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

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ABSTRACT

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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 TOMCZAK, 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; RAMAMIRTHM 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-

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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 m^{-2}; 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-

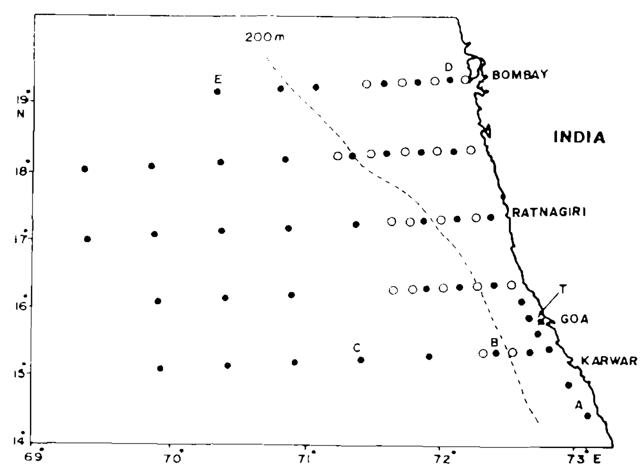

Figure 1. Location of stations (closed circles and a square) where zooplankton were collected. Details of zooplankton composition at station T are given in Table 1 and compared with stations marked A to E (see text). Open circles indicate stations where only physical data were collected.

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 flourometrically (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 (~ 0.2 and 0.4 μg-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-

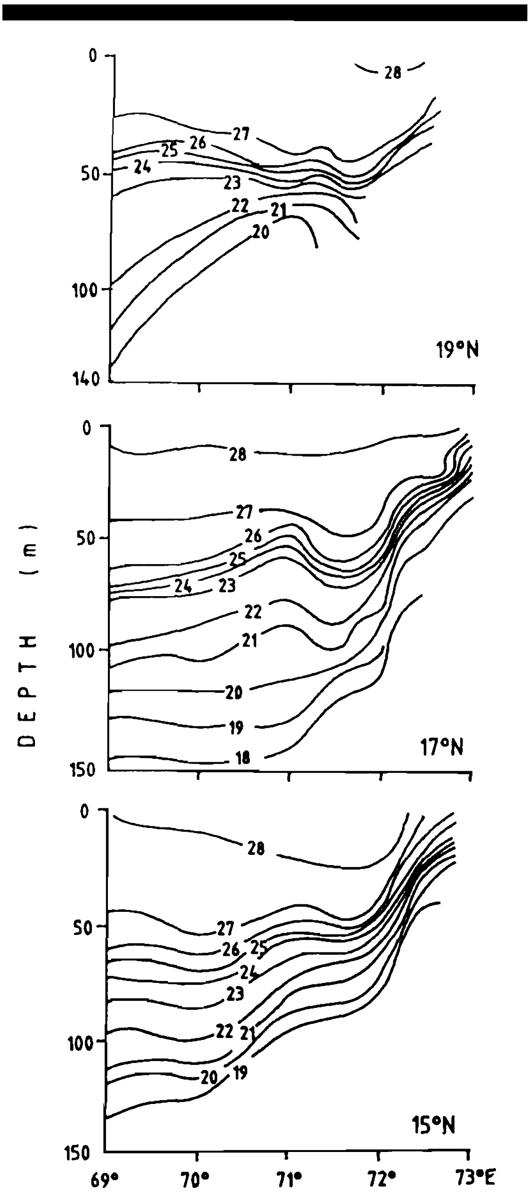

Figure 2. Profiles of temperature (°C) along three sections in the sampling area (Shenoi, unpublished data).

