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The influence of temperature and river runoff on phytoplankton community diversity in Beibu Gulf: insight from 18 S rDNA metabarcoding analysis

Zheng Xiong[1†], Zongsheng Xie[1†], Haochen Li[1†], Chunyan Peng[1], Jixin Jia[1], Xiaobo Liu[1], Jingjing Song[1], Ying Liu[1], Yuyue Qin[1] and Bin Gong[1*]

Abstract

Background Sanniang Bay (SNB) and Dafeng River (DFR), located in the northern Beibu Gulf, is well-known as one of the eight habitats for humpback dolphins in China. This region is representative of typical estuarine and bay ecosystems and produce complex hydrodynamic seawater conditions. Moreover, anthropogenic pressure, such as eutrophication and large-scale infrastructure projects, have caused ongoing habitat deterioration and loss. It is urgent to know the phytoplankton community and their relationships with environmental factors in this region.

Results In this study, we assessed the diversity and assembly mechanisms of phytoplankton communities, as well as their relationship with the physicochemical characteristics of seawater in SNB and DFR region using 18 S rDNA metabarcoding analysis. The results showed that seasonal changes markedly impacted the alpha diversity of the phytoplankton community. From March to July, with the average temperature increasing from 25.2℃ to 28.1℃,the Shannon or Species Richness were negatively correlated with temperature. During hot season (in Sep, average temperature 32.1℃), phytoplankton diversity was negatively correlated with nutrients (NH_4^+, NO_3^-, PO_4^{3-}, TN). Additionally, during the rainy season, the Bray-Curtis similarity of the phytoplankton community was significantly lower than during the dry season. In March, the distance among the sampling sites was most strongly and positively correlated with the Bray-Curtis dissimilarity. Stochastic processes, specifically dispersal limitation and ecological drift, are the primary drivers of community assembly, while deterministic assembly processes (mainly heterogeneous selection) contribute a relatively minor portion (< 17%).

Conclusions Rising temperature diminished the diversity of phytoplankton in SNB and DFR, and nutrient inputs and eutrophication in estuarine areas will aggravate the loss of phytoplankton diversity.

Keywords Phytoplankton, Community assembly, `Metabarcoding, Stochastic processes, Heterogeneous selection

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†Zheng Xiong, Zongsheng Xie, and Haochen Li contributed equally to this work.

*Correspondence:
Bin Gong
gongbin@bbgu.edu.cn

[1]The Guangxi Key Laboratory of Beibu Gulf Marine Biodiversity Conservation, College of Marine Sciences, Beibu Gulf University, Qinzhou 535011, China

Background

Phytoplankton constitute a diverse assemblage of organisms that serve as the foundation of the marine ecosystem [1]. Phytoplankton play a crucial role in the food web as primary autotrophic organisms, and are critical for preserving the equilibrium of entire marine ecosystems [2, 3]. Alterations in the phytoplankton community can serve as crucial indicators of potential changes in global oceanic ecology and biogeochemistry [4]. Carbon fixation (CO_2-fixation) by marine phytoplankton accounts for nearly half of the Earth's primary production [5]. The fluxes of CO_2 and its balance in the Earth's biosphere can significantly affect the ocean's ability to sequester atmospheric CO_2 [6], which will further impact global climate change. Besides carbon fixation, some oligotrophic diatoms, such as *Rhizosolenia* and *Hemiaulus*, are involved in nitrogen fixation process and they convert atmospheric N_2 gas to bioavailable NH_3 by establishing symbiotic associations with heterocystous cyanobacterium *Richelia intracellularis* [7]. The remarkable diversity of marine phytoplankton allows them to play a valuable role in stabilizing the material and energy balance in marine ecosystems and is crucial for sustaining the ecological equilibrium in the oceans [8].

The taxonomic variety of phytoplankton in pelagic environments has captivated ecology researchers for over fifty years [9]. Spatial and temporal distribution patterns in marine phytoplankton communities are heavily influenced by dispersal and environmental selection [10]. Global studies indicate that temperature gradients have a negative effect on marine phytoplankton community structure and biodiversity [11]. Elevated nutrient influx from rivers can substantially alter the phytoplankton assemblage in coastal regions [12, 13]. Accurately measuring the composition and concentration of different phytoplankton taxa is essential for gaining an understanding of the mechanisms of phytoplankton community assembly, which would then allow us to forecast phytoplankton levels [14]. Microscopic-based [15], flow cytometry [16], and high-performance liquid chromatography (HPLC) pigment analysis [17] are techniques that have been to identify and count phytoplankton populations. However, these methods lack precision when identifying diverse phytoplankton in coastal and estuarial environments. DNA metabarcoding employs amplicon sequencing of DNA "barcode" genes, which enables the identification of multiple species from a mixed sample. As a result, DNA metabarcoding has gradually gained wider acceptance in the field of exploring phytoplankton community diversity [14].

Understanding the mechanisms underlying phytoplankton community assembly has long been a central challenge in the fields of ecology and biogeography [18]. The utilization of DNA metabarcoding technology has facilitated our understanding of the mechanisms underlying phytoplankton community assembly [19]. Although some analytical uncertainty regarding this method exists [20, 21], rigorously evaluated workflows for DNA metabarcoding can, in fact, yield accurate and precise estimates of phytoplankton composition [22–24]. Researchers have used DNA metabarcoding to study the diversity and community assembly mechanisms of eukaryotic marine phytoplankton in the coastal waters of Guangdong-Hong Kong-Macao Greater Bay Area [25], Jiaozhou Bay [26], the north South China Sea [27], Maowei sea in Beibu Gulf [28], and the Pacific Ocean [29]. These studies revealed greater diversity of phytoplankton compared to traditional methods, and added more undeniable evidence that environmental heterogeneity and dispersal limitation affects phytoplankton community assembly [27]. However, the relative importance of environmental heterogeneity and dispersal limitation in determining the community assembly varied across regions [25, 26, 28, 30]. Given the intricate characteristics of different environmental factors, such as geomorphological, hydrodynamic, and nutrient levels, in different coastal zones [31], it is imperative to conduct more studies to explore the effects of diverse aquatic environments on the assembly of phytoplankton communities [26]. Furthermore, there is a lack of research on the mechanisms underlying the assembly of phytoplankton communities during different seasonal periods.

Sanniang Bay (SNB) and Dafeng River (DFR) are located in subtropical zones, along the coast of northern Beibu Gulf near Qinzhou city, Guangxi province. This region is well-known as one of the eight habitats for humpback dolphins in China [32]. The abundant richness in biological diversity and unique characteristics of that ecosystem have attracted numerous in-depth studies [33, 34]. Moreover, the region is representative of typical estuarine (Dafeng River) and bay (Sanniang Bay) ecosystems. The intricate topographical characteristics produce complex hydrodynamic seawater conditions in this region [35].

