

The Arabian Sea: Physical environment, zooplankton and myctophid abundance

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The Arabian Sea is one of the most productive regions of the world oceans. This productivity mainly results from coastal and open ocean upwelling in summer and cooling effects during winter. Earlier and more recent studies showed that there are considerable spatial and temporal variations in the area in primary productivity. Nonetheless, contrary to earlier thinking, it would seem that the mesozooplankton abundance in the Arabian Sea is fairly high in the mixed layer all through the year. This paradox of the Arabian Sea could be partly resolved by explaining the microbial loop and a fresh set of data is presented here in support. This is because most of the herbivorous forms are either small filter feeders like copepods or larger mucous filter feeders like tunicates which are able to feed on very small particles. It would seem that the Arabian Sea sustains a large biomass of mesopelagic fishes (about 100 million tonnes), mainly myctophids. They mostly live in the core of oxygen minimum layer and ascend to the surface layers during night to feed on the abundant zooplankton.

The Arabian Sea is a unique geographic area known for its high seasonally oscillating biological primary productivity resulting from monsoon-driven circulation^{1,2}. Upwelling along its western boundary^{3,4} and to a lesser extent along the west coast of India⁵ during summer (southwest) monsoon are the main causative factors for this. Recent studies, however show that Arabian Sea's northern regions experience high biological productivity in winter which results from convective overturning associated with winter cooling^{6,7}, and its open areas also are known to be productive during summer monsoon due to open ocean upwelling^{8,9}. Thus our recent understandings are somewhat contrary to the earlier belief that the coastal regions of the Arabian Sea alone are productive and that too only during summer.

A reasonable extent of information on the primary production and secondary standing stock from this region¹⁰⁻¹⁷ is available. However, only few of the earlier reports¹⁵⁻¹⁷ have addressed the seasonal cycles of zooplankton abundance and variability. In recent years, because of the renewed interest in the region, as a part of the Joint Global Ocean Flux Study (JGOFS) programme, several cruises were undertaken in the Arabian Sea on primary production,

zooplankton abundance and also to include measurements on microzooplankton and bacteria and their spatial and temporal variations¹⁸⁻²¹. JGOFS is an international programme and several countries participated in the Arabian Sea cruises between 1993-97. Arabian Sea was chosen as one of the special area because it forms an ideal natural laboratory to understand the time-varying fluxes of carbon (one of the aims of JGOFS) due to monsoonal effects. The aim of this paper is to put together some of the new information generated under this and relate the physical and chemical changes in the environment over seasons to the biological events. In fact these cruises form the first of its kind in recent times where many biological, physical and chemical parameters were simultaneously measured.

Materials and Methods

The area of investigation under the Indian programme was centred around central Arabian Sea along an open ocean track (64°E) and eastern areas (Fig. 1). Five cruises were undertaken onboard *ORV Sagar Kanya* during April-May 1994 (spring inter-monsoon), February-March 1995 and 1997 (winter monsoon) and July-August 1995 and 1996 (summer monsoon). These months were carefully chosen because they represent the peak oceanographic

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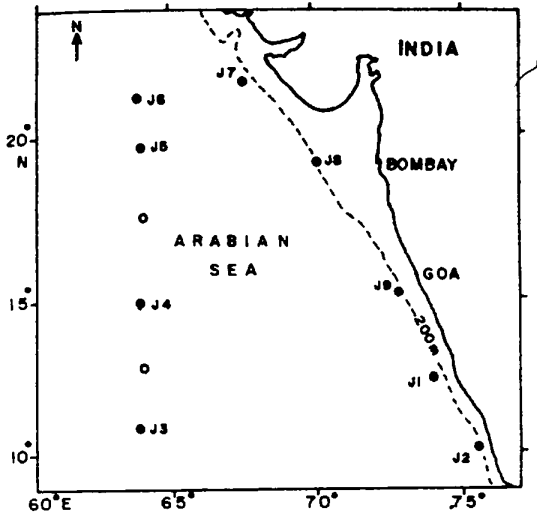


Fig. 1—Location of sampling stations for biological parameters. Unnumbered open circles denote those stations where biological data were collected in some cruises.

conditions representing the season. All cruises followed more or less the same track, except in winter 1997 when a time-series observation was made for two weeks at 21°N, 64°E to study in detail the effects of winter cooling, a phenomenon that is being newly understood from the Arabian Sea. Summer monsoon values for the open ocean are mostly for 1996 since hazardous conditions prevented data collection at many stations in 1995.

