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Diel patterns in Copepods of the Ganges estuary: A time series approach

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ABSTRACT

Research on copepods is vital for understanding estuarine ecosystem functioning, as they are linked with secondary productivity. Diurnal fluctuations of the estuarine copepod diversity and community structure are less known for Indian estuaries. Three separate 12-hour-long time series of hourly intervals were conducted on the Muriganga section of India's Ganges estuary in February, August and December 2019. It was hypothesized that significant variations exist in the copepod richness and abundance between day and night. Results showed that the community's diversity and abundance were higher at night compared to day. The study identified a total of 28 species, with *Bestiolina similis*, *Paracalanus parvus*, *Acartia spinicauda*, and *Acartiella tortaniformis* dominating the community throughout the study. *Bestiolina similis*, *Paracalanus parvus*, *Acartiella tortaniformis* and *Pseudodiaptomus binghami* exhibited no diurnal variations in their abundances; they were also the main contributors to overall abundance of the community. Day Vs. night differences in species richness and abundances were not consistent across the three time-series. Throughout the study Acartiidae, Paracalanidae, and Oithonidae families were the dominant taxa in terms of abundance, making up to 70–90% of the total abundance of the community. SIMPER analysis found day vs. night dissimilarities for several copepod species within the community. The current research underscores the importance of incorporating day-night scale for zooplankton monitoring, an often-overlooked aspect of plankton ecology for Indian estuaries.

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1. Introduction

The equilibrium of a plankton community is primarily maintained by species composition, and abundance; therefore, variation in any one of them or both the components can destabilize the trophic relationships, potentially with cascading impacts on the lower food web of an estuary (Biswas *et al*., 2010; Winder & Jassby, 2011; Paul *et al.*, 2019). Tropical river estuaries are dynamic ecosystems where ecological communities may experience considerable variability of species composition, abundance, and dominance between day and night (Chew *et al.,* 2015; Paul *et al*., 2019). Copepods usually dominate the mesozooplankton communities of those estuaries (da Costa *et al*., 2008; Bhattacharya *et al*., 2015) despite that only a few studies have looked into their day-night variability and suggested that such a variation affects functioning of estuarine food webs (Wooldridge, 1976; Ringelberg *et al*., 1984; Bollens & Frost, 1991; Williamsom *et al.*, 2001; Marques *et al*., 2009; Chew & Chong, 2011; Chew *et al*., 2015; Paul *et al*., 2019). Selvakumar *et al*. (1986) and Vineetha *et al*. (2015) suggested density of the copepods peaked at night during the high tides in the estuaries of Kerala, India. Similar observation was made in the Amazon estuaries and Matang mangroves of Malaysia which affected the community structure of the copepods (da Costa *et al*., 2008; Chew *et al*., 2015).

The taxonomic composition of the copepod community of the Ganges estuary (GE) has been previously well studied for hourly to seasonal scales and those studies suggested *Bestiolina similis*, *Acartiella tortaniformis*, *Paracalanus* spp., *Acartia* spp., and *Oithona* spp. dominated the community (Sinha *et al*., 1996; Bhattacharya *et al*., 2015; Paul *et al.*, 2019). Paul *et al.* (2019) suggested that an intense competition between *Bestiolina similis* and *Paracalanus parvus* influenced the spatial variation of the community dynamics in the Muriganga section of the GE but hourly variability of estuarine environment played limited role in that. The objective of the current study was to provide a better understanding of the structural variations of the estuarine copepod community between day and night. It is, therefore, hypothesized that the copepods would exhibit day vs. night variability in terms of their richness and abundance; however, that variability may not be consistent in different sampling occasions, and such diurnal fluctuations would not influence the predominant copepod populations of the GE.

2. Materials and Methods

2.1 Study area

Near its mouth, the GE divides into two channels; the main channel (known as 'Hooghly') directly mixes with the BoB, whereas the other smaller channel, known as the Muriganga (Fig.1) has similar physical-chemical properties of the main channel but it takes a longer route before it meets the BoB (Mukhopadhyay *et al*., 2006; Dutta *et al.,* 2019). The present study was conducted on the Muriganga section of the GE (see Fig.1), which is shallow and predominantly influenced by mixed semidiurnal tides that often range from 1.8 m to 5.2 m (Mukhopadhyay *et al*., 2006). The catchment of the Muriganga has low to moderate mangrove vegetation, with rural land use with some human settlements

