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Research Article

Aggregation of *Euphausia sibogae* during Summer Monsoon along the Southwest Coast of India

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The influence of environmental parameters on the spawning aggregation of *Euphausia sibogae* was investigated along the southwest coast of India during the peak phase of summer monsoon 2005. The prevailing ecological conditions between the aggregation period (peak phase) and non-aggregation period (early phase) were also compared. The aggregation was observed at station 1 (8°N; 76.5°E, 480 ind$\cdot$m^{-3}) and 6 (10°N; 75.5°E, 839 ind.m^{-3}) during the peak phase of the summer monsoon. Eggs (14769 eggs m^{-3}) and different developmental stages were observed in higher abundance at station 6. The physicochemical conditions indicated that the aggregation coincided with the upwelling. The nutrient enrichment due to the upwelling triggered phytoplankton blooms, and this appeared to provide a conducive environment for spawning and development of *E. sibogae*.

1. Introduction

The euphausiids (Class: Crustacea; Order: Euphausiacea) are keystone members of planktonic food webs in the coastal and oceanic waters. They act as a link between primary and tertiary producers in the pelagic food web. Being omnivores, their diet includes a broad spectrum of food items, ranging from phytoplankton to small zooplankton to detritus, and even some higher trophic level consumers. Euphausiids are considered as one of the potential prey items for many fish species especially tunnies. According to Roger [1], they contribute to about 15.5% of the total crustacean prey items of *Thunnus albacares* and *Katsuwonus pelamis* from the Western Indian Ocean. The young ones (100–119 mm) of *Selar crumenophthalmus* prefer 59.9% euphausiid as their main food item. Thus, studies on euphausiids, especially their survival and reproductive strategies are attaining greater importance among researchers. Early studies on euphausiids of the Indian Ocean were carried out by many researchers [2–8]. Spatial and temporal variations of euphausiid population along the southwest coast of India have been described by Mathew et al. [9].

Spawning and rapid development of euphausiid characterize the high potential of growth to supply energy and matter to higher trophic levels. Along the southwest coast of India, the breeding of euphausiid species usually coincides with the coastal upwelling during the summer monsoon [10]. The present study aimed to understand (a) the ecological conditions prevailing during the breeding period of *E. sibogae*, (b) the relationship between phytoplankton

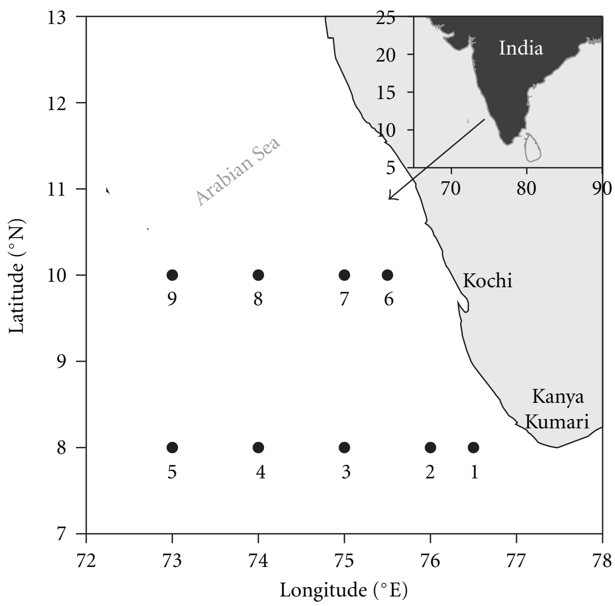


Figure 1: Location of sampling stations.

standing crop and breeding behaviour of *E. sibogae,* and (c) the variations in the ecological conditions between the breeding and nonbreeding periods.

Coastal upwelling is a regular phenomenon occurring off the southwest coast of India during the summer monsoon season when the winds blow predominantly from the southwest. During this season, the nutrient concentrations increase in the euphotic zone, not only as a result of upwelling of cool nutrient-rich water from subthermocline depths, but also through inputs from the large volumes of riverine water outflows. The substantial increases in near-surface nutrient concentrations stimulate increased biological production along the coast [11–13]. Enhanced primary production has also been reported during this period [14, 15]. Many secondary producers like cladocerans, ostracods, decapods, thaliaceans, chaetognaths, and siphonophores have also been found in abundance, often forming swarms/aggregations during this season [14].

2. Study Area and Methodology

Two sets of samples were collected onboard *FORV Sagar Sampada* during the summer monsoon months of 2005. The first set of sampling was carried out in the early summer monsoon (May-June) at the time of the onset of upwelling, and the second set of sampling was carried out in the late summer monsoon (August-September) at the peak phase of upwelling (Table 1). Stations were fixed along two transects (along 8° and 10°N), perpendicular to the southwest coast of India (Figure 1).

A seabird CTD was used to collect temperature-salinity profiles. Salinity was calibrated against water samples analyzed by an Autosal onboard. Sea surface temperature (SST) was measured using a bucket thermometer. For the estimation of dissolved oxygen (DO) and nitrate, water samples were collected from 11 standard depths (0, 10, 20, 30, 50, 75, 100, 150, 200, 250, and 300 m) using Niskin samplers mounted on CTD rosette. DO was estimated by Winkler's method, and nitrate concentrations were analyzed using a SKALAR autoanalyzer.

For estimation of chlorophyll *a* and phytoplankton abundance, water samples were collected from 7 discrete depths (0, 10, 20, 50, 75, 100 and 120 m). One liter of water was filtered through a GF/F filter (pore size 0.7 μm), and chlorophyll was extracted with 10 mL of 90% acetone and estimated spectrophotometrically (Perkin-Elmer UV/Vis at 640 nm). Total water column (upper 120 m) chlorophyll *a* (mg m^{-2}) concentrations were calculated by integrating the profile values.

Quantitative analyses of phytoplankton (>5 μm) were carried out on 500 mL of seawater samples from each depth, initially fixed in 1% Lugol's iodine and then preserved in 3% seawater formalin. The preserved samples were stored in the dark at low temperature until they could be enumerated. A settling and siphoning procedure was followed to obtain 20–25 mL concentrates. One mL of the concentrated sample was examined microscopically (in triplicate) under a stereoscope binocular inverted microscope (magnification 100x) in a Sedgewick-Rafter counting chamber. Phytoplankton groups were identified based on standard references [16, 17].