Conductivity, temperature and salinity (CTD) measurements were conducted at every degree interval along the cruise track up to 500 m. Water samples from the CTD cast were also analysed for nutrients.

Sampling of mesozooplankton was carried out during day and night at the main stations designated J1 to J9. Additional samples were also collected at 13°N and 17°E along 64°E for all biological parameters in some cruises. Samples were collected using a Multiple Plankton Closing Net (MPN-Hydro Bios, mouth area 0.25 m², mesh size 200 µm). Five depths were sampled at open ocean stations: 1000-500 m, 500-300 m, 300-base of thermocline (BT), BT to top of the thermocline (TT) and TT to surface (mixed layer). At coastal stations the two shallow depths were always sampled, deeper sampling was done wherever depths permitted. Zooplankton samples were preserved in 4% buffered seawater-

formalin and biomass was estimated as displacement volume after removing excess water on absorbent paper. A Wilcoxon rank test was employed to assess variations in biomass distributions (day vs night and coastal vs open waters). In this paper, composition of zooplankton from the upper layers (mostly from mixed layer) which constituted the bulk of the biomass is presented. Below the mixed layer, biomass and mesozooplankton abundances were reduced, more so as the depth increased¹⁹. However, regardless of depths, the adults and larvae of myctophids, though caught in low numbers by the MPN, received special attention.

Production and abundance (chlorophyll *a*) of phytoplankton, microzooplankton and bacteria were estimated during all seasons from water samples collected using 30-l-Go Flo bottles operated along with CTD frame. The depths sampled for phytoplankton and bacterial flora were 0, 10 and thereafter at 20 m interval up to 120 m depth. Primary productivity was measured following ¹⁴C clean *in situ* methods by deploying a drifting buoy. Three light bottles and one dark bottle were deployed at the depths where other biological measurements were made (dawn to dusk, local time). Chlorophyll *a* was determined with a fluorometer and phytoplankton cells (>5 µm) were enumerated with an inverted microscope. Samples for microzooplankton were collected from surface to a depth of 200 m at 50 m interval and 20 liters of water was filtered through 20 µm mesh after initially passing through 200 µm. Bacteria were counted with an epifluorescence microscope.

A conversion factor of 0.075 g dry weight per ml displacement volume²² was used to estimate the dry weight of mesozooplankton and 34.2% of it was considered as carbon equivalent²³. For carbon estimation in microzooplankton, a factor of 0.19 pgCµm⁻³ for ciliates²⁴ and 0.14 pgCµm⁻³ for dinoflagellates²⁵ were used. A conversion factor of 16 ngC/individual was used for metazoan microzooplankton²⁶. Cell abundance of bacteria were converted using a value²⁷ of 2 × 10⁻¹⁴ g C per cell.

Results

During the winter monsoon (February-March) the mixed layer depth was around 100 m to the north of 14°N (Fig. 2). In February 1997 it fluctuated between 85-120 m over the two weeks of observation at the northern station. During the inter-monsoon (April-

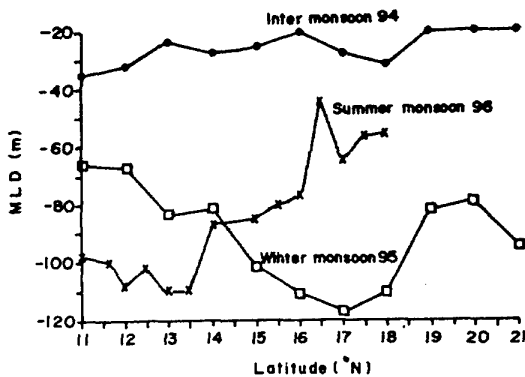


Fig. 2—Mixed layer depths during various seasons in the open ocean areas in the Arabian Sea along 64°E. (•) inter-monsoon 1994, (□) winter 1995 and (x) summer 1996.

May) it shoaled up and remained shallow (20-40 m) more or less throughout the Arabian Sea. During summer monsoon (July-August) it was relatively deeper (>100 m) in south and domed to around 40 m in north in both years.