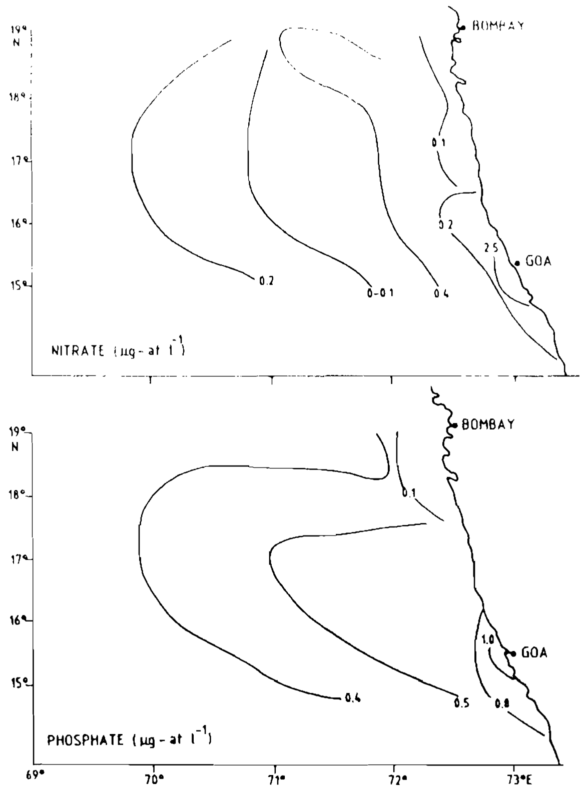

Figure 3. Surface concentrations of nitrate (NO_3-Nµg at l^{-1}) and Phosphate (PO_4-P µg at l^{-1}) in the study area (Chemical Oceanography Division, unpublished data).

sented here. Other differences, *e.g.* as between zooplankton in non-upwelling versus offshore areas, are highlighted in the ensuing account.

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., *Oncaea* 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, Scolecithricella ctenopus* and *Temora discaudata*, occurred in low abundance in southern coastal waters. Across the shelf, near the upwelling areas, several other species, viz.

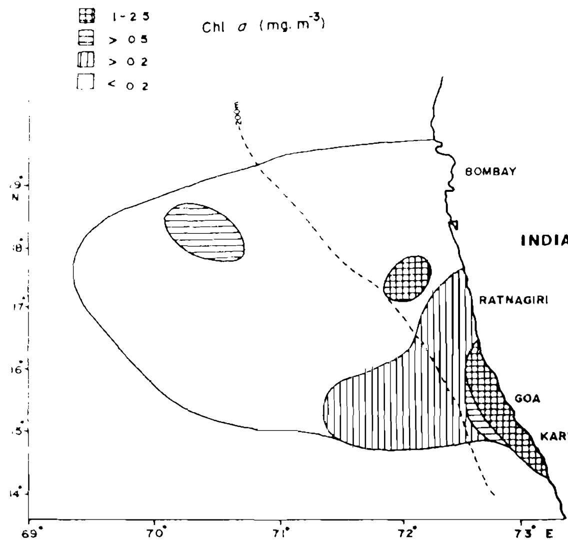

Figure 4. Distribution of surface chlorophyll *a* in the study area (DEVASSY and GOES, unpublished data).

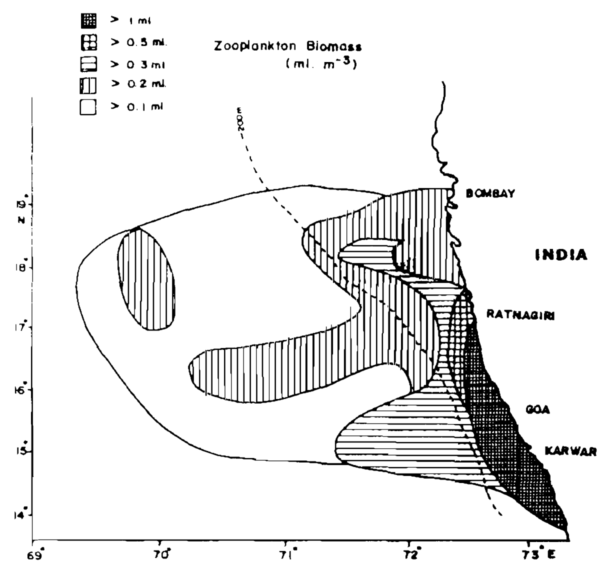

Figure 5. Distribution of zooplankton biomass in the study area.

