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Original Article

Environmental controls on zooplankton community composition across the Bangladesh coast: integrating hydrochemistry, multivariate ordination, and threshold indicator analysis

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Abstract
Understanding the impact of hydrochemical variability on zooplankton communities is fundamental for assessing the ecological status of coastal ecosystems. This study investigated how seasonal and spatial hydrochemical conditions shaped zooplankton communities across three contrasting coastal ecosystems of Bangladesh using multivariate approaches and threshold indicator taxa analysis (TITAN). Hydrochemical variables exhibited strong significant seasonal and spatial variations ($p < 0.05$). Salinity, electrical conductivity, transparency, and pH were higher in pre-monsoon, whereas phosphate, nitrate, chlorophyll-*a*, and dissolved oxygen were higher in post-monsoon. A total of 42 zooplankton genera belonging to four major taxonomic groups were identified, where a subclass of small crustaceans within the phylum Arthropoda such as Copepoda was the dominating group (42.4–52.7%) of zooplankton throughout the study periods. Zooplankton abundance, species richness, and diversity were significantly higher in the western and central coastal zones

than in the eastern coastal zone, with abundance reaching 320±24.6 individuals L^{-1} during the post-monsoon. Redundancy analysis (RDA) identified TDS, chlorophyll-*a*, COD, temperature, DO, and salinity as significant environmental correlates of zooplankton community composition, with the first two canonical axes accounting for 94.83% of the constrained variation. Comparative TITAN analyses identified community thresholds along salinity, TDS, EC, and pH gradients, with the salinity response showing a distinct ecological transition between approximately 8.9 and 13.9 ppt. These findings highlight the association of salinity with zooplankton distribution across the Bangladesh coast and provide a quantitative ecological threshold that can support long-term biomonitoring, biodiversity conservation, and adaptive coastal ecosystem management.

Keywords: coastal ecosystems; estuarine ecology; salinity gradient; TITAN; zooplankton bioindicator

1 | INTRODUCTION

Coastal ecosystems are among the most productive and biologically diverse environments on Earth, supporting fisheries, biodiversity conservation, nutrient cycling, carbon sequestration, and the livelihoods of millions of people (Vinayachandran *et al*. 2022). The interconnected systems, including rivers, estuaries, mangroves, and coastal waters, are characterized by dynamic physicochemical conditions resulting from interactions between freshwater and marine processes (Kim *et al*. 2017). Zooplankton play a vital role in the aquatic ecosystems by transferring energy from primary producers to higher trophic levels while contributing to nutrient regeneration and biogeochemical cycle (Ratnarajah *et al*. 2023). Because of their short life cycles, rapid reproduction, and high sensitivity to environmental change, zooplankton respond quickly to natural and anthropogenic disturbances. Consequently, changes in their abundance and community composition provide reliable indicators of ecosystem health and environmental quality (Goździejewska *et al*. 2024).

Zooplankton communities are structured by the combined effects of physicochemical and hydrological variables operating across spatial and temporal scales (Zhao *et al*. 2017). Salinity, temperature, dissolved oxygen, nutrients, pH, conductivity, and turbidity regulate species distribution, physiological performance, reproduction, and trophic interactions, whereas hydrodynamic processes such as freshwater discharge, tidal exchange, and water circulation influence habitat connectivity and resource availability (Dorak *et al*. 2025). Because these environmental drivers interact simultaneously, their relative importance differs among riverine, estuarine, and coastal ecosystems, resulting in pronounced spatial and seasonal variation in zooplankton communities (Zeng *et al*. 2025). Understanding these complex ecological responses therefore requires integrated analytical approaches capable of evaluating multiple environmental drivers and their combined influence on community organization.

Despite extensive research on zooplankton ecology, significant knowledge gaps remain. Most previous studies have focused on individual aquatic ecosystems or examined spatial and seasonal variations using conventional diversity indices and univariate statistical analyses (Modéran *et al*. 2010; Rollwagen-Bollens *et al*. 2020). Consequently, the mechanisms through which multiple environmental variables jointly regulate zooplankton communities across contrasting coastal ecosystems remain poorly understood (Zhang *et al*. 2022). Furthermore, although multivariate ordination techniques have been widely used to investigate species–environment relationships, studies combining hydrochemical characterization with multivariate ordination and threshold indicator analyses are still limited, particularly in tropical coastal regions (Mantovano *et al*. 2019). Such an integrated approach is essential for identifying the dominant environmental drivers, detecting ecological thresholds, and improving ecosystem assessment and management under rapidly changing environmental conditions (Baker and King 2010).

The Bangladesh coast is one of the most dynamic regions in the world, where riverine, estuarine, and marine ecosystems are interconnected through the combined influence of the Ganges–Brahmaputra–Meghna river system, semidiurnal tides, monsoonal rainfall, and the northern Bay of Bengal (Rahman *et al*. 2024; Khan *et al*. 2025). These processes create strong spatial and seasonal variability in hydrochemical conditions across the Bangladesh coast (Rahman *et al*. 2025). The western region is represented by the tidally influenced Shibsa River within the Sundarbans mangrove ecosystem, the central region by the Lower Meghna Estuary, and the eastern region by the open coastal waters of the Bay of Bengal (Yeasmin *et al*. 2026). Although these ecosystems differ markedly in hydrology and water quality, they have generally been investigated separately, limiting regional-scale understanding of environmental controls on zooplankton communities across the Bangladesh coast (Abdullah Al *et al*. 2020; Sultana *et al*. 2026).

To address the knowledge gap how hydrochemical conditions influence on zooplankton diversity and community composition across three contrasting coastal ecosystems of Bangladesh, a comprehensive understanding of species–environment relationships show ecological significance within a single regional framework. The objectives of this study were to (i) characterize the spatial and seasonal variability of hydrochemical conditions across the western Shibsa River, central Lower Meghna Estuary, and eastern coastal waters of the Bay of Bengal;

(ii) evaluate seasonal and spatial patterns of zooplankton community composition; (iii) identify key hydrochemical variables associated with variation in zooplankton community structure using multivariate approaches; and (iv) identify community-level thresholds and indicator taxa associated with salinity, TDS, EC, and pH gradients using Threshold Indicator Taxa Analysis (TITAN). The findings provide new insights into the environmental regulation of zooplankton communities, and sustainable environmental management under increasing anthropogenic and climatic pressures.

2 | METHODOLOGY

2.1 Study area

The study was conducted across the Bangladesh coast, encompassing three contrasting coastal ecosystems: the western Shibsa River, the central Lower Meghna Estuary, and the eastern coastal waters of the Bay of Bengal (Figure 1). These regions represent a broad hydrochemical gradient resulting from varying influences of freshwater discharge, tidal exchange, and marine intrusion. The western zone comprises the tidally influenced Shibsa River within the Sundarbans mangrove ecosystem, where freshwater inflow and tidal dynamics strongly regulate water quality. The central zone includes the Lower Meghna Estuary, a highly dynamic river–estuary transition influenced by the Ganges–Brahmaputra–Meghna river system (Rahman *et al*. 2025). In contrast, the eastern zone represents the open coastal waters of the Bay of Bengal, characterized by stronger marine influence and distinct hydrographic conditions (Yeasmin *et al*. 2026).

Samples were collected from 15 sites across three coastal regions, comprising five sites each in the western (W1–W5), central (C1–C5), and eastern (E1–E5) zones. Sampling was conducted during three seasonal periods: pre-monsoon (12–19 April), monsoon (5–8 July), and post-monsoon (2–10 November). The same 15 sites were sampled during each seasonal survey to characterize spatial and seasonal variability in hydrochemical conditions and zooplankton communities, resulting in 45 sites × season sampling combinations. The geographical coordinates of all sampling sites are provided in Supplementary Table S1, and their locations are shown in Figure 1.