In 2012, the Sandun Island Petrochemical Dock was constructed in Qinzhou Bay [36]. This reclamation project resulted in a 10-km-long transport embankment that hindered freshwater input and seawater exchange in the eastern part of Qinzhou Bay [35]. It profoundly changed the hydrodynamic conditions and sediment transport processes of the region [35, 37], which may distinctively alter the diversity of the plankton. However, until now, there have been no reports regarding the spatio-temporal distribution of the phytoplankton community, the diversity of the species, and their relationships with environmental factors.

The aim of this study is to investigate all the above questions. Our research holds great significance for the

exploration of biodiversity and the underlying formation mechanisms within the coastal ecosystem of Beibu Gulf.

Materials and methods

Field sampling

Sixteen sites were sampled for this study near Sanniang Bay in northern Beibu Gulf (21.63°N, 108.69°E-21.56°N, 108.93°E), China. The samples were taken at depths less than 11 m, with a salinity of 17.78–31.99‰ during the months of March (Mar) 2019, July (Jul) 2019, September (Sep) 2018, and December (Dec) 2018. The sampling area included typical estuarine (Dafeng River) and bay (Sanniang Bay) ecosystems. Moreover, the site was selected because it is well-known for being one of eight habitats for humpback dolphin subpopulations in Beibu Gulf, China [38]. Seawaters were collected at the surface, middle, and bottom layers in 5 L sterile containers, and then mixed together at a 1:1:1 ratio. Each sampling site was a square area measuring 6 m × 6 m, and seawater samples were collected in triplicate. The seawater samples were stored on ice and then transferred immediately to the lab. 2 L of seawater was pre-filtered with 20-µm nylon mesh to remove large zooplankton, phytoplankton and other particles. Then the filtered seawater was re-filtered with 0.45-µm hydrophilic PVDF membranes. After filtration, each membrane was placed in a sterile plastic self-sealing bag and stored at -80℃ until the eDNA was extracted and analyzed.

Analysis of seawater physico-chemical characteristics

In situ measurements of temperature (TEMP), depth and salinity of the seawater were taken using a CTD (conductivity-temperature-depth) sensor (SBE19 Plus V2, SeaBird, USA) [39]. Turbidity was measured using a portable turbidimeter (2100Q, HACH) [40]. The pH of the seawater samples was measured by a portable pH meter (FiveGo, METTLER TOLEDO, Switzerland). Nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}) were detected in the filtered seawater samples using an autonomous nutrient analyzer (CleverChem Anna, DeChem-Tech, Germany) [41]. The seawater was filtered with 0.65-µm polycarbonate films (Whatman, England), and then the chlorophyll a (Chl-a) was extracted from the membrane with 90% (V/V) acetone and measured by the spectrophotometric method [42]. Total organic carbon (TOC) of the seawater was measured using a TOC analyzer (Aurora 1030 C, OI Analytical, USA). Real-time online measurement of dissolved oxygen (DO) was conducted with a portable dissolved oxygen meter (LDO10110, HACH, USA) [43]. Total nitrogen (TN) was estimated using the Pyrolysis-Chemiluminescence method (ASTM D5176-08) [44]. Total phosphorus (TP) level was assessed using a simple neutral digestion method [45].

DNA extraction, PCR amplification and sequencing

The environmental DNA (eDNA) from the 0.45-µm pore size filter was extracted with a MagIso Environmental Samples DNA Kit (GBCBIO Technologies Inc., China) according to the manufacturer's protocols. The eDNA was quantified with NanoDrop One (Thermo Scientific™, USA), then the V4 region of the 18 S rDNA gene was amplified using universal primers (R: GCTTGTCTCAAA GATTAAGCC; F: GCCTGCTGCCTTCCTTGGA) [46]. Sequencing was conducted on the Illumina HiSeq2500 platform of Majorbio Bio-pharm Technology Company (Shanghai, China). After obtaining the raw sequencing data, Btrim software was utilized to eliminate adapters and low-quality regions [47]. Next, merging of paired-end reads was performed using AdapterRemoval v2 [48]. To minimize the random sequencing error, the chimeric sequences [49], low quality reads, and barcode sequences were removed. Amplicon sequence variants (ASVs) were constructed from the amplicon data that was processed using the above-mentioned procedure [50]. Taxonomic assignment was conducted for the ASVs against an available SILVA database (SSU r138.1) [51]. The ASVs were first annotated as sequences of phylum in phytoplankton (such as Chlorophyta, Cryptophyceae, Diatomea, Streptophyta) and then filtered out into tables for the follow-up analysis.

Statistical analysis

The longitude and latitude coordinates of the sampling sites were transformed to geographical distances using the R "geosphere" package [52]. The alpha diversity index of the samples was determined by calculating the Shannon, Simpson, and species richness indices using the R "vegan" package [53]. The Bray-Curtis similarity of the phytoplankton was computed with the "vegdist" function in the R "vegan" package [53]. The α-diversity and β-diversity indices of the four seasons were calculated and compared using the analysis of variance (ANOVA) method [54], with $p < 0.05$ considered as a significant difference. The correlations (spearman's correlation) between the α-diversity index (or Bray-Curtis similarity) and the environmental elements (NH_4^+, NO_2^-, NO_3^-, PO_4^{3-}, TP, TOC, TN, Chl-a, DO, pH, TEMP, turbidity, sanility) or geographic distances were determined with the mantel test analysis using the R "reshape2" package [55]. We used the R "picante" package to apply the Bray-Curtis based Raup-Crick (RCBray) and β-nearest taxon indices (βNTI) to evaluate the prevalence of Stochastic or Deterministic assembly processes across the four seasons [56].

The community assembly mechanisms consist of two primary categories: Determinism (Non-random fraction, |βNTI| > 2) and Stochasticity (Random fraction, |βNTI| < 2). The Determinism processes can further

be divided into Heterogeneous selection (βNTI > 2) and Homogeneous selection (βNTI < -2) [57]. The Stochastic processes can be classified into Probabilistic Dispersal (|RCBray| > 0.95) (if RCBray < -0.95, the dominance of Homogenizing Dispersal in shaping the community composition; if RCBray > 0.95, community assembly was dominated by Dispersal Limitations) and Drift (|RCBray| < 0.95) [58, 59].