Scolecithrix danae, Lucicutia flavicornis, Acartia amboinensis and *Subeucalanus mucronatus*, were present. Further offshore, other species such as *Aetideus* sp., *Scolecithricella tenuiserrata, S. marginata, Amallothrix indica, Haloptilus 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-*

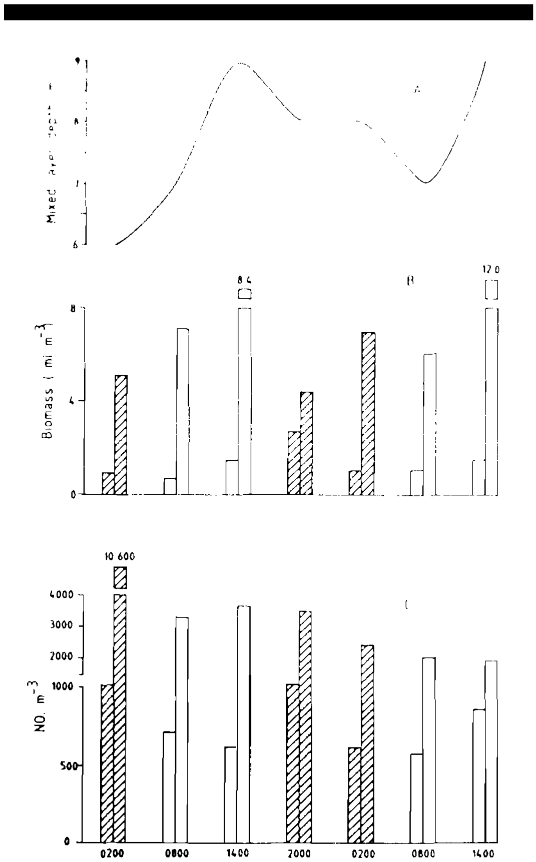

Figure 6. Variations in depth of upper mixed layer (A), zooplankton biomass (B) and total zooplankton densities (C) at station T over 36 h (against each observation in B and C, bars on the left and right side denote values below and above thermocline, respectively).

mamma indica and *P. abdominalis*. In northern coastal waters, species composition of copepods was similar to its southern counterpart, but densities were much lower (32 m ^{3} at station D *versus* 549 m^{-3} at station A).

Among chaetognaths, however, while *Sagitta enflata* was the dominant or often the only form in coastal upwelling areas, *S. bedoti* was more abundant in the north. Across the shelf and in offshore waters, many more species (such as *S. hexaptera, S. pacifica, S. ferox, S. bipunctata, S. regularis* and *S. neglecta*) occurred throughout the area of study, but at lower numbers. Similarly a few more species, such as *Paraconchoecia procera* and *Spinoecia porrecta* among ostracods and *Chelophyes contorta* and *Diphyes dispar* among siphonophores, occurred in the offshore samples. The sergestid *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 parantheses) and at representative stations (marked A to E in Figure 1).*