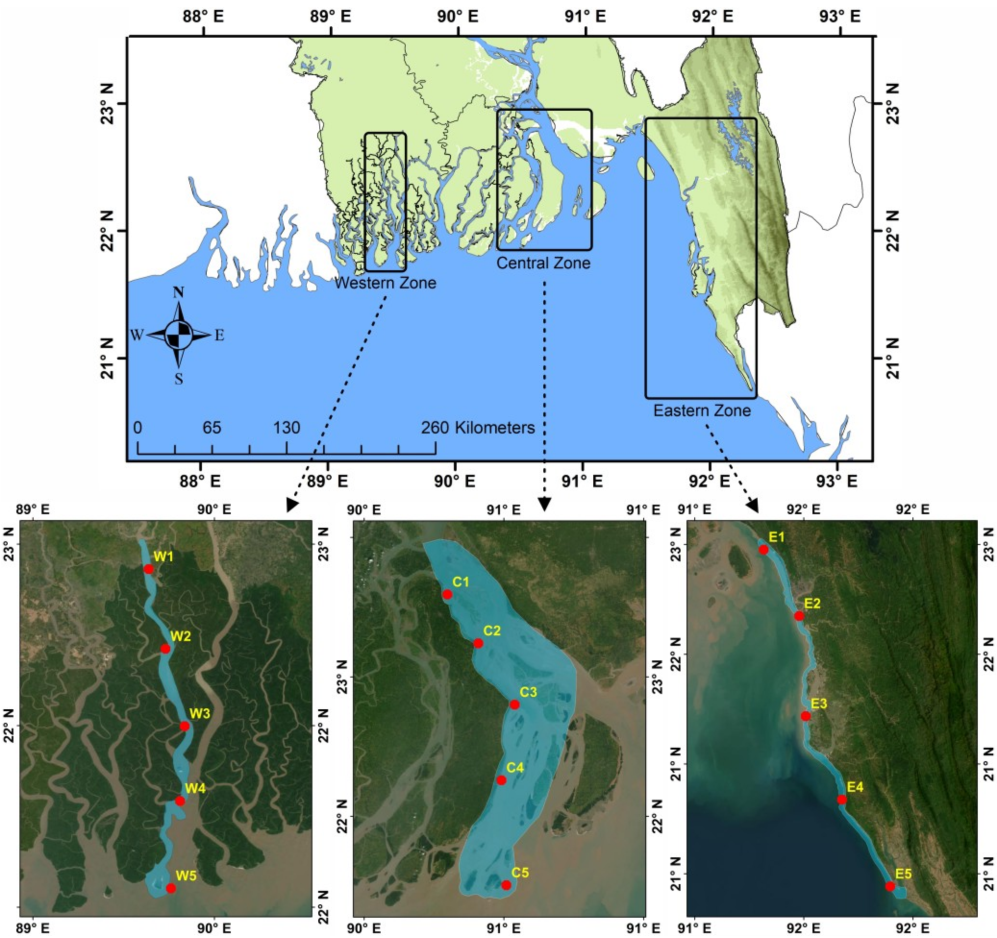

FIGURE 1 Map of the study area and sampling locations across the western, central, and eastern coastal zones of Bangladesh. Fifteen sampling stations were established in the western (W1–W5), central (C1–C5), and eastern (E1–E5) coastal zones.

2.2 Sample collection

Surface water and zooplankton samples were collected simultaneously at all sampling sites during each survey. Sampling was not standardized to a specific tidal phase because multiple geographically separated sites were surveyed within each seasonal sampling campaign. Consequently, tidal state may have varied among sites during sample collection. Immediately after collection, selected hydrochemical parameters were measured in situ, whereas water samples intended for laboratory analyses were transferred into pre-cleaned polyethylene bottles, preserved following standard procedures (APHA 2017), and transported to the laboratory in an icebox.

Hydrochemical parameters were measured using standard field and laboratory procedures. Water temperature (°C) and salinity (ppt) were measured in situ using a multiparameter meter (HI 9829, Hanna Instruments, Woonsocket, RI, USA), while water transparency (cm) was determined using a Secchi disk. Other in situ parameters, including pH, dissolved oxygen (DO; mg L^{-1}), electrical conductivity (EC; dS m^{-1}), and total dissolved solids (TDS; mg L^{-1}), were measured using calibrated field instruments, with detailed instrument specifications provided in Supplementary Table S2. Surface water samples were stored in pre-cleaned polyethylene bottles, transported to the laboratory under chilled conditions, and analyzed for nitrate (NO_3–N), phosphate (PO_4), chemical oxygen demand (COD), biochemical oxygen demand (BOD), and chlorophyll-*a* (Chl-*a*). Nutrient concentrations were determined using a HACH DR/2020 spectrophotometer, while COD, BOD, and chlorophyll-*a* were analyzed according to standard methods (APHA 2017).

Quality assurance and quality control (QA/QC) procedures were applied throughout field measurements and laboratory analyses to ensure data reliability and consistency. Field measurements were conducted using calibrated instruments, and water transparency was determined using a Secchi disk. Laboratory determinations of NO_3–N, PO_4, BOD, COD, and chlorophyll-*a* followed the specified analytical procedures, including APHA (2017) methods where applicable (Table S2). All instruments were operated according to the manufacturers' instructions and checked before measurements to minimize analytical and instrumental errors.

Surface zooplankton samples were obtained from the upper 0–0.5 m of the water column. At each sampling site during each season, three 10-L subsamples were filtered through a 50 µm mesh plankton net and pooled after filtration to form a single composite sample, yielding a total filtered volume of 30 L per site × season combination. The retained organisms were concentrated to 50 mL, transferred to labelled sample bottles, immediately fixed with 5% buffered formalin, and transported to the laboratory for subsequent analysis. Thus, the three 10-L subsamples were not treated as independent replicates in the statistical analyses; each site × season combination represented a single sampling unit (n = 45). Prior to enumeration, each sample was mixed gently to obtain a uniform distribution of organisms. A 1 mL aliquot was loaded into a Sedgwick–Rafter counting chamber (Cat. Ref. S50), and all individuals within the chamber were identified and counted using a fluorescence microscope (Olympus BX51, Olympus Corporation, Tokyo, Japan). Identification was performed to the genus level using standard taxonomic references (Martin and Davis 2001; Conway *et al*. 2003; Goswami 2004; Conway 2012). Zooplankton abundance was calculated relative to the original volume of filtered water and reported as individuals L^{-1}. Taxonomic names were verified against the World Register of Marine Species (WoRMS) to ensure consistency.

2.3 Abundance, diversity indices and statistical analyses

Zooplankton community structure was characterized using total abundance and composition across seasonal and spatial scales. Diversity indices namely, species richness (S), Shannon–Wiener index (H'), Margalef richness (D), and Pielou's evenness (J') (Shannon and Weaver 1949; Margalef 1958; Pielou 1966) were measured. Seasonal and spatial differences in hydrochemical variables and zooplankton community indices were evaluated using linear mixed-effects models, with zone, season, and their interaction (zone × season) included as fixed effects and site included as a random intercept to account for repeated seasonal observations at the same sampling sites. Where significant fixed effects were detected, post hoc pairwise comparisons were performed with appropriate adjustment for multiple comparisons. Model assumptions were evaluated using residual diagnostics. Data normality and homogeneity of variance were assessed using the Shapiro–Wilk and Levene's tests, respectively.

Principal component analysis (PCA) was performed on standardized hydrochemical variables to identify the major environmental gradients across the study area (Abdullah Al *et al*. 2020). Relationships between zooplankton communities and hydrochemical variables were examined using redundancy analysis (RDA). Prior to RDA, detrended correspondence analysis (DCA) was conducted to determine the appropriate ordination method. The gradient length of the first DCA axis was 1.77 SD units, indicating that a linear ordination method (RDA) was appropriate (ter Braak and Šmilauer 2012). The significance of the RDA model and individual environmental variables was evaluated using permutation tests. Because salinity, TDS, and EC represent closely related dissolved-ion gradients, partial RDA was additionally performed to quantify their independent associations with zooplankton community composition by conditioning on the other two variables. Threshold Indicator Taxa Analysis (TITAN) was applied separately to salinity, total dissolved solids (TDS), electrical conductivity (EC), and pH to evaluate nonlinear community- and taxon-level responses along these hydrochemical gradients (Baker and King 2010). TITAN was conducted using 45 sites × season observations and all 42 recorded genera, with a minimum split size of five observations, 1,000 permutations, and 1,000 bootstrap replicates. Taxa were considered robust indicators when purity and reliability were both ≥ 0.95. Community-level thresholds were identified from the filtered sums of standardized indicator values for decreasing (z−) and increasing (z+) taxa. To assess robustness, the analyses were repeated after excluding genera occurring in all 45 samples. All statistical analyses were performed in R version 4.6.1 (R Core Team, 2026) using the packages vegan, TITAN2, ggplot2, multcompView, and dplyr, with statistical significance accepted at $p < 0.05$.

3 | RESULTS

3.1 Dynamics of physicochemical parameters

Seasonal and spatial variations in physicochemical parameters across the western, central, and eastern coastal zones are illustrated in Figure 2, while detailed descriptive statistics and one-way ANOVA results are provided in Table S3. Most hydrochemical variables exhibited significant seasonal variation ($p < 0.05$). Water temperature, transparency, salinity, pH, electrical conductivity (EC), phosphate (PO_4), nitrate (NO_3–N), dissolved oxygen (DO), and chlorophyll-*a* varied significantly among seasons, whereas total dissolved solids (TDS), chemical oxygen demand (COD), and biochemical oxygen demand (BOD) showed no significant seasonal differences (Table S3). Temperature was the only parameter that did not differ significantly among coastal zones, whereas all other variables exhibited significant spatial variation.