Mesozooplankton was collected using a Multiple Plankton Net Sampler (MPN, Hydrobios, 0.25 m^2 mouth area, 200 μm mesh size). The net was hauled vertically sampling the wind-mixed layer and the thermocline (the lower depth of the wind-mixed layer depth was that at which the water temperature was 1°C lower than the SST, and the base of the thermocline was taken as the depth of the 15°C isotherm). The hauling speed was limited to one metre per second. At the "aggregation stations" (station 1 and station 6, where the aggregation of *E. sibogae* was observed), samples were collected at 6-hourly intervals over a 24 hour period to assess the quantitative implications of diel vertical migration (DVM). During early phase, diurnal observation carried out along 10°N transect only. The mesozooplankton biomass (mL m^{-3}) was determined by displacement volume prior to preservation [18, 19]. After measuring the displacement volume, the samples were preserved in 5% formalin-seawater for qualitative and quantitative analysis. Samples >5 mL displacement volume were subsampled either by splitting with a Folsom plankton splitter or by subsampling using a Stempel pipette. Each sample (or subsample) was sorted into different taxonomic groups [20, 21] under a dissecting stereomicroscope and abundance estimated as ind$\cdot m^{-3}$.

3. Results

3.1. Hydrography. During the early and peak phases of summer monsoon, the average SST recorded from the study region was 30.5 ± 0.2 and 27 ± 1°C, respectively. The surface waters were relatively more saline during the peak phase (av. 35.2 ± 0.49) than those during the early phase (av. 34.5 ± 0.3) except at the coastal stations. Significant variation was observed in the distribution of SSS between the two phases

Table 1: Details of sampling during early and peak phases of summer monsoon 2005. (Values in the parenthesis denotes the early phase.)

Station no.	Position	Sampling date	Sampling time (hrs)	Sampling depth intervals (m)
1	8°N and 76.5°E	11.09.05 (27.05.05)	08 : 30, 11 : 50, 18 : 30, 22 : 30 (09 : 00, 12 : 00, 18 : 09)	162–28, 28–0 (152–29,29–0)
2	8°N and 76°E	11.09.05 (28.05.05)	02 : 05 (10 : 00)	140–28, 28–0 (149–20,20–0)
3	8°N and 75°E	10.09.05 (28.05.05)	16 : 50 (07 : 45)	136–20, 20–0 (163–26,26–0)
4	8°N and 74°E	10.09.05 (28.05.05)	08 : 45 (16 : 35)	146–40, 40–0 (161–37,37–0)
5	8°N and 73°E	09.09.05 (29.05 05)	08 : 30 (05 : 30)	142–38, 38–0 (184–24, 24–0)
6	10°N and 73°E	08.09.05 (01.06.05)	08 : 30 (14 : 55)	127–55, 55–0 (174–35,35–0)
7	10°N and 74°E	07.09.05 (01.06.05)	19 : 00 (23 : 20)	150–41, 41–0 (153–53, 53–0)
8	10°N and 75°E	07.09.05 (02.06.05)	07 : 50 (07 : 20)	140–24, 24–0 (175–33, 33–0)
9	10°N and 75.5°E	06.09.05 (02.06.05)	07 : 30, 12 : 30, 18 : 30, 23 : 30(07 : 15, 12 : 00, 18 : 15, 00 : 10)	156–13, 13–0 (158–22, 22–0)

($P < 0.05$). At station 6, SSS values showed a decreasing trend (∼1.2) during the peak phase (Figure 2(d)).

The seasonal variation of hydrographical features at stations 1 and 6 were remarkable during this study. During the early phase, the SSTs recorded at both stations (1 and 6) were 30°C whereas during the peak phase it dropped by 3°C and 5°C at stations 1 (27°C) and 6 (25°C), respectively. Surface salinity values recorded during the early phase were 34.95 at station 1 and 35.4 at station 6. During the peak phase, it increased by 0.2 at station 1 and decreased by 1.8 at station 6 (Figures 3(c) and 3(d)). The mixed layer depth (MLD) was relatively deep during the early phase (30 and 22 m at stations 1 and 6, resp.) compared to the peak phase (25 and 13 m stations 1 and 6, resp.).

During the early phase, the upwelling of cool, oxygen-deficient, nutrient-rich subsurface water (DO: <190 μM and NO_3: > 2 μM) was observed from the oceanic (∼50 m) to the coastal (∼20 m) stations along 8°N whereas, along the 10°N transect, the upwelling signatures (DO: <180 μM and NO_3: >2 μM) were observed in the surface layers of the coastal station. Similarly, during the peak phase of the monsoon, the effects of upwelling were more clearly seen in the emergence of low-DO/high-nitrate water at the surface of the coastal waters both the 8° and 10°N transects (Figure 4).

The surface waters were well oxygenated (225 μM) during the early phase, with the upper limit of the nitracline and oxycline at around 50 m at station 1, but both were much shallower (∼10 m) at station 6. During the peak phase of the monsoon, station 1 was characterised by more or less uniform concentration of DO and NO_3 in the upper 20 m water whereas, at station 6, sharp gradient was observed in DO and NO_3 concentrations from the surface layers. At station 1, nitrate concentration was higher during the peak phase compared to the early phase. At station 6, the depth profiles of both nitrate and oxygen showed much clearer evidence of upwelling during the peak phase of the monsoon.

3.2. Chlorophyll a and Phytoplankton. In the mixed layer, concentration of chlorophyll *a* varied between 2.61 and 5.21 mg m^{-2} during the early phase and increased to 14.33 and 9.01 mg m^{-2} during the peak phase at stations 1 and 6, respectively (Figure 5). In the subsurface water column (MLD to 120 m), the concentrations of chlorophyll *a* were almost similar during both of the seasons.

During the early phase, total phytoplankton cell densities in the surface water at station 1 and 6 were 3660 and 22800 cells L^{-1}, respectively. Three major groups of phytoplankton occurred at station 1 during the early phase (blue-green algae, diatoms, and dinoflagellates) in more or less similar cell densities (1420 cells L^{-1} (38%), 1100 cells L^{-1} (30%), and 1140 cells L^{-1} (31%), resp.). In contrast, the phytoplankton community was dominated by blue-green algae (>85%, 19400 cells L^{-1}) at station 6 followed by diatoms (13.3%, 3040 cells L^{-1}) and dinoflagellates (1.5%, 360 cells L^{-1}) (Table 2).

