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RESEARCH ARTICLE

Ecology of the copepods in Ganges estuary of India

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Abstract

Estuarine plankton studies on often consider the estuary a single continuous habitat. The author hypothesized that a statistical analysis which captures ecological variabilities within a specific stretch of the estuary is more likely to yield statistically significant associations (both spatial and temporal) between copepods and physicochemical gradients than the same analysis targeted to analyze data when an estuary is considered as a single continuous habitat. Copepod assemblages and water were sampled monthly from November 2021 to October 2023 from the three contrasting stretches of the Ganges estuary, each having distinct physicochemical gradients and ecological communities. Copepod diversity was the highest near the estuary mouth, followed by mesohaline and oligohaline stretches. Results suggested Ganges is a Phosphate limited estuary which has significant seasonal variations of Nitrate. Copepod abundance peaked in postmonsoon, but seasonal variability of total abundance was not significant. *Bestiolina similis* was the most abundant; however, in certain stretches and seasons, *Acartiella tortaniformis* and *Paracalanus aculeatus* were the most abundant species. Multivariate analysis could establish the relations between physicochemical gradients and species distribution only to a limited extent. Many temporal associations between copepod abundance,diversity indices with physicochemical gradients could only be established within certain stretches of the estuary but not when the estuary was taken as a single continuous habitat. Suggesting existence of microhabitats within the estuary, which may limit realised niches of certain copepod species. Under a resource limited condition, author recommends monitoring of the transitional zones of Ganges estuary during seasonal change and after any stochastic perturbation.

Keywords Diversity and distribution · Niche partitioning · Physicochemical gradients · Mesozooplankton

Introduction

The author defines an estuary as inland water, which may or may not receive regular tides from an adjacent sea; however, the wide variability in the morphological, physical, chemical, and biological characteristics of estuaries around the world complicates the establishment of a global definition of this ecosystem (Paul et al. 2019). The ecological communities that reside in the different morphological types of estuaries are affected by their physicochemical gradients, which vary with time and the distance from the estuary mouth (Teixeira et al. 2008). Regular monitoring of water qualities of estuaries is crucial because of their ecosystem services; for example, estuaries act as the nurseries for numerous coastal marine fisheries across the world, including India (Sarkar et al. 2007). Countries such as the USA, UK, South Africa, China, and many others have invested in long-term monitoring of estuarine water quality programs, which include physicochemical gradients and various representative taxa from different trophic levels, starting from plankton to fish, and even in some cases birds and other apex predators (Imperial et al. 1992; Ferreira et al. 2007; Cillier and Adams 2016; Bisinicu and Lazar 2024). Monitoring ecological communities, such as the plankton, traditionally requires extensive field and laboratory work, and long-term engagement of human resources, such as taxonomists, field ecologists, water quality experts, and so on (Vaughan et al. 2001; Giering et al. 2022; Bisinicu and Lazar 2024). Even after such resource consuming nature, plankton monitoring programs in the estuaries around the world are not uncommon, because they form the base of the estuarine food webs

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(Chew et al. 2015; David et al. 2016; Paul et al. 2016, 2026; Bisinicu and Lazar 2024). The macrotidal (tidal amplitude > 4 m) river estuaries are habitats which may host multiple ecoclines where many species (including zooplankton) coexist through spatial niche partition by adapting the local physicochemical gradients, ecological interactions within and between species, and unique behaviors such as diel movements (David et al. 2016; Paul 2026). In these estuaries, the zooplankton community comprises predominantly allochthonous species sourced mainly from the adjacent sea or ocean, and to a limited extent inclusion also happens from the freshwater end of an estuary (Hwang et al. 2010; Tweedley et al. 2016). The mesohaline reaches of these estuaries are often inhabited by a few specialized zooplankton, which are widely tolerant to fluctuating physicochemical gradients and seasonal cycles; thus, they build high population densities (David et al. 2016; Paul et al. 2024). Near the estuary mouth, the zooplankton community is generally made of species that are mostly stenohaline; species richness remains high because of inclusion from the sea side , but abundances of individual species are generally low owing to continuous exposure to high energy environment such as wave dashing (Dahms et al. 2012; Hedayati et al. 2017; Bisinicu and Lazar 2024; Paul 2026). In the freshwater to brackish zones of a river estuary, only a few species reside permanently because of the higher osmotic costs; thus, those stretches generally remain less species rich, and less abundance of individual species is not uncommon there (Hwang et al. 2010; Bhattacharya et al. 2024).

India has no institutionalized long-term estuarine monitoring program that includes any plankton (Paul et al. 2026). Academics in India, however, over the years, have conducted detailed research on estuary water quality, including plankton (both on phytoplankton and zooplankton), especially in the Ganges, Cochin, Chilika, Mandovi–Zuari, and Godavari estuaries (Sinha et al. 1996; Panda et al. 2015; Mitra et al. 2018; Sarma et al. 2023; Divakaran et al. 2025; Patil et al. 2026). Zooplankton such as the copepods in the tropical estuaries generally have lifespans that range from a few weeks to a few months, and they reproduce continuously throughout the year (Allan 1976; Chew et al. 2015; Suthers et al. 2019). Copepods dominate the zooplankton communities of Indian estuaries and transfer energy to predators such as macroinvertebrates and fishes; consequently, changes in their structural dynamics affect the sustainability of the lower food webs (Bhattacharya et al. 2015). Therefore, ecological variations, which arise both at the habitat level or within certain unique stretches of a macrotidal river estuary related to physicochemical gradients, are worth studying because those variations to a large extent determine the realized niches (both spatial and temporal) of many copepod species (David et al. 2016; Paul 2026). Ecological variations of the copepods that are restricted within specific stretches of an estuary are often gets overlooked because in the most estuarine studies across the world an estuary is generally considered a single continuous habitat irrespective of its shape, size, physical-chemical-biological properties (Attrill and Rundle 2002; Peterson 2003; David et al. 2016; Paul et al. 2016; Bisinicu and Lazar 2024). Except studies that followed high-frequency temporal sampling (e.g., hourly, weekly, fortnightly) or and monthly or seasonal sampling on the copepods of only a certain stretch of a macrotidal river estuary (Paul et al. 2024; Nandy et al. 2026), providing detailed perspectives on the temporal changes of their community structure is difficult. Many estuarine studies concentrate only on analyzing the habitat-level data, mostly by pooling the temporal and/or spatial data together; thus, they fail to detect many significant and subtle ecological variabilities that arise from the associations between physicochemical gradients and the community at a certain stretch of an estuary (Pasquaud et al. 2012; Bashevkin et al. 2022; Bisinicu and Lazar 2024; Bhattacharya et al. 2024).

The lower course of the Ganges River of India flows hundreds of kilometres before meeting the Bay of Bengal (BoB) near Sagar Island, West Bengal (Jena et al. 2018; Bhattacharya et al. 2024). The Ganges estuary (GE) has a long tidal zone, which remains salt-free throughout the year (Bhattacharya et al. 2024). From the mouth of the GE, the salt water penetration generally remains restricted 90–100 km inside the estuary (Jena et al. 2018; Bhattacharya et al. 2024). After the salt-free zone of the GE, there is a short brackish zone, which remains salinity-limited (i.e., salinity < 5) throughout the year (Bhattacharya et al. 2024). Then, there is a long mesohaline stretch (Paul et al. 2024); thereafter, the GE opens to the BoB, and this region is generally polyhaline in nature (Paul 2026). Beyond the mouth of the GE, there is an outer estuary, which remains in polyhaline to euhaline (i.e., salinity > 30) conditions; the outer estuary stretch depends on the seasonal cycle which affects the volume of freshwater that the estuary receives from the upstream (Mukhopadhyay et al. 2006; Jena et al. 2018). Each of those stretches of the GE has their own distinct physicochemical gradients, which then influence the structure of plankton communities, including copepods (Sinha et al. 1996; Choudhury and Pal 2012; Rakshit et al. 2017; Bhattacharya et al. 2024; Paul et al. 2024; Paul 2026). Copepod ecology research in the GE began in the early 1950s, with diversity and distribution described over various sampling timescales (such as in the intervals of hours, days, weeks, months, and seasons) by generations of authors, and those authors have concluded that the copepod community of the GE are going through decadal changes in their composition, size classes, and feeding guilds (Dutta et al. 1954; Sarkar et al. 1986; Sinha et al. 1996; Paul et al. 2019, 2024; Basu et al. 2022; Bhattacharya et al. 2024; Nandy et al. 2026; Paul 2026). Paul et al. (2019) noted that the spatial niche

partitioning among the copepod of the GE could happen even within 500 m in the mesohaline stretch. Nandy et al. (2026) suggested that the diel behavior of the copepods leads to the spatial niche separation in the mesohaline stretch of the GE, and the spatial niche segregations are further modulated by seasonal cycles. Paul (2026), while studying the tidal creeks of Sagar Island of the GE, noticed physicochemical variabilities within certain sampling stations influenced the structural composition of the copepod community more than the influence of the seasonal cycles which also brings compositional changes in the mesozooplankton community including copepods (Basu et al. 2022).