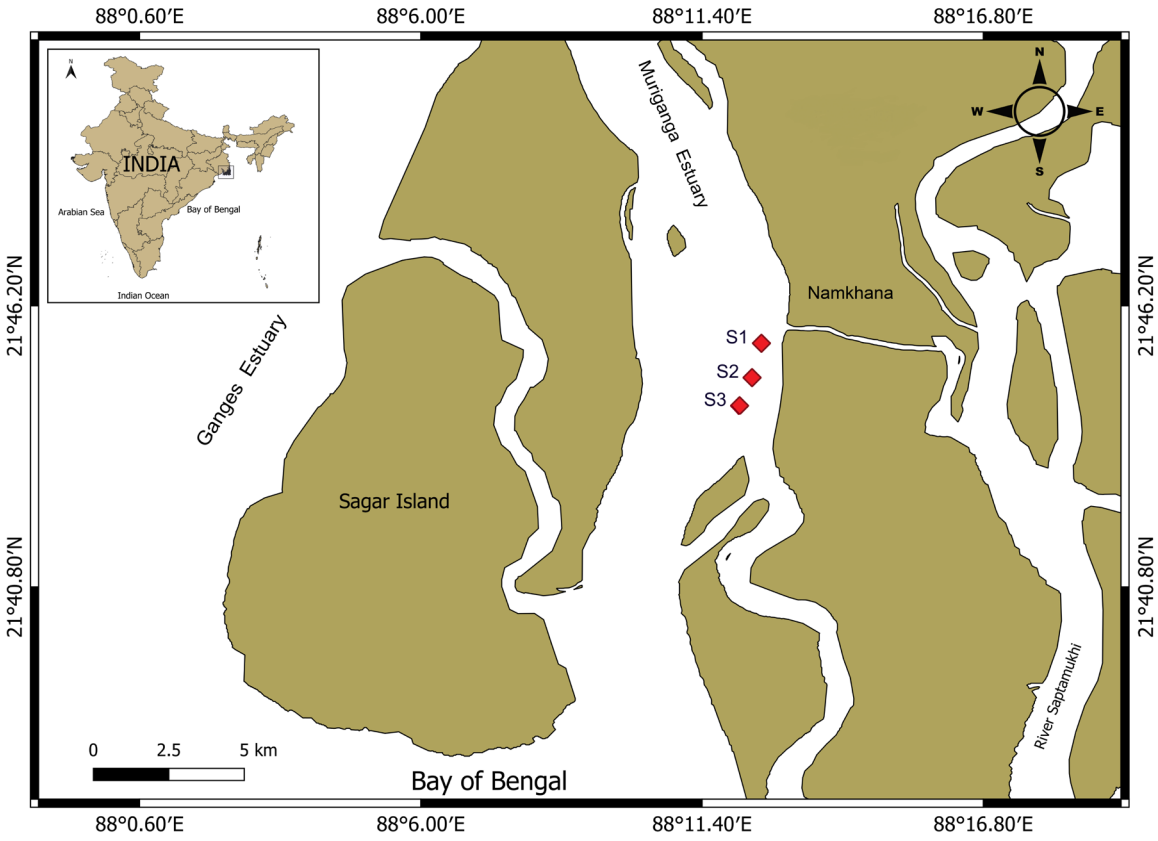


Fig. 1. Map of the sampling sites (S1 to S3) on the Muriganga stretch of the Ganges estuary of India

and agricultural fields (Choudhury & Bhadury, 2015). The surface water temperature of the Muriganga varies from 24-30°C annually with alkaline pH (> 7) and the salinity profile generally stays meso-haline (Mukhopadhyay *et al*., 2006; Choudhury and Bhadury, 2015). The region experiences monsoonal precipitation from June to September, with an average of 60-75% of annual rainfall (range 1400-1600 mm) occurring during monsoon (Mukhopadhyay et al., 2006). Generally, October to January and February to May are designated as postmonsoon and premonsoon seasons, respectively (Mukhopadhyay *et al*., 2006).

2.2 Sampling strategy

A total of three replicate sampling sites S1 (21°44'53.8" N; 88°12'46.2" E), S2 (21°44'55.7" N; 88°12'40.0" E) and S3 (21°44'55.4" N; 88°12'36.8" E) were selected along the north-south direction (Fig.1). The entire time series observation was conducted in triplicate, once in every season for a 12h period in hourly interval. The first time series was conducted on 24 February 2019 (i.e., assumed as a premonsoon time series), the second was on 24 August 2019 (i.e., assumed as monsoon time series), and the final time series was on 28 December 2019 (i.e., assumed as postmonsoon time series). For all the time series samplings were done from 1 pm to 12 am at one-hour intervals. The samples collected before the sunset (i.e., 1 pm to 5 pm: H1-H5) were assumed to be the day samples, and the samples collected after the sunset (i.e., 6 pm to 12 am: H6-H12) were considered night samples. The present study; therefore, has the design of 12 (hourly collection) X 3 (stations) X 3 (seasons).

