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Productivity regime and phytoplankton size structure in the Arabian Sea

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Abstract—The productivity regime and size structure of phytoplankton are described for three different epipelagic systems in the Arabian Sea during the inter-monsoon period in spring 1987: (1) the coast of Oman; (2) the central Arabian Sea; and (3) the shelf off Pakistan. These results are related to the functioning of the specific ecosystem. Off the coast of Oman, the transition from a surface maximum of autotrophic biomass and production to a more oligotrophic system, with a chlorophyll subsurface maximum, was observed. Concomitantly, the size spectrum changed towards a higher significance of picoplankton. In the central Arabian Sea, a typical oligotrophic system with a pronounced subsurface maximum of autotrophic biomass and primary production was encountered. Here, the epipelagic system could be divided into two distinct sub-systems: the surface layer "regenerated" production, the predominance of picophytoplankton and minor losses due to sedimentation, thus a "closed" system; and the subsurface maximum layer at the nutricline characterized by higher sedimentation losses and more diatoms. Both sub-systems showed about the same productivity, the turnover in the surface layer having been much greater than in the subsurface maximum. The system on the shelf off Pakistan is seen as a decay stage of the open ocean system when water from offshore is transported onto the shelf during the onset of monsoon winds.

INTRODUCTION

THE Indian Ocean is distinguished from the Atlantic and Pacific oceans by the Arabian continent which closes it to the north at 25°N and causes a variety of specific climatic and hydrographic features. The northeastern part of the Indian Ocean, the Arabian Sea, is one of the most productive oceanic provinces (RYTHER *et al.*, 1966), because of the special hydrographic situation in this area (SASTRY and DESOUZA, 1972; QASIM, 1982).

A great effort to investigate the Indian Ocean was undertaken by the International Indian Ocean Expedition 1959–1965 (ZEITZSCHEL, 1973). Since then, however, relatively little information on this ocean has been published in comparison to the Atlantic and Pacific Ocean. Another expedition has been described by ANGEL (1983).

Data presented here were obtained during cruise no. 5 of the German Research Vessel *Meteor* from March to June 1987. Since the investigation period fell within the inter-monsoon period, no, or only minor, upwelling could be expected south of the Arabian peninsula, and since it was the warmest and driest period of the year the outflow of the Indus River could be expected to be negligible. High temperatures should lead to a

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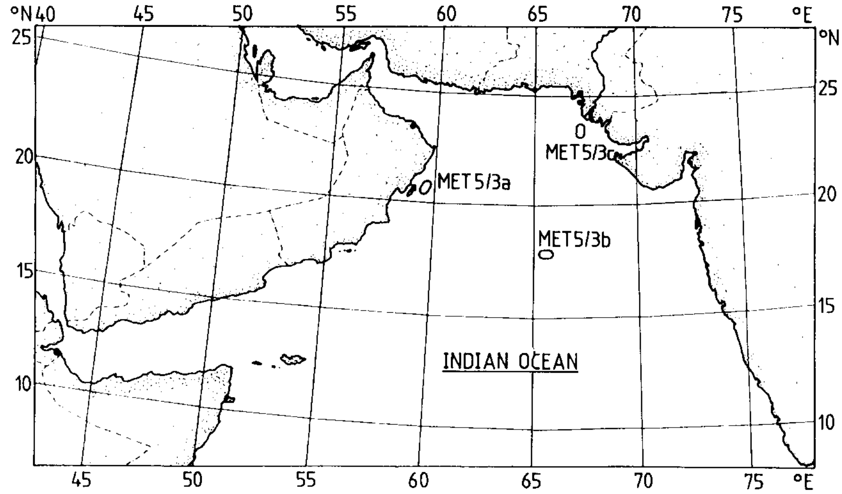


Fig. 1. Study sites of R.V. *Meteor* cruise no. 5 into the Arabian Sea in spring 1987: MET5/3a off the coast of Oman; MET5/3b in the central Arabian Sea; and MET5/3c on the shelf off Pakistan.

thermally stratified and stable water column and more or less oligotrophic conditions in the surface layer.

We describe here three different epipelagic systems: (1) the coast of Oman, (2) the central Arabian Sea; and (3) the shelf off Pakistan (Fig. 1). The productivity regime and the size structure of phytoplankton have been studied and set in relation to the general characteristics and functioning of the specific ecosystem. It will be shown that the significance of the autotrophic picoplankton is generally comparable to that in the Atlantic and Pacific Oceans, and that a close relationship between the ecosystem's functioning and the size distribution of plankton can be established.

MATERIALS AND METHODS

Leg 3a of R.V. *Meteor* cruise no. 5 was situated off the coast of Oman at 21°N, 60°E, mean depth about 2000 m. The 14 days drogue station lasted from 29 March to 11 April. Leg 3b, in the central Arabian Sea, took place at 18°N, 65°E, mean depth 3300 m, 29 April–12 May. The last leg, 3c, was situated on the shelf off Pakistan at 23°N, 67°E, mean depth 115 m, drift period 22 May–2 June.

Since the vertical structure of dynamic processes of the epipelagic system was the main goal of this study, a "Lagrangian" drogue study was carried out. Samples were taken along the track of a drifter carrying sediment traps just below the euphotic zone (80–120 m). During sampling, the ship stayed as close as possible to the drifter. A detailed description of the drifter itself is given elsewhere (PASSOW *et al.*, 1993; POLLEHNE *et al.*, 1993b).

Temperature and salinity profiles were taken with a Kiel Multisonde (ME Electronic, Trappenkamp, Germany). *In situ* chlorophyll fluorescence was recorded by a Variosens fluorescence probe and analog data output.

Water samples were taken with a 12 bottle multisampler with black 12 l Niskin type water bottles. Dissolved inorganic nutrients (NO_3, NO_2, PO_4, silicate) were measured according to GRASSHOFF *et al.* (1983) with an autoanalyzer. Samples were filtered onto 25 mm Whatman GF/F filters, except for particulate silicate analysis where 0.45 μm membrane filters were used. Particulate organic carbon and nitrogen were estimated using a Perkin-Elmer B-140 elemental analyzer, after the removal of inorganic carbonates with hydrochloric acid. Particulate silicate was measured according to PAASCHE (1980). These values were slightly underestimated due to analytical problems, but linearity of the measurements was verified. Chlorophyll *a* was determined either trichromatically (STRICKLAND and PARSONS, 1972) and calculated after JEFFREY and HUMPHREY (1975), or with a Turner Designs Model 10 fluorometer calibrated against trichromatically determined Chl *a*.

Primary production was measured by *in situ* $H^{14}CO_3$ incubations (STEEMANN NIELSEN, 1952) of 5–6 h duration (sunrise–local noon) in 250 ml glass bottles (25 μCi/bottle). [During leg 3a, an additional afternoon incubation (local noon–sunset) was performed]. Three–four bottles, treated with 10^{-5} mol l^{-1} DCMU [3-(3,4-dichlorphenyl)-1,1-dimethylurea; LEGENDRE *et al.*, 1983], were used as a dark correction and subtracted from light bottles. After incubation, samples were treated with 1.5×10^{-5} mol l^{-1} DCMU to prevent carbon uptake. ^{14}C-uptake was determined by liquid scintillation measurements in a Packard TriCarb.

For size fractionation into the size classes "total", "<20 μm" and "<2 μm", post-incubation screening was used. For each depth, one light bottle was incubated. Seventy-five ml aliquots were used for fractionation, to avoid variance because of different bottles. Estimates for "total" were obtained from untreated aliquots, the other two aliquots were filtered through 20 μm net gauze and 25 mm 2.0 μm Nuclepore filters (pressure <300 m*bar*), respectively. The filtrates were again filtered onto 0.45 μm membrane filters. The same size fractionation procedure was used for chlorophyll, but 2 l were fractionated and the filtrates were filtered onto Whatman GF/F. For <2 μm fractionation of chlorophyll, three filters were used for each 2 l sample.