In recent studies, more than 60 species of mesozooplankton have been reported from the GE; most of them are copepods that reside in the mesohaline and polyhaline zones of the estuary (Bhattacharya et al. 2015; Basu et al. 2022; Nandy et al. 2026). In the GE, the diversity of the copepods decreases towards the salinity-limited Diamond Harbor (DH) stretch of the estuary, and the maximum species diversity is found in the mesohaline to polyhaline creeks near the estuary mouth (Basu et al. 2022; Paul et al. 2024). Among those copepod species, Calanoids are the majority, with a few Cyclopoids observed throughout the year; Harpacticoid copepods are mostly restricted to the estuary mouth (Basu et al. 2022; Bhattacharya et al. 2024; Paul et al. 2024; Paul 2026). Species such as *Bestiolina similis*, *Paracalanus parvus*, and *Acartiella tortaniformis* are among the highly abundant Calanoid copepods of the GE (Bhattacharya et al. 2024; Paul et al. 2024; Paul 2026). Multiple species of genus *Oithona* are highly common among the Cyclopoid copepods; their abundances do vary on the basis of the different salinity zones of the estuary as well as with the seasonal cycle (Sarkar et al. 1986; Sinha et al. 1996; Basu et al. 2022; Paul 2026; Nandy et al. 2026). All the zooplankton (microzooplankton and mesozooplankton) diversity and distribution studies previously conducted on the GE considered the estuary a single dominant continuous habitat (Sinha et al. 1996; Rakshit et al. 2017). However, there are multiple distinct salinity stretches within the estuary that have their own unique physicochemical characteristics and have reports of localized zooplankton communities, including specialized copepod assemblages (Basu et al. 2022; Bhattacharya et al. 2024; Paul et al. 2024; Paul 2026).

The author had conducted a continuous 2-year monthly sampling on the copepod community of the Diamond Harbor (DH), Kakdwip (KW), and Frasergunj (FZ) of the GE. All the spatial and temporal data were pooled at first and analyzed through univariate and multivariate techniques as and when required. After that, data of all three sampling stations were analyzed separately through matching univariate and multivariate techniques that were applied in the first instance. The author hypothesized that any statistical analysis (either univariate or multivariate in nature) targeted to capture the variabilities of the physicochemical gradients of the estuary, copepod community composition, and relationships between copepod diversity and physicochemical gradients of each sampling station of the GE would yield more statistically significant spatial or temporal relationships than a matching data analysis targeted to analyze those relationships on the pooled data. The aim was to find out what could be a better approach for monitoring the copepod community of the GE and similar tropical river estuaries, considering a resource-limited situation; is it ecologically optimal to monitor the entire estuary or monitor certain transitional stretches of a river estuary? Finally, the author proposed a national estuary monitoring program for India under institutional patronage, where zooplankton monitoring could be included on a long-term basis.

Materials and methods

Study area

The GE is a macrotidal estuary with mixed semidiurnal tides; the estuary has a wide and shallow mouth, which causes time–velocity asymmetry for tides (Mukhopadhyay et al. 2006; Jena et al. 2018). In 2021, three sampling stations were established in the estuary. This study was conducted at the DH (22° 10′ 53.7492″ N; 88° 11′ 8.4048″ E), which is situated in the upstream of the estuary (Bhattacharya et al. 2024); the FZ (21° 34′ 42.4416″ N; 88° 13′ 44.544″ E), which is close to the estuary mouth; and in the KW (21° 53′ 3.1632″ N; 88° 8′ 44.5164″ E), which is situated between the DH and FZ stations (Fig. 1). The region has three seasons: premonsoon (PRM) is hot and humid (March to May), monsoon (MON) is warm and rainy (June to September), and postmonsoon (POM) is cooler and dry (October to February) (Paul et al. 2024). The estuary receives 60–75% of its 1600–1800 mm annual rainfall in the monsoon, which at times turns it from a oligohaline to mesohaline habitat for a few days by washing away many heterogeneous physicochemical gradients that gather during the premonsoon and postmonsoon seasons (Mukhopadhyay et al. 2006; Paul et al. 2024). The DH and KW stretches of the GE are semi-urban, the FZ stretch is rural in nature, and all the stretches have semi-intense mangroves dominated by *Avicennia* spp.

Fieldwork

Copepod assemblages and water samples were collected monthly from November 2021 to October 2023 for analysis. On each sampling occasion, a motor boat traveled from the FZ to DH in the estuary, riding on a high tide, deploying a horizontal plankton net (200 µm mesh, 3 m

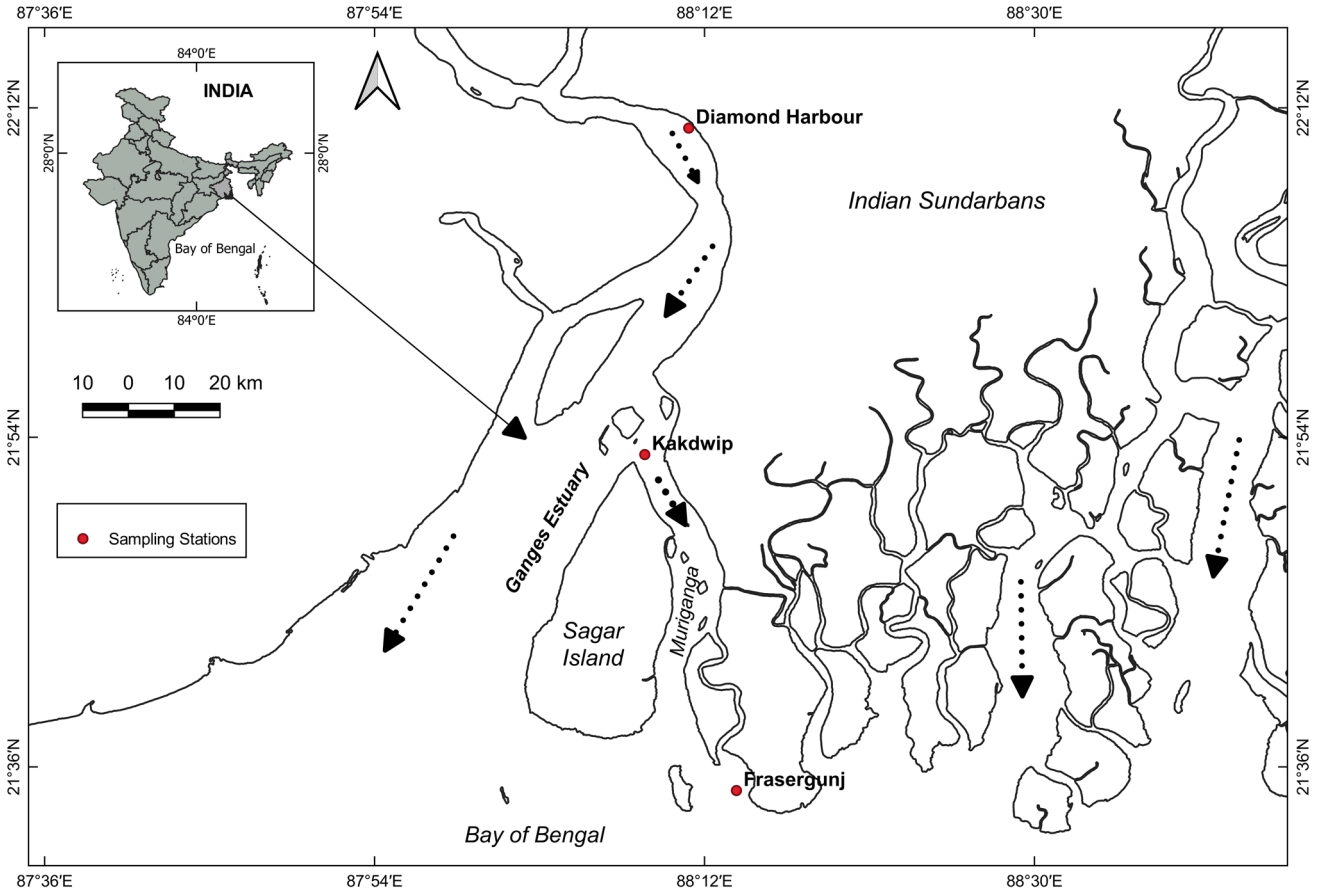


Fig. 1 Study area map and the sampling locations along the Ganges estuary

length, 60 cm diameter) for 5 min at each station to sample copepod assemblages. A mechanical flow meter (438115; HYDRO-BIOS, Germany) was used to measure the water volume for quantitative sampling. Samples were collected from 0.3 to 0.5 m depth. Concurrently, 5 L water samples were collected using a horizontal Niskin water sampler (101008H; General Oceanics, USA) to analyze Nitrate, Phosphate, Silicate and Chlorophyll *a* (chl *a*) in the laboratory. Water salinity (HI98319; Hanna Instrument, Japan), pH (HI98108; Hanna Instrument, Japan), and temperature (Z423513; Easy-Read, USA) were measured. The thermometer broke several times while collecting data of the POM. Considering that the author avoided analyzing the water temperature data or exploring any relations of other data with water temperature, a supplementary figure is provided to familiarize the readers with possible water temperature regimes of the estuary in the PRM and MON. Collected samples were fixed with 4% formaldehyde in 1 L glass jars, and water samples were placed inside HDPE reagent bottles (583460; Tarsons, India) and transported in ice boxes.

Laboratory work

On every occasion, laboratory work began within 12 h of field completion. Water samples were filtered through GF/F filter papers (0.47 µm pore size) and analyzed for Nitrate, Phosphate, Silicate, and chl *a* using a UV–Vis spectrophotometer (119; Systronics, India) following Grasshoff et al. (2009). At least 10% of the copepod assemblages were quantitatively analyzed. Samples were split using Folsom's plankton sample divider (435100; HYDRO-BIOS, Germany), and 1 ml aliquots were placed in a Sedgwick counter chamber for taxonomic identification up to species level (adults only) and enumeration under a compound microscope (B1; Motic, Hong Kong, China). Identification followed Kasturirangan (1963), Conway et al. (2003), and Al-Yamani et al. (2011). Species abundance was expressed as individuals per cubic meter (ind.m^{-3}).

Database preparations and analysis

Field ecological databases are often small; this study spanned 2 years monthly, but the author considered this is a

small database; thus, only nonparametric analysis was used. At first, the following databases were created: (1) a pooled database considering all the physicochemical data (i.e., salinity, pH, Nitrate, Phosphate, Silicate, chl *a*) and biological data (i.e., copepod abundances, richness, and different alpha diversity indices), and is henceforth termed "Habitat database;" and (2) separate databases for each of the sampling stations, which consist of all the physicochemical and biological data related to the respective sampling stations. The aim of the data analysis was to apply similar statistical methods for both levels of databases to compare the statistical variabilities in terms of significance of spatial–temporal associations between the physicochemical and biological data.