These seasonal changes happen because during winter, cool air from the continents blowing into the northern Arabian Sea leads to low SST (ca. 24°C) and evaporation. This combined with reduced solar insolation and high ambient salinity cause densification of surface waters. These waters sink leading to a convective mixing and upward pumping of nutrients from the top of the thermocline⁷. Later during inter-monsoon (April-May), the SST increases to more than 29°C and results in stratification and shallow MLDs (around 30 m). During summer monsoon due to the downwelling effects south of the Findlater jet (a low level jet flowing across Somalia to India) mixed layer is deep to about 100 m, but north of it, positive windstress curl and thereby shoaling of the thermocline causes open ocean upwelling (ca. north of 15°N)^{8,9}.

The nutrient levels in the upper water column typically responded to the changes in physical conditions. During inter-monsoon period the entire upper Arabian Sea was oligotrophic with nitrate at undetectable levels (Fig. 3). On the other hand, during winter, as a result of cooling effects, nutrients became available in the northern regions followed by an increase in productivity (Fig. 4). In fact during 1997 winter, we observed chlorophyll *a* averaging 50 mg m⁻² with primary productivity rates of 845 to

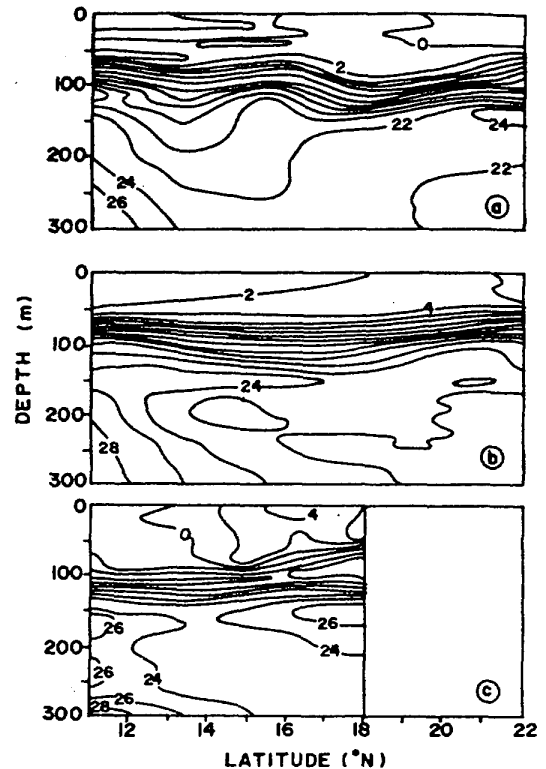


Fig. 3—Distribution of nitrate in the upper 300m during (a) inter-monsoon (1994), (b) winter (1995) and (c) summer monsoon (1995) season. The contour of zero (0) represents undetectable levels.

984 mg C m⁻² d⁻¹. The increase was because of an interannual variability whereby the SST became 1°C cooler in 1997 compared to 1995 and as a result, nitrate level in the upper water column was about 4 μM compared to 2 μM in 1995.

During summer, positive windstress curl north of the Jet and open ocean upwelling resulted^{8,9} in high production (Fig. 4). However, the southern latitudes of the open Arabian Sea was also fairly productive during this season probably as a result of nutrients advected from the coastal upwelling regions off Somalia¹⁶. Coastal waters along southwest coast of India also showed high productivity associated with coastal upwelling¹⁸ (up to 1760 mg C m⁻² d⁻¹). Phytoplankton cell counts were also highest during summer followed by winter and were dominated by diatoms²⁸.

Vertical distribution of chlorophyll *a* (Fig. 5) corresponded to the nutrient profiles. Lowest column values were obtained during the inter-monsoon. In

