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Seasonal patterns and environmental drivers of gastropod distribution in southeastern Bangladesh

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ABSTRACT

Gastropods serve as important indicators of biodiversity in coastal ecosystems, fulfilling critical ecological roles. This study comprehensively assessed gastropod diversity across three southeastern coastal islands of Bangladesh (Kutubdia, Moheskhali, and Sonadia) and examined its relationship with seasonal environmental factors. We documented 144 gastropod species from 65 genera, 28 families, and 3 orders. Monthly *in-situ* measurements of key environmental variables—including salinity, temperature, dissolved oxygen, nutrient concentrations, and suspended/dissolved solids—revealed marked seasonal fluctuations. For example, the monsoon season featured high total suspended solids alongside low salinity and total dissolved solids, whereas the post-monsoon period exhibited peak temperature and pH levels. Gastropod species richness varied significantly across seasons, peaking in winter and pre-monsoon. Principal Component Analysis identified salinity and total dissolved solids as primary environmental drivers influencing gastropod abundance and community composition. Generalised Linear Mixed Models confirmed that elevated salinity and total dissolved solids were major determinants of species richness, particularly enhancing it during winter. Additionally, species composition displayed pronounced seasonal shifts, with distinct assemblages characterising the post-monsoon period. Indicator species analysis highlighted *Oliva* sp. as a key indicator of the post-monsoon season and *Umbonium* sp. for winter assemblages. Our findings underscore that gastropod diversity in southeastern Bangladesh is intricately shaped by dynamic seasonal environmental changes. Understanding these patterns is critical for advancing knowledge of coastal ecosystem dynamics and for guiding conservation efforts in this climate-sensitive region. Several edible gastropods were documented—e.g., *Littorina undulata*, *Umbonium* spp. (*U. vestiarium*), *Telescopium*, and *Babylonia* spp.—which were locally abundant at multiple study sites. These species play important functional roles and are economically significant, contributing to food security and coastal livelihoods.

1. Introduction

Gastropods are among the most diverse groups of molluscs, with an estimated 40,000 to 76,000 species distributed across marine, freshwater, and terrestrial environments. With diverse feeding strategies—including herbivory, predation, and parasitism—gastropods play pivotal roles in both intertidal and subtidal ecosystems (Coleman et al., 2006). Their sensitivity to environmental fluctuations, particularly in intertidal zones, makes them valuable bioindicators for assessing ecological responses to environmental change, including those induced by climate change (Rubal et al., 2013).

Environmental factors such as temperature, salinity, dissolved oxygen, and nutrient concentrations are known to drive patterns of gastropod distribution and abundance (Zeybek et al., 2012; Savić et al., 2016). Studies have shown that molluscan distributions are often constrained by specific environmental conditions and thresholds (Maltchik et al., 2010; Dillon, 2000). For instance, intertidal gastropods display varying tolerances to salinity, pH, and temperature fluctuations, which

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in turn influence their survival, reproductive success, and community structure and composition (Underwood, 1980; Sørensen and Surlyk, 2011). Nutrient dynamics—including nitrate, nitrite, and phosphate availability—can influence directly primary productivity and food web structure supporting gastropod populations, while excessive nutrient input may trigger eutrophication and habitat degradation (Wang et al., 2022; Smith et al., 2006).

Climate-induced rises in sea surface temperatures (SSTs) are rapidly transforming marine ecosystems globally, with the Bay of Bengal—this study's focal region—among the most affected (Lima and Wethey, 2012; Burrows et al., 2011). In addition, the Bay experiences strong monsoon seasonality and substantial riverine inflows, resulting in pronounced variations in salinity, turbidity, and sedimentation—key environmental filters for intertidal communities (Unger et al., 2003; Brewer et al., 2015).

Despite the established ecological importance of molluscs, spatial and seasonal patterns of gastropod diversity in Bangladesh's coastal regions remain underexplored. Past studies in the Bay of Bengal have primarily focused on broad ecological surveys or isolated taxonomic inventories (Ahmed, 1990; Siddique et al., 2007), with limited attention given to the influence of environmental factors in shaping gastropod communities. This research gap highlights the need for comprehensive studies that link environmental variability and spatial and seasonal patterns of gastropod diversity.

This study seeks to fill that gap by examining seasonal distribution patterns of gastropods along the southeastern coastal islands of Bangladesh and exploring their relationships with key physicochemical parameters. By identifying the environmental drivers of gastropod species richness and community structure, this research aims to enhance our understanding of molluscan biodiversity under dynamic environmental conditions and to inform conservation strategies for coastal ecosystems in Bangladesh.

2. Materials and methods

2.1. Study area

The study was conducted on three coastal islands in southeastern Bangladesh (Fig. 1): Kutubdia (21.8167°N, 91.8583°E), Moheskhali (21.653175°N, 91.998628°E), and Sonadia (21.4879°N, 91.8798°E). These islands represent distinct coastal ecosystems, each characterised by unique geomorphological and ecological features. Kutubdia is characterised by sandy-muddy beaches and extensive mangrove plantations, interspersed with patches of natural salt marshes. In contrast, Moheskhali is dominated by muddy beaches and dense mangrove vegetation along the nearshore zone, contributing to significant sediment deposition. Sonadia, the smallest of the three, features sandy beaches and prominent sand dunes lining both shores.

These ecosystems are significantly influenced by human activities. Deep-sea fishing and sea salt production are common across all three islands. Kutubdia and Moheskhali, in particular, host well-established salt production sites that play a vital socio-economic role in local communities.

