above-mentioned processes result in a north–south gradient in the OMZ, with larger oxygen deficiencies occurring in the north. These features make the Arabian Sea an interesting and almost unique area in which to analyze patterns of horizontal and vertical distributions of flora and fauna. Similar oxygen-deficient zones exist only in two other major oceanic regions: a thinner layer (200–600 m) in the Bay of Bengal and between 100–900 m in the eastern tropical Pacific Ocean (Olson et al., 1993).

The first reference to the OMZ and its relation to zooplankton in the Arabian Sea was by Sewell and Fage (1948), followed by Vinogradov and Voronina (1961). There have been more recent attempts to characterize the vertical zonation of zooplankton of the northern Arabian Sea (Smith, 1982; Madhupratap and Haridas, 1990; Madhupratap et al., 1990; Paulinose et al., 1992; Bottger-Schnack, 1994, 1996; Madhupratap et al., 1996b; Padmavati et al., 1998; Wishner et al., 1998) from coastal as well as open-ocean waters. A recently emerging finding is a ‘paradox’ of the northern Arabian Sea with regard to mesozooplankton in the upper layers: its biomass remains almost invariant despite seasonal variations in the primary productivity regime (Madhupratap et al., 1992, 1996a,b; van Couwelaar, 1997; Baars and Oosterhuis, 1998; Baars, 1999). Onshore–offshore gradients in zooplankton biomass have been recorded during upwelling in the summer (Southwest Monsoon) season and in the Fall Intermonsoon in the western Arabian Sea (Smith et al., 1998; Stelfox et al., 1999). Many of these authors also noticed the absence of pronounced diel variations with respect to surface plankton in the area, which may indicate the inhibition due to the OMZ.

This paper describes the distribution of mesozooplankton, particularly calanoid copepods, and the influence of the north–south gradient of the OMZ between 3 and 21°N on zooplankton distribution in the upper 500 m of the Arabian Sea. We describe spatial variations in biomass and findings on horizontal and vertical patterns in assemblages. The present results are from a period when the Arabian Sea is not strongly forced by either monsoon, the Fall Intermonsoon. This season has not been studied in detail with regard to zooplankton. A brief overview of the seasonality of the mixed layer and primary production and findings on mesozooplankton from other expeditions are also included.

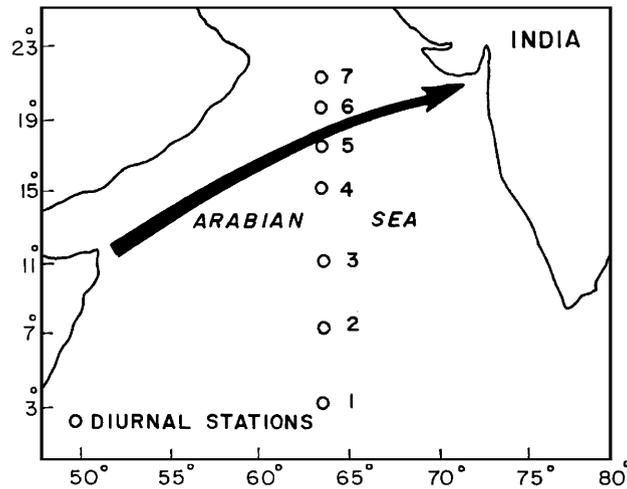


Fig. 1. Station positions in the Arabian Sea between 3 and 21°N along 64°E where diurnal sampling of mesozooplankton was conducted. The thick arrow across the Arabian Sea shows the position of the Findlater Jet which passes 64°E at approximately 16°N during the Southwest Monsoon.

## 2. Materials and methods

Mesozooplankton were collected from five depths in the upper 500 m with a Multiple Closing Plankton Net (Hydro-Bios, mouth area 0.25 m<sup>2</sup>, mesh size 200 μm). Samples were collected in vertical hauls from seven stations (Fig. 1) on two JGOFS-India cruises between 3°N and 21°N along 64°E. Collections from 3°N to 15°N (4 stations) were between 21 September and 3 October 1992, and sampling from 17 to 21°N (3 stations) was between 13 and 22 September 1993. Vertical tows with this net give an accurate picture of vertical distribution of zooplankton (Weikert and John, 1981). The stations were occupied for 24 h, and collections were made around noon and midnight at each station. Sampling was stratified according to the temperature profiles (obtained with a CTD cast prior to the collection) and the conventional OMZ of the north, and were between 500–300, 300–200, 200 m–bottom of thermocline (BT), BT to top of thermocline (TT) and TT to surface (mixed layer, ML).

The net was retrieved at a speed of 1 m/s, and the volume filtered was calculated from the sampling depth, the distance towed and hauling speed (Weikert and John, 1981). Samples from each depth were filtered, drained of excess water on absorbent paper, and added to a known volume of water to estimate biomass as a displacement volume. Samples were preserved in 4% formaldehyde for later enumeration and identification, which was done from 20% aliquots for upper layer samples and the entire sample for deeper layers. Copepods were identified to genus/species level. Carcasses were ignored. Trophic groups of zooplankton were classified according to Timonin (1971) and Longhurst and Williams (1979). Conversion of biomass was done by using the following formulae: 1 ml displacement volume = 0.075 g dry weight and 34.2% (dry weight) = carbon (Madhupratap and Haridas, 1990; Madhupratap et al., 1981).

Table 1

Mixed-layer depth (MLD) and chlorophyll *a* values ( $\text{mg m}^{-2}$ , integrated for upper 120 m) at various latitudes

Station	3°	7°	11°	15°	17°	19°	21°
MLD	70	40	90	40	100	75	40
Chl <i>a</i>	14	20	20	19	18	12	11

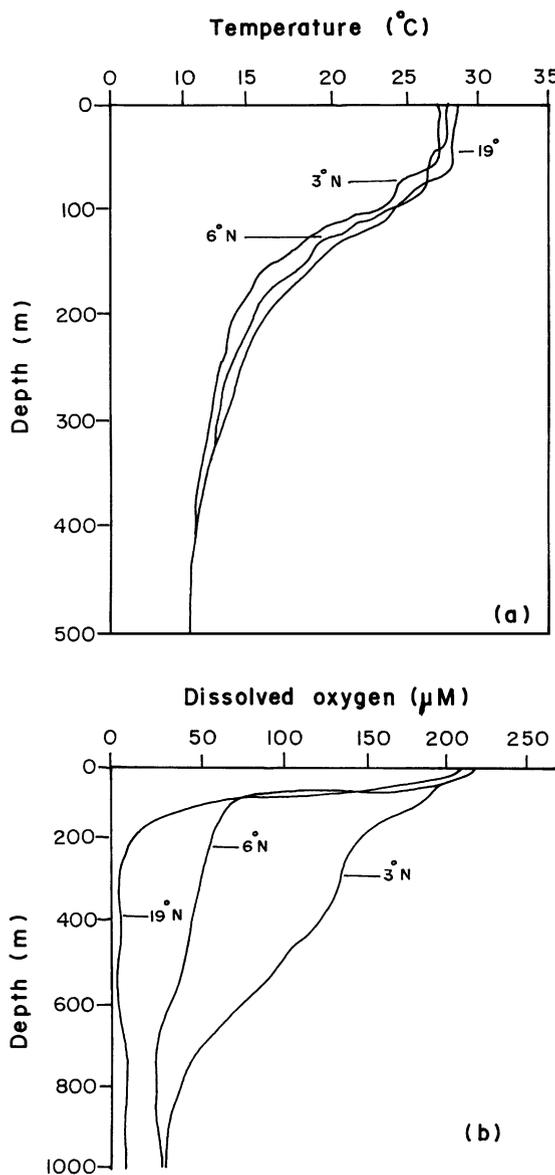


Fig. 2. Vertical profiles of temperature (a) and oxygen (b) at 3°, 6° and 19°N in the Arabian Sea.