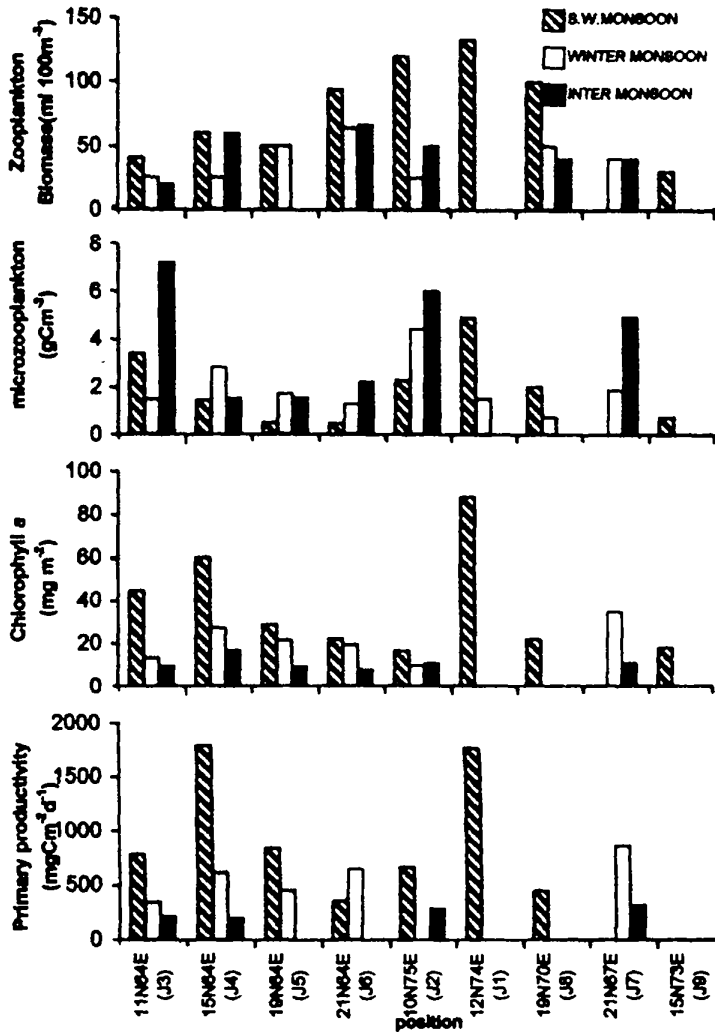


Fig. 4—Column values for primary production (a), chlorophyll a (b) microzooplankton (c) and mixed layer mesozooplankton biomass (d) in the open ocean along 64°E and coastal areas during various seasons.

this season their values were low at surface because of low nutrient availability but showed a clear subsurface chlorophyll maximum below the thermocline at about 50 m depth where nitrate became available. It then decreased because of low light availability. In winter and summer, chlorophyll had higher values in the upper water column concomitant with nutrient availability, but once again decreased with depth and waning light (Fig. 5).

An interesting observation was that, inspite of low primary production during the inter-monsoon (April-May), abundance of bacteria and microzooplankton

showed an increase compared to other two seasons (Fig. 4). Highest bacterial counts were 0.09 ; 0.6 and $0.96 \times 10^9 \text{ l}^{-1}$ for winter, summer and inter-monsoon respectively²¹. These were 56 , 139 and $188 \times 10^3 \text{ m}^{-2}$ for microzooplankton²⁰. Among microzooplankton, protozoans mostly consisting of ciliates were dominant in all areas irrespective of seasons. Among metazoans, copepod nauplii constituted the bulk. The main population of microzooplankton and bacteria generally remained above 100 m depth. These seem to have implications in the overall food web of the Arabian Sea.

Although the mesozooplankton biomass in the mixed layer in coastal and oceanic waters ranged between 25-120 ml.100m⁻³ within or between seasons (Fig. 4), the variations were not statistically significant. Average column standing stock of zooplankton in the mixed layer varied between 1.5-1.8 and 1.3-1.6 g. m⁻² (dry wt.) in the open ocean and coastal waters respectively¹⁹. The uppermost isothermal layer and the layer just below it (thermocline layer) accounted for 95% of the biomass. Pronounced increase in biomass in the mixed layer during night which would have resulted from vertical migration was not evident except in some coastal stations. Below the thermocline there was a sharp decrease in biomass similar to earlier observations²².

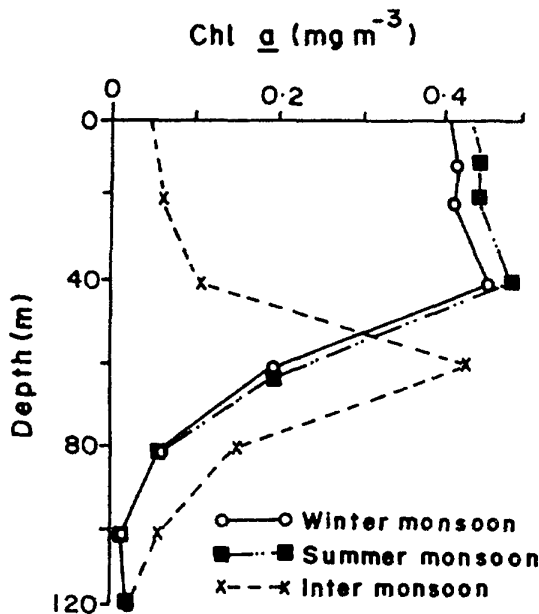


Fig. 5—Profiles of chlorophyll a (mg m⁻³) during 3 different seasons at 15°N and 64°E.