2.2. Sampling

Each island was designated as a sampling station: Station 1 (Kutubdia), Station 2 (Moheskhali), and Station 3 (Sonadia). At each station, three fixed sites were selected along the intertidal zone to ensure spatial representation and monitored across all four seasons to capture spatial

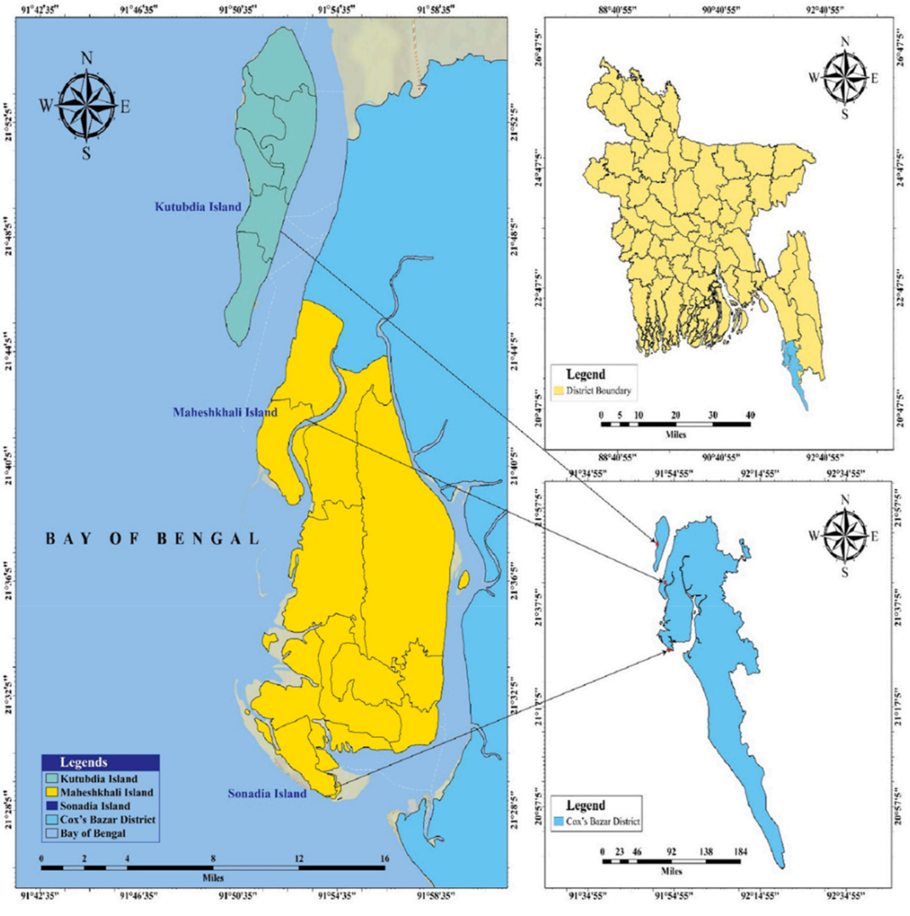

Fig. 1. Map of the southeastern coastal zone of Bangladesh showing the sampling sites: (a) Kutubdia Island, (b) Moheskhali Island, and (c) Sonadia Island.

and temporal variability. While the stations differ in geomorphology and ecological context (e.g., sandy–muddy substrates at Kutubdia, mangrove-dominated shores at Moheskhali, and sandy dunes at Sonadia), stations were included as random effects in the statistical model to account for local variation. The distances between islands were 53.2 km (Kutubdia–Moheskhali), 74.1 km (Kutubdia–Sonadia), and ~14 km (Moheskhali–Sonadia), while the three fixed sites within each island were separated by ~2–3.5 km in Kutubdia, ~1–2.5 km in Sonadia, and ~2–6 km in Moheskhali, ensuring adequate spatial coverage of intertidal habitats.

Sampling was conducted monthly from January to December 2013, and timed to coincide with the new moon periods. This timing was informed by local fishermen's observations, which indicated increased mollusc activity and accessibility during these phases—likely due to tidal influences. This approach is supported by the literature, which suggests that lunar cycles, particularly new moons, can influence mollusc behaviour and density (Chapman et al., 2011; Nishida et al., 2006).

Sampling occurred during low tide on three consecutive days each month, following tidal charts to maintain consistency and maximise specimen availability. Data collection was carried out across four climatic seasons—winter, pre-monsoon, monsoon, and post-monsoon—defined by the annual reversal of the South Asian wind circulation system (Shahid and Khairulmaini, 2009; Shahid, 2010, 2012; Khan et al., 2019). Monthly samples were grouped into seasonal categories: winter (December–February), pre-monsoon (March–May), monsoon (June–September), and post-monsoon (October–November). Independent climatological records, such as Weather Atlas (https://www.weather-atlas.com/) or WeatherAPI (https://www.weatherapi.com), confirm that December already reflects winter conditions in the study region, with temperatures and rainfall closely resembling those of January–February. Accordingly, December 2013 was grouped with January–February as winter in our analyses.

2.3. Mollusc identification

Each month, 10 % of the gastropod catch at each site was collected for analysis. Sampling was consistently conducted at the fixed sites throughout the year to ensure representative data. This standardised '10 % catch sampling method' enabled both sustainable sampling and reliable population-level insights. Individuals were chosen randomly, ensuring that each had an equal chance of inclusion and that the subset was representative of the monthly catch. To assess the adequacy of the 10 % subsample, individual-based rarefaction analyses were conducted across sites and seasons. Rarefaction curves (Fig. S1) reached an asymptote, indicating that the 10 % subsample adequately captured the species pool.

Specimens were transported to the Institute of Marine Sciences (IMS) at the University of Chittagong for further examination. In the laboratory, they were rinsed with tap water to remove debris and separated into live and dead individuals. Live specimens were preserved in either 4 % formalin or 90 % alcohol/rectified spirit, following Tan and Chou's (2000) methodology. Dead shells were stored separately for taxonomic identification and cataloguing.

Species were identified using authoritative taxonomic keys and monographs, including Patil et al. (2012), Khade and Mane (2012), Siddique et al. (2007), Abbott and Dance (2000), and Ahmed (1990). Taxonomic validation was further supported by additional literature (see supplementary references), online databases such as the World Register of Marine Species (WoRMS) and the Worldwide Mollusc Species Database (WMSDB). All specimens were meticulously catalogued and archived at the IMS museum for future reference and research.