Phytoplankton cell density increased substantially during the peak phase compared to the early phase. At station 1, it recorded a 4-fold increase from early (3660 cells L^{-1}) to peak phase (15140 cells L^{-1}). However, at station 6 the variability was only marginal (early phase: 22800 cells L^{-1}, peak phase: 29080 cells L^{-1}). Abundance of green flagellates in the phytoplankton community was the peculiar feature observed during the peak phase. Green flagellates (5000 cells L^{-1}) and diatoms (6250 cells L^{-1}) were the dominant components at station 1, whereas at station 6, along with green flagellates (4620 cells L^{-1}, 15%) and diatoms (15780 cells L^{-1} 55%), dinoflagellates (8680 cells L^{-1}, 29%) were also observed during this phase. Variations in the abundance of green flagellates between stations were only marginal during the peak phase (Table 2). (See Habeebrehman et al. [22] for distribution of chlorophyll *a* and abundance and composition of phytoplankton community during these periods.)

3.3. Mesozooplankton Biomass and Abundance of Euphausiids. The average mesozooplankton biomass recorded during the early phase was 0.52 ± 0.2 mL m^{-3}. In the wind mixed layer, the highest biomass was recorded at station 2 (0.9 mL m^{-3}), followed by station 6 (0.74 mL m^{-3}) (Figure 6). Along the 8°N transect, the average biomass recorded was 0.55 ± 0.2 mL m^{-3}, as against 0.49 ± 0.24 mL m^{-3} recorded along the 10°N transect. At stations 1 and 6, the biomass observed in the mixed layer was 0.74 and 0.16 mL m^{-3}, respectively. During the peak phase of the monsoon, the average mesozooplankton biomass in the MLD showed a fivefold increase (2.18 mL m^{-3}) than the early phase (0.41 mL m^{-3}). Along 8°N transect, the average biomass noticed was 2.32 ± 0.24 mL m^{-3} and along 10°N, it was 2.8 ± 4.5 mL m^{-3}. In the upper 150 m water column, the zooplankton biomass varied

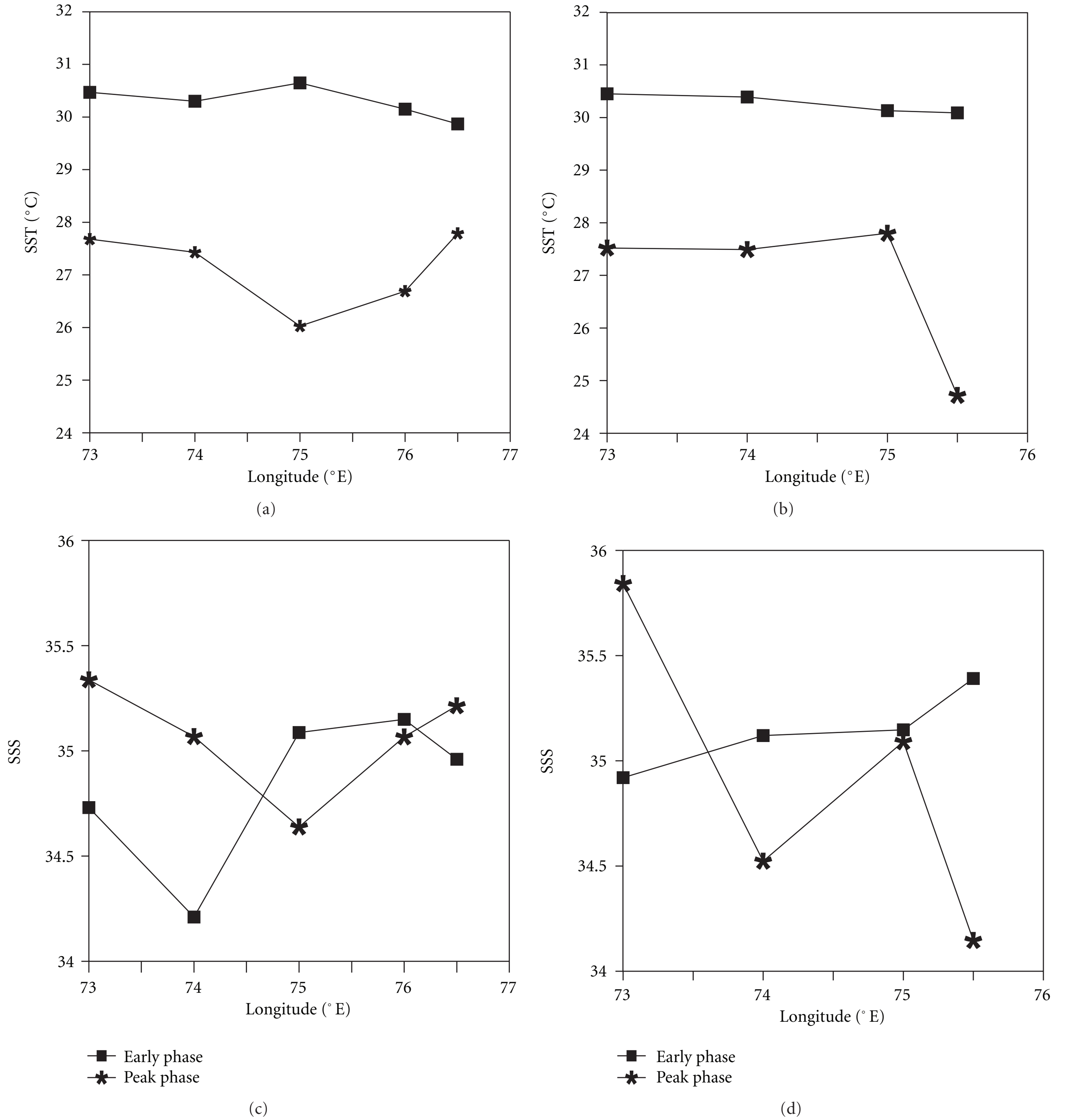


Figure 2: Distribution of sea surface temperature (SST, °C; (a, b) and sea surface salinity (SSS; (c, d)) along 8 and 10°N during early and peak phases of summer monsoon.

between 0.45 mL m^{-3} (station 7) and 9.57 mL m^{-3} (station 6). Along both transects, the coastal stations contributed the major share of the biomass.

The coastal stations of 8°N (station 1) and 10°N (station 6) were considered as aggregation stations where higher abundance of euphausiids was observed (Figure 7). The zooplankton taxa recorded were comparatively higher in the early phase (~13 zooplankton taxa). At station 1, the dominant taxa in the MLD were Copepoda (66.39%) and Ostracoda (27.73%), and, in thermocline layer, their contribution was 83.79 and 10.65%, respectively. At station 6, Copepoda contributed 69.30% followed by Chaetognatha and Pteropoda (8.1 and 8.9%, resp.) in the mixed layer. In the thermocline layer, 83% was contributed by Copepoda and 8.93% by Ostracoda. Relative abundance of euphausiids during this phase was <1% irrespective of layers and stations.

