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Abundance and biomass of nano- and microplankton during the 1995 Northeast Monsoon and Spring Intermonsoon in the Arabian Sea

Mark R. Dennett^{a,*}, David A. Caron^a, Sergey A. Murzov^b,
Igor G. Polikarpov^b, Nelli A. Gavrilova^b, Ludmila V. Georgieva^b,
Ludmila V. Kuzmenko^b

^a*Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*

^b*Institute for the Biology of the Southern Seas, Sevastopol 335011, Crimea, Ukraine*

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Abstract

Phototrophic and heterotrophic nanoplankton (PNAN, HNAN; 2–20 µm protists) and microplankton (PMIC, HMIC; 20–200 µm protists and micrometazoa) are major components of the producer and consumer assemblages in oceanic plankton communities. Abundances and biomasses of these microorganisms were determined from samples collected along two transects during the Northeast Monsoon and Spring Intermonsoon process cruises of the US JGOFS Arabian Sea Program in 1995. Vertical profiles of these assemblages were strongly affected by the presence of a subsurface oxygen minimum layer. Abundances of all four assemblages decreased dramatically below the top of this layer. Depth-integrated (0–160 m) abundances and biomasses of nanoplankton and microplankton were of similar magnitude for most samples. Exceptions to this rule were primarily due to PMIC (mostly diatom) species which dominated phytoplankton assemblages at a few stations during each season. Depth-integrated biomasses for the combined nano- and microplankton averaged over all stations for each cruise were surprisingly similar for the Northeast Monsoon and Spring Intermonsoon seasons in this ecosystem (2.0 and 1.8 g C m⁻² [170 and 150 m moles C m⁻²] for the two seasons, respectively). Nano- and microplankton biomass for these two time periods constituted a significant portion of the total amount of the particulate organic carbon (POC) in the water column.

* Corresponding author. Fax: 001-508-457-2169.

E-mail address: mdennett@whoi.edu (M.R. Dennett)

Summed over all stations, these assemblages constituted approximately 25–35% of the POC in the top 160 m of the northern Arabian Sea. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

A fundamental goal of the Joint Global Ocean Flux Study (JGOFS) is to relate, on a global scale, oceanographic processes in the surface waters of the ocean to the sinking of carbon out of surface waters (SCOR, 1990). This goal cannot be accomplished without an understanding of the standing stocks and elemental flows among planktonic populations because biological processes are instrumental in the transformation and vertical flux of carbon in aquatic ecosystems. Accordingly, a major effort for JGOFS has been the acquisition of accurate assessments of the biomass of plankton assemblages in each of the study areas examined during the existence of this multi-national program.

Microorganisms constitute an important percentage of the living biomass of marine pelagic environments. Phototrophic prokaryotes and protists (microalgae) dominate primary production in the plankton. In addition, recent studies have indicated major roles for bacteria and protozoa as repositories of living biomass in these ecosystems and as instruments of respiration and elemental remineralization (Fuhrman et al., 1989; Cho and Azam, 1990; Li et al., 1992; Stoecker et al., 1994b; Caron et al., 1995; Stoecker et al., 1996). Therefore, microbial community structure affects energy flow and elemental cycling in the plankton (Goldman and Caron, 1985) and thus the sinking of material into the deep ocean. Based on these realizations of pelagic food web structure and function, assessing the standing stocks of microorganisms in the plankton is an essential aspect of establishing the total amount of living biomass in these ecosystems, and characterizing the major contributors to significant biogeochemical processes.

The northern Arabian Sea is an environment in which biological productivity is influenced by strong physical forcing that results from seasonally changing atmospheric conditions (Findlater, 1969). This environment is affected by a Northeast (NE) Monsoon from November through February at which time the predominant wind direction is from the northeast off the Asian continent. Severe wind stress occurs again from June to October during the Southwest (SW) Monsoon, and is characterized by winds moving from the southwest off the coast of Somalia and along the coast of Oman. The SW Monsoon is characterized by wind speeds ($> 14 \text{ m s}^{-1}$) nearly twice the speeds observed during the NE Monsoon. Periods of relatively calm weather (Spring Intermonsoon, March–May, and Fall Intermonsoon, October–November) separate the two monsoonal seasons.

Historical overviews and data summaries have indicated a highly productive, albeit spatially and seasonally variable, phytoplankton assemblage in the northern Arabian Sea in response to upwelling events driven by these meteorological conditions (Banse and McClain, 1986). High concentrations of POC ($200\text{--}600 \mu\text{g C l}^{-1}$) were observed during the 1966 Southwest Monsoon particularly in coastal areas north of 10°N (Finenko and Zaika, 1969). Similarly, high chlorophyll concentrations and rates of

primary production were observed near the coast of Oman during the 1986 SW Monsoon, shifting to more oligotrophic conditions in the southern Arabian Sea (Owens et al., 1993). A dramatic shift in the size distribution of primary production was observed in the latter study. Algae $> 5 \mu\text{m}$ strongly dominated production in the upwelling region near the coast of Oman (90%), while much of the production in the southern portion of the study area was contributed by algae $< 5 \mu\text{m}$. Reported phytoplankton standing stocks, growth, and grazing mortality observed during the 1993 NE Monsoon, were less than reports of these properties during the SW Monsoon; nevertheless, phytoplankton growth rates were nearly twice their mortality rates during that NE Monsoon (Reckermann and Veldhuis, 1997).

In contrast to studies during monsoonal seasons, observations conducted during intermonsoonal periods seem to indicate more oligotrophic conditions in the northern Arabian Sea. For example, more modest concentrations of POC ($33\text{--}99 \text{ mg C m}^{-3}$; $2.7\text{--}8.2 \mu\text{M C}$) were observed during the 1980 Spring Intermonsoon (Burlakova and Eremeeva, 1994) north of the equator to 9°N and west of 68°E . That study determined that microzooplankton biomass contributed approximately 5% of POC, while total phytoplankton biomass contributed 6–20% of POC. Studies of phytoplankton size structure during intermonsoon periods have indicated the predominance of picoplankton (Burkill et al., 1993; Jochem et al., 1993). These latter measurements indicate contributions of microbial assemblages that are reasonably consistent with reports from other oligotrophic oceanic environments (Sorokin et al., 1985; Caron et al., 1995; Buck et al., 1996).

Taken as a whole, these past observations have resulted in the perception that the Arabian Sea alternates between highly productive, upwelling-dominated situations during the SW Monsoon, and oligotrophic phases during the Spring and Fall Intermonsoon periods. While this characterization may be generally true, much of the detail is lacking concerning the magnitude of the seasonal shift in the abundance and biomass of phytoplankton in the Arabian Sea, and the contribution of microbial consumers ($\geq 2 \mu\text{m}$) to standing stocks of biomass and grazing impact on these phytoplankton assemblages.

This study was part of a multi-investigator program designed (in part) to address these unresolved issues. This manuscript presents the results of a study designed to quantify the contribution of phototrophic and heterotrophic nanoplankton and microplankton (protists and micrometazoa $2\text{--}200 \mu\text{m}$ in size) in the carbon budget of the surface waters of the northern Arabian Sea during two seasons, the NE Monsoon and Spring Intermonsoon periods of 1995. An accompanying manuscript (Caron and Dennett, 1999) reports phytoplankton growth and grazing mortality during these seasons. Subsequent manuscripts will consider these features of the biotic community in the Arabian Sea over larger temporal scales.

2. Materials and methods

Samples were collected aboard the R/V *Thomas G. Thompson* in the Arabian Sea during process cruises TN043 (January 8–February 4, 1995, Northeast Monsoon) and

TN045 (March 14–April 10, 1995, Spring Intermonsoon) of the US JGOFS Arabian Sea Process Study. The same 15 stations were occupied during both cruises in a clockwise fashion beginning at N2 (see Fig. 5). The stations are presented here as a “northern” (N2–N11) and a “southern” transect (S1–S15) because they represent two nearshore–offshore transects through different hydrographic regimes.

Up to 11 depths over a range 0–250 m were sampled directly from 10-l Niskin bottles attached to a CTD rosette. Nutrients, oxygen and POC were obtained from the US JGOFS data base for samples from which we measured microbial abundance and biomass. Density profiles for each hydrocast also were provided by the US JGOFS data base. Samples for the enumeration of phototrophic and heterotrophic nanoplankton (PNAN, HNAN, 2–20 μm algae and protozoa, respectively) were preserved with 1% formalin (from 10% stock solution prepared with filtered natural seawater) and refrigerated. Samples were processed for epifluorescence microscopy within 24 h of collection. Aliquots were stained with DAPI at 50 $\mu\text{g ml}^{-1}$ final stain concentration, filtered onto blackened 0.8 μm polycarbonate filters, sealed with paraffin onto microscope slides and stored at -20°C (Sherr et al., 1993; Sherr and Sherr, 1993). Slides were returned to the laboratory for counting using epifluorescence microscopy. Nanoplankton were visualized using DAPI fluorescence, and PNANs were distinguished from HNANs by the autofluorescence of chlorophyll *a* using appropriate filter sets.

Samples for the enumeration of microplankton were preserved with a 10% final concentration of acid Lugols in 1-l amber glass bottles and stored in the dark (Stoecker et al., 1994a). Samples were presettled and concentrated 10-fold before final settling in counting chambers for the enumeration of 20–200 μm organisms using transmitted light inverted microscopy. Microplankton were grouped by major taxa (diatoms, dinoflagellates, other algae, non-loricate ciliates, tintinnid ciliates, planktonic foraminifera + actinopods, nauplii). The high concentration of Lugol's solution used for preservation (to minimize losses of ciliate protozoa) precluded distinguishing phototrophs from heterotrophs by autofluorescence. Clearing the solution with sodium thiosulfate (Sherr and Sherr, 1993) did not result in unambiguous determinations of phototrophs and heterotrophs. For this determination, formalin-preserved samples from two depths at each of 8 stations during the Northeast Monsoon cruise and seven stations during the Spring Intermonsoon cruise were stained with DAPI and filtered onto polycarbonate filters. Dinoflagellates $> 20 \mu\text{m}$ were observed at 400X and examined for chlorophyll autofluorescence. The average ratio of phototrophic to heterotrophic dinoflagellates from the two depths at each station counted was applied to the samples from that station and to samples from neighboring stations. The ratio of phototrophic to heterotrophic dinoflagellates obtained in this manner averaged 1.78 and 1.32 for the two cruises (range = 0.71–3.75).

