

Biological Processes of the Northern Indian Ocean

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With 6 Figures

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- Abstract

Physical processes such as wind-driven coastal upwelling, coastal run-off during the monsoons and convective overturning of surface waters due to winter cooling bring in nutrients into the euphotic zone and enhance primary productivity of the northern Indian Ocean. Nitrogen import, on decay of extensive blooms of *Trichodesmium*, appears to be another mechanism through which production increases in the eastern Arabian Sea. Zooplankton abundances usually match trends in phytoplankton production. However, at times, increases in the abundances of microzooplankton may lead to higher standing stocks of mesozooplankton. Blooms of phytoplankton and swarms of zooplankton are common in the northern Indian Ocean and influence rates of particle fluxes into the ocean interiors. High primary production, microbial activity and zooplankton abundances are characteristic of atoll lagoon waters. Microbial community appears to have a key role in food-chains and biogeochemical processes. Available data show that at least in the Arabian Sea, the high production modifies the ocean physics and chemistry of surface/subsurface waters.

1. Introduction

In the north, around 22° to 25° latitudes, the Bay of Bengal and the Arabian Sea are cul-de-sacs. This unique geographical situation has a decisive influence on the processes of the northern Indian Ocean. Associated with the southwest (summer) and northeast (winter) monsoon seasons, the surface currents exhibit semi-annual reversal.

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This and other physical and chemical features of the region such as restricted renewal of bottom waters, very low oxygen content in the oxygen minimum layer in the northern Arabian Sea, arid conditions over the continents alternating with cooling atmosphere along its northern boundary and low salinity in the northern Bay of Bengal, all have bearings on the biological events.

The International Indian Ocean Expedition (IIOE, 1960-65) was the first concerted effort to gather synoptic data from this region. From the biological angle, this resulted in the general mapping of some of the biological elements (e.g. Rao, 1973; Krey and Babenerd, 1976) and studies on distribution and zoogeographical patterns, especially of zooplankton (e.g. Zeitzschel, 1973; Rao, 1979). More data bases are available from several subsequent efforts (e.g. National Institute of Oceanography, 1977; Swallow, 1980). However, some of the processes oriented studies are just beginning to be conducted. In this review, we will attempt to blend them with earlier data wherever appropriate. We will briefly recapitulate the known features in biological productivity and distributions and try to identify the processes leading to them. We will also try to point out areas where major gaps exist and finally relate the biology to the geochemical processes.

Along coastal areas, upwelling during southwest monsoon is one major process influencing the productivity. Unlike other oceans, in the Arabian Sea, wind-driven upwelling is stronger along the western boundary than the eastern boundary system. Upwelling occurs along the Somali and Arabian coasts and offshore as a consequence of turning of offshore boundary current or Ekman transport in response to winds blowing parallel to the coast (see Schott, 1983; Swallow, 1984 for overviews). Along the west coast of India, wind-driven upwelling of moderate intensity occurs. It apparently starts at the southern tip of peninsular India and intensifies later in the northern areas, tapering off at about 17° - 18°N (Madhupratap et al., 1990 and references therein; Shetye et al., 1990). There are yet other physical and chemical processes influencing the biology of both coastal and offshore waters which will be discussed later.

2. Phytoplankton Biomass and Production

2.1. Western and Northern Arabian Sea

Coastal waters off Somali and Arabia are recognized to be some of the most productive areas in the world (Currie et al., 1973; Krey, 1973). Chemical changes due to upwelling and phytoplankton response in the Somali region (5° - 10°N) are summarized by Smith and Codispoti (1980). Upwelling starts in May and peaks by July-August. Sea surface temperature is low (17° - 22°C) and high concentrations of nutrients (e.g. nitrate, 13 - 20 $\mu\text{mol l}^{-1}$) occur. Offshore depths of water rising to the surface are about 100 m at 5°N and 200 m at 10°N. Phytoplankton biomass is generally high, surface chlorophyll *a* values range between 0.4 and 5 mg m^{-3} (Fig. 1); primary productivity is about 1.3 to 1.8 $\text{g C m}^{-2} \text{day}^{-1}$. A diatom *Nitzschia delicatissima* is dominant. A general inverse relationship between biomass and nutrients suggests active utilization of the latter. In contrast, primary production is only about 0.3 $\text{g C m}^{-2} \text{day}^{-1}$ during the northeast monsoon.

Further north, the Arabian coastal waters are also very productive as a result of upwelling. Here, the breadth of the upwelling zone is much greater, extending about 400 km offshore, and parallels the Arabian coast for a distance of over 1000 km

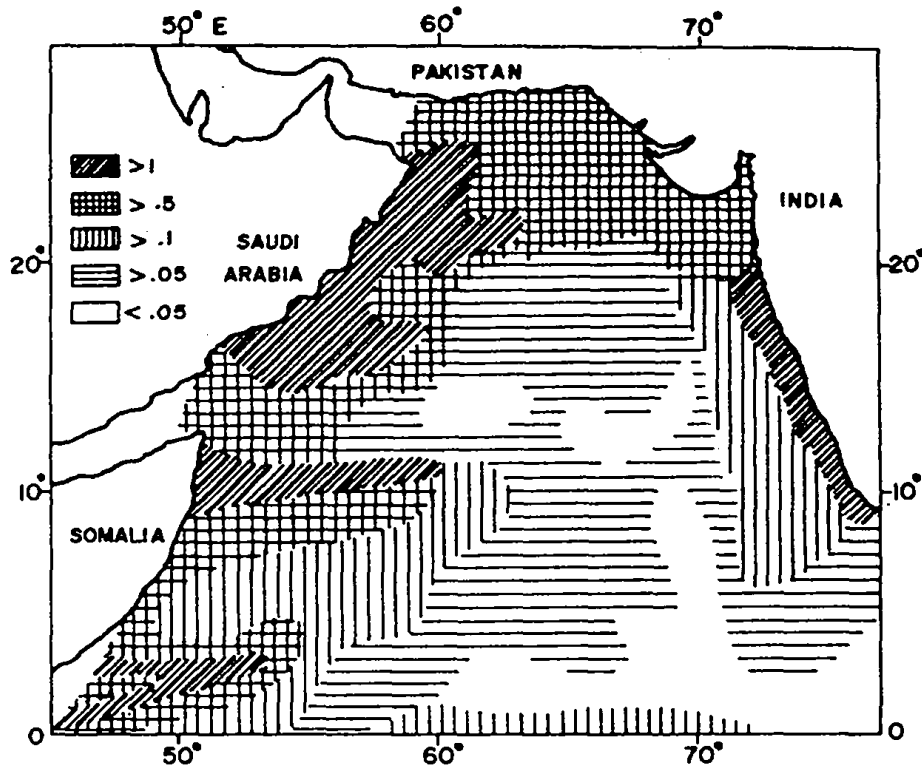


Fig. 1: Distribution of surface chlorophyll *a* (mg m^{-3}) in the Arabian Sea during the southwest monsoon (generalised from sources mentioned in the text).