Statistical analysis was conducted on CRAN R.4.6.0 (R Core Team 2026) with significance at 95% (i.e., $\alpha = 0.05$), reporting only significant test statistics with values of *K-W* chi-squared, *t*, *p*, pseudo-*F*, *F*, and degrees of freedom (d.f.). Medians and standard errors (using "plotrix" version 3.8–14) were presented where required. Spatial (sampling station) and temporal (seasonal) variabilities were analyzed with Kruskal–Wallis tests and pairwise Nemenyi tests if needed in case the result of a Kruskal–Wallis test was found to be significant (using "PMCMRplus" version 1.9.12). Diversity indices (e.g., richness, Shannon diversity, Simpson dominance, and Pielou's evenness) were calculated using the "Vegan" package (version 2.7–2). Diversity indices were compared among stations and seasons for the "Habitat database," whereas only seasonal variations were compared among sampling stations. For such comparisons, generalized linear models (GLMs) were used. While constructing the GLMs, families of quasi-Poisson (in case of species richness), quasibinomial (for Simpson dominance and Pielou's evenness data), and log normal (for Shannon diversity) families were used on the basis of the data distribution of the response variable. For analyzing "Habitat database," random variables (such as 1|station or 1|season as required) were added to the intercept of each GLM equation. This was to account for the variability arising from the nested sampling design of the study. For this purpose, the "glmmPQL" function of the "MASS" package (version 7.3–65) was used. For analysis, databases attached to each sampling station a random variable; i.e., 1|season was added to the intercept of each GLM to account for the seasonal variability. The manuscript also aimed to establish the temporal associations between different alpha diversity indices and physicochemical gradient; thus, mixed-effect GLMs were also built for both the "Habitat database" and databases of each sampling station following the abovementioned method.

Another objective was to explore the compositional heterogeneity (e.g., spatial and/or seasonal) of the copepod assemblages. For that reason, a series of multivariate analysis was conducted one after another using the "Vegan" package (version 2.7–2). At first, the species abundance data were square root transformed to reduce the variability within 1–10 ratio. After that, the NMDS analysis was conducted on the basis of the Bray–Curtis principle with two dimensions ($K = 2$), and a NMDS biplot was drawn. For statistical confirmation of the heterogeneity within and between the copepod assemblages, first a permutational multivariate analysis of variance (PERMANOVA) test was conducted considering 999 permutations, followed by a permutational analysis of multivariate dispersions (PERMDISP) using the "adonis2" function. If the results of a PERMANOVA test were found to be statistically significant, then a similarity percentage (SIMPER) test was conducted (not on transformed data) to assess the weightage of each copepod species for bringing the variability within an assemblage. Canonical Correspondence Analysis (CCA) was conducted (not on transformed data) to explore relationships of individual species of the copepod assemblages with the physicochemical gradients of the GE and the biplots were drawn. These analytical steps were repeated for the "Habitat database" as well as the databases related to each sampling station.

Results

Physicochemical variabilities in "Habitat database"

Overall, physicochemical variability is summarized in Fig. 2. Only the pH (*K-W* chi-squared = 28.99, d.f. = 2, $p < 0.001$) and Nitrate (*K-W* chi-squared = 30.15, d.f. = 2, $p < 0.001$) levels varied significantly among seasons (Fig. 2). The salinity (*K-W* chi-squared = 89.18, d.f. = 2, $p < 0.001$), pH (*K-W* chi-squared = 10.83, d.f. = 2, $p = 0.004$), Phosphate (*K-W* chi-squared = 21.30, d.f. = 2, $p < 0.001$), Silicate (*K-W* chi-squared = 44.62, d.f. = 2, $p < 0.001$), and chl *a* (*K-W* chi-squared = 33.53, d.f. = 2, $p < 0.001$) levels were significantly different among the sampling stations (Fig. 2, 3).

Physicochemical variabilities of sampling stations

Physicochemical variabilities of the DH, KW, and FZ are summarized in Fig. 3. At the DH, Nitrate (*K-W* chi-squared = 9.44, d.f. = 2, $p = 0.008$) and Silicate (*K-W* chi-squared = 10.71, d.f. = 2, $p = 0.004$) levels varied significantly between the PRM and POM. Nitrate (*K-W* chi-squared = 9.70, d.f. = 2, $p = 0.007$), Phosphate (*K-W* chi-squared = 11.06, d.f. = 2, $p = 0.003$), and Silicate (*K-W* chi-squared = 11.058, d.f. = 2, $p = 0.004$) levels significantly varied between the MON and POM and the PRM and POM at the KW. At the FZ, pH (*K-W* chi-squared = 10.31, d.f. = 2, $p = 0.005$), Nitrate (*K-W* chi-squared = 13.96, d.f. = 2, $p < 0.001$), Silicate (*K-W* chi-squared = 13.77, d.f. = 2, $p = 0.001$), and chl *a* (*K-W* chi-squared = 13.57, d.f. = 2,

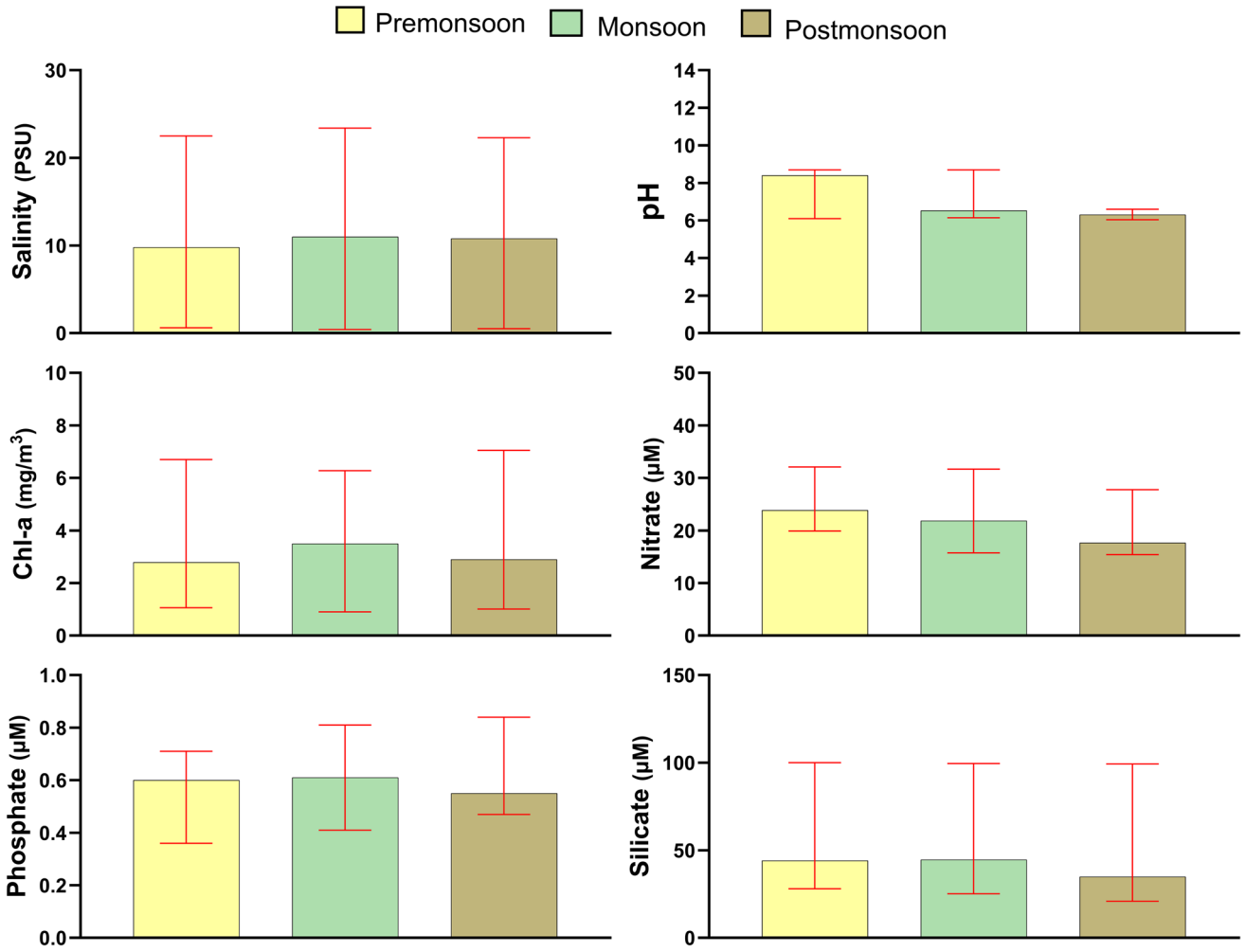


Fig. 2 Seasonal variations of the physicochemical gradients measured along the Ganges estuary between November 2021 and October 2023

$p = 0.001$) showed significant seasonal variations: the pH level varied between the PRM and POM, Nitrate and Silicate varied between the MON and PRM and between the PRM and POM, and the chl *a* varied among all three seasons (Fig. 3).