Biovolume estimates were determined for nanoplankton from microscopical measurements of cell dimensions and assuming spherical or ellipsoidal shape. Microplankton biovolumes were determined from measurements of their linear dimensions using volume equations for appropriate geometric shapes. Volume determinations were made of all assemblages at four depths from each station, and these values were extrapolated to adjacent depths in the water column. Biovolume estimates were

converted to carbon biomass for each of the plankton categories using published conversion factors. Phototrophic and heterotrophic nanoplankton were converted to carbon based on $183 \text{ fg C } \mu\text{m}^{-3}$ (Caron et al., 1995). Diatoms were converted to carbon using the modified Strathmann equation (Smayda, 1978). For other microplankton, conversion factors were $183 \text{ fg C } \mu\text{m}^{-3}$ for PMIC other than diatoms or dinoflagellates (Caron et al., 1995), $140 \text{ fg C } \mu\text{m}^{-3}$ for dinoflagellates and non-loricated ciliates (Stoecker et al., 1994b), $53 \text{ fg C } \mu\text{m}^{-3}$ for tintinnid ciliates (Verity and Langdon, 1984), $89 \text{ fg C } \mu\text{m}^{-3}$ for planktonic foraminifera, $45 \text{ fg C } \mu\text{m}^{-3}$ for actinopods (Michaels et al., 1995) and $80 \text{ fg C } \mu\text{m}^{-3}$ for nauplii (Beers et al., 1975).

Depth-integrated values of abundance and biomass were obtained for the interval 0–160 m. Comparison of these values to depth-integrated particulate organic carbon (POC) were performed using POC values obtained from the US JGOFS data base.

3. Results

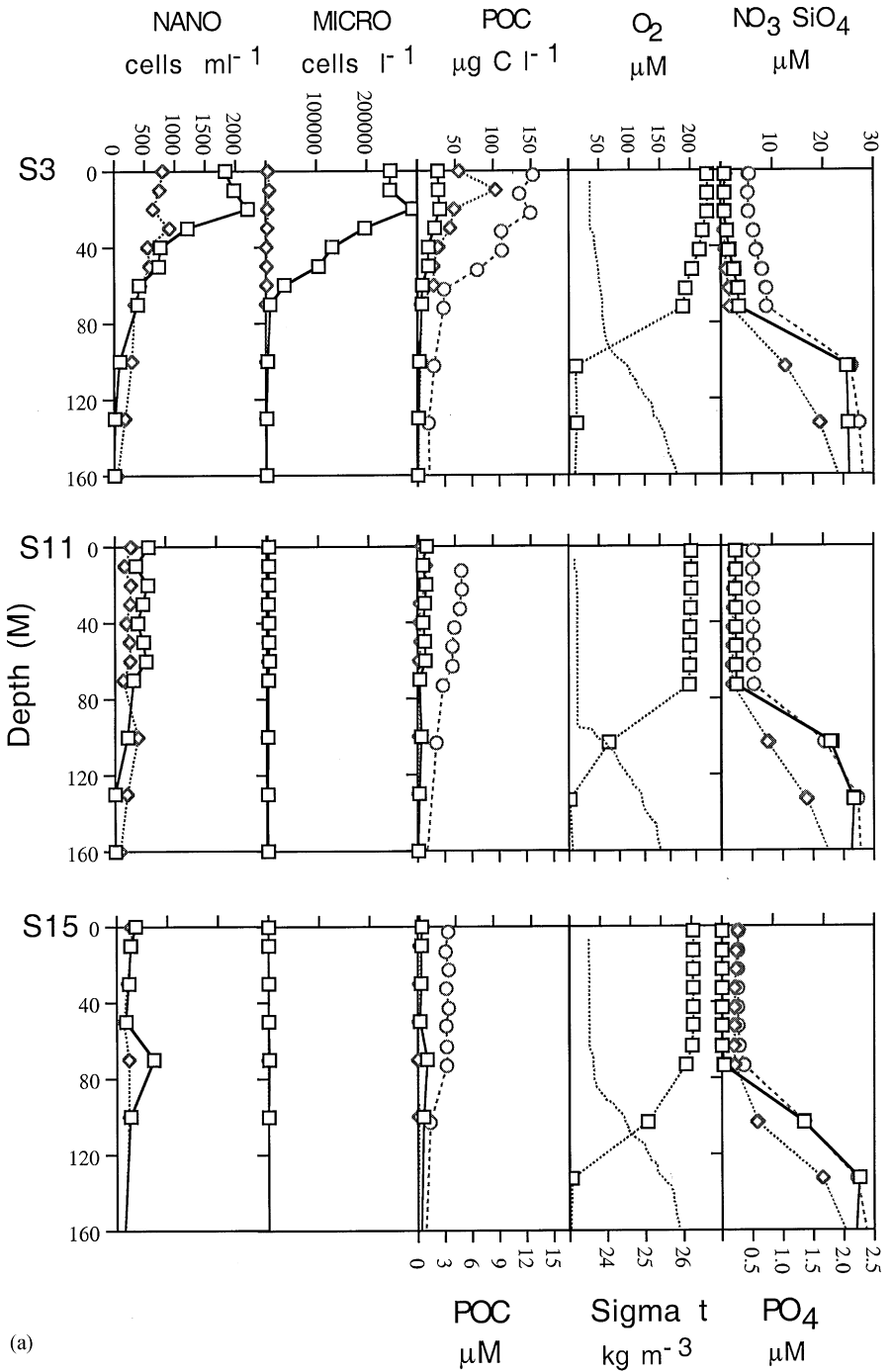
There was a strong similarity in the overall vertical and horizontal patterns of chemical/physical parameters and nanoplankton and microplankton abundances during the Northeast Monsoon and Spring Intermonsoon cruises. A pronounced oxygen minimum layer was present at all stations during both cruises. Population abundances decreased substantially within this minimum with concomitant increases in nutrient concentrations (Fig. 1). In general, phototroph abundances were highest at the nearshore stations and lowest at the eastern-most stations of both the northern and southern transects. There was considerable station-to-station variability presumably due to complexity in the meso- and fine-scale circulation patterns present during these periods. Subsurface maxima in abundances were present at a number of stations, particularly in the eastern-most stations of the southern transect during the Spring Intermonsoon.

Abundance and biomass of PNAN and HNAN assemblages were remarkably comparable between the two cruises. Overall depth-integrated abundance ranges for PNAN and HNAN during the two cruises were $1.88\text{--}8.29 \times 10^5 \text{ l}^{-1}$ and $1.67\text{--}4.10 \times 10^5 \text{ l}^{-1}$, respectively. Averages were $4.03 \times 10^5 \text{ PNAN l}^{-1}$ and $3.08 \times 10^5 \text{ HNAN l}^{-1}$ for the NE Monsoon cruise and $3.84 \times 10^5 \text{ PNAN l}^{-1}$ and $2.60 \times 10^5 \text{ HNAN l}^{-1}$ for the Spring Intermonsoon cruise (Table 1). There were no clear trends apparent in the spatial distribution of abundances of PNAN or HNAN when averaged over the 0–160 m depth interval for each station (Fig. 2). These abundances corresponded to depth integrated (0–160 m) biomass ranges of $0.27\text{--}0.90 \text{ g C m}^{-2}$ ($22.5\text{--}75 \text{ m moles C m}^{-2}$) and $0.23\text{--}0.69 \text{ g C m}^{-2}$ ($19.2\text{--}57.5 \text{ m moles C m}^{-2}$) for PNAN and HNAN. Averages were 0.53 g C m^{-2} ($44.2 \text{ m moles C m}^{-2}$) for PNAN and 0.45 g C m^{-2} ($37.5 \text{ m moles C m}^{-2}$) for HNAN during the NE Monsoon and 0.48 g C m^{-2} ($40 \text{ m moles C m}^{-2}$) and 0.45 g C m^{-2} ($37.5 \text{ m moles C m}^{-2}$) for these assemblages during the Spring Intermonsoon. As with the average abundances, depth-integrated nanoplankton biomass indicated no specific spatial trends along either transect for the two cruises (Fig. 2).