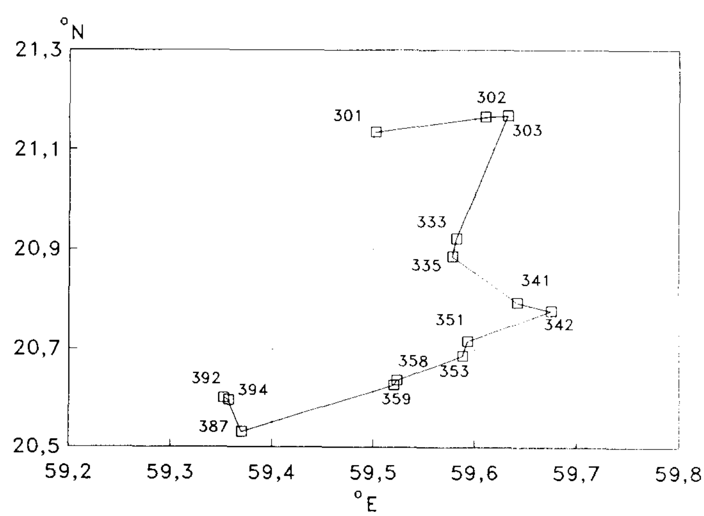
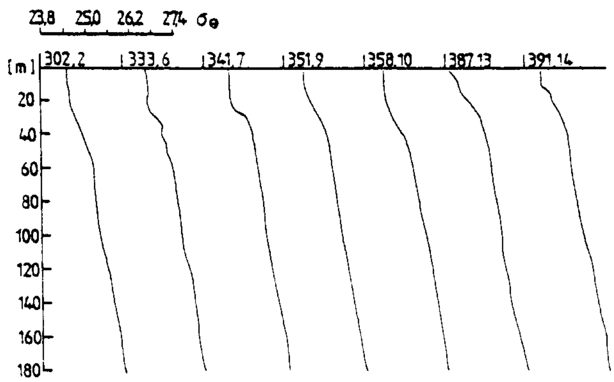


Fig. 2. Drifter trajectory of the drogue station off the coast of Oman, leg 3a. Station numbers indicated.

(a)



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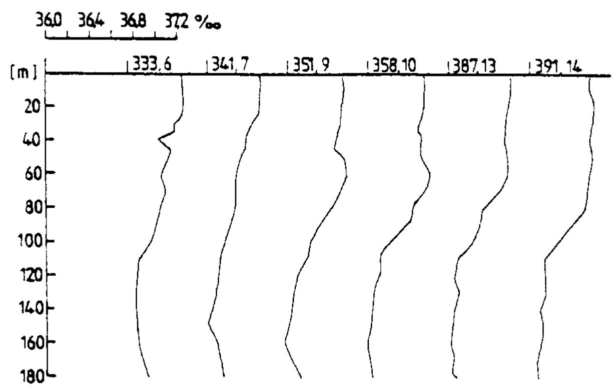


(c)

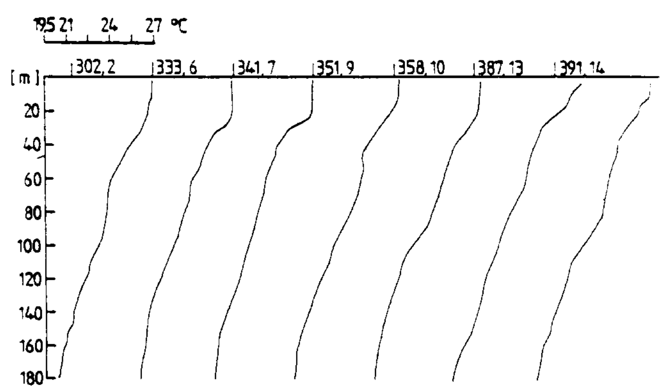
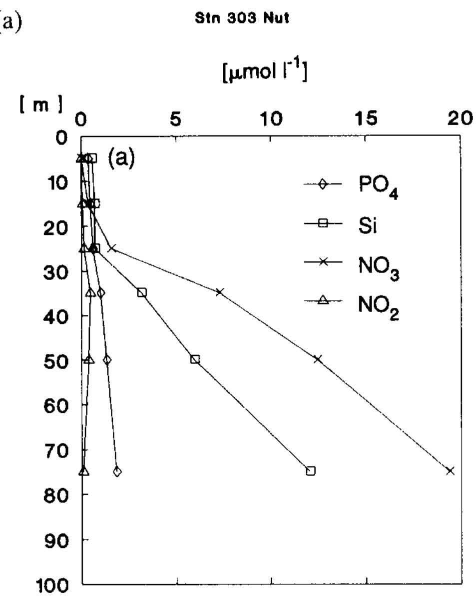


Fig. 3. Profiles of density σ_θ (a), temperature (°C; b), and salinity (‰; c) on leg 3a. Numbers indicate station and day of drift study.

(a)



(b)

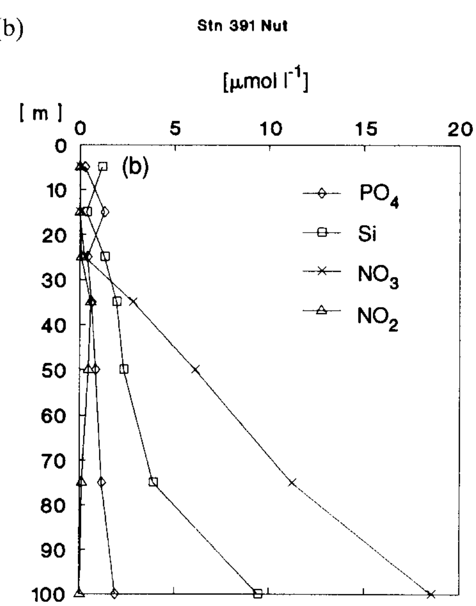


Fig. 4. Inorganic nutrients (μmol l^{-1}) on leg 3a; (a) Sta. 303, day 2; (b) Sta. 391, day 14.

RESULTS

Leg 3a: the coast of Oman

The drogue station off the coast of Oman was investigated over three periods: the first 2 days (Stas 301–303); days 6–10 (Stas 333–359); and days 13 and 14 (Stas 387–392) (Fig. 2).

Surface temperature [Fig. 3(c)] was 25.0–26.5°C and increased slightly over the investigation period; surface salinity ranged from 36.5–36.7‰ [Fig. 3(b)]. A thermocline, prominent at about 20 m depth but at 10 m on the last day [Fig. 3(c)], defined the density structure [σ_θ; Fig. 3(a)] and the depth of the surface layer. During drift phase II (Stas 351, 358), a region of higher salinity was found at 50–80 m depth, which might have been the "Arabian Sea High Salinity Water" (Gallagher 1966). On the last 2 days, however, salinity was almost constant down to the halocline at 65 and 85 m depth, respectively. Changes in the hydrographic structure suggest that the drifter did not stay within the same water body but moved into another one between days 7 and 9 (Stas 341 and 351). A change in the drift trajectory, from cyclonic to straight westward (Fig. 2) confirms the change in hydrographic conditions. Data presented here, therefore, cannot be seen as a true time series. Data elaborated on two 40 × 80 miles grids comprising 40 stations around the drogue (Passow *et al.*, 1993) indicated that the "temporal" development of the epipelagic system observed near the drifter was, however, representative for the temporal development of the whole area.

Nutrient concentrations [Fig. 4(a) and (b)] in the surface layer were 0.4–0.5 μmol l^{-1} of phosphate, about 1.2 μmol l^{-1} of silicate, less than 0.03 μmol l^{-1} of nitrite. The latter exhibited a primary maximum (up to 0.9 μmol l^{-1}) at 35–50 m depth. Nitrate was measurable at <0.3 μmol l^{-1} in the surface layer at the beginning of the study; at the end, it was detectable only below 30 m, and concentrations in the lower part of the euphotic zone (30–75 m) decreased with time.

Vertical profiles of *in situ* fluorescence (Fig. 5) were very "spiky" during the first half of the study period, suggesting the occurrence of larger phytoplankton. Between days 7 and 9 (Stas 341 and 351), the fluorescence profiles became much smoother and the subsurface

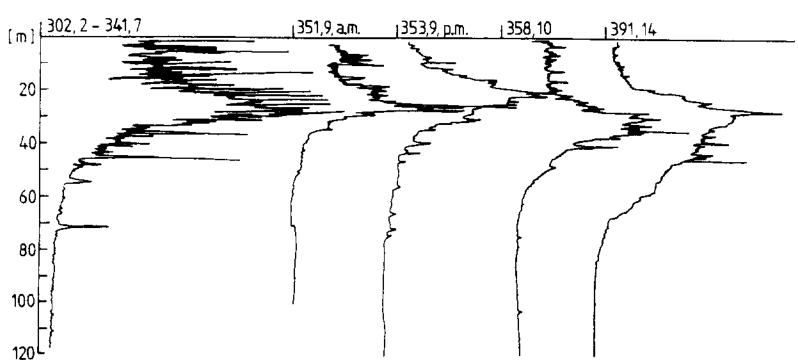


Fig. 5. *In situ* fluorescence on leg 3a, arbitrary units. Numbers indicate station and day of drift study.