An analysis of variance of biomass showed some significant ( $p < 0.05$ ) latitudinal variations. While in the ML biomass increased towards north, in the deeper strata it decreased in this direction. Depth-wise decreases were prominent at all latitudes ( $p < 0.01$ ). The same treatment for the total number of zooplankton showed that the numbers varied significantly between latitudes and depths ( $p < 0.01$ ), but diurnal fluctuations were only due to sampling fluctuations ( $p > 0.05$ ). In order to determine some of the aspects such as the percentage of dominant groups, trophic composition and relative abundance of copepod orders, data were pooled station-wise or depth-wise (Tables 4–7).

The mixed layer was taken as the subsurface depth where temperature was  $1^{\circ}\text{C}$  less than that at the surface using CTD profiles. The depth of the mixed layer varied between 40 and 100 m (Table 1; Fig. 2a, also see Fig. 3 for actual depth of ML, TT and BT at each station). Water samples collected with Go Flo bottles on a rosette around the CTD from various depths during the second cruise were analysed for dissolved oxygen and nitrate by Winkler titration and a SCALAR auto-analyser, respectively. Water samples for the analysis of chlorophyll *a* on both cruises were collected from 8 depths (surface to 120 m) and determined using a Turner Designs Fluorometer (see Bhattathiri et al., 1996, for procedural details).

Distributions of copepod species could be categorized based on their habitats (Fig. 3). In order to obtain a holistic picture of their variability between north and south, a cluster-analysis was performed based on night distributions for 50 calanoid species at  $21^{\circ}\text{N}$  and  $3^{\circ}\text{N}$ . Abundance of species at each depth was accounted for by group-average sorting with a Bray-Curtis analysis after normalising the data using a root-root method (Field et al., 1982). Status of each species in the cluster is assigned (Figs. 4 and 5) according to the classification under Section 3.3.1 (see below); the genera *Acrocalanus* and *Paracalanus* are not marked. Those species that occurred without any spatial/depth pattern are bracketed (S); three deep-living species, *Lucicutia ovalis*, *Gaetanus pileatus* and *Scolecithricella abyssalis* (included to highlight the distributions) are designated (D). The copepod *Scolecithricella ctenopus* was absent at  $3^{\circ}\text{N}$ .

### 3. Results

#### 3.1. Environmental conditions

In order to assess the possible differences in the study area between 1992 and 1993, we examined the sea-surface temperature (SST) maps derived from the advanced very high-resolution radiometer (AVHRR, data not presented) for September–October for 2 years. There was hardly any difference over the entire Arabian Sea between the 2 yrs. Sea-surface temperature was around  $28\text{--}29^{\circ}\text{C}$  along  $64^{\circ}\text{E}$  (Fig. 2a), indicating a warming period the after the cessation of the Southwest Monsoon and prior to onset of the Northeast Monsoon. The mixed layer was variable, being shallow at  $15$  and  $21^{\circ}\text{N}$  ( $\sim 40$  m) and deeper (70–100 m) at  $3^{\circ}$  and  $17^{\circ}\text{N}$  (Table 1). Nitrate was generally undetectable in the upper water column in 1993 (not presented). However, chlorophyll *a* values were slightly higher (Table 1) compared to the Spring Intermonsoon (Madhupratap et al., 1996a) except at the northernmost stations. A well-defined subsurface chlorophyll *a* maximum (SCM) was not evident (unlike the Spring Intermonsoon); concentrations were more or less constant in the upper 60 m, and below this depth, values decreased.

Table 2

Mesozooplankton day and night biomass (latter in parentheses) at different strata from 7 stations from 3° to 21°N along 64°E<sup>a</sup>

Station	0-TT	TT-BT	BT-200	200–300	300–500	Total
3°	24.4 (12.1)	6.4 (12.8)	6.4 (38.6)	5.3 (4.2)	4.2 (4.2)	46.7 (71.9)
7°	6.4 (21.3)	21.3 (25.6)	21.3 (30.5)	12.8 (6.4)	12.8 (2.1)	74.6 (85.9)
11°	23.7 (23.7)	21.3 (42.6)	19.0 (40.6)	8.5 (8.5)	25.6 (8.5)	98.1 (123.9)
15°	42.6 (44.3)	32.1 (37.2)	21.3 (32.1)	5.3 (4.2)	4.2 (2.1)	105.5 (119.9)
17°	230.8 (136.8)	34.2 (4.2)	2.1 (2.1)	2.1 (1.1)	1.1 (1.1)	270.3 (145.3)
19°	45.5 (70)	33.9 (57.0)	34.2 (8.5)	2.5 (2.1)	1.2 (1.1)	117.3 (138.7)
21°	192.3 (235.1)	78.8 (23.3)	2.1 (ND)	1.2 (0.8)	0.6 (0.8)	275.0 (260.0)

<sup>a</sup>Totals obtained for upper 1000 m are given in the last column. Values are in units of millimoles carbon m<sup>-2</sup>. Surface to top of thermocline (TT); BT – bottom of thermocline, for actual depths see Fig 3. ND – No data.

The OMZ showed a distinct gradient from north to south (Fig. 2b). Oxygen concentrations were very low in the north of 12°N, but the layer became thinner and values increased appreciably (to more than 50 μM) toward the south.

### 3.2. Zooplankton biomass and general composition

Zooplankton biomass in the upper 500 m (Table 2) was greater in the northern latitudes. This was mainly due to higher biomass in the upper layers, particularly the ML. However, in deeper strata, below 200 m, values were higher in the south. The reduction in the north may be because of low oxygen content. An increase in biomass during night at some of the northern stations was mostly attributable to ostracods. Total zooplankton counts also followed a similar trend, with highest values north of 15°N in the ML (Table 3). Somewhat higher counts were obtained in some of the deeper strata in the south, but both biomass and counts decreased with depth at all latitudes. Maximum biomass and counts were obtained from the upper 200 m and mainly above the thermocline.

Among the zooplankton, copepods generally dominated numerically, but in the northern latitudes spectacular swarms of ostracods replaced the dominance of copepods (Table 4). These swarms were generally confined to the mixed layer or sometimes up to the bottom of the thermocline, the latter mostly during daytime (Table 5). Swarms of ostracods are frequent in the northern areas of the Arabian Sea in this season (Kumari and Achuthankutty, 1989; Madhupratap et al., 1992). In the upper layers, these two groups dominated the counts, followed by chaetognaths.

Table 3

Mesozooplankton counts obtained at different strata during day and night (latter in parentheses) at 7 stations from 3° to 21°N along 64°E; values are as 10<sup>3</sup> per 100 m<sup>3</sup>. Depth definitions as in Table 2

Station	0-TT	TT-BT	BT-200	200–300	300–500
3°	11.1 (7.4)	1.9 (4.9)	1.9 (8.1)	1.9 (2.3)	1.5 (1.5)
7°	2.3 (5.0)	10.9 (20.6)	13.7 (10.5)	5.4 (1.8)	2.4 (0.4)
11°	27.6 (14.1)	14.8 (15.9)	3.8 (7.5)	1.8 (1.6)	0.5 (0.5)
15°	65.6 (117.5)	29.0 (19.1)	18.7 (20.0)	0.7 (0.5)	0.3 (0.3)
17°	90.7 (101.3)	6.0 (5.3)	4.0 (1.5)	0.8 (0.7)	0.2 (0.1)
19°	52.0 (86.2)	91.6 (20.7)	22.2 (8.4)	0.9 (0.7)	0.2 (0.1)
21°	214.4 (253.7)	82.1 (32.0)	5.9 (ND)	0.2 (0.02)	0.3 (0.1)

Table 4

Percentage of abundances of dominant groups of zooplankton at different stations (all depths, both day and night combined)

Groups	STATIONS						
	1	2	3	4	5	6	7
Siphonophora	1.2	3.6	8.7	0.3	1.8	0.9	1.4
Ostracoda	2.3	1.7	4.2	0.1	62.5	54.8	43.3
Copepoda	83.0	76.6	66.5	88.7	26.6	38.4	49.1
Euphausiacea	2.2	2.1	1.5	1.0	0.9	1.1	0.4
Chaetognatha	7.6	8.6	8.8	4.2	2.7	1.5	3.5
Tunicata	1.8	0.7	8.5	1.5	3.2	0.2	0.8

Siphonophores and tunicates were occasionally present in fairly high numbers. *Thalia democratica* was the common salp observed in the present study.