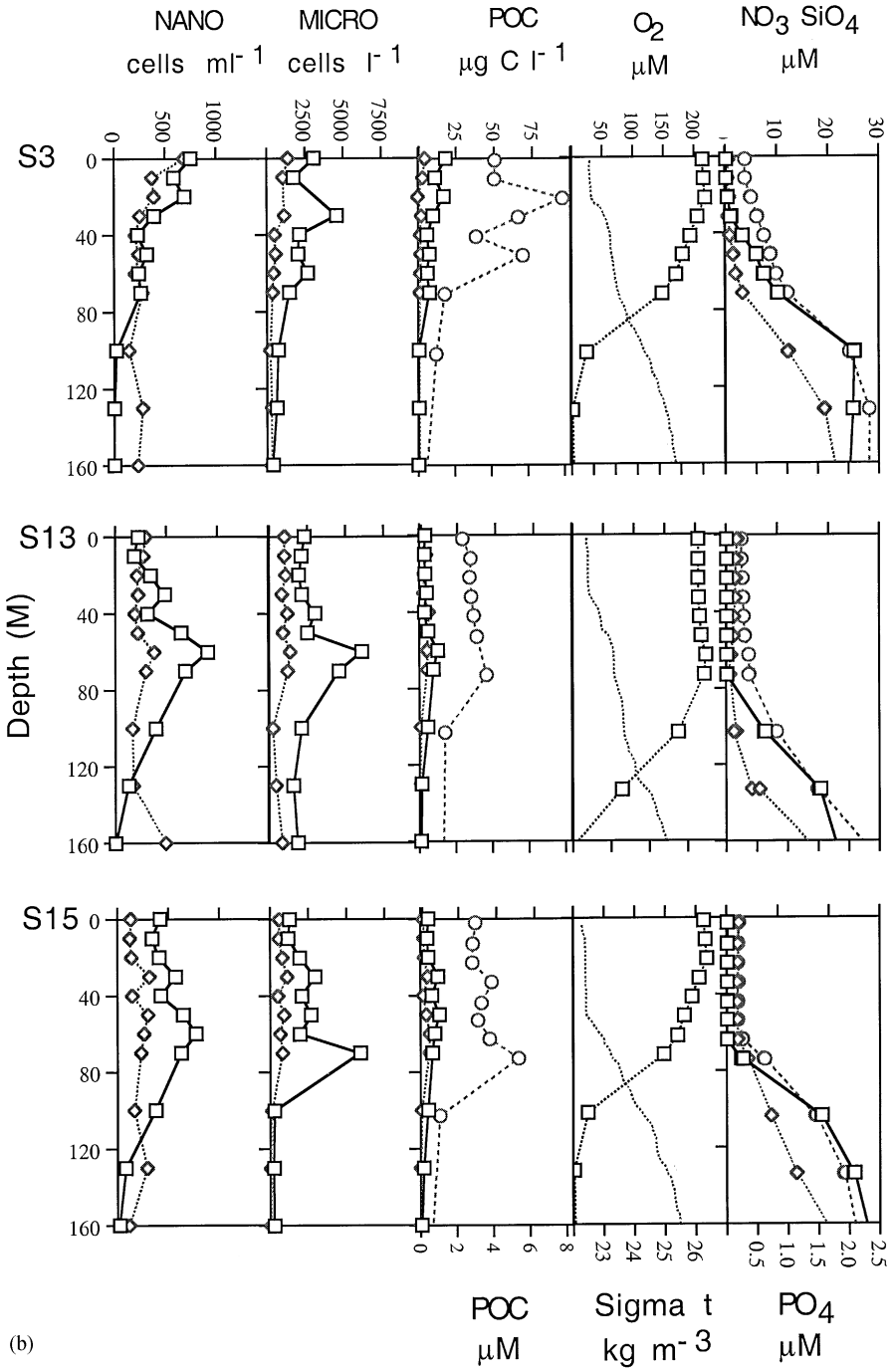
PMIC/HMIC assemblages during the NE Monsoon and Spring Intermonsoon were abundant and diverse (Plate 1). PMIC abundances and biomasses were more heterogeneous spatially and temporally during the cruises than HMIC or the nanoplankton assemblages. Ranges of PMIC abundances were approximately two orders of magnitude for both cruises (Table 1). HMIC abundances ranged over one order of magnitude. Overall ranges for depth integrated abundances were $0.07\text{--}7.17 \times 10^4 \text{ l}^{-1}$ for PMIC and $0.03\text{--}0.23 \times 10^4 \text{ l}^{-1}$ for HMIC. The highly variable nature of PMIC was due primarily to fluctuations in diatom abundances. Diatoms were abundant at the nearshore stations (N2–N6 and S1–S3) during the NE Monsoon cruise (Fig. 3a). Diatom abundances were consistently low on the southern transect during the Spring Intermonsoon cruise, but some stations on the northern transect had high values (Fig. 3b). Several taxonomic groups contributed to spatial variability in the abundances of HMIC. Dinoflagellates and foraminifera/actinopods each showed high abundances only at a few stations on each of the cruises. Tintinnid ciliate abundances were relatively low in all samples ($\leq 70 \text{ cells l}^{-1}$), but non-loricate ciliate and copepod naupliar abundances varied by a factor of 2–3X across all stations (Fig. 3). Microplankton biomass also was more variable than nanoplankton biomass and ranged approximately one order of magnitude. Overall depth integrated biomass ranges were $0.07\text{--}1.93 \text{ g C m}^{-2}$ ($5.83\text{--}161 \text{ m moles C m}^{-2}$) for PMIC and $0.09\text{--}1.17 \text{ g C m}^{-2}$ ($7.5\text{--}97.5 \text{ m moles C m}^{-2}$) for HMIC (Table 1).

Biomass of the four plankton components were integrated down to a depth of 160 m at each station for the two cruises (Fig. 4). Averaged over each cruise, combined nanoplankton and microplankton biota accounted for 1.97 g C m^{-2} ($164 \text{ m moles C m}^{-2}$) for the NE Monsoon and 1.76 g C m^{-2} ($147 \text{ m moles C m}^{-2}$) for the Spring Intermonsoon (Fig. 4a and b). During the NE Monsoon, depth-integrated biomass for PMIC was nearly double that for the other three plankton assemblages at the nearshore stations (N2–N4; S1–S4), while nanoplankton constituted approximately 66% of the biomass at offshore stations (N6–N11; S7–S15), indicating a shift in the overall size structure of the microbial community along the transects due largely to substantial changes in PMIC biomass (Fig. 4c and e). Differences in the relative importance of nano- and microplankton biomasses along the nearshore-offshore transects were not apparent during the Spring Intermonsoon when summed in this manner (nanoplankton = 58% of biomass nearshore and 56% offshore; Fig. 4d and f).

Fig. 1. Vertical profiles of nano- and microplankton abundance, particulate organic carbon (POC), oxygen (O_2), density (Sigma t) and nutrients (nitrate, silicate, phosphate) from three stations (S3, S11, S15) along the southern transect during the (a) 1995 NE Monsoon and (b) Spring Intermonsoon in the Arabian Sea. In plots of abundance, squares are PNAN and HMIC, diamonds are HNAN and PMIC. In plots of POC, squares are PNAN + HNAN, diamonds are PMIC + HMIC, circles are total POC. POC values are depicted in units of $\mu\text{g C l}^{-1}$ and $\mu\text{M C}$ ($12 \mu\text{g C l}^{-1} = 1 \mu\text{M C}$). In hydrographic plots, squares are oxygen, dashed lines are sigma t . In nutrient plots, squares are nitrate, diamonds are silicate, circles are phosphate.



(a)



(b)

Fig. 1. Continued.

Table 1
 Mean, minimum, and maximum values for nano- and microplankton integrated (0–160 M) abundance and carbon biomass along the two transects of the 1995 Northeast Monsoon and Spring Intermonsoon

	Abundance $\times 10^4$ cells l^{-1}			Biomass $g C m^{-2}$ (m moles $C m^{-2}$)			Biomass % of POC					
	PNAN	HNAN	PMIC	HMIC	PNAN	HNAN	PMIC	HMIC	PNAN	HNAN	PMIC	HMIC
<i>Northeast Monsoon</i>												
Northern transect												
Mean	35.4	32.5	1.59	0.10	0.46(38)	0.32(27)	0.60(50)	0.40(33)	9.04	6.60	10.6	8.33
Min	29.1	28.4	0.23	0.06	0.29(24)	0.23(19)	0.15(12)	0.32(27)	6.62	5.08	4.20	6.74
Max	42.0	41.0	7.17	0.13	0.82(68)	0.44(37)	1.75(145)	0.52(43)	12.3	9.68	26.3	10.2
Southern transect												
Mean	43.6	29.6	1.84	0.09	0.57(47)	0.54(45)	0.61(51)	0.45(37)	9.30	9.28	8.96	6.92
Min	21.6	17.7	0.07	0.05	0.28(23)	0.29(24)	0.07(6)	0.16(13)	6.15	6.37	1.65	3.51
Max	82.9	37.7	6.51	0.14	0.90(75)	0.69(57)	1.93(161)	1.17(97)	12.1	15.1	27.5	16.2
<i>Spring Intermonsoon</i>												
Northern transect												
Mean	47.6	30.2	1.54	0.09	0.52(43)	0.49(41)	0.74(62)	0.43(36)	7.88	7.56	11.4	6.39
Min	35.6	23.6	0.19	0.03	0.39(32)	0.35(29)	0.12(10)	0.10(8)	4.53	5.50	2.59	2.37
Max	56.5	39.9	5.14	0.23	0.64(53)	0.57(47)	1.77(147)	0.82(68)	9.60	11.5	24.3	12.4
Southern transect												
Mean	32.2	23.2	0.20	0.09	0.45(37)	0.43(36)	0.21(17)	0.25(21)	8.64	7.97	4.06	4.87
Min	18.8	16.7	0.08	0.05	0.27(22)	0.30(25)	0.08(7)	0.09(7)	4.41	6.82	1.45	1.90
Max	45.5	34.6	0.35	0.17	0.57(47)	0.58(48)	0.44(37)	0.39(32)	11.9	10.3	8.14	8.90