Water temperature was highest during the pre-monsoon (30.49±0.61°C) and lowest during the post-monsoon (23.13±1.47°C). Similarly, transparency and salinity reached their maximum values during the pre-monsoon (41.49±22.09 cm and 19.61±8.18 ppt, respectively), whereas transparency declined markedly during the monsoon (17.70±10.52 cm). Water pH also peaked during the pre-monsoon (7.46±0.19) and decreased to its minimum during the monsoon (6.69±0.33). Electrical conductivity exhibited a similar seasonal trend, with the highest mean value recorded during the pre-monsoon and the lowest during the monsoon.

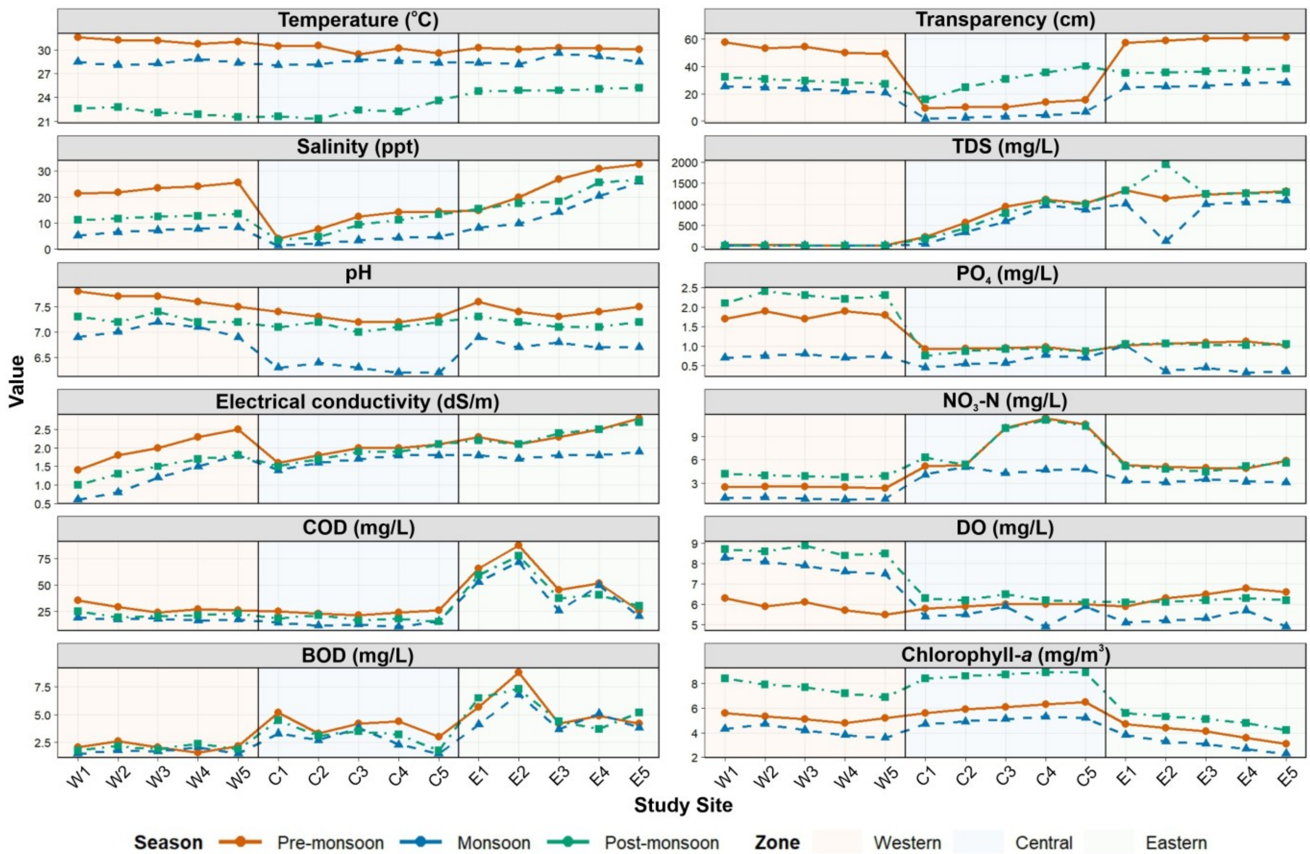

FIGURE 2 Seasonal and spatial variations in physicochemical parameters across the Bangladesh coast.

Among the nutrient- and productivity-related variables, both PO_4 and chlorophyll-*a* attained their highest concentrations during the post-monsoon (1.39±0.64 mg L^{-1} and 7.11±1.67 mg m^{-3}, respectively), while NO_3–N increased from 2.96±1.54 mg L^{-1} during the monsoon to 5.88±2.50 mg L^{-1} during the post-monsoon. Dissolved oxygen also reached its maximum during the post-monsoon (7.02±1.18 mg L^{-1}) and was lowest during the pre-monsoon (6.09±0.35 mg L^{-1}). In contrast, TDS, COD, and BOD exhibited relatively small seasonal fluctuations and did not differ significantly among seasons despite showing significant zonal variation (Table S3).

Principal component analysis (PCA) revealed the multivariate patterns of environmental parameters across the Bangladesh coast (Figure 3). The first two principal components explained 57.6% of the total environmental variation, with PC1 and PC2 accounting for 33.5% and 24.1%, respectively. The ordination showed partial seasonal separation, with pre-monsoon samples predominantly distributed on the positive side of PC1, post-monsoon samples mainly located on the negative side of PC1, and monsoon samples occupying the lower portion of the ordination space with partial overlap among seasons. Salinity, electrical conductivity (EC), transparency, pH, COD, BOD, TDS, and temperature were positively associated with PC1, whereas dissolved oxygen (DO), chlorophyll-*a*, and phosphate (PO_4) were associated with the opposite direction of PC1. NO_3–N was positioned close to the origin of the ordination plot.

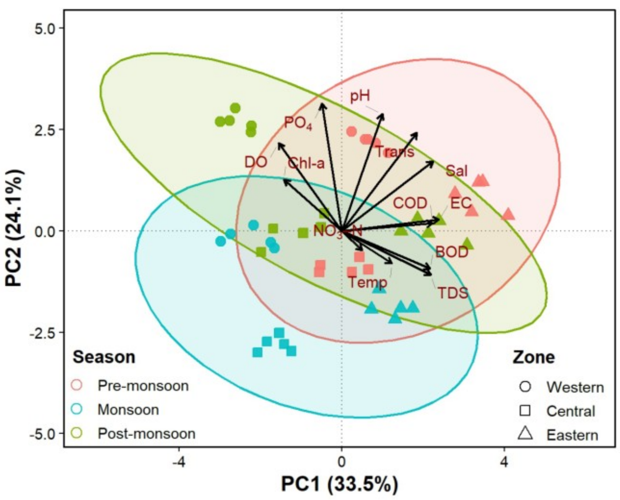

FIGURE 3 Principal component analysis (PCA) of environmental parameters across the Bangladesh coast.

3.2 Zooplankton community compositional variation

A total of 42 zooplankton genera belonging to four major taxonomic groups were recorded during the study period. Copepoda was the most diverse group, comprising 22 genera, followed by Rotifera and Cladocera with nine genera each, while Protozoa was represented by two genera. The complete checklist of zooplankton genera, their overall relative abundance, and seasonal–spatial occurrence is provided in Table S4.

The relative composition of the major zooplankton groups exhibited clear seasonal variation (Table 1). Copepoda dominated the zooplankton community throughout the study period, accounting for 52.71%, 42.43%, and 48.31% of the total abundance during the pre-monsoon, monsoon, and post-monsoon seasons, respectively. Rotifera was the second most abundant group and showed a pronounced seasonal increase during the monsoon, contributing 33.34% of the total abundance compared with 21.68% in the pre-monsoon and 26.12% in the post-monsoon. Cladocera contributed 15.34–18.60% of the total abundance, with its highest proportion observed during the monsoon season. In contrast, Protozoa consistently represented the smallest component of the zooplankton assemblage, decreasing from 10.27% in the pre-monsoon to 5.63% during the monsoon before increasing slightly to 7.99% in the post-monsoon.

Among the four taxonomic groups, the monsoon season was characterized by a relative decline in the contribution of Copepoda and Protozoa, accompanied by increased proportions of Rotifera and Cladocera. The post-monsoon community showed a partial recovery of copepod dominance, whereas the contribution of rotifers declined relative to the monsoon. These seasonal shifts indicate substantial changes in zooplankton community structure in response to seasonal environmental variability across the Bangladesh coast.