Results

Abundance and distribution of phytoplankton communities

The abundance of phytoplankton in Sanniang Bay and Dafeng River was analyzed and the results are displayed in Figure S1. In all four seasons, the predominant phytoplankton classes in Sanniang Bay (SNB) and Dafeng River (DFR) were Bacillariophyceae, Chlorodendrophyceae, Chlorophyceae, Mamiellophyceae, Mediophyceae, Prasinophytae, Trebouxiophyceae, and Ulvophyceae. However, the phytoplankton composition in Sanniang Bay

and Dafeng River did vary significantly during the different seasons. In spring, the unidentified_Cryptophyceae and Mamiellophyceae were significantly more abundant in SNB, while there was a significantly higher abundance of Mediophyceae in DFR. In September, Mamiellophyceae, Trebouxiophyceae, and Mediophyceae were more abundant in SNB, and only one genus, *Thalassiosira* of Mediophyceae, was more abundant in DFR. In December, the Mediophyceae, unidentified_Streptophyta, and unidentified_Cryptophyceae were significantly more abundant in SNB, while only one genus, *Cerataulina* in Mediophyceae, was dominant in DFR.

The alpha diversity indices and their relationship with environmental factors

The values of the Simpson and Shannon diversity indices were significantly higher in March than in July, and the species richness was higher in March than in December or September (Fig. 1). Coincidentally, the temperature (TEMP) in March and September showed a significant
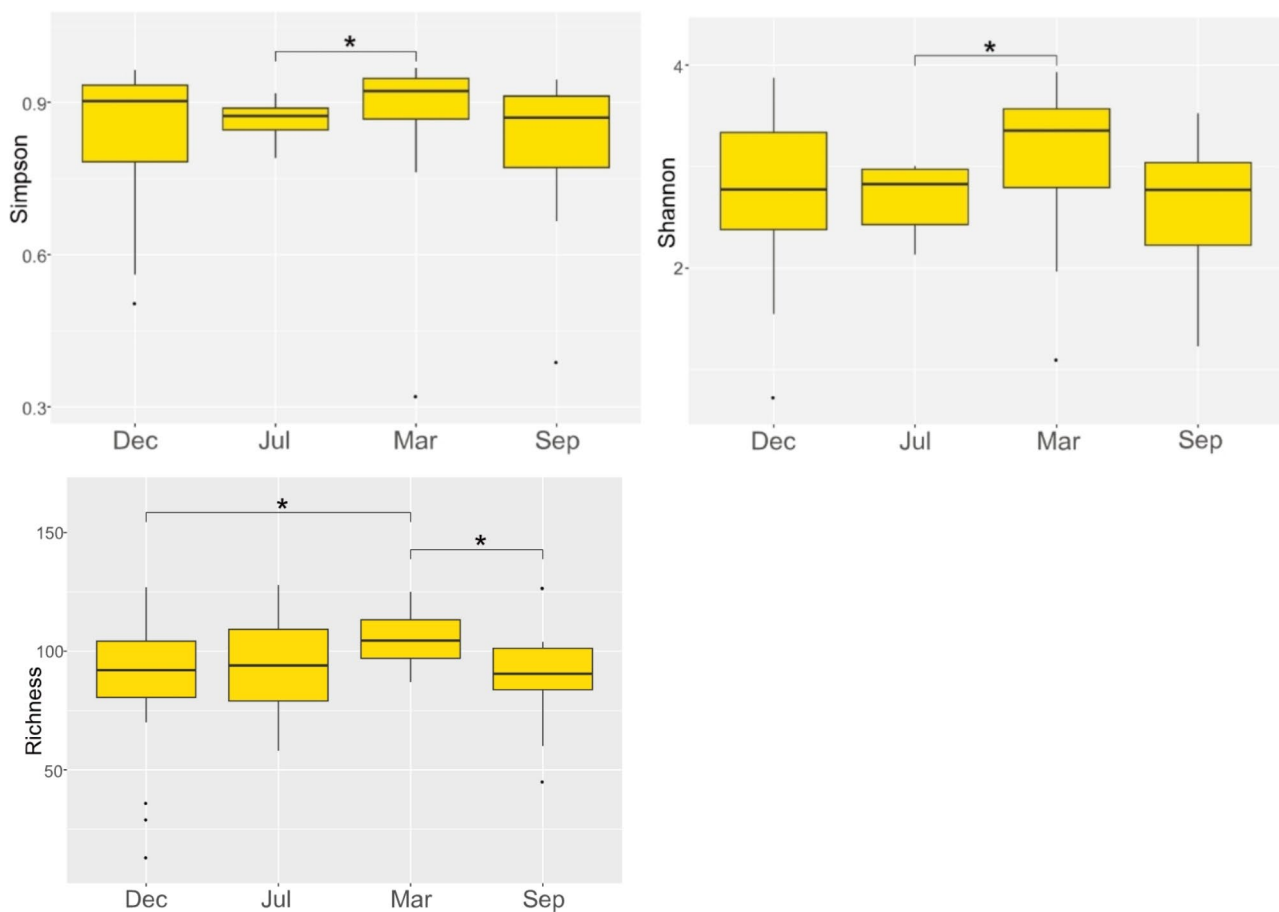
Fig. 1 The α-diversity indices (Shannon, Simpson, and species richness) during different seasons. The significant difference in the α-diversity indices between the groups was calculated using one-way ANOVA (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$)

negative correlation with the Shannon and species richness indices. From the analysis of environmental factors, the temperature gradually increased from March to July. The rising seawater temperatures were likely harmful to the alpha diversity of the phytoplankton. Interestingly, the Shannon index values were negatively correlated with Chl-a, while the Simpson diversity index was negatively correlated with pH and DO in March (Fig. 2). This result was somewhat contrary to our previous understanding regarding the diversity of phytoplankton. Another poorly interpreted result was that an increase in seawater nutrient levels, such as NH_4^+, NO_3^-, PO_4^{3-}, and TN, resulted in a decrease in the Shannon and Simpson diversity indices (Fig. 2).

Relationship between the bray-curtis dissimilarity and environmental factors

The Bray-Curtis dissimilarity values during seasonal shifts are shown in Figure S2. It was found that the Bray-Curtis dissimilarities in the low-flow period (March and December) were significantly higher than those in the high flow period (July and September). This result indicates that seasonal runoff variations have a distinct impact on phytoplankton communities. Next, we conducted linear regression analysis of environmental factors vs. Bray-Curtis dissimilarity values. In March, the distance among sampling sites was most strongly and positively correlated with the Bray-Curtis dissimilarity values ($r=0.665$, $p<0.001$), and the phytoplankton community structure became more distinct as the dispersal distances increased (Fig. 3). The influence of distance was significantly greater than that of any other environmental factors ($r<0.5$, $p<0.001$). However, in September (rainy season), nutrients (NH_4^+ and TN) had a greater influence ($r=0.33$, $p<0.5$) on the similarity of the phytoplankton community structure than distance ($r=0.27$, $p<0.5$) across the sampling sites (Fig. 4). Moreover, the DFR estuarine region received more nutrient inputs from rivers in September than in other months. Therefore, seasonal runoff variations (high flow or low-flow period) and nutrient input from rivers may exert a direct impact on phytoplankton communities.