	Station T										
	Above thermocline		Below thermocline		Above thermocline Day & night combined	Below thermocline Day & night combined	St.A	St.B	St.C	St.D	St.E
	Day	Night	Day	Night							
Biomass	8.4	5.7	0.7	1.0	7.5	0.8	1.9	0.3	0.4	0.2	0.1
	(2.5)	(1.4)	(0.6)	(1.1)	(2.4)	(0.7)					
Total	2618	5405	680	1419	3812	824	898	354	409	65	52
zooplankton	(893)	(4337)	(137)	(1076)	(2981)	(743)					
Hydromedusae	48	25	10	6	38	8	7	0	0	1	1
	(68)	(23)	(8)	(6)	(52)	(7)					
Amphipoda	16	11	2	4	14	2	10	1	1	0	1
	(6)	(10)	(.5)	(2)	(7)	(2)					
Polychaeta	98	60	10	14	81	11	93	2	1	0	1
	(87)	(41)	(7)	(13)	(69)	(9)					
Appendicularia	6	4	2	3	4	2	0	0	0	0	4
	(5)	(2)	(.5)	(1)	(4)	(1)					
Chaetognatha:											
Sagitta enflata	380	363	59	65	373	61	15	9	17	1	1
	(243)	(75)	(48)	(69)	(177)	(52)					
Siphonophora:											
Bassia	46	88	5	4	64	4	4	2	0	0	1
bassensis	(7)	(51)	(4)	(2)	(37)	(3)					
Abylopsis	13	11	16	4	13	10	21	0	3	0	0
tetragona	(9)	(6)	(9)	(2)	(7)	(9)					
Diphyes	54	86	11	9	67	9	3	0	0	2	0
chamissonis	(29)	(27)	(5)	(7)	(31)	(9)					
Lensia	50	64	7	11	56	8	5	0	0	0	0
subteloides	(36)	(10)	(2)	(7)	(27)	(8)					
Cladocera:											
Penilia	7	56	0	0	28	0	0	0	0	0	0
avirostris	(14)	(34)			(31)						
Evadne	0	5	0	0	4	0	0	0	0	0	0
tergestina		(3)			(7)						
Ostracoda:											
Cypridina	8	11	3	4	8	3	3	1	59	0	2
dentata	(7)	(7)	(2)	(3)	(6)	(3)					
Pteropoda:											
Creseis acicula	6	15	9	2	14	5	3	0	0	0	0
	(7)	(20)	(6)	(2)	(20)	(5)					
Copepoda:											
Centropages	54	358	21	189	184	16	51	0	1	0	0
tenuiremis	(54)	(596)	(23)	(7)	(382)	(18)					
Pseudodiaptomus	15	23	4	7	18	5	2	0	0	0	0
serricaudatus	(7)	(9)	(2)	(3)	(7)	(2)					
Temora	601	521	257	158	567	214	35	1	0	4	0
turbinata	(331)	(34)	(98)	(135)	(310)	(117)					
Clausocalanus	104	619	36	235	567	121	10	13	15	2	1
arcuicornis	(76)	(690)	(22)	(376)	(384)	(242)					
Euchaeta rimana	9	27	5	9	16	6	0	4	12	1	2
	(7)	(15)	(6)	(8)	(13)	(6)					
Subeucalanus	168	753	56	140	418	53	64	12	13	3	0
pileatus	(165)	(991)	(41)	(62)	(662)	(38)					
S. crassus	99	312	12	97	190	48	29	3	4	2	1
	(61)	(175)	(9)	(97)	(158)	(72)					
S. subcrassus	86	158	36	77	117	53	13	3	0	1	0
	(84)	(198)	(71)	(104)	(134)	(74)					

Table 1. *Continued.*

	Station T										
	Above thermocline		Below thermocline		Above thermocline Day & night combined	Below thermocline Day & night combined	St.A	St.B	St.C	St.D	St.E
	Day	Night	Day	Night							
S. subtenuis	44	128	22	18	80	20	40	1	8	0	0
	(30)	(164)	(23)	(17)	(107)	(19)					
Canthocalanus pauper	20	23	10	2	32	6	25	4	8	3	0
	(13)	(10)	(16)	(1)	(25)	(12)					
Paracalanus spp.	165	1062	18	216	472	31	35	48	27	2	1
	(136)	(882)	(10)	(30)	(729)	(25)					
Acrocalanus spp.	132	482	13	73	282	38	56	92	29	3	1
	(95)	(582)	(10)	(78)	(391)	(56)					
Oithona spp.	43	26	19	12	35	15	28	10	19	1	0
	(27)	(6)	(17)	(8)	(21)	(13)					
Oncaea spp.	40	39	23	11	42	11	22	63	14	1	2
	(15)	(8)	(30)	(3)	(12)	(22)					
Corycaeus spp.	137	57	12	34	102	21	41	19	13	1	1
	(115)	(36)	(17)	(38)	(94)	(28)					
Sapphirina spp.	8	7	1	2	7	1	0	0	1	0	0
	(14)	(3)	(1)	(1)	(10)	(1)					
Euphausiacea:											
Thysanopoda monocantha	4	5	1	6	4	2	0	0	0	0	1
	(4)	(3)	(.5)	(6)	(10)	(4)					
T. tricuspidata	1	0	0	0	4	0	0	0	0	0	0
	(1)				(1)						
Stylocheiron suhmii	0	0	1	1	0	4	0	0	0	0	1
			(.5)	(1)		(1)					
Sergestidae:											
Lucifer hanseni	21	20	6	7	20	6	19	1	1	0	0
	(11)	(18)	(4)	(5)	(13)	(4)					

