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RESEARCH ARTICLE

Use of a broad β-diversity measure of pelagic ciliate communities for assessing vertical heterogeneity of water columns in the Pacific Arctic Ocean

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Abstract
Multivariate dispersion has proven to be a broad β-diversity measure that shows the heterogeneity of environmental conditions. The dispersion patterns of pelagic ciliate communities were investigated at eight water depths in the northern Bering Sea of the western Arctic Ocean and Chukchi Sea. Multivariate analysis indicated that (1) pelagic ciliates showed significant variability in multivariate dispersion on a vertical scale, (2) dispersion patterns were shaped by both the species composition and individual abundance, (3) vertical variation in species occurrence was significantly related to nutrients and chlorophyll *a*, and (4) the dispersion measures at both species occurrence and species abundance resolutions were significantly negatively related to salinity and dissolved oxygen. This suggests that multivariate dispersion measures driven by both species composition and the individual abundance of pelagic ciliates may be a useful indicator of environmental heterogeneity in marine ecosystems.

Keywords Multivariate dispersion · β-diversity · Bioassessment · Vertical heterogeneity · Pelagic ciliate · Arctic Ocean

Introduction

Pelagic ciliates are the primary factors in the microbial food webs in the ocean ecosystems (Cairns et al., 1972; Sherr and Sherr 1987; Stoecker and McDowell-Cappuzzo 1990; Sime-Ngando et al. 1995; Kchaou et al. 2009; Xu et al. 2017). They are important in the ecosystem processes, as they transfer the energy flux and carbon from the lower trophic levels to higher ones in most marine biotopes (Finlay et al. 1979, 1988; Caron and Goldmann 1990; Jiang et al. 2015). Thus, variation in the ciliate community structure can lead to significant changes in the ecosystem processes in marine environments (Yang et al. 2004, 2009, 2010; Jiang et al. 2013, 2014, 2015; Xu and Xu 2017). Furthermore, due to their sensitivity to environmental changes, short and simple life histories, and ease of sampling, they have been widely used to indicate water quality in marine ecosystems (Jiang et al. 2011, 2013; Xu et al. 2014b).

Whittaker (1972) originally proposed the concept of α, β, and γ components to represent different aspects of diversity. Subsequently, Anderson et al. (2006) proposed that the β-diversity can be measured as the variability in species composition among sampling units for a given area at a given spatial resolution and that this concept of β-diversity can be used to test the significance of differences in β-diversity among areas or groups through multivariate tests of homogeneity in dispersion. This measure is currently widely applied to assess the environmental heterogeneity of many ecosystems (e.g., Veech and Crist, 2010). The Jaccard and Sorensen dissimilarities are the classic measures for exploring the compositional pattern of a community (Sørensen 1948; Jaccard 1900; Chao et al. 2005; Anderson et al. 2006). Recent investigations have demonstrated that the Bray–Curtis dissimilarity is also a robust measure for summarizing the β-diversity of a community, as it is calculated from both relative abundance and compositional occurrence data (Bray and Curtis 1957; Ellingsen and Gray 2002; Magurran 2004; Olszewski 2004). However, a very important ecological issue is how much of the dissimilarity is driven by species composition and how much is driven by the relative abundance of species in a community (Anderson

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et al. 2006). This is difficult to solve using the Bray–Curtis dissimilarity matrix. Therefore, to articulate the degree of heterogeneity in species composition or in dispersions with greater specificity and confidence, it is better to use a range of dissimilarity measures that cover the spectrum from compositional change to changes in abundances (Anderson et al. 2006).

Anderson et al. (2006, 2008) proposed that multivariate dispersion can explain the β-diversity of a community on a broad scale and can be used as an index to assess the environmental heterogeneity. As a multivariate measure, however, multivariate dispersion has an advanced statistical property that may affect the difference in β-diversity of samples among different regions compared with the traditional β-diversity index (Anderson et al. 2008). Although studies indicate that multivariate dispersion is useful for indicating environmental heterogeneity (Ellingsen and Gray 2002; Xu et al. 2015a), very few studies have applied multivariate dispersion based on pelagic ciliate communities to the assessment of environmental heterogeneity.