Responses of phytoplankton communities to environmental variables

CCA biplots of phytoplankton community and environmental variables are shown in Fig. 5. In March, the phytoplankton communities in the SNB region were considerably impacted by NO_3^-, PO_4^{3-}, and salinity, whereas the phytoplankton in DFJ were most significantly affected by temperature (Fig. 6A). In July, the algal assemblages within both SNB and DFJ were moderately distinct, and these populations were most substantially correlated with temperature and TN (Fig. 5B). In September,

the phytoplankton communities in the majority of the sampling locations had similar characteristics, and environmental variables had a negligible influence on them (Fig. 5C). In December, the phytoplankton populations were not discernibly related to their sampling locations within the SNB or DFJ; instead, they were most significantly impacted by NO_3^-, NH_4^+, Chl-a, TOC, temperature, and Chl-a.

Assembly processes of phytoplankton communities

In order to understand the Deterministic or Stochastic processes shaping phytoplankton communities, we employed "within community" (nearest-taxon index [NTI]) and "between community" (βNTI) assessments methods. In all the four seasons, Stochastic processes, which included Dispersal Limitation (47.5-81.8%) and Ecological Drift (16.7-43.9%), contributed a larger fraction and dominated the phytoplankton community assembly (Fig. 6). In contrast, Deterministic assembly processes contributed a relatively small fraction (1.45–16.7%) to the community assembly. The relative contributions of Deterministic processes varied across seasons. The contribution of Deterministic processes gradually increased from March through to September, reaching its peak in September (16.7%). Moreover, we also found that the Deterministic processes tended to significantly strengthen during the dry season (March to December).

Discussion

In this study, we investigated the phytoplankton communities from typical estuary and bay areas in Beibu Gulf, China. Using the 18 S rDNA metabarcoding analysis method, we assessed the seasonal variations, alpha diversity, Bray-Curtis dissimilarity, and assembly processes of the main groups of phytoplankton. Moreover, we also identified the main environmental factors driving the changes of phytoplankton communities. Bacillariophyceae, Chlorodendrophyceae, Chlorophyceae, Mamiellophyceae, Mediophyceae, Prasinophytae, Trebouxiophyceae, and Ulvophyceae were the main classes of phytoplankton. Xu et al. (2022) had conducted a similar study in Maowei Sea in Beibu Gulf, and they found that Bacillariophyceae, Coscinodiscophyceae, Mediophyceae, Fragilariophyceae, and Bangiophyceae were the dominant phytoplankton classes, which are substantially different from our findings [29].