2.4. Physicochemical parameters

Physicochemical parameters were measured monthly at each sampling site to characterise environmental conditions influencing gastropod distribution. The variables measured included: water temperature, salinity, pH, dissolved oxygen (DO), nitrite (NO_2-N), phosphate (PO_4-P), nitrate (NO_3-N), total suspended solids (TSS), total dissolved solids (TDS), and water transparency.

Water temperature was measured with a mercury thermometer (0–100 °C range). Salinity was determined using a calibrated refractometer (NewS-100, TANAKA, Japan). pH was measured with a digital pH pen meter (HANNA Instruments, model HI 98107). Dissolved oxygen was quantified using the Winkler titration method, a widely accepted technique in marine environments (Grasshoff et al., 1999; UNESCO, 1988). Total dissolved solids were measured with an electro-conductivity meter (HANNA Instruments, model EC 98107). Nitrite, phosphate, and nitrate concentrations were determined using spectrophotometric methods, while total suspended solids were assessed via a gravimetric method at the Institute of Marine Sciences (Miranda et al., 2001; Narayana and Sunil, 2009; Xia et al., 2004). Water transparency was measured using a Secchi disk, providing reliable estimates of water clarity at each station.

2.5. Data analysis

All statistical analyses were conducted in R (v4.4.1), and figures were generated using the "ggplot2" package (Wickham, 2016).

2.5.1. Species richness estimation and PCA of physicochemical parameters

Alpha diversity, measured as species richness, was estimated from the abundance data collected at each sampling station using the 'specnumber' function from the "vegan" package (v2.5-7; Oksanen et al., 2020).

To explore the relationship between gastropod diversity and environmental conditions, a Principal Component Analysis (PCA) was performed. Physicochemical parameters were standardised using z-scores to normalise for differences in units. PCA was conducted using the 'prcomp' function from the "stats" package (v4.1.2; R Core Team, 2021). The Broken-stick criterion (Jackson, 1993) was applied to determine the number of principal components that explained a significant proportion of the variance and should be retained for subsequent analysis.

2.5.2. Seasonal variation in species richness

Seasonal variation in species richness was analysed using a Generalised Linear Mixed Model (GLMM) implemented in the "lme4" package (v1.1–27.1; Bates et al., 2015), with a Poisson distribution appropriate for count data.

Given that species richness data are often overdispersed (i.e. variance exceeds the mean), overdispersion was assessed by examining the ratio of residual deviance to residual degrees of freedom. This was confirmed using the 'check_overdispersion' function from the "DHARMa" package, which indicated no significant overdispersion (dispersion ratio $= 0.553$, $p = 0.136$).

Sampling stations were treated as random effects to account for repeated measures and spatial autocorrelation, while seasonal categories (winter, pre-monsoon, monsoon, and post-monsoon) and PCA scores were included as fixed effects. The inclusion of PCA scores allowed the evaluation of indirect environmental effects while minimising multicollinearity from testing individual physicochemical variables.

The significance of fixed effects was tested using a Wald Chi-square test ('Anova' function, "car" package, v3.0-12; Fox and Weisberg, 2019), with a significance threshold set at $p < 0.05$. To determine which specific seasons significantly differed in terms of species richness, pairwise seasonal comparisons were performed using Tukey's post-hoc tests ('glht' function, "multcomp" package, v1.4-18; Hothorn et al., 2008), with adjustments for multiple testing using the Tukey correction.

2.5.3. *Community composition and beta-diversity*

Seasonal differences in gastropod community composition were analysed using Permutational Multivariate Analysis of Variance (PERMANOVA) based on Bray–Curtis dissimilarities, via the ‘adonis’ function in “vegan” (Oksanen et al., 2020). A total of 999 permutations were performed, with sampling stations used as strata to account for spatial structure. PCA scores were included as covariates to evaluate the influence of environmental gradients. Post-hoc pairwise comparisons between seasons were conducted with the ‘pairwise.adonis’ function (“vegan” package), with Bonferroni correction applied to adjust for multiple comparisons.

To visualise seasonal differences in community composition, Non-metric Multidimensional Scaling (NMDS) was used (‘metaMDS’ function, “vegan” package). Beta-diversity was further assessed through a multivariate dispersion analysis, measuring the distance of each community to its group centroid (‘betadisper’ function). Homogeneity of group dispersions was tested via 999 permutations. This analysis distinguished between shifts in community structure (differences in centroids) and within-group variability (dispersion).

2.5.4. *Indicator species*

Indicator species associated with each season or seasonal combination were identified using the ‘multipatt’ function from the “indicspecies” package (v1.7.12; Caceres and Legendre, 2009). Two metrics were computed: specificity (A), indicating the probability that a species occurs exclusively in a given season; fidelity (B), reflecting the probability of encountering the species consistently within that season. The statistical significance of indicator values was tested using 999 permutations to validate species-season associations.

3. Results

3.1. *Species richness and physicochemical parameters*

A total of 144 gastropod species were identified, encompassing 65 genera, 28 families, and 3 orders across the three sampling stations (Fig. 1; Table S1). Rarefaction analyses confirmed that the 10 % subsample was sufficient to capture gastropod species richness, with curves reaching asymptotes across stations (Fig. S1). This indicates that the subsampling design was adequate to represent community composition without oversampling. The family *Trochidae* exhibited the highest species richness, while other families—such as *Fissurellidae*, *Buccinidae*, *Bursidae*, *Littorinidae*, *Ovulidae*, *Tonnidae*, *Bullidae*, and *Melongenidae*—were represented by fewer species.

