Indian Journal of Geo Marine Sciences
Vol. 54 (12), December 2025, pp. 676-693
DOI: 10.56042/ijms.v54i12.22009

Research Article

Seasonal succession in mesozooplankton community in the tropical coastal waters: A study at Kalpakkam, southeast coast of India, Bay of Bengal

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Received 25 July 2025; revised 22 November 2025

Spatio-temporal variations in mesozooplankton diversity and abundance were assessed over 3 years at 6 coastal stations off Kalpakkam, along the Tamil Nadu coast. Samples were collected seasonally for eight consecutive seasons. Spatial variations were observed with respect to two transects, one at 0.5 km and the other at 5 km inside the sea, with three stations in each transect covering ~ 20 km stretch of the coastline. The results showed relatively high zooplankton diversity and density during the pre- and post-monsoon seasons compared to the monsoon season. Zooplankton density ranged from 0.54–6.10×10^4 individuals per 10 m^3 in the nearshore waters and 0.44–4.83×10^4 individuals per 10 m^3 in the offshore waters. A total of 183 taxa were recorded. Out of which, 97 were copepods, 47 Non-Copepod Holoplankton (NCH), and 39 meroplankton. As expected, the copepod group dominated the zooplankton community, belonging to 25 families and 39 genera. Copepodite stages were recorded for 12 copepod taxa. A relatively low number of species was recorded during the monsoon seasons. Seasonally, copepods were found to contribute 26–65 % of the total zooplankton community, followed by NCH (22–69 %), meroplankton (2–19 %), and copepodite (1–5 %). Zooplankton species abundance showed a strong positive correlation with salinity and a negative correlation with turbidity. Non-metric Multidimensional Scaling (nMDS) and similarity percentage (SIMPER) analyses indicated an almost uniform distribution of zooplankton communities across the spatio-temporal scale.

[**Keywords**: Bay of Bengal, Coastal waters, India, nMDS, SIMPER, Spatio-temporal variations, Zooplankton]

Introduction

Seasonal succession pattern in any biotic community is an inevitable process of an ecosystem. It reflects and influences the ecosystem at both spatial and temporal scales. Such processes tend to provide insights into the ongoing interactions between biotic and abiotic components of the environment[1-3]. Long-term ecological alterations in seasonal succession may change the inter-annual and intra-annual components of ecosystem functioning[4]. Although the succession process is a crucial part of biotic life, it is most prominent in planktonic habitats, such as the life cycles of phytoplankton and zooplankton, compared to benthic habitats. Zooplankton is the principal modulator of carbon and energy transfer mechanisms, as it serves as the main link between lower and higher trophic levels in the pelagic and benthic food chains[5-6]. They also play an important role in the cycling & vertical flux of elements in the marine environment. Zooplankton, considered the primary index of secondary production, is highly diverse in its geographical distribution, size fractions, taxonomic composition, trophic levels, environmental tolerance, etc. Zooplankton, as both primary and secondary consumers, play a significant role in the fishery potential of the marine environment due to their large biomass, which accounts for about one-tenth of total marine biomass. Moreover, many zooplankton species are used as environmental and pollution indicators owing to their shorter life spans, high population densities, drifting nature, high diversity, and environmental tolerance, which facilitate the study of physical, chemical, and biological processes in aquatic ecosystems. Thus, given the important ecological and economic roles of zooplankton, zooplankton studies have been recognised as significant as those of phytoplankton.

As the mesozooplankton community is a major component of the total zooplankton assemblage, both functionally and in terms of contribution, it is considered a core area of investigation in marine biology. Mesozooplankton (200 µm – 2 mm, largely

dominated by copepods) are key intermediaries in marine trophic pathways, efficiently transferring energy from phytoplankton to higher trophic levels such as fish larvae and pelagic predators[7]. They contribute significantly to the oceanic biological pump by producing fast-sinking fecal pellets and facilitating vertical carbon export, thereby influencing global biogeochemical cycles[8-9]. Through selective grazing, mesozooplankton regulate phytoplankton community composition and can influence the development and termination of blooms, including harmful algal events[10]. Additionally, their rapid life cycles and sensitivity to environmental variability make them effective indicators of climate-driven changes in marine ecosystems[11]. Although mesozooplankton play a critical role in regulating marine food webs and biogeochemical processes, regional understanding of their distribution and dynamics remains uneven across the Indian Seas. While phytoplankton and physicochemical characteristics have been extensively investigated, zooplankton studies are disproportionately concentrated in the Arabian Sea, which accounts for a substantial share of the available literature relative to the Bay of Bengal (BOB)[12-15]. In particular, the southwestern Bay of Bengal (SW-BOB) remains poorly studied, with relatively sparse and fragmented information on zooplankton community structure and dynamics.

The present study area is home to many nuclear establishments that require continuous environmental monitoring to comply with environmental guidelines. Published literature indicates that zooplankton diversity was recorded only in 2000 at this location[16], much later than the commissioning of power plants in the early 1980s. However, the post-operational studies on zooplankton from this coast are very limited. Earlier studies on zooplankton from the same locations were mostly limited to a single location or short durations[17-19]. Hence, the present study was designed to document the zooplankton community composition and to examine the role of water quality parameters in shaping the zooplankton community across a relatively large area spanning eight seasons over three years. The study would generate benchmark data on a spatiotemporal scale for future reference. Such benchmark data would serve as milestones for subsequent changes in environmental interactions, not only for zooplankton but also for all biotic components. The survey comprises a 100 sq. km area covering 10 km on either side of the nuclear site and 5 km into the sea with six sampling locations. The main objectives of the study are 1. To assess the seasonal variations in the community composition of zooplankton, 2. To find out the impact of water quality parameters on the zooplankton community, and 3. Determination of spatiotemporal patterns in zooplankton community structure through statistical analyses.

Materials and Methods

Study site

Kalpakkam site (12°33’ N, and 80°11’ E) is located on the east coast of India, approximately 70 km from Chennai city (Fig. 1). Kalpakkam region is a growing nuclear complex comprising various nuclear facilities. According to the climatology of this area, three prominent seasons are experienced: Post-monsoon (February to May), Pre-monsoon/Southwest monsoon (June to September), and Northeast monsoon (October to January). The Buckingham Canal, which runs parallel to the shore, is connected to two backwaters: Edaiyur and Sadras. These two backwaters discharge large volumes of freshwater into the coastal environment for 2 to 3 months (Oct–Dec) during the northeast monsoon (NEM) and occasionally during the peak southwest monsoon (SWM). The annual precipitation at Kalpakkam is ~1300 mm, of which the bulk of its precipitation (~65 %) is derived from the NE monsoon. Due to the study area's geographic location, it experiences monsoon wind reversal, and consequently, the current reverses. The coastal current direction remains northward from March to September and shifts southward from October to February with the onset of SWM and NEM, respectively. The change in the coastal water current pattern also brings in oceanic water, or diluted coastal water from the northeastern Bay of Bengal, depending on whether the current is northerly or southerly.

Samples were collected seasonally (Post-monsoon: POM, Pre-monsoon: PRM, and Monsoon- MON) during 2016–2018 from six predefined locations under different environmental conditions. The stations were fixed using the Global Positioning System (GPS) and are located along two transects parallel to the shoreline, ~500 m and 5 km offshore (Fig. 1). The average depth of the water column at the sampling locations was about 7–8 m at 1st transect and 25–30 m at the second transect. The P1, E1, and M1