(Bottero, 1969). Extensive areas of high production (surface production $> 50 \text{ mg C m}^{-3} \text{ day}^{-1}$) are located along the east coast of Arabia, off Pakistan and northwest India (Krey and Babenerd, 1976; Qasim, 1982). What is more significant is that this high rate of production is maintained in the area even after the southwest monsoon period. Surface currents are weak, allowing time for biological production/succession to develop (Swallow, 1984). Ryther et al. (1966) report values approaching bloom conditions ($1 - 6.4 \text{ g C m}^{-2} \text{ day}^{-1}$) all along east coast of Arabia and this extends up to 65°E during October-November. Ryther and Menzel (1965) explain that this probably happens as a result of nutrients from deeper waters reaching the surface as a result of divergence. They concluded that the production in the northwestern Arabian Sea is an order of magnitude greater than elsewhere in the world oceans. Satellite imageries show high pigment values in the area from December through mid-February and a sharp decline by April (Banse and McClain, 1986). They suggest that nutrient supply to the mixed layer enhancing algal growth rates might be resulting from wind mixing or convective overturning of the surface layer due to winter cooling. However, satellite imageries could be sometimes misleading since extensive blooms of the bluegreen alga *Trichodesmium* (= *Oscillatoria*) occur during northeast monsoon period (see below).

2.2. Eastern Arabian Sea

Along the south and central west coast of India, fairly high surface production (ca. $20 \text{ mg C m}^{-3} \text{ day}^{-1}$) is observed during southwest monsoon (Krey and Babenerd, 1976).

Sumitra-Vijayaraghavan and Kumari (1989), however, report surface chlorophyll *a* value of 3.2 mg m^{-3} and surface production rate as high as $232 \text{ mg C m}^{-3} \text{ day}^{-1}$ near the southern coastal waters of peninsular India during upwelling in June 1987. As upwelling spreads north by August-September, biomass goes up in these areas also (2.5 mg m^{-3} , Madhupratap et al., 1990). Still higher values ($> 7 \text{ mg m}^{-3}$) occur in inshore waters (Devassy, 1983). A few species of diatoms dominate the phytoplankton composition during this season (Subrahmanyam et al., 1975). The area of high production during upwelling period, however, appears to be narrow, hugging the coastline and overlying the shelf. Fairly high production is sustained until October-November (Radhakrishna, 1969), but surface chlorophyll *a* values of coastal waters diminished to an average 0.07 mg m^{-3} by December in 1987 (Madhupratap et al., 1992).

Satellite imageries clearly demonstrate the seasonal variations in pigment regimes (Fig. 2) in the Arabian Sea (Yentsch and Phinney, 1992). There is a sharp increase in

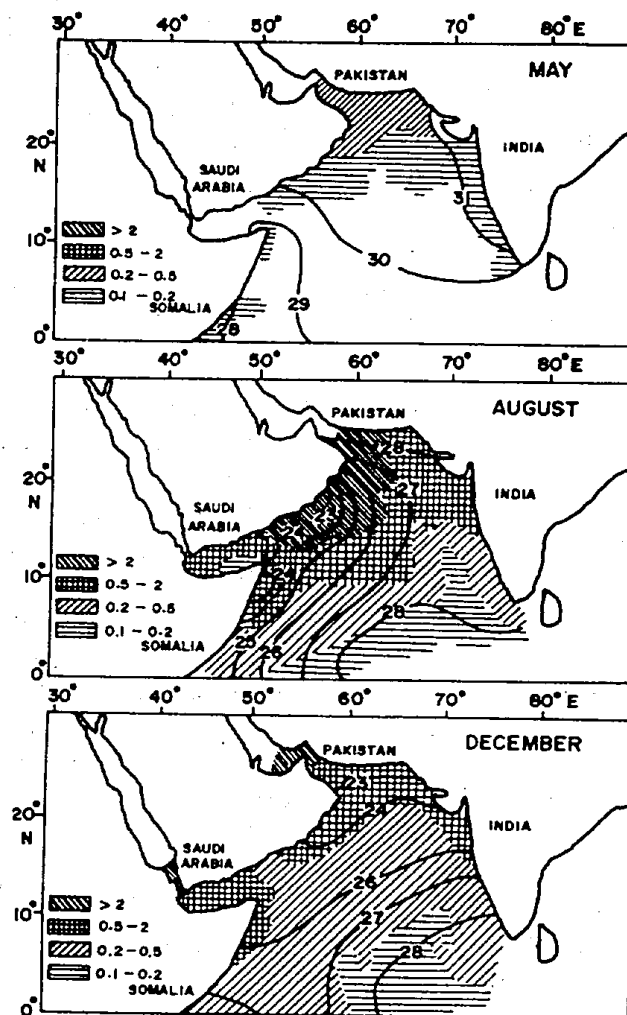


Fig. 2: Chlorophyll (mg m^{-3}) distribution in the Arabian Sea in May, August and December 1979, from satellite images. Line contours are surface temperature in $^{\circ}\text{C}$ (Redrawn from Yentsch and Phinney, 1992).

surface chlorophyll values almost all over the Arabian Sea when upwelling attains a peak (July-August) compared to other months. During winter (December), sea surface temperature is low and biomass is fairly high in northern areas.

Blooms of phytoplankton species are common along the west coast of India (overview by Nair et al., 1991). Diatoms such as *Fragillaria*, *Coscinodiscus*, *Cheatoceros*, *Pleurosigma* and *Skeletonema* occur in bloom conditions during southwest monsoon period. Heterotrophs like *Nocticula* bloom regularly both during and immediately after the monsoon, following diatom blooms. On the other hand, regular and spectacular blooms of the blue-green alga *Trichodesmium* occur all over the eastern Arabian Sea (in offshore waters also) around February-May. Warming of surface waters, calm conditions (well stratified waters during this period in the eastern Arabian Sea, Banse, 1987) and increase of salinity are identified as preconditions for the onset of *Trichodesmium* blooms (Devassy et al., 1978).

2.3. Western Bay of Bengal

The Bay of Bengal is usually considered less productive compared to the Arabian Sea. Although many major world river systems bring in large quantities of nutrients, the narrow shelf, heavy cloud cover and less light penetration have been attributed as reasons for this (Qasim, 1977; Radhakrishna, 1978).

Nonetheless, during southwest monsoon period (August-September), Bhattathiri et al. (1980) report average surface primary production rates during 1976-78 to be 51 to 113 mg C m⁻³ day⁻¹ and surface chlorophyll *a* values of 0.34 to 1 mg m⁻³. Values sometimes exceed 200 mg C m⁻³ day⁻¹ and 5 mg m⁻³ in some areas. They concluded that the productivity in western Bay of Bengal is quite comparable to that in the Arabian Sea during southwest monsoon period.

