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Mesozooplankton community structure in the upper 1,000 m along the western Bay of Bengal during the 2002 fall intermonsoon

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Abstract

Background: Stratification, no upwelling, sediment load, and heavy cloud cover are known to limit primary production in the western Bay of Bengal. Studies on primary consumers in this area are few. Recent studies in the Bay have shown the role of cold-core eddies in enhancing the biological production. This study was carried out to provide a detailed account of variation in mesozooplankton biomass, abundance, and copepod assemblages between cold-core eddy and non-eddy regions in the western Bay.

Results: In this study carried out in the western Bay during fall 2002 intermonsoon, we observed a very high zooplankton biovolume of 2.2 ml/m^3 in the mixed layer at station WB3 located within a shallow cold-core eddy. Zooplankton from 29 groups were observed during this study. Calanoid and poecilostomatoid copepods substantially contributed to the total zooplankton abundance and carbon biomass. Below the 200 m depth, there were fewer groups but higher proportion of copepods. Copepodites of calanoids were more abundant between 500 and 1,000 m at the WB3 eddy station. Invertebrate eggs made up a staggering 65% of the total collection in the 200- to 300-m stratum at WB1, a location in the other cold-core eddy. Copepod species diversity (3.39 to 4.77) and richness (2.32 to 4.84) were lower at WB3. Among 147 copepod species in 69 genera found, *Oncaea venusta* (17% of the total copepod abundance), *Paracalanus indicus* (5.4%), *Lucicutia flavicornis* (5.1%), and *Pleuromamma indica* (4.5%) were the four most dominant ones.

Conclusions: High copepod diversity throughout upper 1,000 m of the western Bay is attributed to the moderate oligotrophy. We reported 93 copepod species for the first time from this region, from which 7 are first records for the Indian Ocean. Cold-core eddies seem to play a pivotal role in sustaining zooplankton in nutrient-limiting regions such as the western Bay of Bengal.

Keywords: Zooplankton; Biomass; Vertical distribution; Copepods; Cold-core eddies

Background

It is increasingly being recognized that eddies bring about mesoscale variability in plankton (The Ring Group 1981). Cold-core eddies upwell nutrient-rich waters into the euphotic layer and subsequently increase chlorophyll (Chl) *a* and primary production and support enhanced biomass and assemblages of grazer populations. In the subtropical North Atlantic and Pacific Oceans, cyclonic eddies were found to significantly contribute to biogeochemical cycles (McGillicuddy and Robinson 1997; Vaillancourt et al. 2003). Such studies which would be of great relevance in tropical oceans where surface waters tend to be nutrient-impoverished are limited. The western Bay of Bengal, off the east coast of India, is known for the perpetual existence of a few cold-core eddies (Prasanna Kumar et al. 2007; Nuncio and Prasanna Kumar 2012) and is therefore an ideal site to study spatial variation in the community structure of zooplankton.

Besides being a warm pool for most of the year, the western Bay receives enormous amounts of freshwater from many Indian rivers which results in its top 20 to 30 m being perennially stratified. In the absence of strong upwelling, this layer is usually devoid of essential dissolved nutrients (Sen Gupta and Naqvi 1984; Sardessai et al. 2007). The persistent cloud cover and sediment-induced

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turbidity shallows the euphotic depth causing the region to remain moderately oligotrophic (Prasanna Kumar et al. 2002). Information on mesozooplankton communities would be useful to understand the secondary productivity potential of such regions.

Studies on mesozooplankton biomass, abundance, taxonomic groups, and ecology from the Bay of Bengal are few (Panikkar and Rao 1973; Nair et al. 1981; Rakhesh et al. 2006; Muraleedharan et al. 2007; Fernandes 2008; Fernandes and Ramaiah 2009), and the information available is mostly for the upper 200 m. This investigation was carried out to provide a detailed account of spatial and vertical variations in the mesozooplankton biomass, density, and copepod assemblages in the upper 1,000 m in the western Bay of Bengal in an area that included two cold-core eddies along the sampling transect.

Methods

Sampling and sample processing

Under the aegis of the Research Program, Bay of Bengal Process Studies (BOBPS), sampling was done onboard *ORV Sagar Kanya* cruise 182 in the western Bay of Bengal in September to October 2002. At each of the four stations (Figure 1), mesozooplankton samples were collected from five discrete depth strata in the upper 1,000 m using a multiple plankton net (Multinet®, Hydro-bios, Kiel, Germany; mouth area of 0.25 m^2 and mesh size of 200 μm) during day and night. The sampled strata were decided based on conductivity, temperature, and depth (CTD) profiles (Sea-Bird Electronics Inc., Bellevue, WA, USA). The strata sampled at each location were as follows: the mixed layer that varied from 20 to 52 m, the thermocline, the base of the thermocline to 300 m, and 500 to 1,000 m. The net was hauled up at a speed of 0.8 m/s, and the volume of water filtered was calculated by multiplying the sampling depth with the mouth area of the net. Upon recovery of the samples, the zooplankton biovolume was measured by the displacement volume method (Harris et al. 2000) and expressed in milliliters per cubic meter of water filtered. A conversion factor of 1 ml displacement volume = 0.075 g dry weight and 34.2% of the dry weight = g carbon (Madhupratap et al. 1981) was used to convert the biovolume to carbon equivalents. Samples were immediately fixed and preserved in a 4% formaldehyde/seawater solution buffered with hexamine.

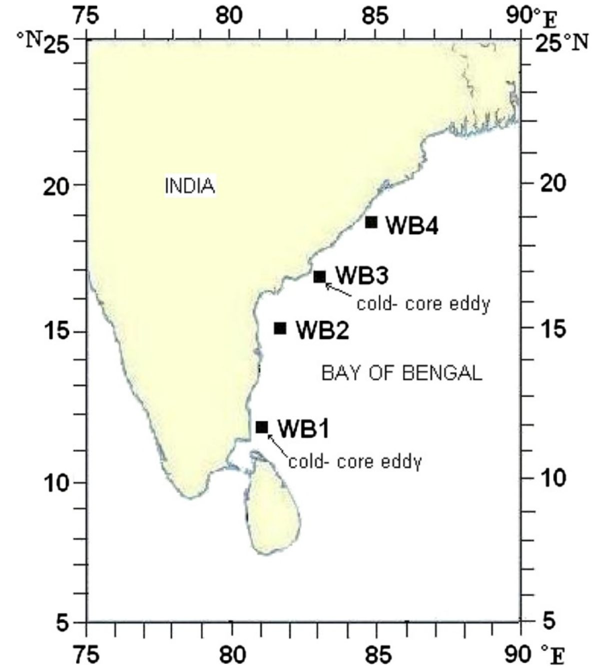

Figure 1 **Map of the study area and sampling locations in the western Bay of Bengal.**

Depending on the size of the sample, either the entire sample or aliquots of the zooplankton were used for enumeration. Generally, the entire samples from depths below 200 m were counted, while from the near-surface layers, they were split with a Folsom splitter to ≤50% and used for the analysis. Under a stereozoom microscope (Olympus, Japan, ×90), the animals were sorted from the original samples and identified into different taxonomic groups using standard identification keys (UNESCO 1968). Detailed taxonomic examination of the copepod species (Kasturirangan 1963; Tanaka 1956) was done from station WB2 to WB4 and expressed as individuals per cubic meter (ind./m^3) of water filtered. The marine Species Identification Portal (http://copepodes.obs-banyuls.fr), the Integrated Taxonomic Information System online database (http://www.itis.gov), and the World Register of Marine Species (http://www.marinespecies.org) were used to aid in the identification of copepod species.

Seawater salinity, temperature, and depth data recorded with the CTD profiler were used to assess their relationships with zooplankton biomass and populations. Water collected by 12-L GO-Flo bottles (General Oceanics, Miami, FL, USA) mounted on a CTD rosette was used to determine dissolved oxygen (DO) by Winkler titration, and inorganic nutrients such as nitrate, silicate, and phosphate were determined by standard methods (Grasshoff et al. 1983). Chl *a* from the top 120 m was measured by fluorometric method (Turner Designs, Sunnyvale, CA, USA, 10-AU-005-CE; UNESCO 1994).