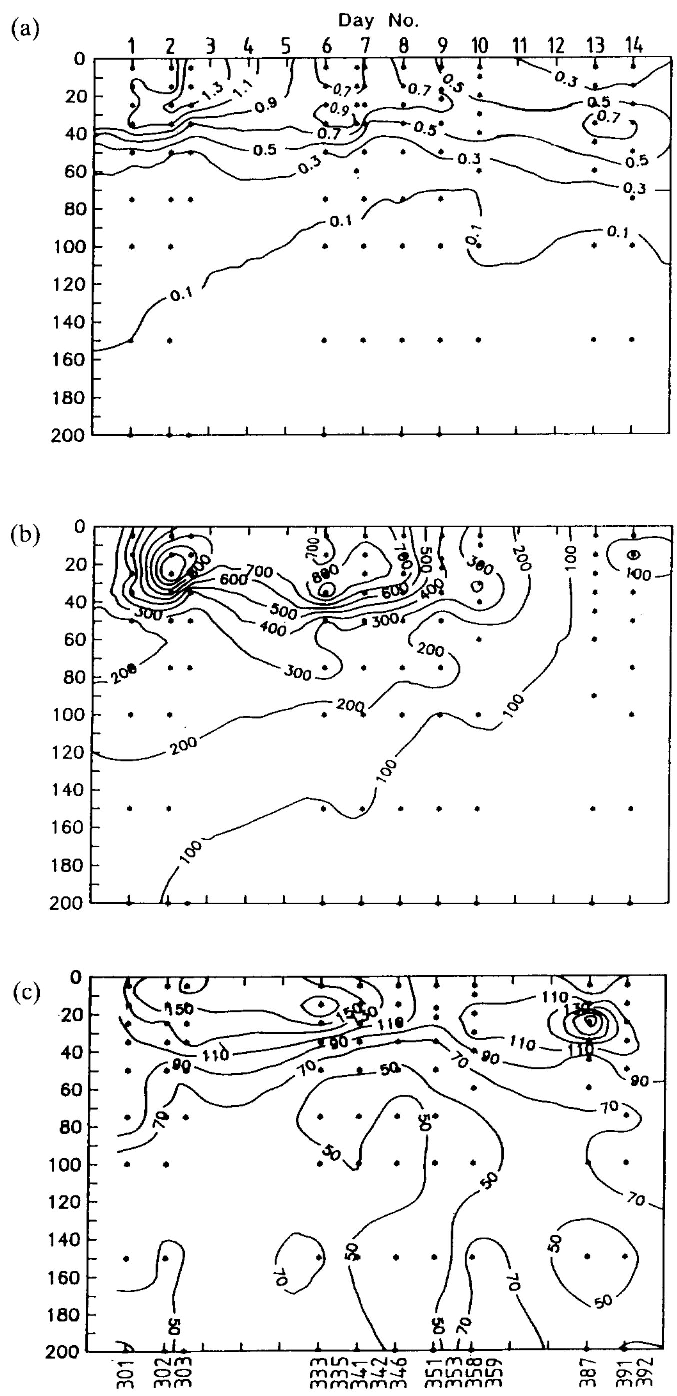


Fig. 6. Profiles of (a) chlorophyll *a* (b) particulate silicate; and (c) particulate organic carbon on leg 3a, all in $\mu g\ l^{-1}$.

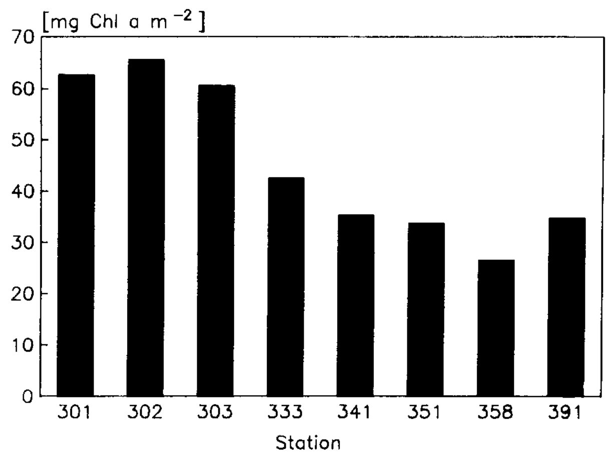


Fig. 7. Integrated chlorophyll *a* (0–75 m) on leg 3a (mg m^{-2}).

maxima [Fig. 6(a)] became more pronounced, whilst the surface layer fluorescence decreased. Integrated chlorophyll decreased from 60 mg m^{-2} to 30–35 mg m^{-2} (Fig. 7).

The decrease and change in the vertical distribution of chlorophyll was concomitant with a significant decrease in particulate silicate, an indicator of diatoms, especially after day 9 [Fig. 6(b)]. At the end of the investigation period only 1/8 of the concentration of chlorophyll was present compared with the beginning.

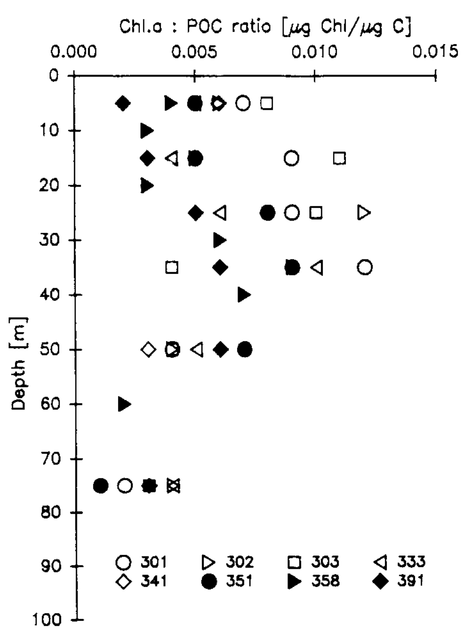


Fig. 8. Chl *a*/POC ratios on leg 3a.

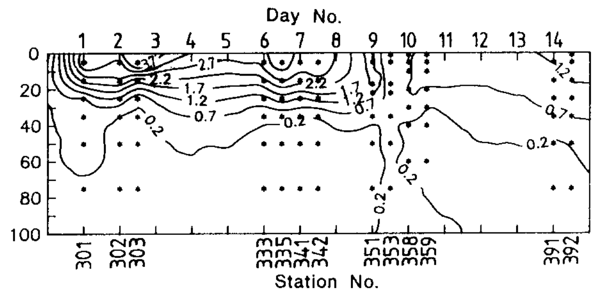


Fig. 9. Primary production (μg C l^{-1} h^{-1}) on leg 3a.

The decrease in autotrophic biomass was not reflected by similar decreases in particulate organic carbon [POC; Fig. 6(c)] and particulate organic nitrogen (not depicted here). However, the maximum of POC was found in subsurface layers towards the end of the study, but the concentration was in the same range as at the start (up to more than 150 μg C l^{-1}). Throughout the upper 200 m of water column, atomic C/N ratios of particulate matter were 5.5–6.5, with no obvious trend with depth, but exhibited a tendency towards lower ratios at the end of the study period. Low C/N ratios, being close to those of bacteria and small phytoplankton, suggest a minor contribution of detrital material to POC. Chl *a*/POC ratios (Fig. 8) were high in the surface waters during the first half of the study period, with maximum values at 20–40 m depth and a sharp decrease below 40 m. Towards the end of the study, the ratios in surface waters were lower and constant down to the depth of the subsurface maximum, and the sharp decrease did not occur until below 50 m depth.

Primary production always showed a surface maximum, which was most pronounced during the first and second drift phase (Fig. 9). At the surface, more than 3 μg C l^{-1} h^{-1} were generally measured and productivity sharply decreased below 30 m depth. The productivity regime also changed after day 9 (Sta. 341), when primary production decreased, and the surface maximum was less obvious. Integrated production (Fig. 10)

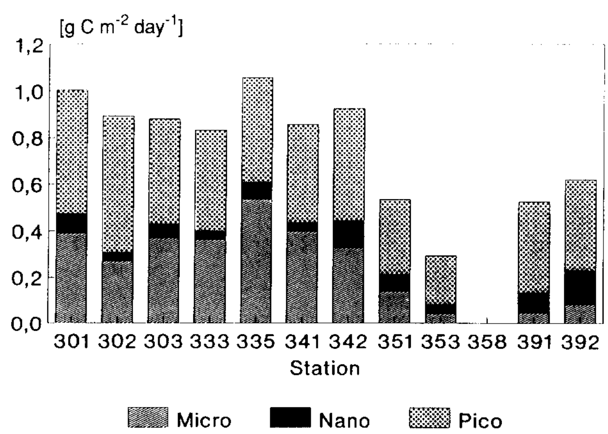


Fig. 10. Daily integrated, size-fractionated primary production (0–75 m; g C m^{-2} day^{-1}) on leg 3a. Pico- <2 μm; nano- 2–20 μm; micro- >20 μm.