It was believed that only mild, localized upwelling occurs along southern parts of east coast of India during southwest monsoon (Murthy and Varadachari, 1968). Results from a recent hydrographic survey of the western Bay during July-August 1989 (Shetye et al., 1991a) give a better explanation to the situation. It was found that almost all along the coast, in an approximately 40 km wide band isopycnals from depths up to about 70 m surfaced due to wind-forced upwelling. However, in northern areas, very high freshwater influx from the Ganges and Brahmaputra overwhelms signatures of upwelling.

Surface production and biomass values along coastal waters of east coast of India during northeast monsoon also appear to be fairly high (Krey and Babenerd, 1976). It should be so, at least during early northeast monsoon, because heavy rains along the east coast during this period (October-November) bring in large quantities of nutrients into coastal waters.

2.4. Open waters

Compared to coastal waters, vast desert areas of low productivity are seen in the open ocean on both sides of the equator (Krey, 1973; Krey and Babenerd, 1976). During southwest monsoon, surface primary production ranges from < 1 to 2 mg C m⁻³ day⁻¹ and surface chlorophyll *a* values are < 0.05 to 0.1 mg m⁻³ in open waters of the Arabian Sea approximately between meridians 65° - 73°E. This region of low productivity further expands during northeast monsoon and only a few areas close to land mass and

some parts of the northern Arabian Sea show higher values (see also Kabanova, 1968). Bhattathiri and Devassy (1979) report low production from the Laccadive Sea during this period. Studies from the Laccadive waters by Wafar et al. (1986) show chlorophyll *a* concentrations of $< 0.1 \text{ mg m}^{-3}$ and carbon fixation rates of < 1 to $5 \text{ mg C m}^{-3} \text{ day}^{-1}$. The situation is similar in the Bay of Bengal. Average surface primary production of the Andaman Sea during February is $12.4 \text{ mg C m}^{-3} \text{ day}^{-1}$ and chlorophyll *a* values are usually less than 0.1 mg m^{-3} (Bhattathiri and Devassy, 1981). Information on primary production from open waters of the Bay of Bengal is generally poor.

In the equatorial waters, however, enhanced production may occur as a result of upwelling as described by Vinogradov (1981). Upwelling results from the piercing of the general westward flow induced by the trade winds by the equatorial undercurrent (Tareev, in the Indian Ocean). Upward vertical transport is intense at the boundaries of opposing zonal flows. As a result of Coriolis force, this deeper water drifts both north and south in the Ekman layer. Downwelling along the margin of the current takes place around 1°N and 1°S . In the narrow band of upwelling along the equator alternating with narrow zones of downwelling, distribution of biomass has a banded pattern in the Indian Ocean (Vinogradov and Voronina, 1962). In August-September, Sorokin et al. (1985) obtained higher primary production rates (0.4 to $1.4 \text{ g C m}^{-2} \text{ day}^{-1}$) near equatorial waters as a result of divergence and these decreased (0.1 to $0.2 \text{ g C m}^{-2} \text{ day}^{-1}$) in areas of convergence. Equatorial upwelling in the Indian Ocean, however, is weaker compared to the Atlantic and Pacific oceans (Swallow, 1984).

3. Zooplankton Standing Stock and Distribution

Trends in distribution of zooplankton biomass closely match phytoplankton biomass and production (Fig. 3). In the following account, for the sake of comparison,

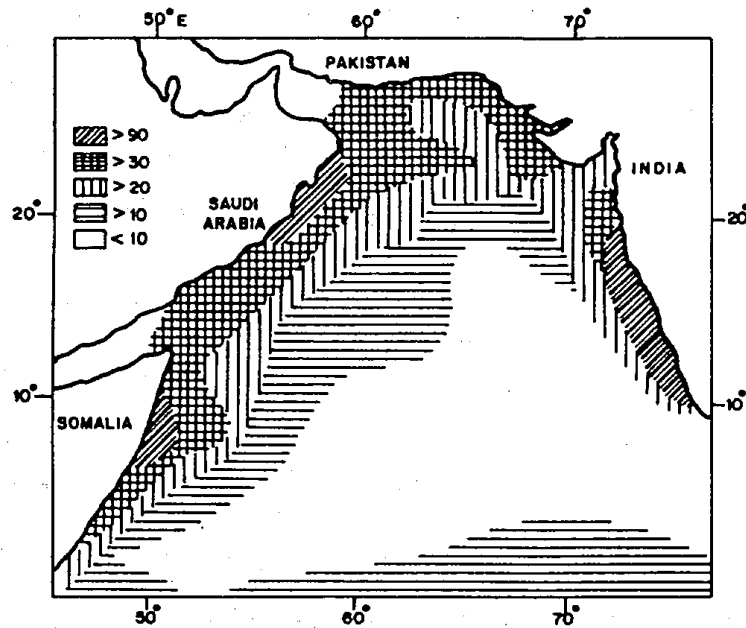


Fig. 3: Distribution of zooplankton standing stock ($\text{mg dry weight m}^{-3}$) in the Arabian Sea during the southwest monsoon (generalised from sources mentioned in the text).

whenever biomass values were available only as displacement volumes per vertical haul, they were converted to values per cubic meter using depth of haul (usually 200 m) and mouth areas of nets used. Wet volumes were converted to dry weight using a factor $1 \text{ ml m}^{-3} = 89.4 \pm 44 \text{ mg dry weight m}^{-3}$ using data from Madhupratap et al. (1992).

Results averaged from the IIOE (Panikkar, 1968) show fairly high standing stocks from near Somali coast ($23 \text{ mg dry weight m}^{-3}$) and upto about 55°E (11 mg) during southwest monsoon. Further north, values are 27 mg near Arabian coast and around 11 mg upto 65°E , paralleling patterns in primary production. During northeast monsoon also, areas in northern Arabian Sea sustain around 23 mg near the coast and 11 mg upto about 52°E . Similar values (23 mg) are seen off Cochin (10°N , 76°E) and upto 73°E (11 mg) during southwest monsoon.

While these averages give a general picture, they appear to be modest with regard to standing stocks in coastal waters. For example, consistently higher values and upto $95 \text{ mg dry weight m}^{-3}$ from Somali and Arabian coasts are reported during July-August (Indian Ocean Biological Centre, 1969). Haq et al. (1973) state that the coastal waters off Pakistan sustain high biomass (upto 187 mg) during November-December. Paulinose and Aravindakshan (1977) also report high standing stock (upto 252 mg) in the northern Indian Ocean during northeast monsoon. It is possible that a more systematic coverage may show still higher zooplankton standing stocks in coastal waters of western and northern Arabian Sea during upwelling season (cf. eastern Arabian Sea, see below).