Variability of the copepod community structure in "Habitat database"

Spatial–temporal variabilities of species diversity are summarized in Table 1. *Parvocalanus crassirostris*, *Subeucalanus crassus*, and *Labidocera euchaeta* were absent in the PRM, and *L. euchaeta* was absent in the POM (Table 1). Seasonal variations of species richness, Shannon diversity, Simpson's dominance, and Pielou's evenness indices and abundances are summarized in Fig. 4. Overall, *Bestiolina similis* was the most abundant species and *Acartia tropica* was the least abundant. *A. tortaniformis*, *P. parvus*, and *A. gracilis* were frequently observed (Table 1). Spatial differences of the copepod abundances were significant (*K-W* chi-squared = 22.31, d.f. = 2, $p < 0.001$), with greater abundances observed in the FZ than the DH and KW ($p < 0.001$). Diversity indices did not vary significantly among seasons. Species richness was significantly higher in the FZ ($t = 4.86$, $p < 0.0001$, d.f. = 71) and KW ($t = 3.19$, $p = 0.0022$, d.f. = 71) than the DH. Shannon index of the DH was significantly lower than that of the FZ ($t = 4.59$, $p < 0.001$, d.f. = 71) and KW ($t = 2.99$, $p = 0.004$, d.f. = 71). Simpson index values of the FZ ($t = 4.46$, $p < 0.0001$, d.f. = 71) and KW ($t = 3.05$, $p = 0.003$, d.f. = 71) were significantly higher than the corresponding values of the DH (Fig. 5). Pielou's index of the DH was significantly lower than that of the KW ($t = 2.72$, $p = 0.008$, d.f. = 71) and the FZ ($t = 2.36$, $p = 0.02$, d.f. = 71) (Fig. 5). Significant positive temporal associations were found between salinity and the species richness ($t = 4.71$, $p < 0.001$, d.f. = 71), Shannon index ($t = 4.55$, $p < 0.001$, d.f. = 71), Simpson index ($t = 4.58$, $p < 0.001$, d.f. = 71), and Pielou's index ($t = 2.35$, $p = 0.028$, d.f. = 71). The pH level

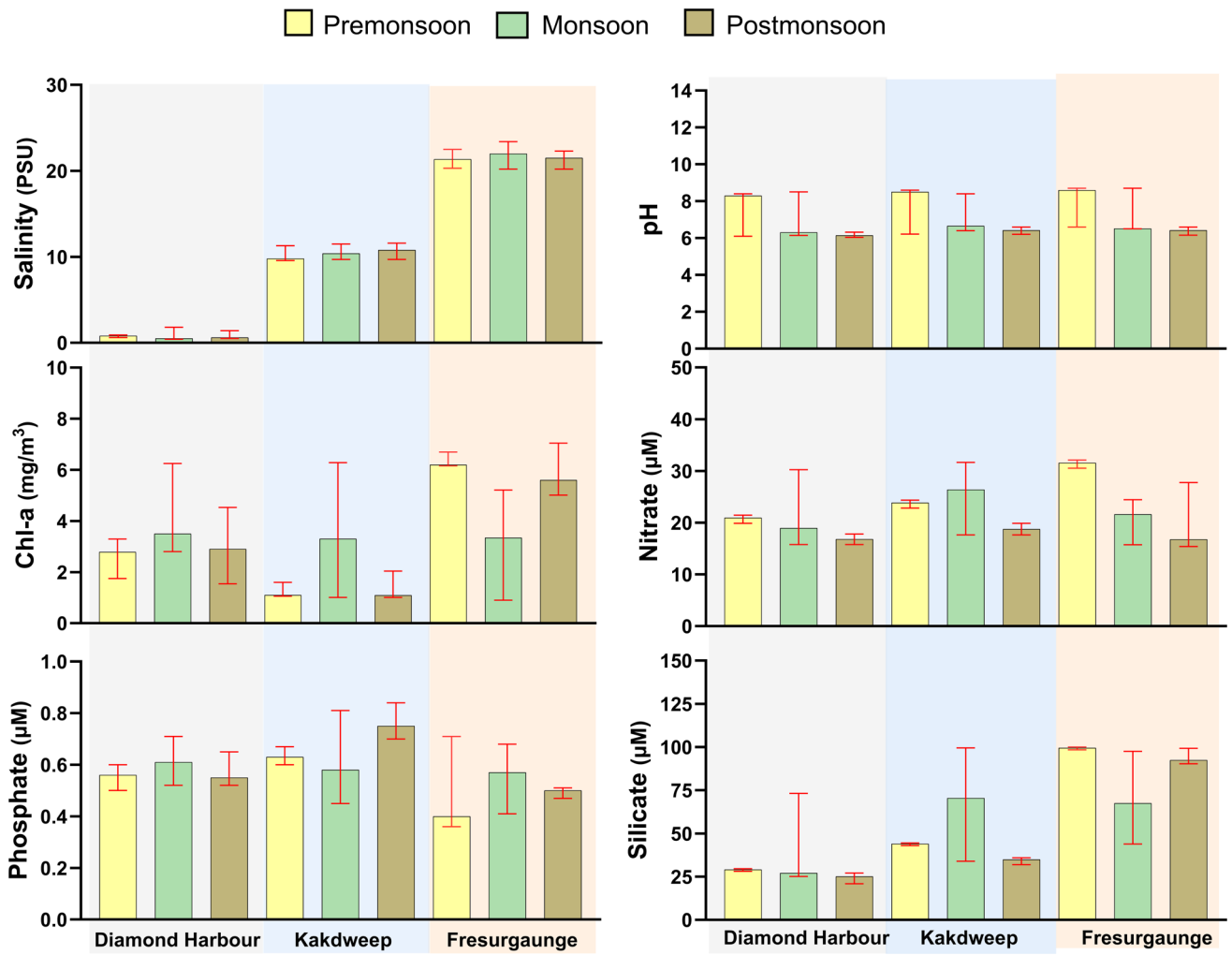


Fig. 3 Spatial and seasonal variations in the physicochemical gradients measured from the different stretches in the Ganges estuary between November 2021 and October 2023

was significantly and positively associated with Simpson index ($t = 2.39$, $p = 0.019$, d.f. = 71) but showed no significant associations with other alpha diversity indices considered in the current study. Nitrate was significantly and positively associated with Simpson index ($t = 3.76$, $p = 0.007$, d.f. = 71) but showed no significant associations with other alpha diversity indices. Phosphate was significantly and negatively associated with species richness ($t = -2.40$, $p = 0.019$, d.f. = 71) and Shannon index ($t = -2.08$, $p = 0.04$, d.f. = 71). Positive significant associations were found between Silicate and species richness ($t = 4.37$, $p < 0.001$, d.f. = 71), Shannon's index ($t = 4.65$, $p < 0.001$, d.f. = 71), Simpson's index ($t = 4.58$, $p < 0.001$, d.f. = 71), and Pielou's index ($t = 2.04$, $p = 0.04$, d.f. = 71).

The NMDS biplot (Fig. 6a), PERMANOVA (pseudo-$F = 1.39$, $R^2 = 0.04$, $p = 0.223$, d.f. = 2), and PERMDISP ($F = 5.49$, $p = 0.006$, d.f. = 2) analyses suggested no significant seasonal variations. However, a significant spatial variation in the copepod assemblages was confirmed by the NMDS biplot (Fig. 6b), PERMANOVA (pseudo-$F = 31.82$, $R^2 = 0.48$, $p = 0.001$, d.f. = 2), and PERMDISP ($F = 0.12$, $p = 0.89$, d.f. = 2) results. The SIMPER analysis suggested that the spatial dissimilarities in the copepod assemblages were largely influenced by *B. similis* (10.4%), *A. spinicauda* (9.9%), and *A. tortaniformis* (8.3%) when the DH and KW stations were compared. For the DH and FZ stations, *B. similis* (9.2%), *Paracalanus aculeatus* (8.1%), and *A. gracilis* (7.5%) majorly contributed to the dissimilarity. *A. spinicauda* (9.4%), *P. aculeatus* (9.2%), and *A. gracilis* (7%) were the chief contributors of dissimilarity between the KW and FZ. The CCA analysis suggested 37.99% constrained variability and 62.01% unconstrained variability within the copepod assemblages, and the biplot (Fig. 7a) showed that the distributions of *B. similis*, *Oithona similis*, and *Pseudodiaptomus serricaudatus* were less associated with the physicochemical variabilities of the estuary (Fig. 7a).

Table 1 Spatial and temporal variations in the species richness and the cumulative abundances of the copepods sampled in the Ganges estuary between November 2021 and October 2023

Species	Diamond Harbour			Kakdwip			Frasergunj		
	PRM	MON	POM	PRM	MON	POM	PRM	MON	POM
Paracalanus parvus	21,746	21,178	24,200	8628	10,686	18,658	20,126	21,450	51,836
Paracalanus aculeatus	0	0	0	9102	11,498	15,048	0	24,000	71,678
Paracalanus indicus	9336	6810	5072	0	0	0	9602	16,932	27,740
Parvocalanus dubia	5370	3404	2536	14,654	13,730	20,642	10,514	12,980	10,286
Acrocalanus gibber	0	0	0	2126	5994	8298	0	14,400	43,006
Acrocalanus gracilis	17,266	15,812	18,928	18,908	12,334	7040	15,204	29,866	55,486
Acrocalanus longicornis	5370	3404	2536	16,068	15,310	8958	3798	6264	10,286
Bestiolina similis	14,710	26,658	32,494	26,612	23,304	40,306	31,620	33,940	42,772
Parvocalanus crassirostris	0	0	0	0	1700	1700	0	2400	7168
Acartia spinicauda	25,454	18,670	22,768	0	0	0	19,006	26,534	37,102
Acartia sewelli	0	0	0	1058	2940	5244	0	0	13,896
Acartia tonsa	0	0	0	11,344	6946	3770	0	9600	14,776
Acatia tropica	0	0	0	1058	2192	1134	0	0	0
Acartiella tortaniformis	29,420	23,720	35,394	17,384	16,872	31,570	22,806	32,800	47,390
Pseudodiaptamus serricaudatus	5370	3952	5898	3780	5892	11,560	6168	11,034	19,824
Pseudodiaptamus binghami	0	0	0	3176	4876	1700	2370	9570	23,874
Canthocalanus pauper	0	0	0	3780	2408	1350	3554	3554	3554
Subeucalanus subcrassus	5370	3404	2536	0	566	566	3798	3864	3118
Subeucalanus crassus	0	0	0	0	1700	1700	0	2400	7168
Euchaeta marina	10,744	7906	11,796	0	0	0	5232	10,162	18,204
Eucalanus elongatus	10,744	6810	5072	0	0	0	5232	5362	3868
Labidocera euchaeta	0	0	0	0	0	0	0	0	10,422
Labidocera acuta	0	0	3600	529	1624	283	1868	7200	7765
Temora turbinata	0	0	2400	3251	2976	1493	3554	8354	15,915
Corycaeus danae	0	0	0	6502	5386	2703	10,530	1184	1751
Oncea venusta	0	0	2400	3251	3826	1918	1184	5984	13,970
Oithona similis	13,264	10,216	8100	6153	2692	2059	12,586	15,184	13,893
Oithona brevicornis	0	0	1900	9756	7514	3771	4740	8540	15,855
Individuals(November 2021 to October 2023)	174,164	151,944	187,630	167,120	162,966	191,471	193,492	323,558	592,603