2.3 Field sampling and laboratory analysis

On each hour of a time-series, water temperature (°C), salinity (in practical salinity unit), and pH were measured in situ by a hand-held multi-parameter probe (YSI-1030, USA), and the copepod assemblages were collected by a 20L bucket from the surface water at each sampling stations following the methodology described by Paul *et. al.* (2019). On each occasion of sampling, 100L of estuarine water was filtered through a 200 µm net for collection of copepods. The filtered sample was fixed immediately with 4% buffered formaldehyde seawater solution and transported to the laboratory for further analysis. In the laboratory, triplicate subsamples (each of 1-5ml) were taken and identified up to species level with the help of the standard manual of Kasturirangan (1963) using a Sedgwick Rafter counting chamber under a stereo-zoom microscope (Bestscope BT2030, China). For each species, only the adults were counted and their median abundance was expressed as individuals per cubic meter of water (Ind.m^{-3}).

2.4 Data analysis

To compare the copepod abundances between day and night, abundance data were square root transformed and used for the Bray-Curtis similarity matrix for drawing the nMDS (non-metric multidimensional scaling) ordination plots. For nMDS, two dimensions were used and the stress scores were calculated. Spatial (among S1, S2 and S3) and temporal (between day and night) variations of the copepod assemblages were evaluated by conducting a permutation (1000 times) multivariate analysis of variance (PERMANOVA). Additionally, to identify the similarity

and dissimilarity of the copepod assemblages between the day and night, Similarity Percentage analyses (SIMPER) were conducted after the square root transformation of the abundance data. Multiple PERMANOVA were conducted to evaluate the day and night variations of the abundances and species richness. Separate analyses were carried out for the samples collected on the different occasions because there was no intention to draw a statistical comparison between them. All the multivariate analyses were carried out using PRIMER-version 7.0 (Clarke & Gorley, 2006).

3. Results

The salinity was 9.92 ± 2.01 (range 13.60 - 7.50) on 24 February 2019, 8.05 ± 0.81 (range 11.10 - 6.81) on 24 August 2019 and 12.25 ± 1.18 (range 14.20 - 10.00) on 28 December 2019. The water temperature was 24.76 ± 1.69°C (range 31.07 - 23.03) on 24 February 2019, 27.69 ± 1.14°C (range 29.00 - 26.00) on 24 August 2019 and 20.82 ± 0.21°C (range 21.20 - 20.40) on 28 December 2019. The pH was 7.55 ± 0.38 (range 8.56 - 7.03) on 24 February 2019, 8.12 ± 0.07 (range 8.30 - 8.00) on 24 August 2019 and 8.51 ± 0.10 (range 8.80 - 8.37) on 28 December 2019.

Overall, 28 copepod species were identified in this study (Table 1). *Bestiolina similis*, *Paracalanus parvus*, *Acartia spinicauda* and *Acartiella tortaniformis* were highly abundant. The copepod community had both the brackish and estuarine species as well as several neritic species under the genus *Labidocera, Temora, Corycaeus* and *Oithona*. Acartiidae, Paracalanidae, and Oithonidae families were the predominant taxa, comprising 70–90% of the community. On 24 February 2019 (Fig. 2 a, b) and 24 August 2019 (Fig. 3 a, b), cumulative abundances and species richness were higher at night than day. On 28 December 2019, the day-night variation of the cumulative abundances was limited but the species richness was moderately higher at night than day (Fig. 4 a, b). Day-night variation of the abundance and species richness was more profound on 24 February (Fig. 2 a, b) and 24 August 2019 (Fig. 3 a, b) compared to the samples collected on 28 December 2019 (Fig. 4 a, b).

On 24 February 2019, cumulative abundance varied between 12,270 and 81,040 ind.m^{-3}, and species richness varied between 9 and 25 (Figs. 2a, b). The day-night variation was presented by a nMDS plot (Stress repeat 25, Dimension = 2, Stress score = 0.11) (Fig.2c). Copepod abundances varied significantly (PERMANOVA: Pseudo F = 25.552, p<0.001) over the day-night cycle but not among the sampling sites. The similarities in the groups of the day and the night samples were 66.77 % and 83.04%, respectively (Table 2). *Bestiolina similis* was the most abundant species and contributed 13.64% and 6.98% of the cumulative abundances of the community during day and night, respectively (Table 2). *Acrocalanus longicornis*, *Subeucalanus crassus, Oncea venusta*, *Eucalanus subcrassus* and *Labidocera euchaeta* were the main contributors to the dissimilarity (i.e., 33.37%) between the day and the night samples (Table 3).