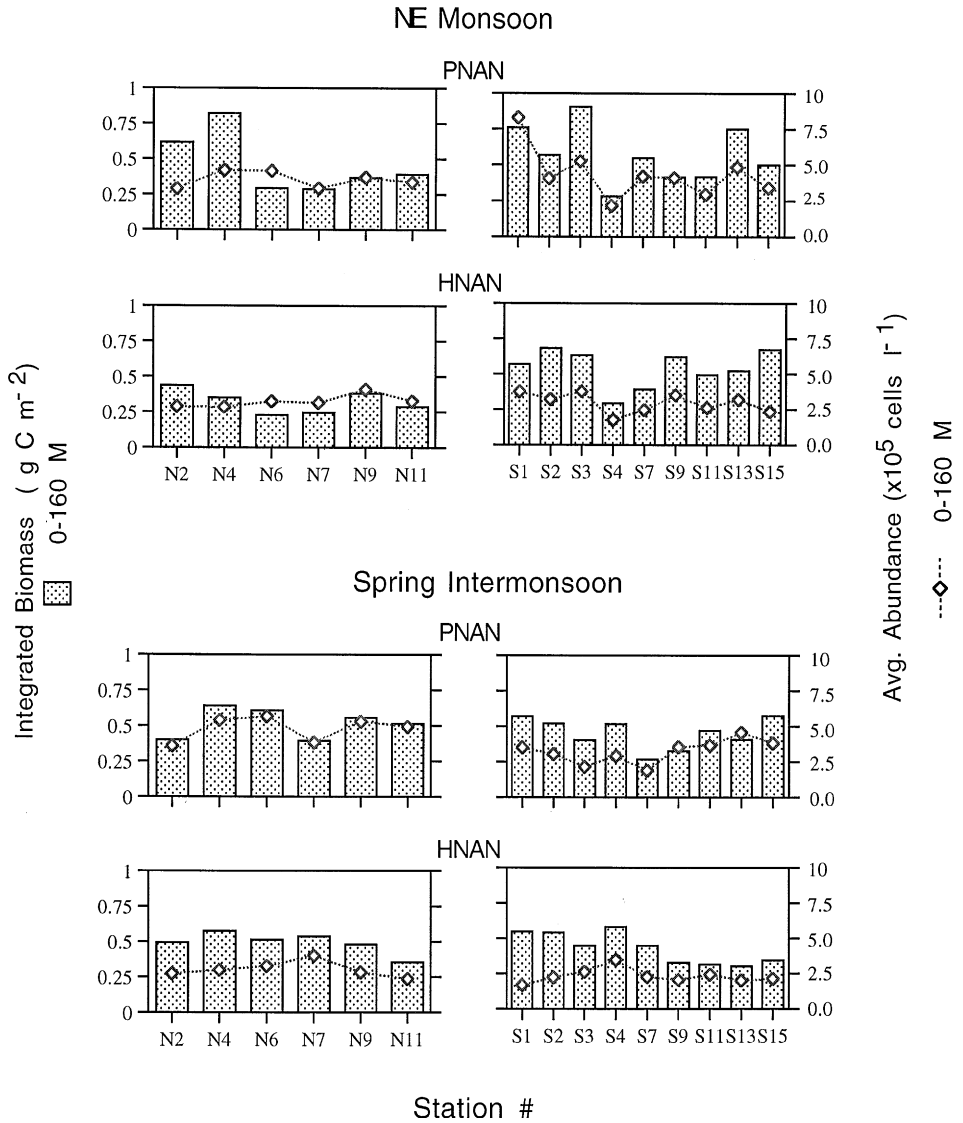


Fig. 2. Nanoplankton integrated biomass (0–160 m) and average cell abundance (0–160 m) along the “northern” and “southern” cruise transects during the 1995 NE Monsoon and Spring Intermonsoon in the Arabian Sea.

Nanoplankton biomass accounted for $\geq 50\%$ of the 2–200 μm biota at most of the stations throughout the study area during both cruises (Fig. 5). PMIC showed the most variability of the four plankton compartments. Three nearshore stations during the NE Monsoon had high biomasses of PMIC (N4, S1, S3), while two stations in the

northern transect during the Spring Intermonsoon had high PMIC and HMIC biomasses (N4, N9). These stations were not adjacent to each other on either cruise.

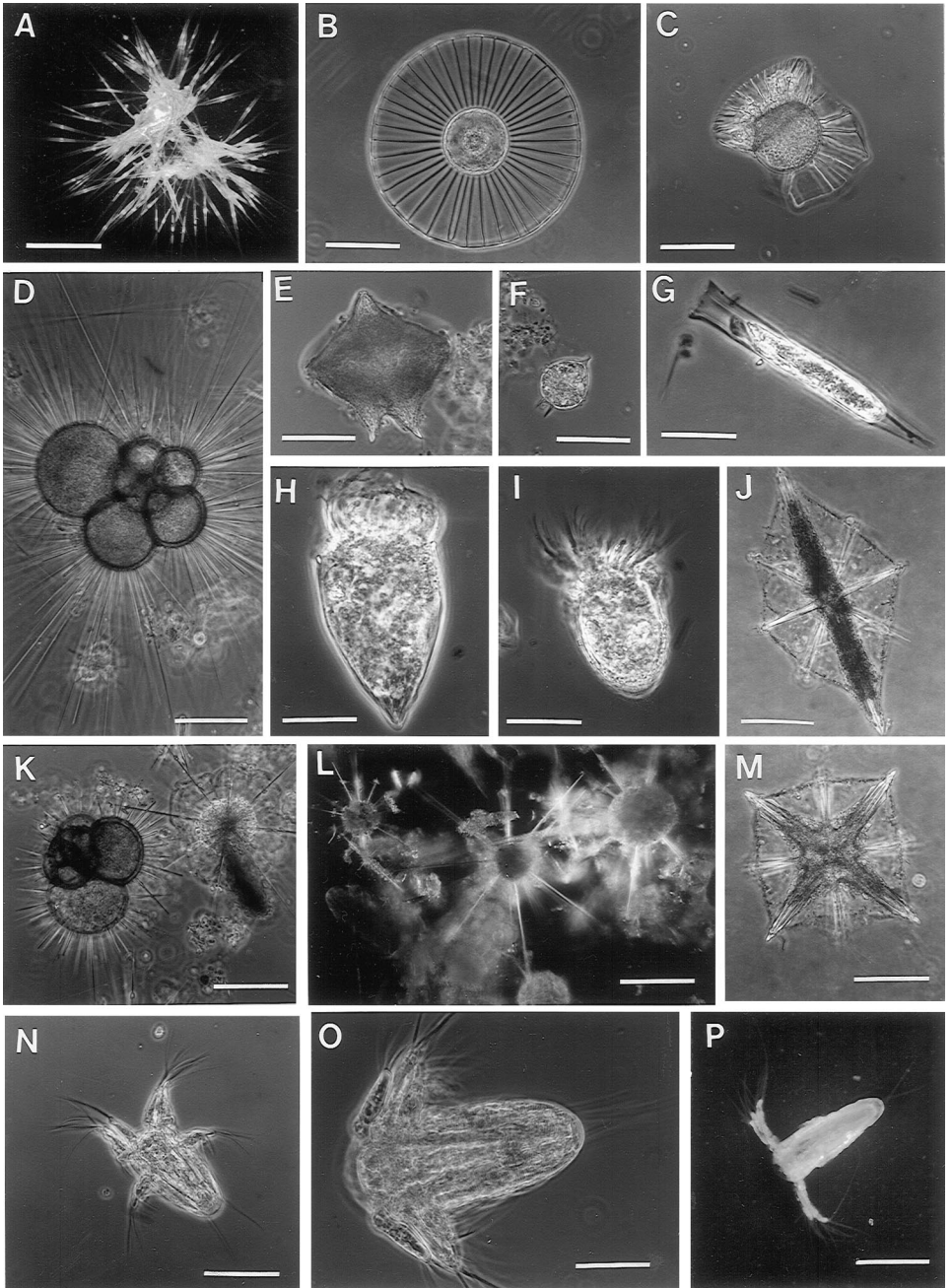
Values of depth-integrated biomass of the nanoplankton and microplankton assemblages were compared to depth-integrated POC values to obtain an indication of the contribution of these living assemblages to total POC in the 0–160 m water column. Overall averages for the two cruises indicate that microorganisms in the 2–200 μm size range constituted approximately 36% (NE Monsoon) and 29% (Spring Intermonsoon) of the total POC (Fig. 6). PMIC averaged for the nearshore stations (N2–N4; S1–S4) during the NE Monsoon constituted 17% of POC (Fig. 6c), but this assemblage contributed $< 8\%$ when samples were averaged for the offshore stations from both cruises or the nearshore stations during the Spring Intermonsoon period (Fig. 6d–f). Nevertheless, PMIC constituted the largest individual contribution to POC of the four assemblages at several stations, contributing $> 21\%$ of total POC at three nearshore stations during the NE Monsoon and up to 24% at two stations along the northern transect during the Spring Intermonsoon (Fig. 7). When examined on a station-by-station basis, PNAN, HNAN, PMIC and HMIC biomass together constituted up to 65% of the total POC during the 1995 NE Monsoon and 55% during the 1995 Spring Intermonsoon (i.e., approximately twice the average contribution).

4. Discussion

4.1. Assessing the accuracy of microbial biomass estimates

Determination of the carbon content of various planktonic organisms might seem relatively straightforward. Nevertheless, accurate determination of the absolute and relative biomasses of microbial plankton assemblages from oceanic ecosystems is still controversial despite the unequivocal importance of establishing these values. There are two basic problems that constitute the crux of this controversy. First, planktonic communities are too diverse to treat each species individually, and therefore community structure must be simplified by combining species into groups. Second, conversion factors must be used to transform the abundance and/or biovolume estimates for these plankton groupings into carbon units.

Plate 1. Epifluorescence (A, P) and transmitted light photomicrographs (B–O) of representative microplankton from the northern Arabian Sea during the 1995 NE Monsoon and Spring Intermonsoon: (A–B) Aggregated pennate diatoms (*Nitzschia* sp.) commonly observed at diatom-dominated stations during the NE Monsoon (A) and the centric diatom *Planktoniella sol* (B), a conspicuous species at oligotrophic stations; C, E, F) Larger heterotrophic dinoflagellates (C, F) such as *Ornithocercus* sp. (C, with epibiotic cyanobacteria) and phototrophic dinoflagellates (E); G–I) Tintinnid and oligotrichous ciliated protozoa; D, J–M) Juvenile planktonic sarcodine protozoa including planktonic foraminifera (D, K) and actinopods, mostly acantharia (J–M); N–P) Copepod nauplii. Scale bars are 40 μm (A, C–J, M, O) or 100 μm (B, K, L, N, P).