Seasonal variations in physicochemical parameters are summarised in Table S2 and visualised in Fig. 2. Elevated levels of total suspended solids (TSS) characterised the monsoon season, accompanied by minima in salinity, total dissolved solids (TDS), and nitrite (NO_2-N). During the post-monsoon period, both water temperature and pH peaked, while nitrate (NO_3-N) reached its lowest concentration. The pre-monsoon season was marked by the lowest levels of temperature, pH, phosphate (PO_4-P), and NO_2-N, without marked increases in other parameters. In winter, salinity, TDS, NO_3-N, NO_2-N, and PO_4-P were elevated, whereas dissolved oxygen (DO) and TSS were comparatively lower.

Species richness displayed both spatial and temporal variation (Fig. 3). Station 1 (Kutubdia) consistently exhibited the highest richness, followed by Station 2 (Moheskhali), while Station 3 (Sonadia) consistently recorded the lowest diversity. Seasonally, richness peaked during winter and declined in the post-monsoon period at Stations 1 and 2. Conversely, Station 3 exhibited highest richness during pre-monsoon and lowest richness during the monsoon.

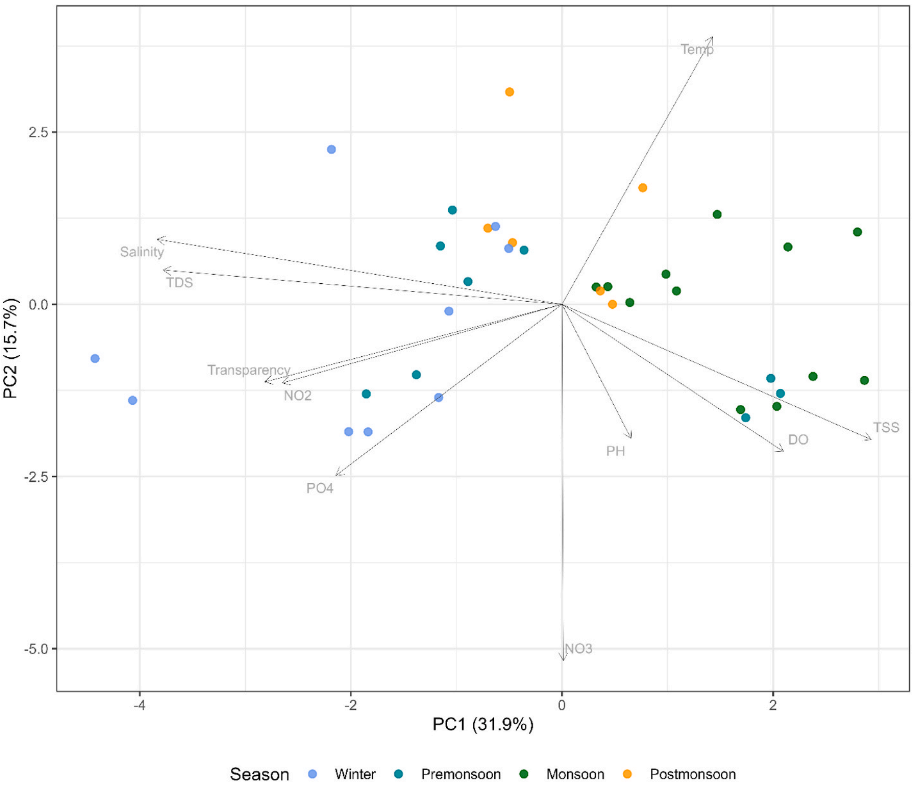

Fig. 2. Biplot of the Principal Component Analysis (PCA) performed on physicochemical parameters, illustrating variable loadings (arrows) and sample scores (points) across seasons (sample size = 36; variables = 10). The first two principal components (PC1 and PC2) explain 31.9 % and 15.7 % of the total variance, respectively, accounting for 47.6 % cumulatively. Arrows represent the direction and strength of the contribution of individual variables: salinity, total dissolved solids (TDS), temperature, pH, dissolved oxygen (DO), total suspended solids (TSS), nitrate (NO_3-N), phosphate (PO_4-P), nitrite (NO_2-N), and transparency. Sampling events are represented by points, colour-coded by season: Blue (winter), Teal (pre-monsoon), Green (monsoon), and Orange (post-monsoon).