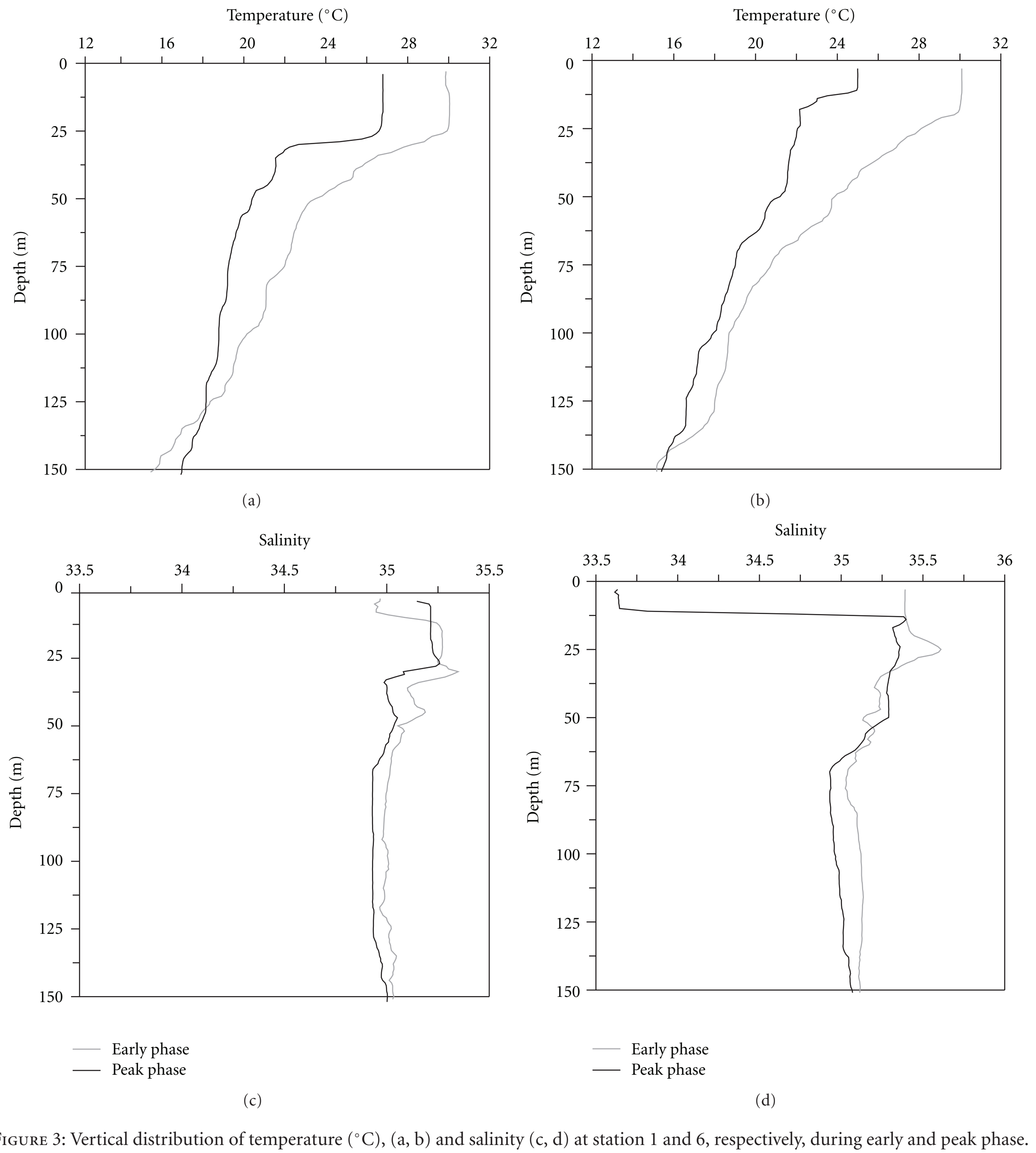


Figure 3: Vertical distribution of temperature (°C), (a, b) and salinity (c, d) at station 1 and 6, respectively, during early and peak phase.

Among euphausiids, the species recorded were *Euphausia sibogae* (65%), *E. diomediae* (25%), and *Pseudeuphausia latifrons* (10%).

Zooplankton diversity during peak phase was relatively less (~9 zooplankton taxa). At station 1, 51% was composed of Copepoda, 42% of Ostracoda, and 3.86% of Chaetognatha. In the thermocline layer, Ostracoda was relatively less (19.87%) whereas Copepoda contributed 56.66%. Density of Chaetognatha in this layer was 12.11%. The remarkable feature observed in the mixed layer at station 6 was the presence of euphausiid eggs (61.11%) followed by Copepoda (30.81%) and Siphonophora (6.36%). The contribution of Copepoda in the thermocline layer was very low (15%) at this station. Euphausiids and euphausiid eggs were abundant in this layer and contributed 55.51% and 20.95%, respectively. During the peak phase, the dominant species of euphausiids identified were *E. sibogae* (90%) and *E. diomediae* (10%). The variation in abundance of euphausiids during the two phases