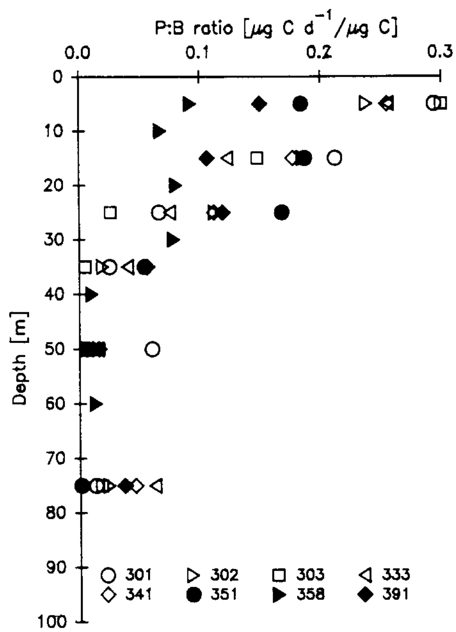


Fig. 11. P:B ratios (daily primary production to particulate organic carbon) on leg 3a.

Table 1. *Size fractionation of euphotic zone chlorophyll and primary productivity. Chlorophyll given in* mg m^{-2}, *production in* g C m^{-2} day^{-1}

Station	Total	Micro-	Nano-	Pico-	% Micro-	% Nano-	% Pico-
Leg 3a							
Chlorophyll							
301	62.7	22.1	10.7	29.9	35.2	17.2	47.6
302	65.6	34.2	1.9	29.5	52.1	2.9	45.0
Leg 3b							
Chlorophyll							
432	31.0	4.5	2.5	24.0	14.5	8.0	77.5
465	35.8	7.7	4.4	23.7	21.5	12.1	66.4
493	28.7	6.3	1.6	20.8	21.8	5.4	72.8
Production							
432	0.70	0.09	0.20	0.40	13.6	28.3	58.1
463	0.74	0.06	0.14	0.54	8.0	19.2	72.8
464	0.68	0.06	0.11	0.51	8.7	15.7	75.6
465	0.79	0.06	0.14	0.59	7.8	17.5	74.7
Leg 3c							
Chlorophyll							
560	26.4	1.8	0.2	24.4	6.9	0.6	92.5
Production							
552	0.18	0.02	0.02	0.14	10.4	9.9	79.7
555	0.31	0.06	0.05	0.20	18.0	15.3	66.7
560	0.35	0.01	0.02	0.32	4.2	5.7	90.1

decreased from about 1 g C m^{-2} day^{-1} to less than 0.6 g C m^{-2} day^{-1}. Whereas chlorophyll concentrations decreased after Sta. 333 (day 6) productivity did not decrease until Sta. 351 (day 9). Differences of daily integrated production based on morning and afternoon incubations were only minor, tending to slightly higher values in afternoon incubations due to higher values in the micro- and nanoplankton size fractions.

P:B ratios (Daily primary production/POC; Fig. 11) showed a steady decrease with depth during the first half of the study period; the shape of the curve strongly resembles that of light penetration into the ocean. After the changes related to Sta. 341, P:B ratios in the surface waters were lower and constant down to 30 m, and sharply decreased below.

All size fractions exhibited surface maxima of primary production. During the first half of the study, productivity was dominated by micro- (>20 μm) and picoplankton (<2 μm) (Fig. 10), producing 0.3–0.5 g C m^{-2} day^{-1} (30–51% of the total) and 0.45–0.6 g C m^{-2} day^{-1} (52–66% of the total), respectively. The nanoplankton (2–20 μm) contribution was minor (0.03–0.08 g C m^{-2} day^{-1}, 4–8%). The same size distribution was reflected in chlorophyll measurements (Table 1). After day 9 (Sta. 351), all size fractions showed reduced productivity but this was most pronounced for microplankton, accounting for only 0.04–0.14 g C m^{-2} day^{-1} (9–26% of the total). Nanoplankton production slightly increased to 0.04–0.14 g C m^{-2} day^{-1} (12–23% of the total). Picoplankton (about 0.4 g C m^{-2} day^{-1}, 60–74%) became the dominant size fraction.

Leg 3b: the central Arabian Sea

The drogue station in the central Arabian Sea also was investigated during three drift phases: the first two days (Stas 432–434); days 6–9 (Stas 463–466); days 13 and 14 (Stas 493–495). Throughout the whole investigation period, the drogue showed a straight southeasterly drift trajectory (Pollehne *et al.*, 1993a).

The hydrographic regime displayed only very minor changes over the whole investigation period, as well as within a 40 × 80 miles grid, comprising 40 stations around the drifter which was surveyed twice (Pollehne, unpublished data). Typical profiles of temperature, salinity and density [σ_θ; Sta. 465 (day 8); Fig. 12] showed a strong pycnocline

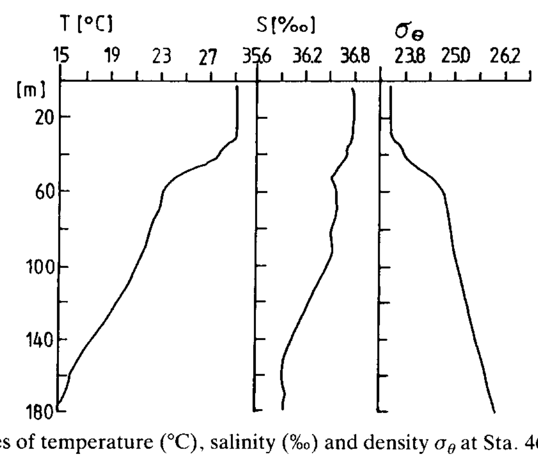


Fig. 12. Profiles of temperature (°C), salinity (‰) and density σ_θ at Sta. 465 (day 8) on leg 3b.

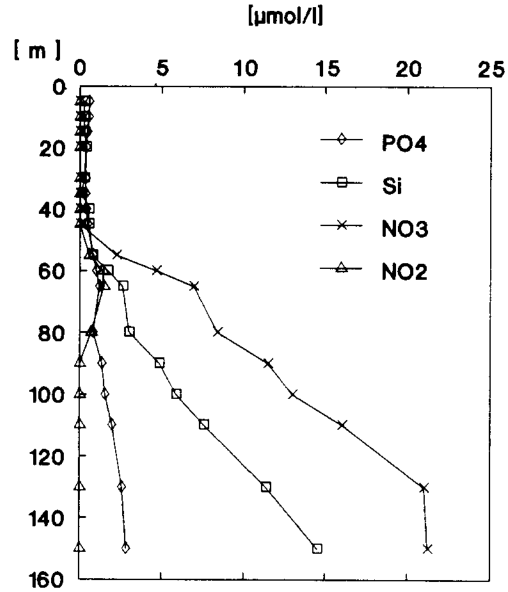


Fig. 13. Inorganic nutrients (μmol l^{-1}) at Sta. 466 (day 9) on leg 3b.

at 20–30 m depth. Surface temperature ranged from 28.0 to 29.5°C, being significantly higher than on leg 3a, and surface salinity was 36.5–36.8‰.