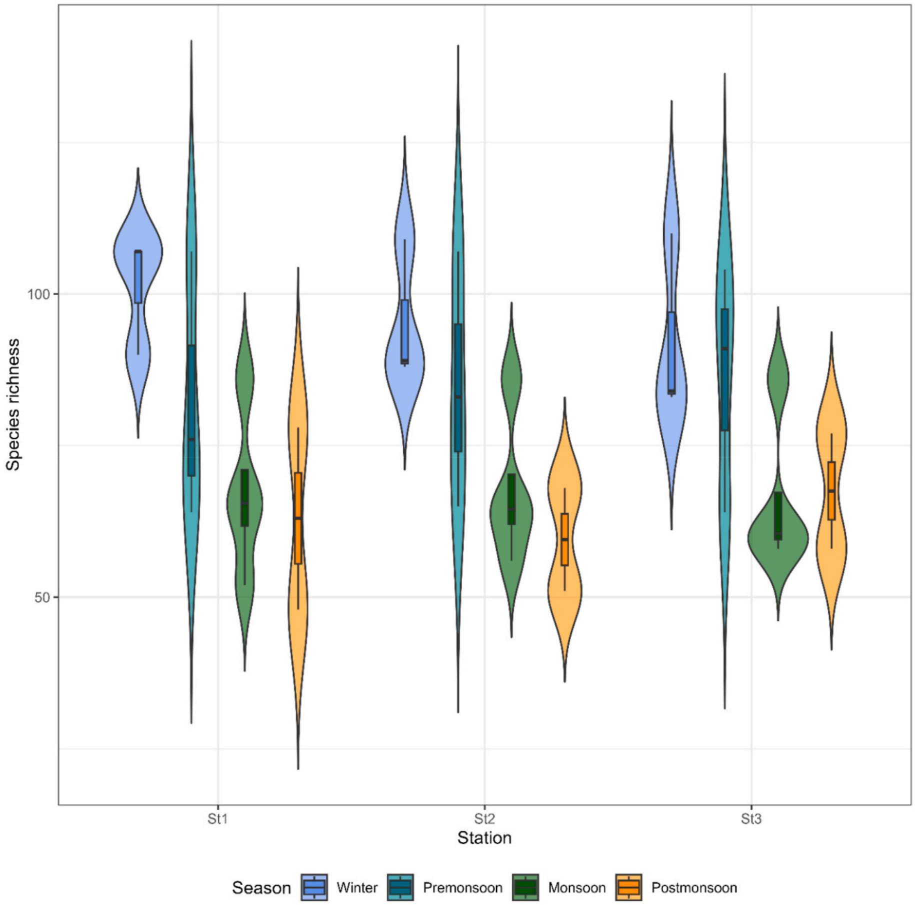

Fig. 3. Violin plots illustrating seasonal variation in gastropod species richness across the three sampling stations. Each plot depicts the distribution and density of species richness values for each season. Seasons are colour-coded as follows: Blue (winter), Teal (pre-monsoon), Green (monsoon) and Orange (post-monsoon). Each violin plot includes an embedded boxplot displaying the median and interquartile range.

Principal Component Analysis (PCA) explained approximately 74 % of the total variance in physicochemical variables across the first four components (Table 1; Fig. 2). PC1 accounted for ~32 % of the variance and was moderately negatively correlated with salinity (−0.480), water transparency (−0.352), and TDS (−0.472). PC2 (~16 %) was negatively associated with NO_3-N (−0.410) and positively with water temperature (0.392). PC3 (~15 %) showed a positive association with DO (0.441) and negative correlation with NO_2-N (−0.381). PC4 (~11 %) was primarily driven by pH with a correlation of −0.405.

Table 1
Principal component loadings (eigenvectors) from PCA on physicochemical variables, showing correlation coefficients and communality values of each variable with the first four principal components (PC1–PC4).

	PC1	PC2	PC3	PC4	Communality values
Temperature	0.179	**0.486**	−0.243	0.215	0.372
pH	0.082	−0.244	0.040	**−0.835**	0.765
DO	0.262	−0.267	**0.446**	0.224	0.389
TSS	**0.366**	−0.245	0.206	0.049	0.239
TDS	**−0.472**	0.062	0.339	−0.121	0.356
Salinity	**−0.480**	0.118	0.179	−0.094	0.284
NO_3^-N	0.002	**−0.647**	−0.235	0.163	0.499
PO_4^-N	−0.268	**−0.311**	−0.301	0.259	0.326
NO_2^-N	**−0.331**	−0.143	**−0.482**	−0.063	0.366
Transparency	**−0.352**	−0.141	0.417	0.287	0.400
Standard deviation	1.786	1.2534	1.2269	1.0605	
Proportion of variance	0.319	0.1571	0.1505	0.1125	
Cumulative proportion	**0.319**	**0.4761**	**0.6266**	**0.7391**	

3.2. *Correlation between species richness and physicochemical parameters*

The Generalised Linear Mixed Model (GLMM) revealed that gastropod species richness was significantly influenced by season ($p = 0.008$) and PC1 scores ($p = 0.001$), whereas spatial differences between stations were not statistically significant (Table 2). The model selection was guided by the Akaike Information Criterion (AIC = 273.54), and the random effect of station was evaluated via likelihood ratio tests.

The negative association of PC1 with salinity (−0.480), TDS (−0.472), NO_2^--N (−0.331), and water transparency (−0.352), alongside its positive correlation with TSS (0.366), suggests that species

Table 2
Results of the Generalised Linear Mixed Model (GLMM) evaluating the effects of environmental factors on gastropod species richness. Model fit is indicated by the Akaike Information Criterion (AIC = 273.54). Significant effects ($p < 0.05$) are highlighted in bold. χ^2-value = chi-square statistic; Df = degrees of freedom; P-value = statistical significance.

Variables	χ^2-value	Df	P-value
Station	0.013	2	0.993
Season	11.821	3	**0.008**
PC1	10.279	1	**0.001**
PC2	1.389	1	0.239
PC3	0.002	1	0.962
PC4	0.024	1	0.877

richness declined during periods of lowered salinity, TDS, and transparency, particularly in pre-monsoon, winter, and post-monsoon seasons (Table 1; Fig. 2). Seasonal post-hoc comparisons (Table 3) indicated significantly higher richness during winter and pre-monsoon compared to post-monsoon. Specifically, significant differences were observed:

- Between pre-monsoon and post-monsoon ($p = 0.0109$)
- Between winter and post-monsoon ($p = 0.0215$)

These results suggest that environmental gradients associated with PC1—particularly salinity and TDS—play a key role in modulating species richness.

An overall decline in richness was observed under low salinity, TDS, NO_2-N, and transparency. Nevertheless, richness patterns during the monsoon season were less consistent across stations. In particular, Station 3 exhibited its lowest richness during the monsoon (Fig. 3), suggesting possible site-specific responses that warrant further exploration in the Discussion.

3.3. *Species composition and indicator species*

Community composition varied significantly across seasons, strongly influenced by environmental gradients represented by PC1, PC2, and PC3 (Table 2). Post-hoc PERMANOVA (Table 4) revealed that post-monsoon assemblages were significantly different from those observed during winter, pre-monsoon, and monsoon seasons. This seasonal differentiation was also evident in the NMDS ordination (stress = 0.087), where post-monsoon communities formed a distinct cluster (Fig. 4) (see Table 5).

Analysis of beta diversity using multivariate dispersion ('betadisper') indicated no significant differences in within-season variability of community composition (p = 0.12). While average community structure shifted seasonally (as revealed by PERMANOVA), variability among samples within each season remained comparable.