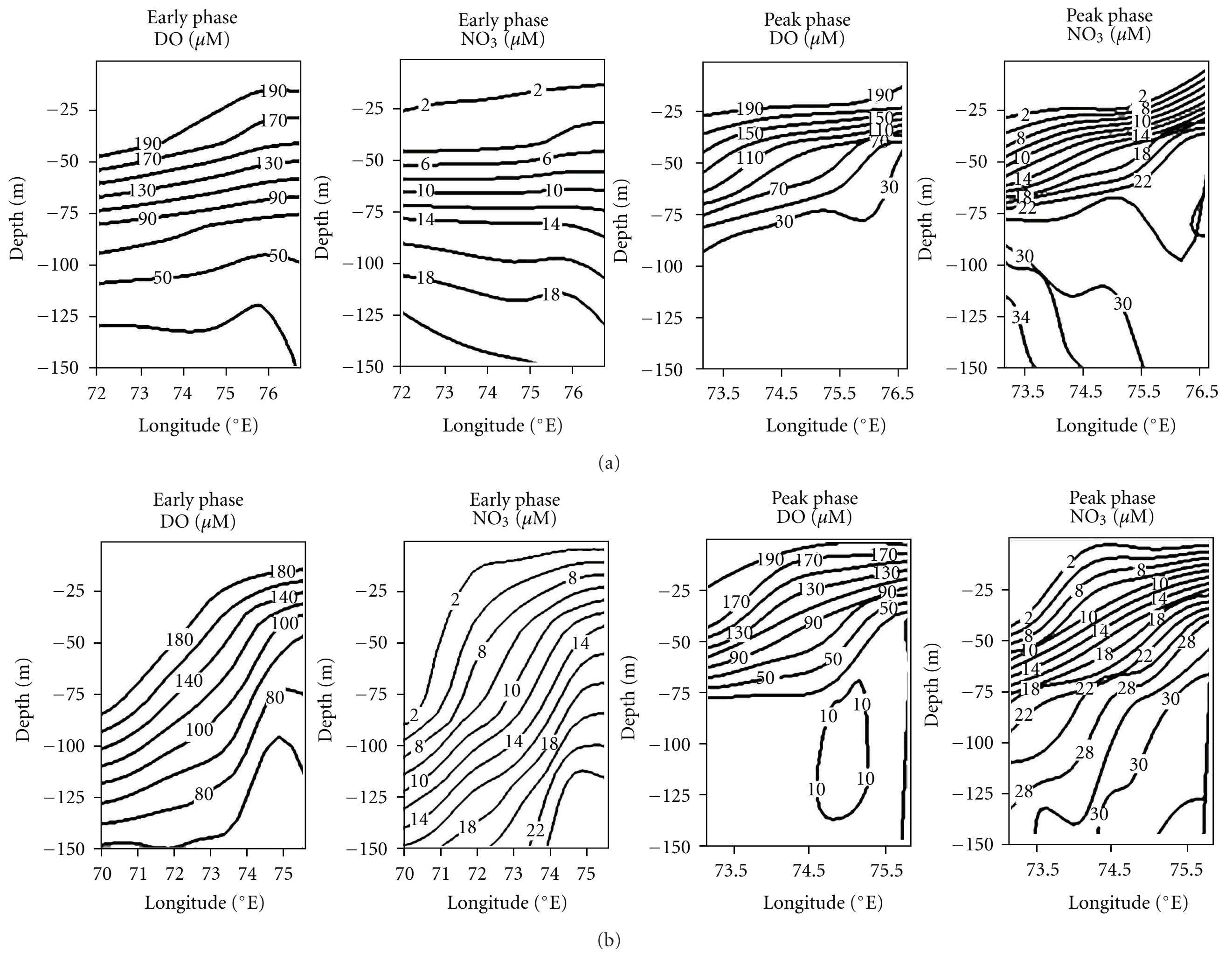


FIGURE 4: Vertical profile of dissolved oxygen (μM) and nitrate (μM) during early and peak phases of summer monsoon along 8°N (a) and 10°N (b).

was significant ($P < 0.05$) in the MLD and thermocline layer (Table 3).

Aggregation of *E. sibogae* was observed both at station 1 and 6 and was composed of actively breeding adults. The lengths of the individuals ranged from 1.0 to 1.5 cm. In other stations, males with spermatophores were relatively more abundant than females.

At station 1, the euphausiid population comprised of 82% males and 18% females. All the females were carrying remnants of spermatophores attached to their thoracic region. The maximum abundance of euphausiids was noticed in the mixed layer during night time (480 ind$\cdot$m^{-3}), whereas in the thermocline layer the abundance was relatively higher during day time (65.7 ind. m^{-3}).

At station 6, the population of euphausiids composed of equal proportions of males and females (50% each), and both sexes were carrying spermatophores. Overall abundance of the euphausiids was relatively very low in the mixed layer (25 ind$\cdot$m^{-3}), where they were observed only during night. In the thermocline layer, the abundance was relatively higher during the evening collection (839 ind$\cdot$m^{-3}). In particular, the *E. sibogae* registered a large number of fertilised eggs at station 6. The examination of eggs revealed an array of developmental stages from four cell to naupliar stage. Empty eggshells were also observed in the samples (Figure 8). Remarkably high density of euphausiid eggs was observed in the mixed layer. The noon sample contained 14769 eggs m^{-3}, the morning sample 8320 eggs m^{-3}, and the evening sample 3692 eggs m^{-3} (Table 4). At station 6 euphausiid eggs contributed about 61% of the total zooplankton. The size of the eggs ranged from 250 to 300 μm. Diurnal variation of presence of eggs in mixed layer was notable with maximum at noon (14769 eggs m^{-3}). Euphausiid distribution also showed remarkable variation during diurnal observations. In the mixed layer, relatively higher abundance was observed during night hours whereas, in the thermocline layer, not much variation in abundance was seen between the sampling times.

Table 2: Density (cells L^{-1}) of major phytoplankton groups during early and peak phases of summer monsoon at station 1 and 6 ("—" absent).

	Station 1		Station 6	
	Early phase	Peak phase	Early phase	Peak phase
Blue-green algae	1420	950	19400	—
Diatoms	1100	6250	3040	15780
Dinoflagellates	1140	2940	360	8680
Green flagellates	—	5000	—	4620

Table 3: Percentage composition of various zooplankton taxa in the MLD and thermocline layer during early and peak phases of summer monsoon at station 1 and 6 (values in the parentheses denotes the peak phase).