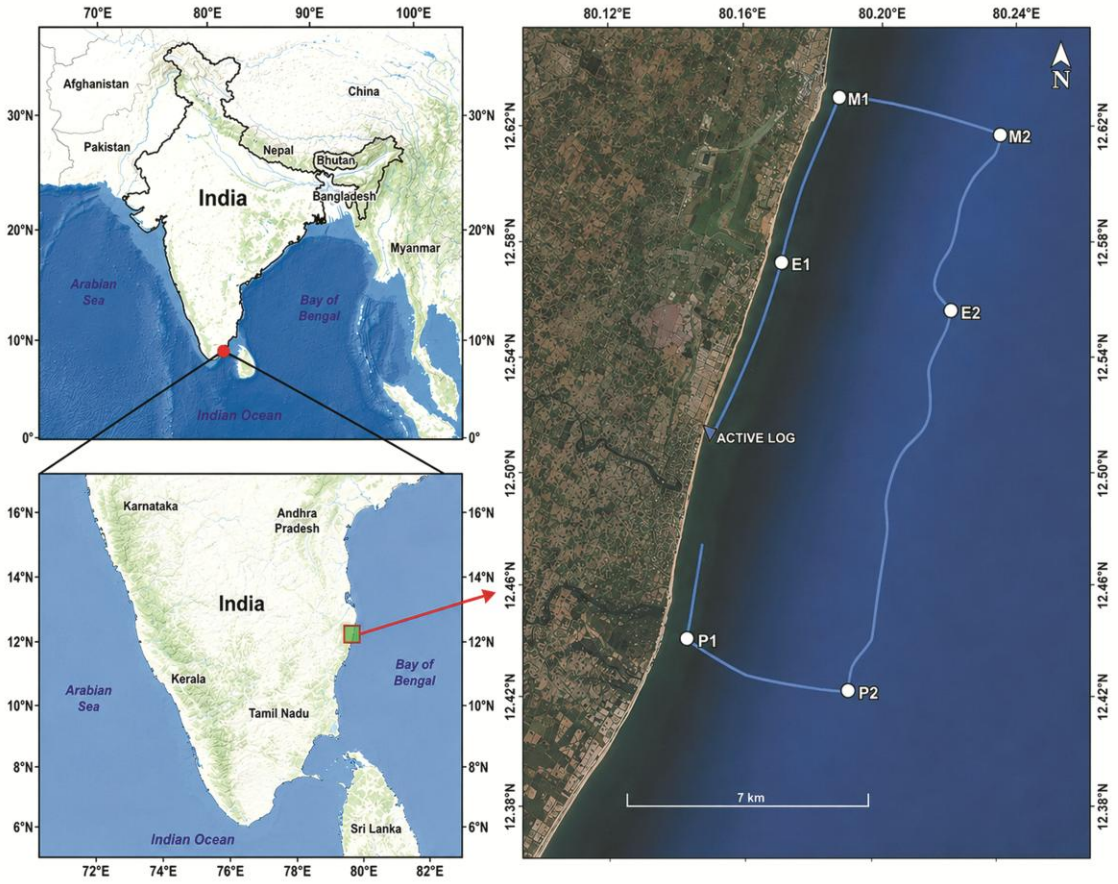


Fig. 1 — Study area map showing the sampling locations (Zooplankton samples were collected at P1, P2, E1, E2, M1, and M2 stations)

stations of the 1st transect are situated opposite to the opening of the Palar River, Edaiyur Backwater, and Mahabalipuram, respectively. The 2nd transect consists of another three stations (P2, E2, and M2) exactly opposite to the stations of the 1st transect at 5 km inside the sea.

Methodology

Water and plankton samples were collected using fibre fishing boats. Water samples were collected using a Niskin sampler (5 L capacity) and transferred to pre-cleaned 1 L HDPE bottles. All water samples were kept in an ice box in dark conditions and transported to the laboratory. Physical parameters such as temperature, pH, salinity, and Dissolved Oxygen (DO) were measured on board using a multi-parameter probe (Hanna Instruments, model HI9829). Secchi disc depth was measured by lowering a Hydrobios-made Secchi disc with a graduated rope. Parameters such as turbidity and chlorophyll-*a* were measured in the laboratory. The turbidity of water samples was measured by a turbidity meter (CyberScan IR TB 100), with 0.01 NTU accuracy. Chlorophyll-*a* samples were filtered through 0.45 µm membrane filters, and the pigment was extracted with 90 % acetone at -4 °C for 24 h. Chlorophyll-*a* was analysed spectrophotometrically following the methods of Parsons *et al*.[20]. A conical plankton net (mouth area 1.25 sq. m) of 200 µm mesh size was used for zooplankton sample collection. The net was fitted with a flow meter (Hydrobios) for quantifying zooplankton. The samples were preserved with 5 % formalin. Zooplankton biomass was determined by the dry-weight and wet-weight methods. The total volume of water filtered (m^3) was calculated using flow meter readings. The total dry weight of the zooplankton was estimated by filtering the organisms through a plankton net (200 microns) and oven-drying at 80–90 °C for 2 h. Biomass is expressed in g. 10 m^{-3}. Wet weight was estimated using the volume-displacement method. The larger organisms, such as Mysids, *Lucifer*, Siphonophores, Dolioloids & Salps, Chaetognaths, Ctenophores, fish eggs & larvae, and large copepods of families Pontellidae, Eucalanidae & Euchaetaidae among the holoplankton and larger

meroplankton components, such as polychaete larvae (Trochophores), larvae of decapods (zoea, megalopa, alima, phyllosoma, mysis), were sorted out from the plankton mixture and counted separately. The residual mixture was then diluted to exactly 100 ml with 5 % formaldehyde solution. 1 ml of this aliquot was examined under an inverted research microscope (Zeiss Axiovert 40) using a Sedgewick-Rafter cell. Species-wise abundance was recorded by counting several repetitions. Plankton density was reported as individuals 10 m^{-3}. The zooplankton was divided broadly into four groups: copepods, copepodites, Non-Copepod Holoplankton (NCH), and meroplankton. The copepods were further categorised into five groups: calanoids, cyclopoids, poecilostomatoids, siphonostomatoids, and harpacticoids. As far as practicable, genera/species levels were assigned to individual animals after thorough microscopic examination of their morphological attributes. Standard literature, such as Kasturirangan[21] for copepods, Rao[22] for Chaetognaths, Conway *et al*.[23] and Newell & Newell[24] for other components, was followed for identification. Based on the qualitative analysis results, a checklist of zooplankton species occurring in the coastal waters of Kalpakkam was prepared.

To assess the possible effects of hydrographical parameters on zooplankton populations, a simple correlation analysis was conducted between biological and hydrographical parameters. Principal Component Analysis (PCA) was performed to assess the relationships among biotic and abiotic parameters across seasons and stations. Non-parametric Multidimensional Scaling (nMDS) with cluster overlay was applied to the three groups, such as copepods, Non-Copepod Holoplankton (NCH), and meroplankton, to assess their distribution pattern during the study. The same treatment was applied to seasonal and station-wise zooplankton abundance to identify similarities across temporal and spatial scales. Further, SIMPER analysis (similarity percentage- species contribution) was carried out for the seasonal and spatial abundance of zooplankton to determine the possible groupings and highest contributors. All statistical analyses were performed using XLStat Pro and Primer 6.

Results and Discussion

Water quality characteristics

Seasonal variations (Average ± SD) in water quality characteristics are shown in Figures 2 & 3. Seawater temperature ranged from 26.1 to 31.0 °C, with marginally higher temperatures observed in the 5 km transect. Seasonal average values of temperature ranged from 28.02 to 30.30 °C for the nearshore transect and 28.40–30.52 °C for the offshore transect (Fig. 2a). Temperature, which is a co-variate[25], influences almost every biochemical interaction in organisms' body tissues, chemical interactions, and the mixing of different water masses. The temperature conditions of the surface layer of the oceans are influenced by several factors that are directly or indirectly involved in heating and cooling processes. In tropical seas, such as the Bay of Bengal, the temperature appears to be influenced by additional processes, including wind stress from the two opposing circulations (clockwise and anticlockwise), cloud cover, monsoon effects, freshwater input from land drainage, and evaporation[26]. The process of phytoplankton productivity is significantly controlled by the pH of the medium water. The pH of seawater ranged from 7.9–8.4 with an average value of 8.15±0.14 for the nearshore transect and 8.1–8.4 with an average value of 8.24±0.10 for the offshore transect. Seasonal average values for pH ranged from 7.98–8.30 and 8.14–8.31 for nearshore and offshore transects, respectively (Fig. 2b). The observed pH values were relatively stable throughout the year, with only sporadic variations. The variations were relatively high in the 0.5 km transect as compared to the offshore transect. pH serves as a true measure of the acidity and alkalinity of the medium water, which are linked to many chemical and biochemical processes taking place within it[27].

Salinity is the most important hydrographic parameter, as it strongly influences other physical and chemical properties of the water column. The distribution of biological communities is also considerably affected by salinity variation. The salinity of seawater ranged from 19.33–37.48 PSU (33.20±4.20) for nearshore waters and ranged from 30.97–35.18 PSU (33.96±2.25) for the 5 km transect. Seasonal average values for salinity ranged from 29.34–36.40 PSU and 31.55–33.67 PSU for nearshore and offshore transects, respectively (Fig. 2c). Relatively low salinity was recorded during the NE monsoon period, whereas higher values were reported during the summer/SW monsoon. The nearshore waters exhibited wide salinity variations, primarily due to land runoff and backwater discharges. The 5 km transect showed relatively stable salinity throughout the study period, due to negligible

freshwater input from terrestrial sources. Perennial sources of freshwater input are absent at this location[28]. The salinity fluctuations in the Bay of Bengal normally range from a low average of 23-34 PSU per year, which has been attributed to the massive influx of freshwater, amounting to 1.625×10^{12} m^3 Y^{-1}, from different rivers debouching into the Bay[29]. The intrusion of high-salinity water masses from the Arabian Sea and the Indian Ocean during the southwest monsoon[30] was also considered an important factor in salinity changes.