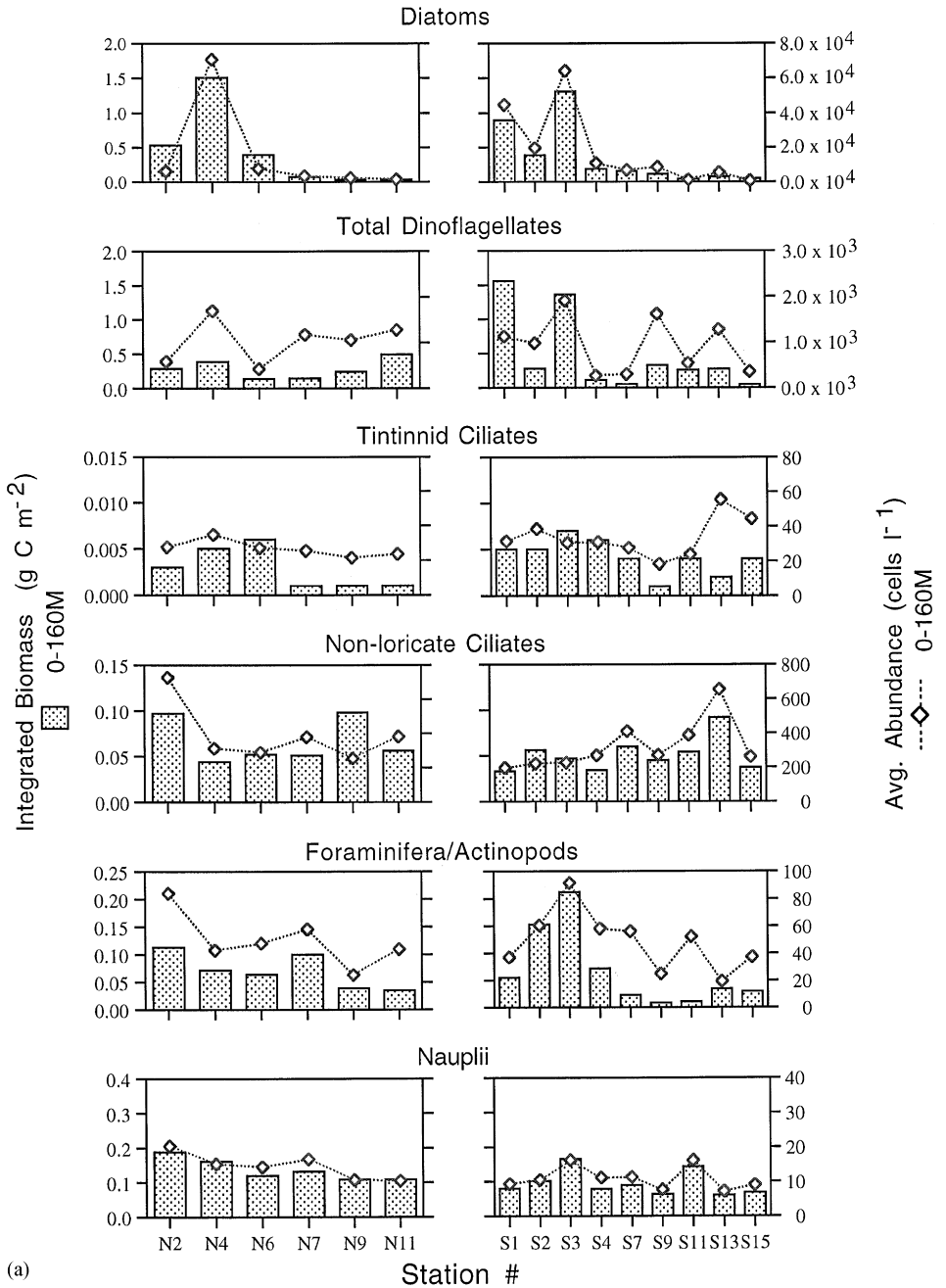
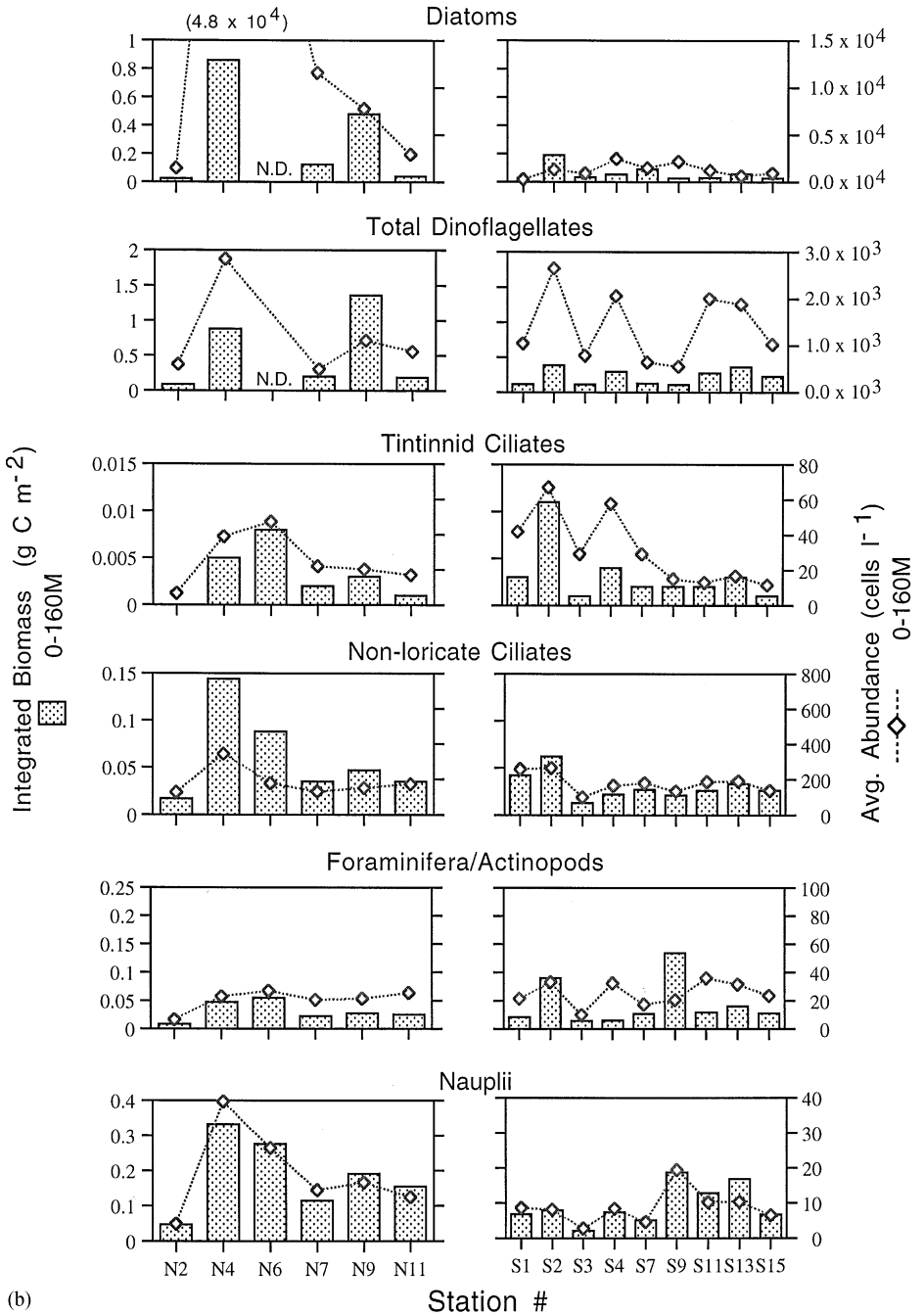


Fig. 3. Microplankton integrated biomass (0–160 m) and average cell abundance (0–160 m) by major taxonomic group along the “northern” and “southern” cruise transects during the 1995 NE Monsoon (a) and Spring Intermonsoon (b) in the Arabian Sea. N.D. indicates sample not counted.



(b)

Fig. 3. Continued.