Zooplankton taxa	Station 1		Station 6	
	MLD (%)	Thermocline (%)	MLD (%)	Thermocline (%)
Polychaeta	0.52 (—)	0.41 (0.12)	— (—)	0.23 (—)
Chaetognatha	1.09 (3.86)	0.86 (12.11)	8.17 (0.24)	0.96 (1.91)
Euphausiids	0.12 (0.86)	0.09 (8.37)	0.03 (0.05)	0.10 (55.51)
Decapoda	0.56 (0.45)	0.45 (0.67)	1.24 (0.04)	0.44 (0.07)
Pteropoda	0.28 (0.00)	0.22 (0.06)	8.91 (0.01)	1.24 (—)
Foraminifera	1.80 (0.67)	1.42 (0.18)	0.75 (—)	— (—)
Ostracoda	27.73 (42.43)	21.92 (19.87)	3.44 (1.27)	8.93 (3.34)
Copepoda	66.39 (51.05)	52.49 (56.66)	69.31 (30.81)	83.7 (15.08)
Amphipoda	0.87 (0.01)	0.69 (—)	0.07 (0.01)	0.06 (—)
Fish larvae	0.10 (—)	0.08 (0.19)	0.68 (—)	0.0 (0.03)
Siphonophora	0.30 (0.03)	0.23 (0.19)	0.01 (6.36)	0.10 (2.69)
Copelata	0.25 (0.28)	0.19 (0.01)	6.00 (0.00)	2.46 (—)
Doliolids	— (—)	— (0.03)	0.06 (0.01)	— (0.02)
Stomatopoda	— (—)	— (0.02)	0.44 (0.03)	0.03 (0.01)
Heteropoda	— (—)	— (—)	0.10 (—)	— (—)
Mysid	— (—)	— (0.32)	— (—)	— (—)
Gastropoda	— (0.29)	— (0.80)	0.09 (—)	0.33 (—)
Fish egg	— (—)	— (—)	— (—)	0.84 (—)
Cephalopoda	— (0.02)	— (—)	— (—)	0.02 (—)
Salp	— (—)	— (—)	0.28 (—)	0.20 (—)
Medusa	— (—)	— (0.03)	— (—)	— (—)
Amphioxus	— (0.04)	— (—)	— (—)	— (—)
Hydrozoa	— (—)	— (0.37)	— (0.13)	— (—)
Euphausiid Egg	— (—)	— (—)	— (61.11)	— (20.95)
Others	— (—)	— (—)	0.18 (—)	0.13 (—)

4. Discussion

The coastal stations along the 8°N (station 1) and 10°N (station 6) transects were characterized by upwelling, particularly during the peak phase. Inshore shoaling of cold, high-saline nutrient-rich subsurface water to the surface during this period was a clear evidence of the prevailing active upwelling process. Relatively high concentrations of chlorophyll *a*, phytoplankton cell abundance, and zooplankton biomass observed at these stations were also in support of the high productivity potential of the upwelled coastal waters. The high biological productivity of the coastal waters along the southwest coast of India, resulting from the upwelling has been well established [14, 23].

The mesozooplankton biomass was higher during the peak phase of the monsoon compared to its onset, especially along coastal stations. Euphausiids are known to be a major component in the zooplankton biomass during the summer monsoon [14]. Similarly, in the Atlantic waters also, higher abundance and biomass of euphausiids have been reported [24] during years of above average upwelling that result in elevated levels of primary and secondary production. The upwelling regions show significant inshore variations of the environmental gradients that may affect the species richness and zooplankton biomass [25].

The abundance of *E. sibogae* in the study area recorded presently was higher (839 ind$\cdot$m^{-3}at station 6 and 483 ind$\cdot$m^{-3} at station 1) than the earlier reports

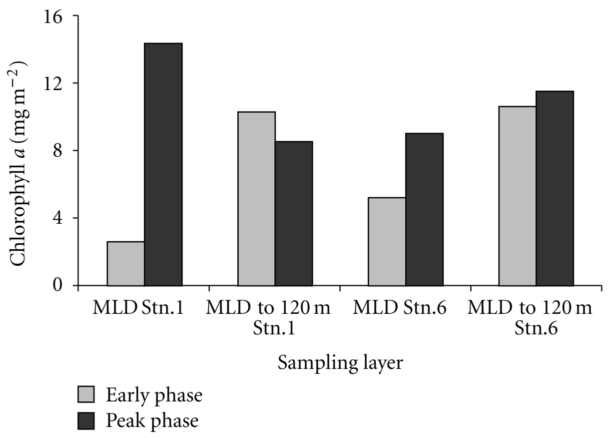


FIGURE 5: Integrated chlorophyll a (mg m^{-2}) concentration during early and peak phases of summer monsoon.

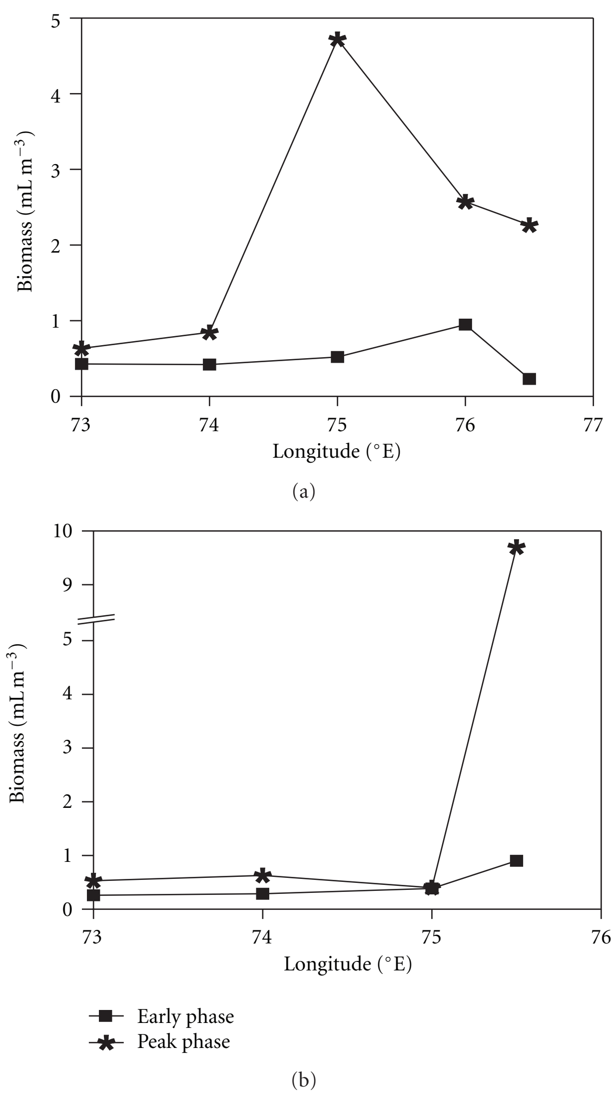


FIGURE 6: Mesozooplankton biomass (mL m^{-3}) from thermocline layer to the surface during early and peak phases of summer monsoon along 8°N (a) and 10°N (b) (note: scales are not same).

(24 ind·m^{-3}) [9]. This species is the most abundant and successful euphausiid in the shelf waters of the southwest coast of India. Its maximum abundance occurs towards the southern region along the west coast of India and is usually associated with the upwelling events [6, 9, 26, 27]. Thiriot [28] also reported that large populations of euphausiids along the shelf break are characteristic of coastal upwelling ecosystems of West Africa. Stelfox et al. [29] have reported increased abundance of large zooplankton in the upwelling area, and we observed increased population of large carnivorous zooplankton associated with the euphausiid aggregation.