Acratia seweli, *A. tonsa*, and *Pseudodiaptomus binghami* distributions were more associated with salinity than other physicochemical gradients, whereas *Paracalanus aculeatus* distribution was more associated with salinity and silicate levels (Fig. 7a). The chl *a* levels may be associated with the distribution of *Labidocera acuta* (Fig. 7a). Phosphate levels could be associated with *Canthocalanus pauper*, *Corycaeus danae*, *Acrocalanus longicornis*, *Paracalanus dubia*, and *Oithona brevicornis* distributions (Fig. 7a).

Structural variability of the copepod community among sampling stations

Seasonal variability of the species richness, Shannon, Simpson, and Pielou's indices and abundances of the DH, KW, and FZ are summarized in Fig. 5 and Table 1. Overall, *A. tortaniformis* was the most abundant species in the DH; however, in the MON, *B. similis* was the most abundant species (Table 1). *Bestiolina similis* was the most abundant species in the KW irrespective of seasons (Table 1). In the FZ, *B. similis* was the most abundant species overall, but *P. aculeatus* was the most abundant species in the POM (Table 1). Seasonal variability of abundances was not significant in sampling station-level databases. In the DH, species richness was significantly associated with salinity ($t = 2.65$, $p = 0.015$, d.f. = 23), pH ($t = 2.09$, $p = 0.04$, d.f. = 23), and nitrate ($t = 2.46$, $p = 0.02$, d.f. = 23); in the KW, that was with the nitrate ($t = 2.45$, $p = 0.02$, d.f. = 23) and phosphate ($t = -2.80$, $p = 0.01$, d.f. = 23); and in the FZ, that was with salinity ($t = -3.18$, $p = 0.004$, d.f. = 23) and nitrate ($t = -3.1$, $p = 0.005$, d.f. = 23). Shannon index was significantly associated with salinity ($t = 2.59$,

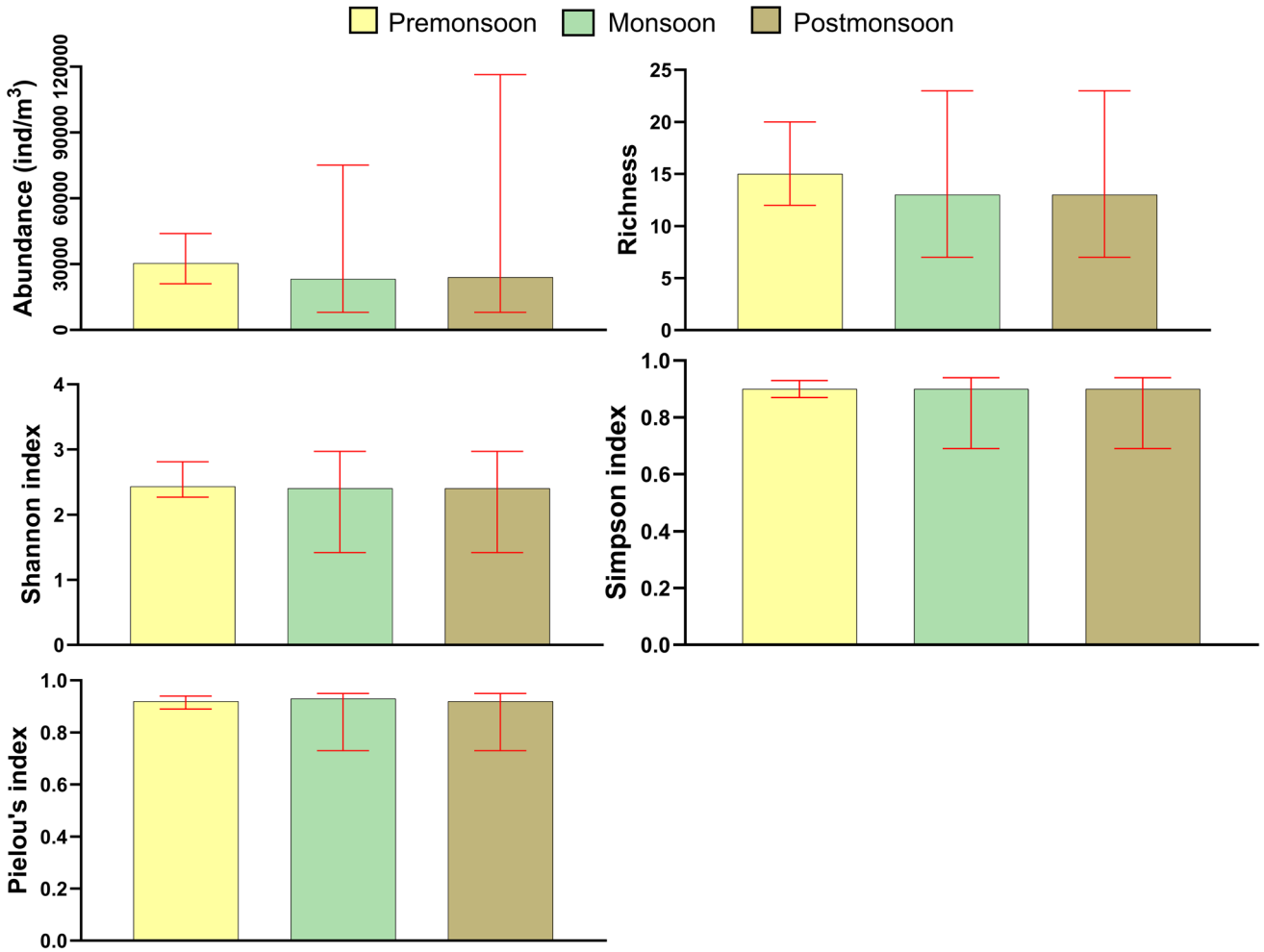


Fig. 4 Seasonal variations in the total abundances and alpha diversity indices of the copepods sampled from the Ganges estuary between November 2021 and October 2023

$p = 0.017$, d.f. = 23), pH ($t = 2.21$, $p = 0.03$, d.f. = 23), and nitrate ($t = 2.74$, $p = 0.01$) in the DH; with nitrate ($t = 2.61$, $p = 0.014$, d.f. = 23), phosphate ($t = -3.07$, $p = 0.005$, d.f. = 23), and silicate ($t = 2.02$, $p = 0.05$, d.f. = 23) of the KW; and salinity ($t = -2.44$, $p = 0.02$, d.f. = 23) and nitrate ($t = -2.54$, $p = 0.01$, d.f. = 23) of the FZ. Simpson index of the DH was significantly associated with salinity ($t = 2.45$, $p = 0.02$, d.f. = 23), nitrate ($t = 2.72$, $p = 0.01$, d.f. = 23), and marginally with the pH ($t = 2.05$, $p = 0.05$, d.f. = 23); in the KW, those were nitrate ($t = 2.82$, $p = 0.009$, d.f. = 23), silicate ($t = 2.13$, $p = 0.04$, d.f. = 23), and phosphate ($t = -3.03$, $p = 0.003$, d.f. = 23); and in the FZ, the Simpson index showed no significant associations with any of the physicochemical gradients. The Pielou's index was only marginally significantly associated with the nitrate ($t = 2.05$, $p = 0.05$, d.f. = 23) in the DH; in the KW, that was with the pH ($t = -2.94$, $p = 0.007$, d.f. = 23); in the FZ, Pielou's index showed no significant associations with the physicochemical gradients.