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

Station	T		A	B	C	D	E
	range	mean					
D	2.6 – 3.4	2.9	4.3	4.6	4.2	4.3	5.0
E	.28 – .32	.30	.45	.41	.51	.71	.56

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

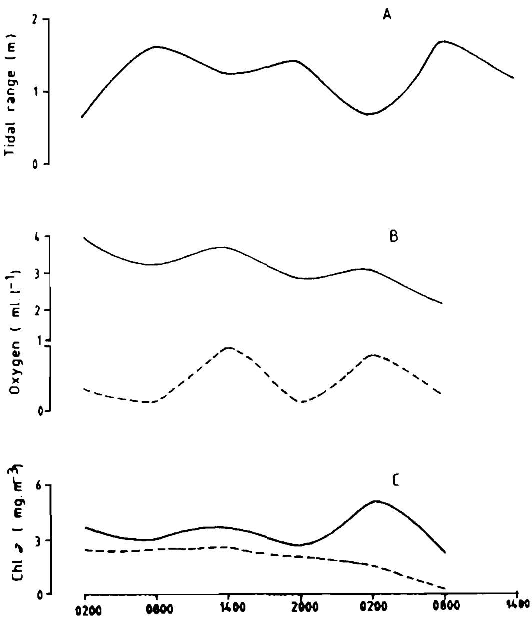

Figure 7. Tidal range (A), distribution of oxygen (B) continuous line represents integrated values for upper 5 m and broken line values at 15 m depth) and chlorophyll *a* (C) continuous line represents integrated values for upper 5 m and broken line values at 15 m depth) at station T over 36 h.

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 (BHATTATHIRI, 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 Diatomacea (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}.

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 post monsoon 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*

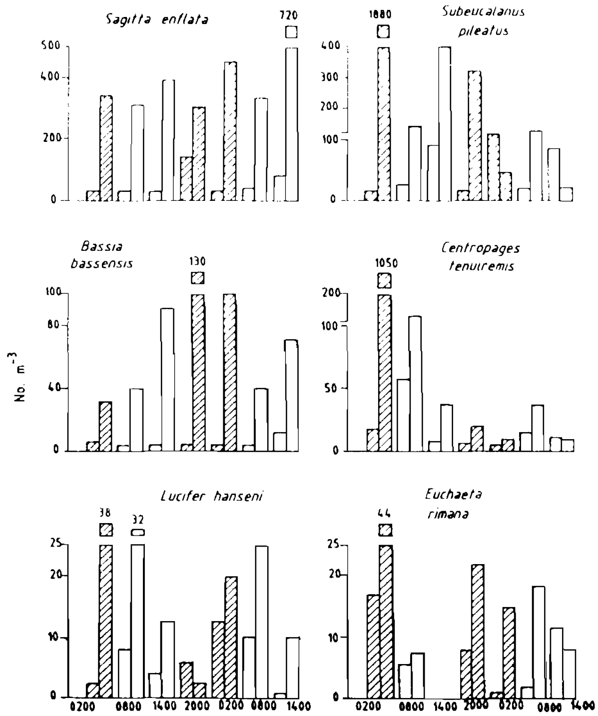

Figure 8. Distribution of representative species of zooplankton at station T over 36 h (against each observation, bars on the left and right side denote values below and above thermocline, respectively).

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. VINOGRADOV 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 tenuiremis, 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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LITERATURE CITED

BANSE, K., 1959. On upwelling and bottom trawling off the southwest coast of India. *Journal of Marine Biological Association of India*, 1, 33–49.

BANSE, K., 1968. Hydrography of the Arabian Sea shelf of India and Pakistan and effects on demersal fisheries. *Deep-Sea Research*, 15, 45–79.

BANSE, K., 1984. Overview of the hydrography and associated biological phenomena in the Arabian Sea, off Pakistan. *In*: B.U. Haq and J.D. Milliman, (Eds.), *Marine Geology and Oceanography of Arabian Sea and Coastal Pakistan*. New York: Reinhold, pp. 271–303.

BARBER, R.T. and SMITH, R.L., 1981. Coastal upwelling ecosystems. *In*: A.R. Longhurst, (Ed.), *Analysis of Marine Ecosystems*. London: Academic Press, pp. 31–68.