The presence of mature males and females, carrying spermatophores at station 6 and with remnants of spermatophores at station 1, indicates that the aggregation was associated with breeding. Mathew et al. [9] opined that *E. sibogae* is a continuous breeder, but its breeding activity intensifies in July, coincident with the onset of upwelling along the south west coast of India as a result of the southwest monsoon. This is clearly reflected in our results.

Presence of spermatophore-bearing males and females and developing eggs at station 6 indicates the active spawning whereas, females bearing remnants of spermatophores indicate the later stage of spawning activity at station 1. In the earlier studies, times of spawning were either back-calculated from the presence of larvae or assumed to be contemporary with the presence of adult females either with mature eggs in their ovaries or with attached spermatophores [9]. The absence of eggs and early larval stages at station 1 may have been a consequence of predation by other carnivorous zooplankton or more likely, the horizontal or vertical movements (or advection) of the larvae. The ontogenic migration of early larval stages of euphausiids has been reported by Makarov [30], and this may be a life history strategy for maintaining the population within upwelling circulation [31].

At station 1, higher abundance of *E. sibogae* was observed in the mixed layer during morning and night hours whereas, at station 6, it was observed in the thermocline layer during the dusk (Table 4). These "ambiguities" in distribution (DVM behaviour) might either be a product of the shallowness of the study area or the physico-chemical characteristics of water column influenced by the upwelling, modifying the attractiveness or habitability of different depths' strata. Alternatively, the breeding population may be utilizing their maximum energy for reproductive activities rather than for normal activities like DVM. According to Tarling et al. [32], ready-to-spawn females of *Meganyctiphanes norvegica* swarm in the uppermost layers at night.

Net avoidance and escapement through mesh are serious concerns when sampling the euphausiids. In our study, the towing speed was 1 ms^{-1} to minimize the net avoidance. The absence of organisms at daytime may be either due to net avoidance because of high visibility in the daylight, or the animals may be concentrated in small dense patches which are often missed or the absence of animals at the sampling depth. According to Mathew [33], the larvae and juveniles of *E. sibogae* did not show any night time abundance, but the adults were exception to this. Thus, it is difficult to arrive

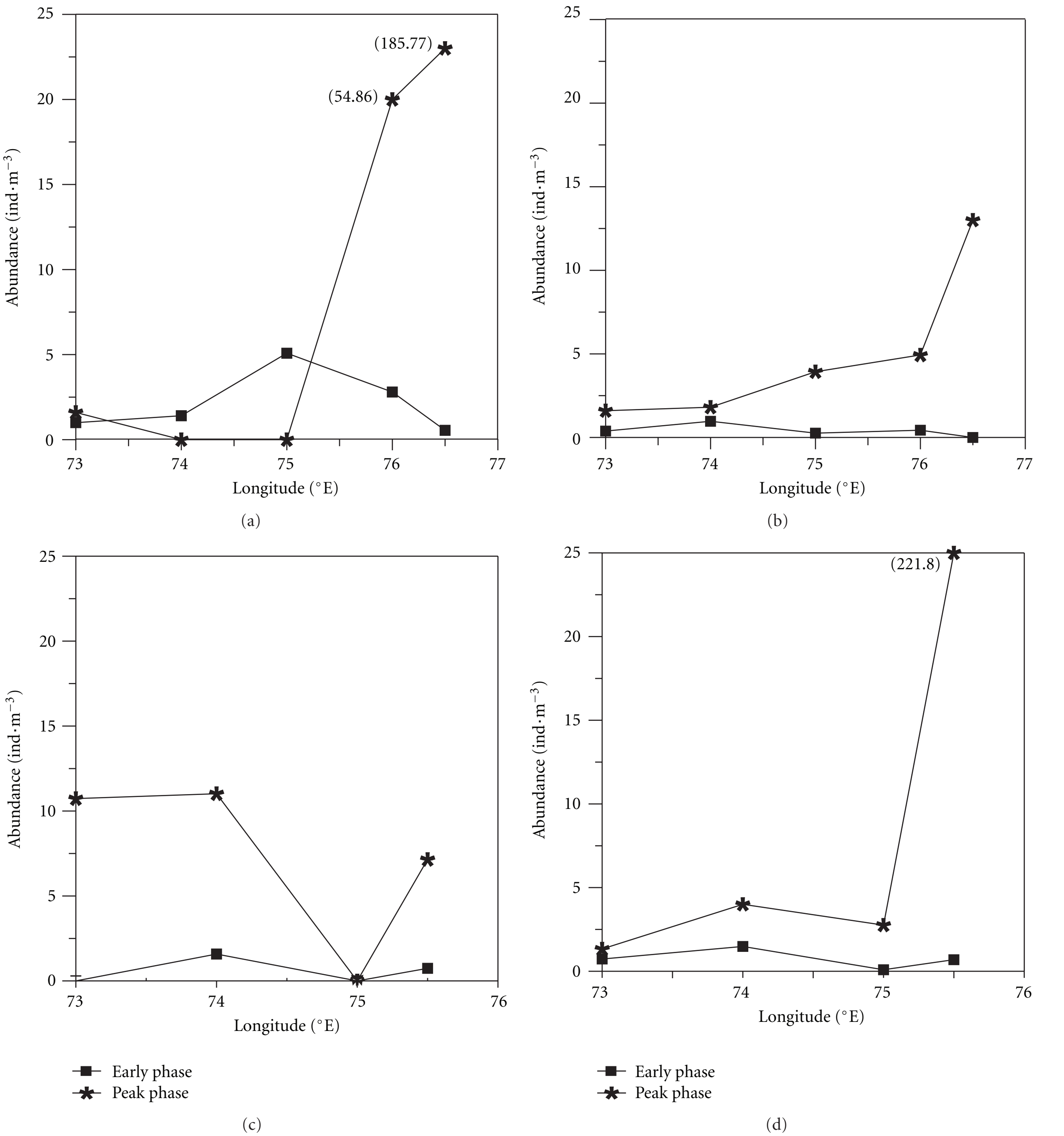
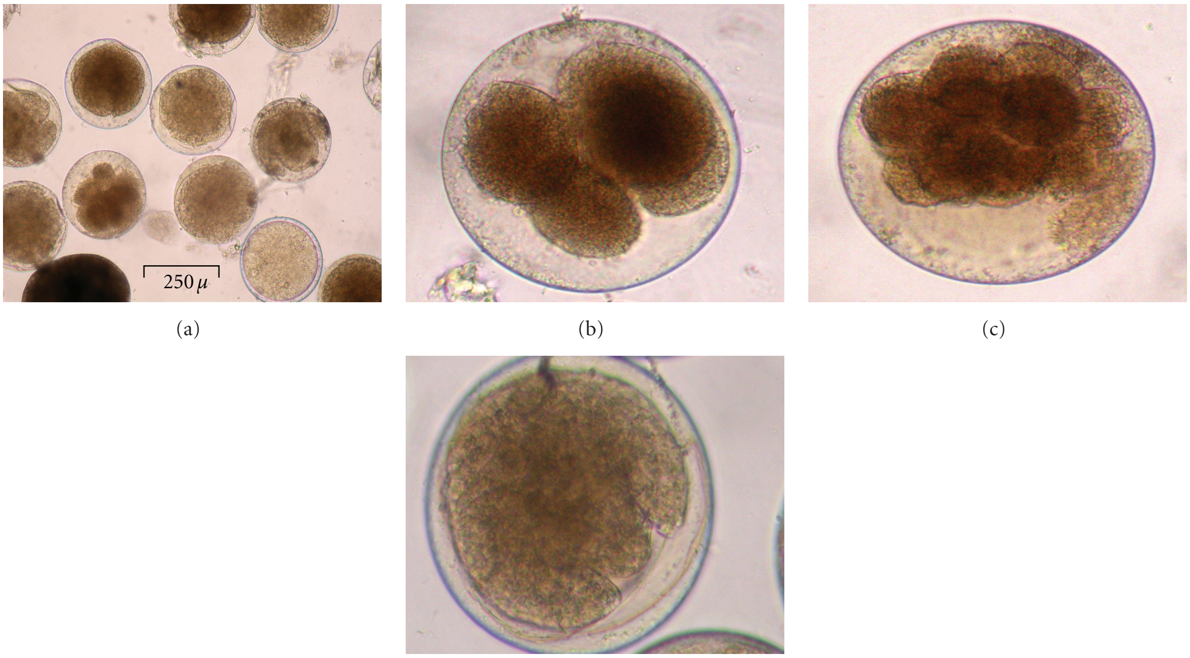