The NMDS biplot (Fig. 8a), PERMANOVA (pseudo-$F = 2.47$, $R^2 = 0.19$, $p = 0.076$, d.f. = 2) analysis suggested no significant seasonal variations in the copepod assemblages of the DH. The PERMDISP ($F = 4.52$, $p = 0.02$, d.f. = 2) conducted on the DH database found that the heterogeneity of the copepod assemblage within a season was significantly higher than the heterogeneity of the copepod assemblages of different seasons. In KW, the NMDS biplot (Fig. 8b), PERMANOVA (pseudo-$F = 3.10$, $R^2 = 0.22$, $p = 0.046$, d.f. = 2), and PERMDISP ($F = 0.49$, $p = 0.62$, d.f. = 2) analyses found only marginally significant seasonal variations in the copepod assemblages. The NMDS biplot (Fig. 8c), PERMANOVA (pseudo-$F = 2.56$, $R^2 = 0.19$, $p = 0.057$, d.f. = 2), and PERMDISP ($F = 1.23$, $p = 0.31$, d.f. = 2) analyses suggested no significant seasonal variations in the copepod assemblages of the FZ. The CCA analysis found 50.16%, 51%, and 62% constrained variabilities and 49.84%, 49%, and 38% unconstrained variabilities for the DH, KW, and FZ, respectively. In the DH, the CCA biplot suggested many species were not

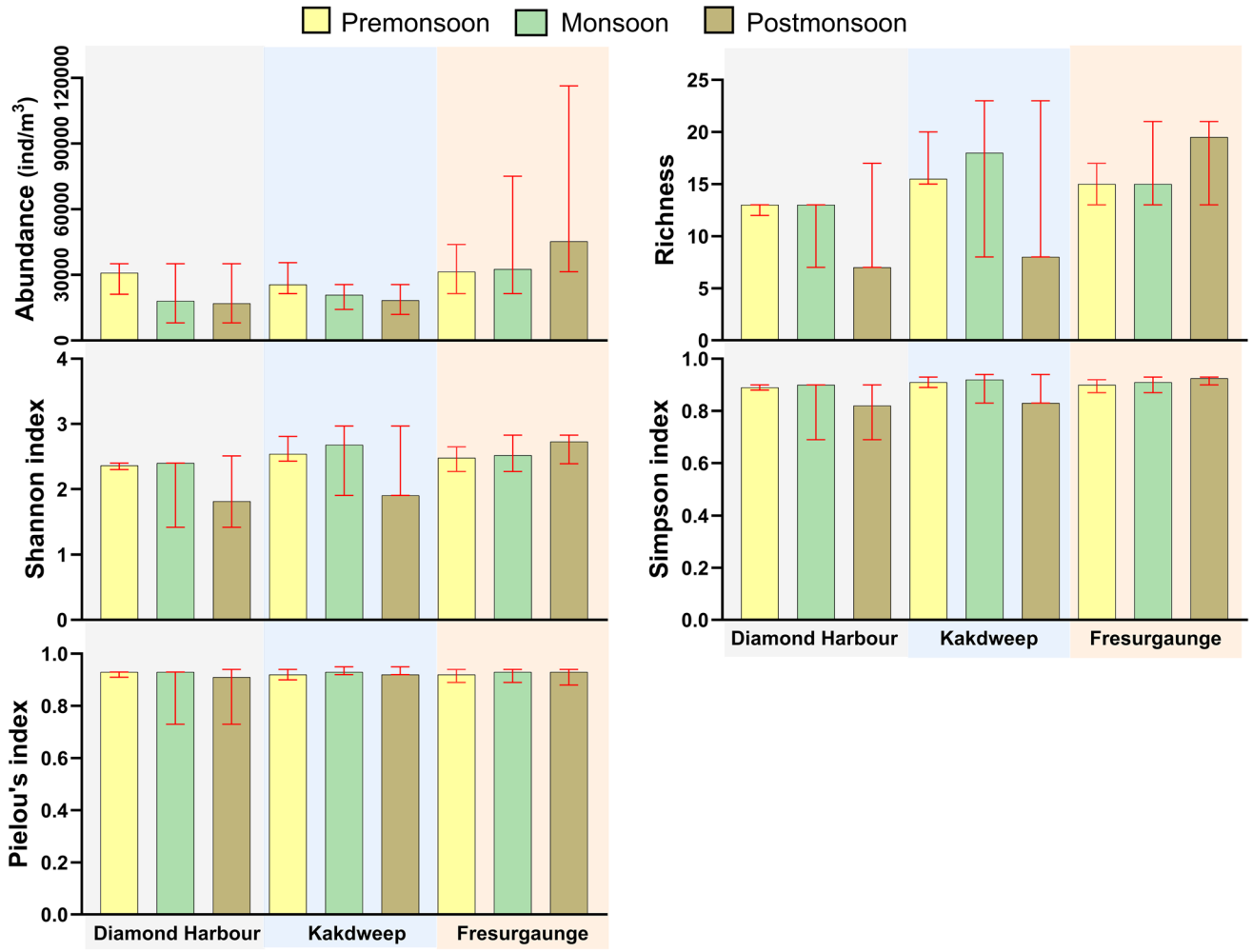


Fig. 5 Spatial and seasonal variations in the diversity indices and the cumulative abundances of the copepods sampled from the different stretches of the Ganges estuary between November 2021 and October 2023

much associated with any specific physicochemical gradients (Fig. 7b). The CCA biplot (Fig. 7c) for the KW indicated that the chl *a* could be associated with *O. similis*, *A. longicornis* distribution could be associated with the Silicate, *O. brevicornis* and *Temora turbinata* may be associated with salinity, *Oncea venusta* may be associated with salinity and nitrate, and *B. similis* and *A. tortaniformis* may have a weak association with pH and Phosphate, while *P. serricaudatus* and *Acrocalanus gibber* could be associated with the negative gradients of salinity (Fig. 7c). In the FZ, the CCA biplot found *Subeucalanus elongatus* may be associated with pH, *C. danae* with Phosphate, *S. subcrassus* with Nitrate, and *L. euchaeta* with Silicate (Fig. 7d).

Discussion

Physicochemical variability of the Ganges estuary

The GE is a degraded and depleted river estuary in terms of its water quality and ecological resources (Mitra et al. 2018; Mishra et al. 2025). Physicochemical variabilities found in the current study closely vindicated the previous results obtained by the different authors who worked on the lower reach of the GE in the current decade (Basu et al. 2022; Bhattacharya et al. 2024; Paul et al. 2024; Mishra et al. 2025; Paul 2026). Sinha et al. (1996) studied the

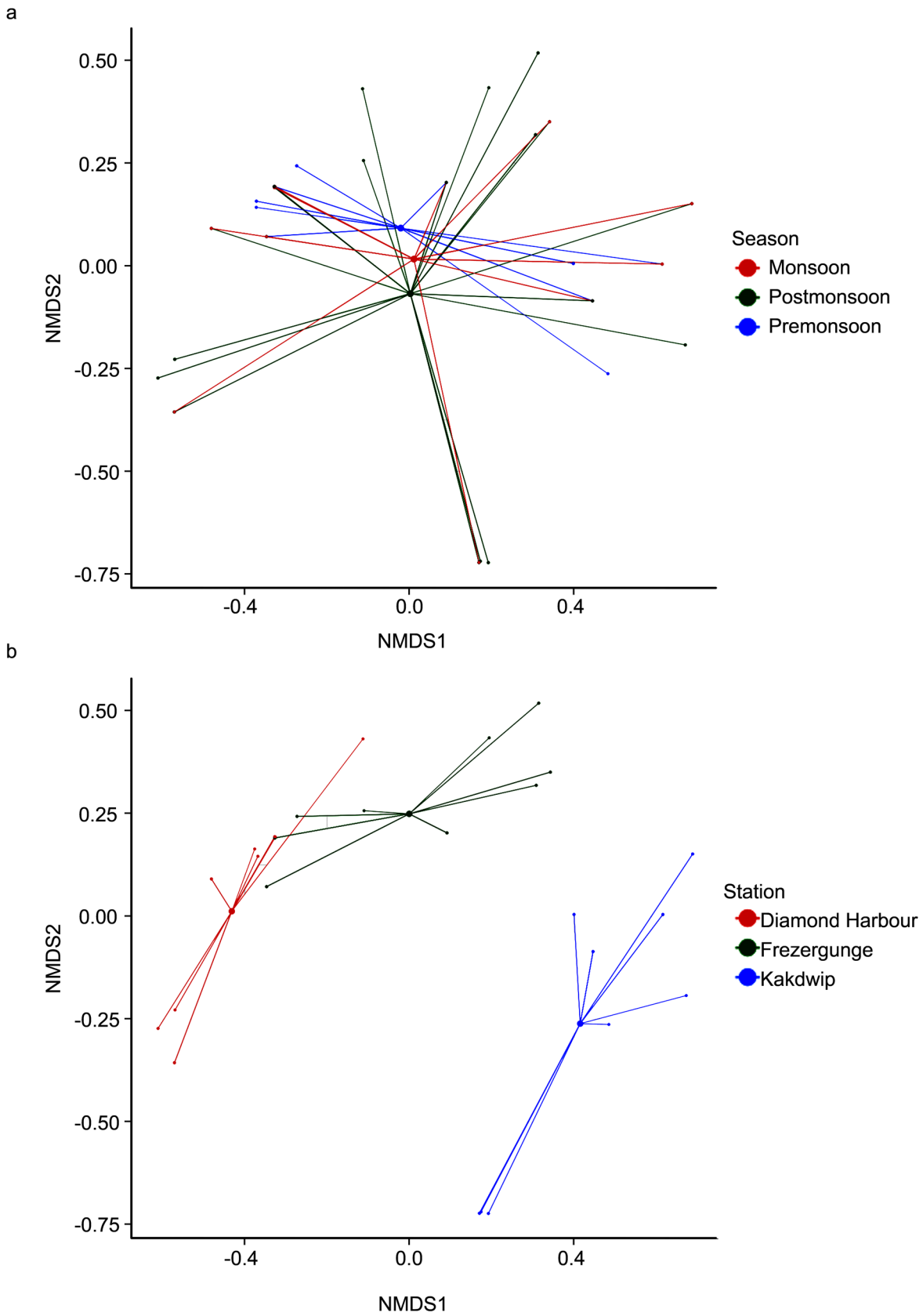


Fig. 6 Variability in the copepod assemblages sampled **(a)** seasonally and **(b)** spatially from the Ganges estuary between November 2021 and October 2023