Herbivores were common at all depths (Table 6), mostly smaller calanoid copepods. However, omnivores and carnivores also were prominent in the total assemblage. Ostracods were considered as omnivores in the present study (Omori and Ikeda, 1984). Appreciable numbers of carnivores are always present in the Arabian Sea, and apart from chaetognaths, they mainly consist of the copepod orders Poecilostomatoida, Cyclopoida and the calanoid *Euchaeta rimana* (Madhupratap and Haridas, 1990; Madhupratap et al., 1992; Padmavati et al., 1998).

Table 5

Percentage abundances of dominant groups in different strata. D – Day, N – Night (all stations combined)

Groups	0-TT		TT-BT		BT-200		200–300		300–500	
	D	N	D	N	D	N	D	N	D	N
Siphonophora	2.2	0.8	1.5	3.6	1.5	3.8	1.5	2.2	0.7	2.2
Ostracoda	12.4	56.6	56.1	3.5	12.8	2.9	8.8	13.9	2.5	16.9
Copepoda	74.1	38.3	35.7	71.6	77.0	73.0	68.8	70.4	78.0	62.0
Euphausiacea	0.3	0.9	0.4	1.7	0.5	2.1	13.1	3.4	3.5	2.0
Chaetognatha	5.9	1.5	3.8	7.7	3.3	6.9	2.7	3.3	4.6	5.1
Tunicata	2.8	0.5	0.7	4.6	0.9	2.3	0.3	1.9	1.0	7.5

Table 6

Average percentage composition of different trophic groups in each stratum ( $\pm$  Standard Deviation); day and night data from all stations are combined

	0-TT	TT-BT	BT-200	200–300	300–500
Herbivores	46.3 $\pm$ 19.1	36.5 $\pm$ 17.7	41.7 $\pm$ 9.1	40.6 $\pm$ 17.3	45.1 $\pm$ 17.7
Omnivores	24.5 $\pm$ 27.6	23.4 $\pm$ 27.7	27.2 $\pm$ 13.8	32.5 $\pm$ 18.8	32.4 $\pm$ 21.7
Carnivores	29.2 $\pm$ 24.1	40.1 $\pm$ 17.9	31.1 $\pm$ 15.1	26.9 $\pm$ 11.7	22.5 $\pm$ 8.1

Table 7

Relative abundance of various orders of copepods in different depth zones (all stations combined, day–night mean  $\pm$  SD); Values given as a percentage of total copepods per 100 m<sup>3</sup> within each zone

Order	0-TT	TT-BT	BT-200	200–300	300–500
Calanoida	73.4 $\pm$ 7.4	72.0 $\pm$ 13.2	80.2 $\pm$ 6.9	76.5 $\pm$ 11.6	84.3 $\pm$ 8.8
Cyclopoida	8.1 $\pm$ 4.7	12.2 $\pm$ 8.9	9.1 $\pm$ 9.9	13.6 $\pm$ 12.7	5.3 $\pm$ 3.3
Poecilostomatoida	18.3 $\pm$ 5.7	15.3 $\pm$ 12.3	9.7 $\pm$ 4.5	9.7 $\pm$ 3.6	9.3 $\pm$ 7.5
Harpacticoida	0.2 $\pm$ 0.2	0.5 $\pm$ 0.2	0.5 $\pm$ 0.1	0.1 $\pm$ 0.1	1.0 $\pm$ 0.6

### 3.3. Composition of the copepod community

Members of the order Calanoida dominated the counts at all depths (Table 7), followed by poecilostomatoids (*Corycaeus* spp. and *Oncaea* spp. plus a few *Copilia* and *Sapphirina* spp.) and cyclopoids (*Oithona* spp.). A few harpacticoid copepods consisting of *Macrosetella gracilis*,

*Microsetella norvegica*, *Aegisthus mucronatus*, *Clytemnestra scutellata* and *Miracia efferata* and the mesopelagic mormonilloid *Mormonilla minor* were also encountered.

### 3.3.1. Distribution of calanoid copepods

Eighty-six species of calanoid copepods belonging to 40 genera were observed in the present collections. However, many were present only in the deeper strata and numbers were too low to detect any pattern. Among the surface-living copepods, the species belonging to the families Paracalanidae, Clausocalanidae, Calanidae, Eucalanidae and Acartiidae were dominant.

Our previous studies of the upper 1000 m of the northern Arabian Sea north of 10°N during November 1983 and February 1995 (Madhupratap and Haridas, 1990; Padmavati et al., 1998) have shown that a large number of common and abundant calanoid species are mainly surface living, but some of them occasionally may occur in deeper waters in very small numbers (~ 10–50 per 100 m<sup>3</sup>). Many of these species were more abundant in surface waters in the present study as well, but one main difference was that some were distributed in greater numbers in the deeper waters of the south. Thus, the predominantly surface-living species (group 1) could be divided into:

(1a) Those species with higher abundance at the surface in the north, but unlike northern regions had higher abundance in deeper strata in the south. Examples of this type of distribution were *Undinula vulgaris* (Fig. 3a), *Calanus minor*, *Cosmocalanus darwini*, *Clausocalanus arcuicornis*, *C. paululus*, *Canthocalanus pauper*, *Eucalanus pileatus*, *E. mucronatus*, *Lucicutia flavicornis*, *Euchaeta rimana*, *Centropages calaninus*, *Acartia negligens* and *Calocalanus pavo*.

(1b) Species distributed only in surface layers regardless of latitude, such as *Acartia amboinensis* (Fig. 3b), *Euchaeta indica*, *Calanopia minor*, *Centropages gracilis*, and *Temora discaudata*.

(1c) A few species that were more common at the surface in the south but exhibited some deeper dispersion, for example, *Eucalanus subcrassus* (Fig. 3c), *Calocalanus plumulosus*, *Scolecithrix danae*, *Paracandacia truncata*, *Eucalanus attenuatus*, *E. elongatus* and *Rhincalanus rostrifrons*. However, these species were recorded from surface waters of the north in other seasons in earlier studies (Madhupratap and Haridas, 1990).

Apart from the taxa above, species belonging to the genera *Paracalanus* (Fig. 3d) and *Acrocalanus*, which were two of the most abundant forms in the collections, were uniformly distributed latitudinally and were mostly surface-living. Occasionally individuals were captured as deep as 500 m. Species of these genera were not identified to ascertain patterns among them. A few others like *Euchaeta acuta*, *Candacia pachydactyla*, *C. catula*, *Labidocera minuta*, *Pontellina plumata* and *Centropages furcatus* occurred in low numbers without any latitudinal pattern at the surface or up to the bottom of the thermocline. Species belonging to group 1 generally did not exhibit diel vertical migrations even in southern latitudes.

