Marine Pollution Bulletin 233 (2026) 120213

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Seasonal drivers of picoeukaryotic community structure and assembly in complex aquatic systems: A case study of the Changjiang (Yangtze) River Estuary and East China Sea

Ran Li [a,b,c], Wenxin Fan [a,b], Xianghui Guo [a], Yan Bai [d], Ping Sun [e], Nianzhi Jiao [a,b], Dapeng Xu [a,b,*]

[a] State Key Laboratory of Marine Environmental Science, College of Ocean and Earth Sciences, Xiamen University, Xiamen, 361102, China
[b] Fujian Key Laboratory of Marine Carbon Sequestration, Xiamen University, Xiamen, 361102, China
[c] College of Advanced Agriculture and Life Sciences, Weifang University, Weifang, 261061, China
[d] State Key Laboratory of Satellite Ocean Environment Dynamics, Second Institute of Oceanography, Ministry of Natural Resources, Hangzhou, 310000, China
[e] Key Laboratory of the Ministry of Education for Coastal and Wetland Ecosystem, College of The Environment and Ecology, Xiamen University, Xiamen, 361102, China

ARTICLE INFO

Keywords:
Community assembly process
Community structure
High-throughput sequencing
Protists
Water masses

ABSTRACT

This study investigates the seasonal dynamics, environmental drivers, and assembly mechanisms of picoeukaryotic communities in the hydrographically complex Changjiang River Estuary and adjacent East China Sea. Using 18S rRNA gene high-throughput sequencing and concurrent environmental profiling, we found pronounced differences in picoeukaryotic assemblages between the winter and summer surveys that were associated with contrasting hydrodynamic conditions. During winter, strong vertical mixing weakened environmental differentiation among water masses, and geographical distance was identified as the strongest correlate of picoeukaryotic community variation. Community assembly was predominantly associated with stochastic processes, particularly dispersal limitation and ecological drift, together with broader ecological niche breadths. In contrast, summer stratification strengthened environmental differentiation among water masses and increased the contribution of heterogeneous selection to community assembly. Taxonomic and network analyses revealed that communities were predominantly composed of Syndiniales-affiliated sequences. Co-occurrence networks demonstrated that parasitic Syndiniales and other potential parasitic groups acted as crucial keystone taxa (hubs and connectors) across seasons, suggesting significant host-parasite co-adaptation and their potential role in carbon transfer within the microbial loop. Notably, these keystone taxa transitioned from widespread, cosmopolitan distributions during winter mixing to highly compartmentalized, water-mass-specific niches during summer stratification. Collectively, our observations suggest that the contrast between winter mixing and summer stratification can alter the selective pressures and spatial gradients governing picoeukaryotic communities. This study underscores the critical importance of seasonal sampling to evaluate microbial interactions and assembly mechanisms in highly dynamic estuary-sea systems.

1. Introduction

Picoeukaryotes encompass a diverse array of microscopic eukaryotic organisms with diameters ≤2–3 μm (Man-Aharonovich et al., 2010; Massana, 2011; de Vargas et al., 2015). Their ubiquitous presence, remarkable diversity, and substantial contributions to biogeochemical cycling and energy flux make them essential components of the marine biota (Massana et al., 2015). Pico-sized eukaryotic algae, which constitute a significant subset of picoeukaryotes, serve as key contributors to marine primary production (Grob et al., 2007; Falkowski et al., 2008; Hartmann et al., 2012). Concurrently, small heterotrophic picoeukaryotic assemblages are essential consumers within the marine food web. Through active feeding, they regulate prokaryotic dynamics (Hartmann et al., 2012; Latorre et al., 2021). Subsequently, larger flagellates and ciliates utilize these small heterotrophic protists as prey, facilitating the transfer of matter and energy to higher trophic levels (Samuelsson and Andersson, 2003). Furthermore, certain fungi in the pico-sized fraction facilitate the decomposition of residual organic

* Corresponding author at: State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen, 361102, China.
E-mail address: dapengxu@xmu.edu.cn (D. Xu).

https://doi.org/10.1016/j.marpolbul.2026.120213
Received 1 June 2026; Received in revised form 30 July 2026; Accepted 31 July 2026

matter, thus contributing significantly to nutrient recycling (Hyde et al., 1998; Sen et al., 2022). These complex trophic linkages highlight the critical roles that picoeukaryotes fulfill in mediating energy transfer within the marine microbial loop (Azam et al., 1983).

Due to their small size and unicellular nature, picoeukaryotes are highly sensitive to changes in environmental variables. Community composition is significantly influenced by diverse factors, including geographical distance (Balzano et al., 2015), depth (Villarino et al., 2018), temperature (Wang et al., 2021), salinity (Jiao et al., 2002), dissolved oxygen (Piscoya et al., 2022), nutrient availability (Qiu et al., 2010), and biological interactions (Sun et al., 2022). Given their intrinsically limited motility, the spatial distribution of picoeukaryotic communities is heavily influenced by prevailing hydrological dynamics, such as river discharge and water mass movement (Piwosz et al., 2018; Wang et al., 2021). Furthermore, the heterogeneity of water masses generates a variety of environmental gradients, which exert diverse selective pressures on resident organisms. Consequently, spatiotemporal variability and water mass dynamics are widely recognized as primary determinants shaping picoeukaryotic community structure (Metfies et al., 2016; Wang et al., 2021). Seasonal transitions introduce further complexity by altering local hydrological and environmental conditions, thereby driving shifts in community dynamics (Zheng et al., 2022). For example, in the nearshore waters of the Pearl River Estuary, phytoplankton communities were primarily composed of micro- and nano-sized cells during early spring, when salinity exceeds 30 and river flow had the least impact. However, during the early autumn, when river flow was minimal impact. However, during early autumn, when river discharge intensified, *Synechococcus* and picoeukaryotes dominated the microbial community (Qiu et al., 2010). Therefore, investigating the seasonal spatial distribution and environmental drivers of picoeukaryotic communities across complex hydrological gradients is critical for understanding marine microbial ecology.

Although seasonal variation in picoeukaryotic abundance, diversity, and taxonomic composition has been documented in coastal, estuarine, and open-ocean environments, the ecological processes generating these patterns remain insufficiently resolved. Previous studies have demonstrated that picoeukaryotic communities can vary substantially in response to seasonally changing freshwater discharge, coastal currents, water temperature, nutrient availability, and water-column mixing (Jing et al., 2010; Kellogg et al., 2019; Rii et al., 2022). However, these investigations have generally focused on describing seasonal changes in abundance, diversity, or community composition and identifying their correlations with environmental variables. Comparatively less attention has been paid to whether the observed seasonal turnover is generated by deterministic processes, such as environmental selection, or by stochastic processes, including dispersal limitation and ecological drift.

Existing studies that explicitly examine microbial eukaryotic community assembly have demonstrated that oceanographic structure, water-mass history, environmental filtering, species sorting, dispersal limitation, and ecological drift can all contribute to community organization (Monier et al., 2015; Logares et al., 2018a, 2018b; Wu et al., 2018; Sun et al., 2020; Xu et al., 2022). Nevertheless, most of these studies have examined spatial gradients, non-estuarine habitats, or particular microeukaryotic groups rather than seasonal changes in entire estuarine picoeukaryotic communities. For example, previous investigations have assessed assembly processes across Arctic water masses, Antarctic aquatic systems, subtropical oceanic gradients, the Taiwan Strait, and broad latitudinal transects. Seasonal shifts in deterministic and stochastic assembly processes have also been studied in coastal prokaryotic communities (Wang et al., 2020), but comparable analyses of estuarine picoeukaryotes remain scarce.

As the third largest river globally, the Changjiang (Yangtze) River delivers massive quantities of freshwater, sediment, and nutrients into the East China Sea (ECS) (Li et al., 2007). Within the ECS, the complex interplay among the Changjiang Diluted Water (CDW), the Taiwan Warm Current (TWC), and China Coastal Currents (CCC) drives highly dynamic physical, chemical, and biological processes (Ichikawa and Beardsley, 2002; Gao et al., 2017; Liu et al., 2021). As the largest marginal sea in the northwestern Pacific Ocean, the ECS is characterized by strong monsoonal circulation (Lee and Chao, 2003). During summer, the Yangtze River Estuary (YRE) and the adjacent ECS region frequently experience water stratification (Chen et al., 2003; Lie et al., 2003; Jiang et al., 2015). This phenomenon is primarily driven by peak freshwater influx from the Changjiang River, which lowers surface salinity and creates a stark vertical salinity gradient. Concurrently, surface solar heating further strengthens this stratification. Conversely, in winter, the cold and dry northeast monsoon from Siberia typically enhances the strength of the CCC (Chen, 2009). These strong monsoonal winds generate vigorous surface currents that transport cold, nutrient-rich waters southward, significantly impacting coastal ecosystems (Chen, 2009). Furthermore, the intensification of these coastal currents enhances oceanic mixing, thereby promoting the reoxygenation of the water column and supporting diverse marine life (Zhang et al., 2020). These strong currents also drive the suspension and transport of benthic particulate matter and sediments, influencing biogeochemical. Consequently, the YRE and adjacent ECS provide a natural setting in which to examine how contrasting hydrodynamic conditions, particularly winter vertical mixing and summer stratification, are associated with changes in environmental heterogeneity, dispersal conditions, ecological niche differentiation, and picoeukaryotic community assembly.

The small size and limited diagnostic morphological features of picoeukaryotes constrain the ability of traditional microscopy-based methods to characterize their diversity and community structure. To address this limitation, this study employed high-throughput sequencing of the V4 hypervariable region of the SSU rRNA gene to investigate picoeukaryotic communities in the YRE and adjacent ECS under contrasting winter and summer hydrographic conditions. We hypothesized that winter mixing would reduce environmental differentiation and increase the relative importance of stochastic processes, whereas summer stratification would strengthen environmental heterogeneity and deterministic environmental selection. By jointly evaluating these ecological dimensions, this study provides an integrated assessment of how contrasting hydrodynamic regimes may restructure PE communities and their assembly processes in a complex river–estuary–shelf system.

2. Methods

2.1. Sample collection and environmental factor analysis

Field sampling was conducted during December 2015 (winter) and August 2016 (summer) across the YRE and adjacent continental shelf of the ECS. Samples were collected on board the *R/V Runjiang I*. At each station, seawater was collected from surface (2 m), mid-depth (10–15 m), and near-bottom (6–90 m, depending on total water depth) layers. In situ measurements of depth, salinity, temperature, and dissolved oxygen (DO) were recorded using a Sea-Bird conductivity-temperature-depth (CTD) rosette.

To remove large zooplankton, 2 L of seawater was pre-filtered through a 200 μm nylon mesh (Sefar Nitex). The filtrate was sequentially through 20 μm, 3 μm, and 0.2 μm pore-size polycarbonate filters (Millipore, USA), and all filters were stored at −80 °C until DNA extraction. This study exclusively analyzed the pico-sized fraction (0.2–3 μm) retained on the 0.2 μm filters. Following the commonly used operational definition of picoeukaryotes as eukaryotic cells approximately ≤2–3 μm in diameter (Man-Aharonovich et al., 2010; Massana, 2011), the material passing through the 3 μm filter and retained on the 0.2 μm filter was considered the 0.2–3 μm pico-sized fraction. Larger eukaryotes were excluded because the present study specifically focused on pico-sized assemblages and to reduce the potential masking of picoeukaryotic sequence signals by DNA derived from larger, higher-biomass plankton (Atteia et al., 2024).

For nutrient analysis, 500 mL seawater samples were filtered through Whatman GF/F filters. The concentrations of nitrate (NO_3-N), nitrite (NO_2-N), silicate (SiO_3-Si), and orthophosphate (PO_4-P) were quantified using an AutoAnalyzer3 (AA3) (Rimmelin and Moutin, 2005; Strickland and Parsons, 1972).

To assess picoplankton abundance, seawater samples were pre-filtered through a 20 μm mesh, and 1.8 mL of filtrates were fixed with glutaraldehyde (1% final concentration) (Brussaard, 2004). A FACSAria flow cytometer (Beckman Coulter, USA) was then used to enumerate *Synechococcus* and phototrophic picoeukaryotes (PPEs) (Marie et al., 1999). The abundances of heterotrophic prokaryotes (HPs) and viral-like particles (VLPs) were quantified using a BD Accuri C6 (Franklin Lake, USA) and Epics Altra II (Beckman Coulter, USA), respectively (Liang et al., 2014; Marie et al., 1999).

For the enumeration of nanoflagellates (NF), 50 mL of seawater was fixed with glutaraldehyde (1% final concentration) for 2–4 h at 4 °C and filtered onto 0.8 μm black polycarbonate membrane filters. The samples were then stained with 4′,6-diamidino-2-phenylindole (DAPI, Sigma, USA; 10 μg mL^{-1}final concentration) for 10 min in the dark. Heterotrophic nanoflagellates (HNFs) and pigmented nanoflagellates (PNFs) were distinguished and enumerated under a fluorescence microscope (Olympus BX51, Japan) according to standard protocols (Sanders and Porter, 1988; Caron et al., 2017).

2.2. DNA extraction, high-throughput sequencing, and sequence data processing

DNA was extracted using the AllPrep DNA/RNA Mini Kit (Qiagen, Germany) according to the protocol described by Xu et al. (2017). PCR amplification of the hypervariable V4 region of the SSU rRNA gene was carried out using the primer pair TAReuk454FWD1 (5′-CCAGCAS-CYGCGGTAATTCC-3′)/TAReukREV3 (5′-ACTTTCGTTCTTGATYRA-3′) (Stoeck et al., 2010). To minimize amplification bias, six independent PCR replicates were performed for each sample, and the resulting products were pooled and purified using the Wizard® SV Gel and PCR Clean-Up System (Promega, USA). Purified PCR products were sequenced on the Illumina MiSeq platform by Majorbio Co. Ltd. (Shanghai, China).