Along the central west coast of India, biomass ranged from 108 to 315 mg and records upto 1080 mg have been made from inshore upper mixed layer during upwelling season (Madhupratap et al., 1990). However, all along the coastal eastern Arabian Sea, standing stocks were high (45 to 630 mg) during early southwest and early northeast monsoon in 1987 even when upwelling was not operative (Madhupratap et al., 1992). Enrichment of coastal waters through river run-off during southwest monsoon appears to be one of the reasons leading to this situation. The Indus, Narmada and Tapti are the major river systems emptying into the northern and northeastern Arabian Sea. But along the central and southwest coasts of India, a dense network of smaller rivers originating from the western ghats brings in freshwater into the region.

Availability of abundant microzooplankton as a direct food source for mesozooplankton in coastal waters, also related to river run-off, appears to be another factor influencing the situation (Madhupratap et al., 1992). A model by Parsons and Kessler (1986) shows that the initial presence of microzooplankton in freshwater plumes might increase secondary production by several orders of magnitude. Further, the northward surface flow along the west coast of India, carrying low salinity waters from the Bay of Bengal during northeast monsoon (Shetye et al., 1991b), is also probably nutrient-rich during early northeast monsoon (October-November). This is because the low salinity is mainly caused by heavy rains and river run-off along the east coast of India where many major rivers empty into the Bay of Bengal. Thus, apart from upwelling, river run-off appears to be a major mechanism influencing productivity in coastal waters around peninsular India. During southwest and early northeast monsoon seasons, although the very high biomass is generally confined to the shelf, the effects percolate offshore, showing values around 10 mg upto $300 - 600 \text{ km}$ away from the coast. During the later part of the northeast monsoon, standing stocks decline in this area (Johannessen et al., 1987).

Once again, there is no good coverage from the Bay of Bengal. Despite fairly high production along its western boundary during southwest monsoon, zooplankton standing stocks appear to be of modest ranges. IIOE data have averages ranging from 10 to 18 mg from the northern Bay. Other data available show 31 to 54 mg during August-September between 10° - 13°N (Achuthankutty et al., 1980) and 18 to 31 mg in June between 13° - 17°N (Nair et al., 1981). Both these reports show much poorer values for the rest of the coastal areas (see also Nair et al., 1977).

In the open waters, zooplankton standing stocks are poor, similar to those of phytoplankton. IIOE data show vast central areas both in the Arabian Sea and Bay of Bengal having poor biomass (< 5 mg) for both seasons. Goswami (1979) reports values ranging from 2 to 16 mg (average 6.5 mg) for the Laccadive Sea. They are 2 to 13 mg (average 5 mg) for the Andaman Sea (Madhupratap et al., 1981), both observations being during later part of northeast monsoon period.

Composition, distribution and zoogeography of epipelagic zooplankton from the IIOE and subsequent studies are summarized in Rao (1979), Nair and Madhupratap (1984), Madhupratap and Haridas (1986) and Rao and Madhupratap (1986). It would appear that species diversity among most groups of zooplankton is higher in the northern Indian Ocean compared to southern subtropical areas. The hydrodynamical front at about 10°S (Wyrki, 1973) appears to limit distributions of some species and there are a few other endemic to the northern Indian Ocean. But a majority of species, many of which enjoy circumglobal distributions, appear to have ranges upto the subtropical convergence.

The northern Indian Ocean, on the whole, appears to be a single geographic area. No major differences in zooplankton faunal elements between the Arabian Sea and Bay of Bengal have surfaced yet, despite differences occurring in hydrographic features. There are, of course, differences in neritic-oceanic ranges of species and there is an increase in species diversity from coastal to open ocean and deeper waters (Madhupratap, 1987; Madhupratap and Haridas, 1990). There appear to be some differences with regard to abundances of phytoplankton species between the Arabian Sea and Bay of Bengal. While a few species dominate blooms along the west coast of India, many species share the composition along the east coast. A similar trend is seen in the species composition of fishes of the two areas (Subrahmanyam et al., 1975).

Available information on vertical distributions of zooplankton is in conformity with patterns found in other oceans. Biomass in the upper 1000 m in the Laccadive Sea was 2.1 g dry weight m⁻² of which 97.7 % was concentrated in the upper 400 m (Madhupratap and Haridas, 1990). Night-time increase of biomass and zooplankton species occurs in the upper 200 m layer as a result of upward migrations, including those of carnivores, from deeper waters. A large number of epipelagic species, however, do not migrate even to mesopelagic depths probably because they can not survive in the poorly oxygenated waters of the oxygen minimum layers. Very little is known on those aspects and the general deep-sea biology of the Indian Ocean.

4. Microplankton

It is becoming increasingly clear that bacteria are not just remineralisers of degrading organic matter but may also be competitors to phytoplankton for nutrients.

The microbial loop (Azam et al., 1983) envisages that water column bacteria utilize dissolved organic matter, mainly of phytoplankton origin, for growth and that their densities are controlled by predation by heterotrophic flagellates. Flagellates, in turn, are preyed upon by microzooplankton. Thus bacterioplankton may also be linked to the metazoan food chain. Ducklow et al. (1986), on the other hand, contend that bacterioplankton are a sink for carbon and serve principally as agents for nutrient regeneration rather than food. The scenario becomes more complicated when we consider evidences of microzooplankton directly ingesting bacteria (e.g. Sherr and Sherr, 1987) thereby short-circuiting the microbial loop and the so called herbivorous zooplankters preferentially feeding upon microzooplankton (e.g. Wiadnyana and Rassoulzadegan, 1989). Further possibilities in the food chain are grazing by microzooplankton on phytoplankton, a process which may even regulate phytoplankton species composition (e.g. Capriulo and Carpenter, 1983; Paranjpe, 1990), or filter/mucus feeding mesozooplankton directly ingesting bacteria (Sorokin, 1981).

These aspects, from the Indian Ocean, are yet to be elucidated. However, certain geochemical activities and biochemical functions of bacterioplankton are recognized. For example, Loka Bharati and Chandramohan (1990) show that sulphate-reducing bacteria (SRB) occur not only in bottom sediments, but also in *aerobic* surface waters. SRB of near-shore sediments are capable of using formate, propionate and benzoate as a source of carbon. SRB are often associated with Thiobacilli-like colourless sulphur oxidizing bacteria. The latter not only oxidize thiosulphate to sulphate but could also reduce nitrate. These chemolithotrophic organisms generate energy through inorganic oxidation and synthesize cell material exclusively from carbondioxide (Loka Bharati, 1989). They appear to achieve higher chemolithotrophic yields in oligotrophic offshore waters. Negligible quantity of nitrate usually encountered in surface waters is probably due to the presence of high numbers of thiosulphate-oxidizing, denitrifying bacteria (Loka Bharati et al., 1988) apart from phytoplankton uptake. Similarly, the high amount of nitrite, especially in intermediate layers of the Arabian Sea (*vide infra*) could be related to these types of bacteria, among other forms. Ferromanganese nodules from the central Indian Ocean basin have been found to harbour a variety of heterotrophic bacteria capable of mobilizing and immobilizing elemental manganese (Chandramohan et al., 1987). Apart from these, other forms like ammonia oxidizers, gelatin liquifiers, hydrogen sulphide producers, fat hydrolyzers etc. and microbial activities such as proteolytic, lipolytic, amylolytic, ureolytic and hydrolytic have been reported from the Arabian Sea (Nair, 1979; Nair and Loka Bharati, 1979).