BAS, C.; MARGALEF, R. and RUBIES, P., 1985. *Simposio Internacional Sobre las areas de afloramiento mas importantes del oeste Africano (Cabo Blancoy Benguela). Vol. 1,* Barcelona: Instituto de Investigaciones Pesqueras, 586p.

BOJE, R. and TOMCZAK, M., 1978. *Upwelling Ecosystems*. Berlin: Springer Verlag, 303p.

BOYD, C.M., 1973. Small scale spatial patterns of marine zooplankton examined by an *in situ* zooplankton detecting device. *Netherlands Journal of Sea Research*. 7, 103–111.

CARRITT, D.E. and CARPENTER, J.H., 1966. Comparison and evaluation of currently employed modifications of the Winkler method for determining oxygen in seawater, A NASCO report. *Journal of Marine Research,* 24, 286–318.

C.M.F.R.I., 1987a. *An Appraisal of the Marine Fisheries of Kerala*. Central Marine Fisheries Research Institute, Special Publication Number 35, 42p.

C.M.F.R.I., 1987b. *An Appraisal of the Marine Fisheries of Karnataka and Goa*. Central Marine Fisheries Research Institute, Special Publication Number 36, 104p.

CODISPOTI, L.A., 1983. On nutrient variability and sediments in upwelling regions. *In*: E. Suess and J. Thiede, (Eds.), *Coastal Upwelling. Its Sediment Record. Part A: Response of the Sedimentary Regime to Present Coastal Upwelling*. New York: Plenum, pp. 125–145.

DARO, M.H., 1985. Feeding rhythms and vertical distribution of marine copepods. *Bulletin of Marine Science*, 37, 487–497.

DENMAN, K.L. and MARA, J., 1986. Modelling the time dependent photoadaptation of phytoplankton to fluctuating light. *In*: J.C.J. Nihoul, (Ed.), *Marine Interfaces Ecohydrodynamics*. Amsterdam: Elsevier, pp. 341–359.

DENMAN, K.L. and POWELL, T.M., 1984. Effects of physical processes in planktonic ecosystems in the coastal ocean. *In*: M. Barnes, (Ed.), *Oceanography and Marine Biology, an Annual Review*. Aberdeen: Aberdeen University Press, pp. 125–168.

DEVASSY, V.P., 1983. Plankton production associated with cold water incursion into the estuarine environment. *Mahasagar-Bulletin of the National Institute of Oceanography*, 16, 221–233.

HARIDAS, P.; MENON, P.G. and MADHUPRATAP, M., 1980. Annual variations in zooplankton from a polluted coastal environment. *Mahasagar Bulletin of the National Institute of Oceanography*, 13, 239–248.

HEIP, C., 1974. A new index measuring evenness. *Journal of Marine Biological Association of United Kingdom*, 54, 555–557.

HEMPEL, G., 1982. The Canary Current: Studies of an upwelling system. *Rapports et Proces-Verbaux des Reunions*, 180, 455p.

HUTCHINGS, L.; ARMSTRONG, D.A. and MITCHELL, B.A., 1986. The frontal zone in southern Benguela Current. *In*: J.C.J. Nihoul, (Ed.), *Marine Interfaces and Ecohydrodynamics*. Amsterdam: Elsevier, pp. 67–94.

KOROLEFF, F., 1983. Determination of nutrients. *In*: K. Grasshof; M. Ehrhard, and K. Kremling, (Eds.), *Methods of Seawater Analysis*. Weinheim:Verlag, Chemie, pp. 125–187.

MADHUPRATAP, M., 1978. Studies on the ecology of Cochin Backwater. *Mahasagar-Bulletin of the National Institute of Oceanography,* 11, 45–56.

MADHUPRATAP, M.; DEVASSY, V.P.; NAIR, S.R.S. and RAO, T.S.S., 1980. Swarming of pelagic tunicates associated with phytoplankton bloom in the Bay of Bengal. *Indian Journal of Marine Science*. 9, 69–71.

MADHUPRATAP, M. and HARIDAS, P., 1986. Epipelagic calanoid copepods of the northern Indian Ocean. *Oceanologica Acta*, 9, 105–117.