The raw reads underwent quality filtering, demultiplexing, and assembly using Trimmomatic and Flash (Bolger et al., 2014; Magoč and Salzberg, 2011) and criteria employed as below: (i) reads were truncated at any site that obtained an average quality score of <20 over a 50-bp sliding window and the truncated reads shorter than 50 bp were discarded; (ii) reads with any mismatch in the barcode, more than two nucleotide mismatches in the primer or containing ambiguous characters were removed; and (iii) overlapping sequences shorter than 10 bp or with a mismatch ratio of more than 0.2, were eliminated (Li et al., 2021). MOTHUR v.1.40.5 was used to retain reads between 300 and 500 bp (Schloss et al., 2009). USEARCH 11 (Edgar, 2010) was employed to delineate zero-radius operational taxonomic units (ZOTU) using UNOISE3 (Edgar, 2016a). Taxonomic assignments of the ZOTUs were determined by searching against the Protist Ribosomal (PR2) Reference database v.5.0.0 (Guillou et al., 2013) using SINTAX (Edgar, 2016b). ZOTU tables were generated in USEARCH 11, and only Eukaryota affiliated ZOTUs were retained. Finally, to ensure comparability, the ZOTU table was rarefied to the lowest read counts (39,091) across all samples for downstream analyses.

2.3. Statistical analyses

The sampling station map and distributions of environmental parameters were generated using Ocean Data View (ODV) version 5.6.5 (Schlitzer, 2023). Pairwise geographic distances between sampling sites were computed in R using the geosphere package. The fpc package in R was used to cluster samples into four water masses based on water temperature and salinity (Li et al., 2017). Comparisons of environmental parameters across water masses were performed using the Wilcox test. Principal component analysis (PCA) was conducted using the vegan package in R to examine the effect of environmental variables on sample variation during winter and summer.

Alpha diversity indices, including ZOTU richness, Shannon index, and Faith's phylogenetic diversity (PD), were calculated using the vegan package in R (Dixon, 2003). Comparisons of alpha diversity indices across different seasons, depths, and water masses were performed using the Wilcox test. Correlations between environmental factors and alpha diversity indices were assessed with Spearman's rank correlation using Paleontological Statistics (PAST) (Hammer and Harper, 2001).

Prior to downstream analyses, environmental factors were z-score transformed, and sequence data were Log (x + 1) transformed. Based on the Bray-Curtis dissimilarity matrix, community ordination of the 59 samples was visualized via non-metric multidimensional scaling (NMDS) and principal coordinate analysis (PCoA) using the vegan package in R. Unweighted Unifrac distances between communities were also computed using the Generalized UniFrac Distances (GUniFrac) package in R to verify sample grouping (Chen et al., 2012). Differences in community structures among water masses were tested using analysis of similarity (ANOSIM) (Chapman and Underwood, 1999) and permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2014).

To reveal relationships between major taxonomic groups, co-occurrence networks for winter and summer picoeukaryotic communities were constructed separately. Pairwise Spearman rank correlations (r) between ZOTUs were calculated using the psych package (Pan et al., 2020). Only strong and significant pairwise correlations ($|r| > 0.7$ and $p < 0.05$) were considered. Networks were visualized using Gephi version 0.10.1. Significantly discriminant taxa within each water mass were identified using linear discriminant analysis effect size (LEfSe) (Segata et al., 2011). Keystone species in the network, including module hubs and connectors linking different modules, were identified based on within-module connectivity (Zi) and between-module connectivity (Pi) metrics (Deng et al., 2012; Guimera and Nunes Amaral, 2005).

Simple and partial Mantel tests (9999 permutations) were used to explore the effects of geographic distance, depth, water mass, and environmental factors on beta diversity (Legendre and Legendre, 1998)., Variance partitioning analysis (VPA) was performed using the vegan package in R to assess the relative contributions of geographic distance, depth, and environmental factors to community variance. The neutral community model (NCM) was employed to evaluate the potential significance of neutral processes in community assembly (Sloan et al., 2006). R^2 represents the overall goodness-of-fit of the NCM, with higher R^2 values indicating a closer fit and suggesting a greater influence of stochastic processes on community assembly. Dispersal among communities was estimated by Nm, the product of metacommunity size (N) and migration rate (m) (Sloan et al., 2006). The relative significance of different ecological processes governing community assembly was quantified using the infer Community Assembly Mechanisms by Phylogenetic-bin-based null model analysis (iCAMP) package (Stegen et al., 2013). A Z-test for two proportions was employed to assess whether there were significant differences in the relative contributions of these ecological processes between the winter and summer eukaryotic communities. Recognizing niche breadth was a critical factor influencing community assembly, we calculated and standardized Levins' niche breadth index to facilitate seasonal comparisons (Hurlbert, 1978; Levins, 1968). Subsequently, the average niche breadth of all ZOTUs within the picoeukaryotic communities was calculated for each season to serve as a community level indicator (Wang et al., 2020; Wu et al., 2018).

3. Results

3.1. Determination of water masses

Based on water temperature and salinity, four prevalent water masses were identified across the sampling area during both summer and winter (Fig. 1). Water mass I, designated as Changjiang Diluted Water (CDW), forms through the mixing of Changjiang River discharge with ECS seawater, resulting in distinctly low salinity. During winter, CDW exhibited the lowest salinity (29.5 ± 0.62, mean ± SD) and temperature (12.8 ± 1.74 °C) among all water masses (Table S1). In summer, it maintained the lowest salinity (19.30 ± 1.41) but reached a comparatively higher temperature (22.7 ± 1.30 °C). Water mass II, identified as the Taiwan Warm Current (TWC), exhibited the highest salinity (34.28 ± 0.19) and temperature (19.62 ± 0.22 °C) during winter. In summer, the TWC retained a relatively higher salinity (27.89 ± 2.75) and the highest temperature (28.21 ± 1.11 °C) of the identified water masses, consistent with prior studies (Lian et al., 2016). Notably, TWC flow rates displayed seasonal fluctuations, with stronger currents in summer driving the warm water mass as far north as 31°N. Water mass III, designated as Mixed Water (MW), possessed a relatively high salinity (33.87 ± 0.24) and temperature (17.54 ± 0.63 °C) in winter. Conversely, in summer, MW recorded the highest salinity (32.60 ± 1.59) alongside the lowest temperature (22.67 ± 1.24 °C). Finally, Water mass IV was identified as China Coastal Current (CCC). Compared to the CDW, the CCC was characterized by higher salinity (31.96 ± 0.17) and temperature (15.49 ± 0.93 °C) in winter, and a higher salinity (29.56 ± 1.06) but lower temperature (24.91 ± 1.16 °C) in summer.

3.2. Environmental parameters

Environmental variables varied distinctly between seasons (PERMANOVA, $R^2 = 0.513$, $p < 0.001$) and among water masses (Adonis, $R^2 = 0.240$, $p < 0.001$) (Table 1). The environmental factors characterizing the four water masses exhibited significant differences in both summer ($R^2 = 0.605$, $p < 0.001$) and winter ($R^2 = 0.584$, $p < 0.001$) (Table 1; Fig. S2). Based on water temperature and salinity profiles, vertical mixing of the water column was pronounced in winter, whereas strong water stratification became established in summer (Fig. 2). Consequently, environmental factors among the three water layers did not differ significantly during winter (PERMANOVA, $R^2 = 0.060$, $p = 0.364$) but exhibited significant differences during summer (Adonis, R^2 =

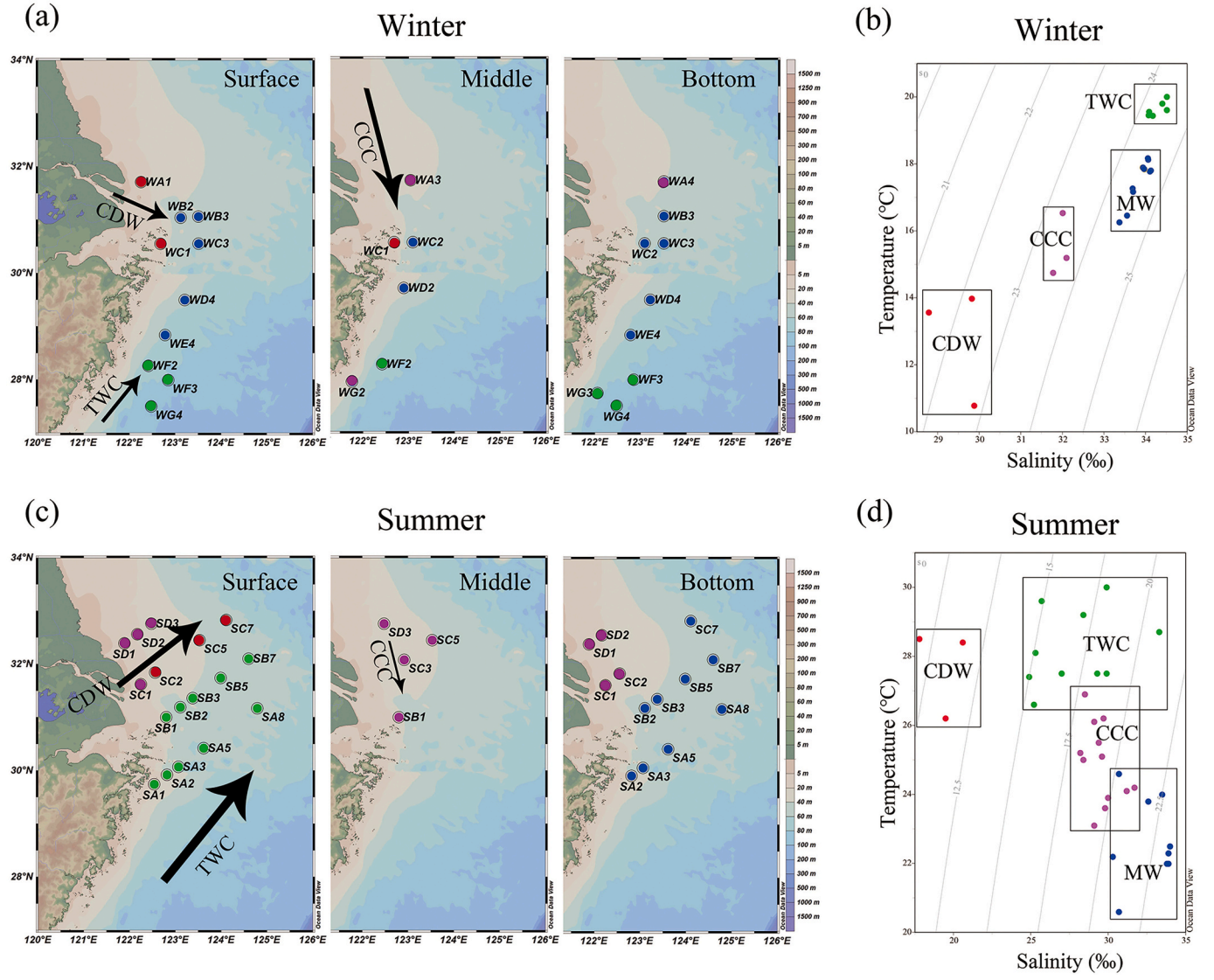

Fig. 1. Map of the Changjiang River Estuary and the adjacent East China Sea, highlighting the sampling sites and the distribution of the four identified water masses across depth strata based on water temperature and salinity during winter (a, b) and summer (c, d), respectively. CCC, China Coastal Current; CDW, Changjiang Diluted Water; MW, Mixed Water; TWC, Taiwan Warm Current.

Table 1
PERMANOVA results comparing environmental variables across sampling seasons (winter vs. summer), water masses, and vertical water layers (surface, middle, and bottom).

PERMANOVA (R^2)	Seasons	Water masses	Layers
All samples	0.513***	0.240***	0.066
Winter		0.584***	0.060
Summer		0.605***	0.305***

Significance: ***, $p < 0.001$.

0.305, $p < 0.001$) (Table 1; Fig. S1).

3.3. Alpha diversity indices

Alpha diversity indices, including ZOTU richness, Shannon index, and PD, did not vary significantly between summer and winter (Fig. 3a, d, g). During winter, no significant differences in alpha diversity were observed among the vertical water layers. Conversely, during summer, both ZOTU richness and PD differed significantly between the surface and bottom layers (Fig. 3b, e, h). Except for the Shannon index, ZOTU richness and PD showed significant pairwise differences among water masses in summer. In winter, however, significant differences were restricted to specific pairwise comparisons among the water masses (Fig. 3c, f, i).

Spearman correlation analyses revealed that alpha diversity indices were influenced by distinct environmental factors across seasons (Table S2). In winter, ZOTU richness and PD showed significant correlations with latitude, longitude, temperature, salinity, DO, NO_3-N and NO_2-N concentrations, as well as the abundances of viruses, HP, *Synechococcus*, and PPE. In summer, ZOTU richness and PD exhibited significant correlations with water depth, temperature, salinity, PO_4-P concentration, and the abundances of viruses, HP, and HNF. Notably, geographical distance exhibited the strongest correlation with alpha diversity during winter (Table S3). In contrast, summer alpha diversity showed the strongest correlation with water mass (driven by temperature and salinity), followed by environmental factors and depth (Table S3). Ultimately, water mass significantly influenced alpha diversity independent of environmental variations and depth. Conversely, when controlling for water mass, these secondary variables had no significant effect on alpha diversity.

3.4. The spatiotemporal distribution of picoeukaryotic communities

After being normalized to the minimum sequence count (39,091 sequences) across all samples, the final dataset contained 2,306,369 sequences assigned to 5079 ZOTUs. These ZOTUs were assigned to ten major taxonomic groups (Fig. 4).

