Response of Zooplankton to Physical Changes in the Environment: Coastal Upwelling Along the Central West Coast of India

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ABSTRACT

Zooplankton composition and abundance were studied in a coastal upwelling situation from the central west coast of India. Upwelling and associated high biomass was found confined to a narrow coastal span. Zooplankton composition was dominated by a few species of herbivores and carnivores and was generally distinct from non-upwelling and offshore waters. Zooplankton had higher aggregations in the shallow upper mixed layer compared to the stratum below. High variability in zooplankton abundance occurred over short periods. Diel patterns in distribution or migration of zooplankton in inshore waters were not detectable.

ADDITIONAL INDEX WORDS: Coastal upwelling, zooplankton abundance, composition, diel pattern, vertical zonation, Arabian Sea.

INTRODUCTION

It is well known that coastal upwelling enhances biological production. Coastal upwelling events in the Atlantic and Pacific oceans have been well studied (e.g. BOJE and TONCZAK, 1978; BARBER and SMITH, 1981; RICHARDS, 1981; HEMPEL, 1982; SUESS and THIEDE, 1983; DENMAN and POWELL, 1984; BAS et al., 1985 among others), but very little information is available from upwelling areas in the Indian Ocean (PACKARD et al., 1984). This is particularly true of the west coast of India where upwelling occurs during the summer (southwest) monsoon (May-September) along with the establishment of clockwise circulation in the northern Indian Ocean.

Upwelling along the west coast appears to start in the southern regions (ca 9°N) with the onset of summer monsoon in May-June and intensifies in July-August. It gradually proceeds north and has been observed up to 15°N (BANSE, 1959, 1968, 1984; RAMAMIRTHMI and JAYARAMAN, 1960; SANKARANARAYANAN et al., 1978). There had been some uncertainty on the nature of the processes that induce and maintain upwelling in this region. It had been thought that the general wind field during this period was non-conducive to upwelling (SHARMA, 1978). BANSE (1959) regarded the prevailing current and not the wind system favoring upwelling in the region. Recent studies (SHETYE, 1984; SHETYE et al., 1985), however, show that the longshore component of the wind stress along the west coast of India is conducive to upwelling throughout the year but reaches a peak in July-August. These studies concluded that the coastal processes in the west coast during April-October are generally controlled by the local wind stress and are consistent with the classical wind induced upwelling systems.

Zooplankton are a major link in the marine food chain and their dynamics in the upwelling areas have received considerable attention. For example, in the Oregon upwelling area, the finding of PETERSON et al. (1979) that the distribution of a neritic copepod is governed by the interaction of upwelling circulation with that of the animal’s vertical distribution, was theoret-
ically confirmed by applying a zonal, two celled circulation model (WROBLEWSKI, 1982). SMITH et al. (1981b) found that temporal variations of zooplankton in an upwelling area off Peru were largely caused by onshore-offshore advection in the upper water column. Similarly, nearshore upwelling off Pt. Conception, California, was found to contribute significantly to offshore peaks in zooplankton biomass (SMITH et al., 1986). These and many other studies in upwelling areas emphasize the importance of short term variability in zooplankton populations caused by physical and biological factors. Along the west coast of India, increase in zooplankton standing stock associated with upwelling has been observed (HARIDAS et al., 1980), but no detailed study has been made. This paper attempts to focus on the changes brought about in zooplankton populations in an upwelling situation along the central west coast of India although physical data explaining some aspects of the distribution patterns are lacking.

MATERIALS AND METHODS

Zooplankton samples were collected on board R.V. Gaveshani from 35 stations along five transects (15°–19°N; 69°–73°E) between 12 and 26 September 1986 (Figure 1). Six additional samples were also collected between 14°–16°N, within the same period along the coastal belt where upwelling was indicated by vertical profiles of temperature. Collections were made with a Heron-Tranter net (mouth area—0.25 m²; mesh size—300 μm) equipped with a calibrated flow meter from 200 m to surface or from bottom to surface in shallower areas. The time of collection of these samples varied depending on time of arrival at the station. A 36 h time series with 6 h interval was also conducted at an inshore anchor station (depth—30 m; marked T in Figure 1) beginning at 0200 h on 28 September. At this station samples were taken from 30 m to the thermocline depth (using a closing mechanism) and subsequently above thermocline to the surface. Separate nets were used to avoid contamination. The time series was undertaken in order to assess the variability over depth and effects of diel migration and thermocline depth on zooplankton distributions.