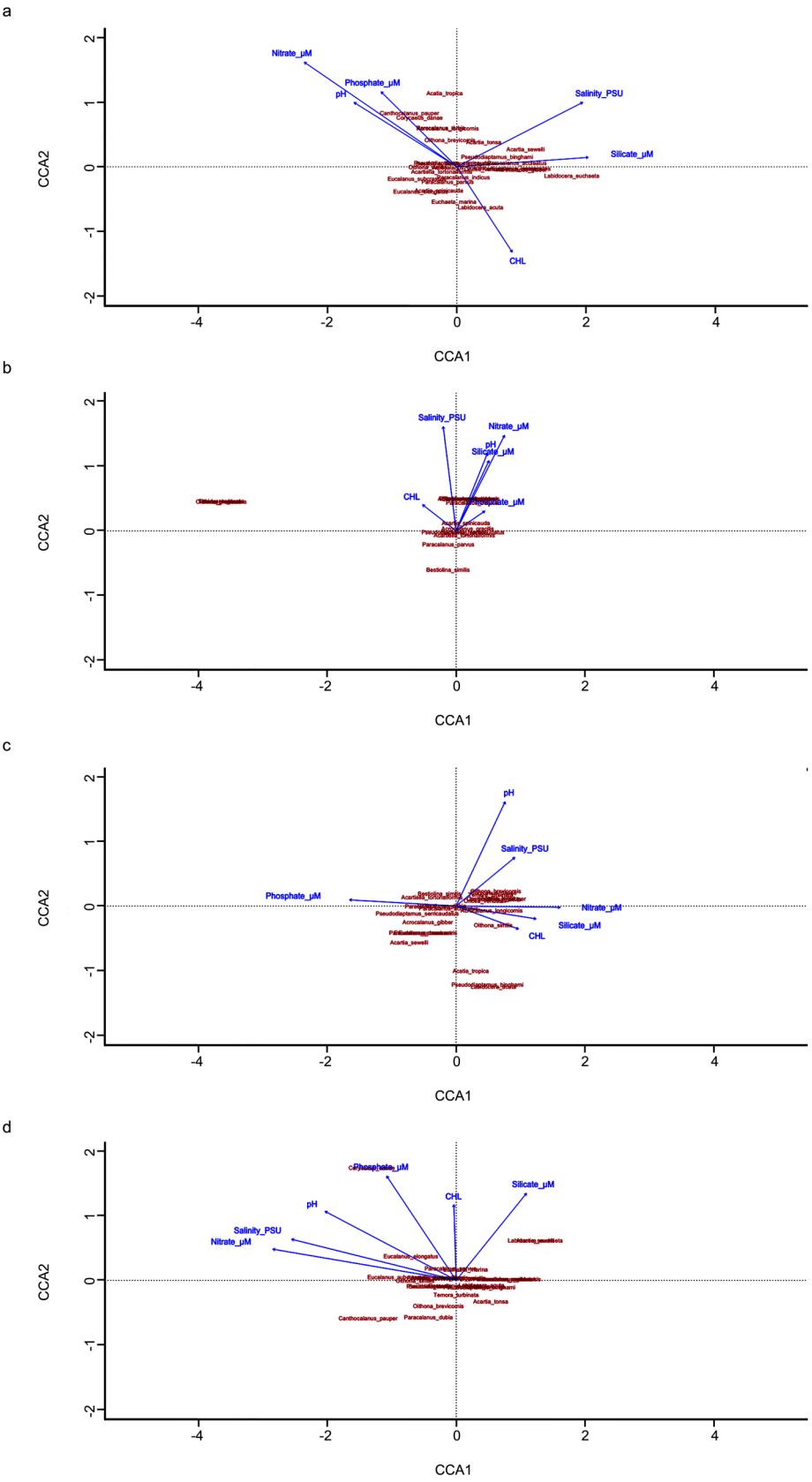


Fig. 7 Relationships between the component species of the copepod community and physicochemical gradients of the Ganges estuary and within the different stretches of estuary

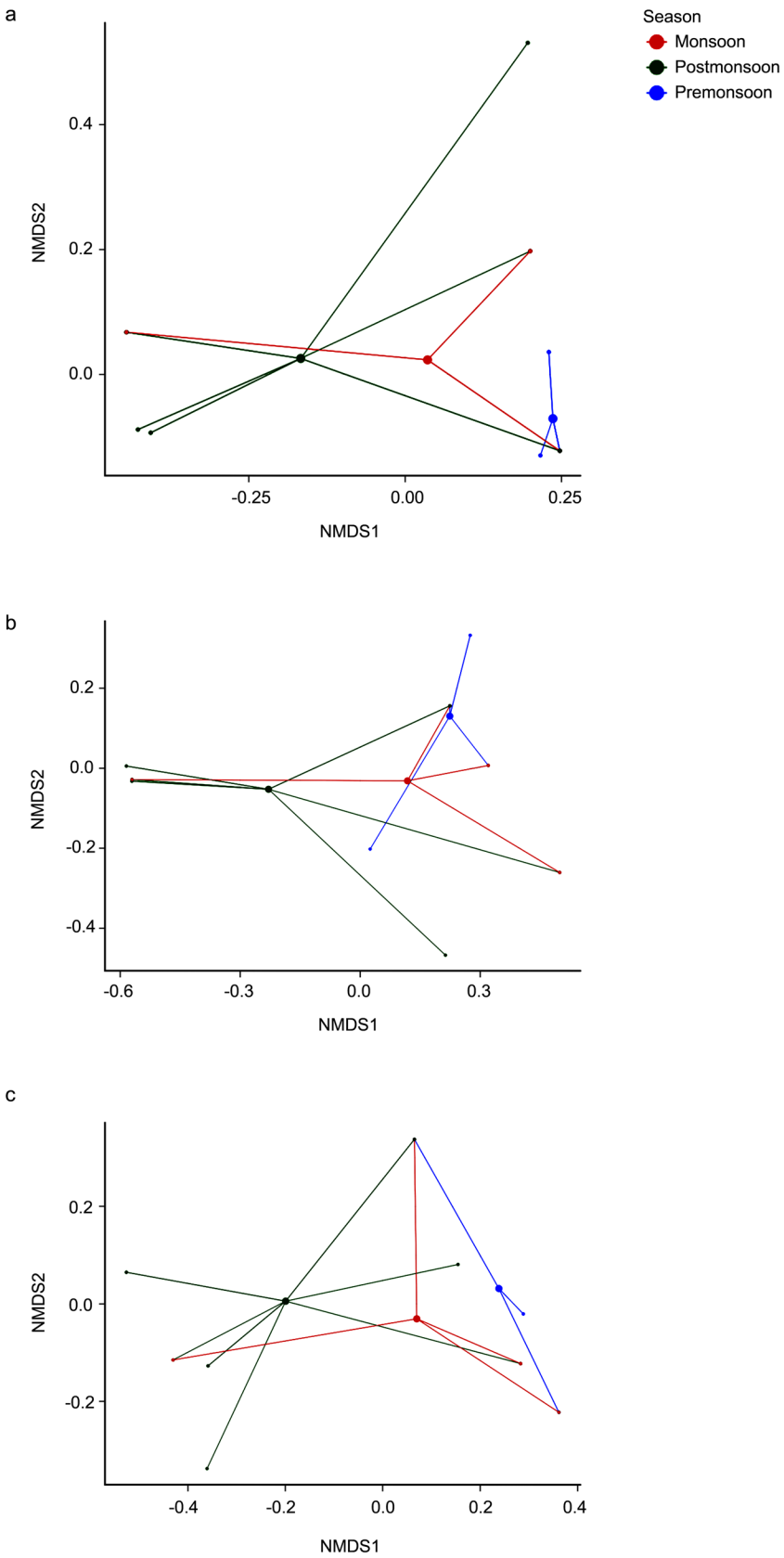


Fig. 8 Seasonal variability of the copepod assemblages sampled in the **(a)** Diamond Harbor, **(b)** Kakdwip, and **(c)** Frasergunj stretches in the Ganges estuary between November 2021 and October 2023

impact of the Farakka barrage on the hydrology and ecological communities (including copepods) of the GE and suggested that the barrage led to the progressive desalination of the GE over the decades, which affected the physicochemical gradients of the GE and spatially shifted the salinity transitional zones within the estuary. The DH is currently the salinity-limiting zone (Bhattacharya et al. 2024), but it used to be the mesohaline zone before the commission of the Farakka barrage in 1975 (Sinha et al. 1996). The KW to Namkhana is currently the mesohaline stretch of the GE (Paul et al. 2024), but they were previously polyhaline in nature (Sinha et al. 1996). Currently, the estuary mouth characteristics are restricted only to the FZ and beyond the Sagar Island stretch of the GE (Sinha et al. 1996; Paul 2026). Those distinct salinity zones have their unique physicochemical properties (Bhattacharya et al. 2024; Paul et al. 2024; Paul 2026); this is also found in the results. The estuary as a single habitat has neutral to slightly alkaline pH, which closely matches the current results (Mukhopadhyay et al. 2006; Basu et al. 2022; Paul et al. 2024; Paul 2026). The pH remains alkaline in the FZ year-round owing to higher salt concentration near the estuary mouth (Mishra et al. 2025), and this is also evident in the results. Mitra et al. (2018) described the GE as a mesotrophic estuary. The results, however, suggested oscillations between oligotrophic and hypertrophic conditions of the estuary depending on the certain stretch of the estuary and seasonal cycles. The GE is a Phosphate-limited estuary with some degree of seasonal variation (Mukhopadhyay et al. 2006), which is consistent with the present results. This is possible because the riverine sediments of the GE act as a major sink for the Phosphate, and the terrestrial runoffs contribute to the variations of nutrient cycles, including Phosphate (Vaithiyanathan et al. 1993; Mitra et al. 2018). Kumar et al. (2023) suggested significant seasonal variability of Nitrate in the GE and linked that with the use of synthetic fertilizers and soil organic matter nitrification. Low chl *a* and Silicate levels in the DH stretch of the GE suggested a limited growth of its phytoplankton resources; a possible reason of that could be the maximum turbidity, which is often the consequence of a higher fetch effect arising from strong wind and uneven shallow bathymetry of the DH stretch of the estuary (Choudhury and Pal 2012).