Data analysis

Differences in biomass and numerical abundance of zooplankton between day and night samples were evaluated by the Wilcoxon test (Sokal and Rohlf 1981), and variations between depths and between stations were by Friedman analysis of variance (ANOVA). The Shannon-

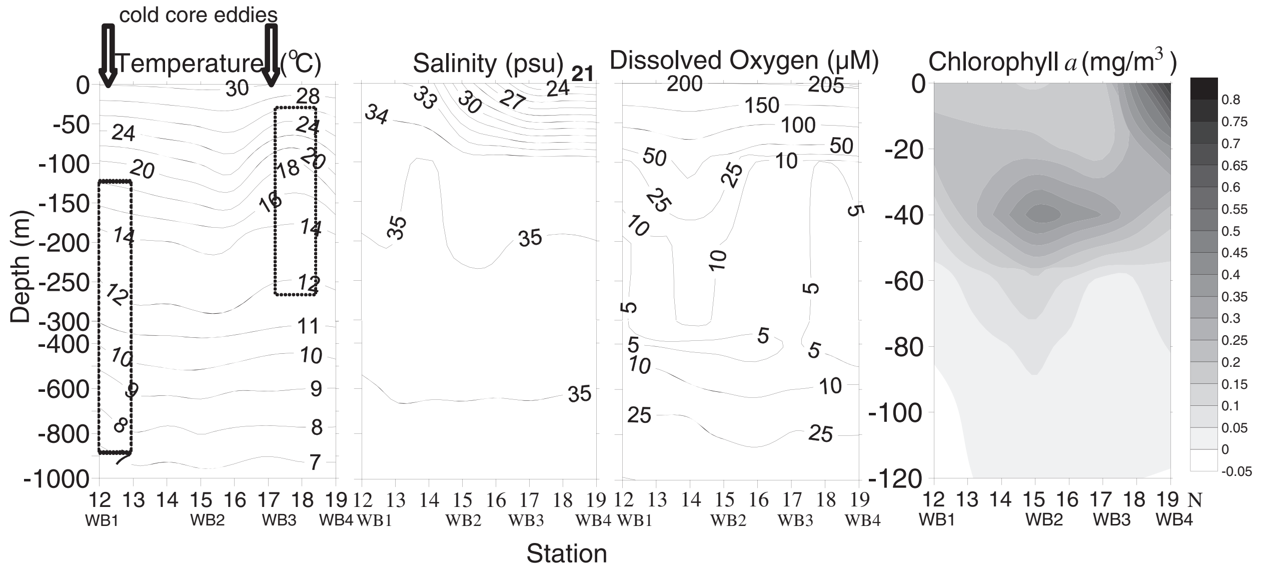

Figure 2 Spatial distribution of temperature, salinity, dissolved oxygen, and chlorophyll *a*.

Wiener diversity index (Omori and Ikeda 1984), species richness index (Margalef 1951), and species evenness index (Heip 1974) were used to calculate the diversity of the copepod community. Spearman correlations were computed to test the effect of environmental parameters on the zooplankton biomass and abundance and copepod species diversity indices. Cluster analysis was carried out using Ward's approach of linking Euclidean distances in Statistics 6.0 (Statsoft Inc. 2001, Tulsa OK, USA). This was done to check if there were differences in copepod species compositions within and outside the eddies.

Results

Hydrography

During the fall 2002 intermonsoon, the sea surface temperature in the western Bay was 30°C (Figure 2). At all locations, a steep thermocline was evident within the top 200 m. Surface salinity decreased from 34 to 21 psu towards the northern stations. It did not vary much below 100 m. The oxygen minimum zone (OMZ) with oxygen concentrations of 5 to 10 μM was found in the 120- to 500-m column. Pockets of DO concentrations of as low as about 3 to 4 μM were also observed at various depths

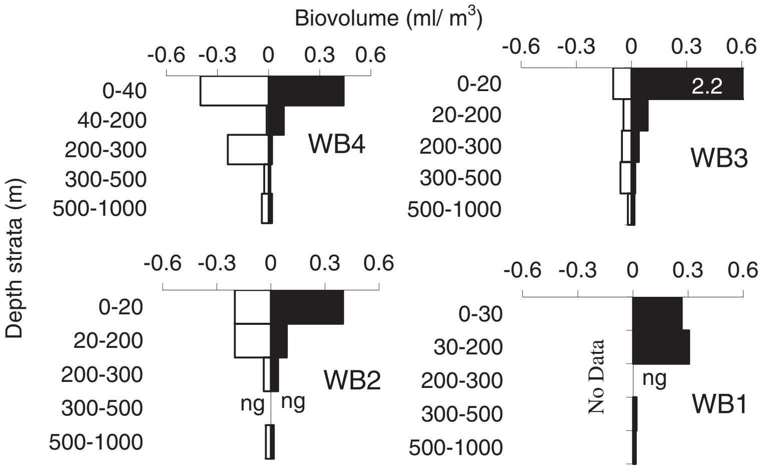

Figure 3 Vertical distribution of zooplankton biovolume during the day (white square) and night (black square). ng, negligible.

Table 1 Vertical distribution of zooplankton density (individuals/m^3) at different sampling locations in the western Bay of Bengal during day and night

Depth strata (m)	WB1 (12°N, 81°E)		WB2 (15°N, 82°E)		WB3 (17°N, 83°E)		WB4 (19°N, 85°E)	
	Day	Night	Day	Night	Day	Night	Day	Night
Mixed layer	ND	1,363	1,122	861	100	2,482	290	2,336
Thermocline	ND	412	601	182	9	165	12	145
BT to 300	ND	55	87	8	863	24	291	12
300 to 500	ND	28	2	14	276	41	259	9
500 to 1,000	ND	7	17	30	21	20	57	15

BT, base of the thermocline; ND, no data.

(data not shown in the graph) in the OMZ. Between depths of 20 and 200 m, the temperature and DO at WB1 and WB3 were lower than at the other two stations.

The Chl *a* concentration in the surface ranged from 0.14 mg/m^3 to its highest value of 0.77 mg/m^3 at the northernmost station, WB4. Subsurface Chl *a* maxima were observed at depths of about 20 to 40 m. The 120-m column Chl *a* concentration for WB1 to WB4 was 19, 13, 19, and 11 mg/m^2, respectively.

Two cold-core eddies along the sampling transect were identified from the *in situ* temperature-salinity data and remotely sensed sea-level anomaly data. Cold-core eddies are circulating water columns with cold water and a low sea level at their center. They are generally formed either by separation of a meander from a relatively swiftly moving main boundary current or due to force exerted by the wind stress curl and maintained by the balance among the pressure gradient, centrifugal, and Coriolis forces (Robinson 1983; Gopalan et al. 2000). In the northern hemisphere, where their movement is counterclockwise (cyclonic), the top layer diverges allowing cold, denser, nutrient-rich deep water to reach the surface. Hydrographic and certain biological characteristics of the Bay of Bengal eddies were described by Prasanna Kumar et al. (2007). Briefly, the effect of eddy was felt at up to 1,000 m at WB1 unlike at only up to 250 m at WB3. In these eddies, 1 μM nitrate as well as silicate isopleths showed shoaling within the upper 50 m. At the northernmost station (WB4), a silicate concentration of up to 16 μM was found that coincided with the highest surface concentrations of Chl *a* and primary production (45 mg C/m^3/day). Nutrient enrichment in the cold-core eddies also led to higher water column Chl *a* concentrations at WB1 and WB3.

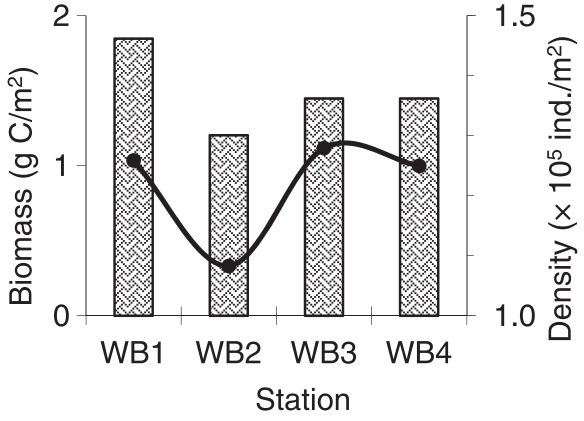

Figure 4 **Distribution of depth-integrated zooplankton carbon biomass (checkered box) and density (line with dot) at different sampling locations in the western Bay of Bengal.**

Zooplankton biovolume, biomass, and abundance

Over 80% of the zooplankton biovolume and abundance was concentrated above the thermocline, i.e., within the upper 200 m. At WB3, the surface peak value was conspicuously an order higher than at the neighboring stations during the night. Biovolume of zooplankton varied from 0.02 to 0.4 ml/m^3 during the daytime and from 0.01 to 2.2 ml/m^3 at night (Figure 3). Likewise, numbers were 2 to 1,122 and 7 to 2,482 ind./m^3 in respective day and night samples (Table 1). Statistically, no significant difference in either biovolume or abundance between the day and night samples ($p > 0.05$) was discernible. The water column-integrated zooplankton carbon biomass that ranged from 1.20 to 1.85 g C/m^2 (Figure 4) was highest at WB1, and the abundance which varied from (1.1 to 1.3) × 10^5 ind./m^2 was highest at WB3.