Indicator species analysis identified *Oliva* sp. as the only significant indicator for the post-monsoon period, while *Umbonium* sp.2 emerged as an indicator for winter. Most other gastropod species were distributed across multiple seasons, reflecting a pattern of overlapping temporal occurrences rather than strong seasonal specialisation (Table S3). Seasonal co-occurrence patterns revealed complex assemblage dynamics: eight species were shared between monsoon and pre-monsoon, and five between post-monsoon and winter. The strongest overlap was observed between pre-monsoon and winter (25 species), while broader overlaps across three-season combinations involved 29 species (monsoon, pre-monsoon, winter) and 21 species (post-monsoon, pre-monsoon, winter). It should be noted that *Oliva* sp. and *Umbonium* sp.2 were identified only to genus or morphospecies level; further taxonomic work is required for species-level confirmation.

Table 3

Post-hoc pairwise comparisons of gastropod species richness across seasons, based on the Generalised Linear Mixed Model (GLMM). P-values were adjusted using Tukey's correction for multiple comparisons. Significant differences ($p < 0.05$) are highlighted in bold. Estimate = difference in means; SE = standard error; Z-value = test statistic; P-value = statistical significance.

Contrasts	Estimate	SE	Z-value	P-value
Post-monsoon- Monsoon	−16.7096	7.9168	−2.111	0.1484
Pre-monsoon- Monsoon	7.8806	8.009	0.984	0.7568
Winter- Monsoon	7.4224	9.278	0.8	0.8532
Pre-monsoon- Post-monsoon	24.5902	7.958	3.09	**0.0109**
Winter- Post-monsoon	24.132	8.413	2.868	**0.0215**
Winter- Pre-monsoon	−0.4582	7.835	−0.058	0.9999

Table 4

Permutational Multivariate Analysis of Variance (PERMANOVA) testing for differences in gastropod species composition across seasons. P-values were calculated based on 999 permutations; significant results ($p < 0.05$) are highlighted in bold. Df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; F-value = pseudo-F statistic; R^2 = proportion of variance explained; P-value = statistical significance.

Variables	Df	SS	MS	F-value	R^2-value	P-value
Season	3	2.134	0.711	6.086	0.326	**0.001**
PC1	1	0.378	0.378	3.235	0.058	**0.018**
PC2	1	0.369	0.369	3.155	0.056	**0.026**
PC3	1	0.343	0.342	2.930	0.052	**0.020**
PC4	1	0.056	0.056	0.476	0.008	0.578
Residuals	28	3.273	0.117	0.500		
Total	35	6.552	1.000			

Table 5

Pairwise comparisons of seasonal gastropod species compositions based on 999 permutations. P-values were adjusted using the Bonferroni correction; significant differences ($p < 0.05$) are highlighted in bold. Df = degrees of freedom; SS = sum of squares; F-value = pseudo-F statistic; R^2 = proportion of variance explained; P-value = statistical significance.

Pairs	Df	SS	F-value	R^2-value	P-value
Winter vs Pre-monsoon	1.000	0.244	1.860	0.104	0.840
Winter vs Monsoon	1.000	0.733	4.937	0.206	0.090
Winter vs Post-monsoon	1.000	0.929	8.729	0.402	**0.012**
Pre-monsoon vs Monsoon	1.000	0.383	2.396	0.112	0.450
Pre-monsoon vs Post-monsoon	1.000	1.145	9.330	0.418	**0.006**
Monsoon vs Post-monsoon	1.000	0.994	6.847	0.300	**0.006**

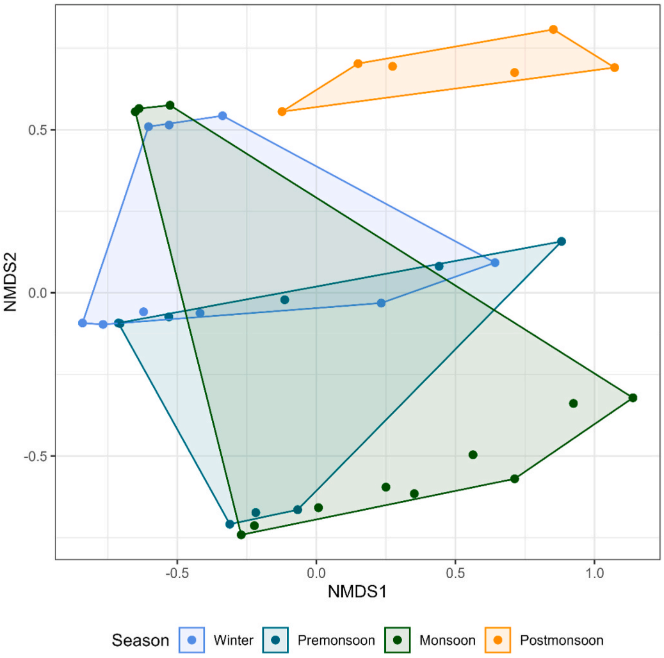

Fig. 4. Non-metric Multidimensional Scaling (NMDS) ordination plot illustrating gastropod species composition across seasons (stress value = 0.087). Distinct seasonal clustering of assemblages is evident, reflecting shifts in community composition across the monsoonal cycle. Points represent seasonal observations, colour-coded by season: Blue (winter), Teal (pre-monsoon), Green (monsoon) and Orange (post-monsoon).

4. Discussion

4.1. Context and knowledge gaps in gastropod diversity

This study presents the most comprehensive assessment to date of gastropod diversity across three coastal islands in southeastern Bangladesh, documenting 144 species spanning 65 genera, 28 families, and 3 orders (Archaeogastropoda, Mesogastropoda, and Neogastropoda). Despite the ecological significance of molluscs as key components of benthic ecosystems, research on their diversity in Bangladesh remains limited and fragmented.