Copepod diversity and distribution in the Ganges estuary

Results of species diversity are aligned with the previous studies conducted on the oligohaline, mesohaline, and polyhaline stretches of the GE separately in the recent decade (Basu et al. 2022; Bhattacharya et al. 2024; Paul et al. 2024; Paul 2026). The FZ station had the highest total abundance of the copepods, possibly because it is near the estuary mouth, receiving many neritic species, and the station is within a semi-intense mangrove patch thus facing less wave dashing, which is otherwise common for beaches of Sagar Island (Basu et al. 2022; Paul 2026). Hedayati et al. (2017) in the Mond River estuary of Iran and Dahms et al. (2012) in the Lanyang River estuary of Taiwan reported higher abundances of copepods near the mouth of those estuaries, compared with the inland sampling sites owing to the neritic inclusions coming from the sea. Limited species diversity of the copepods at the DH is possibly linked to the low salinity which exert higher osmotic costs for maintaining stasis under such environment, as suggested by Bhattacharya et al. (2024). The maximum diversity and abundances of the copepods in the KW were found in the POM, which vindicated the previous results of Basu et al. (2022), who reported higher abundances of the copepods in the Kachuberia opposite to the KW. Sarkar et al. (1986) found that the copepod abundances in the GE peaked during PRM, especially in the mesohaline creeks of Sagar Island, which contradicts the present results. Bhattacharya et al. (2024) suggested *P. parvus* was the most abundant species in the DH, followed by *B. similis*. Paul (2026) found *A. spinicauda* was the most abundant species followed by *B. similis* near the estuary mouth, which starts beyond Sagar Island. Basu et al. (2022) suggested *B. similis*, *P. parvus*, *A. spinicauda*, and *Oithona* spp. were ubiquitous, breeding continuously with high reproductive capacity owing to suitable conditions in the mesohaline creeks of the GE. Alpha diversity indices considered in the current study are chiefly derived from species richness and abundance (Thukral 2017) and did not show significant seasonal variations, indicating localized communities are less affected by seasonal cycles because they were well adapted to the physicochemical gradients of the GE, as found for the copepod community in the mesohaline to polyhaline creeks of the Sagar Island by Paul (2026). Most previous studies, including the current one, were conducted during the daylight owing to feasibility and travel restrictions, except the studies of Paul et al. (2019) and Nandy et al. (2026), who found higher species richness and abundances of the copepods of the GE at night owing to diel patterns; the present study has a limitation in that regard. Comparing the recent species diversity of the copepods of the GE with the species diversity observed in the studies conducted in the late 20th century is difficult owing to the decadal changes in species composition that are possibly ongoing in the estuary, which may be linked with broad-scale changes of physicochemical gradients of the system (Dutta et al. 1954; Sarkar et al. 1986; Sinha et al. 1996; Bhattacharya et al. 2015, 2024; Paul et al. 2019, 2024; Basu et al. 2022; Paul 2026). In future too, decadal comparisons of the species composition, size class, and feeding guilds of the copepod community of the GE and other estuaries of India will continue to face challenges

unless there is a long-term plankton monitoring program in place (Bhattacharya et al. 2015; Paul et al. 2019, 2026).

Copepod assemblages exhibited specialized distributions with significant spatial variability. The distribution of copepods within certain stretches of the GE largely remained unexplained by physicochemical gradients, suggesting that the realized niches might also be segregated by ecological interactions, the intensity of which in the GE varies on the basis of the seasonal changes of the physicochemical gradients (Paul et al. 2019; Nandy et al. 2026). Most estuarine studies on the copepods suffer from scale versus sampling frequency trade-off (Paul and Calliari 2019; Paul et al. 2019), and the resultant databases that arise from such studies are often statistically analyzed in a way that is insufficient to capture many significant and subtle ecological variations that are exclusive (be it physicochemical gradients or species-specific interactions) to specific stretches within an estuary or coastal marine ecosystems because an estuary is generally considered as a single continuous dominant habitat (David et al. 2016; Bisinicu and Lazar 2024). The replacement of *A. tortaniformis* by *B. similis* in the MON as the most abundant species in the DH exemplifies this, as it could not be detected in the habitat-level data analysis in the current study. Dissimilarity in the copepod assemblages found in the results are not unexpected, because *B. similis*, *A. spinicauda*, and *A. tortaniformis* are estuarine residents and euryhaline in nature (Bhattacharya et al. 2024; Paul et al. 2024); therefore, their ideal niches are well spread along the salient gradient, but the centers of their distributions are more concentrated towards the mesohaline stretch of the GE (Basu et al. 2022; Bhattacharya et al. 2024; Paul et al. 2024; Paul 2026). *Acrocalanus gracilis* and *P. aculeatus* prefer polyhaline conditions, as observed in the Hooghly (also referred as the GE) and off the Rushikulya estuaries of India (Srichandan et al. 2015; Basu et al. 2022). Copepod diversity and distribution in the DH and FZ were significantly limited positively and negatively by the gradients of salinity, respectively, but the salinity gradient hardly limited copepod distribution in the KW stretch of the estuary; this result is on par with the previous studies conducted on the copepods of the GE (Bhattacharya et al. 2024; Paul et al. 2024; Paul 2026). Inconsistencies in the relationships between nutrient dynamics and copepod distributions were observed when results of the "Habitat database" and databases of each sampling station were compared with each other. This is not unexpected owing to the specific adaptability of certain copepod species to the water mass properties of a certain stretch of the estuary, as previously observed in the Hooghly and Asthamudi estuaries of India, the Gironde Estuary of France, and the coastal marine waters of the Black Sea (Sinha et al. 1996; David et al. 2016; Hani and Jayalakshmi 2023; Basu et al. 2022; Bisinicu and Lazar 2024; Paul 2026). The CCA conducted on both the "Habitat database" and databases of each sampling station revealed that the distributions of a few copepod species were influenced by one or more physicochemical gradients, but the majority were not much associated with water mass properties of the GE; this possibly suggested a considerable role of species interactions and diel behaviors of the copepod, as found in the studies of Paul et al. (2019) and Nandy et al. (2026). Unfortunately, both of those studies were confined to only the mesohaline stretch of the GE; thus, the author is cautious of extrapolating those results to the DH and FZ stretches of the GE. Bhattacharya et al. (2024) suggested that the distribution of certain stenohaline species in the DH was constrained by salinity, pH, and nutrients, which to some extent supports the present results. Basu et al. (2022) found that the distribution of the copepods in the mesohaline and polyhaline tidal creeks of the GE were largely influenced by salinity, temperature, and nutrient dynamics, which also supports the present results. Finally, when ecological databases are pooled together, many variations get lost; thus, it is difficult to tease out those microscale ecological variabilities from a habitat-level data analysis. In the present study, data arose from different stretches of the GE, which are exclusive from the standpoint of their physicochemical gradients, and it may have implications for the copepod assemblages that inhabit therein. This is not uncommon—the higher number of significant results in the disaggregated analyses—because it reflects the loss of resolution from pooling heterogeneous stations independent of any genuine ecological-scale effect.

Monitoring zooplankton in the Ganges estuary

Only a few river estuaries of the world have decadal water quality monitoring programs that cover ecologically sensitive zones and the zooplankton communities that reside there (Ferreira et al. 2007; Pinto et al. 2010; Nieman et al. 2021; Richardson and Soloviev 2021; Bisinicu and Lazar 2024). The GE is serving millions of humans ecologically and economically since the dawn of civilization in India (Sarkar et al. 2007). The Ganges River has had the Ganga Action Plan since 1984, and this plan is stretched from the sources to the sink of the river, generating a huge wealth of regular water quality data, both physical and chemical in nature, but biological data are often scarce and intermittently collected (Srinivas et al. 2020). Indian universities and research institutions have gathered significant knowledge of zooplankton diversity and ecology in the lower stretch of the GE over the decades starting from the 1950s (Dutta et al. 1954; Sarkar et al. 1986, 2007; Sinha et al. 1996; Rakshit et al. 2017; Basu et al. 2022; Bhattacharya et al. 2024; Paul et al. 2024; Paul 2026). Those datasets could be used as a baseline for long-term monitoring of zooplankton and water quality of the GE. However, institutional support and guidance are essential for the long-term,

so the author proposes that the Ministry of Earth Sciences (MoES) of India forms a National Estuarine Committee (NEC) for the management of Indian estuaries, including the GE. On the basis of the recommendations of the NEC, a task force shall be constituted for "Estuary Monitoring (EM)," which shall present a comprehensive report on how baselines shall be drawn for water quality monitoring, keeping the compliance on par with the Ministry of Environment Forest and Climate Change (MoEFCC), India, guidelines. The monitoring could be initiated in the United Nation's Ocean Decade (2021–2030), keeping the GE as a model estuary for the northeastern coast of India. Monitoring zooplankton including copepods shall consider the optimal choices of sampling frequency (Paul et al. 2019) and heterogeneity in habitat characteristics, including biogeochemical gradients of the GE (Mukhopadhyay et al. 2006; Bhattacharya et al. 2024; Paul 2026). If the monitoring is on a monthly basis, then higher sampling efforts before and after seasonal transitions and stochastic changes such as cyclone and floods are required (Paul et al. 2024, 2026; Paul 2026). If the monitoring is seasonal, then at least sampling efforts before and after the transition of the monsoon are required because on those occasions the GE experiences the maximum ecological variabilities owing to rapid changes in the physicochemical gradients of the entire estuary (Bhattacharya et al. 2024; Paul et al. 2024; Paul 2026). If the resources are constrained for monitoring the entire estuary, then a few distinct stretches (e.g., salinity limiting zone, estuary mouth etc.) within the estuary characterized by unique physicochemical gradients shall at least be monitored for the long-term.

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Author contributions S.P.: conceptualization, validation, funding acquisition, methodology, formal analysis and investigation, data curation, visualization, software, resources, project administration, writing—original draft, and writing—review and editing.

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Data availability Data and materials would be provided after reasonable request.

Declarations

Conflict of interest Author declares no competing interests.

Ethical approval This is not applicable.

Consent to participate This is not applicable.

Consent for publication Author provides consent for publication.

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