3.3 Zooplankton abundance and taxa richness

Zooplankton abundance exhibited significant seasonal and spatial variation across the Bangladesh coast (Figure 4A and 4B; Table S5). Seasonally, abundance differed significantly among seasons *(F = 87.55, p < 0.001)*, with the highest mean abundance recorded during the post-monsoon (320±24.6 individuals L^{-1}), followed by the pre-monsoon (205±24.6 individuals L^{-1}), whereas the monsoon exhibited the lowest abundance (171±24.6 individuals L^{-1}). Pairwise comparisons indicated significant differences among all three seasons. Spatially, zooplankton abundance also varied significantly among sampling sites (F = 23.88, p < 0.001). The highest abundance was recorded at W5 (399 individuals L^{-1}), followed by W4 (365 individuals L^{-1}) and W3 (337 individuals L^{-1}), whereas the lowest abundance occurred at E1 (94 individuals L^{-1}). Overall, zooplankton abundance was generally higher in the western coastal sites than in the central and eastern coastal sites.

Zooplankton taxa richness also varied significantly with season and sampling site (Figure 4C and 4D). Mean taxa richness was highest during the post-monsoon (31.1±2.0 genera) and pre-monsoon (30.5±2.0 genera), both of which were significantly greater than that recorded during the monsoon (25.9±2.0 genera) ($F = 20.73$, $p < 0.001$). Significant spatial variation in taxa richness was also observed ($F = 27.07$, $p < 0.001$). The highest richness was recorded at W3 (36.0 genera), while richness remained consistently high across the western and central coastal sites (31.7–36.0 genera). In contrast, the eastern coastal sites supported substantially lower richness, ranging from 18.0 genera at E1 and E2 to 21.0 genera at E5.

TABLE 1 Seasonal relative composition of major zooplankton groups and representative genera recorded across the Bangladesh coast.

Taxonomic group	Genera	%		
		Pre-monsoon	Monsoon	Post-monsoon
Protozoa	*Eutintinnus*, *Tintinnopsis*	10.27	5.63	7.99
Rotifera	*Asplanchna*, *Brachionus*, *Colurella*, *Filinia*, *Hexarthra*, *Keratella*, *Lecane*, *Polyarthra*, *Trichocera*	21.68	33.34	26.12
Copepoda	*Acartia*, *Calanopia*, *Calanus*, *Candacia*, *Canthocalanus*, *Centropages*, *Cyclops*, *Diaptomus*, *Eucalanus*, *Euterpina*, *Labidocera*, *Merocyclops*, *Mesocyclops*, *Microcalanus*, *Microsetella*, *Oithona*, *Oncaea*, *Paracalanus*, *Pseudodiaptomus*, *Subeucalanus*, *Temora*, *Tigriopus*	52.71	42.43	48.31
Cladocera	*Alona*, *Bosmina*, *Bosminopsis*, *Chydorus*, *Daphnia*, *Diaphanosoma*, *Evadne*, *Moina*, *Simocephalus*	15.34	18.60	17.59

Note: Values represent the relative abundance (%) of each major zooplankton group within each season. Representative genera are listed for each taxonomic group; detailed genus-level occurrence across seasons and coastal zones is provided in Table S4.

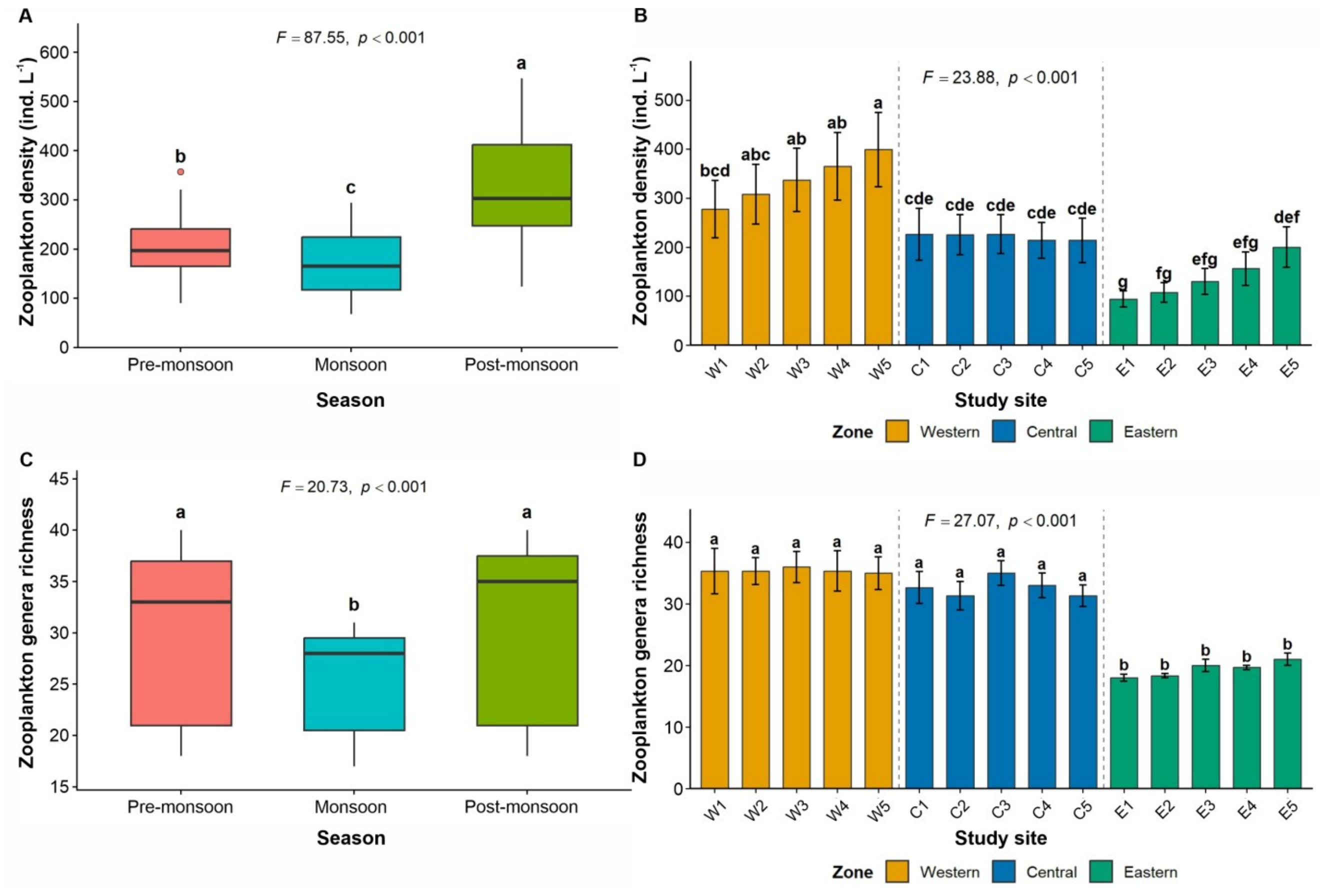

FIGURE 4 Seasonal and spatial variations in zooplankton abundance and taxa richness across the Bangladesh coast. (A, B) zooplankton abundance (individuals L^{-1}) and (C, D) zooplankton genera richness.

3.4 Zooplankton diversity indices

Seasonal and spatial variations in Shannon diversity (*H′*), Margalef richness (*D*), and Pielou's evenness (*J′*) are presented in Figure 5. All three diversity indices varied significantly among seasons and sampling sites. Shannon diversity differed significantly among seasons (F = 4.07, p = 0.028), with the highest mean value recorded during the post-monsoon (2.90±0.58), followed by the pre-monsoon (2.88±0.57), whereas the monsoon exhibited the lowest value (2.80±0.43) (Figure 5A).

Margalef richness also showed significant seasonal variation (F = 8.26, p = 0.002), reaching its highest value during the pre-monsoon (5.55±0.97) and lowest during the monsoon (4.89±0.73) (Figure 5C), while Pielou's evenness was highest during the monsoon (0.861±0.077) and lowest during the pre-monsoon (0.845±0.094) (F = 3.62, p = 0.040; Figure 5E). Significant spatial variation was also observed for Shannon diversity (F = 75.52, p < 0.001), Margalef richness (F = 16.58, p < 0.001), and Pielou's evenness (F = 74.46, p < 0.001) (Figure 5B, 5D and 5F). Shannon diversity ranged from 2.05±0.12 at E1 to 3.32±0.13 at W5, Margalef richness from 3.75±0.18 at E2 to 6.30±0.40 at C3, and Pielou's evenness from 0.684±0.049 at E1 to 0.933±0.011 at W5, with the western and central coastal sites consistently exhibiting higher diversity than the eastern coastal sites.