A second group consisted of a few species that seem to have the core of their abundance in the OMZ in the north, but were also present in the deeper waters of the south in lesser numbers. They were *Pleuromamma indica* (Fig. 3e), *P. abdominalis*, *P. xiphias*, *P. gracilis*, *Rhincalanus nasutus*, *Metridia brevicauda*, *M. princeps*, *Heterorhabdus papilliger*, *Amalothrix indica*, *Haloptilus spiniceps*, *H. longicornis*, *Scolecithricella tenuiserrata* and *Temoropia mayumbaensis*. All these species appeared to be active diel migrants and hence had some overlap in distribution with species of group 1c.

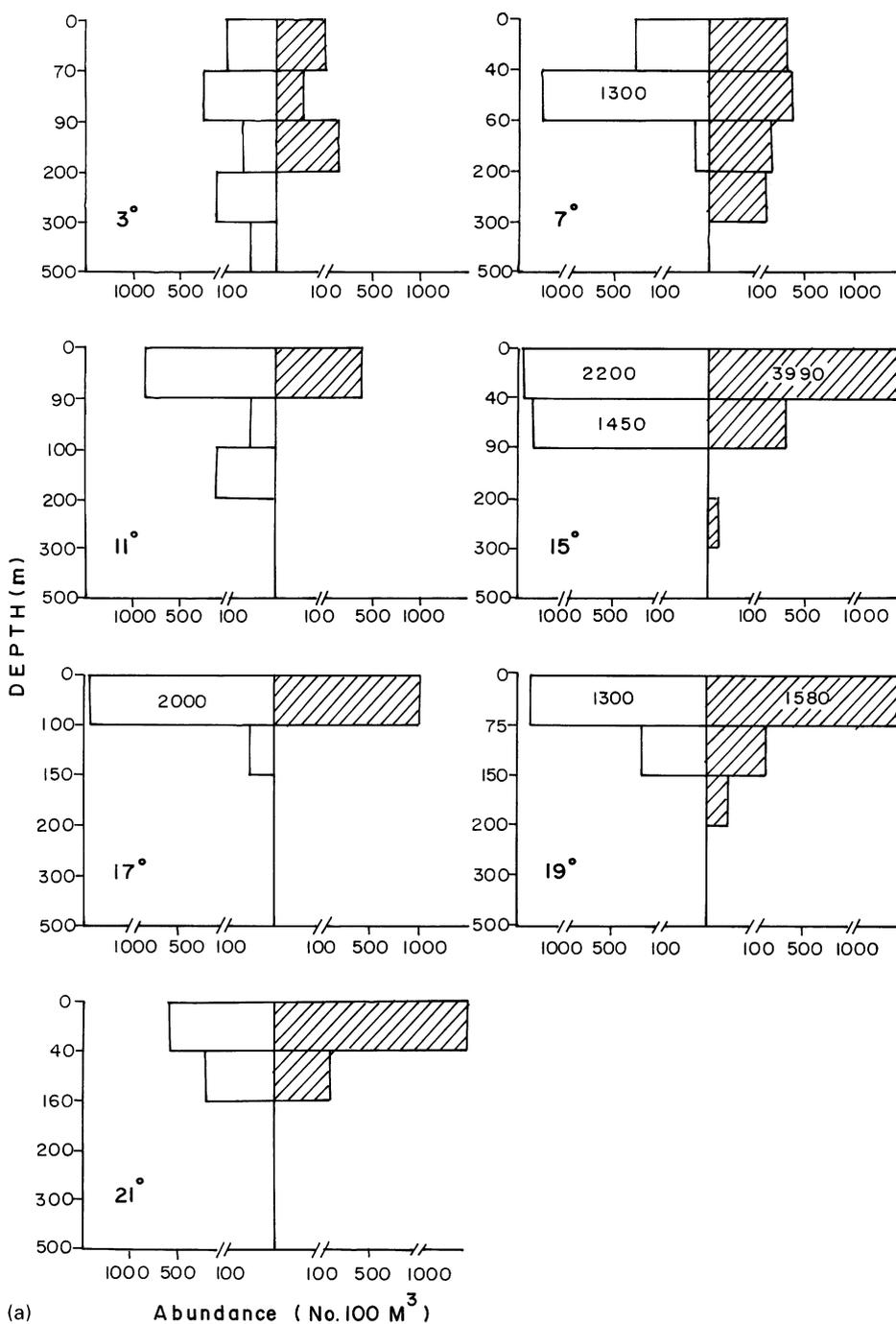


Fig. 3. Latitudinal and vertical distribution (number per 100 m<sup>3</sup>; night shaded) of (a) *Undinula vulgaris* (representing group 1a; see text); (b) *Acartia amboinensis* representing group 1b; (c) *Eucalanus subcrassus* representing group 1c; (d) *Paracalanus* spp. (see text); and (e) *Pleuromamma indica* representing group 2 species.

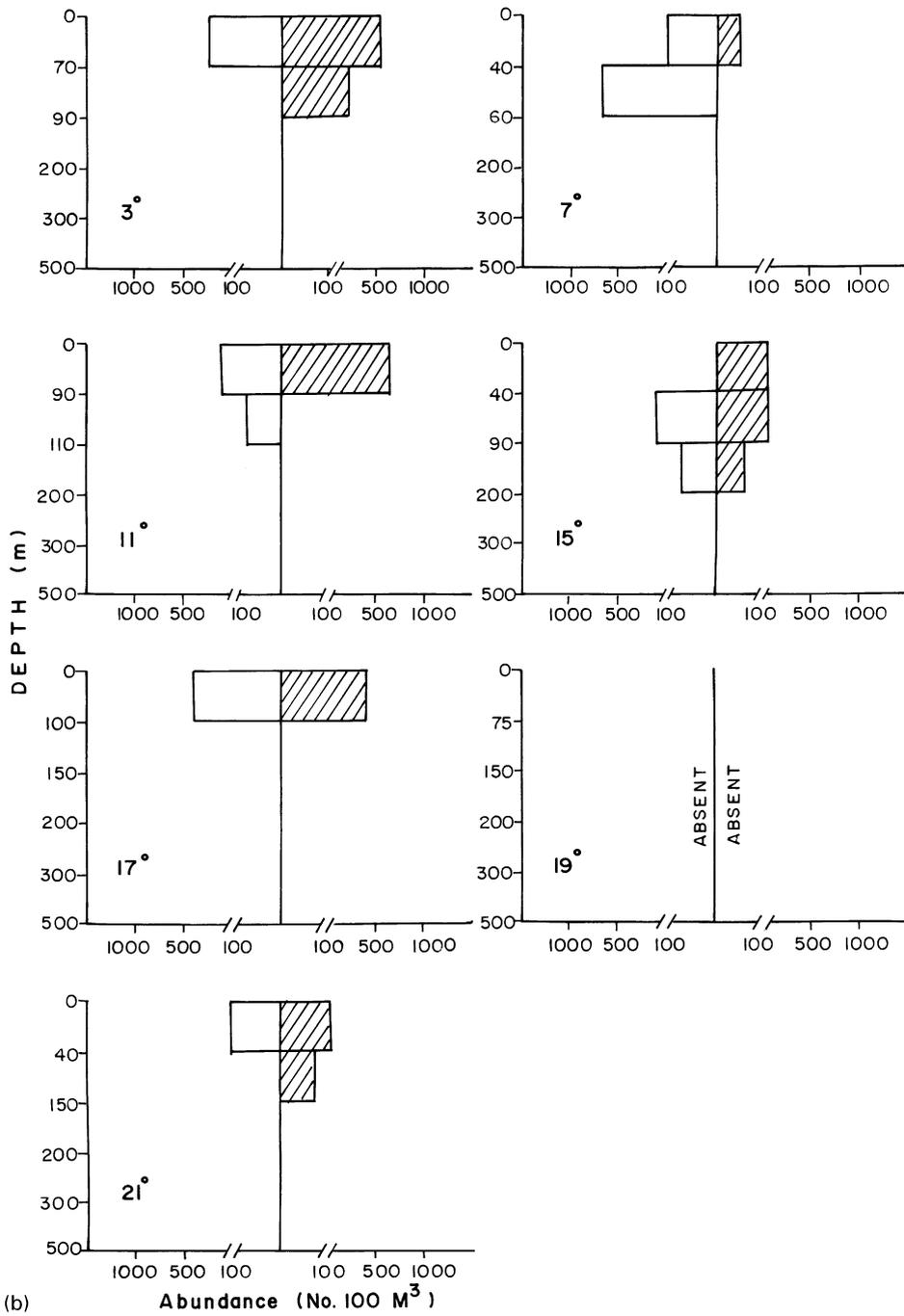


Fig. 3. (continued)