Free living bioluminescent bacteria are common in coastal areas but their abundances are considerably reduced in oligotrophic waters. Below a depth of 200 m, luminescent bacteria are generally symbionts (Ramaiah and Chandramohan, 1987, 1988). Large numbers of these, exhibiting chitinoclastic activity, are found attached on zooplankton. Marine fungi are also remineralisers and have an active role in the detrital food chain. Thraustochytrids, the single celled zoosporic fungi, are common in the Arabian Sea and are particularly more abundant during southwest monsoon and in upwelled waters (> 1100 cells l^{-1} , Raghukumar et al., 1990). These fungi show high protease activity suggesting their involvement in the break-down of matter of animal origin (S. Raghukumar, unpublished data). Phycomycetous fungi parasitic on filamentous algae are often important regulators of densities of algal populations (Raghukumar, 1986).

In the northwestern Indian Ocean, Chepurnova (1984) observed minimal bacterial biomass ($< 50 \text{ mg m}^{-3}$, biomass estimates based on cell volumes and counts) in upwelled waters rich in phytoplankton. Concentrations increased ($> 80 \text{ mg m}^{-3}$) in offshore areas and deeper (50 - 100 m) waters as a result of transport of surface waters (author does not explain the mechanism) rich in organic matter and their sinking in zones of convergence. Similarly, in the upwelled waters off west coast of India, bacterial counts were low ($2.2 \times 10^5 \text{ ml}^{-1}$, S. Nair, pers. comm.). Higher concentrations (10^9 l^{-1}) of cyanobacteria occur in the oligotrophic gyral waters compared to eutrophic upwelling regions (10^7 l^{-1}) in the northwest Indian Ocean (Burkill et al., 1991). Similarly, retrievable number of bacteria (heterotrophic, nitrate reducing and sulphate reducing) in nearshore waters are sometimes lower by an order of magnitude as compared to offshore regions (Loka Bharati et al., 1992). Sorokin et al. (1985) report average bacterial counts of $15 \times 10^4 \text{ ml}^{-1}$ and biomass of 40 to 100 mg m^{-3} from the equatorial divergence. Maxima of phytoplankton, bacterioplankton and protozoans usually occur in the upper thermocline boundary where mesozooplankton utilize microplankton stock. On the whole, it would appear that higher bacterial concentrations are associated with oligotrophic rather than enriched waters. This could arise as a result of high abundances of microzooplankton in enriched waters and their controlling bacterial populations as mentioned earlier.

5. Coral Reefs

Coral reefs are specialized ecosystems with rich and highly diverse communities. They form a kind of oasis in the middle of oligotrophic waters. The Maldivo-Laccadive Archipelago is speckled with a number of atolls luxuriant in coral fauna, In the Andaman Sea fringing reefs occur. Some information is available on the reef biology from the Laccadive atolls.

In contrast to the open ocean waters which surround them, reef ecosystems are highly productive. The main reason for this is the efficient retention and recycling of available energy within the reef community. A variety of food-chains from autotrophy to symbiosis and diverse forms of heterotrophy are characteristic of reef functions (see Lewis, 1981). Corals themselves exhibit several modes of feeding. They are autotrophs by virtue of having zooxanthellae, carnivores feeding on zooplankton, filter feeders of microplankton, suspension feeders of organic particles and can even be saprophytes capable of removing dissolved organic matter from ambient waters.

Primary productivity in the Laccadive atolls typically ranges from $5 \text{ to } 10 \text{ g C m}^{-2} \text{ day}^{-1}$ (Nair and Pillai, 1972; Qasim et al., 1972). which is comparable to reef production anywhere in the world. Contribution of phytoplankton to this is as little as a few tens $\text{mg C m}^{-2} \text{ day}^{-1}$, this mainly through nanoplankton (Wafar, 1977). The main sources of the high production are benthic macroalgae and extensive sea-grass beds, the latter having production rates as high as $12 \text{ g C m}^{-2} \text{ day}^{-1}$ (Qasim and Bhattathiri, 1971). Other contributors are zooxanthellae, calcareous algae, boring filamentous algae and benthic microalgae.

Among the several symbiotic relationships that occur in reef systems, the commonest one is that between coral polyps and zooxanthellae. Studies on nitrogen balance of atoll waters (Wafar et al., 1985) show that zooxanthellae can derive all their nitrogen requirements from coral excretion alone and that the translocation of

photosynthate from the algae to corals can satisfy 40 to 100 % of the basal energy requirements of the latter.

Reef waters have a high load of dissolved and particulate organic matter mainly arising from continuous mucus production by corals. Production of POC in these waters is as high as $95 \text{ mg C m}^{-2} \text{ h}^{-1}$ (Qasim and Sankaranarayanan, 1970). Consistent with this is the high microbial activity in reef waters. Coral lagoons harbour the highest number of thraustochytrids ($10,700 \text{ l}^{-1}$) recorded from the Arabian Sea and contribute to about 3 % of microbial ATP in lagoon waters (Raghukumar, 1987; Raghukumar et al., 1987). Population of urea-hydrolysing bacteria is among the highest recorded from several ecosystems, with urea decomposition rates exceeding $14 \text{ ng-at l}^{-1} \text{ h}^{-1}$ (Wafar et al., 1985). Such high rates are significant in the nutrient cycle since urea which is a less preferred N nutrient by autotrophs is converted to the more preferred ammonium. The processes are not only rapid but highly coupled too. For example, ammonium excreted by corals is competitively removed by autotrophs and nitrifiers and is returned to corals via photosynthate translocation or as nitrate for assimilation by zooxanthellae, without the N being lost from coral-algal symbiosis (Wafar et al., 1990).

Zooplankton of the lagoons were thought to be mainly of oceanic origin and to form a source of coral nutrition as the water passes over the reef (e.g. Tranter and George, 1972). Recent studies (Madhupratap et al., 1991a, b) show that lagoons have a highly diverse and rich resident population of pelagic zooplankton. Besides, there are large numbers of epibenthic forms (ca. $50,000$ to $100,000 \text{ m}^{-2}$, highest densities yet recorded from anywhere in the world) and about 80 % of these migrate into the water column each night. Such high abundances have implications not only in nutrition of corals and other planktivores in the lagoons, but also assume significance in nutrient regeneration in the lagoon ecosystem.