All samples were preserved in 4% buffered formalin. Biomass of zooplankton was estimated as displacement volume after removing the larger gelatinous organisms (hydromedusae and siphonophora). Subsamples (25–50%) were taken from larger samples using a Folsom plankton splitter. Aliquots or whole samples were analyzed and groups of zooplankton were enumerated using a counting chamber. Species belonging to the groups Chaetognatha, Siphon-
ophora, Cladocera, Ostracoda, Pteropoda and Copepoda were identified. Zooplankton biomass and counts were transformed to numbers per unit volume using flow meter data. Species diversity was calculated using two indices: $D$ (MARGALEF, 1968) which gives species richness and $E$ (HEIP, 1974) which derives the equitability component.

Oxygen was estimated using the Winkler method as modified by CARRITT and CARPENTER (1966). Phosphate and nitrate were estimated using method described by KOROLEFF (1983). Chlorophyll $a$ was estimated fluorometrically (Turner Designs) as described by STRICKLAND and PARSONS (1972).

RESULTS

The upward slope of isotherms in the southern area of study (Figure 2) indicated upwelling, stronger in the southern area (15°N) with intensity gradually decreasing to the north. Upwelling appeared to be confined to a narrow zone, 50–70 km from shore. The shoreward proximity of upwelling was also reflected in concentrations of nutrients and chlorophyll $a$ (Figures 3 and 4). Concentrations were fairly high in the coastal belt in the southern areas, but rapidly decreased to the north and west of the upwelling centre. Offshore concentrations of nutrients and chlorophyll were quite low ($\sim 0.2$ and $0.4$ $\mu g$-at L $^{-1}$ NO$_3$ and PO$_4$ respectively, $<0.2$ mg m$^{-3}$ chl $a$), typical of oligotrophic open ocean conditions, showing that the area was little influenced by upwelling.

Spatial Variations in Zooplankton

Zooplankton standing stock was high in the coastal zone, coincident with upwelling (range 1.2 to 3.5 ml.m$^{-3}$, Figure 5). Further inshore, at station T, zooplankton biomass in the deepest mixed layer was the highest observed (up to 12 ml.m$^{-3}$, Figure 6B). High zooplankton biomass was confined to the shelf overlying the upwelling field, where peak concentrations of nutrients and chlorophyll occurred. In the southern area, high standing stocks were observed up to approximately 200 km offshore. In contrast, lower zooplankton biomass and densities were observed in the weakly upwelling northern areas.

Composition and abundance of dominant groups and species of zooplankton in the upwelling area (stations T and A) and nearby (stations B and C) are given in Table 1. The occurrences and abundances of these from two stations located outside the upwelling area (stations D and E) are included for comparison. Similar trends in composition and abundances were observed at other stations and are not pre-
Copepods generally comprised the largest percentage of zooplankton numbers both above (range 35–87%, mean 65%) and below (range 55–95%, mean 87%) the thermocline in the time series; they also constituted 50–90% of the total counts at other stations. In the upwelling area, the dominant representatives were mainly herbivorous/omnivorous calanoids (except Euchaeta sp.) and carnivorous cyclopoids and poecilostomatoids. Species like Centropages tenuiremis, Temora turbinata, Clausocalanus arcuicornis, Subeucalanus spp., Paracalanus spp., Acrocalanus spp., Oithona spp., Oncoea spp. and Corycaeus spp. were typically abundant in inshore and coastal waters. Their abundances decreased substantially across the shelf even in areas near the upwelling belt (contrast densities at stations T, A and B-E, Table 1).

A significant component of the biomass in the upwelling area, however, was comprised by larger carnivores such as Chaetognatha, Siphonophora and Hydromedusae. At station T, Sagitta enflata was the only chaetognath present. Similarly, Pteropoda and Ostracoda were represented by only one species each but in smaller numbers (Table 1). Other suspension feeders known to occur in high abundances in upwelling situations were represented in low numbers (appendicularians, cladocerans and euphausiids; THIRIOT, 1978; WEIKERT, 1982; PAFFENHOFER et al., 1984).

Other copepod species such as Centropages furcatus, Scoleleithricella ctenopus and Temora discoidata, occurred in low abundance in southern coastal waters. Across the shelf, near the upwelling areas, several other species, viz.
Figure 4. Distribution of surface chlorophyll $a$ in the study area (DEVASSY and GOES, unpublished data).

Figure 5. Distribution of zooplankton biomass in the study area.