Almost no changes in nutrient concentrations could be observed over the investigation period. Surface layer concentrations were 0.3–0.4 μmol l^{-1} of phosphate and 0.4–1.0 μmol l^{-1} of silicate. Nitrite showed a maximum of up to 1.4 μmol l^{-1} at 50–80 m depth, being undetectable above and below this depth. Nitrate was mostly below the limit of detection

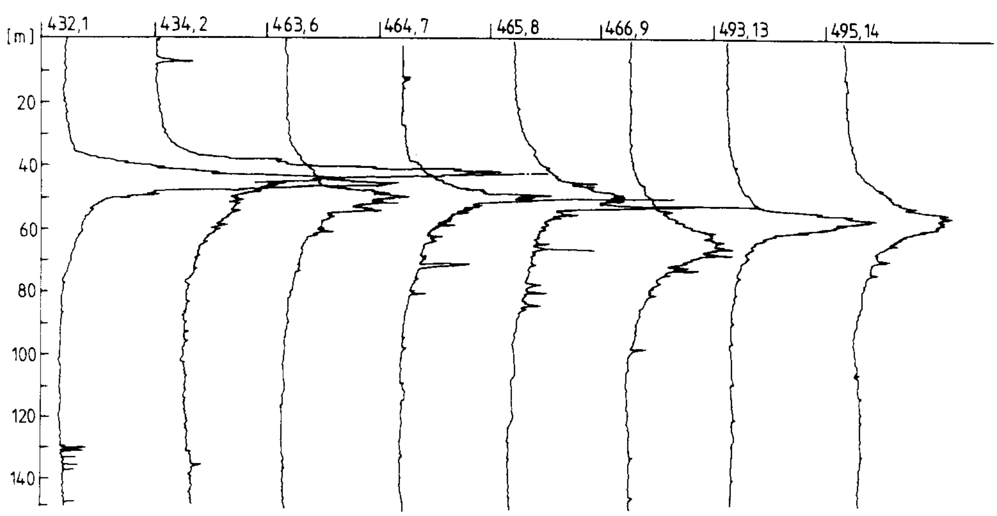


Fig. 14. *In situ* fluorescence on leg 3b, arbitrary units. Numbers indicate station and day of drift study.

down to 45 m. Below 120 m the anomaly of nitrate distribution due to bacterial denitrification typical for the Arabian Sea became obvious (see MANTOURA *et al.*, 1993) (Fig. 13).

Vertical profiles of *in situ* fluorescence (Fig. 14) and chlorophyll [Fig. 15(a)] show a prominent subsurface maximum, decreasing from 35–50 m, at the beginning, to 45–70 m. Chlorophyll concentrations were 0.11–0.18 $\mu g\, l^{-1}$ in the surface layer and as high as 1.40 $\mu g\, l^{-1}$ (always >0.8 $\mu g\, l^{-1}$) in the subsurface maximum. The distinct subsurface maximum of

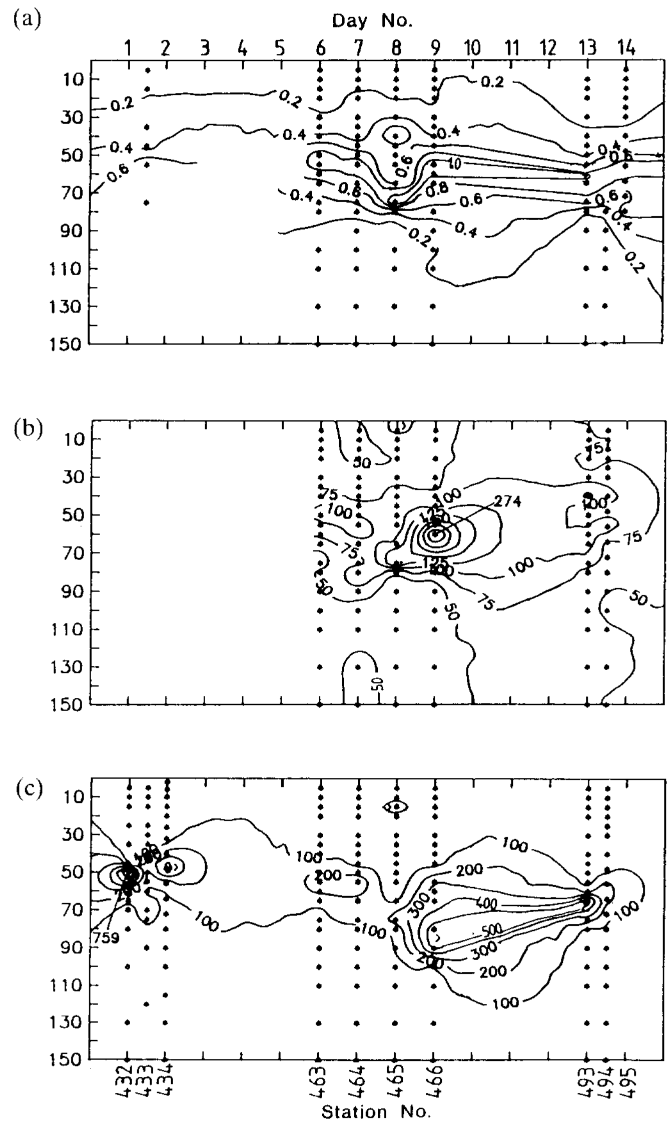


Fig. 15. Profiles of (a) chlorophyll *a*, (b) particulate organic carbon and (c) particulate silicate on leg 3b, all in $\mu g\, l^{-1}$.

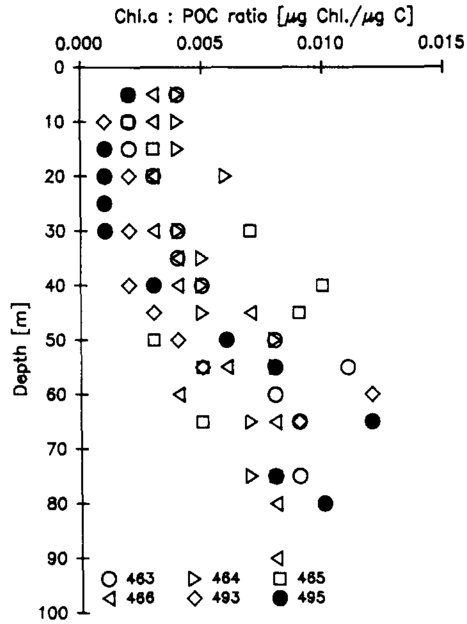


Fig. 16. Chl *a*/POC ratios on leg 3b.

particulate silicate [Fig. 15(c)] in the lower part of the chlorophyll maximum indicated the occurrence of diatoms.

POC, [up to 274 $\mu g\ l^{-1}$; Fig. 15(b)] and PON (up to 47 $\mu g\ l^{-1}$; not depicted) also showed distinct subsurface maxima coinciding with the chlorophyll maximum. The highest integrated chlorophyll was observed at Sta. 466 (day 9) and coincided with the highest values of POC, PON and particulate silicate. Atomic C/N ratios ranged between 5 and 7.3, tending to slightly lower values in the surface layer. The low ratios again suggest a minor contribution from detritus; this was supported by microscopic observations. In the surface layer, Chl *a*/POC ratios (Fig. 17) were constant and much lower compared to leg 3a, indicating a higher significance of heterotrophic organisms. Chl *a*/POC ratios decreased from 30 m down to the bottom of the productive zone (75 m) and remained constant between 75 and 90 m.

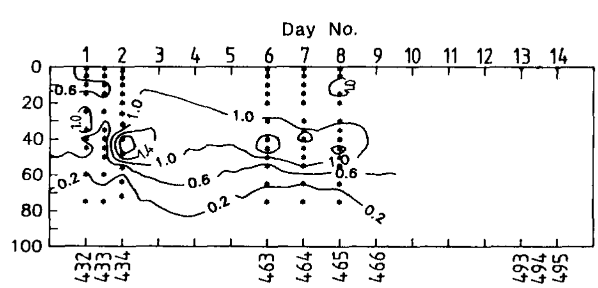


Fig. 17. Primary production ($\mu g\ C\ l^{-1}\ h^{-1}$) on leg 3b.

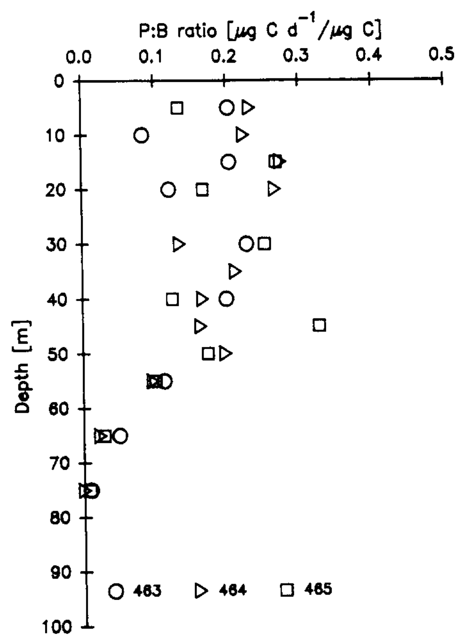


Fig. 18. P:B ratios (daily primary production to particulate organic carbon) on leg 3b.

Except on day 1 (Stas 432 and 433), primary productivity showed a distinct subsurface maximum at 30–50 m depth [that is in the upper half of the subsurface chlorophyll maximum (Fig. 18)]. Surface production was about 0.6 μg C l^{-1} h^{-1} and as high as 2.1 μg C l^{-1} h^{-1} within the subsurface maximum (always >1 μg C l^{-1} h^{-1}). Low rates of production could still be measured at 75 m depth. Integrated production amounted to about 0.7 g C m^{-2} day^{-1} (Table 1).