Vertical distribution patterns of taxonomic groups

Twenty-nine groups of mesozooplankton (Table 2) were identified in this collection. The number of groups was greater in the upper 200 m at all stations (Figure 5). Cladocerans were restricted to the surface layer (Table 2). Four other groups (anthozoans, ctenophores, cephalochordates, and echinoderms) were not found in any sample below 200 m. Out of the large number of groups identified, only eight groups dominated at most depths. As can be seen in Figure 6, chaetognath abundance was higher in the upper 200 m, although they were present in the entire water column. Other carnivores such as siphonophores and polychaetes were also found in higher proportions in the upper 300 m especially at WB3. In fact,

Table 2 The percentage abundance of mesozooplankton taxonomic groups in the upper 1,000 m

Category	Mixed layer	Thermocline	BT to 300 m	300 to 500 m	500 to 1,000 m
Amphipods	0.11	0.08	0.02	0.04	0.08
Anthozoans	0.01	0.21	-	-	-
Appendicularians	5.37	4.31	2.67	5.09	0.48
Bivalves	0.07	0.06	0.02	0.00	0.04
Cephalochordates	0.05	0.01	-	-	-
Cephalopod larvae	0.01	0.15	-	0.01	0.01
Chaetognaths	2.66	3.20	1.19	1.72	1.18
Cladocerans	0.67	-	-	-	-
Crustacean larvae	0.01	0.02	0.01	-	0.03
Copepods	80.54	76.58	67.29	87.16	89.04
Ctenophores	0.01	-	-	-	-
Decapods	0.68	0.70	0.62	1.54	0.16
Doliolids	0.15	0.48	0.15	0.03	0.04
Euphausid larvae	0.81	1.20	0.35	0.12	0.26
Echinoderm larvae	-	0.01	-	-	-
Fish eggs and larvae	0.11	0.15	0.07	0.06	0.04
Foraminifera	0.34	0.93	3.27	0.19	0.23
Gastropods	0.29	0.15	0.27	0.14	0.01
Invertebrate eggs	4.43	2.72	17.45	0.64	0.41
Isopods	0.03	-	-	-	0.01
Medusae	0.18	0.61	0.31	0.10	0.05
Mysids	0.06	0.04	0.03	0.02	0.02
Ostracods	1.39	2.17	2.93	1.64	6.71
Polychaetes	1.11	2.99	2.04	0.93	0.90
Pteropods	0.07	0.16	0.02	-	-
Radiolaria	-	0.06	0.07	0.06	0.03
Salps	0.09	0.22	0.01	0.04	0.02
Siphonophores	0.82	2.76	1.22	0.65	0.23
Stomatopods	-	0.04	-	-	0.01

BT, base of the thermocline.

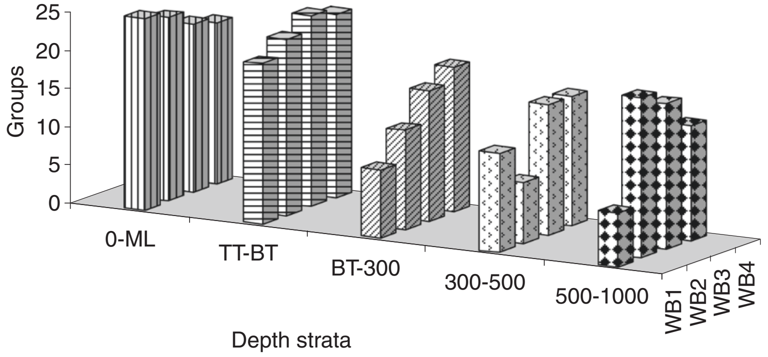

Figure 5 Station-wise distribution of the total number of zooplankton groups in various depth strata (m) sampled in the western Bay of Bengal. 0, surface; ML, mixed layer; TT, top of the thermocline; BT, base of the thermocline.

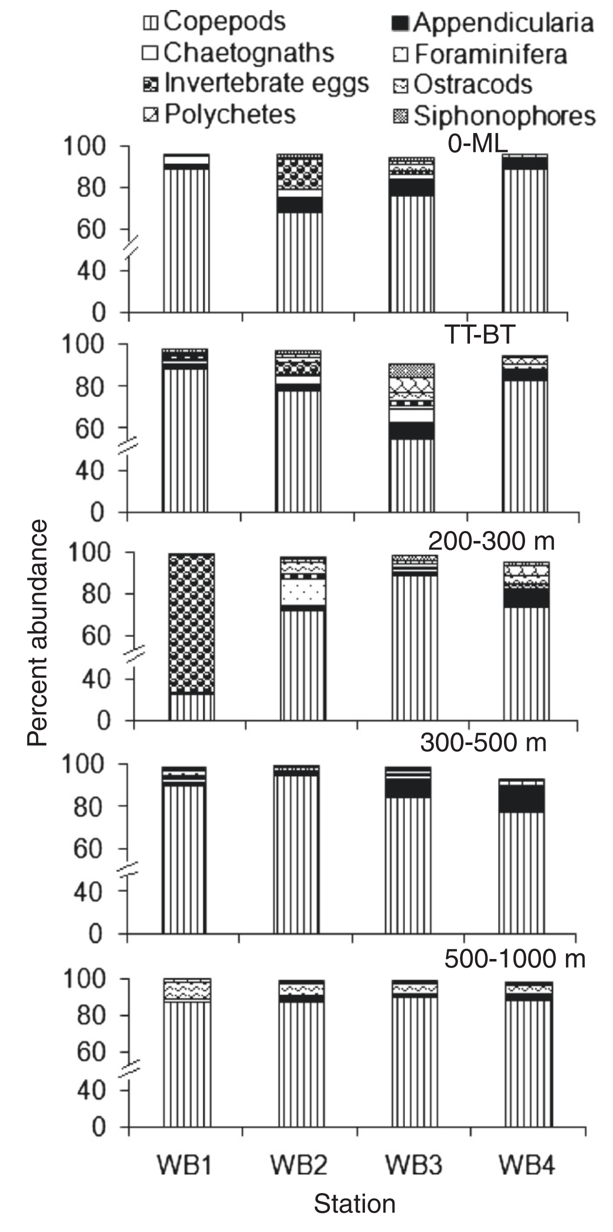

Figure 6 **Distribution of dominant zooplankton groups in various strata sampled in the western Bay of Bengal.** 0, surface; ML, mixed layer; TT, top of the thermocline; BT, base of the thermocline.

there was a swarm of siphonophores in the thermocline region of this station that housed the cold-core eddy. Appendicularians (at 0% to 10%) were relatively abundant in the upper 500 m at WB3 and to a lesser extent at WB4. The highest proportion of invertebrate eggs, which ranged from 0% to 65% in the top 3 strata, was observed in the 200- to 300-m stratum at WB1, where the other cold-core eddy existed. The largest percentage of foraminifera was also observed in this stratum. Ostracods (0.2% to 9.5%) were relatively more abundant in the 500- to 1,000-m stratum especially at WB1. The ubiquitous copepods representing around 34% to 95% of the total mesozooplankton were generally the most important taxon particularly at greater depths (Figure 6).

Copepoda

Copepods from five orders were recorded during the present study (Figure 7). Copepods from the order Calanoida dominated throughout the 1,000-m column contributing 63% to 78% to their total, followed by the Poecilostomatoida (15.7% to 24.5%). Calanoids were more abundant near the surface and in the 300- to 500-m stratum, a trend contrary to that of poecilostomatoids. Cyclopoid copepods which contributed 1.2% to 9.3% of the total copepods were preponderant in the 200- to 300-m stratum. Mormonilloida individuals (1.8% to 8.4%) were mostly found in samples from the deep stratum and thermocline. The harpacticoid population was rare to moderate (0.9% to 3.4%) and was mostly observed in the thermocline.

Copepod diversity was high from the surface to 1,000 m at all four stations examined. In total, 147 copepod species from 69 genera were identified in this study

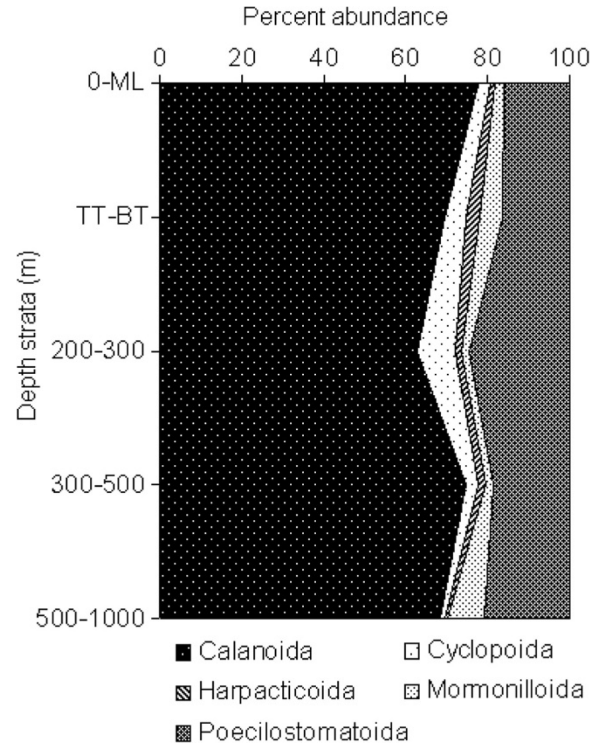

Figure 7 **Distribution of various orders of copepods in the upper 1,000 m in the western Bay of Bengal.** 0, surface; ML, mixed layer; TT, top of the thermocline; BT, base of the thermocline.