Following Syndiniales and Metazoa, Chlorophyta comprised ca. 10.8% of the total sequences in winter (vs. 2.8% in summer), while Dinophyceae accounted for ca. 10.9% in summer (vs. 4.6% in winter). Compared to the other water masses, the CDW harbored the highest relative abundance of Metazoa (ca. 58.1%) in winter, and the highest relative abundance of Fungi and Gyrista (ca. 28.9% and 14.0%, respectively) in summer. In contrast, the MW exhibited a higher relative abundance of Ciliophora (ca. 12.8%) in winter and Radiolaria (ca. 15.7%) in summer than the other water masses. In terms of ZOTU richness, picoeukaryotic communities exhibited slight variations between seasons and across water masses, being predominately composed of Syndiniales, followed by Gyrista, Dinophyceae, Ciliophora, Cercozoa, and other groups (Fig. 4).

Ordination based on Bray-Curtis dissimilarities (PCoA) and unweighted UniFrac distances (NMDS) revealed significant differences between the winter and summer communities (Fig. 5a, ANOSIM: $R = 0.443$, $p < 0.001$). Community heterogeneity among water masses was significantly higher in summer (ANOSIM: $R = 0.577$, $p < 0.001$) than in winter (ANOSIM: $R = 0.285$, $p < 0.005$) (Table S4). In winter, picoeukaryotic communities within the TWC formed a distinct cluster, while those in the other water masses were not well separated (Fig. 5b and Table S4). In summer, however, picoeukaryotic communities formed distinct clusters corresponding to their respective water masses (Fig. 5c and Table S4).

LEfSe analysis revealed a greater number of discriminant taxa within the identified water masses during summer (Fig. S3). In winter, the CCC harbored the highest number of discriminant taxa compared to the other water masses, including Fungi, Cryptophyta, and Cercozoa affiliated ZOTUs. Conversely, in summer, the TWC contained the highest number of discriminant taxa, harboring more Haptista, Archaeplastida,

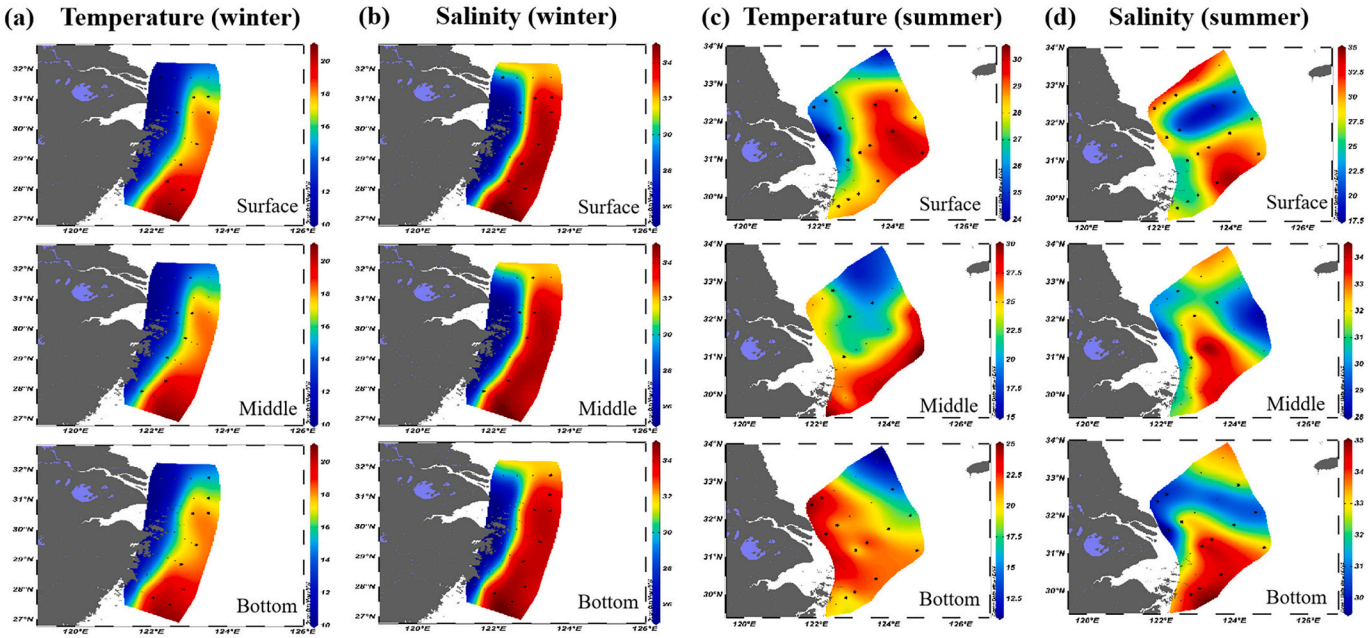

Fig. 2. Vertical distribution of water temperature (°C) (a, c) and salinity (b, d) across three sampling depths (surface, middle, and bottom) during winter (a, b) and summer (c, d) in the study area.

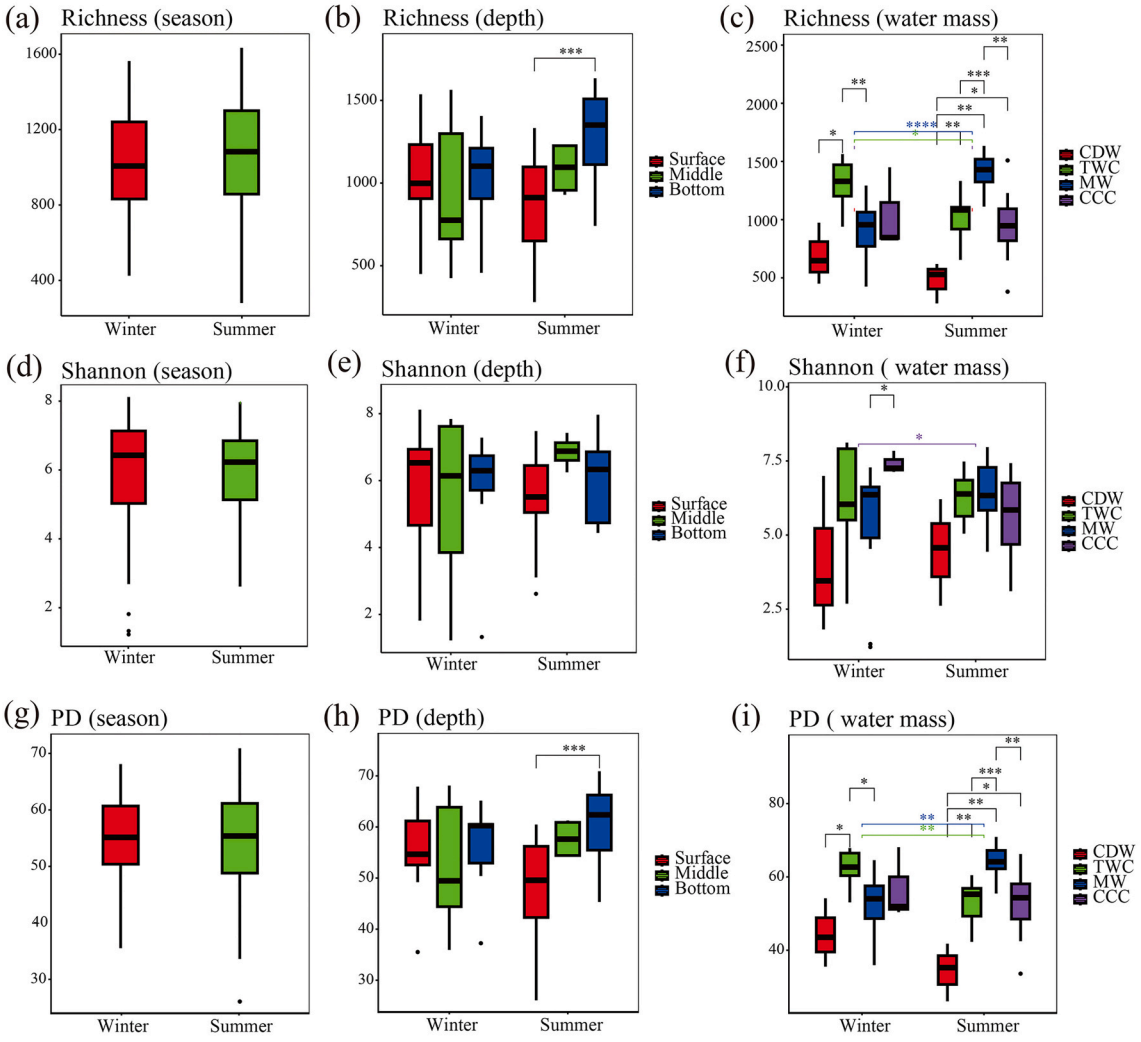

Fig. 3. Boxplots comparing alpha diversity indices, including ZOTU richness (a–c), Shannon index (d–f), and phylogenetic diversity (PD) (g–i), across seasons (a, d, g), depths (b, e, h), and water masses (c, f, i). The upper and lower boundaries of each box represent the 75th and 25th percentiles, respectively, while the horizontal line within each box indicates the median. Significant differences are marked by asterisks based on pairwise Wilcoxon tests (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$).

Dinoflagellata, and Telonemia affiliated ZOTUs than the other water masses. Additionally, more Radiolaria and Apusomonada-affiliated ZOTUs were found in the CCC and MW, respectively, while Ciliophora, Picozoa, and Cryptista were more abundant in the CDW.

3.5. Co-occurrence networks of picoeukaryotes

The winter and summer co-occurrence networks contained 4998, and 2800 edges connecting 391, and 541 nodes, respectively (Fig. 6a). Positive associations predominated in both networks, accounting for 98.7% of winter edges and 97.6% of summer edges. Within-module associations were primarily positive, whereas most negative associations occurred between modules (Fig. 6a). The three largest modules accounted for approximately 82.35% of all nodes in winter but only approximately 60% in summer, indicating that summer nodes were more evenly distributed among a larger number of modules. Thus, the summer network exhibited a more dispersed and compartmentalized modular organization, consistent with the stronger environmental and community differentiation observed among summer water masses and water layers.

During winter, members affiliated with Syndiniales, Ciliophora, Gyrista, Bigyra, and Dinophyceae were the major contributors to Module 1 (Fig. 6b). Module 2 was dominated by Gyrista and Bigyra, while Module 3 consisted primarily of Syndiniales ZOTUs and a few Radiolaria ZOTUs, exhibiting mainly positive correlations (Fig. 6c). Conversely, significant negative correlations were observed between two Ciliophora ZOTUs (ZOTU_282 and ZOTU_253) and several Syndiniales ZOTUs (Fig. 6c). ZOTU_282 was closely related with the parasitic genus *Cryptocaryon* (Table S5) and reached its highest average abundance in the CCC (173 reads), followed by the CDW (67 reads), MW (32 reads), and TWW (1 read). ZOTU_253 was closely related to Scuticociliatia, also peaking in the CCC (145 reads), followed by the CDW (54 reads), MW (48 reads), and TWW (3 reads). In summer, Module 1 included a broader assortment of taxa, with Syndiniales and Bigyra predominating (Fig. 6b). Module 2 was primarily composed of Syndiniales and Dinophyceae. Finally, Module 3 consisted predominantly of numerous Gyrista ZOTUs, accompanied by only a few ZOTUs representing Ciliophora and Cercozoa.

To assess the topological roles of taxa in the microbial networks, nodes were classified into four categories based on their within-module (Zi) and among-module (Pi) connectivity values: peripherals, connectors, module hubs, and network hubs (Deng et al., 2012). Most nodes in both networks were classified as peripherals, exhibiting predominantly intra-module connections. In the winter network, six module hubs and six connectors were identified, whereas the summer network contained nine module hubs and three connectors. These module hubs originated

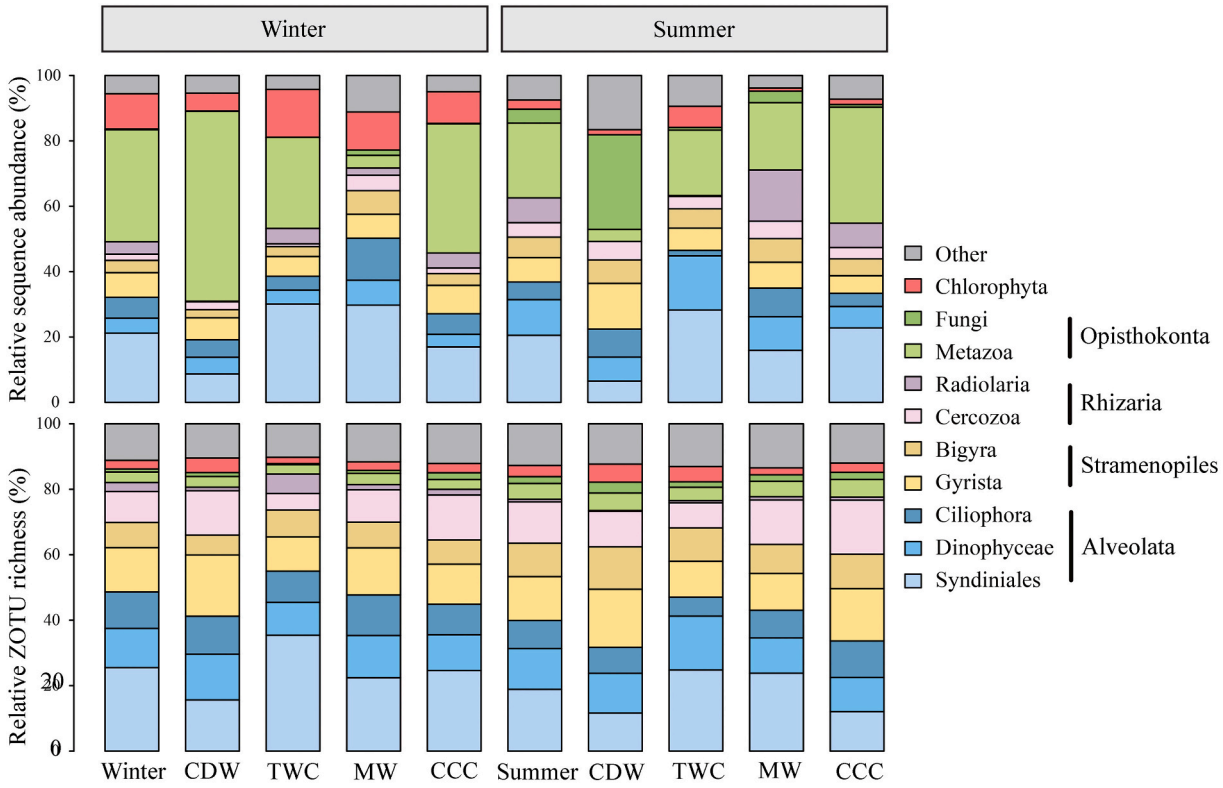

Fig. 4. Relative abundance of sequences (upper) and ZOTU richness (lower) for major taxonomic assemblages of picoeukaryotes across different seasons and water masses. CCC, China Coastal Current; CDW, Changjiang Diluted Water; MW, Mixed Water; TWC, Taiwan Warm Current.

from a diverse array of taxonomic groups, including Bigyra (with three belonging to Labyrinthulomycetes), Dinophyceae, Cercozoa, Ciliophora, Cryptophyceae, Gyrista, and Picozoa. A total of nine connectors were detected. Three belonged to Dinophyceae, while the remainder were affiliated with Ciliophora, Cryptophyceae, Gyrista, Picozoa, and Bigyra (Table S6). No network hubs were observed in either season.