6: Overview

This brief review shows that we have a fairly good picture of some of the basic aspects of biology and the processes which regulate them in the Arabian Sea. Data from the Bay of Bengal are sparser. On the whole, the overall production in the northern Indian Ocean, especially the Arabian Sea, is quite high. Coastal upwelling during summer monsoon is a major physical process forcing the nutrients into the euphotic water column. Lateral advection and/or Ekman transport may enhance production in offshore areas of the northwestern Arabian Sea. Winter cooling and consequent convective overturning of surface waters in the northern Arabian Sea, wind induced entrainment of subsurface waters and equatorial divergence are other mechanisms of enrichment. Along the waters off the southern Asian sub-continent, river run-off during both monsoons also brings nutrients into coastal waters. However, it must be remembered that during the last glacial maximum (ca. 18,000 yr BP), southwest monsoon was weaker than today whereas northeast monsoon was stronger (Duplessy, 1982). Hence, the paleo-productivity patterns would have been different from what we experience now as evident from sedimentary records.

Relationships between enrichment, primary production and zooplankton may appear linear, but these are not necessarily always coupled. As mentioned earlier, zooplankton abundances along the west coast of India were found to be very high during early southwest and northeast monsoons, when no coastal upwelling was taking

place (Madhupratap et al., 1992). During the same period, nutrient concentrations and phytoplankton biomass were extremely low. Abundance of microplankton in the freshwater plume and a short-circuit in the microbial loop (bacteria - microzooplankton - mesozooplankton) appeared to have led to the situation.

Taking the carbon equivalent of chlorophyll *a* as 50 (Tranter, 1973) and that of zooplankton as 35 % dry weight (Madhupratap et al., 1981), there is an almost 1:1 ratio between phytoplankton biomass and zooplankton standing stock in the Arabian Sea (Fig. 1 & 3). However crude this calculation might be, it points towards unconventional food chains in the Arabian Sea. Dortch and Packard (1989) show that in oligotrophic waters, inverted biomass pyramid (biomass of heterotrophs such as bacteria and zooplankton exceeding plant biomass) is typical and that this could sometimes happen even in upwelling systems. In oligotrophic waters primary production is typically controlled by the availability of regenerated inorganic nitrogen (mainly ammonium, through zooplankton excretion) whereas in coastal areas new production (nitrate based) may account for bulk of the production. However, in upwelling waters also, phytoplankton may preferentially utilize nitrogen excretory products of zooplankton (ammonium and urea) even when nitrate concentrations are high (Probyn, 1988). Sukshina et al. (1984) calculate the ratio of primary production to heterotrophic destruction in epipelagic layers of world oceans to be 2.8 even after making allowance for probable overestimates of bacterial production.

The postulated time lag and spatial dislocation between nutrient enrichment, development of phytoplankton and succession of herbivores and carnivores is not always apparent. In areas of mild upwelling or divergence, swift responses from all these categories of biota have been observed (Madhupratap and Haridas, 1986) Further, during upwelling, confinement of the high biomass, less diverse zooplankton community (consisting of both herbivores and carnivores) to a narrow shelf area, probably through a two layered circulation across the shelf, has been observed along the central west coast of India (Madhupratap et al., 1990). Food chains in the Indian Ocean have received very little attention.

The effect of the enormous production, in turn, modify the physics and biogeochemical dynamics of the ocean. Photosynthetic pigments in autotrophic microplankton are major absorbers of irradiance and alter sea surface temperature depending on their abundances (Satyendranath et al., 1991). In the Arabian Sea, upwelling during southwest monsoon reduces sea surface temperature but enhances pigment concentrations and thereby biological heating. Thus the phytoplankton reduce the rate of cooling during this period, but enhance the rate of heating during the heating period. Effects of surface heating might further translate into affecting other physical processes, ocean heat budget or ocean atmosphere heat exchange (see Satyendranath et al., 1991, for details).

The thickness (ca. 100 to 800 m) of the oxygen minimum layer ($O_2 < 5 \mu\text{mol dm}^{-3}$) in the Arabian Sea increases from south to north accompanied by steady northward decrease in oxygen concentration (Naqvi, 1987). The high rate of productivity leads to elevated oxygen demand in subsurface waters. The northward decrease of oxygen is well correlated with highly productive overlying waters and is a combined effect of the high oxidation rates and oxygen depletion in water available for renewal (Swallow, 1984). However, this low is also seen in the central parts of the Arabian Sea where production is low suggesting that organic matter is carried to this

region from adjacent productive areas. A physical mechanism through which this might happen during the southwest monsoon is the Monsoon Current which transports waters from west to east in the Arabian Sea (Wyrki, 1973).

Rates of particle flux (Fig. 4) obtained through sediment traps in the Arabian Sea (Nair et al., 1990) show patterns agreeing with production rates described earlier. Highest fluxes are in the western Arabian Sea, with seasonal peaks corresponding to production 'highs'. A time lag observed in peaks between western and eastern Arabian Sea (ca. 15°N) during southwest monsoon is because of a delay in upwelling and associated increase in biological production at this latitude in the eastern Arabian Sea (*vide supra*). The lowest fluxes obtained from the eastern Arabian Sea from January through May are also explained by the generally poor productivity in this area during that period. Relatively high fluxes observed in the central Arabian Sea should be

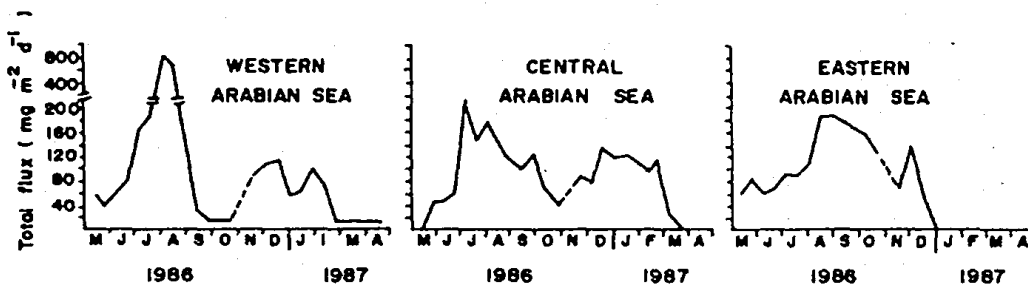


Fig. 4: Seasonal variations in particle fluxes to the deep Arabian Sea from time-series sediment trap deployments (Redrawn from Nair et al., 1989).

through a transport of particles from vicinages as mentioned earlier (see also Walsh et al., 1988). Although elevated pigment levels might occur for a couple of months in the area (Fig. 2; see also Banse, 1987), the overall productivity (both primary and secondary) is not high enough that far south in central regions (especially during winter) to generate fluxes comparable to western or eastern Arabian Sea.

The low oxygen content leading to near anoxic conditions also triggers (facultative) nitrate reducing and denitrifying bacteria to switch over to the use of nitrate as an alternate electron acceptor in energy generation. Studies by Naqvi et al. (1992) show that the Arabian Sea is one of the largest oceanic nitrate reducing sites accounting for ca. 1/3 of global water column denitrification. The secondary nitrite maximum lies within the core of the oxygen minimum at about 200 to 300 m depth. The anomalous feature is that unlike other world regions of intense denitrification (e.g. eastern tropical Pacific), Arabian Sea denitrification zones are not tied up with high production areas (Fig. 5). Rather, these vast areas underlie the central desert regions described earlier (Naqvi, 1991).