On 24 August 2019, hourly cumulative abundances varied from 24,167 to 40,833 ind.m^{-3}, and species richness varied between 11 and 22 (Fig.3a, b). Variations of the abundances between day and night was represented by a nMDS plot (Stress repeat = 25, Dimension = 2, Stress score = 0.21) (Fig.3c). The PERMANOVA analysis found significant variation in the copepod abundance between day and night (Pseudo F = 136.97, p <0.001) but not among the sampling sites. The similarity in the group of the day and night samples was 78.20% and 82.08%, respectively (Table 2). *Bestiolina similis* contributed 12.49% and 9.39% of

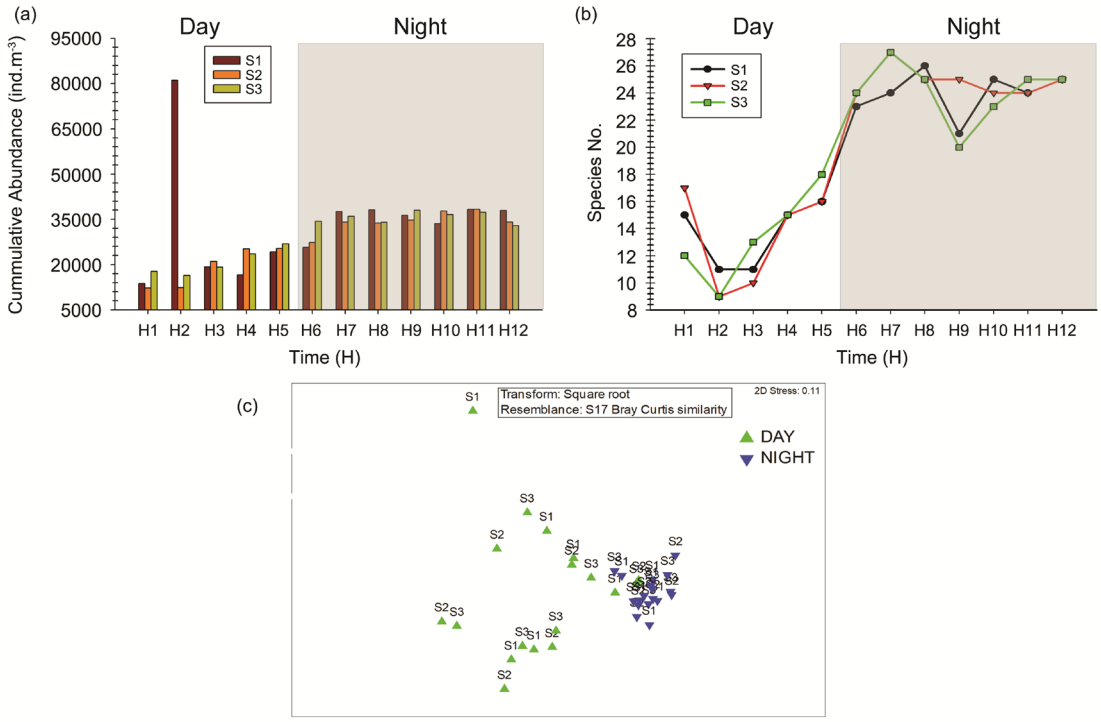


Fig. 2. Spatial and day-night variations of diversity and abundances of the copepod community sampled on 24 February 2019 from the Muriganga stretch of the Ganges estuary of India.

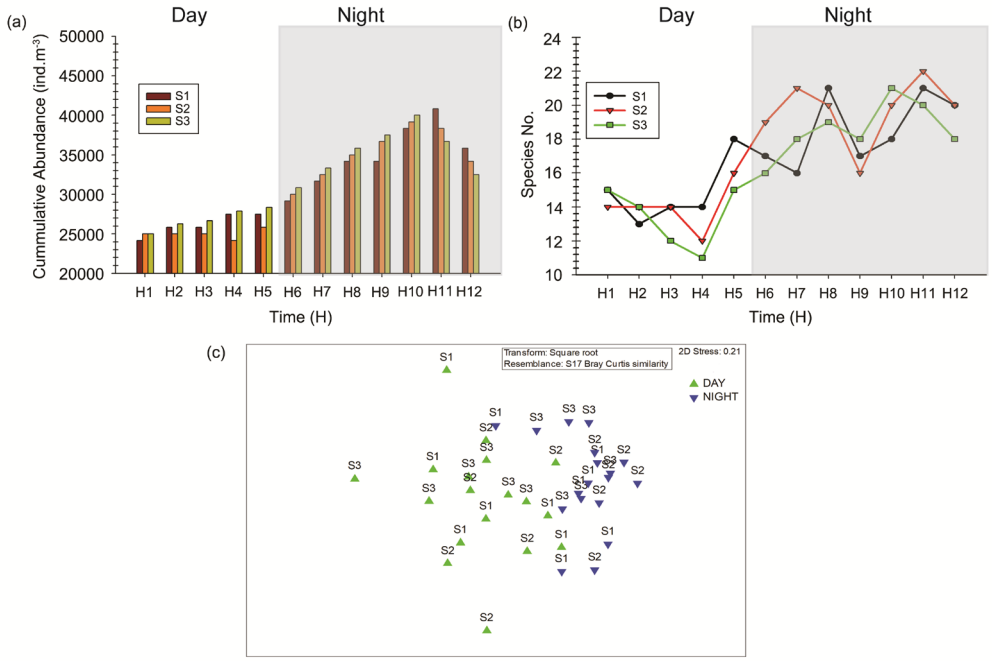


Fig. 3. Spatial and day-night variations of the diversity, and abundance of the copepod community sampled on 24 August 2019 from the Muriganga stretch of the Ganges estuary of India.