Table 3 Percentage distribution of copepod species in the upper 1,000 m at three locations in the Bay of Bengal

Species	WB2 (15°N, 82°E)					WB3 (17°N, 83°E)					WB4 (19°N, 85°E)				
	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
Calanoida															
Acartia amboinensis Carl,1907	-	-	-	-	-	-	-	-	-	-	0.80	-	0.05	1.47	-
Acartia (*Odontacartia*) *erythraea* Giesbrecht, 1889	-	0.70	-	-	-	-	-	-	-	-	-	-	-	-	-
Acartia negligens Dana, 1849[a]	-	-	2.0	-	-	-	-	-	-	-	1.65	0.30	-	0.04	-
Acartia (*Odontacartia*) *spinicauda* Giesbrecht, 1889[a]	-	-	-	-	-	11.0	-	-	0.70	0.30	12.0	-	0.15	1.43	-
Aetideopsis tumorosa Bradford, 1969[b]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.09
Aetideus acutus Farran, 1929	-	-	-	-	-	-	-	-	-	-	-	0.30	-	-	2.08
Euaugaptilus bullifer Giesbrecht, 1889	-	-	-	2.08	-	-	-	-	-	0.70	-	-	-	-	-
Euaugaptilus hecticus Giesbrecht, 1893	-	-	-	-	-	-	-	-	-	-	-	-	-	0.99	17.9
Euaugaptilus oblongus Sars G.O., 1905	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-
Euaugaptilus rigidus Sars G.O., 1907	-	-	-	-	-	-	-	-	-	1.20	-	-	-	-	-
Haloptilus longicornis Claus, 1963	-	-	-	-	-	-	0.70	-	-	-	-	0.70	0.49	-	0.69
Haloptilus ornatus Giesbrecht, 1893	-	-	2.0	-	0.90	-	-	-	-	-	0.16	-	-	-	0.69
Haloptilus spiniceps Giesbrecht, 1893	-	-	-	-	-	-	1.33	-	-	-	-	-	-	-	-
Chiridius longispinus Tanaka, 1957[b]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.69
Chirundina streetsii Giesbrecht, 1895	-	-	-	-	-	-	-	-	0.18	-	-	-	-	-	-
Euchirella amoena Giesbrecht, 1888[a]	-	-	-	-	0.09	-	-	-	-	-	-	-	-	-	-
Euchirella curticauda Giesbrecht, 1888[a]	-	-	-	-	-	0.33	-	-	-	-	-	-	-	-	-
Euchirella indica Wolfenden, 1906	-	-	-	-	-	-	-	-	-	0.36	-	-	-	-	0.69
Euchirella galeata Giesbrecht, 1888	-	0.70	-	-	-	-	-	-	-	-	-	-	-	-	0.69
Euchirella rostromagna Farran, 1929	-	-	-	-	0.09	-	-	-	-	-	-	0.35	-	-	-
Euchirella sp.	-	-	-	-	0.09	-	0.08	-	-	-	-	0.09	-	0.01	0.07
Gaetanus minor Giesbrecht, 1888	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.69
Gaetanus pileatus Farran, 1903	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.69
Undeuchaeta plumosa Lubbock, 1856	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.40
Undeuchaeta sp.	-	-	-	-	-	-	-	-	-	-	-	1.05	-	-	0.40
Valdiviella brevicornis Sars G.O., 1905	-	-	4.0	-	0.88	-	-	-	-	0.93	-	-	-	-	-
Arietellus giesbrechti Sars G.O., 1905	-	-	-	-	-	-	-	-	-	-	0.83	-	-	-	-
Canthocalanus pauper Giesbrecht, 1888[a]	2.72	-	-	2.08	0	1.0	0.67	-	10	-	-	-	0.49	1.43	-
Mesocalanus tenuicornis Dana, 1849[a]	0.54	0.70	-	-	-	-	-	-	-	-	-	-	-	-	-
Undinula vulgaris Dana, 1849[a]	2.72	-	-	-	-	4.16	0.15	2.31	3.35	-	-	0.04	-	10	0.69
Candacia bradyi Scott A., 1902[a]	-	-	-	-	-	-	-	-	-	0.36	1.81	0.70	0.05	2.86	0.69
Candacia catula Giesbrecht, 1889[a]	-	-	-	-	0.09	-	-	-	-	-	-	-	-	0.04	-
Candacia discaudata Scott A., 1909[a]	-	1.41	-	-	-	-	-	-	-	-	-	-	-	1.43	-
Candacia pachydactyla Dana, 1849[a]	-	-	-	-	-	2.78	-	-	-	-	-	-	-	-	-
Candacia truncata Dana, 1849[a]	-	-	-	-	-	-	-	-	-	-	-	-	0.81	0.04	-
Centropages alcocki Sewell, 1912	-	-	-	-	-	-	-	-	0.67	-	-	-	-	-	-
Centropages furcatus Dana, 1849[a]	-	-	-	-	-	-	-	-	0.18	-	-	1.40	0.98	-	-
Clausocalanus arcuicornis Dana, 1849[a]	-	-	-	-	-	-	-	-	-	-	-	0.04	-	-	1.38
Clausocalanus furcatus Brady, 1883	3.80	5.63	-	-	-	6.55	9.41	0.01	4.02	0.62	0.83	2.10	2.95	1.43	-
Clausocalanus pergens Farran, 1926	-	1.41	-	2.08	-	-	-	-	-	-	-	1.40	0.10	0.04	-
Farrania frigida Wolfenden, 1911	-	0.70	-	-	-	-	-	-	-	-	-	-	-	-	-
Subeucalanus crassus Giesbrecht, 1888[a]	-	-	-	-	-	1.98	0.2	-	-	-	-	-	0.07	-	0.02

Table 3 Percentage distribution of copepod species in the upper 1,000 m at three locations in the Bay of Bengal *(Continued)*

Subeucalanus monachus Giesbrecht, 1888[a]	8.15	5.63	-	-	1.76	0.33	12.2	0.01	2.37	0.31	1.65	5.69	0.05	7.06	-
Subeucalanus mucronatus Giesbrecht, 1888[a]	-	-	-	-	-	-	-	-	-	0.36	-	0.09	0.98	-	-
Eucalanus elongatus Dana, 1848[a]	-	0.70	6.0	8.33	3.51	0.33	1.28	7.02	0.18	-	0.16	2.75	0.66	0.04	0.69
Eucalanus sp.	-	2.11	-	-	-	-	0.08	-	-	-	3.31	-	-	-	-
Paraeuchaeta concinna Dana, 1849[a]	0.54	-	-	-	-	-	-	-	-	-	-	-	0.49	-	-
Euchaeta indica Wolfenden, 1905[a]	-	-	-	-	-	-	-	-	-	-	0.83	-	0.05	-	-
Euchaeta marina Prestandrea, 1833[a]	2.72	1.41	-	-	-	-	-	-	-	-	-	4.24	4.92	1.47	1.09
Euchaeta sp.	-	-	-	-	0.09	-	0.67	-	-	-	-	0.35	0.49	-	-
Hemirhabdus grimaldi Richard, 1893	-	-	-	-	-	0.33	-	-	-	-	-	-	-	-	-
Heterorhabdus abyssalis Giesbrecht, 1889	-	-	-	-	0.88	0.33	-	0.02	-	1.09	-	1.35	0.46	-	1.38
Heterorhabdus pacificus Brodsky,1950[b]	-	-	-	-	0.88	-	-	0	-	-	0.63	-	-	-	-
Heterorhabdus papilliger Claus, 1863[a]	-	-	8.0	2.08	1.76	-	1.33	0.01	-	-	-	-	0.10	0.30	0.69
Heterorhabdus sp.	-	-	4.0	2.08	-	-	-	-	-	-	-	-	-	-	-
Heterostylites longicornis Giesbrecht, 1889[a]	-	-	-	-	0.88	-	-	0.01	-	-	-	-	-	-	-
Lucicutia flavicornis Claus, 1863[a]	2.17	2.82	8.0	8.33	10.5	2.05	4.23	0.05	2.11	5.48	5.94	8.09	3.58	0.08	8.99
Lucicutia gaussae Grice, 1963	-	-	-	2.08	-	0.33	-	2.31	0.18	-	0.16	0.22	-	-	2.08
Lucicutia lucida Farran, 1908	-	-	-	-	-	-	-	-	-	-	-	-	-	0.49	1.21
Lucicutia magna Wolfenden, 1903	-	-	-	-	-	-	-	-	-	0.67	0.16	-	-	0.04	0.69
Lucicutia maxima Steuer, 1904	-	-	-	-	1.76	0.33	-	0.02	0.18	3.00	0.31	-	-	-	0.69
Mecynocera clause Thompson I.C., 1888	-	0.70	-	2.08	-	-	-	-	-	-	-	0.35	-	0.15	2.42
Gaussia princeps Scott T., 1894	-	-	-	-	-	-	-	-	-	0.36	-	-	-	-	-
Metridia brevicauda Giesbrecht, 1889	-	-	-	-	-	-	0.67	0.01	-	1.40	0.31	-	-	0.15	3.57
Metridia curticauda Giesbrecht, 1889	-	-	-	-	0.03	-	-	-	-	0.01	-	-	-	-	0.03
Metridia sp.	-	-	-	-	-	-	0.08	-	-	-	-	0.04	0.05	-	-
Pleuromamma gracilis Claus, 1863	-	-	-	2.08	-	1.0	0.67	0.04	0.18	0.67	0.47	0.74	0.15	0.11	6.34
Pleuromamma indica Wolfenden, 1905[a]	4.35	6.34	10	10.4	3.51	1.39	2.23	2.48	0.18	1.76	0.63	10.8	7.93	1.47	0.81
Pleuromamma robusta Dahl F., 1893	-	1.41	4.0	4.17	2.63	-	-	-	0.18	0.93	-	-	0.05	0.11	-
Pleuromamma sp.	-	-	-	-	-	-	-	-	-	0.31	0.83	2.45	-	-	-
Nullosetigera sp.	-	-	-	-	-	-	-	-	-	-	-	0.35	-	-	-
Acrocalanus gibber Giesbrecht, 1888[a]	-	-	-	-	-	-	0.74	6.94	0.67	-	0.83	-	2.95	5.72	-
Acrocalanus gracilis Giesbrecht, 1888[a]	3.26	0.70	-	-	0.88	-	-	0.01	4.02	-	-	-	-	1.43	0.69
Acrocalanus longicornis Giesbrecht, 1888[a]	-	-	-	-	-	1.72	0.15	4.62	0.67	-	0.16	-	0.98	2.86	-
Calocalanus pavo Dana, 1852[a]	1.09	-	-	-	-	-	1.33	0.01	-	-	-	-	-	-	-
Calocalanus pavoninus Farran, 1936	2.17	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02
Paracalanus aculeatus Giesbrecht, 1888[a]	2.72	1.41	-	-	-	4.16	-	0.01	0.18	-	1.65	1.44	0.98	5.72	-
Paracalanus indicus Wolfenden, 1905	8.70	1.41	-	-	-	2.38	5.51	11.6	26.8	-	0.31	0.44	5.96	4.29	0.69
Paracalanus parvus Claus, 1863[a]	9.24	1.41	-	2.08	0.88	5.88	4.67	2.3	8.70	-	-	0.61	7.38	2.86	2.08
Xanthocalanus crassirostris Tanaka, 1960[b]	-	-	-	-	2.63	0.30	-	-	-	0.40	-	0.30	-	-	-
Xanthocalanus pectinatus Giesbrecht, 1893[b]	-	-	-	-	-	-	-	-	0.20	-	3.3	1.40	-	-	-
Onchocalanus affinis With, 1915	-	-	-	-	-	-	-	-	-	0.31	-	0.04	0.98	1.43	0.69
Phaenna spinifera Claus, 1863	-	-	-	-	-	-	-	-	-	0.31	4.96	1.05	0.05	0.34	-
Calanopia elliptica Dana, 1849[a]	-	-	-	-	-	-	-	-	0.85	-	-	-	-	-	-
Labidocera acuta Dana,1849[a]	-	-	-	-	-	-	-	-	-	-	0.47	-	-	-	-
Labidocera minuta Giesbrecht, 1889	-	-	-	-	-	-	-	-	-	-	0.83	-	-	-	-