Scoleithrix danae, Lucicutia flavicornis, Acartia amboinensis and Subeucalanus mucronatus, were present. Further offshore, other species such as Aetideus sp., Scoleithricella tenuiserrata, S. marginata, Amallothrix indica, Halopilus longicornis, Centropages gracilis, Pareucalanus attenuatus, Euchaeta concinna and some pontellids, were present. In the offshore waters in the northern region, most of these oceanic species were supplemented by a few others such as Eucalanus attenuatus (usually dominant), Candacia pachydactyla, Pleuro-
Sergerstid Lucifer hanseni in the upwelling area and nearby waters was replaced by L. typus in the northern area. Species diversity was low in the upwelling area compared to offshore waters (Table 2). This was also true for equitability component since a few species made up the majority of population in inshore upwelling waters.

### Short Term Variations at Station T

At station T, oxygen concentrations were low in deeper waters (< 1 ml L⁻¹) while it was uniformly high at the surface (Figure 7B). Similarly, chlorophyll a concentrations were also higher in surface compared to deeper waters and did not change much over the period of observation (Figure 7C).

Zooplankton were concentrated in the layer above the thermocline with biomass and densities being about 5.5 and 5 times higher compared to the water column below the thermocline (Figure 6B and C). Abundances of all species were significantly higher above the thermocline (p > .05 - .001, t-test, also see Figure 8 and Table 1). However, all groups and species of zooplankton except Cladocera occurred below the thermocline as well.

Biomass in the mixed layer showed a clear increase with increase in the mixed layer depth (Figure 6A and B). This was not so with total zooplankton counts indicating that the high biomass values were caused by the accumulation of larger organisms. In fact, larger numbers of hydromedusae, Sagitta, siphonophores and polychaetes, all carnivores, occurred in samples taken when the mixed layer depth was highest.

No diel pattern emerged from the time series either for biomass or total zooplankton counts for the column or above and below the thermocline (p < .05, also see Figure 6B and C). The same was true for groups and species (distributions of some common and representative species are given in Figure 8). The high standard deviations derived from the day and night distributions and above and below the thermocline for most groups and species (Table 1) clearly show the large scatter and that variations over time were not uniform.

### DISCUSSION

This study is in an area where seasonal upwelling is known to occur annually during
Table 1. Biomass (ml m$^{-3}$), total number of zooplankton and abundance of major groups and species (No. m$^{-3}$) at station T (SD in parentheses) and at representative stations (marked A to E in Figure 1).

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<th>Above thermocline</th>
<th>Below thermocline</th>
<th>Above thermocline Day &amp; night combined</th>
<th>Below thermocline Day &amp; night combined</th>
<th>St.A</th>
<th>St.B</th>
<th>St.C</th>
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late August and September (BANSE, 1968; SANKARANARAYANAN et al., 1978), but very little information exists on physical and biological characteristics of the region or event. Earlier studies indicate that upwelling along the Indian west coast comes to an end by October. The importance of upwelling areas can be underscored considering that about 50% of the world fish catch comes from 0.1% of upwelling sea areas (RYTHER, 1969). This pattern is duplicated along the west coast of India where maximum fish catches are taken during or immediately after the upwelling season (C.M.F.R.I., 1987a,b) and indicates the economic importance of monsoon generated upwelling to India’s local economy.

Upwelling in this region begins in the south accompanying the arrival of monsoon in this area and gradually moves north. Upwelling was localized to the nearshore region although effects of enrichment were evident in offshore waters as well. Higher concentrations of nutrients were evident in the southern coastal region. Subsurface waters in nearshore areas with low oxygen concentrations were probably advected from deeper sources as a result of upwelling. Other studies have noted similar effects of seasonal nearshore upwelling, e.g. at the mouths of the Cochin backwaters (an estuary) of Kerala (9°55’N) in June-August and Zuari estuary of Goa (15°30’N) in late August-September (SANKARANARAYANAN and JAYARAMAN, 1972; MADHUPRATAP, 1978). In contrast, coastal waters are nutrient-poor prior to upwelling in the region. For example, nitrate values in the upper 30 m were undetectable in nearshore waters off Goa in early

Table 2. Diversity indices at representative stations (species richness – D, equitability – E).