MARGALEF, R., 1968. *Perspectives in Ecological Theory*. The University of Chicago Press, 111p.

MARGALEF, R., 1978a. What is an upwelling ecosystem. *In*: R. Boje and M. Tomczak, (Eds.), *Upwelling Ecosystems*. Berlin: Springer Verlag, pp. 12–14.

MARGALEF, R., 1978b. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta*, 1, 493–509.

McGOWAN, J.A. and HAYWARD, T.L., 1978. Mixing and oceanic productivity. *Deep-Sea Research*, 25, 771–793.

MINAS, H.J.; CODISPOTI, L.A. and DUGDALE, R.C., 1982. Nutrients and primary production in the upwelling region off northwest Africa. *Rapports et Proces-Verbaux des Reunions*, 180, 148–183.

NAIR, V.R.; PETER, G. and PAULINOSE, V.T., 1978. Zooplankton studies in the Indian Ocean II. From the Arabian Sea during the post-monsoon period. *Mahasagar-Bulletin of the National Institute of Oceanography*, 11, 35–43.

PACKARD, T.T.; BLASCO, D. and BARBER, R.T., 1978. *Mesodinium rubrum* in the Baja California upwelling system. *In*: R. Boje and M. Tomczak, (Eds.), *Upwelling Ecosystems*. Berlin: Springer Verlag, pp. 73–89.

PACKARD, T.T.; BLASCO, D. and DUGDALE, R.C., 1984. Coastal upwelling: a synopsis of its physical, chemical and biological characteristics. *In*: B.U. Haq and J.D. Milliman, (Eds.), *Marine Geology and Oceanography of Arabian Sea and Coastal Pakistan*. New York: Reinhold, pp. 339–350.

PAFFENHOFER, G-A.; WESTER, B.T. and NICHOLAS, W.D., 1984. Zooplankton abundance in relation to state and type of intrusions on to the southeastern United States shelf during summer. *Journal of Marine Research*, 42, 995–1017.

PETERSON, W.T.; MILLER, C.B. and HUTCHINSON, A., 1979. Zonation and maintainance of copepods in the Oregon upwelling zone. *Deep-Sea Research*, 26, 467–494.

RAMAMIRTHM, C.P. and JAYARAMAN, R., 1960. Hydrographical features of the continental shelf waters off Cochin during the years 1958 and 1959. *Journal of Marine Biological Association of India*, 2, 199–207.

RICHARDS, F.A., 1981. *Coastal Upwelling. Coastal and Estuarine Sciences, 1*. Washington: American Geophysical Union. 529p.

RYTHER, J.H., 1969. Photosynthesis and fish production in the sea. *Science*, 166, 72–76.

SANKARANARAYANAN, V.N. and JAYARAMAN, R., 1972. Intrusion of upwelled water in the Mandovi and Zuari estuaries. *Current Science*, 41, 204–206.

SANKARANARAYANAN, V.N.; RAO, D.P. and ANTONY, M.K., 1978. Studies on some hydrographical characteristics of the estuarine and inshore waters of Goa during the southwest monsoon 1972. *Mahasagar-Bulletin of the National Institute of Oceanography*, 11, 125–136.

SAMEOTO, D.D., 1984. Environmental factors influencing diurnal distribution of zooplankton and ichthyoplankton. *Journal of Plankton Research*, 6, 767–792.

SCHULZ, S., 1982. A comparison of primary production in upwelling regions of north west and south west Africa. *Rapports et Proces-Verbaux des Reunions*, 180, 202–204.

SCROPE-HOWE, S. and JONES, D., 1986. The vertical distribution of zooplankton in the western Irish Sea. *Estuarine, Coastal and Shelf Science*, 22, 785–802.

SHARMA, G.S., 1978. Upwelling off the southwest coast of India. *Indian Journal of Marine Science*, 7, 209–218.

SHETYE, S.R., 1984. Seasonal variability in the temperature field off the south-west coast of India. *Proceedings of the Indian Academy of Sciences*, 93, 399–411.

SHETYE, S.R.; SHENOI, S.S.C.; ANTONY, M.K. and KUMAR, K.K., 1985. Monthly mean wind stress along the coast of north Indian Ocean. *Proceedings of the Indian Academy of Sciences*, 94, 129–137.