The topological analysis of the microbial networks reveals distinct seasonal and spatial preferences among keystone taxa, highlighting the impact of environmental heterogeneity on network structure (Fig. 8). During winter, module hubs and connectors were broadly distributed across multiple water masses, indicating a more cosmopolitan ecological role likely facilitated by seasonal vertical mixing. Conversely, keystone taxa in summer exhibited relatively strict spatial sorting and highly specific water mass preferences. For example, summer module hubs within Module 2 were almost entirely restricted to the TWC, while hubs in Modules 1 and 3 were heavily concentrated in the MW and CCC, respectively. Summer connectors displayed similar environmental filtering, with specific taxa such as ZOTU_48 completely dominating within the CDW. This pronounced transition from widespread winter distributions to highly specialized summer compartmentalization suggests that summer water mass stratification strongly partitions the ecological niches of network hubs and connectors.

3.6. Effects of environmental factors on picoeukaryotic communities

Mantel tests indicated that, in winter, picoeukaryotic community composition was strongly influenced by geographic distance, water mass (represented by temperature and salinity), and environmental variations (represented by all biotic and abiotic factors except water temperature and salinity) (Table 2). After controlling for water mass and environmental variations, geographic distance maintained a significant effect on β-diversity. Conversely, when controlling for geographic distance, the effects of water mass and environmental variations on β-diversity became insignificant. In summer, community composition was primarily influenced by environmental variations and water mass, while geographic distance and depth exerted comparatively less influence (Table 2). When controlling for environmental factors and water mass, geographic distance showed a weaker influence on β-diversity. Environmental variation and water mass retained significant effects on β-diversity independent of other factors, whereas the effect of depth was not significant when other variables were controlled.

The goodness-of-fit (R^2) and the *Nm* values of the winter communities were greater than those of the summer communities (Fig. 7a), indicating that the winter communities were more heavily influenced by stochastic processes and exhibited higher species dispersal. Null model results further revealed that, in both seasons, dispersal limitation (a stochastic process) predominated in community assembly (Fig. 7b). However, heterogeneous selection contributed more significantly to the assembly of summer communities, whereas ecological drift was a stronger driver in winter community assembly. Furthermore, the average Levins' niche breadth of picoeukaryotic communities (Bcom) was significantly higher in winter than in summer (Mann-Whitney *U* test, $p < 0.001$) (Fig. 7c).

4. Discussions

4.1. Community composition and co-occurrence networks of picoeukaryotes

Metazoa-affiliated sequences, predominantly assigned to Arthropoda, were detected in the pico-sized fraction (Fig. S4). Given the body and cell sizes of the corresponding organisms, these sequences are unlikely to represent intact metazoans inhabiting the pico-sized fraction. Instead, aquatic environmental DNA may originate from cells or genetic material released through excretion, tissue shedding, mortality, predation, and decomposition (Geisen et al., 2015). It can occur as dissolved extracellular DNA, DNA adsorbed to suspended mineral or organic particles, DNA enclosed within detached cells or organelles, and DNA

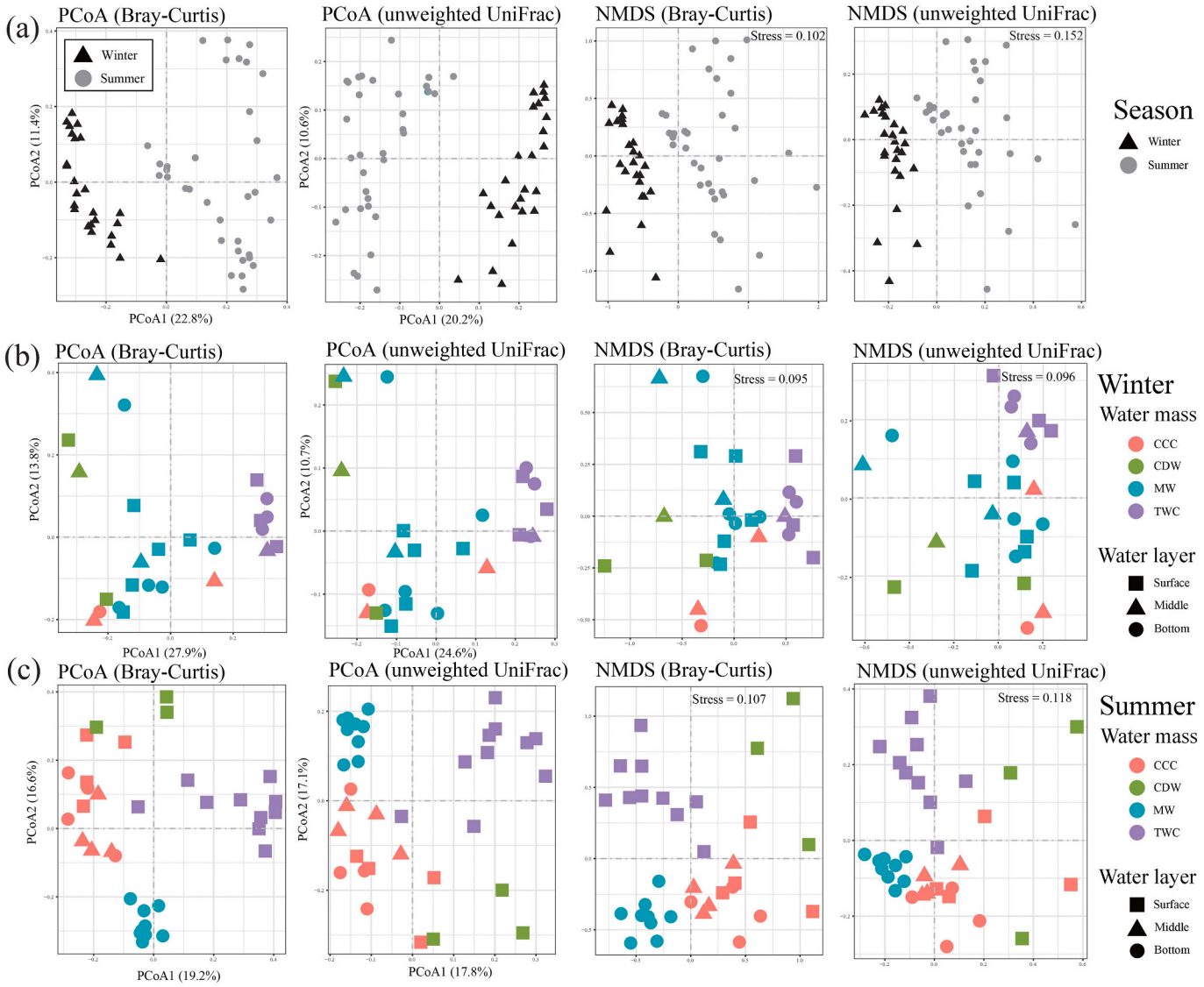

Fig. 5. Ordination plots of picoeukaryotic communities based on principal coordinate analysis (PCoA) of Bray-Curtis dissimilarities and non-metric multidimensional scaling (NMDS) of unweighted UniFrac distances. Plots display community structuring between seasons (a), as well as among water masses during winter (b) and summer (c). CCC, China Coastal Current; CDW, Changjiang Diluted Water; MW, Mixed Water; TWC, Taiwan Warm Current.

contained in tissue fragments (Mauvisseau et al., 2022). Compared with DNA-based metabarcoding, environmental RNA-based approaches may reduce signals derived from persistent extracellular or relic DNA and thereby improve the representation of metabolically active microbial eukaryotes, although RNA-based detection also has taxon-specific and methodological limitations (Hu et al., 2016; Kong et al., 2023; Xu et al., 2017).

The predominance of Dino-Group-I and Dino-Group-II further suggests that the pico-sized assemblage contained diverse parasitic lineages with potentially different host ranges and environmental preferences (Fig. S4). The dinoflagellate lineage Syndiniales represents a major parasitic group of protists capable of infecting diverse marine organisms, including ciliates, other dinoflagellates, and even multicellular animals (Guillou et al., 2008). Syndiniales have been reported to be ubiquitously distributed in both coastal and open-ocean waters worldwide (Christaki et al., 2017, 2023; Guo et al., 2020; Kong et al., 2023; Sassenhagen et al., 2020; Sehein et al., 2022) and sometimes dominate microbial eukaryotic communities (Fu et al., 2024; Nagarkar and Palenik, 2023). Morphological characterization of species within Syndiniales remains limited, as only a few species have been successfully isolated and studied (Jung et al., 2016). Among them, the genus *Amoebophrya* is one of the few groups that has been morphologically and experimentally studied. Studies on *Amoebophrya* have shown that the free-living stages (dinospores) are 2–5 μm in size (Park et al., 2019). Given that our sample fraction was restricted to <3 μm, the high proportion of Syndiniales affiliated sequences observed is likely indicative of these free-living dinospores. This life stage alternates between free-living infective dinospores and intracellular trophonts (Nagarkar and Palenik, 2023).

Syndiniales may influence estuarine carbon cycling by redirecting host biomass through both microbial recycling and trophic transfer. Intracellular infection converts host material into parasite biomass, while host rupture releases dinospores, cellular remains, and dissolved and particulate organic matter. Labile released material may stimulate heterotrophic bacterial production and nutrient remineralization, whereas dinospores and infected cellular remains may be consumed by microzooplankton or incorporated into sinking particles (Li et al., 2014; Anderson and Harvey, 2020; Anderson et al., 2024). Previous observations of *Amoebophrya* infection in the Changjiang River Estuary confirm that this pathway is potentially relevant to the regional plankton community (Li et al., 2014).