Table 1. List of identified copepod species sampled from the Muriganga stretch of the Ganges estuary of India. (√=present, X=absent)

Species	24.02.2019	24.08.2019	28.12.2019
Paracalanus parvus	√	√	√
Paracalanus aculeatus	√	√	√
Paracalanus indicus	√	√	√
Acrocalanus gibber	√	×	×
Acrocalanus gracilis	√	√	√
Acrocalanus longicornis	√	√	√
Bestiolina similis	√	√	√
Parvocalanus crassirostris	√	√	√
Parvocalanus dubia	√	√	√
Acartiella sewelli	√	×	×
Acartia tonsa	√	√	√
Acatia tropica	√	√	√
Pseudodiaptomus binghami	√	√	√
Temora turbinata	√	√	×
Oncaea venusta	√	×	×
Oithona similis	√	√	√
Oithona brevicornis brevicornis	√	√	√
Corycaeus danae	√	√	√
Acartia spinicauda	√	√	√
Acartiella tortaniformis	√	√	√
Pseudodiaptomus serricaudatus	√	√	√
Canthocalanus pauper	√	√	√
Eucalanus subcrassus	√	√	×
Subeucalanus crassus	√	√	√
Euchaeta marina	√	×	×
Eucalanus elongatus elongatus	√	×	×
Labidocera euchaeta	√	√	√
Labidocera acuta	√	√	×

the cumulative abundance of the community by day and night, respectively (Table 2). Contrasting abundances of *Subeucalanus crassus*, *Parvocalanus crassirostris*, *Labidocera acuta*, *Labidocera euchaeta* and *Acartia tropica* 23.75% dissimilarity between the day and night samples (Table 3).

On 28 December 2019, the hourly variation of the cumulative abundance was 3967 ind.m^3 to 1,50,000 ind.m^{-3}, and in total 10 copepod species were documented on that sampling occasion (Figs.4a, b). Variation in the copepod abundance between day and night presented by a nMDS plot (Stress repeat = 25, Dimension = 2, Stress score = 0.13) (Fig.4c). Results of the PERMANOVA on the variability of the copepod abundances among the sites and day vs night were not significant. The similarities in the samples of the day and night groups were 57.79% and 69.18%,

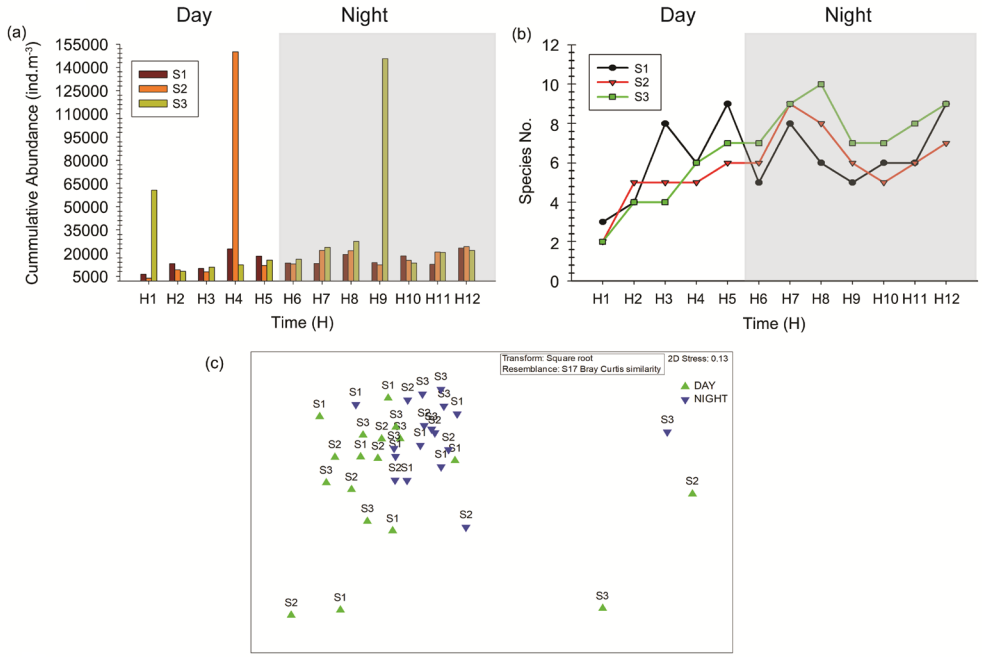


Fig. 4. Spatial and day-night variations of the diversity, and abundance of the copepod community sampled on 28 December 2019 from the Muriganga stretch of the Ganges estuary of India.

Table 2. Similarity percentages of a few abundant species of the copepod community sampled at the day-night scale on different sampling occasions from the Muriganga stretch of the Ganges estuary of India.