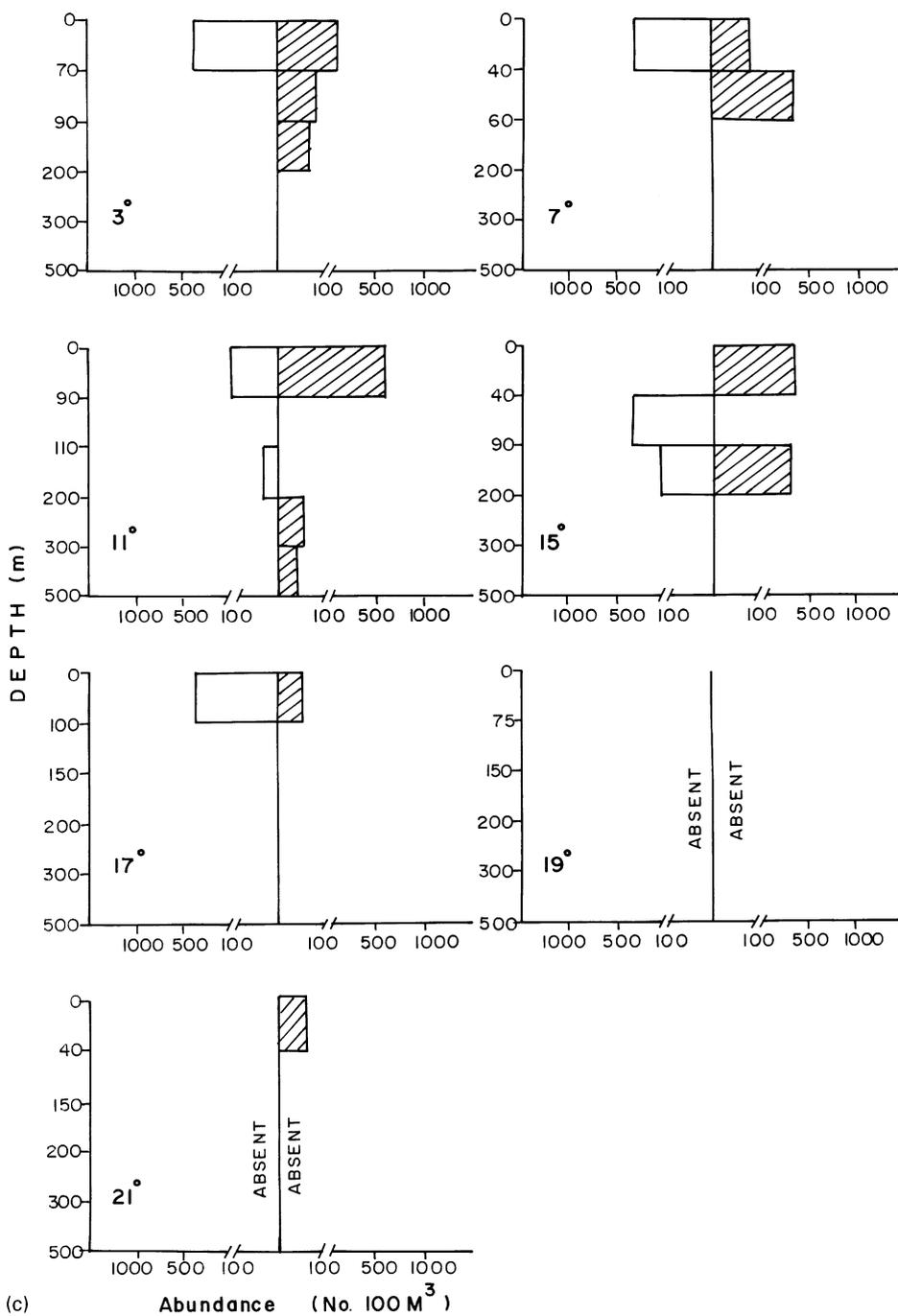


Fig. 3. (continued)