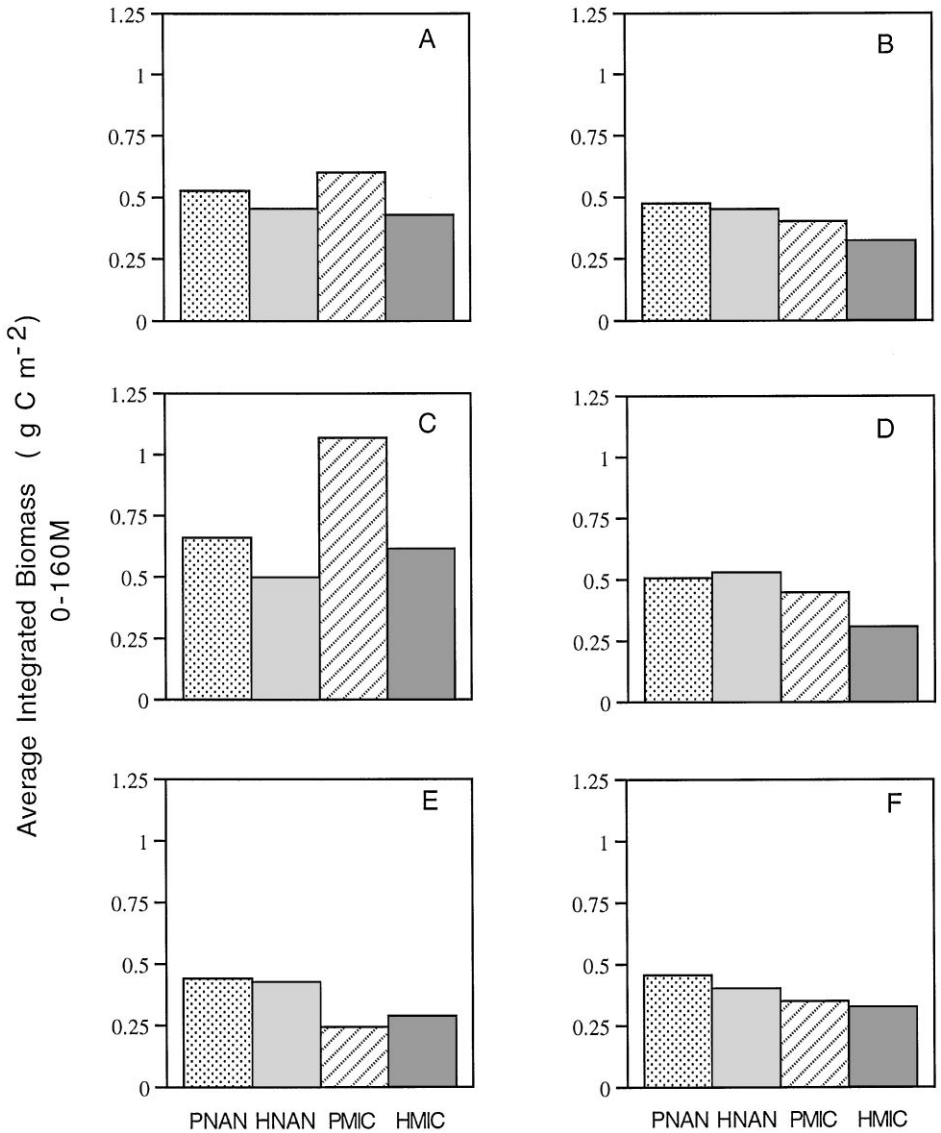


Fig. 4. Average integrated biomass (0–160 m) of PNAN, HNAN, PMIC and HMIC from (a) 15 stations (refer to Fig. 5) during the 1995 NE Monsoon, (b) 15 stations during the Spring Intermonsoon, and then divided into nearshore stations (N2, N4, S1, S2, S3, S4) during the NE Monsoon (c) and Spring Intermonsoon (d), and offshore stations (N6, N7, N9, N11, S7, S9, S11, S13, S15) during the NE Monsoon (e) and the Spring Intermonsoon (f).

The process of grouping planktonic microorganisms into a few defined compartments is an attempt to arrange them into ‘guilds’ based on similar ecological function. In this way, the complexity of natural communities can be reduced to units that

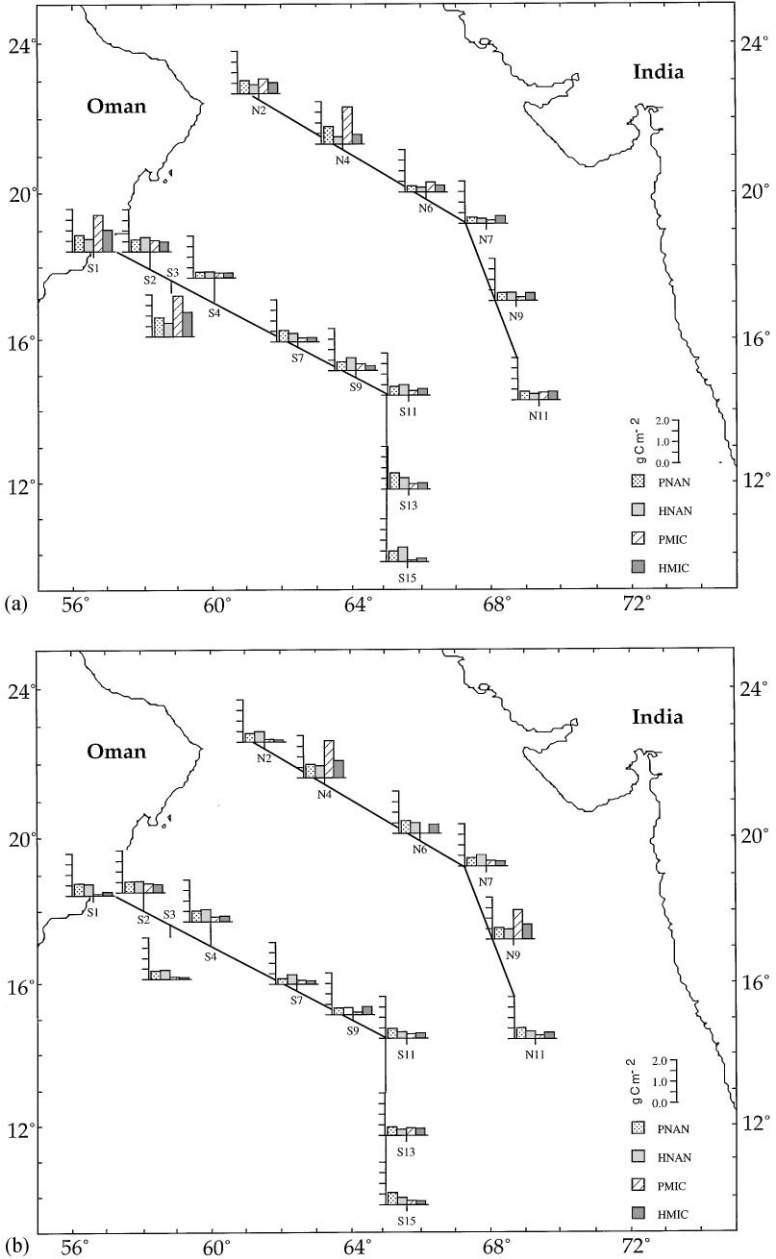


Fig. 5. Integrated biomass (0–160 m) of PNAN, HNAN, PMIC and HMIC at 15 stations in the Arabian Sea during the 1995 NE Monsoon (a) and the Spring Intermonsoon (b).

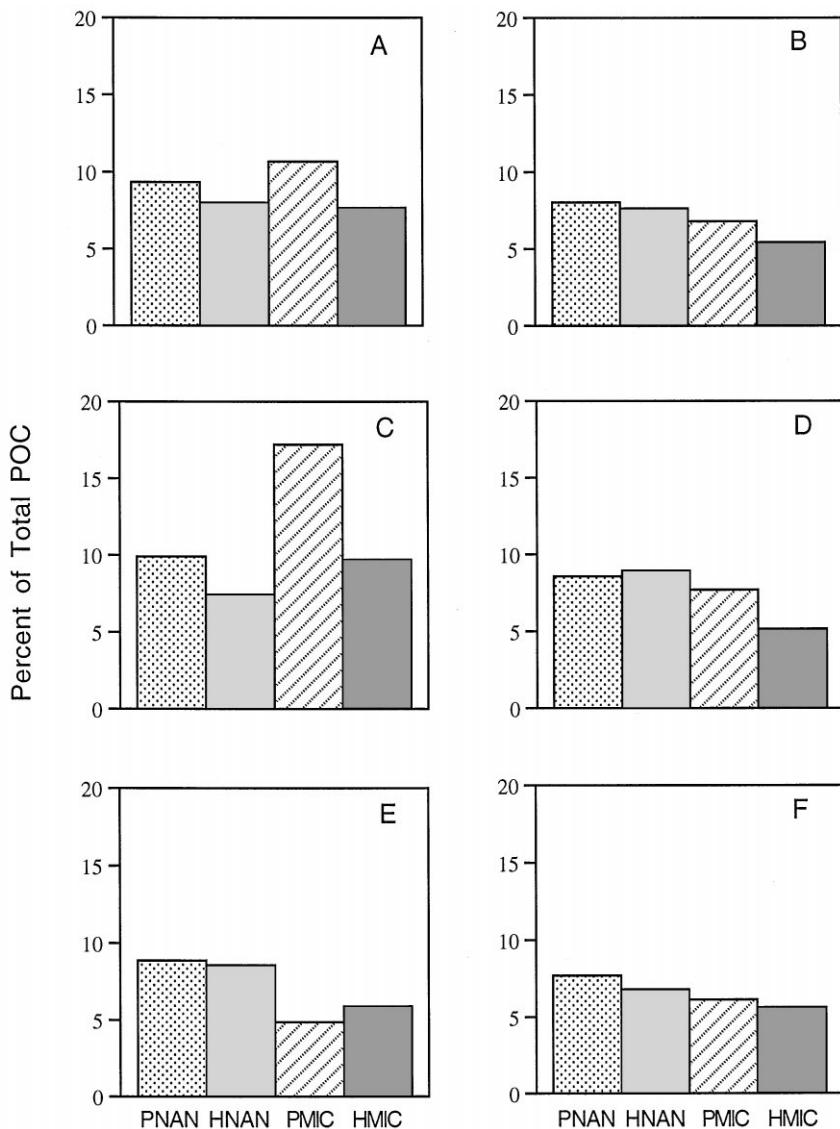


Fig. 6. Average integrated biomass of PNAN, HNAN, PMIC and HMIC as a percent of particulate organic carbon (0–160 m) from (a) 15 stations (refer to Fig. 5) during the 1995 NE Monsoon, (b) 15 stations during the Spring Intermonsoon, and then divided into nearshore stations (N2, N4, S1, S2, S3, S4) during the NE Monsoon (c) and Spring Intermonsoon (d), and offshore stations (N6, N7, N9, N11, S7, S9, S11, S13, S15) during the NE Monsoon (e) and the Spring Intermonsoon (f).

represent the major biological processes in the ecosystem but also are manageable for modeling and experimental investigations. The most popular of these groupings are based on size according to the scheme of Sieburth et al. (1978), which assumes