P:B ratios (Fig. 18) were more or less constant down to 50 m, but decreased sharply below this depth. This shape of profile is similar to that found during the last 3 days of leg 3a, but the P:B ratios were lower off the coast of Oman.

The production of all three size fractions was highest in the subsurface maximum, but the picoplankton maximum appeared in the upper half of the chlorophyll maximum, whereas that of micro- and nanoplankton occurred in the lower part. This vertical zonation within the subsurface maximum could, however, not be detected in chlorophyll measurements (JOCHEM, 1990). The picoplankton was the dominant size fraction, both in integrated primary production and chlorophyll.

Leg 3c: the shelf off Pakistan

The drogue station on the shelf off Pakistan was investigated in two drift phases: days 1–2 (Stas 521–525); and days 6–12 (Stas 552–561). The drifter trajectory of this leg was very complicated, with the drogue frequently changing direction (Fig. 19). This indicates a highly dynamic area and makes it difficult to determine whether the data presented below can be seen as a true time series, particularly because hydrographic data were available only for three stations. The hydrographic data however, showed very similar profiles (Fig.

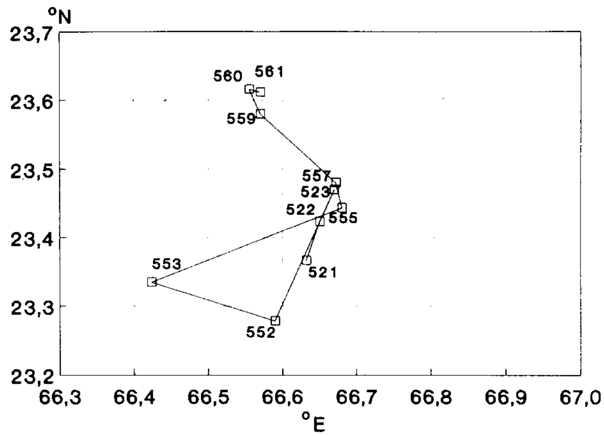


Fig. 19. Drifter trajectory of the drogue station on the shelf off Pakistan, leg 3c. Station numbers indicated.

20), with surface temperature being 28.7–29.8°C and surface salinity 36.9–37.1‰. The temperature and salinity were the highest of the three investigation areas. A salinity minimum was recorded between the main pycncocline (at about 20 m depth) and 60 m depth.

The nutrient regime on the shelf off Pakistan was very similar to that in the central Arabian Sea (Fig. 21) Surface layer concentrations were 0.3–0.45 μmol l^{-1} of phosphate and 0.6–1.3 μmol l^{-1} of silicate; the latter was variable but higher than on leg 3b. Both nitrate and nitrite were below the limit of detection down to 50 m. The anomaly of nitrate distribution was obvious below 80 m depth. The nitrite maximum at 50–70 m was as high as 0.96 μmol l^{-1}.

In situ fluorescence (Fig. 22) and chlorophyll [Fig. 23(a)] showed subsurface maxima at 30–50 m during drift phase I, and 40–60 m during drift phase II. Chlorophyll concentrations were about 0.15 μg l^{-1} in the surface layer and as high as 1.1 μg l^{-1} in the subsurface maximum. During drift phase II, a decrease of chlorophyll within the

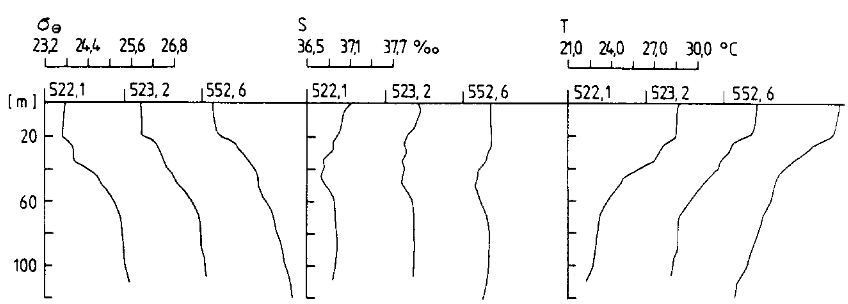


Fig. 20. Profiles of density σ_θ, salinity (‰), and temperature (°C) on leg 3c. Numbers indicate station and day of drift study.

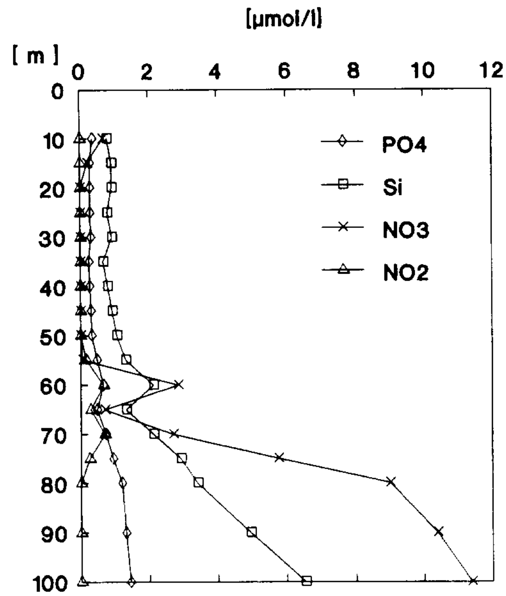


Fig. 21. Inorganic nutrients (μmol l^{-1}) at Sta. 555 (day 8) on leg 3c.

subsurface maximum was noted. This decrease can also be seen in integrated values (Fig. 24), which decreased from 28 mg m^{-2} to 14 mg m^{-2} at Sta. 558, but increased to 24.6 and 26.5 mg m^{-2} on the last 2 days.

Again, subsurface maxima of POC [$\leq 156\,\mu g\,l^{-1}$; Fig. 23(b)] and PON ($\leq 34\,\mu g\,l^{-1}$; not depicted) were recorded in the chlorophyll maximum. Like in the Arabian Sea, atomic C/N ratios ranged between 5 and 7, and between 7 and 8 in some samples from the depth range 60–100 m. Particulate silicate had its maximum in the lower part of the chlorophyll maximum, indicating higher diatom abundance there [Fig. 23(c)]. Vertical profiles of Chl *a*/POC (Fig. 25) strongly resembled those from the central Arabian Sea, i.e. constant ratios down to 30 m, and an increase within the subsurface maximum. The ratios were, however, at the lower end of the range found in the central Arabian Sea.

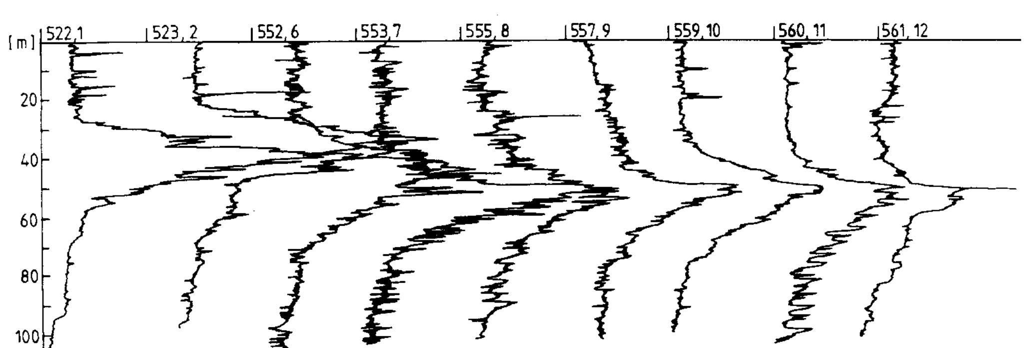


Fig. 22. *In situ* fluorescence on leg 3c, arbitrary units. Numbers indicate station and day of drogue station.