	24.02.2019	
	Day (Avg. similarity=66.77%)	**Night** (Avg. similarity=83.04%)
Species	Contribution %	Contribution %
Bestiolina similis	13.64	6.98
Paracalanus parvus	11.11	6.86
Acartiella tortaniformis	9.51	5.8
	24.08.2019	
	Day (Avg. similarity=78.20)	**Night** (Avg. similarity=82.08%)
Species	Contribution %	Contribution %
Bestiolina similis	12.49	9.39
Paracalanus parvus	11.76	8.52
Pseudodiaptomus binghami	10.63	7.67
	28.12.2019	
	Day (Avg. similarity=57.79%)	**Night** (Avg. similarity=69.18%)
Species	Contribution %	Contribution %
Bestiolina similis	40.68	28.37
Paracalanus parvus	27.44	19.87
Acartiella tortaniformis	16.61	20.91

respectively (Table 2). *Bestiolina similis* contributed 40.68% and 28.37% behind such similarity (Table 2). Differences in the abundances of *Acartia spinicauda*, *Acartiella tortaniformis*, *Bestiolina similis*, *Paracalanus parvus* and *Pseudodiaptomus serricaudatus* were mainly responsible for the 39.81% dissimilarity between the day and night samples (Table 3). The hourly variation of the different species of copepods described in detail in Fig. 5, whereas Fig. 6 described some commonly found copepod species identified from this region.

4. Discussion

The observed salinity ranges in the Muriganga corroborate findings of the previous studies conducted in the same stretch of the GE (Mukhopadhyay *et al.*, 2006; Choudhury & Bhadury, 2015; Bhattacharya & Paul, 2023). The shallow nature of the Muriganga estuary plays a crucial role in regulating water temperature, which is primarily influenced by ambient air temperatures (Mukhopadhyay *et al.*, 2006). The water temperature fluctuations observed across different time series can be attributed to seasonal variations in the air temperature during sample collection periods. The pH values recorded during the study ranged from neutral to alkaline. These findings align with the previous research conducted near the current study sites on the Muriganga section of the GE (Rakshit *et al.*, 2016; Mitra *et al.*, 2018; Paul *et al.*, 2019).

Diel variations in the habitat utilization is not uncommon among estuarine copepods (Hutchinson, 1967; Fancett & Kimmerer, 1985). Diel variations may be attributed to several factors e.g., migrating to deeper waters during daylight