DO values during the study ranged from 4.13 to 8.30 mg/l, and the seasonal average values ranged from 4.64 to 6.16 mg/l and 5.82 to 6.77 mg/l for the nearshore and offshore transect, respectively (Fig. 2d). Proper mixing and year-round phytoplankton production lead to well-oxygenated coastal waters at this location[31]. Various factors, including reaeration, photosynthesis, and the degradation of organic matter[32] govern oxygenation in aquatic systems. The turbidity of water samples ranged from 0.38 to 14.23 NTU. Seasonal average values of turbidity ranged from 1.83–3.58 NTU and 0.62–2.56 NTU for the nearshore and offshore transect, respectively (Fig. 2e). Relatively high turbidity values were recorded in the nearshore transect, which could be attributed to greater churning of coastal waters at 0.5 km from the coast than at 5 km offshore. Moreover, as discussed earlier, turbidity is directly related to the terrestrial runoff and freshwater input from rivers and backwaters. The above observation was further supported by the Secchi disc depth measurements, which showed that the water at the 5 km transect was more transparent with relatively

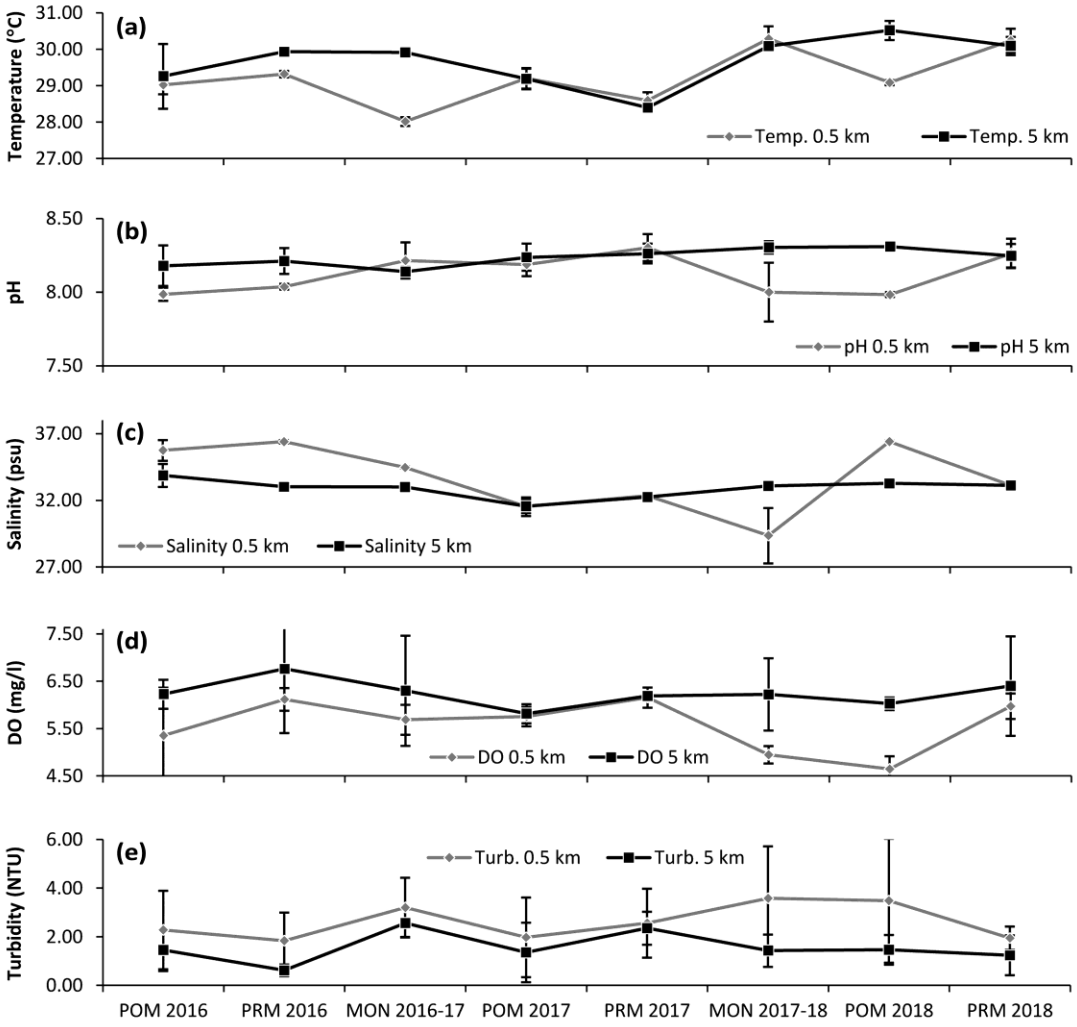


Fig. 2 — Seasonal variations (Average ± Standard deviation) in a) Temperature (°C), b) pH, c) Salinity (psu), d) Dissolved oxygen (mg/l), and e) Turbidity (NTU) in the coastal waters of Kalpakkam

high light penetration. It ranged from 1.0–7.5 m in the nearshore transect and 4.1–15 m in the offshore transect. Seasonal average values of Secchi disc depth ranged from 1.65–5.73 m and 5.51–9.84 m for the nearshore and offshore transect, respectively (Fig. 3a). Transparency refers to the optical properties of the water column and has far-reaching implications. Since it is the major factor influencing photosynthesis in the sea, it also controls the distribution of gases such as oxygen and carbon dioxide in the ambient medium. On the other hand, it also indirectly affects nutrient enrichment and depletion in seawater. The transparency of seawater is governed by several factors, such as surface irradiance and concentration of suspended particles, including phytoplankton and yellow substances[33-34]. Chlorophyll-*a* (chl-*a*), which is the universal photosynthetic pigment, ranged from 0.04 to 8.63 mg m^{-3}, with a nearshore average of 1.19 mg m^{-3} and an offshore average of 1.70 mg m^{-3}. Seasonal average values of Chlorophyll-*a* ranged from 0.13–2.49 mg m^{-3} and 0.60–4.08 mg m^{-3} for the nearshore and offshore transect, respectively (Fig. 3b).

Role of water quality on zooplankton distribution

The distribution, abundance, and diversity of zooplankton are influenced directly by several environmental parameters like pH, salinity, temperature, light, dissolved oxygen, tidal rhythm, rainfall, wind force, and phytoplankton abundance[35]. The addition of freshwater during the monsoon enriches coastal waters, leading to spring phytoplankton blooms that trigger herbivorous zooplankton production[36]. The relationship among zooplankton abundance, temperature, and salinity in coastal waters shows a strong association between salinity variations and zooplankton abundance[37-39].

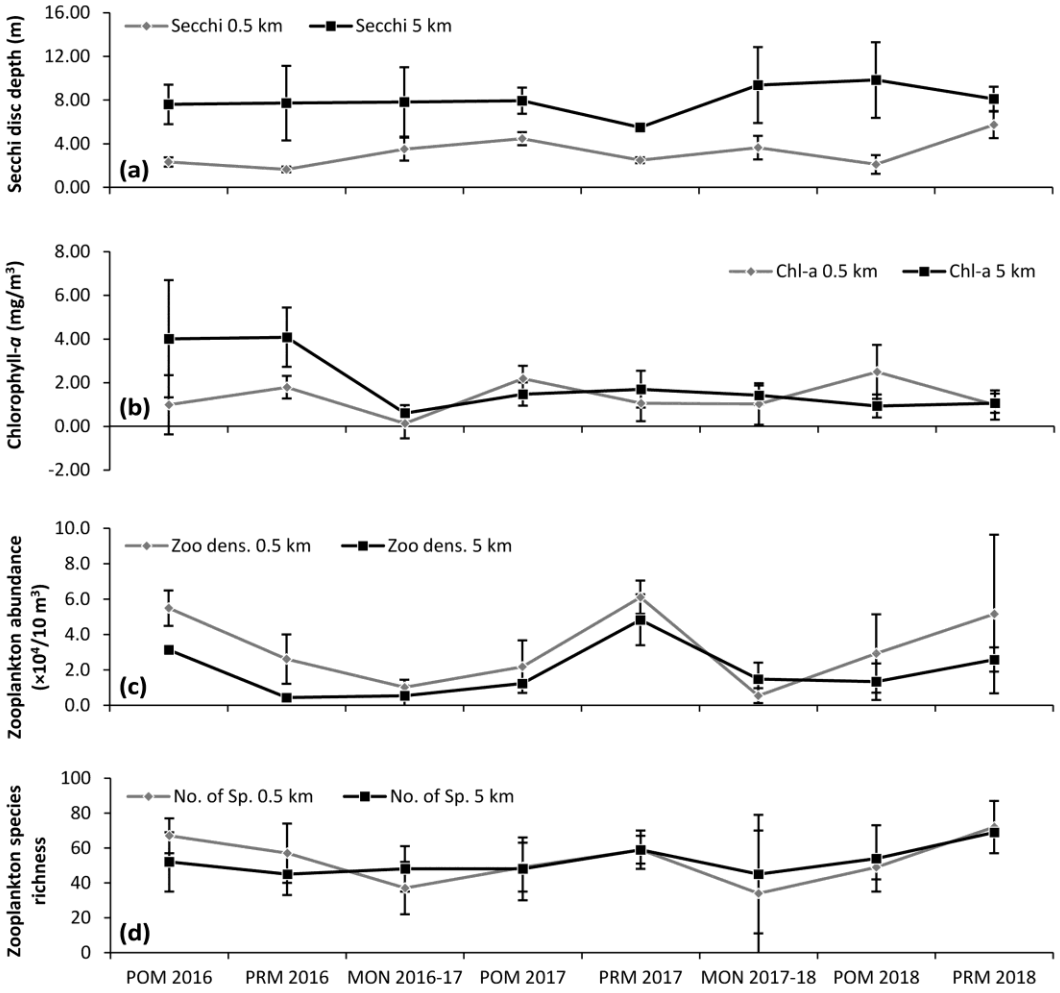


Fig. 3 — Seasonal variations (Average ± Standard deviation) in a) Secchi disc depth (m), b) Chlorophyll-*a* (mg/m^3), c) Zooplankton population density (×10^4 individuals per 10 m^3), and d) Number of zooplankton species in the coastal waters of Kalpakkam