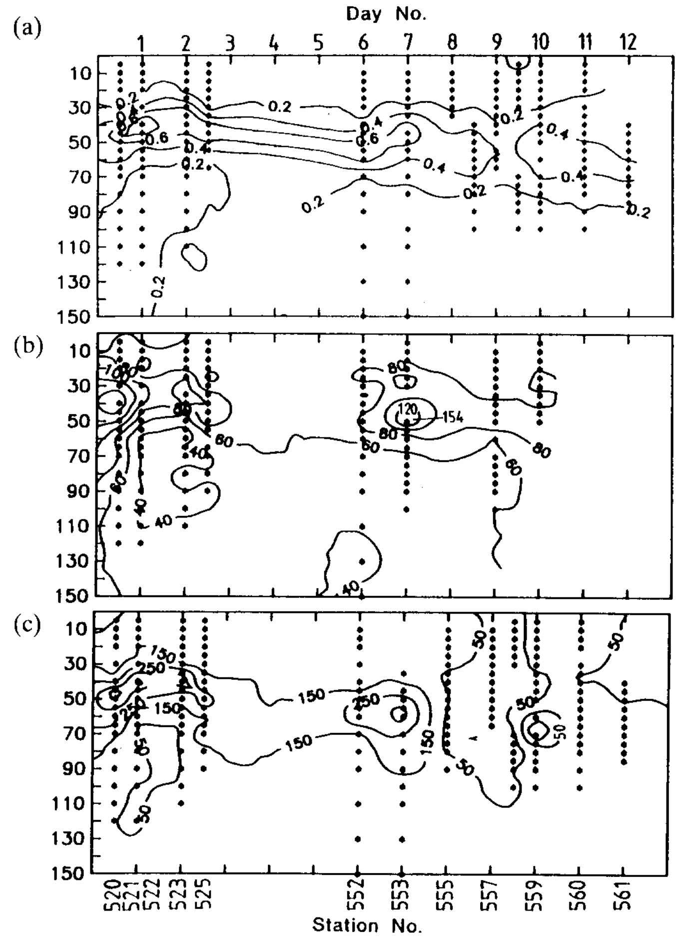


Fig. 23. Profiles of (a) chlorophyll *a*, (b) particulate organic carbon and (c) particulate silicate on leg 3c, all in $\mu g\ l^{-1}$.

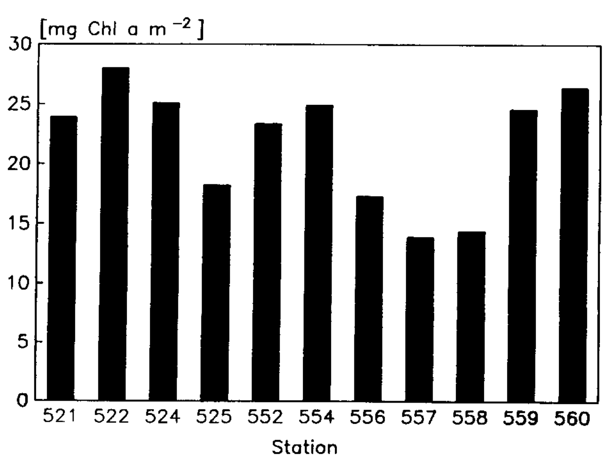


Fig. 24. Integrated chlorophyll *a* (0–75 m) on leg 3c (mg m^{-2}).

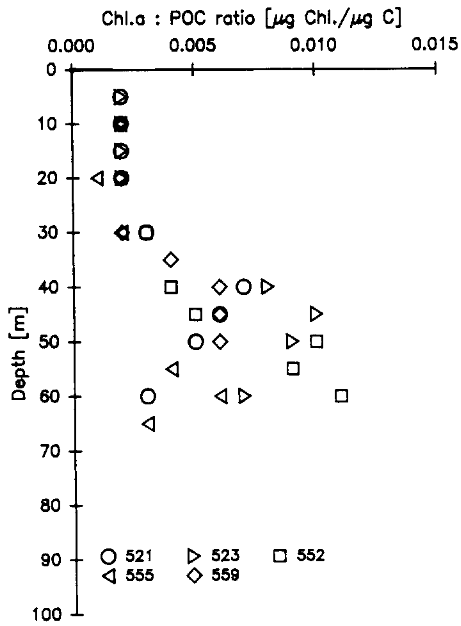


Fig. 25. Chl *a*/POC ratios on leg 3c.

Primary production showed a subsurface maximum ($\leq 1.2\,\mu g\ Cl^{-1}\ l^{-1}$) at 40–50 m depth during drift phase I (Fig. 26) corresponding to fluoresence and chlorophyll profiles. During drift phase II, both a subsurface and a surface maximum occurred. The latter was most prominent ($\leq 2.6\,\mu g\ C\ l^{-1}\ h^{-1}$) at Sta. 557 (day 9), and coincided with the occurrence of filamentous cyanobacteria which resulted in a more pronounced effect on productivity than on chlorophyll measurements. The integrated primary production (upper 75 m) was 0.2–0.4 g C m^{-2} day^{-1} but was as high as 0.6 g C m^{-2} day^{-1} during the period of surface maxima (Fig. 27).

P:B ratios (Fig. 28) were only half of those in the central Arabian Sea. Except for the last two days, the shape of the vertical profile was similar to that in the central Arabian Sea, displaying almost constant ratios from the surface down to 60 m. On the last 2 days (Stas 555 and 559), however, the productivity surface maximum of filamentous cyanobacteria caused higher ratios in the surface waters, and thus a decrease with depth. The highest P:B

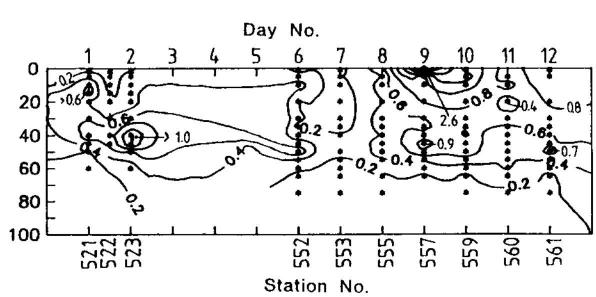


Fig. 26. Primary production ($\mu g\ C\ l^{-1}\ h^{-1}$) on leg 3c.

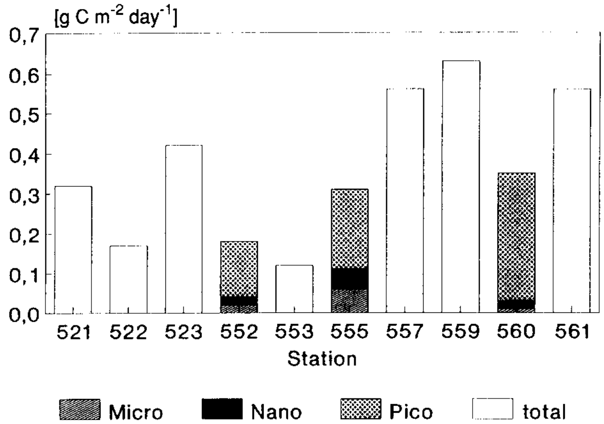


Fig. 27. Daily integrated, size-fractionated (where available) primary production (0–75 m; g C m^{-2} day^{-1}) on leg 3c.

ratios of the entire cruise were encountered during this phase of the investigation, and the shape of the profiles resembled that of the beginning of leg 3a off the coast of Oman.

Only three size fractionation experiments for productivity, and one for chlorophyll, were available on leg 3c (Table 1). They showed picoplankton dominated both the primary production and autotrophic biomass (66–92% of total). At Sta. 552 (day 6), however, 40% of the production was measured in the microplankton size class in the surface sample (5 m).

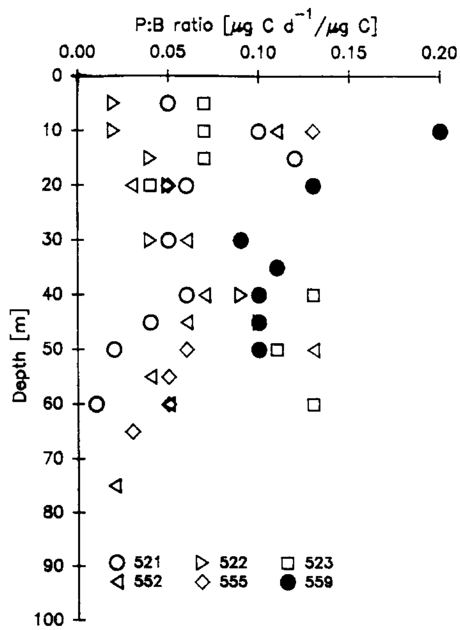


Fig. 28. P:B ratios (daily primary production to particulate organic carbon) on leg 3c.

DISCUSSION

The investigation area off the coast of Oman showed the highest spatial and temporal variability among the three regions investigated. The relatively low temperatures (25°C) may indicate that cold and nutrient-rich subsurface water may have been entrained into the euphotic zone immediately prior to the study. This is supported by low, but still measurable, nitrate concentrations in the surface layer at the beginning of the study. At the start of the drogue station, autotrophic biomass consisted of microplankton, namely diatoms like *Rhizosolenia* spp. (Passow *et al.*, 1993), and picoplankton in similar quantities. This size distribution changed with an increased significance of picoplankton along with decreasing nutrient concentrations, and the consolidation of the subsurface maximum. This change was accompanied by the highest sedimentation rates observed during this study, namely the sedimentation of diatoms, and auxospore-formation by *Rhizosolenia* spp. (Passow *et al.*, 1993), and a decrease in water column productivity. The decrease in autotrophic biomass and productivity was primarily governed by the decreased microphytoplankton.