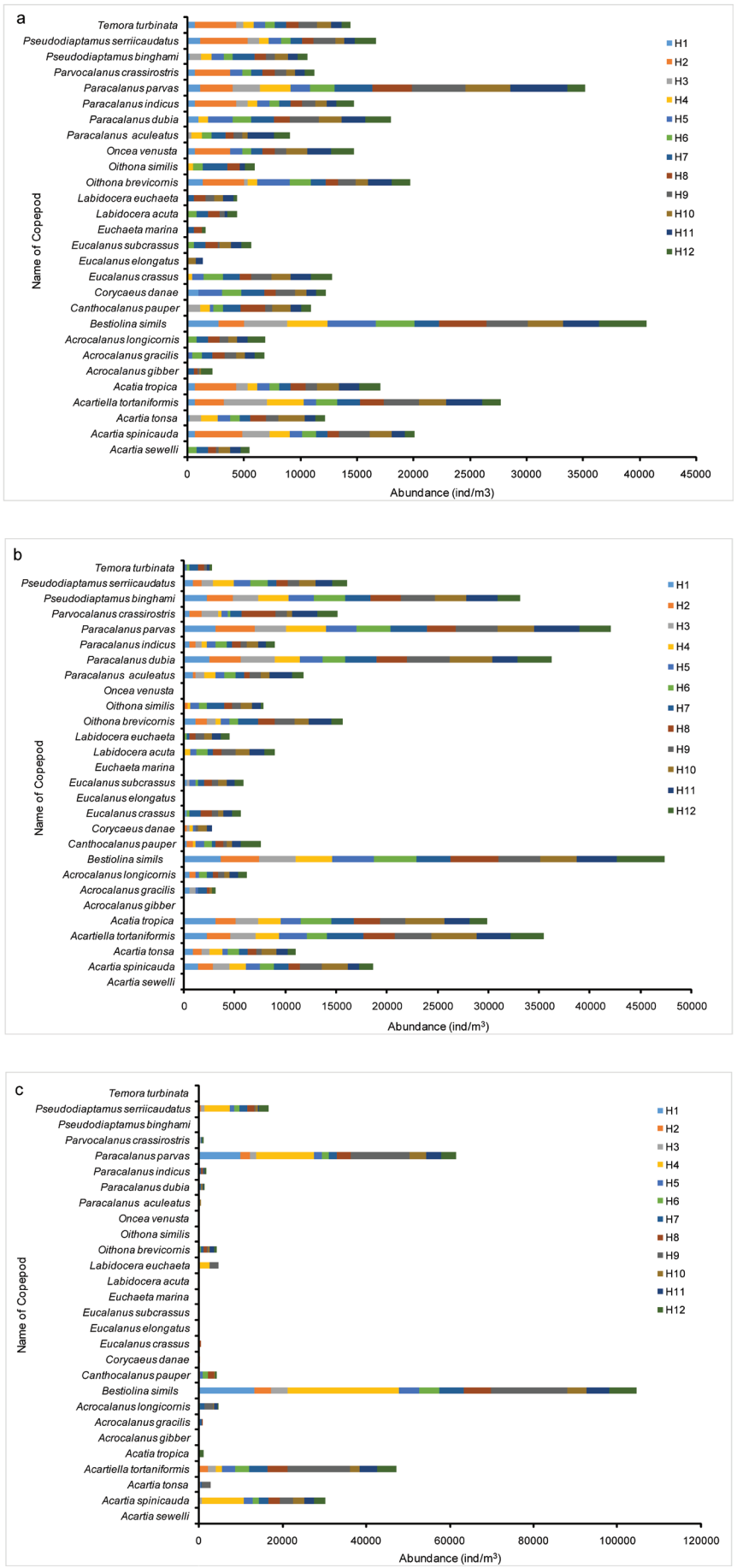


Fig. 5. Hourly variation of the copepod sampled during three study periods. a 24.02.2019 (premonsoon); b 24.08.2019 (monsoon); c 28.12.2019 (postmonsoon)

Table 3. Dissimilarity percentages of a few major species of the copepod community sampled at day-night scale on different sampling occasions from the Muriganga stretch of the Ganges estuary of India.

24.02.2019			
Average dissimilarity between day and night = 33.67%			
Species	Avg. abundance during day	Avg. abundance during night	Contribution %
Acrocalanus longicornis	04.82	31.16	05.64
Subeucalanus crassus	15.05	39.48	05.54
Oncea venusta	19.96	38.08	05.15
Eucalanus subcrassus	03.44	27.11	05.11
Labidocera euchaeta	00.00	24.49	05.00
24.08.2019			
Average dissimilarity between day and night = 23.75%			
Species	Avg. abundance during day	Avg. abundance during night	Contribution %
Subeucalanus crassus	03.21	26.05	07.42
Parvocalanus crassirostris	22.01	37.97	07.01
Labidocera acuta	12.07	30.82	06.67
Labidocera euchaeta	01.60	23.12	06.55
Acartia tropica	44.55	47.08	06.42
28.12.2019			
Average dissimilarity between day and night = 39.81%			
Species	Avg. abundance during day	Avg. abundance during night	Contribution %
Acartia spinicauda	32.02	50.24	12.98
Acartiella tortaniformis	38.92	68.01	12.49
Bestiolina similis	83.33	82.68	10.92
Paracalanus parvus	59.05	62.79	10.24
Pseudodiaptomus serricaudatus	26.62	26.94	09.72