Figure 7: Abundance (ind$\cdot$m^{-3}) of euphausiids during early and peak phases of summer monsoon (a) in the mixed layer and (b) thermocline layer along 8°N, (c) in the mixed layer and (d) thermocline layer along 10°N.

Table 4: Abundance (ind$\cdot$m^{-3}) of euphausiids and euphausiid eggs (eggs m^{-3}) observed during the diurnal collection at station 6 ("—" absent).

Time of collection	Mixed layer		Thermocline layer	
	Euphausiids (ind$\cdot$m^{-3})	Egg (eggs m^{-3})	Euphausiids (ind$\cdot$m^{-3})	Egg (eggs m^{-3})
Morning	—	8320	13.80	—
Noon	—	14769	0.97	55
Evening	2.77	3692	839	279
Night	25	—	33.29	—



(a) (b) (c) (d)

Figure 8: Eggs of *Euphausia sibogae* collected from station 6. (a) Eggs of *E. sibogae*, (b, c) enlarged view of eggs with various stages of cell division, and (d) enlarged view of nauplii development inside the egg.

at any firm conclusion as to whether or not the euphausiids were undertaking DVM in the study area.

Males dominated the population, particularly at station 1, suggesting that there were irregularities in the sex ratio. According to Mauchline and Fisher [34], there are shifts in the sex ratios of euphausiid populations, both at the time of spermatophore transfer from the males to females and during the period of egg laying. Similar shifts in the observed sex ratios during breeding seasons have been reported in several other species of euphausiid, such as *Meganyctiphanes norvegica, Thysanoessa inermis,* and *T. raschii* in the Byfjord and Hardangerfjord, Norway [35].

A density of 839 $\text{ind}\cdot\text{m}^{-3}$ is somewhat less than the typical abundance reported in breeding swarms (~ 1000 $\text{ind}\cdot\text{m}^{-3}$) by Mauchline [36]. He stated that breeding aggregations are self-regulating and seasonal, and they disperse once breeding is finished. Such postbreeding declines in the density may be the result of the dispersal, but predation may also play a role. Madhuprathap et al. [14] defined densities of $\geq$100 $\text{ind}\cdot\text{m}^{-3}$ as swarms and up to 50 $\text{ind}\cdot\text{m}^{-3}$ as aggregations, the former may be the result of the behaviour while the latter may be the result of passive aggregation by physical processes. Considering this view, the present observation can be termed a swarm (breeding behaviour) rather than an aggregation.

The aggregation of *E. sibogae* coincided with high concentrations of chlorophyll *a* and green flagellates (Table 2). Relatively higher abundance of small phytoplankton (but not as small as picoplankton) provides a trophic advantage not only for the spawning adults but also for the first feeding larval stages. Studies carried out in other species like *E. pacifica* also concur this observation. The reproductive rate of this species is closely coupled with availability of phytoplankton [37]. In contrary to the present findings, Feinberg and Peterson [38] suggested that the adult spawning habitat was purely seasonal, and there was no significant association between abundance of eggs spawned and phytoplankton biomass. Our study implies that the spawning success of *E. sibogae* along the southwest coast of India may be associated with availability of small-sized phytoplankton (chlorophyll *a* concentration) and favourable SST. Egg production is reliant on the resources available to adult females and consequently may be food limited, but egg hatching and postembryonic development show strong temperature dependence [39]. Even though salinity showed significant variation between the two stations during the peak phase, the presence of females with spent ovary and spermatophore at both stations implies that salinity may not be an important factor influencing the spawning potential. The low salinities in the upper water column at station 6 may have restricted the passive sinking of the eggs due to stabilization of the water column. Thus, the breeding aggregation of *E. sibogae* is related directly and indirectly to the seasonal events like coastal upwelling which provide optimal or conducive environmental condition.

5. Summary

The study provides the ecological context off the southwest coast of India during the early and peak phases of the summer monsoon associated with upwelling and aggregation of

E. sibogae. The abundance of this species recorded in the present study was several times higher than that of earlier reports and was associated with the breeding behaviour. The high phytoplankton biomass (both cell density and chlorophyll *a*) might be nutritionally more favourable for the growth of the first larval stages of the euphausiids than the adult population. The nutrient-rich upwelled waters with low SST support very high phytoplankton densities and hence chlorophyll *a* concentrations, creating a highly suitable environment both for spawning and successful development of the eggs of euphausiids.

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