The investigation area in the central Arabian Sea displayed high spatial (Nellen *et al.*, 1988; Pollehne *et al.*, 1993a) and temporal homogeneity, and the epipelagic system can be considered to be in steady-state. As on the other legs, the depth of the nutricline showed no relation to physical structures and, therefore, was determined predominantly by biological activity.

Subsurface maxima of *in situ* fluorescence and chlorophyll, a well documented phenomenon in oligotrophic oceans, were related to the nutricline. Both accumulation of autotrophic biomass and an increase in cellular pigment content due to photoadaptation can cause such a maximum. There are several reports that subsurface maxima of chlorophyll do not necessarily reflect biomass maxima (Steele, 1964; Beers *et al.*, 1975; Cullen and Eppley, 1981; Kimor *et al.*, 1987; Taguchi *et al.*, 1988; Pillen, 1989). However, microscopic cell counts (Jochem, 1990), HPLC pigment analysis (Pollehne *et al.*, 1993a) and profiles of particulate silicate proved the subsurface chlorophyll maximum to be a biomass maximum as well. Since Chl *a*/POC ratios increased below 30 m, the subsurface maximum of POC also indicates the chlorophyll maximum being an algal biomass maximum. The subsurface maxima of primary production proved this subsurface population to be actively growing, and not a result of sedimenting biomass. Picoplankton was the dominant size fraction in both autotrophic biomass and primary production throughout the water column. While *Synechococcus*-type cyanobacteria were almost the only algae in surface layers, some larger phytoplankton occurred in the lower half of the subsurface maximum (Jochem, 1990; Passow *et al.*, 1993; Pollehne *et al.*, 1993a).

The vertical structure of physical, chemical and biological variables was very similar on the shelf off Pakistan and the central Arabian Sea. However, there was a prominent difference between autotrophic biomass and primary production, primarily due to lower values in the subsurface maximum layer and its decay over the study period. The epipelagic system of leg 3c can be interpreted as a water mass from offshore advected towards the coast of Pakistan/India and onto the shelf with the start of southwesterly monsoon winds in May. This advection, due to the nature of Ekman-transport, was most pronounced near the surface. Thus with decreasing depth on the shelf, the lower part of the water column was effectively "cut-off", leaving the euphotic zone without the underlying nutrient-rich waters. Consequently, the upward flux of nutrients decreased,

decreased, and the euphotic zone became depleted of nutrients. This was clearly indicated by the depth below which nitrate could be detected; surface to 30 m at the beginning, but 55–60 m at the end of the drogue station.

The N:P ratios of inorganic nutrients never reached the Redfield uptake ratio of 15 (REDFIELD *et al.*, 1963) and, therefore, phosphorus tended to accumulate in the euphotic zone of the Arabian Sea. This may favour the occurrence of filamentous diazotrophic blue-greens observed at the end of the study, leading to surface maxima in primary production. Primary productivity originating from the surface layer increased from <50 to 60–70% of water column productivity. Since picoplankton productivity also increased near the surface after filamentous cyanobacteria occurred (JOCHEM, 1990), it is possible that fixed nitrogen was very rapidly channelled through the microbial loop, possibly via exudation by the cyanobacteria and subsequent remineralization by bacteria and microzooplankton. This was also reflected by an increase of N-dependent bacterial processes (GIESENHAGEN, 1988).

Different functional systems in the Arabian Sea

Within a spatially homogeneous and temporally stable environment, the epipelagic system in the central Arabian Sea can be divided into two functionally different sub-systems whose co-existence might be considered characteristic for (sub)tropical oceans (POLLEHNE *et al.*, 1993a), the oligotrophic surface layer (SL) and the subsurface maximum layer (SML) at the nutricline.

In the SL, vertically constant P:B ratios of phytoplankton suggest that primary production was not limited by light availability, but rather nutrient cycling dependent on heterotrophic activity. 50% of the water column productivity originated from the SL, having a much lower phytoplankton standing stock as compared to the SML. Turnover, therefore, was much faster in the SL [chlorophyll-specific production at the surface >4 mg C (mg Chl)$^{-1}$ h^{-1}, as high as 9.7 mg C (mg Chl)$^{-1}$ h^{-1}; JOCHEM, 1990]. GIESKES and KRAAY (1986) report a similar high biomass-normalized productivity [as high as 15 mg C (mg Chl *a*)$^{-1}$ h^{-1}] in the surface layer of the tropical North Atlantic (20°N, 20–40°W), but no increase of chlorophyll, indicating a high turnover of primary production rather than biomass accumulation. Losses of nutrient elements (N, P, Si) must be kept to a minimum; therefore sedimentation can be expected to be very low. In fact, sedimentation of chlorophyll measured in a Kiel sediment trap at 30 m depth was only minor, 9 μg Chl *a* m^{-2} day^{-1} or 0.05–0.2% of the standing stock (NELLEN *et al.*, 1988).

Within the SML, Chl *a*/POC ratios increased, probably reflecting both the increased contribution of phytoplankton to POC and the increase of cellular chlorophyll content due to photoadaptation. GIESKES and KRAAY (1986) report increased cellular chlorophyll for phytoplankton from the SML in the tropical North Atlantic in contrast to the SL, they also found an increase of chlorophyll within incubation bottles over 12 h, indicating primary production leading to autotrophic biomass accumulation, thereby balancing sedimentation losses and stabilizing the subsurface maximum. At 80 m depth, sedimentation of 22 mg C m^{-2} day^{-1} was measured (POLLEHNE *et al.*, 1993b). Assuming that almost all of this sedimentation originated from the SML, it amounted to about 6% of daily production within this layer; it further accounted for 30–60% of microphytoplankton production, the size fraction most likely to sediment out of the water column. Some amounts of zeaxanthin, characteristic for picocyanobacteria, were also measured in the sediment traps so that some active pathways, most probably via grazing, contribute to the sedimentation. In contrast to the relatively closed surface system, the SML is open at its base. It is interesting that, despite high nutrient concentrations, small phototrophs, i.e. organisms less likely to sink, are the major primary producers at the bottom of the euphotic zone (JOCHEM, 1990). A detailed description of the two-layer system is given elsewhere in this volume (POLLEHNE *et al.*, 1993a,b).

On leg 3a off the coast of Oman, successional stages towards the development of a two-layer system and the concomitant consolidation of the subsurface chlorophyll maximum could be observed. At the beginning of the study, surface Chl *a*/POC ratios were much higher than on leg 3b, increasing with depth which most likely reflects photoadaptation. Profiles of P:B ratios resembled those of light penetration into the ocean and indicate primary production probably being light- rather than nutrient-limited. After the hydrographic changes (days 7–9, stas 341–351), the subsurface maximum was more pronounced and profiles of P:B ratios became more similar to those of leg 3b, no longer resembling light penetration curves and indicating a higher significance of nutrient limitation near the surface. Generally decreasing Chl *a*/POC ratios point towards an increasing importance of heterotrophic biomass, accompanied by higher sedimentation. Size-fractionation as well as decreasing C/N ratios throughout the euphotic zone reflected the change towards the predominance of smaller organisms. While 27–88% of community respiration was attributed to nanozooplankton ($<20\ \mu m$) at the start of leg 3a, this was 66–97% at the end; the change in community size structure, thus, was also obvious in the heterotrophic compartments (NELLEN *et al.*, 1988).

The epipelagic system encountered on the shelf off Pakistan, on the other hand, can be seen as a decay stage of the two-layered system of the open oligotrophic ocean. While the vertical structure was very similar to that of leg 3b, autotrophic biomass and productivity were lower (except during the occurrence of filamentous cyanobacteria near the surface). Chl *a*/POC ratios were in the lower range and P:B ratios only half of those in the central Arabian Sea. The decrease of nutrients and heterotrophic processes gaining higher importance in community dynamics will, on a longer time scale, lead to a breakdown of this ecosystem. By the increasing monsoon winds, the water body will be advected further onto the shelf, and mixing with coastal waters will destroy the vertical structure and the equilibrium of processes in this ecosystem. Due to the drastic changes in wind direction and wind stress by the different monsoon regimes, this should be a recurrent seasonal phenomenon.

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