Table 3 Percentage distribution of copepod species in the upper 1,000 m at three locations in the Bay of Bengal *(Continued)*

Labidocera pavo Giesbrecht, 1889[a]	-	-	-	-	-	1.39	-	-	-	-	-	-	-	-	-
Labidocera pectinata Thompson I.C. and Scott A., 1903	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.69
Pontellina plumata Dana, 1849[a]	1.09	0.70	-	-	-	-	-	-	-	-	-	-	-	-	-
Pontellopsis scotti Sewell, 1932	-	-	-	-	-	1.39	-	-	-	-	-	-	-	-	-
Rhincalanus cornutus Dana, 1849	-	-	-	-	-	-	-	-	-	-	-	-	-	1.43	-
Lophothrix frontalis Giesbrecht, 1895	-	-	-	-	0.88	0.33	-	0	0.18	1.76	0.16	-	-	-	1.38
Scaphocalanus echinatus Farran, 1905	-	-	-	-	0.88	-	-	-	0.18	0.36	-	0.04	-	-	0.69
Scaphocalanus major Scott T., 1894	-	-	-	-	-	-	-	-	-	-	0.16	0.04	-	-	-
Scaphocalanus sp.	-	-	-	-	0.09	-	-	-	-	-	-	0.04	-	-	-
Scolecithricella bradyi Giesbrecht, 1888	-	-	-	-	-	-	-	-	-	-	-	0.35	-	-	0.40
Scolecithricella dentata Giesbrecht, 1893	-	-	-	-	-	-	-	-	-	-	-	0.09	-	-	-
Scolecithricella nicobarica Sewell, 1929	1.09	-	-	-	-	-	0.67	0.01	-	-	-	0.35	-	-	-
Scolecithricella vittata Giesbrecht, 1893	-	-	-	-	-	-	-	-	-	0.36	-	-	-	-	-
Scolecithricella sp.	-	0.70	4.0	-	-	-	-	-		-	-	-	-	0.11	-
Scolecitrichopsis ctenopus Giesbrecht, 1888[a]	-	-	-	-	-	-	-	-	-	-	-	0.35	0.49	-	-
Scolecicithrix danae Lubbock, 1856	-	2.11	-	-	-	-	-	-	-	0.36	-	2.54	3.94	-	1.79
Scolecithrix sp.[a]	-	-	-	-	-	-	-	-	0.18	-	-	-	-	-	-
Monacilla gracilis Wolfenden, 1911[b]	-	-	-	-	-	-	-	-	0.18	-	16.6	1.05	0.10	-	0.69
Monacilla tenera Sars G.O., 1907	-	-	-	-	-	-	-	-	-	0.73	-	-	-	-	-
Monacilla typica Sars G.O., 1905	-	-	-	-	5.27	-	-	-	2.19	-	-	0.35	-	-	-
Spinocalanus angusticeps Sars G.O., 1920	-	-	-	2.08	-	-	-	-	-	-	-	-	-	-	-
Spinocalanus magnus Wolfenden, 1904	-	-	-	2.08	-	-	0.08	-	-	-	-	0.25	-	-	-
Spinocalanus sp.	-	-	-	2.08	-	-	-	-	-	-	-	-	-	-	-
Temora discaudata Giesbrecht, 1889[a]	0.54	0.70	-	-	-	1.72	0.08	-	-	-	-	-	0.49	4.33	-
Temora turbinata Dana, 1849[a]	-	0.70	-	-	-	-	-	-	-	-	-	-	-	-	-
Temoropia mayumbaensis Scott T., 1894		0.70	-	-	-	1.72	4	0.01	-	0.98	0.83	1.40	0.10	-	-
Undinella spinifer Tanaka, 1960[b]	-	-	-	-	-	-	-	-	-	0.36	-	-	-	-	-
Harpacticoida															
Aegisthus mucronatus Giesbrecht, 1891	-	-	-	-	-	-	-	-	-	0.67	1.65	4.90	-	-	0.69
Clytemnestra scutellata Dana, 1849[a]	-	-	-	-	-	-	-	-	-	0.36	-	-	0.05	-	-
Euterpina acutifrons Dana, 1847[a]	-	-	-	-	-	-	-	-	-	-	0.83	-	-	-	-
Macrosetella gracilis Dana, 1847[a]	-	-	2.0	-	-	1.72	-	-	1.34	0.31	-	3.19	1.14	2.86	-
Microsetella norvegica Boeck, 1865[a]	1.63	-	-	-	-	-	0.08	-	-	-	-	-	-	-	-
Microsetella rosea Dana, 1848[a]	0.54	-	-	-	0	-	0	-	0.67	-	-	-	-	1.43	-
Mormonilloida															
Neomormonilla minor Giesbrecht, 1891	-	9.86	10	6.25	16.7	1.0	2.67	0.01	-	12.7	0.47	0.57	3.45	2.86	2.08
Mormonilla phasma Giesbrecht, 1891	-	0.70	2.0	-	5.27	-	0.67	0.01	0.18	0.62	-	2.80	0.10	-	-
Cyclopoida															
Oithona brevicornis Giesbrecht, 1891[a]	0.54	0.70	-	-	-	-	-	2.31	-	-	-	-	-	1.43	-
Oithona plumifera Baird, 1843[a]	5.43	2.11	-	-	-	1.39	1.33	2.31	0.67	-	-	-	-	-	-
Oithona setigera Dana, 1852	-	-	2.0	2.08	-	-	-	-	-	-	-	-	-	0.04	-
Oithona similis Claus, 1866[a]	5.98	8.45	8.0	4.17	1.76	-	6.08	0.01	3.35	-	0.16	4.68	3.99	0.04	1.38
Oithona spinirostris Claus, 1863	0.54	2.11	4.0	-	-	-	1.33	-	0.18	-	0.83	-	0.49	-	-
Oithona sp.	-	-	-	-	-	1.0	0.74	13.9	-	0.31	-	-	-	0.04	0.40

Table 3 Percentage distribution of copepod species in the upper 1,000 m at three locations in the Bay of Bengal *(Continued)*