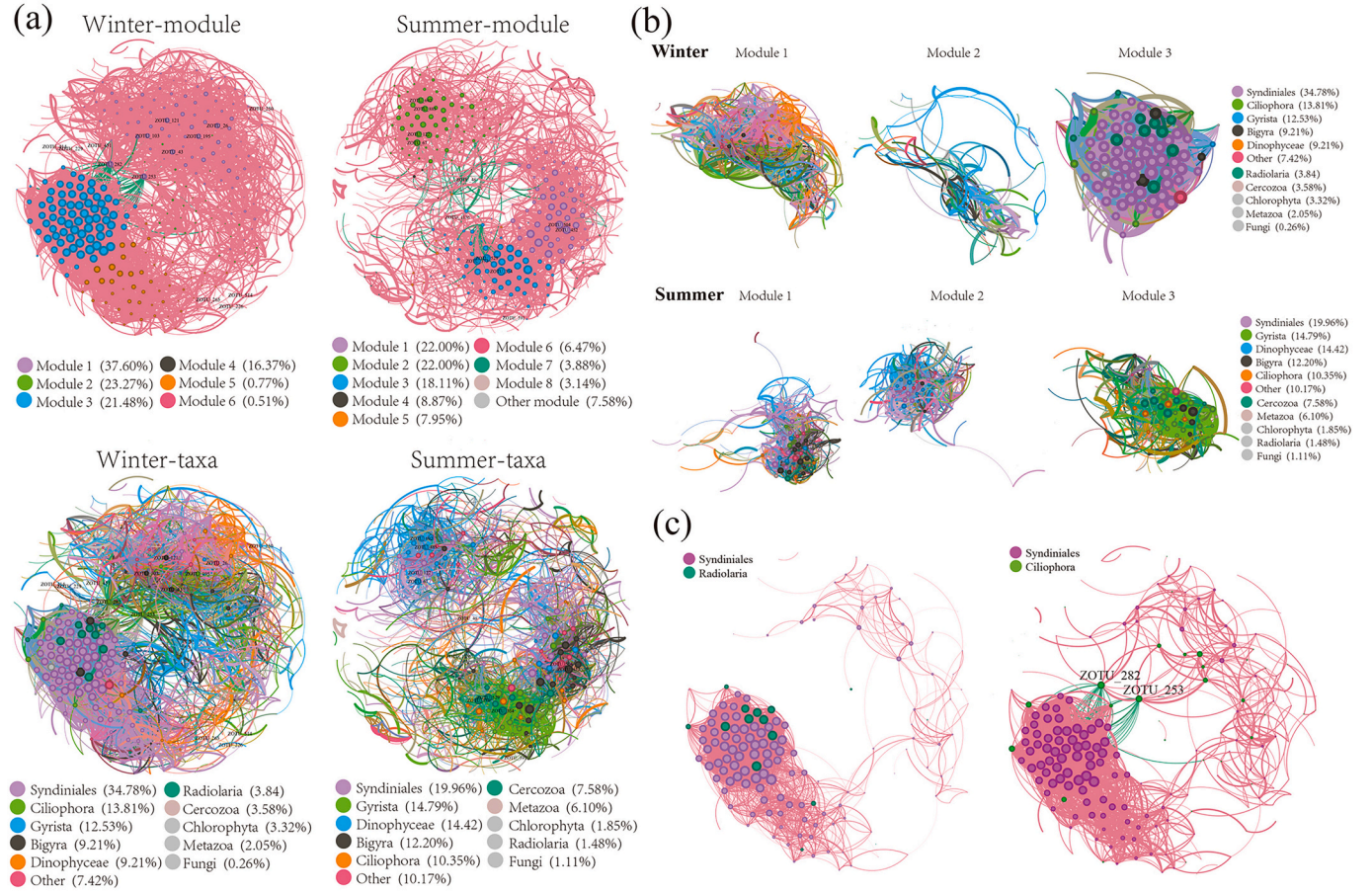

Fig. 6. Co-occurrence networks of picoeukaryotic communities during winter and summer. (a) Nodes are colored according to modularity classes and taxonomic identities. (b) The top three modules of picoeukaryotic communities in winter and summer. (c) Co-occurrence subnetworks between Syndiniales and Radiolaria, and between Syndiniales and Ciliophora during winter. Edges represent for strong (Spearman's $r > 0.7$ or $r < -0.7$) and significant ($p < 0.05$) correlations. Node size is proportional to the number of connections (i.e., degree).

Table 2
Results of simple and partial Mantel tests evaluating the effects of geographic distance, depth, environmental variables, and water mass on the β-diversity of picoeukaryotic communities.

Variables	Controlling factors	Winter		Summer	
		r	*p*	r	*p*
Geographic distance		**0.286**	**0.001**	**0.170**	**0.008**
Environment		**0.231**	**0.014**	**0.601**	**0.000**
Water mass		**0.296**	**0.012**	**0.589**	**0.000**
Depth		−0.080	0.783	**0.153**	**0.029**
Geographic distance	Environment & water mass	**0.252**	**0.001**	**0.167**	**0.010**
	Environment	**0.215**	**0.004**	**0.157**	**0.011**
	Water mass	**0.188**	**0.007**	**0.126**	**0.030**
Environment	Geographic distance	0.130	0.115	**0.599**	**0.000**
	Water mass	–	–	**0.440**	**0.000**
	Depth	–	–	**0.589**	**0.000**
Water mass	Geographic distance	0.204	0.052	**0.582**	**0.000**
	Environment	–	–	**0.420**	**0.000**
	Depth	–	–	**0.589**	**0.000**
Depth	Environment & water mass	–	–	−0.349	1.000
	Geographic distance	–	–	−0.149	0.973
	Environment	–	–	**0.150**	**0.029**
	Water mass	–	–	0.049	0.235

Water mass was represented by water temperature and salinity; environment was represented by all biotic and abiotic factors excluding water temperature and salinity. Numbers in bold indicate statistically significant results.

Seasonal hydrodynamics may determine where these processes occur. Winter mixing likely redistributed Syndiniales dinospores and potential hosts among depths and water masses, producing broadly distributed parasite-associated networks and spatially diffuse recycling of host-derived carbon. Conversely, summer stratification generated water-mass-specific host assemblages and more compartmentalized associations, potentially concentrating infection-driven mortality and organic-matter release within particular hydrographic habitats. Thus, winter mixing may broaden parasite-mediated connectivity, whereas summer stratification may create localized hotspots of host–parasite coupling and microbial remineralization. However, because co-occurrence networks represent statistical associations, the inferred links cannot confirm infection, host identity, or carbon transfer without direct microscopic and biogeochemical measurements.

Network analysis revealed that the picoeukaryotic community was organized into multiple modules of varying sizes (Fig. 6a, b). Modular organization is commonly observed in microbial systems, reflecting the integration and differentiation of ecological niches among taxa (Barberán et al., 2012; Steele et al., 2011). Positively correlated taxa often share similar or complementary functions, whereas negative correlations typically indicate niche differentiation arising from competition, predation, or ecological divergence. In our study, various potential parasitic groups were identified within specific modules, including Labyrinthulomycetes in winter Module 1, Syndiniales in Module 3, and Cercozoa (*Protaspis*) in summer Module 3. Most of these parasitic groups exhibited positive correlations within their respective modules, with negative correlations primarily occurring between different modules.

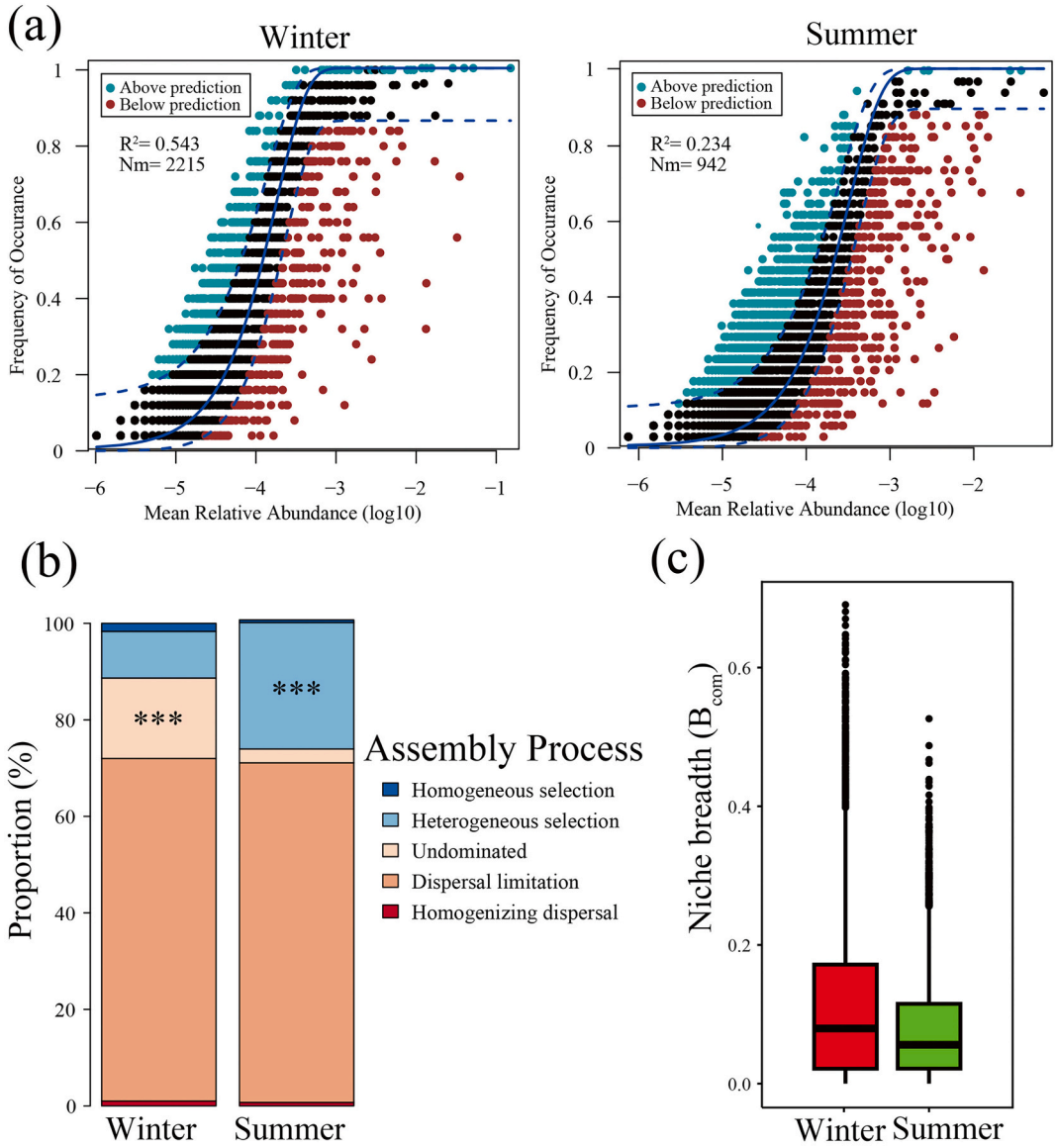

Fig. 7. (a) Fit of the neutral community model (NCM) for community assembly. *Nm* indicates the product of metacommunity size (*N*) and immigration rate (*m*), and R^2 indicates the overall goodness-of-fit to the model. (b) Relative contributions of various ecological processes to community assembly in winter and summer. Significant differences in assembly processes between seasons are denoted by asterisks (pairwise *Z*-test). (c) Boxplots illustrating the standardized Levins' niche breadth of picoeukaryotes at the community level (B_{com}) during winter and summer. Significant differences between seasons are denoted by asterisks (Mann-Whitney *U* test).

This pattern suggests that parasites belonging to a specific module may not induce sufficiently high mortality rates in their local hosts to trigger negative correlations. Interestingly, a similar tendency was reported by Berdjeb et al. (2018) when analyzing a high frequency (daily to weekly) network of parasitic OTUs (e.g., Syndiniales and Chytrids) and other taxa network at the San Pedro Ocean Time-series (SPOT). The mutual selective pressures exerted by hosts and parasites may drive rapid co-adaptation, thereby enhance their collective competitive capabilities when interacting with populations from other modules.

The more dispersed modular organization observed in summer was consistent with the stronger environmental differentiation generated by water-column stratification. Distinct temperature, salinity, nutrient, and dissolved-oxygen conditions among depths and water masses likely filtered taxa according to their environmental preferences, grouping taxa with similar realized niches into separate modules and reducing co-occurrence among different environmental compartments. In contrast, winter mixing homogenized water-column conditions and redistributed taxa across water masses and depths, resulting in a larger proportion of nodes being concentrated within a few dominant modules. Therefore, the network results suggest that summer stratification promoted water-mass-specific ecological compartmentalization, whereas winter mixing promoted a more integrated network structure. However, because these networks were based on correlations, the inferred links represent statistical co-occurrence patterns rather than confirmed ecological interactions (Barberán et al., 2012; Steele et al., 2011).

In the present study, Fungi constituted a significant proportion of sequences, reaching as high as 28.9% in the CDW during summer (Fig. 4). Previous research has indicated that in coastal environments, the copy number of the fungal SSU rRNA gene peaks in summer and autumn, a pattern associated with environmental factors including temperature, pH, Chl *a*, sunlight, salinity, and dissolved inorganic carbon (Derelle et al., 2016).

During summer, Cryptophyta emerged as a highly discriminant taxon in the CDW (Fig. S3). This distribution is likely attributable to the

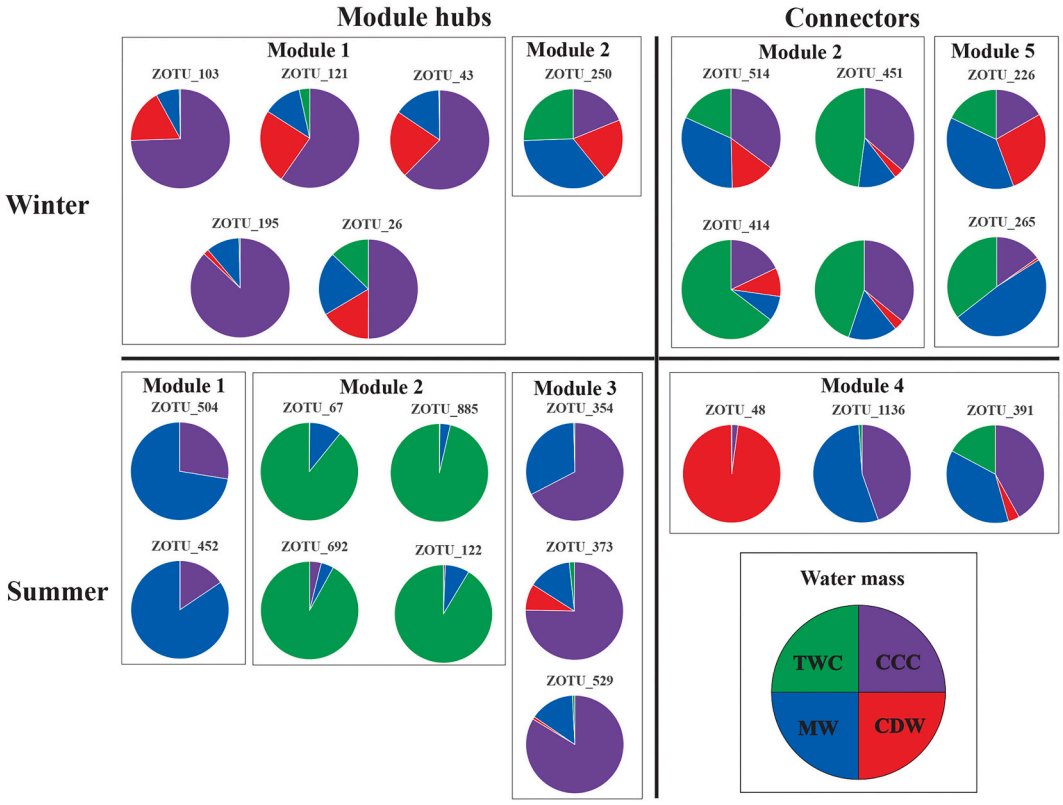

Fig. 8. Distribution of ZOTUs identified as connectors and module hubs in the co-occurrence networks across different water masses and seasons. CDW, Changjiang Diluted Water; TWC, Taiwan Warm Current; MW, Mixed Water; CCC, China Coastal Current.

relatively high bacterial abundance in this water mass (Fig. S1). Interestingly, although traditionally considered primarily autotrophic, Cryptophyta have been identified as key bacterivores in both freshwater (Grujcic et al., 2018) and marine systems (Unrein et al., 2014). Furthermore, Picozoa was also identified as a discriminant taxon within the CDW. Picozoa represents a group of phagotrophic protists discovered almost two decades ago. Recent studies have revealed that they are among the ten most abundant eukaryotic groups and are widely distributed across diverse marine environments (Huber et al., 2024). The presence of viral and bacterial genes within Picozoa genomes suggests that they actively graze on these organisms (Yoon et al., 1979). Consequently, the higher abundances of bacteria and viruses in the CDW compared to other summer water masses may indicate that Picozoa play a crucial role in mediating the microbial loop within these coastal diluted waters. Finally, Telonemia was identified as a discriminant taxon within the TWC during summer. However, it represents a relatively obscure major phylum of heterotrophic flagellates characterized by unique morphological features (Strassert et al., 2019). Further in-depth research is required to fully elucidate its functional role and grazing impact within the marine microbial food webs.