Naqvi et al. (1992) believe that this anomaly might arise through the introduction of additional bio-degradable organic matter such as dissolved organic carbon (DOC). Naqvi and Shailaja (pers. comm.) found the activity of respiratory electron transport system (ETS) within the oxygen minimum layer to be (i) among the highest in the world oceans at comparable depths (2) showing no decrease with distance from the shore (in other words, ETS was not necessarily correlated to the productivity of overlying waters). Within the euphotic zone, however, microplankton ETS activity

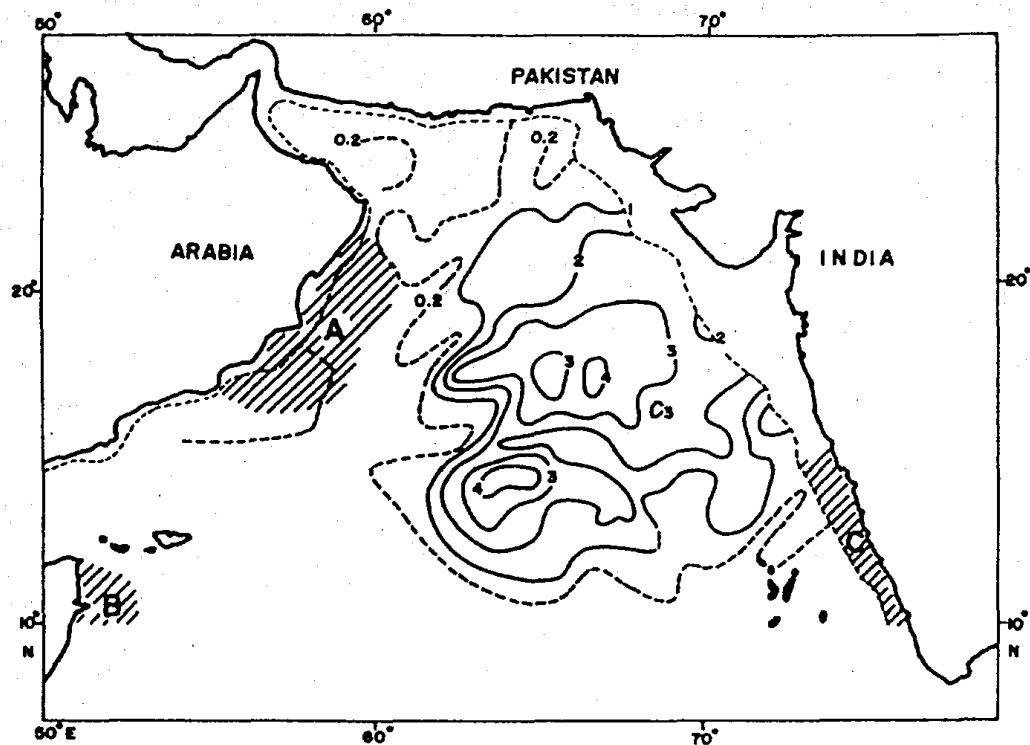


Fig. 5: Distribution of nitrite (μM) at the secondary maximum averaged for each 1-degree square in the Arabian Sea. The hatched areas represent zones of upwelling off (A) Arabia, (B) Somalia and (C) south west India (Redrawn from Naqvi, 1991).

appears to be correlated with primary productivity (U.D. Muraleedharan, unpublished data). This, the low oxygen content and the fairly high flux rates show that there is substantial amount of organic matter available in the subsurface waters of the central Arabian Sea despite low production.

A recent study by Kumar et al. (1990) shows DOC values in the Arabian Sea to be 3 - 4 times higher than previously recorded. DOC is more or less equally distributed in the water column of the northern and central Arabian Sea but values increase towards south. Kumar et al. (1990) provide evidence for differential utilisation of oxygen and nitrate for DOC oxidative decomposition. While nitrate is utilised in DOC oxidation in the northern Arabian Sea (minimum DOC was associated with active denitrification depths indicating active uptake), it is produced through nitrification in southern areas as a result of DOC accumulation.

The above discussion might plausibly show that organic matter is available in the subsurface/deeper waters of the central as well as other areas of the Arabian Sea. But it does not explain the original dilemma of Naqvi et al. (1992) as to why denitrification does not happen in subsurface waters of productive areas. Naqvi (1991) suggests that reoxygenation of subsurface layers, through vertical mixing resulting from weak thermocline stratification, could inhibit denitrification beneath centers of upwelling. In addition, high ETS activities occurring away from the shelfbreak point to unusual dynamics of organic carbon in the Arabian Sea.

Alternate explanations/views on this anomaly are possible from a biological angle. One of them is the apparent decrease in bacteria population in upwelling areas as described earlier. Loka Bharati et al. (1988, 1991) show a decrease in the ratio of denitrifiers to nitrate reducers (autotrophic denitrification) in intermediate water depths as one of the factors that could influence nitrite maximum and that enhanced nitrate reducing activity (heterotrophic) at 200 m depth compared to surface waters may result from response of bacteria to increase in nitrate concentrations.

On the other hand, while high ETS activity might indicate intense nitrate reduction, the measure does not exclude other respiratory modes (e.g. aerobic under microaerophilic conditions). Further, nitrate reduction/denitrification need not exclusively depend on the availability of organic carbon because this could happen either through heterotrophic fermentation (organic carbon dependent) or chemosynthetic autotrophs (organic carbon independent). Low concentrations of nitrite in upwelling waters could also arise if further reducing processes are faster than nitrite accumulation. Or, there could be prevalence of a steady state if oxidation rates match reducing rates. Lloyd et al. (1987) show aerobic denitrification processes to be a rule rather than an exception. Hence re-oxygenation of subsurface waters of upwelling areas need not necessarily inhibit denitrification. Both arguments (chemist's and biologist's) may be tenable at the moment, on different grounds, but a more detailed exploration of microbial activities controlling nitrate reduction/denitrification in the Arabian Sea appears to be worthwhile.

Blooms of phytoplankton and swarms of zooplankton which are very common in neritic waters have implications in ocean biogeochemical cycles. Alldredge and Gotschalk (1989) show that during blooms, rapid aggregation and flocculation of chain-forming diatoms (such as *Chaetoceros*, *Nitzschia*, *Fragillaria*, *Skeletonema* etc. which are common bloom forming organisms in the northern Indian Ocean) are of common occurrence and form a major source for marine snow. Their settling velocities are two orders of magnitude faster than those of unaggregated forms and their export would result in significant flux of primary production to the ocean bottom. Somasundar et al. (1990) make a conservative estimate of nitrogen fixed by *Trichodesmium* blooms in the Arabian Sea as 4.79×10^{12} g N year⁻¹. Nitrogen fixed by these extensive blooms and its subsequent release into the environment on their decay will certainly have implications on the nitrogen flux in the Arabian Sea. In fact, within days after the decay of the trichomes, diatom blooms occur (V.P. Devassy, pers. comm.) thus enhancing productivity in an otherwise low production period. Further studies to quantify the import of nitrogen by this mode into the pelagos are essential. *Trichodesmium* produces hydrogen also and this activity may be significant in the hydrogen balance of the mixed layer (Scranton, 1983).