Table 1 — Correlation matrix (Pearson) of environmental parameters and zooplankton dynamics at coastal waters of Kalpakkam, Tamil Nadu, India

Variables	Temp.	pH	Salinity	DO	Turb.	Secchi	Chl-*a*	Zoo dens.	No. of Sp.	Wet weight	Dry weight
Temp.	**1**										
pH	0.069	**1**									
Salinity	-0.275	-0.358	**1**								
DO	0.161	**0.679**	-0.103	**1**							
Turb.	-0.419	**-0.544**	0.021	**-0.753**	**1**						
Secchi	**0.565**	**0.639**	-0.344	**0.582**	**-0.650**	**1**					
Chl-*a*	0.265	0.275	0.026	0.360	**-0.541**	0.419	**1**				
Zoo dens.	-0.379	0.044	0.253	-0.055	0.029	**-0.442**	0.338	**1**			
No. of Sp.	0.034	0.012	**0.444**	0.206	**-0.458**	-0.139	**0.636**	**0.638**	**1**		
Wet weight	-0.295	-0.004	0.245	-0.014	0.032	-0.330	0.146	**0.761**	**0.508**	**1**	
Dry weight	0.065	0.111	0.160	0.260	**-0.432**	-0.064	0.363	**0.539**	**0.669**	**0.742**	**1**

Values in bold are significantly different from 0 with a significance level alpha=0.05

High biomass values have been reported during the pre-monsoon season when salinity was high. Salinity has always been regarded as regulating the distribution and diversity of zooplankton, especially copepods in marine ecosystems[13,14,40-44].

The correlation between zooplankton-related parameters and different environmental factors is shown in Table 1. Zooplankton species abundance showed a strong positive correlation with salinity and chl-*a*. It indicated that marine zooplankton diversity thrived under optimal salinity conditions of ~32–33 PSU and food availability[45,46]. On the other hand, turbidity deterred zooplankton, as evidenced by the negative correlation between them. This could be because turbidity influences light penetration, directly affecting phytoplankton production[47,48], the main food source of zooplankton. Thus, with the increase in turbidity, the food of the primary consumers becomes scarce, and thus, they cannot sustain themselves in the turbid waters. Interestingly, the zooplankton density showed a negative correlation with the Secchi disc depth. In fact, phyto- and zooplankton themselves contribute to water transparency. In the present study, Secchi disc depth was approximately twice as high in offshore waters, and zooplankton density was relatively low there compared to nearshore waters (Fig. 3c). It indicated that the low zooplankton density and possibly the low phytoplankton biomass in the offshore waters had increased transparency. Zooplankton's dry weight showed a moderately negative relation with turbidity. It indicated that zooplankton production is adversely impacted by water turbidity, as discussed earlier.

The PCA biplot shows that PC1 and PC2 accounted for 55.13 % of the total variance (Fig. 4). It represented the affinities of biotic and abiotic factors towards different seasons. It was observed that zooplankton-related parameters (population density, number of species, wet weight, and dry weight) and subgroups of zooplankton (copepod, copepodite, NCH, and meroplankton) showed linkage towards PRM seasons. Collectively, all zooplankton parameters were associated with salinity and chlorophyll-*a*, reconfirming the findings from the correlation analysis. Other water quality parameters, such as temperature, pH, DO, turbidity, and Secchi disc depth, were mostly linked to the POM and MON seasons, during which zooplankton production was relatively low. Similar observations of seasonal zooplankton abundance have been reported from various coastal waters of India and abroad[17,18,49-51].

Zooplankton composition and abundance

A total of 183 taxa were recorded from the study area. Out of which 97 were copepods, 47 Non-Copepod Holoplankton (NCH), and 39 meroplankton (Table S1). As expected, the copepod group dominated the zooplankton community, representing 25 families and 39 genera. Copepodite stages were recorded for 12 copepod taxa. A relatively low number of species was recorded during monsoon seasons (Fig. 3d). It ranged from 34–72 and 45–69 species for the nearshore and offshore transects, respectively. Average zooplankton population density ranged from $0.54–6.10\times10^4$ individuals per 10 m^3 in the nearshore waters and $0.44–4.83\times10^4$ individuals per 10 m^3 in the offshore waters (Fig. 3c). On the other hand, the total average density was higher in nearshore waters of Palar and Edaiyur than at 5 km; whereas, in the Mahabalipuram zone, both densities were almost equal (Fig. 5). Zooplankton biomass

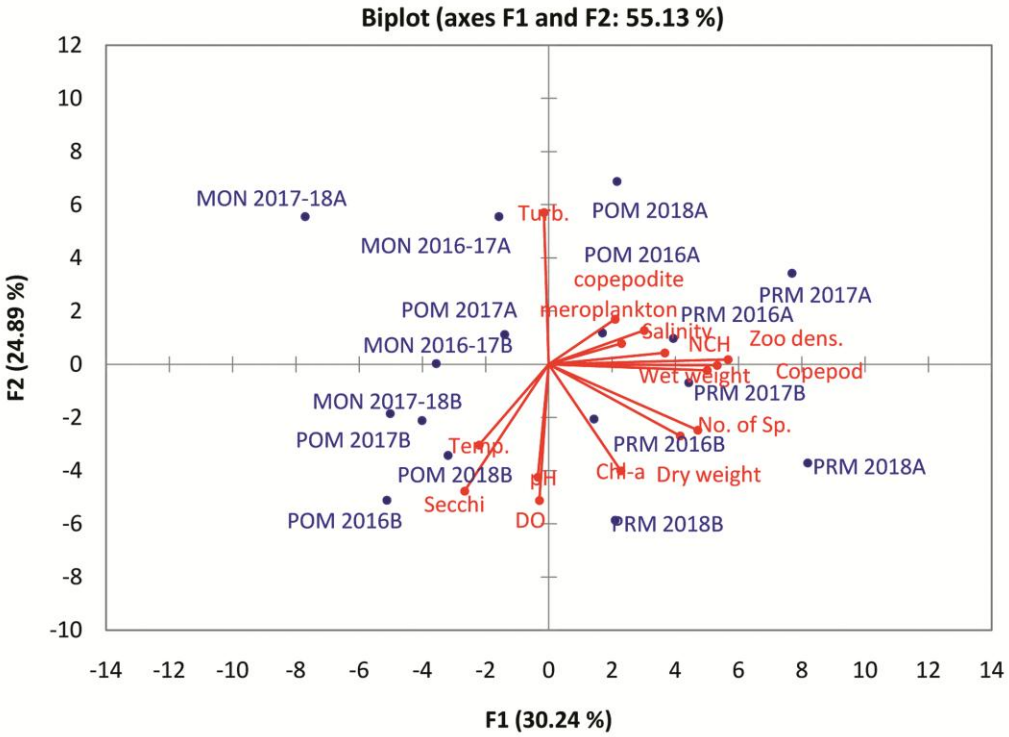


Fig. 4 — Factor plane projection of environmental variables and different seasons derived from PCA

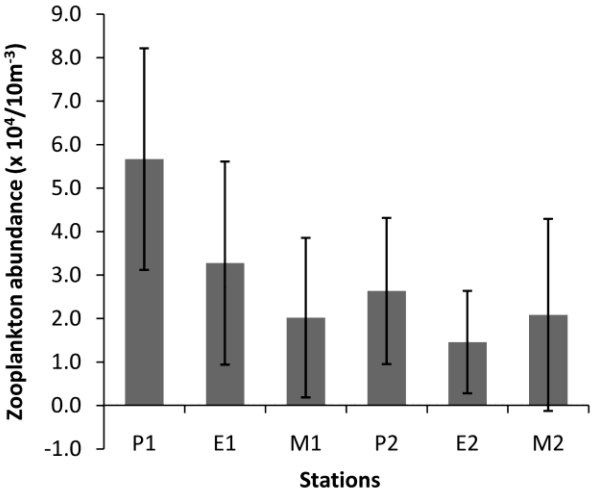


Fig. 5 — Spatial variation in zooplankton population in the coastal waters of Kalpakkam

(wet and dry weight) was found to have peaked during PRM except for PRM-2016. A similar trend in average biomass was found for both wet and dry weight (Fig. 6). The Numerical density, as well as the number of zooplankton species, showed positive correlations with their biomass (both wet and dry weight), indicating that population density was directly proportional to biomass. Diversity indices varied significantly across seasons during the study period (Fig. 7). A well-marked spatial heterogeneity was observed with relatively high species diversity in the 5 km transect compared to the 0.5 km transect. Among the stations, P1 and E1 showed relatively lower species diversity and richness than P2 and E2, unlike those in Mahabalipuram water (Fig. 8).