4.2. Environmental influencing factors on the distribution of picoeukaryotic communities differ between winter and summer

Water masses form different physical and chemical environments, thereby supporting diverse microbial communities. Strong coupling between water masses and microbial-eukaryotic community structure has also been reported in the Pearl River Estuary, Taiwan Strait, East China Sea, and Antarctic waters (Gu et al., 2021; Sun et al., 2020; Yang et al., 2020). However, most previous studies have been limited to a single season (primarily summer), leaving the seasonal influence of water masses on the composition and distribution of microbial eukaryotes largely unexplored. Our results extend this understanding by suggesting that the influence of water masses varies with seasonal hydrographic structure and becomes especially pronounced when stratification preserves their environmental distinctiveness.

In winter, apart from significant differences in picoeukaryotic community composition between the TWC and other water masses, no significant differences were found among the remaining water masses (Table S4). As shown in partial Mantel tests, when controlling for geographic distance, environmental variables, and water depth, the correlation between water masses and picoeukaryotic community composition was no longer significant (Table 2). Geographic distance, however, remained significantly correlated with community composition even when controlling for other variables, emerging as the primary factor droving changes in winter picoeukaryotic communities (Table 2). Summer stratification and winter mixing are persistent hydrographic features of the YRE and its adjacent ECS region (Chen et al., 2003; Chen, 2009; Jiang et al., 2015; Lie et al., 2003; Zhang et al., 2020). The water temperature, salinity, and depth data collected in the present study indicate that summer stratification confined water masses to specific depth ranges, while winter allowed them to span a much wider range of depths (Figs. S1 and 2). This dynamic is further supported by the observation that environmental heterogeneity among water masses was lower in winter than in summer. Thus, the physical separation of water masses is far less pronounced in winter. Consequently, we propose that the reduced influence of water masses on winter community was driven by the vertical mixing of seawater, which disrupted the pronounced stratification of water masses during the summer. This disruption homogenized the vertical spatial gradients and reduced environmental heterogeneity among the water masses, ultimately rendering geographical distance the primary factor dictating picoeukaryotic community distribution in winter.

4.3. Community assembly processes of picoeukaryotes

The coordinated seasonal changes in environmental heterogeneity, niche breadth, neutral-model fit, and iCAMP-inferred processes indicate that hydrodynamic conditions influenced PE community assembly through both habitat filtering and dispersal. Winter mixing homogenized environmental conditions and redistributed taxa across depth layers, reducing the strength of local ecological filters. Under these conditions, broadly distributed taxa were less strongly constrained by individual habitats, allowing passive dispersal, colonization history, and random demographic changes to exert greater influence on community composition. Given their inherently small cell size, picoeukaryotic communities, which, when assessed through DNA-based sequencing, often include spores, deceased individuals, or cellular fragmented, are particularly susceptible to stochastic processes. Previous studies have consistently identified dispersal limitation as a dominant assembly mechanism for marine planktonic microbial eukaryotic communities at both local and global scales, spanning coastal and open ocean waters (Logares et al., 2018a, 2018b; Sun et al., 2020; Xu et al., 2022; Fu et al., 2024). This dispersal limitation is primarily driven by two factors. First, the vast marine environment is partitioned by physical barriers, including distinct ocean currents, temperature gradients, and salinity fronts. For instance, the direction and velocity of prevailing ocean currents significantly dictate the distribution range of protists, impeding their ability to traverse specific water masses. Second, although many protistan taxa possess active micro-scale motility for feeding and local orientation, they lack the capacity for active, long distances migration. Consequently, they rely almost entirely on passive transport mechanisms, such as water currents, for large-scale dispersal. Furthermore, differential adaptive capacities among various protist species further restrict their successful dispersal and colonization in newly encountered habitats.

The seasonal divergence in picoeukaryotic community assembly was associated with simultaneous changes in environmental heterogeneity and realized niche breadth. Winter vertical mixing weakened physicochemical differentiation among depths and water masses, as indicated by the absence of significant environmental differences among the three water layers. Such environmental homogenization reduced the number and strength of distinct habitat filters acting on picoeukaryotic taxa. Taxa that might otherwise have been restricted to particular depths or water masses could therefore occur more evenly among winter samples, resulting in a significantly wider community-level Levins' niche breadth than in summer. Niche breadth can influence the balance between deterministic and stochastic community assembly. Taxa with broad niches can occur under a relatively wide range of environmental conditions and are consequently less strongly constrained by local environmental filters. Previous research suggests that a decrease in habitat heterogeneity reduces selective habitat preference, thereby elevating the relative importance of stochasticity over determinism (Legendre et al., 2009). Consequently, the enhanced water mixing observed in winter likely amplified the impact of stochastic birth and death processes, leading to the increased relative importance of ecological drift. Drift plays a critical role in the assembly of marine eukaryotic communities. For example, in the South China Sea, drift accounts for approximately 40% of the turnover in community composition from the coast to the basin (Sun et al., 2021). Furthermore, the narrower ecological niche width of picoeukaryotes in summer compared to the winter (Fig. 7c) explains why summer communities were subject to stronger heterogeneous selection. Taxa with wider ecological niches are generally less affected by environmental fluctuations, making them more adaptable new environments following passive dispersal (Pandit et al., 2009; Wu et al., 2018). Overall, our observations suggest that seasonal changes in hydrodynamic conditions can alter the relative contributions of stochastic and deterministic processes to picoeukaryotic community assembly.

5. Conclusions

Seasonal hydrological conditions were closely associated with contrasting picoeukaryotic community-assembly regimes in the Changjiang River Estuary and adjacent East China Sea. Winter vertical mixing weakened environmental differentiation among water masses and depth layers, broadened realized niche breadths, and increased the relative influence of stochastic processes, particularly dispersal limitation and ecological drift. In contrast, summer stratification maintained environmentally distinct habitats, promoted water-mass-specific community differentiation and network compartmentalization, and strengthened heterogeneous selection. These findings suggest that seasonal hydrodynamics regulate picoeukaryotic assembly by simultaneously modifying environmental filtering and the redistribution of taxa among habitats. The integration of water-mass classification, spatial and environmental analyses, niche-breadth estimation, ecological null models, and co-occurrence networks provides a mechanistic perspective on seasonal microbial variation in a complex river–estuary–shelf system. The seasonally reorganized distributions and associations of Syndiniales further suggest that hydrological stratification may influence the spatial organization of parasite–host coupling and microbial-loop carbon recycling. Because each season was represented by a single survey, these findings should be interpreted as a hydrodynamically associated winter–summer contrast. Multi-year, seasonally resolved observations are required to establish whether the proposed mechanism represents a stable seasonal pattern.

CRediT authorship contribution statement

Ran Li: Writing – original draft, Visualization, Validation, Investigation, Formal analysis. **Wenxin Fan:** Investigation, Formal analysis. **Xianghui Guo:** Resources, Investigation. **Yan Bai:** Resources, Investigation. **Ping Sun:** Writing – review & editing, Resources, Formal analysis. **Nianzhi Jiao:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Dapeng Xu:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

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.

Acknowledgements

This study was funded by the National Natural Science Foundation of China (no. 42188102, and 42276095) and the Ministry of Science and Technology (MOST) the Global Ocean Negative Carbon Emissions (Global ONCE) Program. Ran Li was also funded by the MEL Visiting Fellowship (MELRS2234) and Shandong Provincial Natural Science Foundation (no. ZR20230D167). We appreciate the assistance of Shixiang Huang and Yizhe Zhang in facilitating field sampling.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2026.120213.

Data availability

Amplicon sequencing data have been deposited in the NCBI Sequence Read Archive (SRA) under accession numbers PRJNA8468 and PRJNA1438588.

References

Anderson, M.J., 2014. Permutational multivariate analysis of variance (PERMANOVA). In: Wiley Statsref: Statistics Reference Online, pp. 1–15. https://doi.org/10.1002/9781118445112.stat07841.

Anderson, S.R., Harvey, E.L., 2020. Temporal variability and ecological interactions of parasitic marine Syndiniales in coastal protist communities. mSphere 5 (3), e00209–e00220. https://doi.org/10.1128/msphere.00209-20.

Anderson, S.R., Blanco-Bercial, L., Carlson, C.A., Harvey, E.L., 2024. Role of Syndiniales parasites in depth-specific networks and carbon flux in the oligotrophic ocean. ISME Commun. 4, ycae014. https://doi.org/10.1093/ismeco/ycae014.

Atteia, A., Bec, B., Gianaroli, C., Serais, O., Quétel, I., Lagarde, F., Gobet, A., 2024. Evaluation of sequential filtration and centrifugation to capture environmental DNA and survey microbial eukaryotic communities in aquatic environments. Mol. Ecol. Resour. 24 (1), e13887. https://doi.org/10.1111/1755-0998.13887.

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, F., 1983. The ecological role of water-column microbes in the Sea. Mar. Ecol. Prog. Ser. 10 (3), 257–263. https://doi.org/10.3354/meps010257.

Balzano, S., Abs, E., Leterme, S.C., 2015. Protist diversity along a salinity gradient in a coastal lagoon. Aquat. Microb. Ecol. 74 (3), 263–277. https://doi.org/10.3354/ame01740.

Barberán, A., Bates, S.T., Casamayor, E.O., Fierer, N., 2012. Using network analysis to explore co-occurrence patterns in soil microbial communities. ISME J. 6 (2), 343–351. https://doi.org/10.1038/ismej.2011.119.

Berdjeb, L., Parada, A., Needham, D.M., Fuhrman, J.A., 2018. Short-term dynamics and interactions of marine protist communities during the spring-summer transition. ISME J. 12 (8), 1907–1917. https://doi.org/10.1038/s41396-018-0097-x.

Bolger, A.M., Lohse, M., Usadel, B., 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinformatics 30 (15), 2114–2120. https://doi.org/10.1093/bioinformatics/btu170.

Brussaard, C.P.D., 2004. Optimization of procedures for counting viruses by flow cytometry. Appl. Environ. Microbiol. 70 (3), 1506–1513. https://doi.org/10.1128/AEM.70.3.1506-1513.2004.

Caron, D.A., Connell, P.E., Schaffner, R.A., Schnetzer, A., Fuhrman, J.A., Countway, P.D., Kim, D.Y., 2017. Planktonic food web structure at a coastal time-series site: I. Partitioning of microbial abundances and carbon biomass. Deep Sea Res. Part 1 Oceanogr. Res. Pap. 121, 14–29. https://doi.org/10.1016/j.dsr.2016.12.013.

Chapman, M., Underwood, A., 1999. Ecological patterns in multivariate assemblages: information and interpretation of negative values in ANOSIM tests. Mar. Ecol. Prog. Ser. 180, 257–265. https://doi.org/10.3354/meps180257.

Chen, C.-T.A., 2009. Chemical and physical fronts in the Bohai, Yellow and East China seas. J. Mar. Syst. 78 (3), 394–410. https://doi.org/10.1016/j.jmarsys.2008.11.016.

Chen, C., Zhu, J., Beardsley, R.C., Franks, P.J.S., 2003. Physical-biological sources for dense algal blooms near the Changjiang River. Geophys. Res. Lett. 30 (10), 1515. https://doi.org/10.1029/2002gl016391.

Chen, J., Bittinger, K., Charlson, E.S., Hoffmann, C., Lewis, J., Wu, G.D., et al., 2012. Associating microbiome composition with environmental covariates using generalized UniFrac distances. Bioinformatics 28, 2106–2113. https://doi.org/10.14814/phy2.14261.

Christaki, U., Genitsaris, S., Monchy, S., Li, L.L., Rachik, S., Breton, E., Sime-Ngando, T., 2017. Parasitic eukaryotes in a meso-eutrophic coastal system with marked *Phaeocystis globosa* blooms. Front. Mar. Sci. 4, 416. https://doi.org/10.3389/fmars.2017.00416.

Christaki, U., Skouroliakou, D.I., Jardillier, L., 2023. Interannual dynamics of putative parasites (Syndiniales Group II) in a coastal ecosystem. Environ. Microbiol. 25, 1314–1328. https://doi.org/10.1111/1462-2920.16358.