Historical surveys by Commans (1940), Ali and Aziz (1976), and Ahmed (1990) provided early taxonomic inventories for regions such as St. Martin's Island and the Sundarbans. More recent studies (Siddique et al., 2007) have emphasised the incomplete nature of regional biodiversity records, citing constraints such as limited sampling, resource limitations, and a shortage of taxonomic expertise. Contemporary work has primarily focused on descriptive taxonomy, morphological assessments, and ecotoxicology (Ahmed et al., 2009; Sultana et al., 2021), while relatively few studies have explored ecological drivers of gastropod community structure. Our study contributes to addressing this gap by integrating environmental and community data to elucidate key abiotic factors influencing gastropod assemblages across dynamic intertidal habitats.

4.2. Key environmental drivers influencing gastropod distribution

Key environmental drivers and their potential effects on the gastropod communities displayed strong emphasis on temporal changes in abiotic conditions, as reflected in the responses of individual stations. Results from the Generalised Linear Mixed Model showed that seasonal factors and abiotic gradients, particularly salinity and total dissolved solids, were significant predictors of gastropod richness ($p = 0.008$ and $p = 0.001$), whereas spatial differences among stations were not significant. Some site-specific responses were observed, such as lower richness at Sonadia during the monsoon, but overall patterns were driven primarily by seasonal changes rather than local context.

Principal Component Analysis (PCA) identified salinity, total dissolved solids (TDS), and total suspended solids (TSS) as primary environmental parameters shaping gastropod distribution patterns. These findings align with prior studies that have highlighted osmotic stress, sediment stability, and turbidity as ecological filters in coastal ecosystems (Sor et al., 2020). Secondary factors, including temperature, nitrate, and dissolved oxygen (DO), also contributed to community variation, reflecting the role of metabolic constraints and nutrient availability.

Salinity emerged as the dominant driver, exhibiting strong seasonal variability linked to the monsoonal cycle. Elevated salinity during the pre-monsoon resulted from high evaporation rates and reduced precipitation, while monsoonal freshwater influx led to marked hyposaline conditions. These rapid shifts may impose physiological stress on stenohaline species, particularly during the monsoon, as evidenced by reduced species richness at Moheskhali (Station 2) during peak freshwater inflow (Deaton, 2009; Muraeva et al., 2016).

Dissolved oxygen (DO) also played a significant role in structuring gastropod communities. DO levels were relatively high during the monsoon and post-monsoon periods, particularly at Sonadia, likely due to increased rainfall and freshwater inflows carrying nutrient-rich materials from upstream sources. Adequate oxygen availability supports greater species diversity, evenness, and influences distribution, abundance, and individual size in gastropods (Chapelle and Peck, 1999; Kuk-Dzul and Díaz-Castañeda, 2016; Imamsyah et al., 2020). Conversely, Kutubdia experienced lower DO levels during winter, which may be attributed to smothering events caused by sediment deposition (2–5 cm) from earlier monsoonal activity, organic loading from river discharge, coastal erosion, increased suspended sediment, and elevated turbidity. These conditions can significantly affect the survival of aquatic organisms, including molluscs (Hossain et al., 2013; Chowdhury et al., 2019).

TSS and TDS fluctuations mirrored salinity variability, with post-monsoon sediment resuspension driven by tidal currents and monsoon-period inputs from terrestrial runoff (e.g., in Moheskhali) (Vinayachandran et al., 2002; Vajravelu et al., 2018). High TSS can reduce primary production by limiting light penetration, negatively affecting filter-feeding gastropods. These impacts were evident in the decline of filter-feeder abundance during periods of elevated TSS, though uncertainties in measurement accuracy should be acknowledged. The observed patterns, however, are consistent with known ecological effects of elevated suspended solids (Raha et al., 2013; Yang et al., 2024).

Nutrient enrichment, particularly nitrate, phosphate, and nitrite availability, further influenced community structure (Wang et al., 2022). Positive correlations between nitrate levels and gastropod abundance suggest enhanced primary productivity supports greater benthic diversity, highlighting bottom-up processes in structuring these communities (Menge et al., 1999; Wang et al., 2022).

4.3. Seasonal dynamics and community structure

Clear seasonal fluctuations in species richness were observed, with richness peaking during winter and pre-monsoon periods when salinity and TDS were elevated, reflecting the tolerance ranges of euryhaline gastropods. In contrast, richness declined during the monsoon due to hyposaline conditions, increased turbidity, and sediment resuspension, which reduce habitat suitability (Urra et al., 2013; Roy et al., 2022).

Multivariate analyses reinforced these patterns. PERMANOVA revealed significant seasonal shifts in community composition, particularly highlighting distinct post-monsoon assemblages. NMDS analysis further visualised this differentiation, showing greater overlap among winter, pre-monsoon, and monsoon communities, while post-monsoon samples formed a distinct cluster, likely due to stabilised salinity, DO, and nutrient conditions after monsoonal perturbation. The overall trend points to a seasonal shift in environmental filters that may shape species turnover and recruitment patterns following the monsoon.

Despite these seasonal changes in species composition, beta diversity analysis did not detect significant differences in community dispersion across seasons ($p = 0.12$), indicating that while mean community composition shifted, within-season variability—or the dispersion of communities around their seasonal centroids—remained stable. This decoupling between turnover and community heterogeneity suggests a structured ecological response to seasonal environmental filters rather than stochastic variability, with deterministic processes synchronising species replacement across seasons. Walter et al. (2021) reported that changes in species richness over time do not always correspond to changes in spatial or temporal dispersion, reflecting a degree of underlying ecological stability. Similarly, Shimadzu et al. (2013) demonstrated that seasonal fluctuations in species abundances can sustain community diversity through coordinated dynamics, rather than through random variability. These results support the interpretation that deterministic processes, such as shared physiological tolerances or synchronised responses to environmental filters, may govern the temporal assembly of intertidal gastropod communities. However, because the present study covers a single year, which may have been anomalous, seasonal variations cannot be generalised beyond this period.