Poecilostomatoida															
Corycaeus asiaticus Dahl F., 1894	-	-	-	-	-	-	-	-	-	-	0.83	-	0.54	-	-
Corycaeus danae Giesbrecht, 1891[a]	3.26	2.82	-	4.17	0.09	4.16	0.67	-	3.35	-	4.29	1.44	0.05	2.94	1.79
Corycaeus longistylis Dana, 1849	-	0.70	-	-	-	1.39	-	-	-	-	-	-	-	-	-
Corycaeus speciosus Dana, 1849[a]	1.09	1.41	2.0	-	-	7.60	2	2.32	1.34	-	0.83	-	0.98	2.86	-
Corycaeus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	4.29	-
Onychocorycaeus agilis Dana, 1849	-	-	-	-	-	-	-	-	-	-	-	-	0.49	-	-
Onychocorycaeus catus Dahl F., 1894[a]	2.17	2.11	2.0	-	-	2.78	0.67	0.01	-	-	1.81	0.70	0.49	1.51	0.69
Lubbockia squillimana Claus, 1863	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08	-
Oncaea gracilis Dana, 1852	-	-	-	12.5	15.8	-	-	-	-	12.0	-	-	-	-	2.77
Oncaea venusta Philippi, 1843[a]	15.8	12.0	16	12.5	16.7	20.4	25.4	37	16.4	10.5	6.26	15.5	28.3	11.9	11.1
Oncaea sp.	-	-	-	-	-	-	-	-	-	0.73	-	-	-	-	0.40
Triconia conifera Giesbrecht, 1891	0.54	-	-	-	-	2.05	-	-	2.01	0.62	-	-	-	-	-
Copilia mirabilis Dana, 1852	0.54	0.70	-	-	-	-	-	-	-	-	-	-	-	-	-
Copilia quadrata Dana, 1849	2.17	-	-	-	-	-	-	-	0.18	0.31	0.16	-	0.05	-	-
Copilia vitrea Haeckel, 1864[a]	0.54	0.70	-	-	-	-	-	-	-	-	-	-	-	-	-
Sapphirina auronitens Claus, 1863	-	0.70	-	-	-	-	0.67	-	-	-	-	0.70	-	-	-
Sapphirina intestinata Giesbrecht, 1891	-	-	-	-	-	-	-	-	-	-	-	0.35	-	-	-
Sapphirina nigromaculata Claus, 1863[a]	1.09	0.70	-	-	-	-	0.67	-	0.67	-	-	-	-	-	-
Sapphirina ovatolanceolata Dana, 1849[a]	-	-	-	-	-	-	-	-	-	-	-	-	0.49	-	-
Sapphirina sp.	-	-	-	-	-	-	0.67	2.31	-	-	-	-	-	-	-
Unidentified copepodites	-	10.6	-	2.08	0.88	1.39	1.41	0.02	-	33.8	16.8	6.60	6.86	2.86	5.25
Total individuals per cubic meter	664	309	41	8	21	947	68	383	126	20	899	60	88	92	31

Roman numbers I to V respectively correspond to strata in the mixed layer, thermocline, base of the thermocline to 300 m, 300 to 500 m, and 500 to 1,000 m. The absence of a species is indicated by a dash (–). [a]Species recorded in the Bay of Bengal prior to BOBPS; [b]new records for the Indian Ocean.

(Table 3). Of these, only 54 species (footnote a in Table 3) were reported from the Bay of Bengal region prior to BOBPS. Most other species were widely reported mainly from the Arabian Sea and South Indian Ocean. However, the following seven species of *Aetideopsis tumorosa*, *Chiridius longispinus*, *Heterorhabdus pacificus*, *Monacilla gracilis*, *Undinella spinifer*, *Xanthocalanus crassirostris*, and *Xanthocalanus pectinatus* are the first reports for the Indian Ocean. Some species such as *Euchirella curticauda*, *Haloptilus spinifer*, *Calanopia elliptica*, *Candacia pachydactyla*, *Centropages alcocki*, *Hemirhabdus grimaldi*, *Labidocera pavo*, *Pontellopsis scotti*, and *Scolecithricella vittata* were found only in the cold-core eddy at WB3 albeit in lower numbers. At this station, a large number of unidentified copepodites, mainly of calanoids, were found in the last stratum.

The Shannon diversity index (H') for copepod species was 3.39 to 4.41 (Figure 8). Species richness (d, range 2.32 to 4.84) was found to increase in the thermocline and deeper strata. Such variation was minimal with evenness (J') in a range of 0.73 to 0.93. Overall, H' and d were lower at WB3.

Vertical ranges of dominant copepod species in the upper 1,000 m

From the large number of species identified (Table 3), only 30 species accounted for ≥2% of the total copepod abundance, and their vertical distributions are depicted in Figures 9 and 10. In mixed-layer strata, *Acartia spinicauda* was the dominant species (Table 3). Other abundant species in the mixed layer included *Onychocorycaeus catus*, *Corycaeus speciosus*, and *Oithona plumifera*, and their proportion gradually diminished towards the deeper strata. Interestingly, the species of *Paracalanus* (*Paracalanus aculeatus*, *Paracalanus parvus*, and *Paracalanus indicus*), *Acrocalanus longicornis*, *Acrocalanus gracilis*, *Undinula vulgaris*, *Canthocalanus pauper*, and *Corycaeus danae* showed two peaks of higher abundance: one in the mixed layer and the other between the base of the thermocline (at 200 m) and 500 m. The relative abundances of

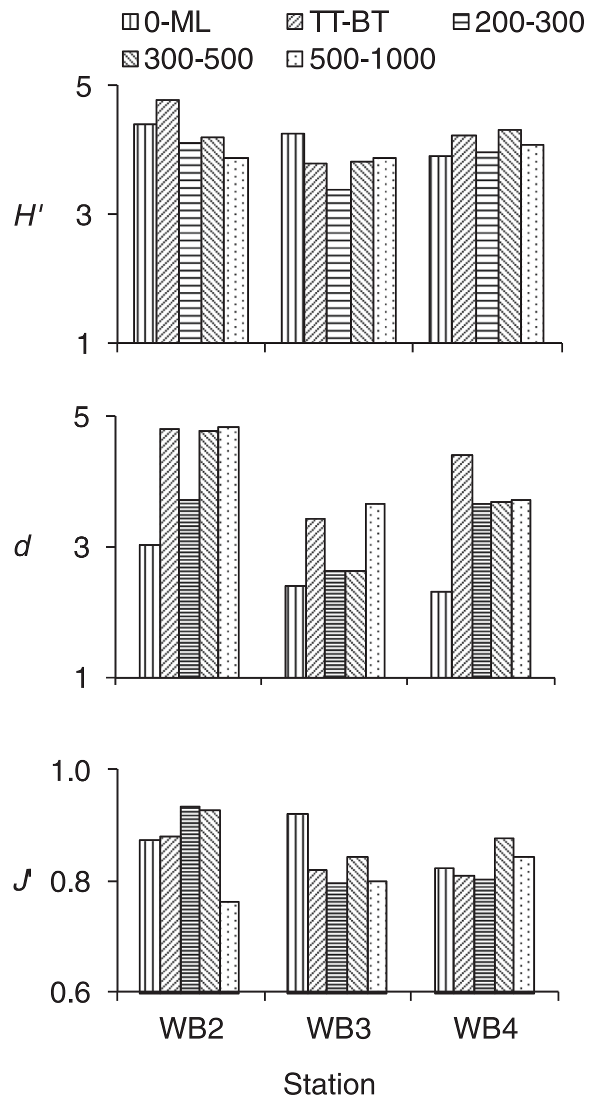

Figure 8 Variations in copepod species diversity, species richness, and evenness indices in the upper 1,000 m of western Bay of Bengal. 0, surface; ML, mixed layer; TT, top of the thermocline; BT, base of the thermocline.

Clausocalanus furcatus, *Subeucalanus monachus*, *Oithona similis*, and *Macrosetella gracilis* were prominent in the thermocline.

Proportions of *Acrocalanus gibber*, *Oithona* sp., *Euchaeta marina*, *Oncaea venusta*, *Pleuromamma indica*, *Pleuromamma robusta*, *Eucalanus elongatus*, and *Heterorhabdus papilliger* were higher in the subsurface (top of the thermocline and 500 m; Figure 10). Individuals of *Lucicutia flavicornis*, *Pleuromamma gracilis*, *Oncaea gracilis*, *Euaugaptilus hecticus*, *Mormonilla phasma*, and *Neomormonilla minor* increased in proportion with increasing depth.

A cluster analysis of the major copepod species revealed assemblages unique to stations. At <10% Euclidean distance, five clusters made up of at least five species were formed (Figure 11). Further, there were two stand-alone species - *O. venusta* and *P. indicus*. Incidentally, these two were the most abundant species in the western Bay with higher abundances at WB3 which is within the cold-core eddy. *A. spinicauda*, *A. gibber*, *A. longicornis*, *U. vulgaris*, *C. speciosus*, and *Oithona* sp. from cluster I and several species (*P. parvus*, *C. furcatus*, and *S. monachus*) from cluster IV also showed a peak at WB3, albeit in lesser proportions. Cluster II contained species such as *E. hecticus*, *Monacilla gracilis*, *E. marina*, *Phaenna spinifera*, *P. gracilis*, *M. gracilis*, and *P. aculeatus* which had the highest relative abundances at the northernmost station WB4. On the contrary, clusters III and V housed species like *A. gracilis*, *O. catus*, *M. phasma*, *O. plumifera*, *H. papilliger*, and *P. robusta*, the relative abundances of which were greatest at station WB2.