De Vargas, C., Audic, S., Henry, N., Decelle, J., Mahe, F., Logares, R., Lara, E., Berney, C., Le Bescot, N., Probert, I., Carmichael, M., Poulain, J., Romac, S., Colin, S., Aury, J.-M., Bittner, L., Chaffron, S., Dunthorn, M., Engelen, S., Flegontova, O., Guidi, L., Horák, A., Jaillon, O., Lima-Mendez, G., Lukeš, J., Malviya, S., Morard, R., Mulot, M., Scalco, E., Siano, R., Vincent, F., Zingone, A., Dimier, C., Picheral, M., Searson, S., Kandels-Lewis, S., Tara Oceans Coordinators, Acinas, S.G., Bork, P., Bowler, C., Gorsky, G., Grimsley, N., Hingamp, P., Iudicone, D., Not, F., Ogata, H., Pesant, S., Raes, J., Sieracki, M.E., Speich, S., Stemmann, L., Sunagawa, S., Weissenbach, J., Wincker, P., Karsenti, E., 2015. Eukaryotic plankton diversity in the sunlit ocean. Science 348 (6237), 1261605. https://doi.org/10.1126/science.1261605.

Deng, Y., Jiang, Y.H., Yang, Y., He, Z., Luo, F., Zhou, J., 2012. Molecular ecological network analyses. BMC Bioinformatics 13, 1–20. https://doi.org/10.1186/1471-2105-13-113.

Derelle, R., López-García, P., Timpano, H., Moreira, D., 2016. A Phylogenomic framework to study the diversity and evolution of Stramenopiles (=Heterokonts). Mol. Biol. Evol. 33 (11), 2890–2898. https://doi.org/10.1093/molbev/msw168.

Dixon, P., 2003. VEGAN, a package of R functions for community ecology. J. Veg. Sci. 14 (6), 927–930. https://doi.org/10.1111/J.1654-1103.2003.TB02228.X.

Edgar, R.C., 2010. Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26, 2460–2461. https://doi.org/10.1093/bioinformatics/btq461.

Edgar, R.C., 2016a. UNOISE2: improved error-correction for Illumina 16S and ITS amplicon sequencing. BioRxiv, 081257. https://doi.org/10.1101/081257.

Edgar, R.C., 2016b. SINTAX: a simple non-bayesian taxonomy classifier for 16S and ITS sequences. BioRxiv, 074161. https://doi.org/10.1101/074161.

Falkowski, P.G., Fenchel, T., Delong, E.F., 2008. The microbial engines that drive earth's biogeochemical cycles. Science 320 (5879), 1034–1039. https://doi.org/10.1126/science.1153213.

Fu, Y., Qu, Z., Wang, Y., Sun, P., Jiao, N., Xu, D., 2024. Biogeographical and biodiversity patterns of planktonic microeukaryotes along the tropical western to eastern Pacific Ocean transect revealed by metabarcoding. Microbiol. Spectr. 12 (4), e02424-23. https://doi.org/10.1128/spectrum.02424-23.

Gao, N., Yang, G.P., Zhang, H.H., Liu, L., 2017. Temporal and spatial variations of three dimethylated sulfur compounds in the Changjiang Estuary and its adjacent area during summer and winter. Environ. Chem. 14 (3), 160–177. https://doi.org/10.1071/EN16158.

Geisen, S., Laros, I., Vizcaíno, A., Bonkowski, M., De Groot, G.A., 2015. Not all are free-living: high-throughput DNA metabarcoding reveals a diverse community of protists parasitizing soil metazoa. Mol. Ecol. 24 (17), 4556–4569. https://doi.org/10.1111/mec.13238.

Grob, C., Ulloa, O., Li, W.K.W., Alarcón, G., Fukasawa, M., Watanabe, S., 2007. Picoplankton abundance and biomass across the eastern South Pacific Ocean along latitude 32.5°S. Mar. Ecol. Prog. Ser. 332, 53–62. https://doi.org/10.3354/meps332053.

Grujcic, V., Nuy, J.K., Salcher, M.M., Shabarova, T., Kasalicky, V., Boenigk, J., Jensen, M., Simek, K., 2018. Cryptophyta as major bacterivores in freshwater summer plankton. ISME J. 12 (7), 1668–1681. https://doi.org/10.1038/s41396-018-0057-5.

Gu, B., Wang, Y., Xu, J., Jiao, N., Xu, D., 2021. Water mass shapes the distribution patterns of planktonic ciliates (Alveolata, Ciliophora) in the subtropical Pearl River Estuary. Mar. Pollut. Bull. 167, 112341. https://doi.org/10.1016/j.marpolbul.2021.112341.

Guillou, L., Viprey, M., Chambouvet, A., et al., 2008. Widespread occurrence and genetic diversity of marine parasitoids belonging to Syndiniales (Alveolata). Environ. Microbiol. 10 (12), 3349–3365. https://doi.org/10.1111/j.1462-2920.2008.01731.x, 2008.

Guillou, L., Bachar, D., Audic, S., Bass, D., Berney, C., Bittner, L., Boutte, C., Burgaud, G., De Vargas, C., Decelle, J., Del Campo, J., Dolan, J.R., Dunthorn, M., Edvardsen, B., Holzmann, M., Kooistra, W.H.C.F., Lara, E., Le Bescot, N., Logares, R., Mahé, F., Massana, R., Montresor, M., Morard, R., Not, F., Pawlowski, J., Probert, I., Sauvadet, A.L., Siano, R., Stoeck, T., Vaulot, D., Zimmermann, P., Christen, R., 2013. The Protist Ribosomal Reference database (PR^2): a catalog of unicellular eukaryote small sub-unit rRNA sequences with curated taxonomy. Nucleic Acids Res. 41 (D1), D597–D604. https://doi.org/10.1093/nar/gks1160.

Guimera, R., Nunes Amaral, L.A., 2005. Functional cartography of complex metabolic networks. Nature 433 (7028), 895–900. https://doi.org/10.1038/nature03288.

Guo, X., Wu, L., Huang, L., 2020. Spatiotemporal patterns in diversity and assembly process of marine protist communities of the Changjiang (Yangtze River) plume and its adjacent waters. Front. Microbiol. 11, 579290. https://doi.org/10.3389/fmicb.2020.579290.

Hammer, Ø., Harper, D.A., 2001. Past: paleontological statistics software package for educaton and data anlysis. Palaeontol. Electron. 4 (1), 1. https://doi.org/10.1016/j.bcp.2008.05.025.

Hartmann, M., Grob, C., Tarran, G.A., Martin, A.P., Burkill, P.H., Scanlan, D.J., Zubkov, M.V., 2012. Mixotrophic basis of Atlantic oligotrophic ecosystems. Proc. Natl. Acad. Sci. U. S. A. 109 (15), 5756–5760. https://doi.org/10.1073/pnas.1118179109.

Hu, S.K., Campbell, V., Connell, P., Gellene, A.G., Liu, Z., Terrado, R., Caron, D.A., 2016. Protistan diversity and activity inferred from RNA and DNA at a coastal ocean site in the eastern North Pacific. FEMS Microbiol. Ecol. 92 (4), fiw050. https://doi.org/10.1093/femsec/fiw050.

Huber, P., De Angelis, D., Sarmento, H., Metz, S., Giner, C.R., De Vargas, C., Maiorano, L., Massana, R., Logares, R., 2024. Global distribution, diversity, and ecological niche of Picozoa, a widespread and enigmatic marine protist lineage. Microbiome 12, 162. https://doi.org/10.1186/s40168-024-01874-1.

Hurlbert, S.H., 1978. The measurement of niche overlap and some relatives. Ecology 59 (1), 67–77. https://doi.org/10.2307/1936632.

Hyde, K.D., Jones, E.B.G., Leaño, E., Pointing, S.B., Poonyth, A.D., Vrijmoed, L.L.P., 1998. Role of fungi in marine ecosystems. Biodivers. Conserv. 7 (9), 1147–1161. https://doi.org/10.1023/A:1008823515157/METRICS.

Ichikawa, H., Beardsley, R.C., 2002. The current system in the Yellow and East China Seas. J. Oceanogr. 58, 77–92. https://doi.org/10.1023/A:1015876701363.

Jiang, Z., Chen, J., Zhou, F., Shou, L., Chen, Q., Tao, B., Yan, X., Wang, K., 2015. Controlling factors of summer phytoplankton community in the Changjiang (Yangtze River) Estuary and adjacent East China Sea shelf. Cont. Shelf Res. 101, 71–84. https://doi.org/10.1016/j.csr.2015.04.009.

Jiao, N., Yang, Y., Koshikawa, H., Watanabe, M., 2002. Influence of hydrographic conditions on picoplankton distribution in the East China Sea. Aquat. Microb. Ecol. 30 (1), 37–48. https://doi.org/10.3354/ame030037.

Jing, H., Liu, H., Bird, D.F., Wong, T.H.C., Chen, X., Chen, B., 2010. Composition and seasonal variability of picoeukaryote communities at two subtropical coastal sites with contrasting trophic conditions. J. Plankton Res. 32 (4), 565–573. https://doi.org/10.1093/plankt/fbq002.

Jung, J., Choi, J., Coats, D.W., Kim, Y., 2016. *Euduboscquella costata* n. sp. (Dinoflagellata, Syndinea), an intracellular parasite of the ciliate *Schmidingerella arcuata*: morphology, molecular phylogeny, life cycle, prevalence, and infection intensity. J. Eukaryot. Microbiol. 63, 3–15. https://doi.org/10.1111/jeu.12231.

Kellogg, C.T.E., McClelland, J.W., Dunton, K.H., Crump, B.C., 2019. Strong seasonality in Arctic estuarine microbial food webs. Front. Microbiol. 10, 2628. https://doi.org/10.3389/fmicb.2019.02628.

Kong, H., Yang, E.J., Jiao, N., Lee, Y., Jung, J., Cho, K.H., Moon, J.K., Kim, J.H., Xu, D., 2023. RNA outperforms DNA-based metabarcoding in assessing the diversity and response of microeukaryotes to environmental variables in the Arctic Ocean. Sci. Total Environ. 876, 162608. https://doi.org/10.1016/j.scitotenv.2023.162608.

Latorre, F., Deutschmann, I.M., Labarre, A., Obiol, A., Krabberød, A.K., Pelletier, E., Sieracki, M.E., Cruaud, C., Jaillon, O., Massana, R., Logares, R., 2021. Niche