Naturally, the phytoplankton taxonomic composition in different marine areas will vary. The phytoplankton in South Sulawesi (Indonesia) included three classes (Bacillariophyceae, Cyanophyceae, Dinophyceae) [60]. Year-round monitoring of phytoplankton dynamics indicated that Bacillariophyta, Pelagophyceae, Dictyochophyceae, Mamiellophyceae, and Pyramimonadophyceae were the dominant classes in the coastal waters of Fildes Bay in the
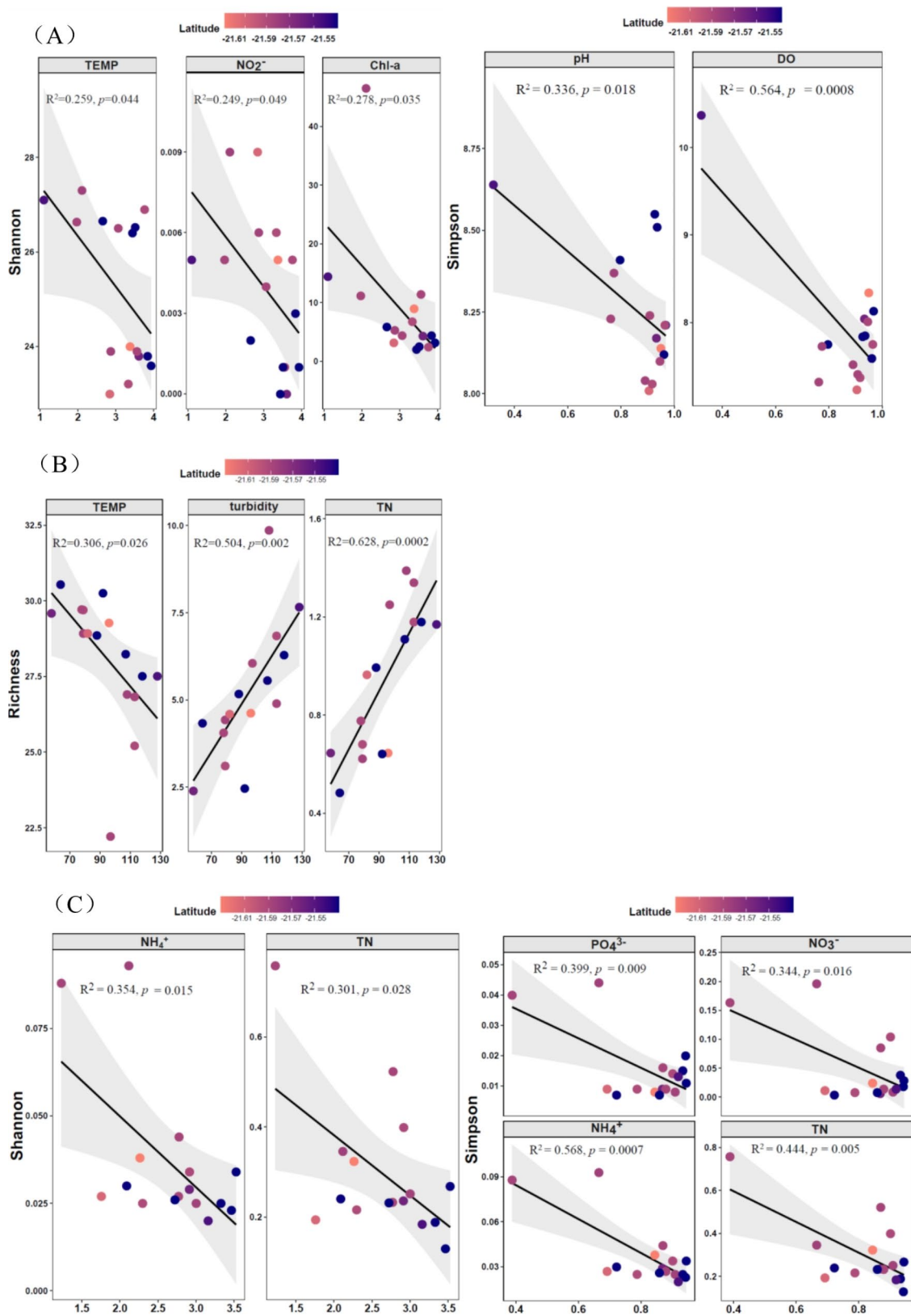
Fig. 2 Relationship between alpha-diversity index and TEMP, NO_3^-, Chl-a, pH, DO in the four seasons. The black line represents the linear regression, R^2 indicates the degree of correlation, and the *p*-values were calculated to indicate significant differences. **A**, **B** and **C** represents March, July, and September, respectively