Correlation analysis

Zooplankton biovolume and abundance and the number of groups showed significant positive correlations with temperature, DO, and Chl *a*, and negative correlations with salinity (Table 4). Diversity indices correlated poorly with the environmental parameters.

Discussion

Our results indicate that the mesozooplankton in the western Bay of Bengal are mostly concentrated in the mixed layer during the fall intermonsoon, irrespective of day or night. During this season, there is pronounced secondary solar heating (Narvekar and Prasanna Kumar 2006) as was clearly evidenced from sea surface temperatures of >29°C at all locations. Monsoonal runoff and increased river outflow (Prasanna Kumar et al. 2007) lowered the surface salinity to as low as 21 psu. The strong thermohaline stratification hinders mixing of surface waters and therefore limits the availability of essential nutrients such as nitrate in the top 20 m. High surface Chl *a* and primary production in the northern region driven by fluvial silicate and phosphate (Sardessai et al. 2007) maintained the observed zooplankton standing stocks at WB4.

As the East India Coastal Current moves from north to south in September to October (Shetye et al. 1996), with no possibility of advection, nutrient concentrations in the surface layer are low to nil towards the southern stations. However, Sardessai et al. (2007) and Prasanna Kumar et al. (2007) reported the persistence of a shallow cyclonic eddy at WB3 and another one that was as deep as 1,000 m at WB1. Those studies also showed that cold-core eddies led to the shoaling of a nitracline into the mixed layer and enhanced Chl *a* and primary production. Paul et al. (2008) reported a typical tropical phytoplankton community mostly comprising centric diatoms that prefer high nutrient regimes and have shorter

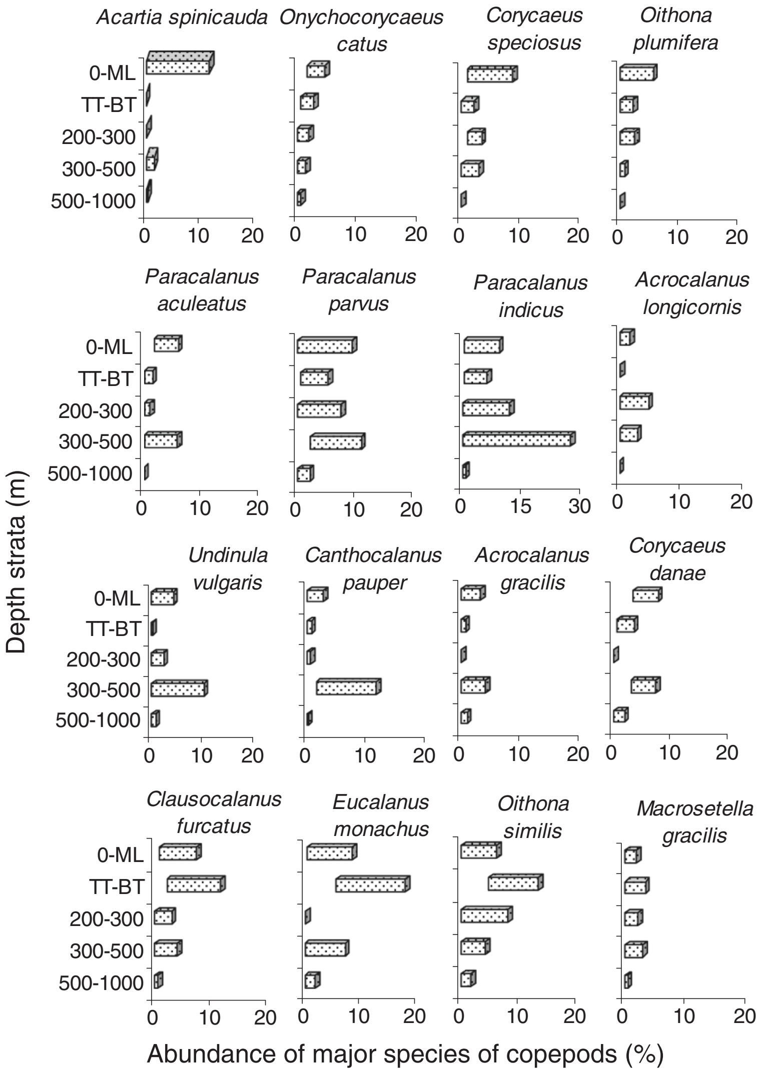

Figure 9 Vertical ranges (%) of dominant copepod species (epipelagic species) in the western Bay of Bengal. 0, surface; ML, mixed layer; TT, top of the thermocline; BT, base of the thermocline.

doubling times of the order of hours (*sensu* Sheldon 1984). Maximum biomass obtained in the western Bay was higher than that reported by Nair et al. (1981). The biomass observed in our study was comparable to those from more productive coasts off Somalia, Saudi Arabia and southwestern India (Madhupratap and Parulekar 1993). We attribute the higher zooplankton biomass levels and abundances at WB3 and WB1 to an outcome of their rapid reproduction and sustenance on diatoms for a long time in the cold-core eddies that have lifespans of around 1 to 5 months (Nuncio and Prasanna Kumar 2012). Ample evidence is available from the Gulf Stream (Beckmann et al. 1987) and Gulf of Mexico (Ressler and Jochens 2003), where higher zooplankton biomass associated with enhanced nutrient and Chl *a* concentration in cold-core eddies was reported. Only a couple of such observations are available from the Bay of Bengal (Muraleedharan et al. 2007; Fernandes 2008).

Sharp declines in zooplankton biomass and density at subsurface depths are a typical feature of tropical oceans (Vinogradov 1997). However, the vertical distribution of zooplankton communities in this Bay is apparently governed by an extremely stable water column. Such a phenomenon was observed by Giller (1984) and also can be inferred from the ANOVA results that show significant impacts of temperature ($p < 0.05$) and salinity ($p < 0.05$) on the vertical distribution. Above the thermocline, many groups such as appendicularia, carnivorous chaetognaths, polychaetes, siphonophores, and phagotrophic foraminifera substantially contributed to the biomass and abundance. Their positive correlations with Chl *a* suggest that there is a close coupling first with the phytoplankton

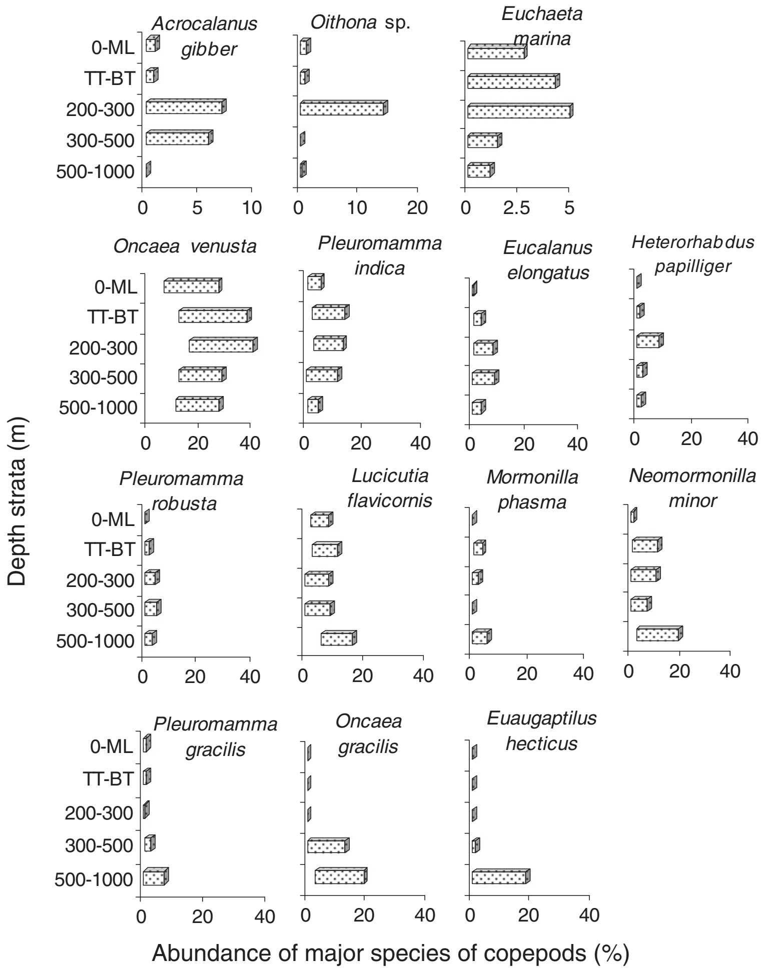

Figure 10 Vertical ranges (%) of dominant copepod species (epi- and mesopelagic species) in the western Bay of Bengal. 0, surface; ML, mixed layer; TT, top of the thermocline; BT, base of the thermocline.

biomass and probably also with microzooplankton and even bacteria. As also proposed by Stoecker and Capuzzo (1990), it is possible to suggest from our results that micro-herbivorous plankton do form a major component of zooplankton food. This is because we found up to two billion bacterial cells and 11,000 microzooplankton per liter in the western Bay during this season. In addition, the rivers also bring in microplankton that might serve as forage for the neritic mesozooplankton (Fernandes et al. 2008). As such, cladocerans and appendicularians are capable of fine filtering even bacteria in their diet (Sorokin 1981). On the other hand, sinking detritus may adequately provide for omnivorous ostracods and copepods which were quite numerous in the mesopelagic zone as was put forth by Lampitt et al. (1993) and Steinberg (1995). It is suggested that increased abundances of *P. indicus*, *P. parvus*, *C. furcatus*, *S. monachus*, and *O. venusta* might reflect a rich nutrition status in eddy regions.