Many zooplankton species which forage in the food-rich surface layers and later migrate to deeper waters form a direct source of flux of organic matter into the ocean interiors. They enhance flux rates into deeper waters through the release of fecal pellets (see also Longhurst and Harrison, 1988). Zooplankton fecal pellets are perhaps one of the most important sources of particle flux at all depths as evidenced from most sediment trap studies. Since more than 80 % of zooplankton standing stock is generally in the upper 200 m or so, closely coupled with phytoplankton and microzooplankton abundances, this is logically the layer from where maximum flux originates. Gliwicz (1986) demonstrates enhanced rates of clearance of suspended clay in water column

reservoirs through cladoceran feeding which would not have been possible through pure physical processes of particle sedimentation. Swarms of filter/mucus feeders such as cladocerans, ostracodes, tunicates, etc. and some carnivores frequent in the Arabian Sea (Fig. 6) and the Bay of Bengal (Madhupratap et al., 1980) should significantly influence

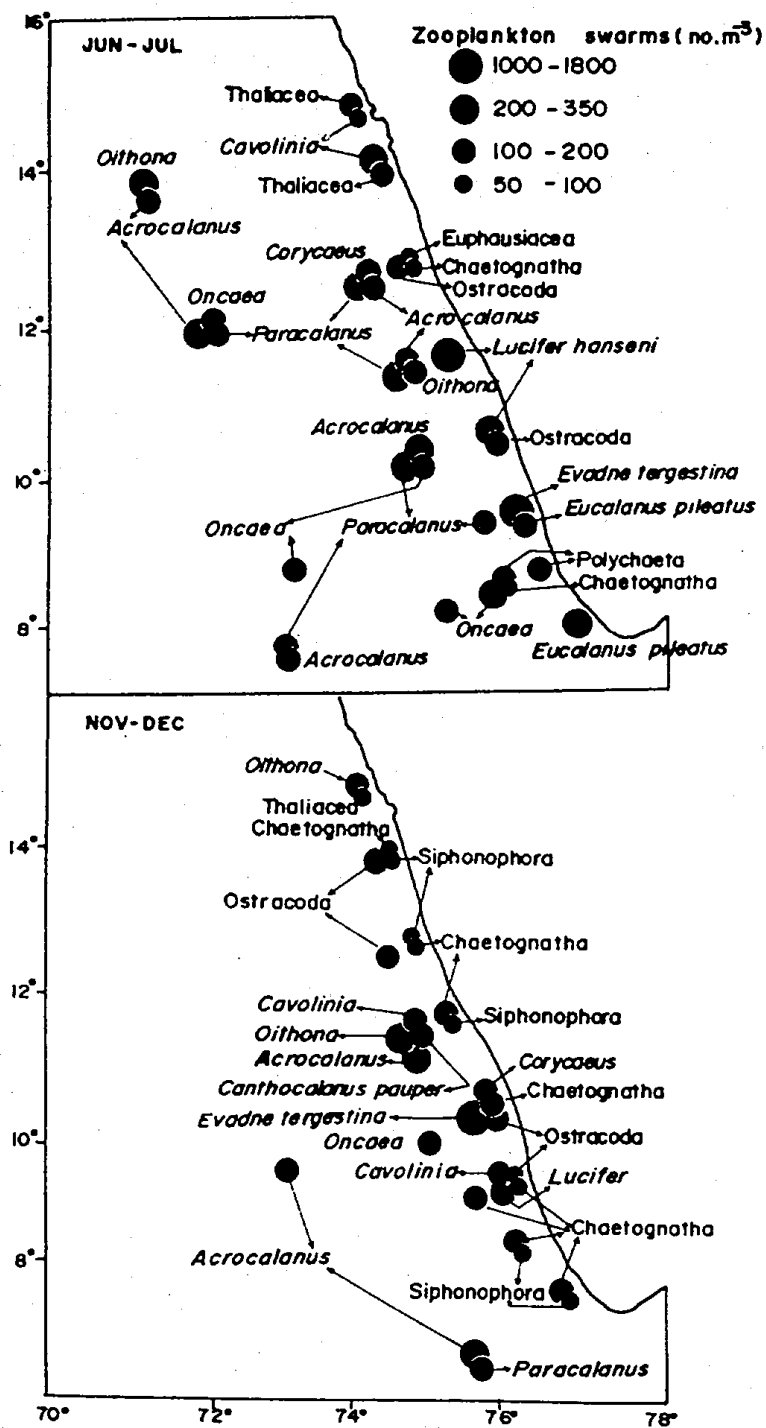


Fig. 6: Zooplankton swarms in the eastern Arabian Sea during 1987 (Redrawn from Madhupratap et al., 1992).

particle production and turnover rates (see also Michaels and Silver, 1988). Discarded houses of appendicularians are another major source of marine snow (Alldredge, 1976). A recent article by Jumars et al. (1989) postulates that less than 10 % of DOC made available to the bacteria arise through phytoplankton exuviae. The major source is through byproducts of animal (zooplankton) ingestion and digestion and rapid diffusion from pellets.

7. Summary

Studies on biological features of the northern Indian Ocean are mainly limited to the Arabian Sea. However, a close coupling of physical processes and biological production is evident in coastal waters of both the Arabian Sea and the Bay of Bengal.

Processes through which nutrients might become available in euphotic waters of the open ocean are poorly understood. It is believed that regenerated nutrients may have an important role. There is a need to differentiate production through recycling and new production from both coastal and open waters.

Reef ecosystems of Laccadive atolls appear to be highly efficient. They sustain a diverse and rich flora and fauna by recycling resources available within the system.

High primary production rates and zooplankton standing stocks occur in the Arabian Sea for a good part of the year (May-June to November-December). Particle flux originating from the high coastal production appears to be transported to (subsurface waters of) central areas. Mechanisms through which this might happen are poorly known. Estimates of secondary production, rates of zooplankton grazing, nutrient regeneration and fecal pellet production are subjects which need attention.

High oxidation rates as a result of the flux of organic matter lead to acute deficiency of oxygen in subsurface waters. This triggers other microbial processes such as nitrate and sulphate reduction.

The role of microplankton is an area requiring thorough elucidation. Microzooplankton appear to be important in food-chains of coastal waters, especially in areas experiencing river run-off. Bacterioplankton seem to control a variety of processes apart from directly forming a part of the food chain. However, very little quantification of these aspects is available at the moment.

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