<table>
<thead>
<tr>
<th>Station</th>
<th>T</th>
<th>A</th>
<th>B</th>
<th>C</th>
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<td>range</td>
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<td>2.9</td>
<td>4.3</td>
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<td>mean</td>
<td>28 - .32</td>
<td>.30</td>
<td>.45</td>
<td>.41</td>
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</table>
Zooplankton, especially herbivores, occurred in high densities in coastal waters where food was plentiful. Biomass values from the inshore station T were higher than those recorded even during zooplankton swarms from the northern Indian Ocean (2.5 to 4.8 ml.m⁻³, MADHUPRATAP et al., 1980). Offshore biomass was low relative to upwelled regions but generally higher than noted in other non-upwelling seasons. Zooplankton biomass in the same area during postmonsoon season (late November) was only around 0.1 to 0.5 ml.m⁻³ in coastal waters and 0.01 to 0.09 ml.m⁻³ in offshore areas (NAIR et al., 1978) whereas it was > 0.1 ml⁻³ throughout the area studied during the present investigation (Figure 1). Mechanisms which cause the confinement of high biomass to the shelf region in the central west coast of India are uncertain, but could probably arise from a front at the shelf break or through a two layered circulation pattern across the shelf (cf PACKARD et al., 1978; PETERSON et al., 1979; HUTCHINGS et al., 1986; SMITH et al., 1986). However, the offshore reduction of zooplankton biomass during upwelling period is not surprising because production is completely utilized within a narrow zone along the coast in other close shore upwelling systems (e.g. 100–150 sea miles, Peru; VINogradov and Shushkina, 1978).

The abundances of zooplankton in the upwelling area were strikingly different from unaffected inshore and offshore areas. In general, it was possible to distinguish a coastal and an offshore community from zooplankton composition. Species diversity and equitability were low in the upwelling area, a few species dominated the community. As has been mentioned, in coastal waters, species composition was more or less similar both in southern and northern areas. Many of these coastal forms are obviously capable of rapid increases in populations when conditions become ideal. They are opportunistic species exploiting the unstable conditions created by upwelling and the auxiliary biological input of energy and are most likely r-strategists (cf MARGALEF, 1978a). Situations where a few species dominate the zooplankton composition have been reported from other upwelling areas, and often, many of the genera which exploit such situations are same as those found in the present study (e.g. Eucalanus, Paracalanus, Clausocalanus, Centropages, Temora, Oncaea among copepods; cf August 1987 (NAQVI, personal communication). Nutrient concentrations were low in the northern coastal waters where upwelling did not occur.

Upwelling also triggers a chain of biological processes. Chlorophyll a in surface waters during premonsoon season (January-February) in the study area was 0.2 to 1 mg m⁻³ in the shelf region and 0.05 to 0.5 mg m⁻³ in offshore areas (BIATTATHIRI, unpublished data). Along the south and central west coast, phytoplankton standing stock increases from May and peaks in July-October, the composition dominated by a few species of Diatomaceae (SUBRAHMANYAN et al., 1975). High primary and secondary production associated with nutrient enrichment of surface waters occurs off Goa through September and October followed by a decline in production (DEVASSY, 1983). Phytoplankton (including both diatoms and dinoflagellates) densities ranged from $13 \times 10^4$ to $55 \times 10^4$ L⁻¹ while chlorophyll a values were frequently above 5 mg m⁻³.

Figure 7. Tidal range (A), distribution of oxygen (B) continuous line represents integrated values for upper 5 m and broken line values at 15 m depth) and chlorophyll a (C) continuous line represents integrated values for upper 5 m and broken line values at 15 m depth) at station T over 36 h.
Figure 8. Distribution of representative species of zooplankton at station T over 36 h (against each observation, bars on the left and right side denote values below and above thermocline, respectively).

THIRIOT, 1978; SMITH, 1982; WEIKERT, 1982). Along southwest coast of India, *Temora turbinata* and *Acrocalanus* sp. have been reported to form swarms during upwelling season (HARIDAS et al., 1980). The study also showed that most of these copepods have either poor abundances or are absent in inshore waters during other seasons.

MARGALEF (1978a,b) suggests that coastal upwelling systems are less mature and organization is prevented from increasing in the upwelling areas by vertical movements and its variability; food chains are kept shorter. VIN-OGRADOV and SHUSHKINA (1978), on the other hand, maintain that distinct successional sequences spread over space/time occur (overview by BARBER and SMITH, 1981). By the end of September upwelling intensity in the present study area appears to slacken, subsiding at the surface, although vertical transport was still directed upwards at mid-depths (data from current meter moorings off Goa at 90 m depth between 15 and 30 September, 1987, ANTONY, personal communication). Thus the area was probably sampled towards the end of the upwelling event, but at a period when upwelling was still occurring at low rate. This is supported by the intermediate concentrations of nutrients and chlorophyll *a* in the upwelling area as opposed to the higher values reported from intensely upwelling fields (e.g. MINAS et al., 1982; SCHULZ, 1982; CODISPOTI, 1983).