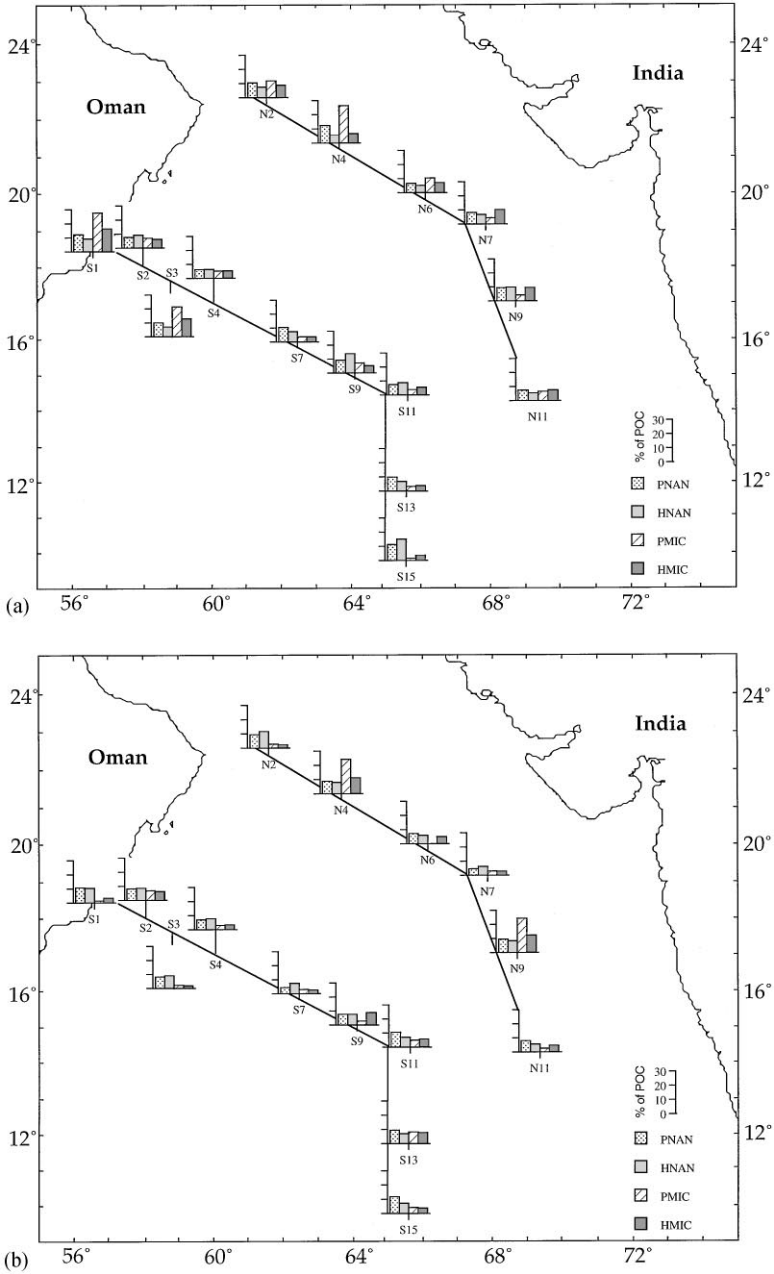


Fig. 7. Average integrated biomass of PNAN, HNAN, PMIC and HMIC as a percent of particulate organic carbon (0–160 m) at 15 stations during the 1995 NE Monsoon (a) and during the Spring Intermonsoon (b).

order-of-magnitude, size-dependent, trophic interactions (e.g., picoplankton, 0.2–2.0 μm ; nanoplankton, 2.0–20 μm ; microplankton, 20–200 μm). Assemblages separated into these size classes typically are further divided according to photosynthetic ability. In this way, complex assemblages of microorganisms are defined by a few major trophic modes (phototrophy/heterotrophy) and size-dependent trophic interactions (i.e., consumers in a size class prey on organisms in the next smallest size class). For example, heterotrophic picoplankton are composed largely of bacteria, while heterotrophic nanoplankton are primarily flagellated protozoa that consume picoplankton.

The use of these characterizations to define ecological components of the plankton is common among plankton researchers, but these devices possess inherent inconsistencies. For example, the existence of photosymbiosis among some sarcodine protozoa, plastid retention by some ciliated protozoa and phagotrophy by some flagellated algae is indicative of the artificiality of the boundary between phototrophy and heterotrophy for many species of protists (Sanders and Porter, 1988; Stoecker et al., 1989; Caron and Finlay, 1994). Furthermore, the assumption of a 10 : 1 ratio for predator–prey size relationships also is inaccurate for some protozoa that can consume prey larger than themselves (Jacobson and Anderson, 1986). Despite these caveats, depiction of microbial plankton assemblages as distinct, definable ecological entities remains a common and useful convention for describing and modeling these communities (Azam et al., 1983).

Solving problems associated with estimating microbial biomass that relate to conversion factors are not so easy. Conversion factors have proven difficult to establish accurately for prokaryote and protistan assemblages. Much of the problem relates to the fact that these conversion factors are not necessarily constant but may vary with species, cell size, the type of preservative, even the type of microscopy employed (Smayda, 1978; Choi and Stoecker, 1989; Verity et al., 1992; Stoecker et al., 1994a). Therefore, conversion factors reported in the literature differ considerably. For example, biovolume:carbon conversion factors reported in the literature for nano- and microplankton vary by a factor of approximately five (Smayda, 1978; Børshem and Bratbak, 1987; Putt and Stoecker, 1989; Verity et al., 1992). Clearly, the choice of a conversion factor can affect the calculated contribution of a specific assemblage to the total living biomass of a community.

In evaluating the accuracy of the biomass values determined in this study and comparing them to other investigations, several issues should be noted. First, we did not separate out mixotrophic/symbiotic species of protists in our studies. Plastid-retaining ciliates and symbiont-bearing sarcodine protozoa were considered 'heterotrophs' in our analyses, while mixotrophic flagellates were not distinguished from purely phototrophic species. Recent field investigations indicate that these populations can contribute significantly to the total abundance and biomass of nano- and microplankton (Sanders and Porter, 1988; Stoecker et al., 1989; Caron and Swanberg, 1990; Dolan, 1992; Bockstahler and Coats, 1993; Arenovski et al., 1995). Our characterizations are not incorrect technically, but they do mask the trophic complexity that was present in this ecosystem. Also, the contributions of heterotrophic and phototrophic dinoflagellates in this study may have been somewhat in error because these

assemblages were not distinguished in all samples. However, recent studies indicate that mixed nutrition is much more widespread among dinoflagellates than previously believed, and therefore characterizing these species as ‘phototrophs’ or ‘heterotrophs’ may be flawed in any event (Jacobson and Anderson, 1996).

A more important consideration, however, is our choice of conversion factors for calculating biomass from biovolume. Our abundance/biovolume data were converted to carbon units using factors that we felt were the most appropriate for each of the plankton groups enumerated (see Materials and Methods). The biomass data are unavoidably influenced by these decisions. For example, our choice of an average conversion factor for nanoplankton was based on a previous empirical effort to constrain this conversion factor for Sargasso Sea plankton (Caron et al., 1995). It is possible that the use of that factor might not have adequately taken into account shifts in the carbon content of nanoplankton relating to cell size (Verity et al., 1992).

Despite possible caveats concerning biomass estimation, our analyses of the contribution of nano- and microplanktonic assemblages to total POC were quite reasonable. Averaged over both cruises, integrations of carbon biomass in the top 160 m for the four plankton groups were 32% of POC. The contribution of living carbon in the nano- and microplankton size classes to total POC is, of course, influenced by the depth of integration. Most of the population abundances decreased rather precipitously well above 160 m while POC concentration typically decreased more slowly. Therefore, there is a possibility that depth-integration to a shallower depth would have increased the contribution of nano- and microplankton to total POC. When integrated over the depth range 0–100 m, however, the overall average percent contribution to POC increased only by 2.5%. We conclude that our estimates of microbial biomass in these size classes of plankton are relatively robust.

4.2. Comparison with other Arabian Sea studies

There are relatively few previous measurements with which to compare our data of the contribution of living microbial biomass to total biomass and particulate organic carbon in the Arabian Sea. Burlakova and Eremeeva (1994) noted that phytoplankton biomass contributed 6–20% of POC during the 1980 Spring Intermonsoon. Similar values were obtained in the Arabian Sea during the 1963 Fall Intermonsoon (Ryther and Menzel, 1965). A crude estimate of ‘living carbon’ calculated by the latter investigators indicated that living phytoplankton biomass in this sea was typically a small percentage of total suspended carbon (not more than 10–20%), although phytoplankton accounted for up to 60% of the particulate carbon at a few “bloom” stations. Our values for PNAN + PMIC biomass during our cruises are in good agreement with these previous studies. Phytoplankton $\geq 2 \mu\text{m}$ in the present study constituted approximately 15% of POC on average, and values reached as high as 40% at a few stations. Our PNAN + PMIC biomass estimates, however, do not include the contribution of picophytoplankton to phytoplankton biomass, and picoplankton have been demonstrated to be significant in this sea (Burkill et al., 1993; Jochem et al., 1993; Campbell et al., 1998).

Our estimates of heterotrophic biomass also are in agreement with the few published reports on these assemblages. One study conducted during the 1980 Spring Intermonsoon indicated that microzooplankton biomass contributed approximately 5% of POC, (summarized in Burlakova and Eremeeva, 1994). Our data for the 1995 Spring Intermonsoon indicated that HMIC constituted approximately 6% (Fig. 6). Reckermann and Veldhuis (1997) reported carbon biomasses for HNAN (HNF in that study) and ‘total protozoa’ (HNAN + HMIC) from stations in the Somali Basin to the south of our study area obtained during the 1993 NE Monsoon. Values for HNAN in that study (2.12–2.98 mg C m⁻³) were virtually identical to our average HNAN biomass during the 1995 NE Monsoon (2.83 mg C m⁻³; from Table 1, obtained by averaging all stations). The values for “total protozoa” estimated by Reckermann and Veldhuis (1997) were slightly less than the value that we observed for HNAN + HMIC during the 1995 NE Monsoon (4.59–4.84 vs. 5.51 mg C m⁻³ in our study), but our values for HMIC include sarcodine protozoa and nauplii (populations not included in the 1993 study). Given the variabilities associated with estimating microbial biovolume and converting these estimates to carbon noted above, these values from past studies seem remarkably consistent with the findings of the present study.