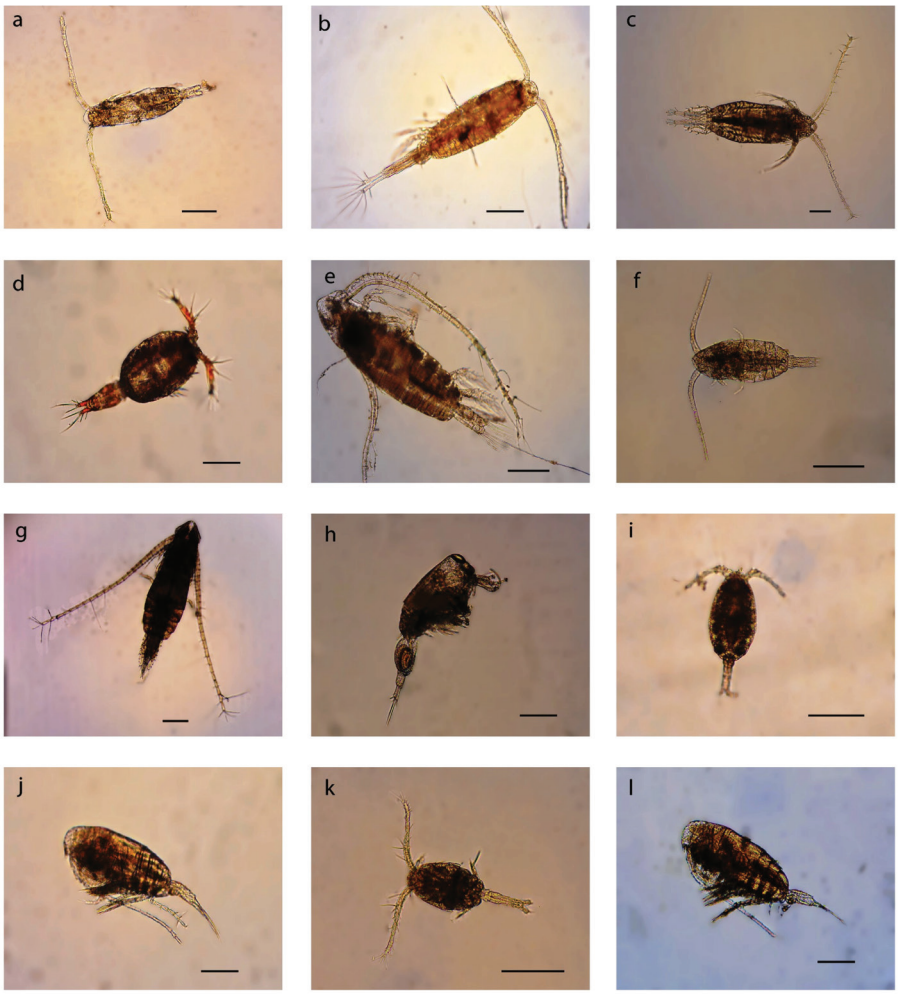


Fig. 6. Some identified copepods of the Muriganga stretch of the Ganges estuary of India. *a Acartia tropica, b Acartiella sewelli, c Labidocera euchaeta, d Oncaea venusta, e Eucalanus elongatus, f Bestiolina similis, g Subeucalanus crassus, h Corycaeus danae, i Oithona brevicornis, j Acrocalanus gibber, k Oithona similis, l Paracalanus parvus.* (Scale:200μM).

for evading visual predators and avoid solar radiation (Ringelberg, 1984; Bollens & Frost, 1991; Williamson *et al.*, 2011), nocturnal grazing behaviour (Rawlinson *et al.*, 2005). Several copepod genera demonstrated increased abundance at the surface during night, potentially as a strategy to avoid predation by planktivorous fishes present in the Muriganga (Kundu *et al.*, 2014; Sarker *et al.*, 2016). Elevated nocturnal abundance of the genus *Acartia* has been reported from the coastal waters of Japan (Ueda, 1991). Chew *et al.* (2015) documented a higher abundance of *Parvocalanus* in the surface waters during night in the Matang estuary of Malaysia. Results also align with the findings of Marques *et al.* (2011), who observed higher copepod abundances at night compared to day in the estuaries of Portugal. *Bestiolina similis, Paracalanus parvus, Acartiella tortaniformis,* and *Pseudodiaptomas binghami*, exhibited no diel variations and they were the major contributors to the community in terms of total abundance. Although semidiurnal tides in the Muriganga estuary can influence plankton transport, but the dominant species appears to be primarily influenced by the light cycle, as evidenced by its consistent abundance patterns irrespective of tidal fluctuations.

The structural and functional equilibrium of estuarine copepod communities are results of complex interplay species composition, population abundance, size class distribution, and feeding guilds (Froneman, 2002; York *et al.*, 2014; Araujo *et al.*, 2020). The diel patterns influences transfer of energy and nutrients between different depths, affecting the overall productivity and trophic dynamics of the system (Armengol et al., 2019; Hays, 2003). Additionally, the varying behaviours of different copepod species may contribute to the niche partitioning, allowing for the coexistence of multiple species within the same micro-habitat (Benedetti et al., 2015; Lindegren et al., 2019). Krills demonstrate fine-scale trophic niche separation throughout the year, exhibiting different degrees of food specialization rather than being purely opportunistic (Cabrol et al., 2018).

In the GE, the abundance of *Paracalanus parvus* had risen during the night, suggesting a diel vertical migration (DVM) pattern influenced by cooler waters (Paul *et al.*, 2019). In the Cochin estuary, higher zooplankton abundance was consistently observed in mesohaline zones, indicating a strong correlation between salinity and copepod distribution (Vineetha *et al.*, 2015). Moreover, the DVM is a common behaviour among copepods, with species exhibiting different migration strategies based on tidal and light cycles (Chew *et al.*, 2015). In the Mondego estuary some copepod species prefer surface waters during flood tides while others remain at the bottom demonstrating varied responses to environmental cues (Goncalves *et al.*, 2012). In the Taperacu estuary, significant shifts in the copepod densities were noted, correlating with salinity changes (Magalhaes *et al.*, 2009) and the dominance of *Pseudodiaptomus marshi* was linked to specific months indicating that community structure is not static throughout a year but highly responsive to seasonal changes (Magalhaes *et al.*, 2009). Implementing sampling protocols that capture diurnal variations necessitates a multifaceted research approach which considers both the spatial and temporal scales (Araujo *et al.*, 2016; Vineetha *et al.*, 2015; Wu *et al.*, 2023). Overall, the findings challenge the traditional focus on seasonal/monthly variability and emphasize the need for more nuanced approaches in studying estuarine copepod dynamics by incorporating diel variations for better monitoring of estuarine resources.

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