Similar observations have been made from the Baja California by WALSH et al. (1977).

We have further evidence from zooplankton composition for the study period coinciding with a late period of upwelling. Although herbivores were still very abundant in the upwelling center, carnivores accounted for 10–60% or on average 25% of total zooplankton numbers and biomass at station *T*. The abundance of carnivores indicated that some time had elapsed after the start of upwelling to allow for development of a tertiary community. Community succession had occurred but development of secondary and tertiary communities was restricted to the upwelling center. BARBER and SMITH (1981) suggested that exploitation of ideally
suited conditions by zooplankton does not occur only if the upwelling area did not have sufficient, or the right kind of, organisms. Our data support this view. For example, tunicates were either absent or had very poor abundances in the present study; on the other hand they were observed to abound in mild upwelling conditions in the Bay of Bengal on another occasion (MADHUPRATAP et al., 1980). Most herbivores and carnivores occurred in large numbers in the upwelling area. Increases in populations of both herbivores and carnivores at upwelling centres have been observed in earlier studies from the northern Indian Ocean and generally, carnivores occur in low numbers in other seasons/areas (summarized in MADHUPRATAP and HARIDAS, 1986). Groups like Hydromedusae, Siphonophora and Chaetognatha and copepod species belonging to a few genera such as Euchaeta, Candacia, Oithona, Oncaea and Corycaeus are typically carnivorous zooplankton.

High aggregations of zooplankton above the thermocline both during day and night, as observed at station T, have been reported from the Irish Sea (SCROPE-HOWE and JONES, 1986). Other similar reports include those by BOYD (1973), SAMEOTO (1984) and DARO (1985). One reason for low numbers of zooplankton below the thermocline might be low oxygen content of the bottom waters (Figure 7B). This is in close agreement with an earlier study by SMITH et al., 1981b) from the Peruvian upwelling region. They found that zooplankton were concentrated in the upper layers when dissolved oxygen was low in deeper waters (less than 1 ml L\(^{-1}\)) and there was very little vertical migration in the upper water column. A second reason might be that chlorophyll \(a\) concentrations were highest in surface waters suggesting abundant food for the dominant herbivores. Finally, tropical zooplankton probably prefer the warmer waters of the mixed layer. These three reasons also account for the observed lack of diel patterns.

High short term variations in the abundances of composite species might be the result of spatial organization being destroyed by turbulence (caused by upwelling, tidal advection etc.). Increase in the zooplankton biomass along with an increase in the depth of the upper mixed layer is also likely to have originated from some physical mechanism. There are several reports indicating that such transport might coincide with internal wave activity (McGOWAN and HAYWARD, 1978; SMITH et al., 1981a; DENMAN and POWELL, 1984; DENMAN and MARA, 1986). Future research might concentrate on the role of physical factors controlling these distributions.

**SUMMARY**

Upwelling leads to increase in nutrients and phytoplankton stocks along coastal waters of the central west coast of India. Apparently in response to this, zooplankton biomass increased and peaked inshore. A few (opportunistic) species such as Sagitta enflata, Centropages tentiremis, Temora turbinata, Clausocalanus arcuicornis, Subeucalanus spp., Paracalanus spp., Acrocalanus spp., Corycaeus spp. were responsible for this. This resulted in a low diversity community. Increase in abundances of both herbivores and carnivores suggested that sequential community development had occurred subsequent to the start of upwelling. But the predicted high diversity terminal community in downstream/offshore areas (cf VINogradov and Shushkina, 1978) did not occur; rather the high biomass community was concentrated over the shelf. Offshore zooplankton community was distinctly different, biomass and densities decreased showing that the influence of upwelling declined. Time series data suggested high short term variability and lack of diel patterns in the upwelling area. Avoidance of low oxygen bottom waters appears to be common and consequently zooplankton accumulated in the upper mixed layer.

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Die Verbreitung und Zusammensetzung des Zooplanktons wurde in einem Gebiet mit Auftriebwasser vor der zentralen Küste Indiens studiert. Das Aufquellen und die damit verbundene hohe Biomasse sind auf einen sehr schmalen Küstenstreifen bes-


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Résumé

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