Measurements made by Garrison et al. (1998), however, during the 1995 SW Monsoon reported nano- and microplankton abundances and biomasses that were substantially higher than values obtained in our study. Ranges for phototrophic and heterotrophic populations observed by Garrison et al. (1998) spanned several orders of magnitude, indicative of highly eutrophic but spatially variable conditions during the SW Monsoon. The highest values reported in that study are consistent with conceptualizations of the northern Arabian Sea as a highly productive environment, and stand in contrast to the values obtained in the present study during the NE Monsoon and Spring Intermonsoon. Our results indicate a productive, but not overly productive ecosystem (see below).

4.3. Comparison with other plankton assemblages in the Arabian Sea

Nano- and microzooplankton biomass in the present study was of similar magnitude to previous reports of net-collected larger zooplankton (Vinogradov, 1962) as summarized in Banse (1994). Concurrent studies of mesozooplankton (> 200 µm) during the NE Monsoon and Spring Intermonsoon periods during 1995 reported a range of approximately 0.3–1.5 g C m⁻² in the upper 200 m along the southern transect of the study site (Smith et al., 1998; Wishner et al., 1998). These estimates of the biomass of larger zooplankton are similar to the ranges of HNAN + HMIC biomass observed in the present study (Figs. 2 and 3; Table 1). This finding that HNAN + HMIC biomass is comparable to the biomass of zooplankton > 200 µm in size seems somewhat surprising in this productive ecosystem, but it is consistent with findings in more oligotrophic oceanic communities (Roman et al., 1995).

Carbon values reported for meso- and macrozooplankton during the SW Monsoon are larger, but not by a great amount. Smith (1982) mapped zooplankton biomass near the Somali coast and obtained values up 0.82–6.96 g dry weight m⁻² in the top

200 m of the water column during the SW Monsoon. These values correspond to approximately $0.3\text{--}2.8 \text{ g C m}^{-2}$ ($25\text{--}230 \text{ m moles C m}^{-2}$) assuming that carbon is 40% of dry weight. Given the concomitant increases in HNAN and HMIC biomass during this season (Garrison et al., 1998), microbial heterotroph biomass might be expected to remain similar to meso- and macrozooplankton biomass.

4.4. Comparison with other oceanic ecosystems

There was considerable station-to-station variability in the proportions of PNAN, HNAN, PMIC and HMIC spatially and temporally in this study. The integrated biomasses in these plankton compartments, however, were quite similar when averaged over the entire data set (Table 1, Fig. 4). Diatom abundances were a notable exception to this pattern. Our finding of relative equity among these four plankton assemblages (PNAN, HNAN, PMIC, HMIC) is dissimilar to a number of other studies in which nanoplankton biomass constituted a larger proportion of the biomass than microplankton (Stoecker et al., 1994b; Caron et al., 1995). It is unlikely that inconsistencies in conversion factors contributed significantly to this difference because these previous studies used conversion factors that were quite similar to the ones that we applied. HNAN, dinoflagellates and ciliates in the present study (Figs. 2 and 3) were not unusually abundant compared to other studies in productive oceanic waters (Davis et al., 1985; Paranjape, 1990; Strom et al., 1993; Stoecker et al., 1994b; Gifford et al., 1995). Our HMIC values are somewhat higher than typically reported, and may be a combined effect of the contributions of sarcodine biomass (see below) and nauplii in this ecosystem (Fig. 3). Based on these latter values, we speculate that HMIC biomass in the Arabian Sea constitutes a significant source of nutrition for mesozooplankton. This speculation is consistent with recent experimental data on the fate of HMIC in pelagic food webs (Stoecker and Capuzzo, 1990; Gifford and Dagg, 1991).

The average contribution of nano- and microplankton to total POC was significant in our study (32% of POC). This contribution is greater than reported for some, but not all other oceanic environments. One study in the Sargasso Sea near Bermuda noted that PMIC + HMIC biomass accounted for $\leq 10\%$ of the POC while PNAN + HNAN constituted up to 20% (Caron et al., 1995). Microplankton always constituted a minor component of the microbial biomass in that study. Another study of broader geographic scope in the South and North Atlantic noted latitudinal trends in the relative contributions of the various plankton assemblages to total living microbial biomass (Buck et al., 1996). That study noted an increasing dominance of nano- and microplankton (relative to picoplankton) when comparing stations from tropical, subtropical and subarctic latitudes. The total contribution of HNAN, PNAN, HMIC and PMIC increased from 26% of total microbial carbon ($5^{\circ}\text{S}\text{--}24^{\circ}\text{N}$) to 40% ($25\text{--}45^{\circ}\text{N}$) to 69% ($50\text{--}61^{\circ}\text{N}$). Such a comparison will be interesting in the context of seasonal cycles in the Arabian Sea as syntheses of the JGOFS study proceed.

4.5. Sarcodine protozoa and the (variable) role of microzooplankton in particle flux

A microplanktonic assemblage of particular note in the Arabian Sea was the sarcodine protozoan fauna. Foraminifer/actinopod abundances enumerated in the HMIC plankton category in this study (Fig. 3) were 2–3 orders of magnitude higher than most previous reports for larger juvenile and adult specimens of planktonic foraminifera and radiolaria, but similar to reported abundances of acantharia from highly productive oceans (Caron and Swanberg, 1990). For example, abundances in the Arabian Sea of several 10 s m^{-3} have been reported for planktonic foraminifera $> 75 \mu\text{m}$ (Auras-Schudnagies et al., 1989). Reports of actinopods from productive ecosystems, however, typically range up to several 10 s l^{-1} (Beers and Stewart, 1971; Michaels, 1988), similar to abundances reported in the present study. Even juvenile planktonic foraminifera can reach abundances of 10 s l^{-1} in productive waters (Bé et al., 1985).

Few investigations of microbial abundances and biomass in oceanic ecosystems have included the contribution of sarcodine protozoa (acantharia, radiolaria and foraminifera) to total microzooplankton biomass (Beers and Stewart, 1969, 1971). This oversight is due probably to the difficulties associated with preservation, the lack of pertinent conversion factors to relate biovolume to biomass for these species, and the fact that adult sarcodines are large (i.e., they are meso- or macrozooplankton by size classification). Nevertheless, juvenile sarcodines fall within the nano- and micro- size classes, and are HNAN or HMIC by commonly accepted descriptions of these plankton categories.

Abundances of foraminifera and actinopods in the microzooplankton size class (20–200 μm) averaged over the 160 m water column during the present study ranged from a few to nearly 100 l^{-1} . These abundances were often an order of magnitude lower than ciliate abundances and two orders of magnitude lower than dinoflagellate abundances observed during these seasons. Their averaged contribution to microzooplankton biomass, however, often was similar to the contribution of these latter assemblages (Fig. 3). Very small juvenile sarcodines contributed to HNAN biomass as well, but these minute specimens were not specifically distinguished from other nanoplankton in our epifluorescence microscopical counts. This finding (the significant contribution of sarcodine biomass to total microbial biomass) is consistent with analyses of microbial plankton assemblages in the equatorial Pacific Ocean during the JGOFS program (Stoecker et al., 1996). Stoecker et al. (1996) concluded that sarcodines were the most important protozoan contributors to particle flux during the JGOFS study in the equatorial Pacific Ocean.

High abundances of sarcodines in surface waters of the Arabian Sea complicate the depiction of trophic relationships, energy flow within surface waters, and particle flux into the deep ocean. A common conceptualization of the trophic activities of nano- and microzooplankton in pelagic food webs is that the food processed by these species remains in surface waters for remineralization and recycling. That is, microbial consumers contribute to recycling processes in surface waters but are not major contributors to sinking particle flux. In general this relationship seems plausible because most non-sarcodine protozoa are not large enough to sink rapidly and typically produce minute fecal particles which are presumed to have slow sinking speeds (Elbrächter, 1991).

Sarcodine species, however, have rather long and complex life histories (for protozoa) that can span weeks or months (Anderson, 1983; Hemleben et al., 1988). These species grow from swarmer cells that are several μm in diameter to macroscopic adults. Some colonial radiolaria form gelatinous ribbons that exceed 1 m in length. In addition, many of these species form skeletal structures of CaCO_3 , silica, or strontium sulfate that increase their overall cell density and can increase their sinking speeds (Takahashi and Honjo, 1983; Takahashi and Bé, 1984). Finally, reproductive behavior of at least some of these species is preceded by, or coincides with, vertical descent in the water column of the adult specimens (Hemleben et al., 1988).

From a biogeochemical point of view, therefore, sarcodines live part of their life cycles as nano- and microzooplankton (i.e., participate in recycling/remineralization processes in surface waters), but ultimately possess the potential for contributing significantly to the vertical flux of particles from surface waters during their adult life stages. The degree to which planktonic sarcodines contribute to the vertical flux of organic carbon from surface waters via their life processes is controversial, but can be substantial (Michaels et al., 1995).

In this manner, sarcodine protozoa play a biogeochemical role in plankton communities that is more analogous to that of metazoan zooplankton that possess larval or juvenile stages $< 200 \mu\text{m}$. For example, copepod nauplii often fall within the microzooplankton size class (Fig. 3). Trophic activities that take place during the juvenile phases of these larger metazoa, as well as the juvenile stages of planktonic sarcodines, presumably contribute primarily to elemental recycling/remineralization in surface waters rather than sinking particle flux. The ability of planktonic sarcodines to contribute to remineralization in surface waters (versus the vertical flux of organic matter to the deep ocean) is typically ignored in most studies of microbial trophodynamics. Based on the results of this study and that of others (Stoecker et al., 1996), their potential contribution in oceanic ecosystems should not be disregarded.

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