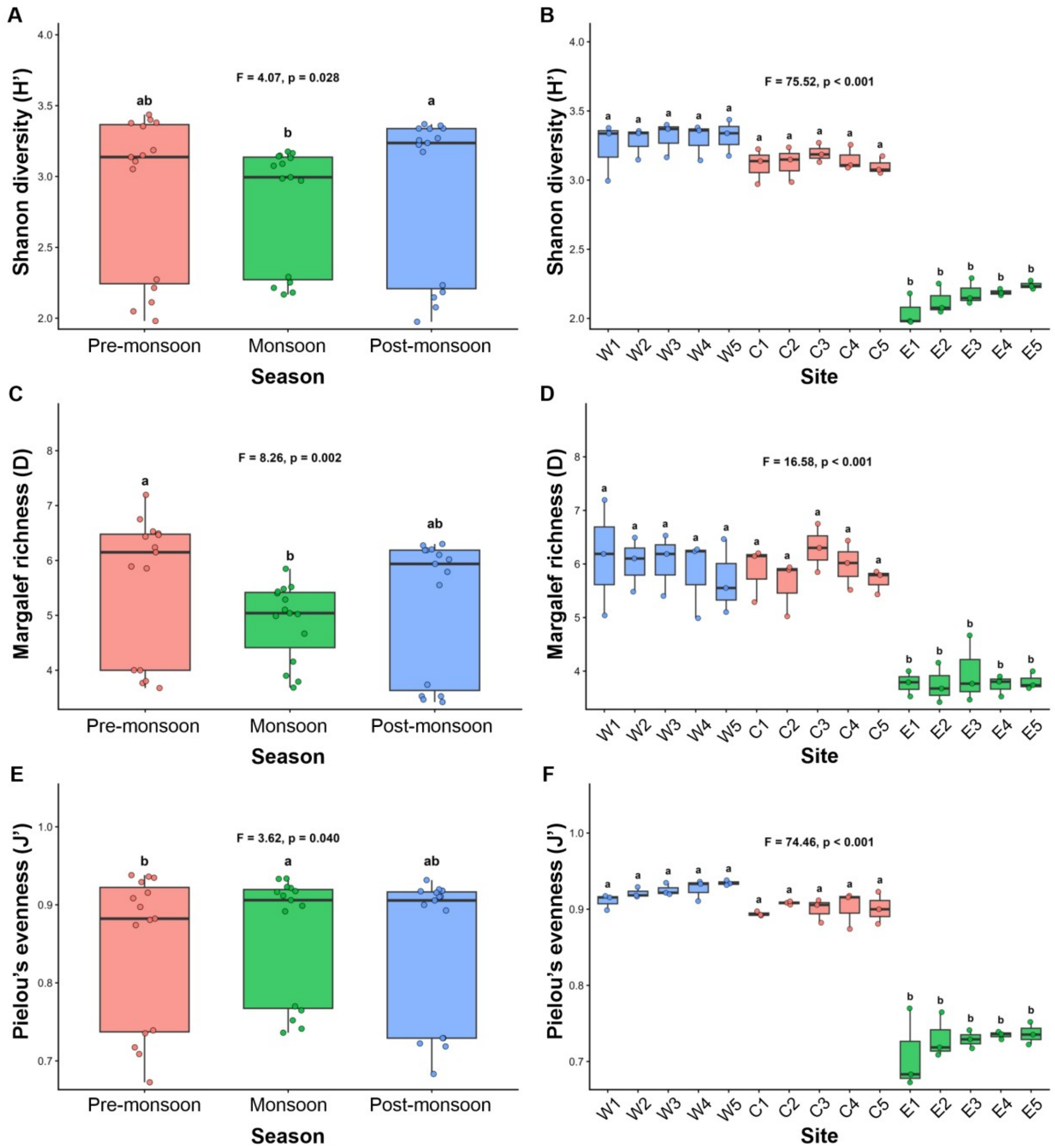

FIGURE 5 Seasonal and spatial variations in zooplankton diversity indices across the Bangladesh coast. (A, B) Shannon diversity (*H′*), (C, D) Margalef richness (*D*), and (E, F) Pielou's evenness (*J′*).

3.5 Relationship between zooplankton and physico-chemical parameters

Redundancy analysis (RDA) revealed a significant relationship between zooplankton community composition and the selected environmental variables (F = 25.48, p < 0.001; adjusted R^2 = 0.796). The first two canonical axes accounted for 94.83% of the constrained variation, with RDA1 and RDA2 explaining 90.35% and 4.48%, respectively (Figure 6). Marginal permutation tests identified TDS (F = 16.06, p < 0.001), Chl-*a* (F = 9.50, p = 0.001), COD (F = 9.43, p < 0.001), temperature (F = 7.61, p = 0.003), DO (F = 5.88, p = 0.011), and salinity (F = 4.93, p = 0.020) as significant environmental variables associated with zooplankton community composition, whereas pH was not significant (F = 2.48, p = 0.103). Pearson correlation analysis showed that salinity was positively correlated with EC (r = 0.70), while weaker-to-moderate correlations were observed between salinity and TDS (r = 0.39) and between TDS and EC (r = 0.65) (Figure S1).

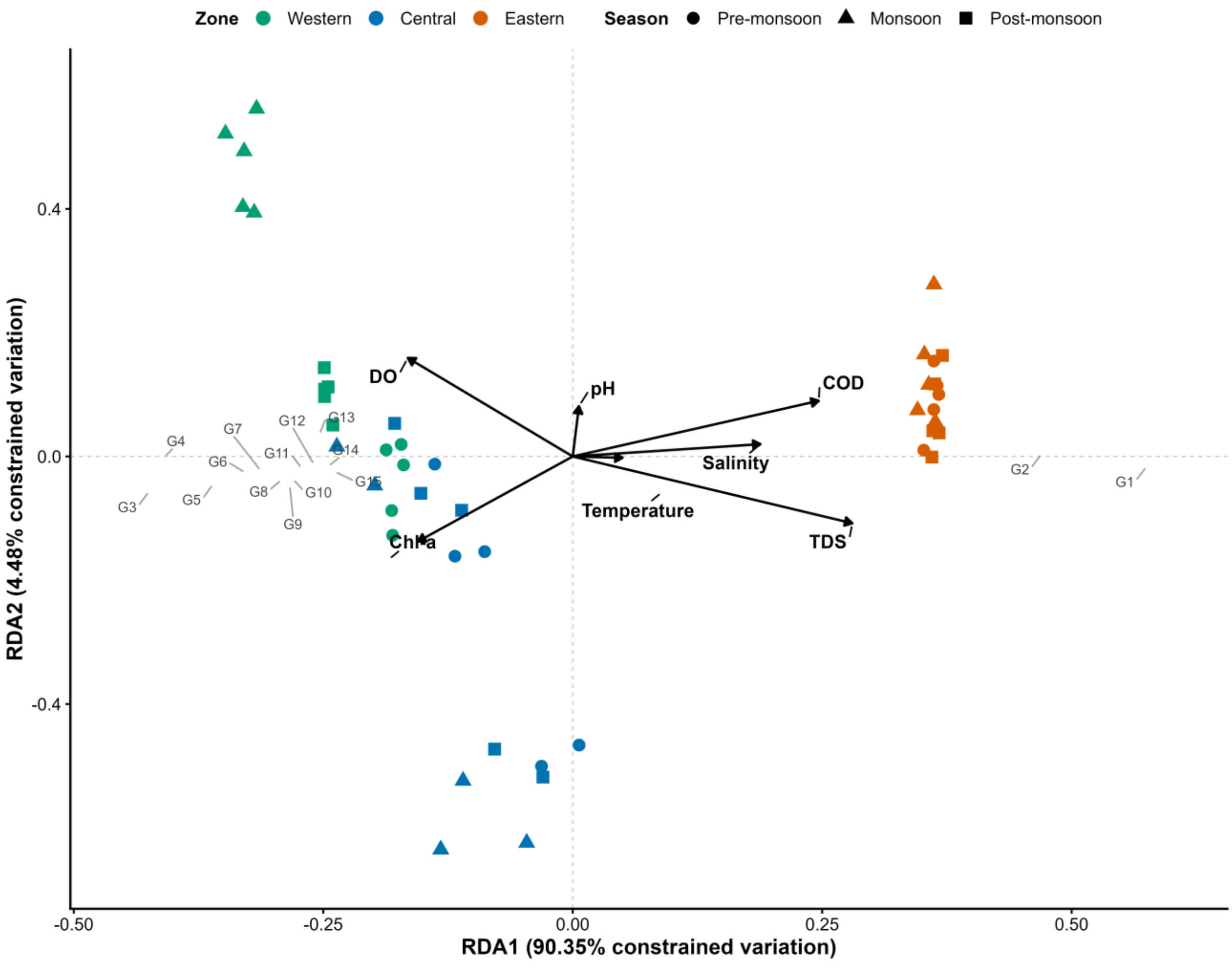

FIGURE 6 Redundancy analysis (RDA) ordination showing relationships between zooplankton community composition and selected environmental variables across the western, central, and eastern coastal zones of Bangladesh. RDA1 and RDA2 explained 90.35% and 4.48% of the constrained variation, respectively. For clarity, the 15 genera with the largest species-score magnitudes across the first two canonical axes are displayed (G1–G15); all 42 genera were retained in the RDA analysis. Genus codes and corresponding identities are provided in Table S6.