Copepods were the most dominant taxa in the zooplankton community in the study. Seasonally, copepods were found to be contributing 26–65 % to the total zooplankton community, followed by NCH (22–69 %), meroplankton (2–19 %), and copepodite (1–5 %) (Fig. 9). Spatially, the copepod community showed higher abundance in the 5 km waters of Palar (P2) and Edaiyur (E2) than in P1 and E1, whereas in the Mahabalipuram (M) water, the trend was reversed (Fig. 10). This could be due to riverine influx during the monsoon period, creating an unfavourable condition in the nearshore environment. On the other hand, the nearshore waters of Mahabalipuram are free of river runoff, resulting in higher copepod abundance (M1 > M2) throughout the study period. Moreover, Mahabalipuram water (M1) supported a high abundance of harpacticoid copepods, mostly benthic. This may have occurred due to heavy churning of coastal sediment from local tourism and recreational

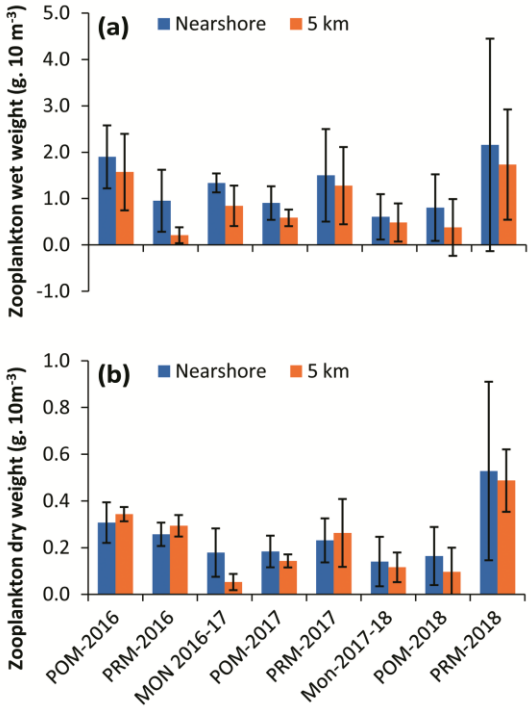


Fig. 6 — Seasonal variations in a) Wet weight, and b) Dry weight of zooplankton, in the coastal waters Kalpakkam

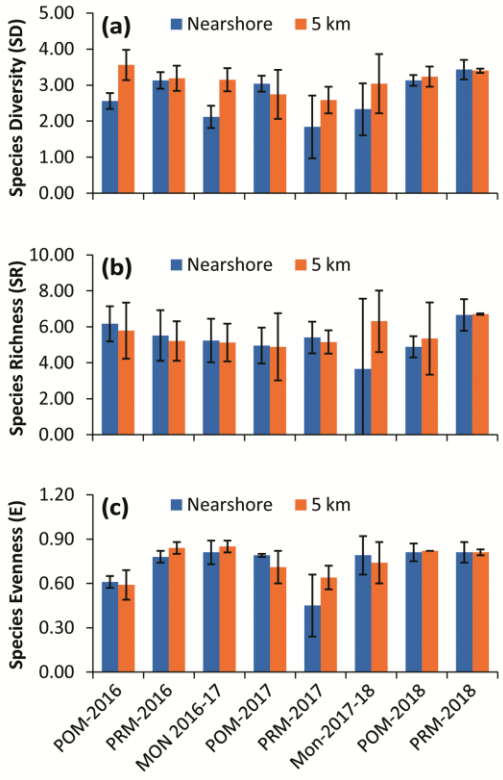


Fig. 7 — Seasonal variations in zooplankton diveristy incices a) Species Diversity (SD), b) Species Richness (SR), and c) Species Evenness (E), in the coastal waters of Kalpakkam

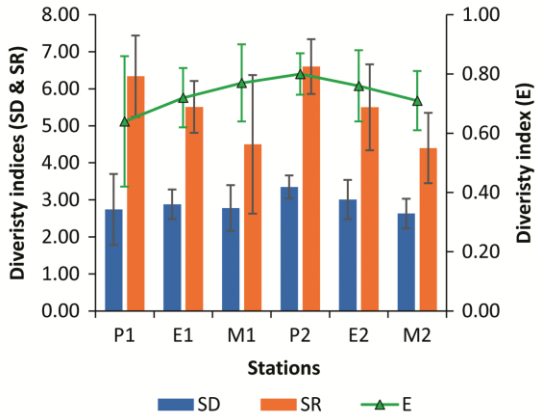


Fig. 8 — Spatial variations in zooplankton diveristy indices in the coastal waters of Kalpakkam

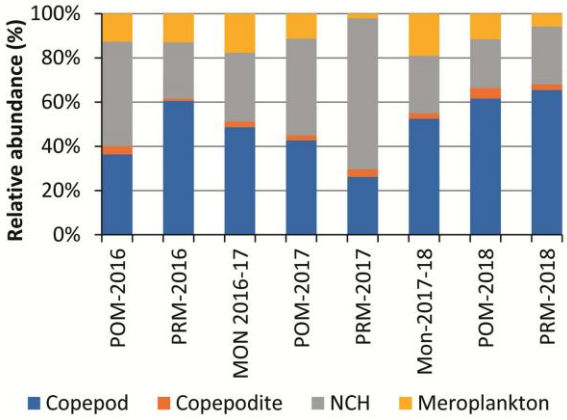


Fig. 9 — Seasonal percentage contribution of copepod, copepodite, non-copepod holoplankton, and meroplankton in the coastal waters of Kalpakkam

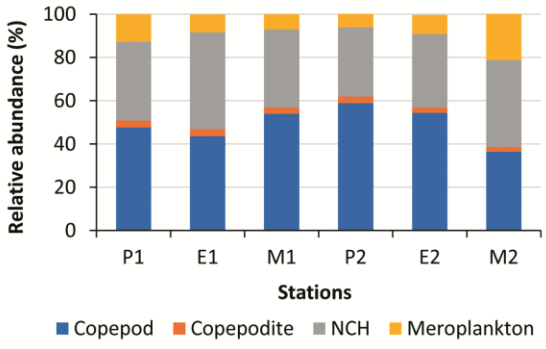


Fig. 10 — Station-wise (Spatial) percentage contribution of copepod, copepodite, non-copepod holoplankton, and meroplankton in the coastal waters of Kalpakkam

activities, leading to an influx of benthic copepods from the sediment into the water column. Zhou *et al*.[52] also observed benthic harpacticoids in the water column of intertidal habitats during tidal flooding.

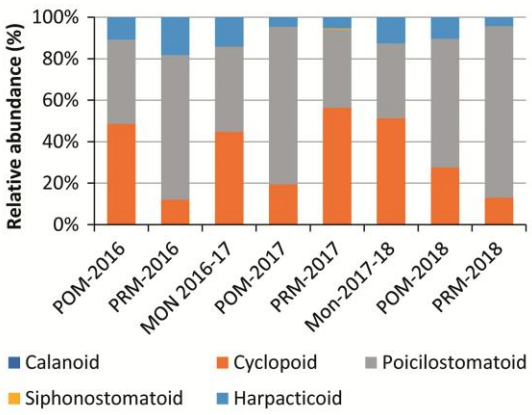


Fig. 11 — Seasonal percentage contribution of different copepod groups in the coastal waters of Kalpakkam

Among copepods, as expected, the calanoid group dominated the community and contributed 45–86 % to the total copepod population (Fig. 11). Seasonal average copepod population was predominated by *Bestiolina similis*, *Pseudodiaptomous serricaudatus*, and *Paracalanus parvus*, which contributed 25.4, 22, and 15.5 % to the total copepod abundance, respectively. The total zooplankton taxa recorded in the present study were similar to those reported from other coastal waters of Indian[53-55]. This result corroborated with various other studies[17,18,42-50,56] where the authors have reported the dominance of copepods in saline water bodies.

Temporal variations in major groups

Copepods

Among copepods, *B. similis* and *P. parvus* were dominant during the POM, which subsequently diminished in abundance in PRM. *Bestiolina similis* reappeared in the MON season with relatively low population density. Predation pressure from fish larvae could be the reason for its low abundance during PRM. Apr–June is considered the primary fish breeding time for this tropical coastal region, and subsequently, the larval dispersion occurs in PRM season (June–Sep.). Calanoid copepods are highly nutritious food for marine invertebrates and fish larvae[57]. Apart from the two species above, others such as *Pseudodiaptomous*, *Canthocalanus*, *Calanopia*, *Temora*, etc., are also preferred as food items because the size range of prey selected by the larvae is similar to the size of these copepods[58]. Moreover, due to the size of its developmental stages, growth rate, and nutritional composition, *B. similis* becomes susceptible to predation by tropical larval fishes[59]. Similarly, studies have reported that *B. similis* is a highly preferred food item for larval fish in aquaculture[58].