Relative abundance of various groups of mesozooplankton is listed in Table 1. Copepods accounted for about 50-88% in coastal waters and in the open ocean their dominance was still higher (77 to 88%). Small herbivorous copepods (<2 mm) belonging to Paracalanidae, Eucalanidae, Calanidae and Clausocalanidae were dominant accounting for more than 50% of the total copepod fauna¹⁹. Other common groups were chaetognaths and tunicates. The salp population was mostly constituted by a single species *Pegea confederata* in winter and it was distributed over a wide area along the open ocean track (64°E) from 15°N to 21°N. The tunicates are also mucous filter feeders capable of inesting very small particles. In all seasons herbivores were abundant both in the coastal as well as open ocean areas, but appreciable number of carnivores (particularly chaetognaths and poecilostomatoid copepods) were also present.

Among the total fish larvae collected from the open ocean, myctophid larvae accounted for more than 70%. They were relatively more common towards the north (15°N to 21°N) in the upper layers during night. Adults of myctophids were also collected in low numbers from DSL (Deep Scattering Layer). It is emphasised that the myctophid larvae caught in zooplankton net were not used to assess their population abundance but rather as an indication of their presence in this region (but see below). However, clear diurnal variations were discernible in the DSL which mainly composed of myctophids (Fig. 6). The general percentage of composition was *Diaphus arabicus* 80%, *Benthosema pterotum* 15% and the rest *Benthosema fibulatum*.

In terms of carbon, average values of microzooplankton during inter-monsoon, winter and summer monsoons were 19, 10 and 12 μgC l⁻¹ respectively. Microzooplankton biomass in terms of carbon was more compared to mesozooplankton in all

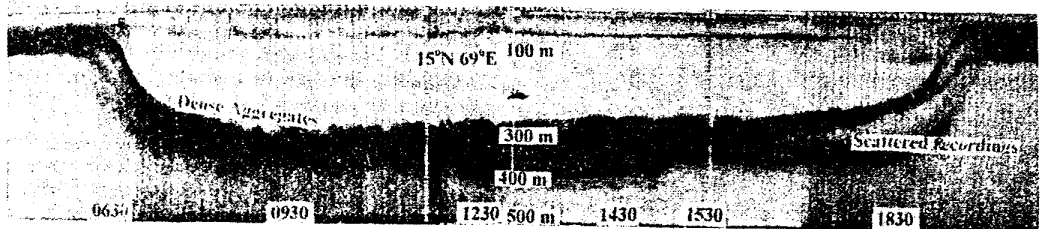


Fig. 6—The Deep Scattering Layer (DSL) in the central Arabian Sea during late summer monsoon.

Table 1—Relative percentage abundance of major zooplankton groups in the mixed layer of coastal and open ocean waters during different seasons

Group	April-May		February-March		July-August	
	(C.O.)	(O.P.)	(C.O.)	(O.P.)	(C.O.)	(O.P.)
Hydromedusae*	0.6	0.1	0.3	0.4	0.002	—
Siphonophoa*	2.2	0.3	0.9	0.9	0.04	0.3
Ctenophora*	0.1	—	—	—	—	—
Polychaeta*	1.2	0.1	0.3	0.4	0.1	0.3
Cladocera	0.3	0.1	—	—	—	—
Ostaracoda	0.5	2.2	0.5	1.5	0.6	2.1
Amphipoda*	0.7	0.9	0.8	0.7	0.2	0.7
Copepoda	50.0	87.3	79.0	82.0	88.0	77.0
Sergestidae	0.2	0.7	0.9	0.3	1.1	2.3
Euphausiacea	0.4	0.1	0.4	0.6	0.2	1.3
Heteropoda*	0.5	0.2	0.2	0.2	0.1	—
Pteropoda	2.1	0.1	0.1	0.1	0.6	0.1
Chaetognatha*	18.0	3.0	10.0	4.9	3.1	7.1
Salps	0.5	0.1	0.1	2.6	0.3	—
Dolioids	0.1	0.2	0.2	0.6	0.2	0.7
Copelata	15.0	3.9	4.5	3.8	0.4	0.2
Fish eggs	0.3	0.3	0.1	0.2	1.8	4.4
Fish larvae*	0.5	0.1	0.2	0.1	0.4	0.3
Decapod larvae	3.5	0.3	0.8	0.2	1.5	2.0

—Indicates absence

*Groups considered as carnivores (trophic group of copepods were classified according to Timonin³⁹).