Swarming and migration of carnivores, such as siphonophores, polychaetes, and chaetognaths that made up most of the biovolume in the productive cold core ring at WB3, for feeding at night were previously recognized (Strzelecki et al. 2007). The large swarm of siphonophores was peculiar not only in the mixed layer but along the entire cold-core eddy depth of 0 to 300 m, and this led to a mismatch in total zooplankton carbon biomass and individual abundances in the upper 1,000 m at this station. This is because gelatinous siphonophores have a very high biovolume: carbon ratio (Bone 1998). The occurrence of invertebrate eggs at depths of 200 to 300 m at WB1 and up to 34% calanoid copepodites in the deepest stratum of WB3 suggests that both of these cold-core eddies are zones of intense zooplankton spawning activity. Large calanoid copepods such as *Subeucalanus crassus* and *Calanoides carinatus* were reported to rest at mesopelagic depths in the western Arabian Sea and surface during upwelling (Smith and Madhupratap 2005). As Madhupratap (1999) suggested, unfavorable conditions related to food and salinity do prevail in the tropics and may require copepods to hibernate. However, such cases are yet to be investigated.

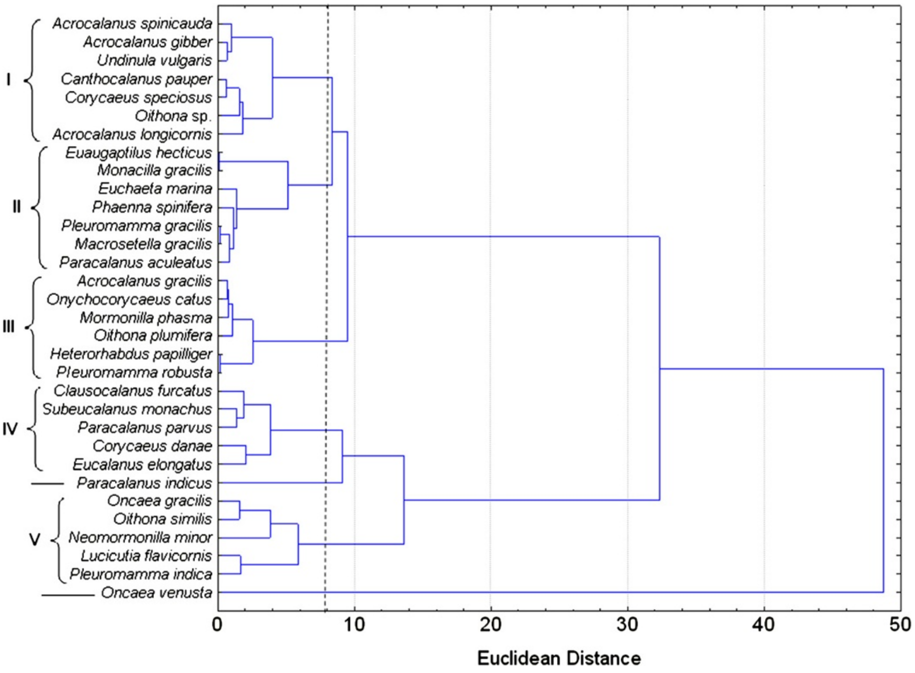

Figure 11 **Cluster analysis of major copepod species found at sampling stations during the study.**

As the two eddies spanned a diameter of around 200 to 300 km, they may also have influenced the primary productivity of neighboring stations, apparently giving rise to insignificant variations in the biomass/abundance of zooplankton among the four stations sampled. Beckmann et al. (1987) reported that aging eddies harbored biomass levels similar to those of the surrounding waters due to organisms migrating away from the core to maintain a similar temperature.

The vertical distribution pattern of copepod species was also mostly dependent on the hydrography of the water. For instance, from the several copepod species identified from the western Bay, only nine with rare abundances were found to be uniquely associated with the cold-core eddy. It is therefore implicit that depth, rather than the cold-core eddies, causes niche separation among copepod species. Like in many other studies (Tranter and Abraham 1971; Dahms et al. 2012), the estuarine copepod *A. spinicauda* preferred lower salinity surface waters found at northern stations of the western Bay. Similarly, poecilostomatoids like *Corycaeus catus* and *C. speciosus*, and the cyclopoid *O. plumifera* were restricted to warmer waters found in the mixed layer. Similar to observations by Siokou-Frangou and Papathanassiou (1989), we found an abundance of the Oncaeidae, Oithonidae, and Corycaeidae in the coastal regions of this Bay. Although the significance of *O. venusta* in the Bay is yet to be established, it is suggested that such preponderance of nutritionally versatile forms may be important in the overall biogeochemistry of the region as also reported by Böttger-Schnack (1996).

Abundances of epipelagic species such as *C. furcatus*, *O. similis*, and *M. gracilis* found in the 1,000- to 500-m stratum suggest favorable temperature ranges (Wiebe et al. 1988; Madhupratap and Haridas 1990). They may

Table 4 Correlation coefficient of major environmental and mesozooplankton parameters

Parameter	Number	Spearman *R*			
		vs. temperature	vs. salinity	vs. dissolved oxygen	vs. chlorophyll *a*
Biovolume	20	0.83*	−0.73*	0.50*	0.83*
Carbon biomass	20	0.22	−0.54*	0.28	0.39
Abundance	20	0.82*	−0.50*	0.34	0.73*
Groups	20	0.69*	−0.72*	0.46*	0.79*
Shannon diversity	15	0.43	−0.29	0.41	0.41
Species richness	15	−0.35	0.26	−0.06	−0.36
Evenness	15	0.33	0.03	0.14	0.19

*Significant at $p < 0.05$.

also be adapted to living at low oxygen concentrations along with copepods such as *A. gibber*, *Oithona* sp., *E. marina*, *O. venusta*, *P. indica*, *P. robusta*, *E. elongatus*, and *H. papilliger* that had higher numbers throughout the OMZ. Similarly, higher abundances of *L. flavicornis*, *P. gracilis*, *O. gracilis*, *E. hecticus*, *M. phasma*, and *N. minor* in the meso/bathypelagic precincts are indicative of the larger role they play in carbon mineralization with lower metabolic costs (Childress 1975).

The high diversity of copepods observed throughout the 1,000-m water column at eddy as well as non-eddy stations in this warm pool region could be attributed to the tropical and moderately oligotrophic nature of the Bay. The smaller number of species in the topmost layer was mostly attributed to strong stratification (Prasanna Kumar et al. 2007). From available studies (see Krishnamurthy 1967; Lawson 1977; Nair et al. 1981; Rakhesh et al. 2006) prior to BOBPS on mesozooplankton communities in the Bay, it is clear that the number of recorded copepod species was only 54. This was largely due to sampling mainly near the coast and/or from the upper 200 m. We recorded an additional 93 species. The spatially and vertically extended sampling attempt used in this study highlights the occurrence of many more species of copepods in the Bay. Although the western Bay supports a higher mesozooplankton biomass (1.5 g C/m^2) in the upper 1,000 m during the fall intermonsoon, the number of copepod species was lower compared to the central transect (1.3 g C/m^2, 170 species; Fernandes 2008). Nonetheless, the western transect is much richer in copepod species during this season than during summer (Fernandes and Ramaiah 2009). Notably, the generic and species compositions of copepods in general were quite similar to reports from the Arabian Sea by Madhupratap and Haridas (1990) and Madhupratap et al. (2001).

Conclusions

It is apparent that cold-core eddies are special oceanic features that sustain zooplankton grazer populations due to nutrient enrichment and subsequent phytoplankton production in the euphotic zone. Mesoscale cold-core eddies assume importance in stratified bays such as this one where production is severely nutrient-limited. The reporting for the first time of over 90 copepod species from this study, including 7 species as the first records from the Indian Ocean region, is an indication that copepod species deserve to be examined in greater detail from the deep realms of the Bay of Bengal.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

VF and NR collected the samples. VF analyzed and drafted the manuscript. NR obtained grants from the Ministry of Earth Sciences and CSIR-NIO and read and edited the manuscript. Both authors read and approved the final manuscript.

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