A group of copepods consisting of *Bestiolina similis*, *Paracalanus parvus*, *P. aculeatus*, *Acrocalanus longicornis*, *A. gibber*, *Corycaeus danae*, *C. catus*, *C. erythraeus*, *Euterpina acutifrons*, *Oithona rigida*, *O. setigera*, and *Pseudodiaptomous serricaudatus*, which appeared predominantly during all the seasons, formed a common association showing about 80 % similarity (Figs. 12, 13). This association formed the core of the copepod community, and the abundance of the other copepod species revolved around it. Species which appeared in a highly sporadic manner, *viz*. *Microsetella norvegica*, *Pontella* sp., and *Centropages gracilis* that appeared only once during the entire study were distinctly separated from others (Figs. 12, 13). Species such as *Oithona speciosus*, *Cosmocalanus darwinii*, and *Paracalanus attenuatus* formed a separate group due to their rare appearances. Another group of copepods, which appeared 4–5 times across the 48 samples, formed an association that included *Pontella danae*, *Calanopia elliptica*, *C. minor*, *Euchaeta marina*, *Lucicutia flavicornis*, *Corycaeus longistylis*, *Sapphirina opalina*, *Acartia tropica*, and *Labidocera kroyeri*. The 4th minor group of copepods is formed by *Centropages dorsispinatus*, *Paracalanus indicus*, *Pseudodiaptomous aurivilli*, *Bomolochus* sp., *Oithona nana*, *Candacia bradyi*, *Labidocera* sp., *Macrosetella gracilis*, *Copilia quadrata*, *Clausocalanus arcuicornis*, *Candacia catula*, and *Longipedia weberi*. These species appeared at relatively high frequency compared to other minority groups, and their appearances were associated with one another in many cases.

Non-Copepod Holoplankton (NCH)

Among NCH, *Oikopleura dioeca* and *Oikopleura* sp. (appendicularians) were abundantly found during all the seasons. POM was dominated by *Evadne tergestina*, *Lucifer* zoea/ nauplius, *Oikopleura dioeca* & *Oikopleura* sp., and *Sagitta bedoti* (contributed 10–49 % of abundance) among NCH. The PRM period showed the greatest contribution (~30 %) from *Oikopleura dioeca* and *Sagitta bedoti* to the NCH population, except during PRM-2017, when only *Noctiluca scintillans* dominated the NCH community. The monsoon period was represented solely by *Oikopleura dioeca*, which accounted for 73.1 % of the total NCH population. Appendicularians, which filter food particles, live within mucosal structures

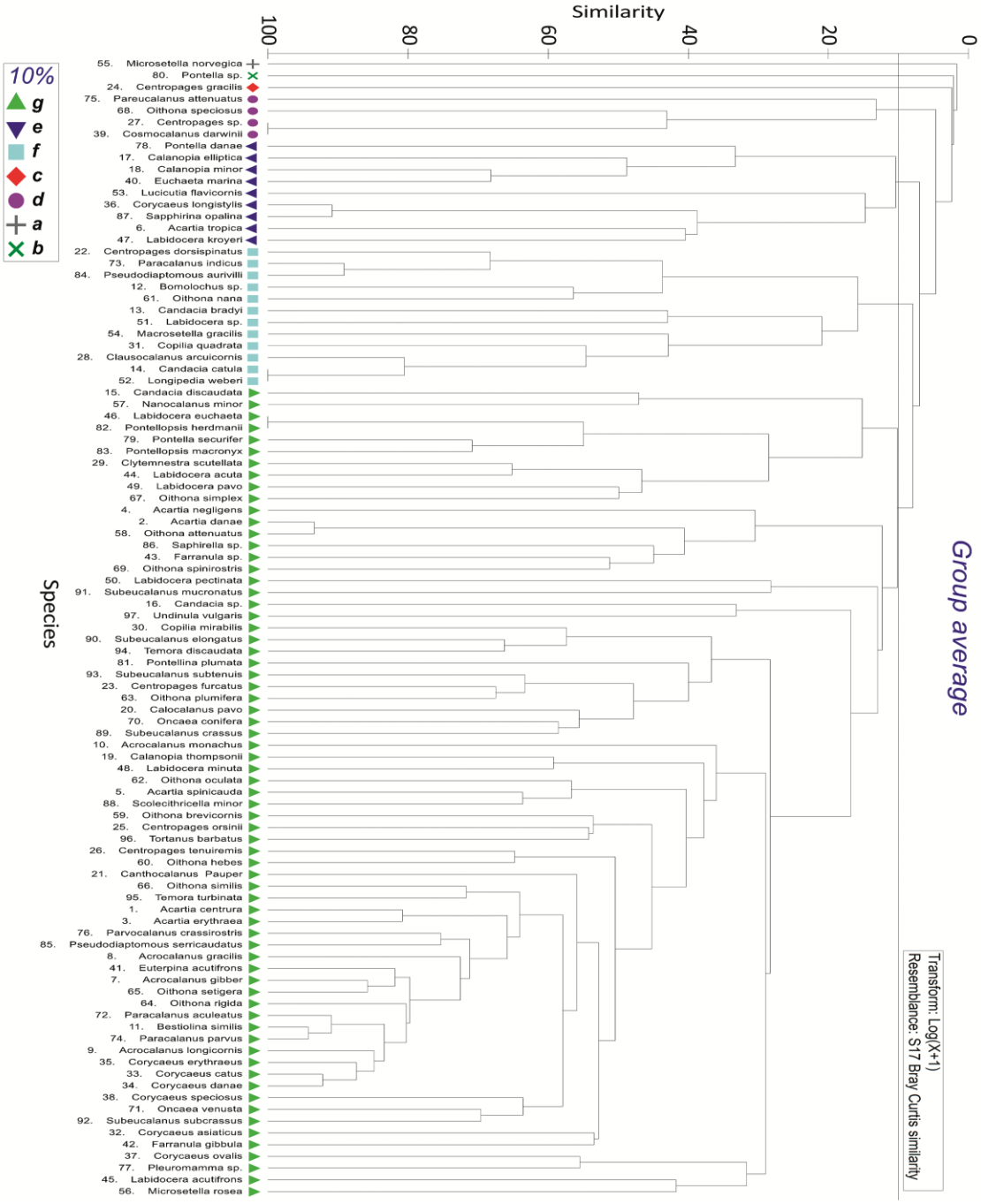


Fig. 12 — Cluster analysis showing the association of copepods in the coastal waters of Kalpakkam

commonly called 'houses'. These mucosal structures protect the organism from adverse environmental conditions[60]. The mucous encasement also helps them escape predation by fish larvae[61]. High *Oikopleura* abundance throughout the study could be attributed to the above factors, which enhance the survival rate of these organisms relative to other forms. Partially supporting the present finding of *Sagitta bedoti* and *Lucifer* zoea dominance during POM, Antony *et al*.[62] elucidated the presence of *Lucifer* during the SW-monsoon period (*i.e*., PRM at SE coast of India) and the immediate POM period (*i.e*., NE-monsoon at SE coast of India) along the SW coast of India and also at localised centres on the east coast, such as Chennai,

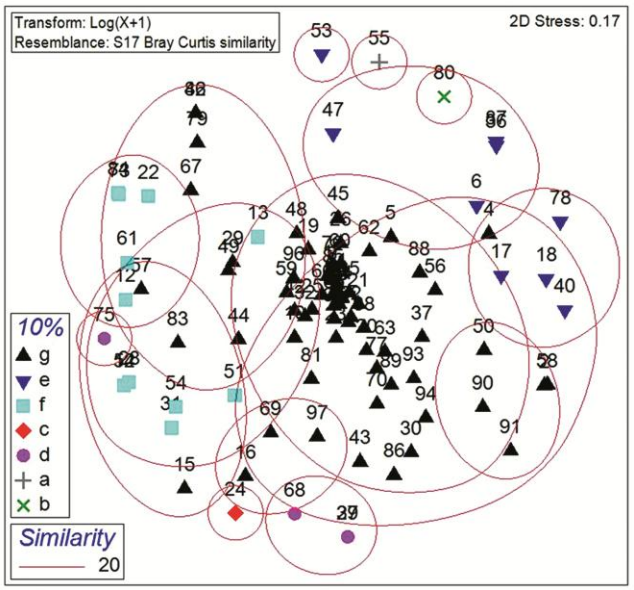


Fig. 13 — nMDS plot showing the association of copepods in the coastal waters of Kalpakkam

Visakhapatnam, and Odisha. *Noctiluca scintillans*, which dominated the NCH community during PRM season, were not abundant during other periods of this study. As is well known, *N. scintillans* requires high salinity and cool water for growth and survival[63], and it appeared during PRM in this study. This period is characterised by high-salinity, low-temperature water masses that support the growth of *N. scintillans*. Similar observations on *N. scintillans* abundance during the PRM period have been reported from Indian coasts[64-67]. In NCH, the core group that appeared during almost all observations was formed by *Noctiluca scintillans*, *Lucifer hanseni*, *Sagitta inflate*, *Sagitta bedoti*, *Oikopleura dioeca*, *Obelia* sp., *Evadne tergestina*, *Doliolum* sp., and a few others (Fig. 14). Unlike Copepods, the minor associations in NCH were numerous, indicating that their appearance and abundance were independent. Many of these minor groups included organisms that were broadly identified (up to the order level in some cases) and were rare.