Note: Genus codes: G1, *Acartia*; G2, *Oithona*; G3, *Brachionus*; G4, *Bosmina*; G5, *Keratella*; G6, *Daphnia*; G7, *Asplanchna*; G8, *Hexarthra*; G9, *Diaptomus*; G10, *Filinia*; G11, *Alona*; G12, *Cyclops*; G13, *Chydorus*; G14, *Colurella*; and G15, *Polyarthra*. All 42 genera were retained in the RDA analysis; genus codes were used only for visualization.

Partial RDA further showed that salinity retained a significant independent association with zooplankton community composition after controlling for TDS and EC (F = 5.44, p = 0.005; adjusted R^2 = 0.042). TDS showed a stronger independent association after controlling for salinity and EC ($F = 27.06$, $p < 0.001$; adjusted $R^2 = 0.245$), whereas the independent contribution of EC was not significant ($F = 0.88$, $p = 0.395$).

The RDA ordination showed clear spatial separation among coastal zones along RDA1. Eastern-zone samples were positioned predominantly on the positive side of RDA1 and were associated with higher salinity and TDS, whereas western and central samples were distributed mainly on the negative side. Among the 15 genera displayed for visualization, *Acartia* (G1; RDA1 = 0.5761) and Oithona (G2; RDA1 = 0.4708) showed the strongest positive RDA1 scores. In contrast, *Brachionus*, *Bosmina*, *Keratella*, *Daphnia*, *Asplanchna*, *Hexarthra*, *Diaptomus*, *Filinia*, *Alona*, *Cyclops*, *Chydorus*, *Colurella*, and *Polyarthra* had negative RDA1 scores, indicating their association with the opposite side of the principal constrained gradient (Figure 6; Table S6).

3.6 Threshold responses of zooplankton communities along hydrochemical gradients

TITAN revealed distinct community-level responses along the salinity, TDS, EC, and pH gradients, although the direction and magnitude of the thresholds differed among variables (Table S7). Along the salinity gradient, increasing-response taxa (z+) exhibited a community threshold at 8.90 ppt (95% CI: 8.60–10.75 ppt), whereas decreasing-response taxa (z−) showed a threshold at 13.85 ppt (95% CI: 13.05–25.55 ppt), defining a broad community transition zone between approximately 8.9 and 13.9 ppt (Figure 7). TDS showed thresholds at 23.80 mg L^{-1} for increasing taxa and 827.50 mg L^{-1} for decreasing taxa, whereas EC exhibited closely spaced thresholds at 1.90 and 1.80 dS m^{-1} for increasing and decreasing taxa, respectively. For pH, only an increasing-response community threshold was detected, centered at pH 7.00 (95% CI: 6.90–7.10); no robust decreasing-response community threshold was identified. Sensitivity analyses excluding genera occurring in all 45 samples produced nearly identical community thresholds for all four gradients (Table S8), indicating that the identified threshold patterns were not driven by ubiquitous taxa. Taxon-specific threshold analysis identified 31 pure and reliable indicator genera, comprising 13 increasing (z+) and 18 decreasing (z−) indicators (Figure S2). Increasing-response genera exhibited threshold salinities ranging from 4.15 to 17.95 ppt, with *Temora* showing the lowest threshold (4.15 ppt) and *Calanus* the highest (17.95 ppt). In contrast, most decreasing-response genera were concentrated within a relatively narrow salinity range of 13.85–14.65 ppt, including *Brachionus*, *Keratella, Filinia*, *Polyarthra*, *Bosmina*, *Daphnia*, *Cyclops*, and *Pseudodiaptomus*. The strongest indicator responses were recorded for Calanus (median z-score = 7.64), followed by *Asplanchna* (6.57), *Brachionus* (6.49), *Filinia* (6.37), and *Centropages* (6.35).

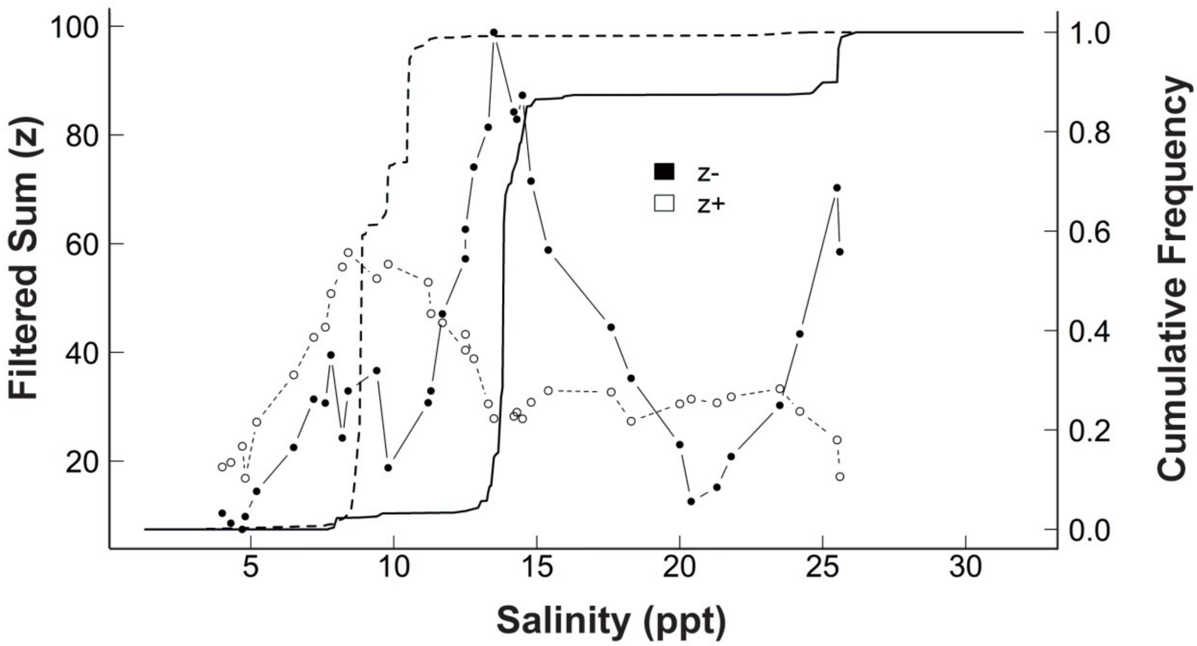

FIGURE 7 Community threshold responses of zooplankton to salinity identified by TITAN. Filled circles (z−) and open circles (z+) represent filtered sum(z) scores for decreasing and increasing taxa, respectively. Solid and dashed curves indicate the cumulative frequency distributions of change points for decreasing (z−) and increasing (z+) taxa. The left y-axis represents the filtered sum(z), and the right y-axis represents the cumulative frequency.

4 | DISCUSSION

4.1 Seasonal and spatial variability of physicochemical parameters

Our results demonstrated pronounced seasonal variation in most hydrochemical parameters, with salinity, electrical conductivity, transparency, and pH reaching their highest values during the pre-monsoon, whereas phosphate, nitrate, chlorophyll-*a*, and dissolved oxygen increased during the post-monsoon. The PCA further showed a clear seasonal separation of samples, indicating that monsoon-driven hydrological processes were the primary drivers of environmental variability across the Bangladesh coast. These findings reflect the seasonal balance between freshwater discharge from the Ganges–Brahmaputra–Meghna (GBM) river system and marine water intrusion from the Bay of Bengal (Sultana *et al*. 2026). During the dry pre-monsoon period, reduced river discharge allows greater seawater intrusion, increasing salinity, electrical conductivity, pH, and water transparency (Rahman *et al*. 2025). In contrast, intense monsoonal runoff dilutes coastal waters and transports large quantities of suspended sediments, reducing salinity, conductivity, and transparency (Shaha *et al*. 2022; Yeasmin *et al*. 2025). Similar hydrochemical responses have been widely reported in tropical estuarine ecosystems where freshwater inflow governs seasonal water quality (Raulo *et al*. 2026).