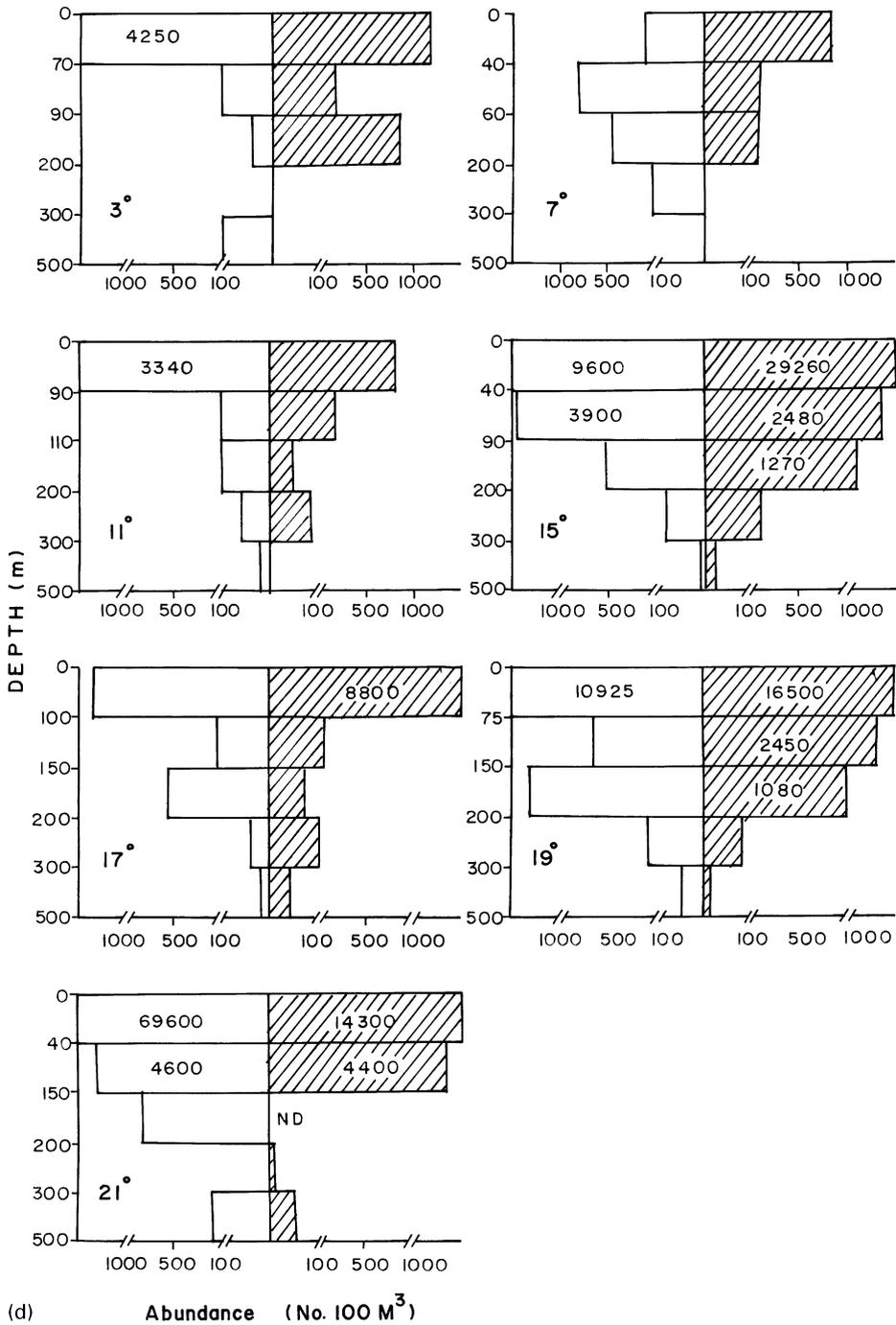


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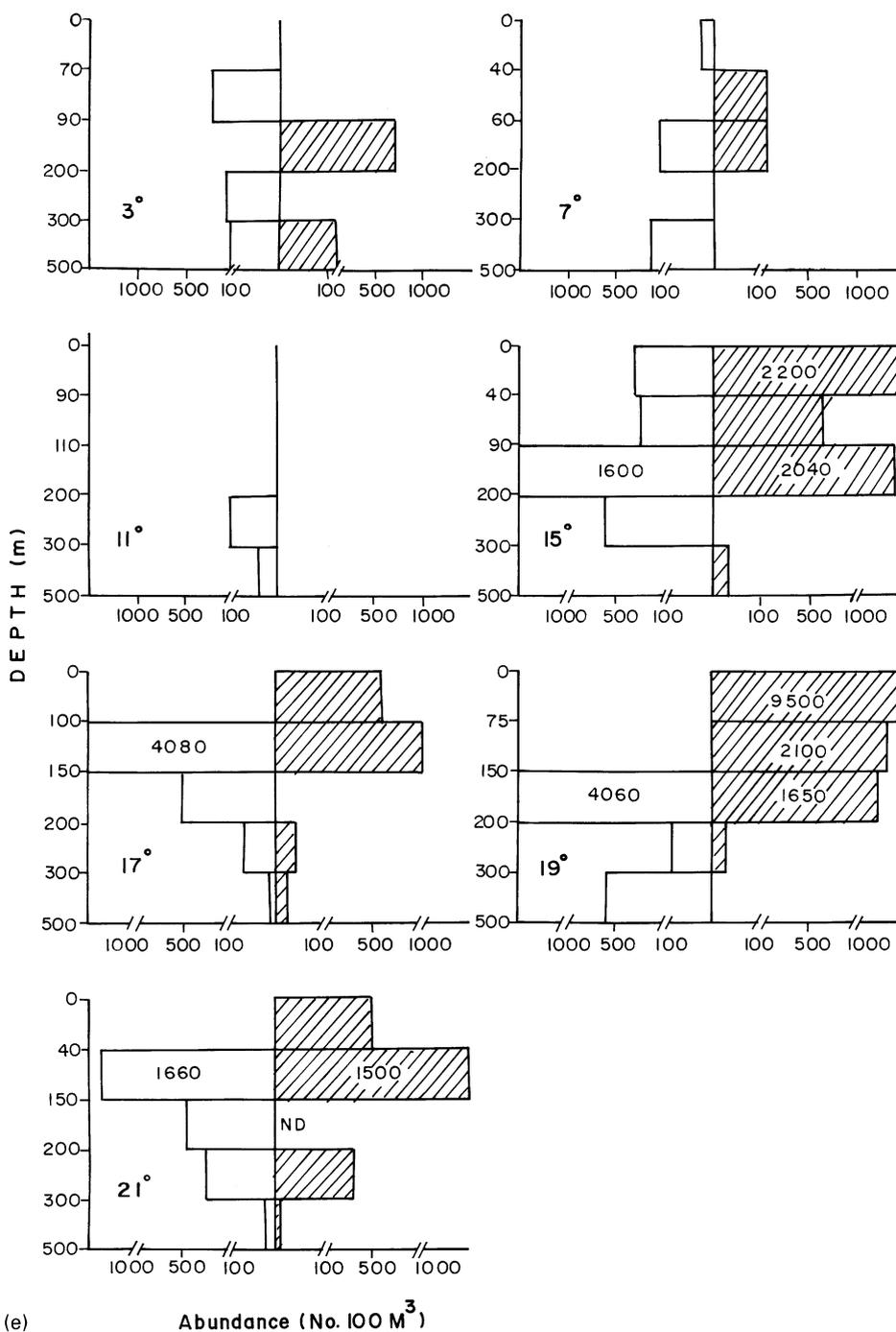


Fig. 3. (continued)

The third group consisted of deeper-living species, which mostly occurred in the bottom strata without any spatial patterns. Thirty-nine species in this category were present in the collections in small numbers. They generally belonged to the families, Aetideidae (*Euchirella*, *Gaetanus*), Phaenidae, Scolecithricidae, Metridinidae (*Gaussia*), Lucicutiidae, Augaptilidae (*Augaptilus* spp.) and Arietellidae. These species are also diel migrants, as reported in our earlier studies, and are found

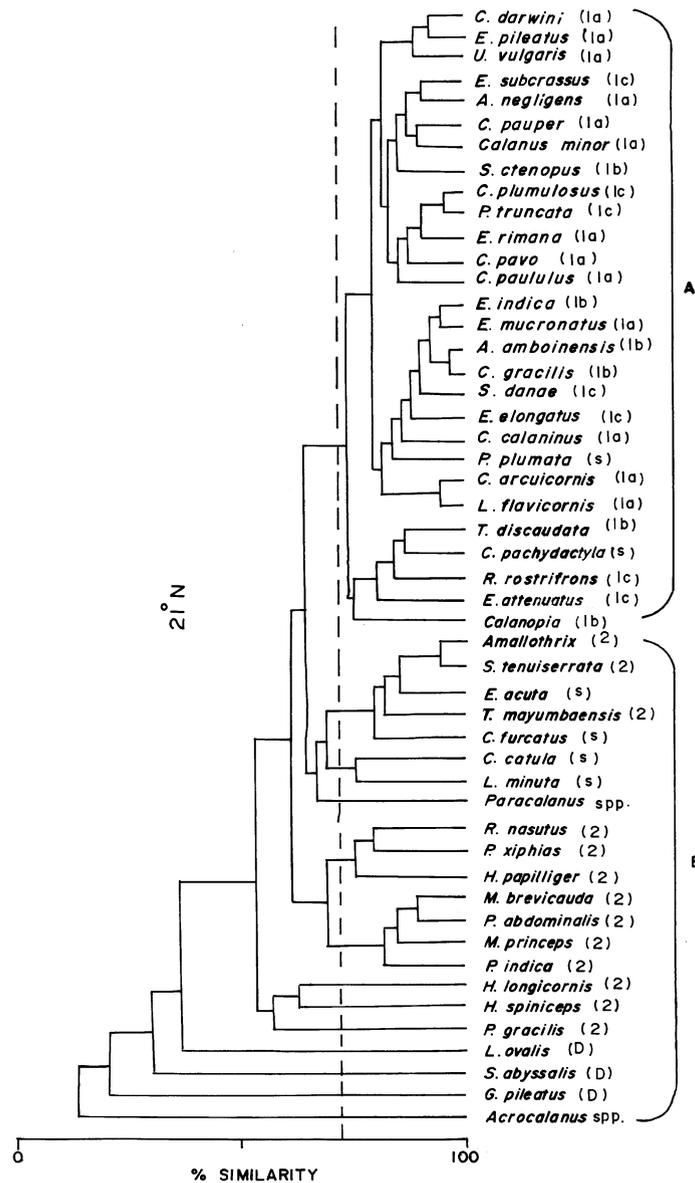


Fig. 4. Species cluster formation based on Bray-Curtis analysis showing affinities (night distributions) of 50 species at 21°N. For explanation of bracketed symbols and groups, see text.



without specific patterns (S) were grouped together (cluster A). Species predominant in the OMZ (group 2) were mostly separated and were found in cluster B along with some designated without pattern (S) and deep-living (D). Cluster B species were mostly active diel migrants at both latitudes.