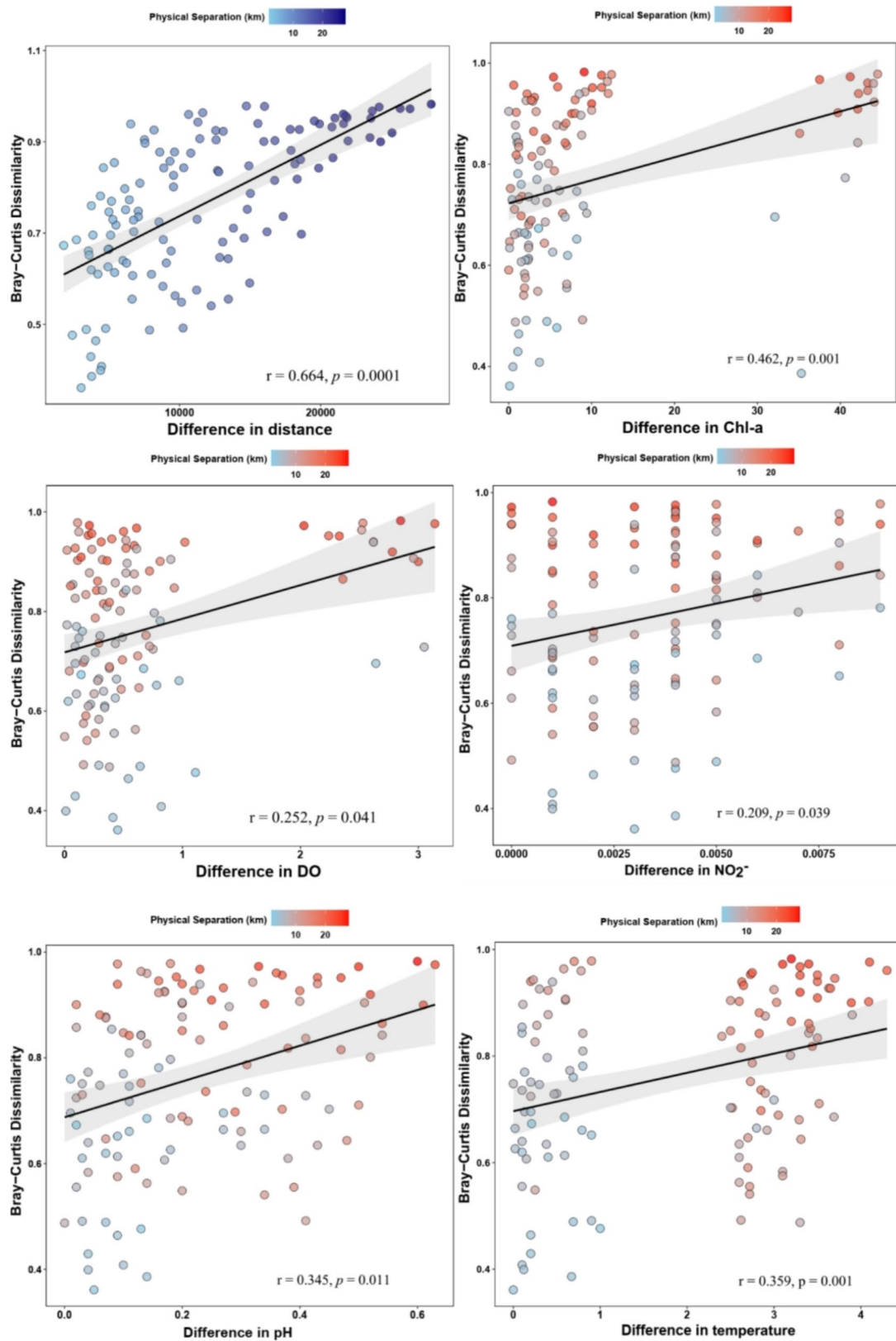
Fig. 3 Relationship between Bray-Curtis dissimilarity values and geographical distance, TEMP, pH, Chl-a, DO, and NO_3^- in March. The black line represents the linear regression, r indicates the degree of correlation, and *p*-values were calculated to indicate significant differences
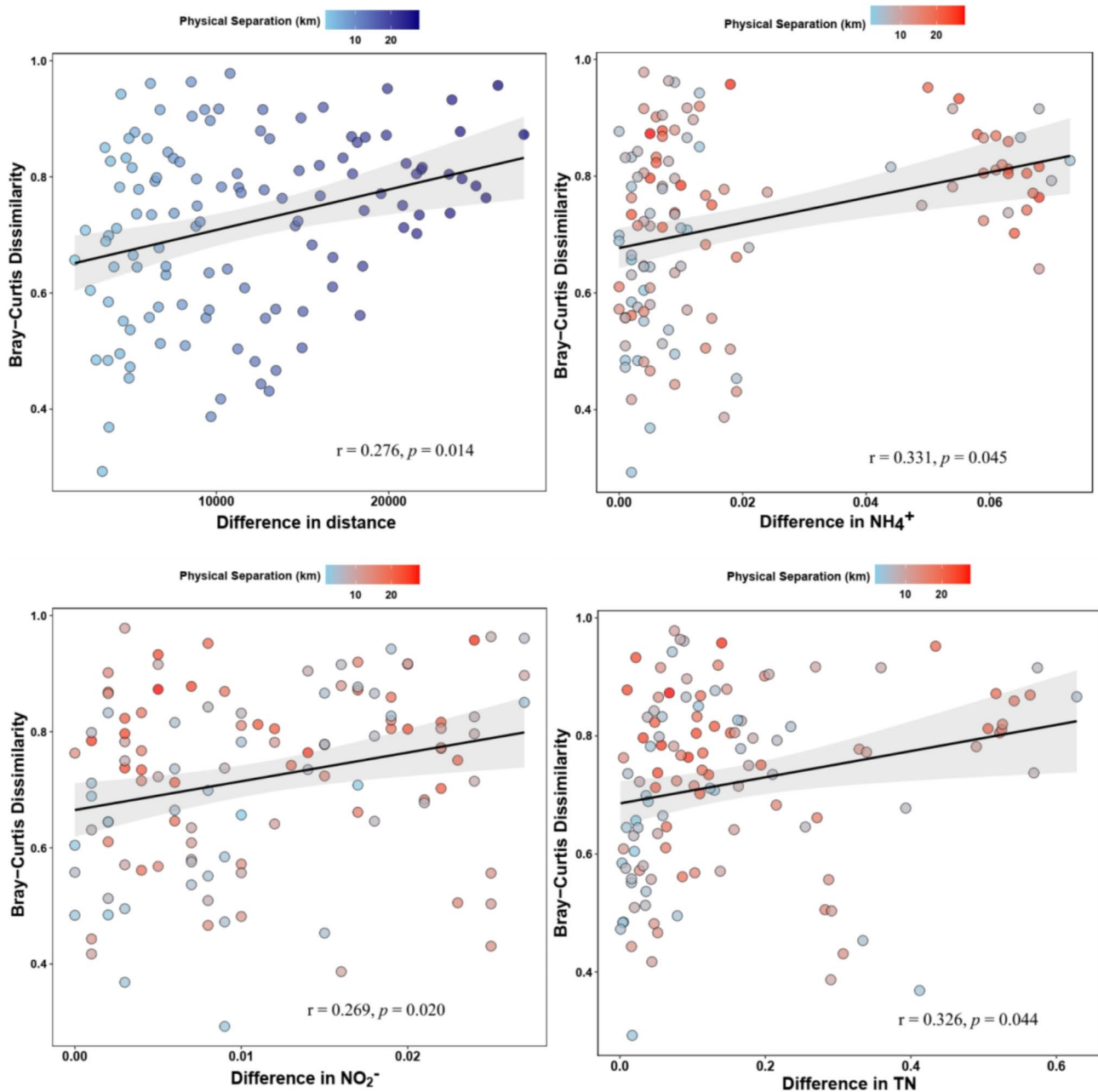
Fig. 4 Relationship between Bray-Curtis dissimilarity values and geographical distance, NH_4^+, TN, and NO_3^- in September. The black line represents the linear regression, r indicates the degree of correlation, and *p*-values were calculated to indicate significant differences