Unlike salinity-related variables, nutrient concentrations and chlorophyll-*a* exhibited different spatial patterns, with consistently higher chlorophyll-*a* concentrations in the central coastal zone throughout the study. This suggests that phytoplankton production in the Lower Meghna Estuary is sustained by continuous nutrient inputs rather than seasonal nutrient pulses alone. The Lower Meghna receives nutrient-rich freshwater from the GBM basin, while runoff from surrounding agricultural and terrestrial catchments may further enhance nutrient availability in the estuary (Krishna *et al*. 2016; Rahman *et al*. 2025). Although nutrient delivery is greatest during the monsoon, high turbidity and short water residence times restrict phytoplankton growth by limiting light penetration. As turbidity declines after the monsoon, improved light availability and greater water-column stability promote phytoplankton production, contributing to the elevated chlorophyll-*a* and dissolved oxygen concentrations observed during the post-monsoon (Cloern *et al*. 2014).

The marked spatial variation in hydrochemical characteristics further reflects the contrasting hydrographic settings of the three coastal zones. The western coast is dominated by tidal exchange within the Sundarbans estuarine network, the central coast by freshwater discharge from the Lower Meghna Estuary, and the eastern coast by stronger marine influence from the Bay of Bengal (Rahman *et al*. 2025; Yeasmin *et al*. 2025). These contrasting hydrological conditions generated the environmental gradients identified by both the univariate analyses and PCA, particularly along the salinity axis, providing the physicochemical framework that subsequently shaped zooplankton community composition across the Bangladesh coast (Telesh and Khlebovich 2010; Cloern *et al*. 2017).

4.2 Seasonal dynamics of zooplankton community composition

Our results showed that Copepoda consistently dominated the zooplankton community (42.4–52.7%) throughout the study, whereas Rotifera, Cladocera, and Protozoa contributed comparatively smaller proportions. The predominance of copepods is characteristic of tropical estuarine and coastal ecosystems because of their broad salinity tolerance, high reproductive capacity, and ability to efficiently exploit available phytoplankton resources under fluctuating environmental conditions (Mauchline 1998; Turner 2004). The widespread occurrence of dominant genera such as *Acartia*, *Oithona*, and *Paracalanus* across all three coastal zones further indicates their adaptation to the dynamic hydrographic conditions of the Bangladesh coast. Similar copepod dominance has been reported from the Bay of Bengal and other tropical estuarine ecosystems (Bhattacharya *et al*. 2015; Ezhilarasan *et al*. 2025).

Despite the overall dominance of copepods, our results revealed a relative increase in Rotifera and Cladocera during the monsoon, followed by recovery of copepod dominance in the post-monsoon. This seasonal succession is likely driven by monsoon-induced reductions in salinity and increased nutrient availability, which favor the rapid reproduction and short generation times of many freshwater-associated rotifers and cladocerans (Segers 2008). As freshwater influence declines during the post-monsoon, increasing salinity and improved water quality favor the re-establishment of marine and estuarine copepods, resulting in the observed recovery of copepod dominance (Telesh and Khlebovich 2010). Similar seasonal shifts in zooplankton community composition have been documented in estuaries strongly influenced by monsoonal hydrology (Jiarui *et al*. 2025).

Our study also demonstrated that zooplankton abundance, taxa richness, and diversity were consistently higher in the western and central coastal zones than in the eastern coast, with maximum values occurring during the post-monsoon. These patterns likely reflect greater habitat heterogeneity and nutrient availability associated with the Sundarbans and Lower Meghna estuarine systems, which support higher primary productivity and a wider range of ecological niches (Rahaman *et al*. 2013). In contrast, the eastern coastal zone supported comparatively lower abundance and diversity, which corresponded with the higher salinity conditions identified in the hydrochemical analyses and RDA. In addition, the eastern coast of Bangladesh, particularly the Chattogram–Sitakunda coastal region, is exposed to multiple anthropogenic pressures associated with industrial activities, port operations, urban discharges, and extensive shipbreaking activities, which can introduce metals, oils, organic contaminants, and other pollutants into adjacent coastal environments (Rahman *et al*. 2024, 2025, 2026). Although these stressors were not directly evaluated in the present study, they may have contributed to the comparatively lower zooplankton abundance and diversity observed in the eastern coastal zone. Overall, these findings indicate that both natural hydrological variability and anthropogenic pressures jointly influence the seasonal and spatial dynamics of zooplankton communities along the Bangladesh coast.

4.3 Relationship between zooplankton and physicochemical parameters

The RDA demonstrated a strong association between zooplankton community composition and the measured hydrochemical gradients, with TDS, COD, Chl-*a*, temperature, DO, and salinity showing significant marginal associations in the selected model. The first two canonical axes accounted for 94.83% of the constrained variation, indicating that the major species–environment relationships represented by the selected RDA model were concentrated primarily along RDA1. Among these variables, salinity represented a particularly important ecological gradient, as the clear separation of sampling sites along RDA1 corresponded closely with the freshwater-to-marine transition across the Bangladesh coast. However, the partial RDA indicated that this salinity-associated pattern should not be interpreted as evidence that salinity was the strongest independent predictor. Salinity retained a significant independent association with community composition after accounting for TDS and EC (adjusted R^2 = 0.042, p = 0.005), whereas TDS exhibited a substantially larger unique contribution (adjusted R^2 = 0.245, p < 0.001). EC showed no significant independent contribution after controlling for salinity and TDS (p = 0.395). Thus, salinity represents an ecologically meaningful freshwater-to-marine gradient, while TDS showed the strongest independent association among these three related dissolved-ion variables. This pattern reflects the contrasting influence of freshwater discharge and marine water intrusion on zooplankton assemblages (Hossain *et al*. 2026; Monwar *et al*. 2026). The importance of the salinity gradient was further supported by the PCA and TITAN analyses, with TITAN identifying a community transition around 8.9–13.9 ppt. Salinity is widely recognized as a major environmental filter in estuarine ecosystems because it affects osmoregulation, physiological performance, reproduction, and habitat suitability of zooplankton (Telesh and Khlebovich 2010). Similar salinity-associated community patterns have been reported in tropical and temperate estuaries worldwide (Röthig *et al*. 2023; de Lima and Pessanha 2024).

The RDA ordination showed that *Acartia* and *Oithona* were strongly associated with the positive side of RDA1 and the more saline eastern coastal zone. These genera are characteristic estuarine and coastal copepods with relatively broad salinity tolerance (Ezhilarasan *et al*. 2021). In contrast, several freshwater and euryhaline genera, including *Brachionus*, *Keratella*, *Polyarthra*, *Bosmina*, *Daphnia*, and *Cyclops*, were positioned toward the lower-salinity western and central zones (Table S6). This distribution is consistent with differences in salinity tolerance among zooplankton taxa and the greater freshwater influence in riverine and estuarine habitats (Telesh and Khlebovich 2010). Comparable transitions from freshwater rotifers and cladocerans toward marine copepod assemblages along increasing salinity gradients have been documented in other estuarine ecosystems (de Lima and Pessanha 2024). Besides salinity, TDS, COD, Chl-*a*, temperature, and DO were significantly associated with variation in zooplankton community composition in the selected RDA model. Among these variables, TDS showed the strongest marginal association and also retained the largest independent contribution in the partial RDA examining salinity, TDS, and EC. Elevated TDS reflects increased concentrations of dissolved ions associated with marine intrusion and can influence water density, feeding efficiency, and habitat suitability for planktonic organisms (Liu *et al.* 2025). Chlorophyll-*a* represents phytoplankton biomass and thus potential food availability for zooplankton, whereas DO, temperature, and COD characterize additional aspects of water quality and metabolic conditions that may contribute to community differentiation (Bouquet *et al*. 2018). Collectively, these results indicate that zooplankton community composition was associated with multiple interacting hydrochemical gradients rather than with a single environmental variable.

Overall, the RDA indicates that zooplankton community composition across the Bangladesh coast is strongly associated with multiple hydrochemical gradients. Although TDS showed a stronger independent association than salinity in the partial RDA, salinity remained independently significant and represented an ecologically meaningful freshwater-to-marine gradient. Together with the PCA and TITAN results, these findings highlight salinity as an important environmental correlate of spatial variation in coastal zooplankton assemblages, while avoiding attribution to a single environmental driver. These patterns further support the potential use of zooplankton as sensitive biological indicators of environmental change in tropical estuarine and coastal ecosystems (Dehingia *et al*. 2026).