SMITH, S.L., 1982. The northwest Indian Ocean during the monsoons of 1979: distribution, abundance and feeding of zooplankton. *Deep-Sea Research*, 29, 1331–1353.

SMITH, S.L.; BOYD, C.M. and LANE, P.V.Z., 1981a. Short term variation in the vertical distribution of small copepods off the coast of northern Peru. *In*: F.A. Richards, (Ed.), *Coastal Upwelling. Coastal and Estuarine Science, 1*. Washington D.C.: American Geophysics Union, pp. 417–426.

SMITH, S.L.; BRINK, K.H.; SANTANDER, H.; COWLES, T.J. and HUYER, A., 1981b. The effect of advection on variations in zooplankton at a single location near Cabo Nazca, Peru. *In*: F.A. Richards, (Ed.), *Coastal Upwelling, Coastal and Estuarine Science, 1*. Washington D.C.: American Geophysical Union, pp. 400–410.

SMITH, S.L.; JONES, B.H.; ATKINSON, L.P. and BRINK, K.H., 1986. Zooplankton in the upwelling fronts off Pt. Conception, California. *In*: Nihoul, J.C.J., (Ed.), *Marine Interfaces Ecohydrodynamics*. Amsterdam: Elsevier, pp. 195–213.

STRICKLAND, J.D.H. and PARSONS, T.R., 1972. A practical handbook of seawater analysis. *Bulletin of Fisheries Research Board Canada*, 167, 310p.

SUBRAHMANYAN, R.; GOPINATHAN, C.P. and PILLAI, C.T., 1975. Phytoplankton of the Indian Ocean: some ecological problems. *Journal of Marine Biological Association of India*, 17, 608–612.

SUESS, E. and THIEDE, J., 1983. *Coastal Upwelling, its Sediment Record. Part A: Response of Sedimentary Regime to Present Coastal Upwelling*. New York: Plenum Press, 604p.

THIRIOT, A., 1978. Zooplankton communities in the west African upwelling area. *In*: R. Boje and M. Tomczak, (Eds.), *Upwelling Ecosystems*. Berlin: Springer Verlag, pp. 32–61.

VINOGRADOV, M.E. and SHUSHKINA, E.A., 1978. Some development patterns of plankton communities in the upwelling areas of the Pacific Ocean. *Marine Biology*, 48, 357–366.

WALSH, J.J.; WHITLEDGE, J.C.; KELLEY, S.A.; HUNTSMAN, S.A. and PILSBURY, R.D., 1977. Further transition states of the Baja California upwelling ecosystem. *Limnology and Oceanography*, 22, 264–280.

WEIKERT, H., 1982. Some features of zooplankton distribution in upper 200 m in the upwelling region off northwest Africa. *Rapports et Proces-Verbaux des Reunions*, 180, 280–288.

WROBLEWSKI, J.S., 1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone—a simulation. *Deep-Sea Research*, 29, 665–686.

□ RÉSUMÉ □

Composition et abondance du zooplancton ont été étudiées dans une situation d'upwelling de la côte centre ouest de l'Inde. L'upwelling et la biomasse associée sont confinés à un espace côtier étroit. La composition zooplanctonique est dominée par quelques espèces d'herbivores et de carnivores, généralement distinctes de celles des eaux littorales sans upwelling. Le zooplancton est plus fortement agrégé dans les couches mixtes supérieures. On observe une grande variabilité de l'abondance zooplanctonique sur de courtes périodes.—*Catherine Bressolier, Géomorphologie EPHE, Montrouge, France.*

□ ZUSAMMENFASSUNG □

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

chränkt. Die Zusammensetzung des Zooplanktons wird dominiert von wenigen Herbivoren end Karnivoren und unterscheidet sich generell von der außerhalb der Küstengewässer und Auftriebsgebiete. Außerdem ist es in einer flachen Oberflächenschicht dichter als in tieferen Lagen, und eine kurzfristig starke Schwankung in der Zusammensetzung tritt auf. Muster der Wanderung uind Verbreitung des Zooplanktons innerhalb der küstennahen Binnengewässer wurden nicht ermittelt.—*Dieter Kelletat, Essen/FRG.*