All seasons showed high abundance of copepods and appendicularians. The copepod-appendicularian abundance has been grouped into two meaningful categories, *viz.*, routine and opportunistic phytoplankton grazers along the SW coast of India[68]. Earlier findings revealed that appendicularian densities are primarily limited to eutrophic waters and phytoplankton blooms[69]. As a consequence, seasonal competition for food is functioning between copepodites, copepods, and appendicularians, consisting of juveniles and adults. Also, carnivorous copepods were attracted to juvenile appendicularians. In this context, Ohman & Runge[70] also stated that the competitive interaction between copepods and appendicularians for phytoplankton can sometimes trigger carnivorous grazing by copepods when phytoplankton concentration is low, turning them into appendicularian predators. In this way, a food chain relationship, *i.e.*, phytoplankton-appendicularian-copepod-fish, established in coastal waters, further provides evidence for a threshold to research perspectives.

Meroplankton

The distribution of meroplankton depends on various factors, such as reproduction, mortality, predation pressure, and oceanographic processes, which determine their presence in the pelagic realm, not only by dispersing them but also by retaining them in specific areas[71]. Cirripede larvae in the present study dominated the meroplankton community. Barnacles, the adult forms of cirripedes, are the dominant sessile forms at this location[17-19]. Continuous breeding and wide environmental tolerance in this group result in a continuous supply of larval forms throughout the year[72]. Similar observations of cirripede dominance have also been reported from different coastal regions of India, such as Visakhapatnam, Bombay, Mangalore, and Karwar[73,74]. Another dominant form in the meroplankton category was the bivalve larvae (D-shaped larvae). Relatively high densities of bivalve larvae were recorded during POM, followed by MON. Lowest densities were recorded during the PRM season. It is worthwhile to mention here that green mussels have been observed to form the climax community in the macrobenthic settlements at this location[72,75,76]. In addition to green mussels, brown mussels are also highly abundant in this region. Several studies have shown that mussels reach reproductive maturity during the MON season at this location, and their spatfall begins immediately thereafter and continues throughout the POM period. Settlement of juvenile forms takes place during the late POM and PRM periods. The observation of a relatively high population of bivalve larvae during the POM season and lower numbers during the PRM season could be attributed to the above reasons. Common larval forms such as *Echinopluteus* larva,

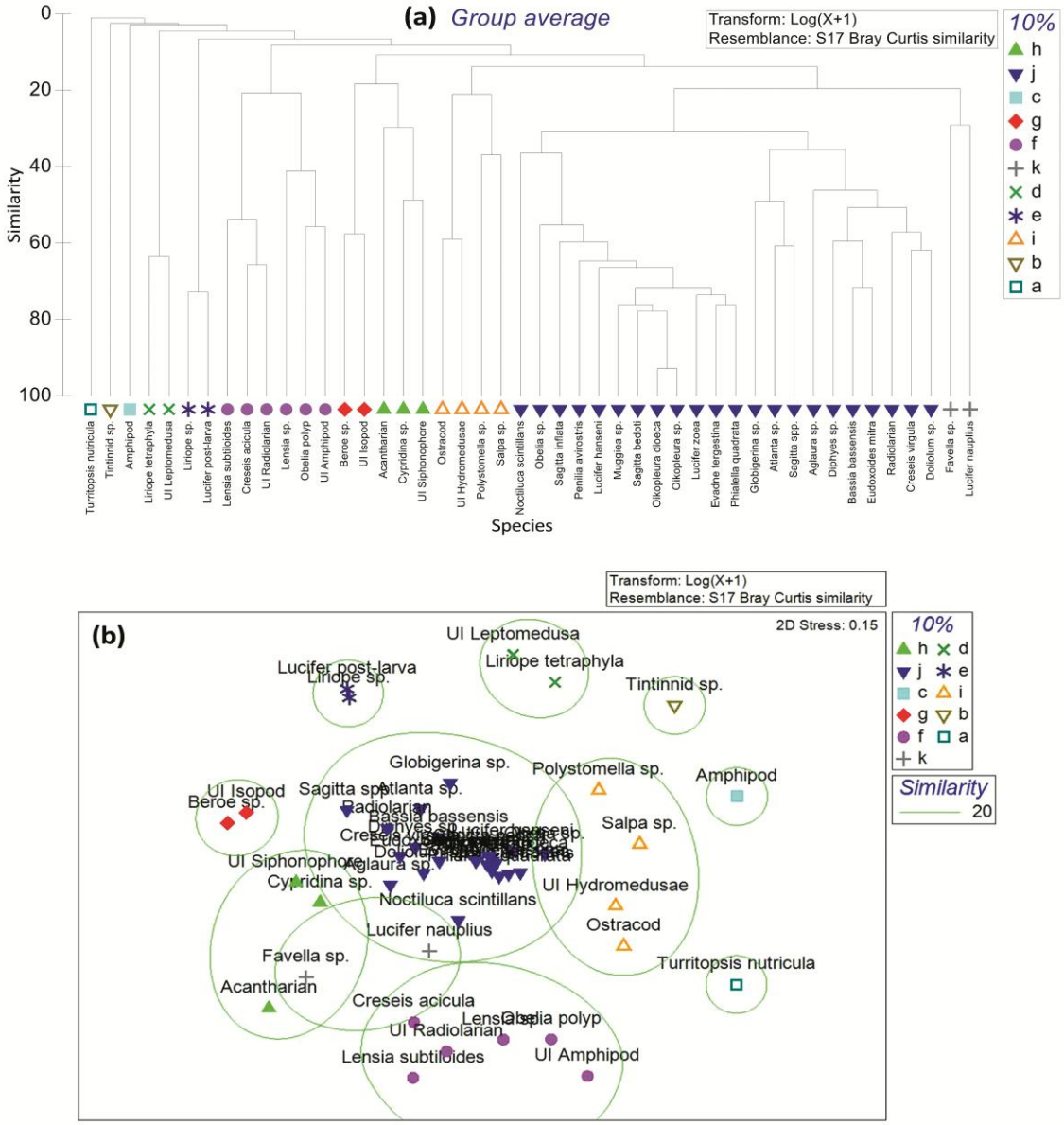


Fig. 14 — Cluster and nMDS analysis showing the association of Non-Copepod Holoplankton (NCH) in the coastal waters of Kalpakkam

Ophiopluteus larva, crab zoea, fish egg, gastropod larvae, polychaete larvae, bivalve larvae, and cirripede nauplius formed the major association in meroplankton. Another association of larvae included brachiopod larvae, rotifer eggs, Squat lobster zoea, rotifer larvae, and *Squilla* zoea. Apart from these two associations, all the other larval distributions were unrelated (Fig. 15).

Temporal and spatial heterogeneity in zooplankton distribution

Non-metric Multidimensional Scaling (nMDS) with a cluster overlay indicated that zooplankton community dynamics across all seasons showed about 60 % similarity (Figure 16a). Only POM 2018 and Mon 2016-17 showed some interrelation at 80 % similarity. It indicated that zooplankton distribution at this location is not highly variable and shows no distinct year-to-year variation. The SIMPER analysis further confirmed the above findings by grouping all the seasons into a single group. The average similarity was 68.23 %. Species such as *Bestiolina similis*, *Oikopleura dioeca*, *Paracalanus parvus*, *Oikopleura* sp., *Paracalanus aculeatus*, *Corycaeus danae*, *Corycaeus catus*, *Acrocalanus longicornis*, etc., were