West Antarctic Peninsula [61]. Prasinophyceae, Cryptophyceae, Dinophyceae, and Prymnesiophyceae were identified at a site near the French coast of the English Channel [62]. Environmental factors, such as nutrients, temperature, CO_2, and salinity, have a significant impact on phytoplankton community composition in coastal areas [63, 64].

The Maowei Sea mentioned in Xu's study [29] is a semi-enclosed inland sea approximately 30–40 km away from our sampling site. From previous studies, we found that Maowei Sea has a higher concentration of nutrients than our site [65]. Moreover, the salinity of Maowei Sea is significantly lower than that of Sanniang Bay and Dafeng River [66]. Undoubtedly, the environmental conditions of the seawater will significantly impact the phytoplankton community structure. However, the huge difference observed between the phytoplankton community in the Maowei Sea and our site still requires thorough investigating in the future.
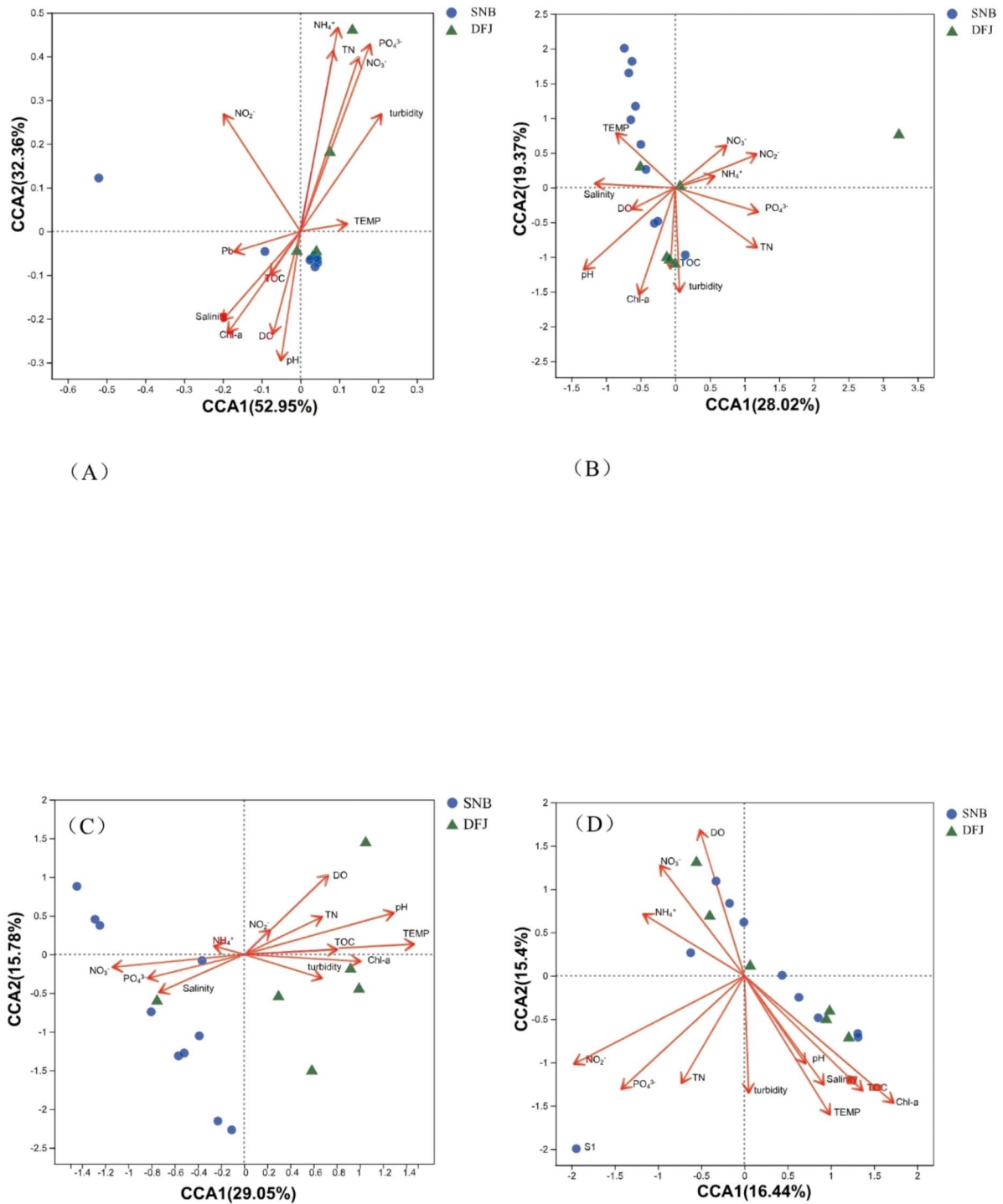
Fig. 5 CCA biplots illustrating the relationship between phytoplankton community composition and environmental variables in four seasons. **A**, **B**, **C** and **D** represent March, July, September, and December, respectively
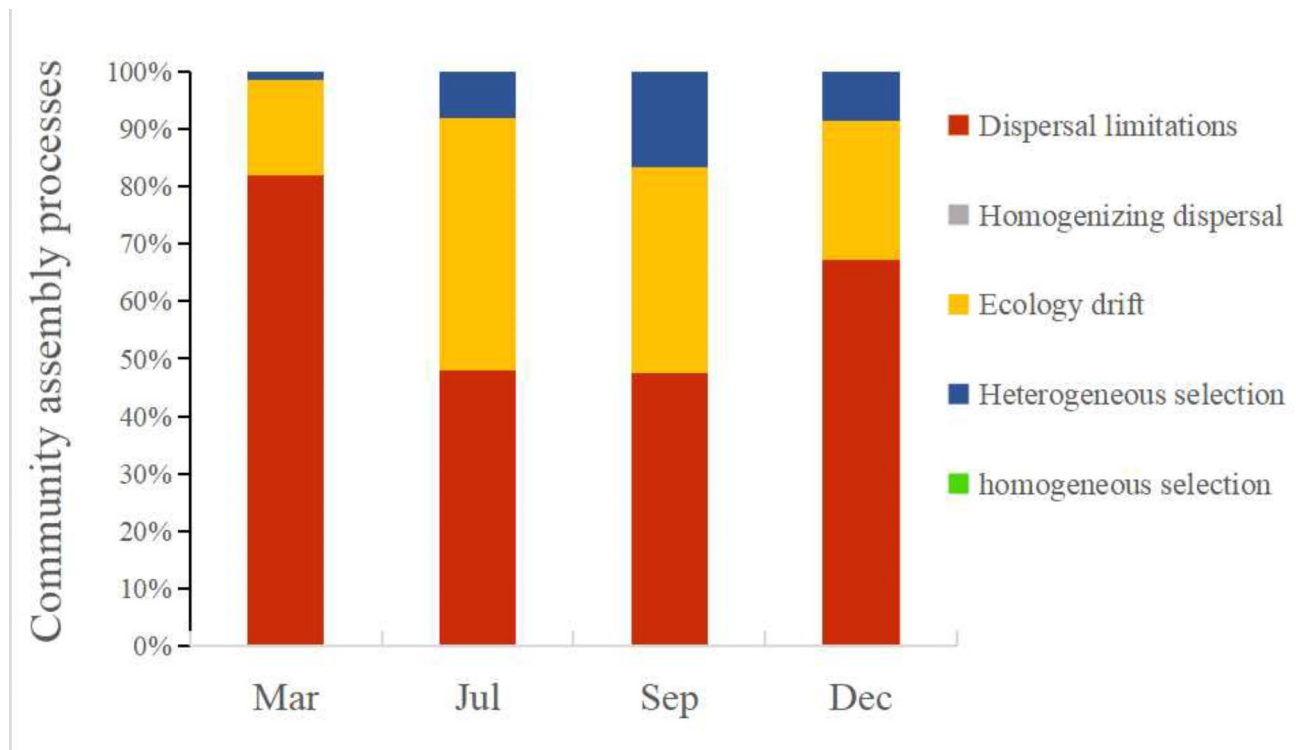
Fig. 6 Seasonal variation in microzooplankton community assembly governed by Deterministic (Homogeneous and Heterogeneous selection), and Stochastic processes (Dispersal Limitations, Homogenizing Dispersal, and Ecology Drift)

Variations in environmental characteristics could significantly impact the diversity of a phytoplankton community. In our study, the temperatures in March and September had a significant negative correlation with the Shannon and species richness diversity indices, which indicates that some alpha-diversity indices may suffer a continuous reduction as the temperature rises from 24 ℃ to 30 ℃. Mesocosm experiments had proven that an increase in temperature significantly decreases phytoplankton diversity [67]. Some researchers have also found that increased temperature resulted in significantly lower growth of some species of phytoplankton [68]. This effect resulted in the phytoplankton community being dominated by some taxa that are better adapted to endure warmer temperatures [67]. However, there is still insufficient relevant field data on the impact of temperature on phytoplankton diversity. Our experimental data will add to the body of evidence to clarify the impact of warmer climates on the alpha diversity of phytoplankton in coastal environments.

Another intriguing finding from our results is that an increase in Chl-a and DO levels was correlated with a decrease in alpha diversity of the phytoplankton community in March. In general, increased phytoplankton biomass corresponds to increased levels of Chl-a and DO [69]. This indicates that an increase in phytoplankton biomass may represent the expansion of only a subset of the taxonomic groups and does not result in a rise in alpha diversity of the community. Several researchers have reported that the study area underwent a bloom of *Phaeocystis globosa* [29, 70–72]. It is plausible that the elevated Chl-a concentration was due to *P. globosa*, which may engage in competitive relationships with other phytoplankton groups [73], resulting in a negative correlation between Chl-a levels and alpha diversity.

Another noteworthy discovery from our study is the observed negative correlation between the alpha diversity of the phytoplankton community and nutrient concentrations (NH_4^+, NO_3^-, PO_4^{3-}, and TN) in September. The input of nutrients, such as NH_4^+ and NO_3^-, had a distinctive influence on increasing the biomass of many phytoplankton species [74]. However, in 2022 Ge et al. had found a positive correlation between phytoplankton alpha diversity (Pielou's evenness index) and NO_3^- in a field investigation of China's Jiulong River estuary [75]. To explain these contrasting results, there are two potential underlying causes for the negative correlation observed in our results between alpha diversity and nutrient concentrations. Firstly, the elevated temperatures during September heightened the environmental pressures and decreased the population of delicate species [76]. Secondly, discharge derived nutrients (such as NH_4^+, NO_3^-, PO_4^{3-}, and TN loading) will enhance the abundance of thermotolerant phytoplankton taxa,

leading to a reduction in phytoplankton alpha. In summary, variations in temperature and the influx of terrestrial runoff can significantly decrease the alpha diversity of phytoplankton.