C.O. = Coastal Waters, O.P. = Open Ocean Waters.

seasons, and it was about 3.5 times higher during inter-monsoon season. Similarly, bacterial carbon was higher than primary produced carbon during inter-monsoon particularly in southern regions where the latter formed only 2% of the biological production²¹.

Discussion

New understanding of the processes that lead to biological productivity shows that apart from coastal upwelling, open ocean upwelling and lateral advection of nutrients lead to fairly high primary productivity throughout the Arabian Sea during summer monsoon. During winter also its northern areas sustain high production. The southern areas during winter and the entire Arabian Sea during inter-monsoon experience low primary productivity. However, a salient feature observed was the maintenance of high mesozooplankton biomass in the mixed layer of open and coastal waters almost round the year.

The Arabian Sea has a well known oxygen

minimum zone (OMZ) between ca. 150 to 1000 m. This results in drastic reduction in zooplankton biomass below the thermocline layer. The OMZ also inhibits diel migration²² to some extent confining the major stocks to the upper layer. The 'Arabian Sea paradox' of maintenance of high mesozooplankton biomass is now a fairly well established fact as observed in other studies as well^{7,14-16,19,29,30}.

Reports on biomass values based on International Indian Ocean Expedition (IIOE) collections³¹ from the Arabian Sea showed much lesser displacement volume in open ocean waters (5-20 ml.100 m⁻³) compared to present observations made from the mixed layer (25-120 ml.100 m⁻³). The low values reported during IIOE should be due to the large mesh size (300 µm) used for sampling. The fact is that the generic composition of mesozooplankton in the Arabian Sea does not vary much over seasons and is dominated by small copepods (usually <2 mm) would have greatly contributed to this artifact. Another reason for the lower biomass reported in IIOE is that the standard hauls were from 200 m depth which

includes the low biomass strata and converted to standing stock for 200 m³. Recent studies clearly show that the mesozooplankton of the Arabian Sea is concentrated above the base of the thermocline with very little migration of smaller forms.

The Arabian Sea paradox by way of maintaining high mesozooplankton biomass in the mixed layer between productive and less productive seasons may be explained as follows. The smaller herbivores appear to be facultative, able to feed on either phytoplankton or microzooplankton. There is considerable evidence that the herbivorous mesozooplankton (including larger forms like tunicates) feed on very small particles including bacteria^{32,33}. Thus, during winter as well as during the southwest monsoon period the major grazing by zooplankton would be on phytoplankton. Considering the available evidence, during the inter-monsoon period (April-May) when primary production less than half compared to other seasons, the feeding mode is mainly through the microbial loop^{7,34}.

Thus as the winter and summer blooms become senescent, a large pool of dissolved organic carbon (DOC) is built up (D. Kumar, Personal Communication) leading to increase of bacteria and microzooplankton. Bacterial number $>1 \times 10^6$ ml⁻¹ from the Arabian Sea during the fall inter-monsoon following summer bloom (September) has been reported³⁵ apart from those high numbers mentioned earlier in April-May following winter bloom. Apart from DOC derived from phytoplankton, metabolic byproducts of mesozooplankton would also support the bacterial population³⁶.

The maintenance of high biomass of mesozooplankton round the year in the northern Arabian Sea apparently sustains a huge stock of mesopelagic fish (more than 100 million metric tonnes³⁷) mostly belonging to Myctophidae. In spite of the prevalence of an acute oxygen deficiency at mid-depths, the myctophids apparently are metabolically adapted to low ambient oxygen levels and feed almost exclusively on zooplankton³⁸. They are strong diel migrators, ascending to the surface layer at night for feeding and descending to 200-400 m during day (Fig. 6). Their occurrence is not confined to coastal upwelling zones; instead they seem to occur everywhere in high densities. Low metabolic rates within the OMZ, high conversion efficiencies³⁷ plus hitherto poorly understood high zooplankton biomass

in upper layers must be sustaining the mesopelagic fish stock.

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