4.4. Indicator species and season-specific responses

Indicator species analysis identified *Oliva* sp. as a strong indicator of the post-monsoon season, exhibiting both high fidelity and abundance during this period. This observation is consistent with prior observations of *Oliva* dominance in pre- and post-monsoon seasons in Honnavar and Majali beaches (D'Souza and Shenoy, 2020). However, species-level identification using molecular approaches would strengthen its value as a seasonal bioindicator.

Umbonium sp.2 emerged as a strong winter indicator, consistent with *Umbonium vestiarium*, which has been shown to peak during cooler seasons along the Digha coast in West Bengal (Das, 2017; Pandya et al., 2021). Its strong seasonal fidelity underscores its potential utility as bioindicator of winter environmental conditions in the study region, particularly in relation to temperature and salinity stability during that time.

Lunatia lewisii (moon snails) was recorded across multiple seasons, indicating a broad ecological niche and high tolerance to environmental variability. Its persistent occurrence during the monsoon, post-monsoon, and winter periods suggests potential seasonal vertical migrations between deeper subtidal zones and the intertidal zone, enabling it to exploit diverse habitat conditions and persist despite fluctuations in salinity, turbidity, and dissolved oxygen.

4.5. Biogeographic influences and conservation implications

Gastropod distribution is shaped not only by local environmental conditions but also by broader biogeographic processes acting over evolutionary timescales. In particular, the legacy of Pleistocene glaciations has played a pivotal role in shaping present-day species distributions. Repeated cycles of sea-level fluctuations, habitat fragmentation, and post-glacial recolonisation have historically structured marine biodiversity, resulting in the formation of distinct faunal assemblages across different regions (Araújo et al., 2008; Svenning et al., 2009; Georgopoulou et al., 2016). These historical dynamics have contributed to the development of latitudinal gradients in gastropod richness, with higher diversity typically concentrated in tropical and subtropical regions where recolonisation of intertidal habitats following glacial retreat was more extensive and uninterrupted.

In the context of Bangladesh, these biogeographic legacies interact with regional hydrodynamics and the monsoonal climate, jointly shaping gastropod community structure. However, contemporary climate change is expected to alter monsoon intensity and rainfall patterns, leading to stronger seasonal salinity fluctuations. Such changes may exacerbate physiological stress during hyposaline periods, with cascading effects on gastropod richness and assemblage structure. Alterations in temperature regimes, accelerating sea-level rise, and shifts in ocean chemistry are transforming marine environments at a pace that challenges the adaptive capacity of many intertidal species. Rising global temperatures have already been linked to poleward range shifts and depth migrations in gastropods, as species seek refuge from thermal stress and desiccation in increasingly inhospitable intertidal habitats (Lima et al., 2006; Pandori and Sorte, 2019). Comparable distributional shifts have been observed along the Atlantic Iberian Peninsula and other coastal region, underscoring the vulnerability of intertidal communities to rapid environmental change.

Gastropods are sensitive to variations in temperature, salinity, dissolved oxygen, and habitat degradation, making them valuable ecological sentinels (Underwood, 1979; Rubal et al., 2013; Kuk-Dzul and Díaz-Castañeda, 2016; Mentino et al., 2025). They occupy multiple trophic levels in intertidal ecosystems as grazers, detritivores, and predators, contributing to algal control, nutrient cycling, sediment aeration, and stabilisation. These processes are particularly important in Bangladesh's dynamic coastal environments, where monsoonal forcing alters turbidity and sediment deposition. Elevated suspended solids are known to reduce primary production and impair filter feeders, with cascading impacts on benthic communities (Sor et al., 2020; Vajravelu et al., 2018). Our study revealed clear seasonal patterns in species richness, with euryhaline species favoured in winter and pre-monsoon, and sharp declines during the monsoon under hyposaline and turbid conditions. Distinct assemblage shifts reflected taxa fidelity to specific environmental regimes, underscoring gastropods' value as indicators of seasonal variability. Sustained population declines due to monsoonal hyposalinity or climate-induced stressors can trigger cascading ecological effects, compromising ecosystem resilience and the livelihoods of coastal communities (Chowdhury et al., 2019; Hossain et al., 2013). By establishing baseline diversity patterns and identifying key environmental drivers, this study emphasises the need for long-term monitoring and targeted conservation to safeguard both ecological integrity and coastal livelihoods.

To mitigate these risks, long-term ecological monitoring is essential for detecting distributional shifts, population declines, and potential local extinctions. Our findings provide a critical baseline for the development of adaptive management strategies and targeted conservation actions, particularly in climate-vulnerable regions such as Bangladesh (Heer and Choudhury, 2025). Integrating species distribution models, genetic analyses, and climate projections will strengthen our understanding of gastropod responses to environmental change, facilitating the identification of potential climate refugia and conservation priority areas.

Safeguarding gastropod diversity is essential for preserving coastal biodiversity and maintaining the ecological integrity of intertidal systems. In this study, 144 species from 65 genera and 28 families were documented across Kutubdia, Moheskhali, and Sonadia, highlighting their ecological richness. Seasonal abundance peaks reflected salinity and total dissolved solids supporting stable communities, with clear indicator species such as *Oliva* sp. (post-monsoon) and *Umbonium* sp. (winter). Post-monsoon assemblages further demonstrated sensitivity to fluctuations in salinity, dissolved oxygen, and suspended solids. These findings highlight the vulnerability of Bangladeshi coastal ecosystems, recognised among the world's climate-vulnerable regions (IPCC et al., 2021; Alam et al., 2017), and underscore the need for proactive, evidence-based conservation strategies that incorporate climate resilience frameworks. Such approaches are essential to mitigate climate-induced pressures, sustain gastropod assemblages, and ensure the long-term health of marine ecosystems.

CRediT authorship contribution statement

Md Royhanur Islam: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Eric Goberville:** Writing – review & editing, Validation. **Anik Saha:** Writing – review & editing. **S.M. Sharifuzzaman:** Writing – review & editing. **M Shahadat Hossain:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107593.

Data availability

Data will be made available on request.

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