The beta diversity results unequivocally demonstrated that the influx of runoff from Dafeng River exerted a significant impact on the phytoplankton community structure. The Bray-Curtis dissimilarity values exhibited a marked decrease during the rainy season (Jul to Sep) as compared to the dry season (Dec to Mar). This indicates a higher degree of similarity in the phytoplankton community taxa in the sampling sites during the rainy season. River runoff can modify the hydrodynamics of estuaries, enhancing the mixing of seawater and migration of phytoplankton [77]. In the dry season (such as in Mar), the distance between sampling sites was most strongly and positively correlated with Bray-Curtis dissimilarity values ($r=0.665$, $p<0.001$). This effect was significantly higher than that from environmental factors ($r<0.5$, $p>0.001$). This validates that, throughout the dry season (in Mar), the primary determinant to variations in phytoplankton populations observed across the different sampling locations is the distance, when weighed against environmental factors. In the rainy season (in Sep), the impact of distance on phytoplankton assemblages was substantially reduced ($r=0.276$, $p=0.014$).

The community assembly of phytoplankton in the ocean has intrigued ecologists for several decades [78]. Most ecologists assume that marine phytoplankton may override spatial constraints and environmental determinants, leading to stochastic distribution of species (everything is everywhere) [79]. Stochastic processes are more prevalent in oligotrophic seawaters as opposed to eutrophic marine environments [28]. In eutrophic coastal environments, the involvement of heterogeneous selection in phytoplankton community assembly may exceed 80% [28]. In this study, stochastic processes, specifically dispersal limitation and ecological drift, are the primary drivers of phytoplankton community assembly, while deterministic assembly processes (mainly heterogeneous selection) had a relatively minor contribution. These findings were consistent with the current understanding of the primary role of stochastic processes in marine phytoplankton community assembly. The phytoplankton diversity in Sanniang Bay experienced minimal impact from the heterogeneous selection process (<17%), which is comparable to that observed in oligotrophic waters. These findings indicate a healthier state in Sanniang Bay comparing to Qinzhou Bay, which exhibited greater susceptibility to anthropogenic disturbances [28]. We also observed a higher susceptibility of phytoplankton to heterogeneous selection processes in September compared to other seasons. This may be attributed to the summer stratification of the seawater in Sanniang Bay, which may

exert a profound impact on phytoplankton assembly. Additionally, the nutrient inputs from rivers are more abundant in September (a rainy season in Beibu Gulf), further affecting the diversity of phytoplankton assembly.

Growing evidence has indicated that alterations in marine environmental conditions can significantly impact the structure of the phytoplankton community [80]. On a global scale, temperature strongly impacts the large-scale biodiversity of phytoplankton, while environmental variability is critical for species turnover and diversity over time [9]. The species richness diversity index of phytoplankton exhibited a positive correlation with temperature under 20 ℃. However, when the temperature exceeded 20 ℃, the species richness diversity index of the phytoplankton remained relatively unchanged [9].

At the small-and medium-scale field range, the mechanisms involved in phytoplankton community assembly are significantly more intricate. In the offshore and deeper area of Beibu Gulf (average depth 40 m, and maximum depth approximately 100 m), Ge et al. pointed out that the relative importance of environmental heterogeneity and dispersal limitations on spatial patterns of phytoplankton communities varied across seasons, wherein environmental heterogeneity dominated in summer and winter, and dispersal limitations dominated in spring and autumn [81]. Moreover, hydrologic distance, pH, alkalinity, and total nitrogen were crucial factors in shaping the beta diversity pattern [81]. Chen et al. studied the phytoplankton in Qinzhou Bay (average 10 m depth) in Beibu Gulf, and suggested that trophic states regulate assembly processes of phytoplankton communities [28]. However, the impact of seasonal temperature fluctuations on phytoplankton community diversity in regional studies remains limited. Similarly, the influence of river runoff on near-shore phytoplankton community diversity has not been sufficiently researched.

In this study, we examined the impacts of temperature and runoff on phytoplankton diversity by analyzing the phytoplankton composition in Sanniang Bay and Dafeng River. Our analysis demonstrated that, in the subtropical region of Beibu Gulf, an increase in seawater temperature is negatively correlated with phytoplankton diversity (with seawater temperatures ranging between 15.4℃ and 32.6℃). In contrast, global scale investigations have shown that phytoplankton diversity does not increase when seawater temperatures exceed 20℃. These results imply that in local marine environments, phytoplankton diversity responds differently to changes in seawater temperature, largely due to the heterogeneity of the local habitat environment and phytoplankton species. This investigation contributes to our understanding of the relationship between phytoplankton diversity and environmental factors. Our study also have broad ecological

implications for climate change and coastal management strategies. First, we should pay more attention to global warming trend. If we fail to cooperate in controlling global warming, the diversity of phytoplankton will decrease markedly and further diminish the species diversity in marine ecosystems, particularly in subtropical regions. Second, greater attention and management practices should be paid to nutrient inputs and eutrophication in estuarine areas, since it will aggravate the loss of phytoplankton diversity caused by temperature rise.

Conclusions

1. Rising temperature diminished the diversity of phytoplankton in SNB and DFR, and nutrient inputs and eutrophication in estuarine areas will aggravate the loss of phytoplankton diversity.
2. Stochastic processes, specifically dispersal limitation and ecological drift, are the primary drivers of community assembly, while deterministic assembly processes (mainly heterogeneous selection) contribute a relatively minor portion (< 17%).
3. Deterministic processes tended to significantly strengthen during the dry season.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12862-024-02315-1.

Supplementary Material 1

Author contributions
Zheng Xiong: Writing-Original draft preparation, Data analysis; Zongsheng Xie: Carried out the experiments, Data analysis; Haochen Li: Carried out the experiments, Writing-Original draft preparation; Chunyan Peng: Data analysis; Jixin Jia: Data curation; Xiaobo Liu: Writing-Reviewing and Editing; Jingjing Song: Conceptualization, Methodology; Ying Liu: Conceptualization, Data analysis; Yuyue Qin: Data analysis; Bin Gong: Data analysis, Methodology, Supervision.

Data availability
Sequence data that support the findings of this study have been deposited in GenBank with the primary accession number PRJNA1060426.

Declarations

Ethical approval
Not applicable.

Consent to publish
Not applicable.

Competing interests
The authors declare no competing interests.

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