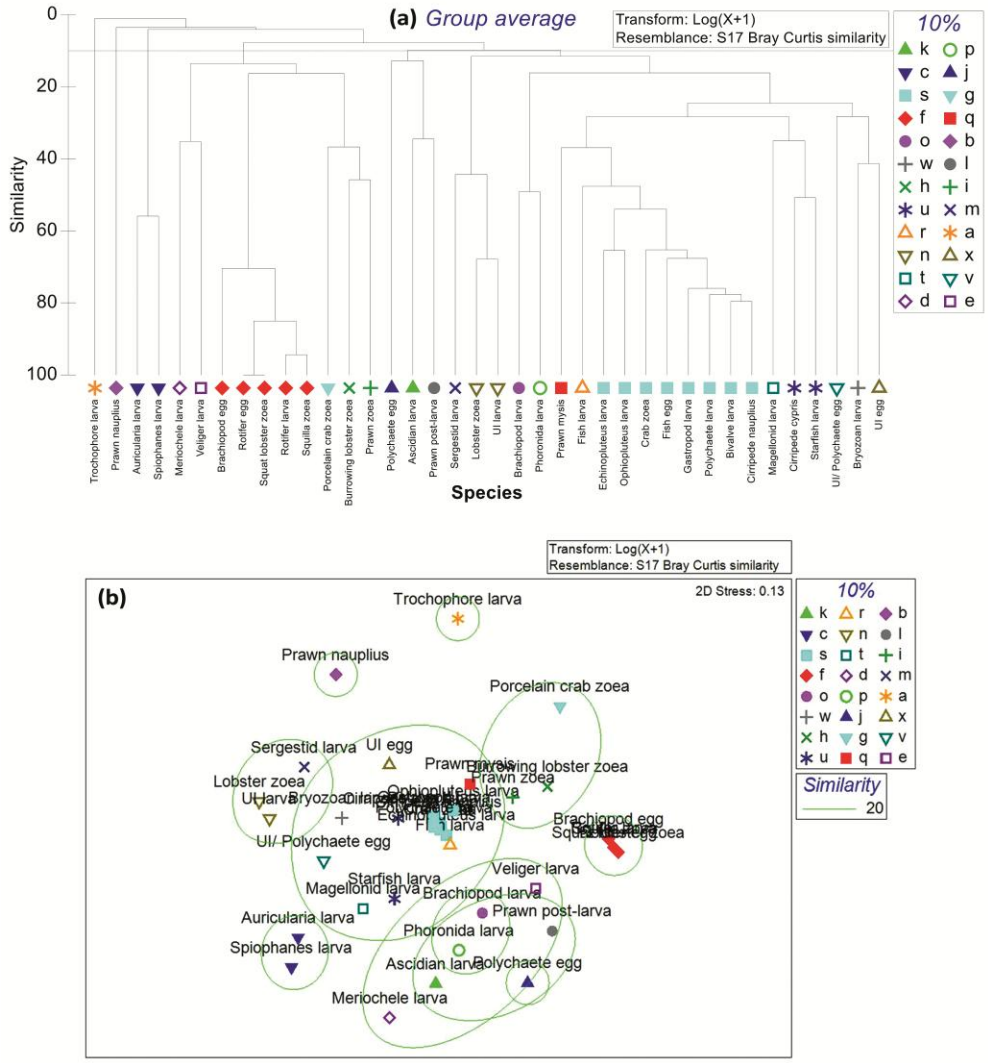


Fig. 15 — Cluster and nMDS analysis showing the association of meroplankton in the coastal waters of Kalpakkam

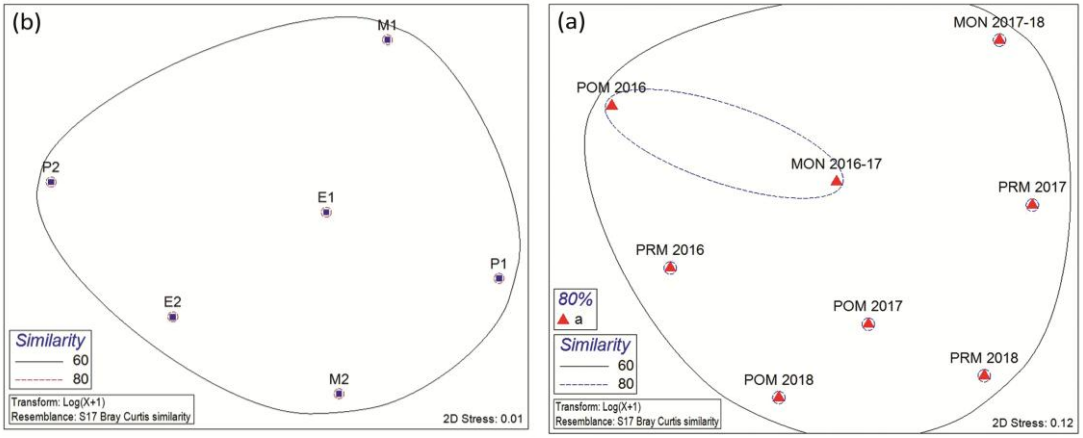


Fig. 16 — nMDS analysis showing the a) Seasonal (Temporal), and b) Station-wise (Spatial) similarities in zooplankton distribution in the coastal waters of Kalpakkam

Table 2 — Results of SIMPER analysis

Seasons - Average similarity: 68.23					
Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Bestiolina similis	7.32	1.62	7.99	2.38	2.38
Oikopleura dioeca	7.11	1.60	8.60	2.34	4.72
Paracalanus parvus	7.01	1.56	6.73	2.29	7.01
Oikopleura sp.	6.65	1.49	9.92	2.18	9.20
Paracalanus aculeatus	6.59	1.45	5.70	2.13	11.33
Corycaeus danae	6.01	1.34	7.72	1.97	13.30
Corycaeus catus	5.99	1.33	6.07	1.95	15.24
Acrocalanus longicornis	6.07	1.32	6.55	1.94	17.18
Euterpina acutifrons	5.91	1.32	7.69	1.93	19.12
Sagitta bedoti	5.93	1.30	6.90	1.90	21.02
Oithona rigida	5.87	1.30	9.52	1.90	22.92
Cirripede nauplius	5.95	1.29	5.31	1.89	24.81
Corycaeus erythraeus	5.78	1.27	8.08	1.86	26.67
Polychaete larva	5.63	1.25	8.84	1.83	28.50
Pseudodiaptomous erricaudatus	6.25	1.24	4.52	1.82	30.32
Acrocalanus gibber	5.47	1.22	8.01	1.79	32.11
Bivalve larva	5.64	1.18	6.54	1.73	33.84
Oithona setigera	5.17	1.09	4.58	1.59	35.43
Muggiea sp.	5.24	1.07	3.49	1.57	36.99
Copepod nauplius	5.24	1.06	6.86	1.55	38.54
Stations - Average similarity: 74.47					
Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Noctiluca scintillans	8.22	1.69	10.37	2.27	2.27
Oikopleura dioeca	7.31	1.50	13.37	2.01	4.28
Oikopleura sp.	6.84	1.40	12.90	1.88	6.16
Bestiolina similis	7.07	1.38	13.11	1.85	8.01
Paracalanus parvus	6.85	1.35	12.78	1.82	9.82
Corycaeus catus	6.19	1.30	12.25	1.74	11.56
Corycaeus danae	6.16	1.29	13.18	1.73	13.29
Acrocalanus longicornis	6.28	1.27	14.78	1.71	15.00
Corycaeus erythraeus	6.00	1.24	11.41	1.67	16.66
Sagitta bedoti	6.01	1.22	10.45	1.64	18.31
Paracalanus aculeatus	6.30	1.20	10.47	1.61	19.92
Copeod nauplius	5.94	1.20	9.38	1.61	21.53
Cirripede nauplius	6.06	1.20	8.84	1.61	23.14
Oithona rigida	6.01	1.19	8.27	1.60	24.74
Pseudodiaptomus serricaudatus	6.39	1.19	8.06	1.60	26.34
Oncaea venusta	5.99	1.18	9.22	1.58	27.92
Muggiea sp.	5.63	1.12	7.48	1.51	29.43
Lucifer zoea	6.08	1.10	6.53	1.48	30.91
Penilia avirostris	6.30	1.10	6.32	1.47	32.38
Oithona setigera	5.49	1.09	11.93	1.46	33.84

the dominant contributors (Table 2). The stations also showed a similar pattern in zooplankton distribution. All the stations showed about 70 % similarity (Fig. 16b). SIMPER analysis showed a similarity of exactly 74.47 %. The dominant contributors in the spatial pattern were the same as those listed for the temporal pattern, except for *Noctiluca scintillans*, which appeared here as the highest contributor.

Conclusion

The results showed relatively high zooplankton diversity and density during the pre-monsoon and post-monsoon seasons compared to the monsoon season. Zooplankton density ranged from 0.54–6.10×10^4 individuals per 10 m^3 in the nearshore waters and 0.44–4.83×10^4 individuals per 10 m^3 in the offshore waters. A total of 183 taxa were recorded.

Out of which 97 were copepods, 47 Non-Copepod Holoplankton (NCH), and 39 meroplankton. As expected, the copepod group dominated the zooplankton community, belonging to 25 families and 39 genera. Copepodite stages were recorded for 12 copepod taxa. A relatively low number of species was recorded during the monsoon seasons. Seasonally, copepods were found to contribute 26–65 % of the total zooplankton community, followed by NCH (22–69 %), meroplankton (2–19 %), and copepodite (1–5 %). Among copepods, the calanoid group dominated the community and contributed 45–86 % to the total copepod population. Among other NCH, *Sagitta bedoti* and *Lucifer* zoea were the dominant ones during POM, and *Lucifer* zoea developed into adults by PRM. Within the meroplanktonic members, cirripede larvae were the most dominant and common larval group. Relatively high species diversity was observed at the 5 km transect as compared to the 0.5 km transect. Salinity and turbidity were the most important factors influencing zooplankton diversity at this location. Non-metric Multidimensional Scaling (nMDS) and similarity percentage (SIMPER) analyses indicated an almost uniform distribution of zooplankton communities across the spatio-temporal scale.

Supplementary Data

Supplementary data associated with this article is available in the electronic form at https://nopr.niscpr.res.in/jinfo/ijms/IJMS_53(03)676-693_SupplData.pdf

Acknowledgments

The authors are thankful to the Head, RDS; Head, EAD; Director, SQRMG; and Director, Indira Gandhi Centre for Atomic Research, for their encouragement and support in carrying out this work. Thanks are also due to Dr. Rosamma Stephen for helping identify some of the zooplankton.

Conflict of Interest

The authors declare that there is no conflict of interest.

Author Contributions

GS: Investigation, formal analysis, and writing original draft; AKM: Conceptualisation, formal analysis, software, and writing- review & editing; RSS: Formal analysis and writing original draft; and NPID: Writing- review & editing.

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