adaptation promoted the evolutionary diversification of tiny ocean predators. Proc. Natl. Acad. Sci. U. S. A. 118 (25), e2020955118. https://doi.org/10.1073/PNAS.2020955118.
Lee, H.J., Chao, S.Y., 2003. A climatological description of circulation in and around the East China Sea. Deep-Sea Res. II Top. Stud. Oceanogr. 50 (6–7), 1065–1084. https://doi.org/10.1016/S0967-0645(03)00010-9.
Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier.
Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I.-F., He, F., 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90 (3), 663–674. https://doi.org/10.1890/07-1880.1.
Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press.
Li, M., Xu, K., Watanabe, M., Chen, Z., 2007. Long-term variations in dissolved silicate, nitrogen, and phosphorus flux from the Yangtze River into the East China Sea and impacts on estuarine ecosystem. Estuar. Coast. Shelf Sci. 71 (1–2), 3–12. https://doi.org/10.1016/j.ecss.2006.08.013.
Li, C., Song, S., Liu, Y., Chen, T., 2014. Occurrence of *Amoebophrya* spp. infection in planktonic dinoflagellates in Changjiang (Yangtze River) estuary, China. Harmful Algae 37, 117–124. https://doi.org/10.1016/j.hal.2014.05.009.
Li, W., Wang, M., Pan, H., Burgaud, G., Liang, S., Guo, J., Luo, T., Li, Z., Zhang, S., Cai, L., 2017. Highlighting patterns of fungal diversity and composition shaped by ocean currents using the East China Sea as a model. Mol. Ecol. 27 (2), 564–576. https://doi.org/10.1111/mec.14440.
Li, R., Hu, C., Wang, J., Sun, J., Wang, Y., Jiao, N., Xu, D., 2021. Biogeographical distribution and community assembly of active protistan assemblages along an estuary to a basin transect of the Northern South China Sea. Microorganisms 9, 351. https://doi.org/10.3390/microorganisms9020351.
Lian, E., Yang, S., Wu, H., Yang, C., Li, C., Liu, J.T., 2016. Kuroshio subsurface water feeds the wintertime Taiwan Warm Current on the inner East China Sea shelf. J. Geophys. Res. Oceans 121 (7), 4790–4803. https://doi.org/10.1002/2016JC011869.
Liang, Y., Li, L., Luo, T., Zhang, Y., Zhang, R., Jiao, N., 2014. Horizontal and vertical distribution of marine virioplankton: a basin scale investigation based on a global cruise. PLoS One 9 (11), 1–11. https://doi.org/10.1371/journal.pone.0111634.
Lie, H.J., Cho, C.H., Lee, J.H., Lee, S., 2003. Structure and eastward extension of the Changjiang River plume in the East China Sea. J. Geophys. Res. Oceans 108 (3). https://doi.org/10.1029/2001jc001194.
Liu, Z., Gan, J., Hu, J., Wu, H., Cai, Z., Deng, Y., 2021. Progress on circulation dynamics in the East China Sea and southern Yellow Sea: origination, pathways, and destinations of shelf currents. Prog. Oceanogr. 193, 102553. https://doi.org/10.1016/J.POCEAN.2021.102553.
Logares, R., Deutschmann, I.M., Giner, C.R., Krabberød, A.K., Schmidt, T.S.B., Rubinat-Ripoll, L., Mestre, M., Salazar, G., Ruiz-González, C., Sebastián, M., 2018a. Different processes shape prokaryotic and picoeukaryotic assemblages in the sunlit ocean microbiome. BioRxiv, 374298. https://doi.org/10.1101/374298.
Logares, R., Tesson, S.V.M., Canbäck, B., Pontarp, M., Hedlund, K., Rengefors, K., 2018b. Contrasting prevalence of selection and drift in the community structuring of bacteria and microbial eukaryotes. Environ. Microbiol. 20 (6), 2231–2240. https://doi.org/10.1111/1462-2920.14265.
Magoč, T., Salzberg, S.L., 2011. FLASH: fast length adjustment of short reads to improve genome assemblies. Bioinformatics 27 (21), 2957–2963. https://doi.org/10.1093/bioinformatics/btr507.
Man-Aharonovich, D., Philosof, A., Kirkup, B.C., Le Gall, F., Yogev, T., Berman-Frank, I., Polz, M.F., Vaulot, D., Béjà, O., 2010. Diversity of active marine picoeukaryotes in the Eastern Mediterranean Sea unveiled using photosystem-II psbA transcripts. ISME J. 4, 1044–1052. https://doi.org/10.1038/ismej.2010.25.
Marie, D., Partensky, F., Vaulot, D., Brussaard, C., 1999. Enumeration of phytoplankton, bacteria, and viruses in marine samples. Curr. Protoc. Cytom. https://doi.org/10.1002/0471142956.cy1111s10.
Massana, R., 2011. Eukaryotic picoplankton in surface oceans. Annu. Rev. Microbiol. 65, 91–110. https://doi.org/10.1146/annurev-micro-090110-102903.
Massana, R., Gobet, A., Audic, S., Bass, D., Bittner, L., Boutte, C., Chambouvet, A., Christen, R., Claverie, J.-M., Decelle, J., 2015. Marine protist diversity in European coastal waters and sediments as revealed by high-throughput sequencing. Environ. Microbiol. 17 (10), 4035–4049. https://doi.org/10.1111/1462-2920.12955.
Mauvisseau, Q., Harper, L.R., Sander, M., Hanner, R.H., Kleyer, H., Deiner, K., 2022. The multiple states of environmental DNA and what is known about their persistence in aquatic environments. Environ. Sci. Technol. 56 (9), 5322–5333. https://doi.org/10.1021/acs.est.1c07638.
Metfies, K., Von Appen, W.J., Kilias, E., Nicolaus, A., Nöthig, E.M., 2016. Biogeography and photosynthetic biomass of arctic marine pico-eukaroytes during summer of the record sea ice minimum 2012. PloS One 11 (2). https://doi.org/10.1371/journal.pone.0148512.
Monier, A., Comte, J., Babin, M., Forest, A., Matsuoka, A., Lovejoy, C., 2015. Oceanographic structure drives the assembly processes of microbial eukaryotic communities. ISME J. 9 (4), 990–1002. https://doi.org/10.1038/ismej.2014.197.
Nagarkar, M., Palenik, B., 2023. Diversity and putative interactions of parasitic alveolates belonging to Syndiniales at a coastal Pacific site. Environ. Microbiol. Rep. 15 (3), 157–169. https://doi.org/10.1111/1758-2229.13138.
Pan, Y., Yang, J., McManus, G.B., Lin, S., Zhang, W., 2020. Insights into protist diversity and biogeography in intertidal sediments sampled across a range of spatial scales. Limnol. Oceanogr. 65 (5), 1103–1115. https://doi.org/10.1002/lno.11375.
Pandit, S.N., Kolasa, J., Cottenie, K., 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. Ecology 90 (8), 2253–2262. https://doi.org/10.1890/08-0851.1.
Piscoya, E., von Dassow, P., Aldunate, M., Vargas, C.A., 2022. Physical-chemical factors influencing the vertical distribution of phototrophic pico-nanoplankton in the Oxygen Minimum Zone (OMZ) off Northern Chile: the relative influence of low pH/low O_2 conditions. Mar. Environ. Res. 180, 105710. https://doi.org/10.1016/j.marenvres.2022.105710.
Piwosz, K., Całkiewicz, J., Gołębiewski, M., Creer, S., 2018. Diversity and community composition of pico- and nanoplanktonic protists in the Vistula River estuary (Gulf of Gdańsk, Baltic Sea). Estuar. Coast. Shelf Sci. 207, 242–249. https://doi.org/10.1016/j.ecss.2018.04.013.
Qiu, D., Huang, L., Zhang, J., Lin, S., 2010. Phytoplankton dynamics in and near the highly eutrophic Pearl River Estuary, South China Sea. Cont. Shelf Res. 30 (2), 177–186. https://doi.org/10.1016/J.CSR.2009.10.015.
Rii, Y.M., Peoples, L.M., Karl, D.M., Church, M.J., 2022. Seasonality and episodic variation in picoeukaryote diversity and structure reveal community resilience to disturbances in the North Pacific Subtropical Gyre. Limnol. Oceanogr. 67 (S1), S331–S351. https://doi.org/10.1002/lno.11916.
Rimmelin, P., Moutin, T., 2005. Re-examination of the MAGIC method to determine low orthophosphate concentration in seawater. Anal. Chim. Acta 548 (1–2), 174–182. https://doi.org/10.1016/j.aca.2005.05.071.
Samuelsson, K., Andersson, A., 2003. Predation limitation in the pelagic microbial food web in an oligotrophic aquatic system. Aquat. Microb. Ecol. 30 (3), 239–250. https://doi.org/10.3354/ame030239.
Sanders, R.W., Porter, K.G., 1988. Phagotrophic phytoflagellates. In: Advances in microbial ecology, pp. 167–192. https://doi.org/10.1007/978-1-4684-5409-3_5.
Sassenhagen, I., Irion, S., Jardillier, L., Moreira, D., Christaki, U., 2020. Protist interactions and community structure during early autumn in the Kerguelen Region (Southern Ocean). Protist 171 (1), 125709. https://doi.org/10.1016/j.protis.2019.125709.
Schlitzer, R., 2023. Ocean Data View. https://odv.awi.de.
Schloss, P.D., Westcott, S.L., Ryabin, T., Hall, J.R., Hartmann, M., Hollister, E.B., Lesniewski, R.A., Oakley, B.B., Parks, D.H., Robinson, C.J., Sahl, J.W., Stres, B., Thallinger, G.G., Van Horn, D.J., Weber, C.F., 2009. Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. Appl. Environ. Microbiol. 75, 7537–7541. https://doi.org/10.1128/AEM.01541-09.
Segata, N., Izard, J., Waldron, L., Gevers, D., Miropolsky, L., Garrett, W.S., Huttenhower, C., 2011. Metagenomic biomarker discovery and explanation. Genome Biol. 12, R60. https://doi.org/10.1186/gb-2011-12-6-r60.
Sehein, T.R., Gast, R.J., Pachiadaki, M., Guillou, L., Edgcomb, V.P., 2022. Parasitic infections by Group II Syndiniales target selected dinoflagellate host populations within diverse protist assemblages in a model coastal pond. Environ. Microbiol. 24 (4), 1818–1834. https://doi.org/10.1111/1462-2920.15977.
Sen, K., Sen, B., Wang, G., 2022. Diversity, abundance, and ecological roles of planktonic fungi in marine environments. J. Fungi 8 (5), 491. https://doi.org/10.3390/jof8050491.
Sloan, W.T., Lunn, M., Woodcock, S., Head, I.M., Nee, S., Curtis, T.P., 2006. Quantifying the roles of immigration and chance in shaping prokaryote community structure. Environ. Microbiol. 8 (4), 732–740. https://doi.org/10.1111/J.1462-2920.2005.00956.X.
Steele, J.A., Countway, P.D., Xia, L., Vigil, P.D., Beman, J.M., Kim, D.Y., Chow, C.E., Sachdeva, R., Jones, A.C., Schwalbach, M.S., Rose, J.M., Hewson, I., Patel, A., Sun, F., Caron, D.A., Fuhrman, J.A., 2011. Marine bacterial, archaeal and protistan association networks reveal ecological linkages. ISME J 5 (9), 1414–1425. https://doi.org/10.1038/ismej.2011.24.
Stegen, J.C., Lin, X., Fredrickson, J.K., Chen, X., Kennedy, D.W., Murray, C.J., Rockhold, M.L., Konopka, A., 2013. Quantifying community assembly processes and identifying features that impose them. ISME J. 7, 2069–2079. https://doi.org/10.1038/ismej.2013.93.
Stoeck, T., Bass, D., Nebel, M., Christen, R., Jones, M.D.M., Breiner, H.W., Richards, T.A., 2010. Multiple marker parallel tag environmental DNA sequencing reveals a highly complex eukaryotic community in marine anoxic water. Mol. Ecol. 1, 21–31. https://doi.org/10.1111/j.1365-294X.2009.04480.x.
Strassert, J.F.H., Jamy, M., Mylnikov, A.P., Tikhonenkov, D.V., Burki, F., 2019. New phylogenomic analysis of the enigmatic phylum Telonemia further resolves the eukaryote tree of life. Mol. Biol. Evol. 36 (4), 757–765. https://doi.org/10.1093/molbev/msz012.
Strickland, J., Parsons, T., 1972. A Practical Handbook of Seawater Analysis.
Sun, P., Wang, Y., Laws, E., Huang, B., 2020. Water mass–driven spatial effects and environmental heterogeneity shape microeukaryote biogeography in a subtropical, hydrographically complex ocean system - a case study of ciliates. Sci. Total Environ. 706, 135753. https://doi.org/10.1016/j.scitotenv.2019.135753.
Sun, P., Huang, X., Wang, Y., Huang, B., 2021. Protistan-bacterial microbiota exhibit stronger species sorting and greater network connectivity offshore than nearshore across a coast-to-basin continuum. mSystems 6 (5), 10–1128. https://doi.org/10.1128/msystems.00100-21.
Sun, P., Wang, Y., Huang, X., Huang, B., Wang, L., 2022. Water masses and their associated temperature and cross-domain biotic factors co-shape upwelling microbial communities. Water Res. 215, 118274. https://doi.org/10.1016/j.watres.2022.118274.
Unrein, F., Gasol, J.M., Not, F., Forn, I., Massana, R., 2014. Mixotrophic haptophytes are key bacterial grazers in oligotrophic coastal waters. ISME J. 8, 164–176. https://doi.org/10.1038/ismej.2013.132.
Villarino, E., Woodil, J., Barton, A., Massana, R., Salazar, G., Irigoien, X., Watson, J.R., Jönsson, B.F., Gasol, J.M., Giner, C.R., Duarte, C.M., Chust, G., 2018. Large-scale ocean connectivity and planktonic body size. Nat. Commun. 9, 142. https://doi.org/10.1038/s41467-017-02535-8.

Wang, K., Yan, H., Peng, X., Hu, H., Zhang, H., Hou, D., Chen, W., Qian, P., Liu, J., Cai, J., Chai, X., Zhang, D., 2020. Community assembly of bacteria and archaea in coastal waters governed by contrasting mechanisms: a seasonal perspective. Mol. Ecol. 29 (19), 3762–3776. https://doi.org/10.1111/mec.15600.

Wang, F., Huang, B., Xie, Y., Cai, S., Wang, X., Mu, J., 2021. Diversity, composition, and activities of nano-and pico-eukaryotes in the northern south China Sea with influences of Kuroshio intrusion. Front. Mar. Sci. 8, 658233. https://doi.org/10.3389/fmars.2021.658233.

Wu, W., Lu, H.-P., Sastri, A., Yeh, Y.-C., Gong, G.-C., Chou, W.-C., Hsieh, C.-H., 2018. Contrasting the relative importance of species sorting and dispersal limitation in shaping marine bacterial versus protist communities. ISME J. 12 (2), 485–494. https://doi.org/10.1038/ismej.2017.183.

Xu, D., Li, R., Hu, C., Sun, P., Jiao, N., Warren, A., 2017. Microbial eukaryote diversity and activity in the water column of the South China Sea based on DNA and RNA high throughput sequencing. Front. Microbiol. 8, 1121. https://doi.org/10.3389/fmicb.2017.01121.

Xu, D., Kong, H., Yang, E.J., Wang, Y., Li, X., Sun, P., Jiao, N., Lee, Y., Jung, J., Cho, K.H., 2022. Spatial dynamics of active microeukaryotes along a latitudinal gradient: diversity, assembly process, and co-occurrence relationships. Environ. Res. 212, 113234. https://doi.org/10.1016/j.envres.2022.113234.

Yang, J., Huang, S., Fan, W., Warren, A., Jiao, N., Xu, D., 2020. Spatial distribution patterns of planktonic ciliate communities in the East China Sea: potential indicators of water masses. Mar. Pollut. Bull. 156, 111253. https://doi.org/10.1016/j.marpolbul.2020.111253.

Yoon, H.S., Price, D.C., Stepanauskas, R., Rajah, V.D., Sieracki, M.E., Wilson, W.H., et al., 1979. Single-cell genomics reveals organismal interactions in uncultivated marine protists. Science 332, 714–717. https://doi.org/10.1126/science.1203163.

Zhang, H., Fennel, K., Laurent, A., Bian, C., 2020. A numerical model study of the main factors contributing to hypoxia and its interannual and short-term variability in the East China Sea. Biogeosciences 17 (22), 5745–5761. https://doi.org/10.5194/bg-17-5745-2020.

Zheng, Z., Zhuang, Y., Chen, H., Ge, R., Li, Y., Liu, G., 2022. Seasonality shapes community structure and functional group dynamics of zooplankton in Changjiang River estuary and its adjacent waters. Divers. Distrib. 28 (10), 2152–2170. https://doi.org/10.1111/ddi.13615.