The cluster at 3°N (Fig. 5) showed a slightly different pattern. Although cluster A consisted predominantly of surface-living forms similar to that at 21°N, it also included a mixture of (1c) and (S) along with some group 2 forms, the latter three also have truncated distributions. Subdivision of this cluster showed AA (species living in the upper layers), AB (consisting of forms which occurred in mid-waters as well, but in low numbers), and AC (those species with high abundance at the surface, as well as in mid-water strata at this latitude). Cluster B at 3°N included some of the surface-living species and 1c, all of which occurred up to 500 m (BA), and deep-living species (BB). At both latitudes, clusters A and B were not closely linked (usually < 75% similarity). *Paracalanus* and *Acrocalanus*, although they have similar depth distributions at both latitudes, were segregated at 21°N because the former occurred in larger numbers at the surface in the north (> 14,000/100 m<sup>3</sup>) compared to about 5000/100 m<sup>3</sup> at 3°N. Their abundance was similar at 3°N and therefore they were more closely linked (Fig. 5).

#### 4. Discussion

The data presented in this paper describe the zooplankton composition from an open ocean transect during the Fall Intermonsoon. There are very few comparable zooplankton data available for this period from the open Arabian Sea.

It is well known that the Arabian Sea, a small tropical/subtropical ocean basin, undergoes regular oscillations intra-annually, between the Southwest (June–mid-September) and Northeast (November–February) Monsoons. Until recently the data generated during the transition periods between these monsoon seasons, the Spring and Fall Intermonsoons, were generally pooled along with the monsoon seasons. The Fall Intermonsoon has been included in the SW Monsoon season, and the Spring Intermonsoon has been included in the NE Monsoon season. An unfortunate consequence was that most of the biological measurements of the past were also usually combined within these two seasons (i.e., the International Indian Ocean Expedition (IIOE) Plankton Atlas, 1968; Krey and Babenerd, 1976).

During the Southwest Monsoon, apart from coastal upwelling along Somalia, Arabia and southwest coast of India, upward Ekman pumping driven by the positive wind stress curl northwest of the Findlater Jet (Fig. 1; our stations 6 and 7) leads to high primary productivity (up to 1700 mg C m<sup>-2</sup> d<sup>-1</sup>; JGOFS-India, unpublished results). South of the Jet, downwelling and deep mixed layers develop (Naidu and Rao, 1990; Brock and McClain, 1992). However, in the south, up to 10°N and west of 64–65°E, primary productivity is also high (800 mg C m<sup>-2</sup> d<sup>-1</sup>; Kumar et al., unpublished manuscript; R. Barber, pers. comm.). The reasons for this are not well understood but have been attributed to lateral advection or filaments arising from the coastally upwelled waters off the Arabian peninsula (Manghnani et al., 1998; Kumar et al., unpublished manuscript). During the Northeast Monsoon, winter cooling and convection results in the development of deep mixed layers, injection of nutrients into surface waters, and primary productivity up to 1000 mg C m<sup>-2</sup> d<sup>-1</sup> in the northern areas (Kumar et al., 2001).

By the Spring Intermonsoon, the Arabian Sea in our study area shows characteristics of a Typical Tropical Structure (TTS, Herbland and Voituriez, 1979). The SST increases to 28–29°C and the mixed layer shoals to form a uniformly shallow layer of 40–50 m or even less (Wyrтки, 1971; Kumar and Prasad, 1996). Primary productivity remains low ( $< 200 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) in this season. The condition of the TTS is more or less regained during the Fall Intermonsoon, but is less pronounced due to the less intense ocean heat gain (Hastenrath and Greischar, 1989).

Thus, the mixed layer and productivity of the northern Arabian Sea undergo large seasonal and spatial variations. The model by Brock et al. (1994) shows that the southern parts remain permanently oligotrophic and are not much influenced by the seasonal regimes.

The near absence of nitrate in the mixed layer during September–October in the open Arabian Sea has been well documented by Mantoura et al. (1993). Their oxygen profiles also match our data, decreasing in the OMZ from  $60 \mu\text{M}$  near the equator to  $< 10 \mu\text{M}$  at  $9^\circ\text{N}$ . The high chlorophyll *a* concentrations found off Somalia and in the central Arabian Sea during the Southwest Monsoon generally disappear by the Fall Intermonsoon (Baars and Oosterhuis, 1998). However, primary productivity values during the latter period (Owens et al., 1993) were not very low (their stations 1–7, range  $236\text{--}533 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) compared to those observed during the Spring Intermonsoon (Bhattathiri et al., 1996). This observation is supported by our chlorophyll *a* values, which were higher than those observed in the Spring Intermonsoon, and were without a subsurface chlorophyll *a* maximum. This would indicate that regenerated nutrients are available in the upper water column (low *f*-ratios obtained by Owens et al., 1993) and presumably zooplankton play a major role through their metabolism and excretion.

The IIOE results (Rao, 1973; his Fig. 7) show that there was no proper coverage of the Arabian Sea for the Fall Intermonsoon except for the Saudi Arabian coast where the mesozooplankton biomass was between 40 and  $85 \text{ m mol C m}^{-2}$  for the upper 200 m (330  $\mu\text{m}$  mesh size). A re-analysis of the data collected during IIOE, the Indian Ocean Experiment (INDEX) and the Netherlands Indian Ocean Programme (NIOP) using the same mesh (Baars and Oosterhuis, 1998; Baars, 1999) did not show significant variations between Southwest and Northeast Monsoons. But, these results also point out that the IIOE data south of  $10^\circ\text{N}$  show low values throughout the year in the open waters, particularly during the Fall Intermonsoon ( $25 \text{ m mol C m}^{-2}$ ). A few more data sets available for the Fall Intermonsoon from the open northern Arabian Sea show average values of 65 and  $127 \text{ m mole C m}^{-2}$  for the upper 200 m (Kumari and Achuthankutty, 1989; Madhupratap et al., 1992).

The average mesozooplankton biomass observed for the northern latitudes ( $179 \text{ m mol C m}^{-2}$  between  $15$  and  $21^\circ\text{N}$ , Table 2) is higher than those observed for the upper 1000 m on the JGOFS-India cruises during winter and summer from the oceanic waters (88 and 94 respectively, Madhupratap et al., 1996b). However, it is comparable to Spring Intermonsoon data (162, considering that below 500 m, the biomass is almost negligible). Wishner et al. (1998) report their highest biomass (128) for the upper 1000 m during the Spring Intermonsoon for offshore areas (see also Smith et al., 1998).

It is interesting that the intermonsoon seasons support high mesozooplankton biomass in open waters, especially in the upper layers, although the primary productivity generally is lower than during the Southwest or Northeast Monsoons. This and the fact that seasonal variations in biomass are small in the upper layers of northern latitudes (Madhupratap et al., 1996b; Wishner

et al., 1998) bring us back to the paradox of the Arabian Sea and the applicability of the microbial loop spatially and temporally (Madhupratap et al., 1996a, b). Highest bacterial counts in the upper 200 m ( $> 1 \times 10^9 \text{ cell l}^{-1}$ ) were obtained during the Spring (Ramaiah et al., 1996) and Fall Intermonsoons (between 9 and 21°N in the present study; Ramaiah, pers. comm.). This was also true for microzooplankton during the Spring Intermonsoon (Gauns et al., 1996; see, however, Burkill et al., 1993 for Fall data and interpretations). Landry et al. (1998) suggested a strong microbial coupling and remineralisation for the open Arabian Sea.