4.4 Ecological significance of salinity thresholds

Comparative TITAN analysis revealed nonlinear zooplankton community responses along salinity, TDS, EC, and pH gradients, although the threshold patterns differed among environmental variables. Salinity showed distinct community change points for increasing- and decreasing-response taxa at 8.90 and 13.85 ppt, respectively, defining a community transition zone of approximately 8.9–13.9 ppt. EC showed closely spaced community thresholds near 1.8–1.9 dS m^{-1}, while TDS also exhibited community-level change points but with greater uncertainty in the location of the increasing-response threshold. In contrast, pH exhibited only an increasing-response community threshold near 7.0, with no robust decreasing-response threshold detected. These contrasting responses indicate that zooplankton community turnover was associated with multiple hydrochemical gradients rather than with salinity alone.

Among these gradients, salinity provides a particularly ecologically interpretable representation of the freshwater-to-marine continuum across the study area. The community transition across a salinity range of approximately 8.9–13.9 ppt complements the RDA results, in which salinity retained a significant independent association with community composition despite the stronger independent contribution of TDS. Thus, the TITAN results should not be interpreted as evidence that salinity is the sole or strongest environmental driver, but rather that it represents an ecologically meaningful gradient along which substantial taxonomic turnover was observed. Similar nonlinear responses have been reported in estuarine ecosystems, where relatively small changes in salinity can produce disproportionate changes in biological communities once species-specific physiological tolerance limits are exceeded (Han and Han 2024; McKenzie *et al*. 2024).

The salinity transition identified in the present study is broadly consistent with community changes reported from other Asian estuarine systems, although direct quantitative comparisons are limited because previous studies generally used different analytical approaches. Across tropical Indian estuaries, Venkataramana *et al*. (2023) reported marked differences in zooplankton assemblages among oligohaline, mesohaline, and polyhaline conditions, demonstrating substantial community turnover along the freshwater-to-marine salinity gradient. Comparable spatial replacement of freshwater-associated rotifers and cladocerans by copepod-dominated assemblages toward more saline waters has also been reported from Asian estuarine systems. These regional observations support the broader ecological pattern of salinity-associated zooplankton turnover, while the 8.9–13.9 ppt transition identified in the present study provides a system-specific quantitative estimate for the Bangladesh coast.

The contrasting responses of indicator taxa further illustrate community reorganization along the salinity gradient. Marine copepods, including *Acartia*, *Oithona*, *Paracalanus*, *Temora*, and *Calanus*, responded positively to increasing salinity, whereas freshwater-associated taxa such as *Brachionus*, *Keratella*, *Polyarthra*, *Bosmina*, *Daphnia*, and *Lecane* declined across the salinity gradient. These contrasting responses reflect differences in osmoregulatory capacity, reproductive performance, and ecological tolerance, which may influence taxon persistence and distribution along the freshwater–marine continuum (Dildar *et al*. 2025). Similar salinity-driven species replacement has been documented in estuarine zooplankton communities worldwide (de Lima and Pessanha 2024).

The identified salinity transition zone has important implications for the management of coastal ecosystems in Bangladesh. Future changes in freshwater discharge, sea-level rise, altered monsoon intensity, and increasing salinity intrusion are expected to modify estuarine salinity regimes (Calvin *et al*. 2023). Such changes could alter the position of this community transition zone and favor shifts between freshwater-, estuarine-, and marine-associated assemblages, with potential consequences for trophic interactions, fish recruitment, and ecosystem functioning (Camatti *et al*. 2023). Therefore, 8.9–13.9 ppt salinity transition zone identified in this study provides a quantitative ecological benchmark for long-term biomonitoring and adaptive management of the Bangladesh coast under increasing climatic and anthropogenic pressures, while the additional TDS, EC, and pH thresholds demonstrate that zooplankton responses occur across multiple, interrelated hydrochemical gradients.

4.5 Ecological implications and management perspectives

The present study demonstrates that seasonal hydrochemical variability, including the freshwater-to-marine gradient represented by salinity and related dissolved-ion variables, is strongly associated with zooplankton community composition across the Bangladesh coast. By integrating hydrochemical analyses with PCA, RDA, and TITAN, this study identified key environmental correlates of community composition and quantified a critical salinity transition zone associated with zooplankton community turnover. This integrated approach provides a more comprehensive understanding of ecosystem responses than conventional diversity assessments alone and highlights the value of combining multivariate and threshold analyses for evaluating ecological change in tropical estuarine and coastal ecosystems (Baker and King 2010; King and Baker 2010).

Zooplankton occupy a pivotal position in aquatic food webs, linking primary producers with higher trophic levels, and their rapid response to environmental fluctuations makes them sensitive indicators of ecosystem health. The salinity threshold identified in this study therefore provides a practical ecological benchmark for long-term biomonitoring of the Bangladesh coast. As climate change, sea-level rise, altered freshwater discharge, coastal urbanization, industrial development, and port activities continue to modify estuarine environments, shifts in salinity regimes are likely to alter zooplankton community composition and, consequently, ecosystem functioning (Calvin *et al*. 2023; Bhattacharjee *et al*. 2025). Incorporating zooplankton-based indicators and salinity thresholds into routine coastal monitoring programs could improve the early detection of ecological change and support evidence-based management strategies aimed at maintaining biodiversity and ecosystem resilience in the northern Bay of Bengal.

One limitation of the present study is that sampling was not standardized to a specific tidal phase because multiple geographically separated sites were surveyed within each seasonal sampling campaign. Consequently, short-term tidal variability may have contributed to some of the observed variation in salinity and other hydrochemical parameters. Future studies incorporating tide-standardized or repeated tidal-cycle sampling would help distinguish short-term tidal effects from broader spatial and seasonal patterns.

5 | CONCLUSIONS

This study provides a comprehensive scenario of the seasonal and spatial dynamics of hydrochemical conditions and zooplankton communities across the Bangladesh coast by integrating hydrochemical characterization, multivariate ordination, and threshold indicator analysis. Pronounced monsoon-driven environmental gradients were associated with marked variation in zooplankton assemblages across the Bangladesh coast. RDA identified TDS, chlorophyll-*a*, COD, temperature, DO, and salinity as significant environmental correlates of community composition, while partial RDA showed that TDS had a stronger independent association than salinity among the closely related salinity–TDS–EC variables. Nevertheless, salinity remained independently significant and represented an ecologically meaningful freshwater-to-marine gradient. Comparative TITAN analyses further revealed nonlinear community responses along salinity, TDS, EC, and pH gradients. Salinity showed distinct community change points for increasing- and decreasing-response taxa at 8.90 and 13.85 ppt, respectively, defining an ecologically interpretable community transition zone of approximately 8.9–13.9 ppt. EC showed closely spaced thresholds near 1.8–1.9 dS m^{-1}, while TDS also exhibited community-level change points, although the increasing-response threshold was associated with greater uncertainty. In contrast, pH showed only an increasing-response community threshold near 7.0. These findings indicate that zooplankton community turnover was associated with multiple, interrelated hydrochemical gradients rather than with a single environmental factor, while salinity provided a particularly meaningful ecological axis for interpreting freshwater-to-marine taxonomic turnover. The salinity transition zone provides a quantitative ecological benchmark for detecting community-level responses to environmental change. Collectively, these findings improve our understanding of the hydrochemical gradients associated with variation in zooplankton communities in tropical estuarine and coastal ecosystems and demonstrate the value of integrating hydrochemical analyses with multivariate and threshold approaches. The identified hydrochemical thresholds, particularly the ecologically interpretable salinity transition zone, together with the associated indicator taxa, provide a scientific basis for long-term biomonitoring, biodiversity conservation, and adaptive management of the Bangladesh coast under increasing climatic and anthropogenic pressures.

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ETHICAL APPROVAL

All applicable international, national and/or institutional guidelines for the care and use of animals were followed in this study.

CONFLICT OF INTEREST

The author declares no conflict of interest.

AUTHORS' CONTRIBUTION

Syeda Maksuda Yeasmin: Writing – Original draft, Validation, Methodology, Investigation and Formal analysis. Md Habibur Rahman: Conceptualization, Writing – Original draft, Methodology, Funding acquisition, Formal analysis, and Data curation. Mamun Abdullah Al: Writing – Review & editing and Resources. Md. Abu Kawsar: Writing – Review & editing and Resources. Syed Tanvir Woalid: Formal analysis, Data curation and Conceptualization. Rion Islam Fardin: Resources, Software, Visualization and Investigation. Md. Hasan: Software, Investigation and Data curation.

AI-USE STATEMENT

During the preparation of this work, the authors used ChatGPT (OpenAI) to assist with language editing, grammatical improvement, and improving the clarity and readability of the manuscript. The authors reviewed and edited the output as needed and take full responsibility for the content of the published article.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on a reasonable request from the corresponding author.

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