The lesser biomass observed at the southern stations (average =  $83 \text{ m mol C m}^{-2}$  between 3 and 11°N) is consistent with other recent findings (station J3 in Madhupratap et al., 1996b; station S-15 in Smith et al., 1998). Stelfox et al. (1999) report the value,  $12.5 \text{ m mol C m}^{-2}$  (using conversion factors applied in the present data set) from the upper 100 m from their southern station (A7) for the Fall Intermonsoon.

Reduction in zooplankton biomass with depth is more or less universal in tropical waters although the patterns might differ with seasons in colder regions (Vinogradov, 1997). However, the severe depletion obtained in the northern latitudes in the present and earlier studies in the Arabian Sea seem to be associated with the OMZ (Paulinose et al., 1992; Smith et al., 1998; Wishner et al., 1998). Similar observations have been made from the eastern tropical Pacific Ocean (Sameoto, 1986) and the Bay of Bengal (Padmavati et al., unpublished manuscript).

An Oxygen Minimum Zone occurs at mid-depths in many seas/oceans (Kamykowski and Zentara, 1990; Wishner et al., 1995), but it is the acute deficiency experienced only in a few regions mentioned earlier that constrains distributions and suppresses diel vertical migrations of many species. This is clear from studies of areas that experience different oxygen stress and an increase in biological activity at the boundaries of the OMZ (see Bottger-Schnack, 1996; Wishner et al., 1995 for details). A large part of the zooplankton community that occurs in the Somali Basin exhibited some vertical migration probably because oxygen concentrations were not very low (van Couwelaar, 1997). The increase in biomass and zooplankton counts obtained from the lower strata (below 200 m) along southern latitudes also supports this.

The percentage compositions of trophic groups (Table 6) and various copepod orders (Table 7) agree fairly well with our earlier studies (Madhupratap and Haridas, 1990; Madhupratap et al., 1996b; Padmavati et al., 1998). However, certain drawbacks in the present data set (some of which were pooled irrespective of the latitudes) and interpretations must be pointed out. Bottger-Schnack (1996) shows that a larger mesh does not effectively sample many small poecilostomatoids and cyclopoids, which occur in large numbers in deeper waters, and that they are carnivores. There may be other inherent problems in the classification of trophic groups; for example, euphausiids were not an abundant group in the present study and were generally classified as herbivores while some species are actually carnivores. The herbivores collected from deeper depths may arise from surface populations sinking out of their usual depths. Moreover, in view of the dwindling food supply, many deeper forms may be detritivores or coprophagous. Some of the copepods assumed to be carnivores may actually be omnivores (i.e., the calanoid copepods of the family Pontellidae; Ohtsuka and Onbe, 1991). Longhurst and Pauly (1987) concluded that there is twice as much biomass of predators relative to herbivores and detritivores in the tropics compared to polar and temperate oceans.

Unfortunately, there are not many data sets available to compare the horizontal and vertical distributions of calanoid copepod species from the Arabian Sea where collections were made

on latitudinal scales in a similar stratified mode with a 200  $\mu\text{m}$  net particularly during Fall Intermonsoon. Over the next few years larger inventories are likely to emerge based on several JGOFS studies from the Arabian Sea (cf. Smith et al., 1998; Wishner et al., 1998).

A list of epipelagic calanoid copepods occurring in the northern Indian Ocean and their distributions based on historical and post-IIOE studies were collated by Madhupratap and Haridas (1986). The general composition and patterns of distributions of calanoid copepod species obtained here are quite comparable with it and subsequent studies (Madhupratap and Haridas, 1990; Madhupratap et al., 1996b; Padmavati et al., 1998; JGOFS-India, unpublished results) from the northern parts of this region. The surface-living species, which are usually in smaller forms ( $< 2$  mm, except Eucalanidae) belonging to a few families mentioned earlier, mostly stay in the upper layers. Although there were deeper distributions in the south for some of these, conspicuous diel migrations were not noticeable. On the whole, the list of surface and deep-living species was similar to those obtained in our earlier studies or those listed from the western Arabian Sea by Smith et al. (1998). There were small differences, such as species like *Lucicutia flavicornis* and members of the family Eucalanidae, which have been found to have deeper distributions. The composition was also more or less similar to earlier findings for groups 2 and 3 species. These point towards genetic adaptations of species to surface or particular depths and a general lack of seasonal variations in species composition in the Arabian Sea.

Although this study is confined to the Fall Intermonsoon, the horizontal patterns in concentrations of oxygen do not vary in the Arabian Sea over the year. Thus, it will not be very surprising if those species clustered in the OMZ show the same pattern in all seasons. Nonetheless, a seasonal coverage of areas in and out of OMZ and particularly concentrating the upper and lower boundaries should be interesting.

The confinement of surface-living species to upper layers of low oxygen zones has been observed in many earlier studies. Even in coastal waters, when the low oxygen isolines surface during upwelling, these species were confined to the upper 10 m or so without any diel migration along the west coast of India (Madhupratap et al., 1990). The copepod *Calanoides carinatus*, which proliferates during upwelling in the western Arabian Sea (Smith, 1982), does not occur in the eastern Arabian Sea, but has been found in diapause in the subsurface waters of the central Arabian Sea during the Northeast Monsoon (Padmavati et al., 1998).

The deep-living copepods found in the present as well as earlier studies have much more extended distributions into deeper waters ( $> 2000$  m) in the Arabian Sea (Grice and Hulsemann, 1967). Most of these species occur circumglobally (Madhupratap and Haridas, 1986).

The species belonging to group 2 are especially interesting since they seem to be adapted to the OMZ. Sewell and Fage (1948) and Vinogradov and Voronina (1961) included *Eucalanus elongatus* in this group. Apart from it and *Rhincalanus nasutus*, the OMZ is occupied mainly by the calanoid families of Metridinidae and Augapatilidae. These and some of the mesopelagic fishes seem to have evolved to tolerate and take advantage of the conditions that exist in the OMZ (Smith et al., 1998). The most remarkable species among this group is *Pleuromamma indica*. It formed 84% of the total numbers of all species of this genus in the IIOE collections (Saraswathy, 1986) and is probably an endemic to the Indian Ocean (Saraswathy and Iyer, 1986) despite stray doubtful records from the Atlantic (Sewell, 1948) and Pacific Oceans. This species is generally confined to the OMZ of the northern Indian Ocean (both Arabian Sea and Bay of Bengal) and rarely occurs at south of  $10^{\circ}\text{N}$  (Goswami et al., 1992). In the IIOE collections, this species occurred in the upper

layers mostly in night samples showing active diel migration (Kasturirangan et al., 1973) as observed in the present study (Fig. 3e).

The OMZ of the Arabian Sea could have evolved when the surface productivity increased associated with the origin of the monsoons. The latter may be associated with the emergence of the Himalayas (Valdiya, 1999). Although, as a result of continental drift, India encountered the southern margin of Asia during early Cenozoic (Dietz and Holden, 1970), and the Himalayas emerged as a highland by middle Miocene, it was not until ca. 8 m.y. ago that the latter rose to its present heights and set the monsoons in motion (Valdiya, 1999). Nonetheless, the intensity of the OMZ has varied on orbital and sub-orbital time-scales in the past, driven by changes in surface productivity and the depth of winter mixing (Reichart et al., 1998). Thus, the evolution of species adapted to the OMZ and the suppression of downward migration of surface living species seems to be of more recent origin, considering that modern copepods evolved some time in the Cretaceous or Cenozoic (Madhupratap and Haridas, 1992).

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