In this study, the multivariate dispersion of pelagic ciliate communities was explored during a cruise in the western Arctic Ocean. Our purposes were (1) to explore the dispersion of pelagic ciliate assemblages at various water depths, (2) to reveal the drivers that shape the homogeneity of the ciliate communities, and (3) to assess the feasibility of using multivariate dispersion to assess the environmental heterogeneity in marine ecosystems using pelagic ciliate communities.

Materials and methods

Study stations

The Korean icebreaker Araon conducted a comprehensive scientific investigation on the Chukchi Sea and Northern Bering Sea in the western Arctic Ocean (including the Northwind Ridge and Chukchi Plateau) from 64°N to 80°N during summer (August 5–24, 2016; Fig. 1). A total of 23 sampling stations were visited (Fig. 1).

Data collection

A total of 85 samples were collected from eight water depths (from surface to 100 m) at 23 sampling stations during the period of August 5–24, 2016 (Fig. 1). The temperature, salinity, dissolved oxygen (DO), and density of water were measured in situ using a CTD rosette system (SBE 911+; Sea Bird Electronics).

Water samples for nutrient analysis (including 24 10-L Niskin bottles) were obtained from the CTD rosette sampler and immediately stored in a 2 °C refrigerator. Following the Joint Global Ocean Flux Study protocols, nitrite + nitrate ($NO_2 + NO_3$), ammonium (NH_4), phosphate (PO_4), and silicic acid [$Si(OH)_4$] were measured with a continuous autoanalyzer (QuAAtro, Seal Analytical). A 300–500 mL of water samples were collected from each depth and grinding glass fiber filters (47 mm; Gelman GF/F) for measurement of total chlorophyll *a* (Chl *a*). With a Turner Trilogy fluorometer, Chl *a* was concentrated after extraction with 90% acetone (Parsons et al. 1984). A 500-mL water samples per layer were collected to calculate the abundance of ciliates and stored at 4 °C after being fixed with Lugol's solution (4% v/v) (Kchaou et al. 2009; Pitta et al. 2001; Yang et al., 2016). A 20-mL concentrated sample was obtained by settling in a cylinder for 48 h by removing the upper water (Choi et al. 2012; Xu et al. 2018).

According to the description by Xu et al. (2018), the ciliates were identified and enumerated. A 1-mL aliquot of concentrated samples was used to measure the individual abundance. For species identification, the morphological features of the ciliates were observed at magnifications of 200–400 × under a light microscope (Olympus BX51). Species identification of tintinnids was performed according to lorica morphology based on the keys from Kofoid and Campbell (1929, 1939); the non-lorica ciliates were identified according to the description by Montagnes and Lynn (1991) and Song et al. (2003). The taxonomic scheme referred to Lynn (2008).

Data analyses

Estimation of species diversity at α, β, and γ levels was done as described by Crist and Veech (2006), Xu et al. (2014a, 2015b). The β-diversity index was calculated following the equation (Ricotta 2008):

$\beta = 1 – \alpha/\gamma$

where α is the α-diversity, β is the β-diversity, and γ is the γ-diversity.

The analyses for multivariate dispersions and community patterns of ciliate samples were conducted using the program PRIMER (v. 7.0.13), in which the routine "PERMANOVA" (v1.0.6) was hosted.

The measurement of multivariate dispersions (Z) was performed according to the average distance of samples to "centroid." Three dissimilarity matrices were selected to evaluate the weights of compositional occurrence (species composition) and/or relative abundance: Sorensen dissimilarity-based dispersion (Z_S) was responsible for species composition, Bray–Curtis dissimilarity-based dispersion (Z_{BC}) was for both species composition and individual abundance, and the modified Gower dissimilarity-based dispersion (Z_{MG}) is for only individual abundance (Anderson et al. 2006).

The community patterns were summarized using the metric multidimensional scaling (MDS) ordinations. For this ordination, the analysis "bootstrap averages" was done at all three resolutions above. The procedures RELATE and BEST\BIOENV were used to test the correlations between

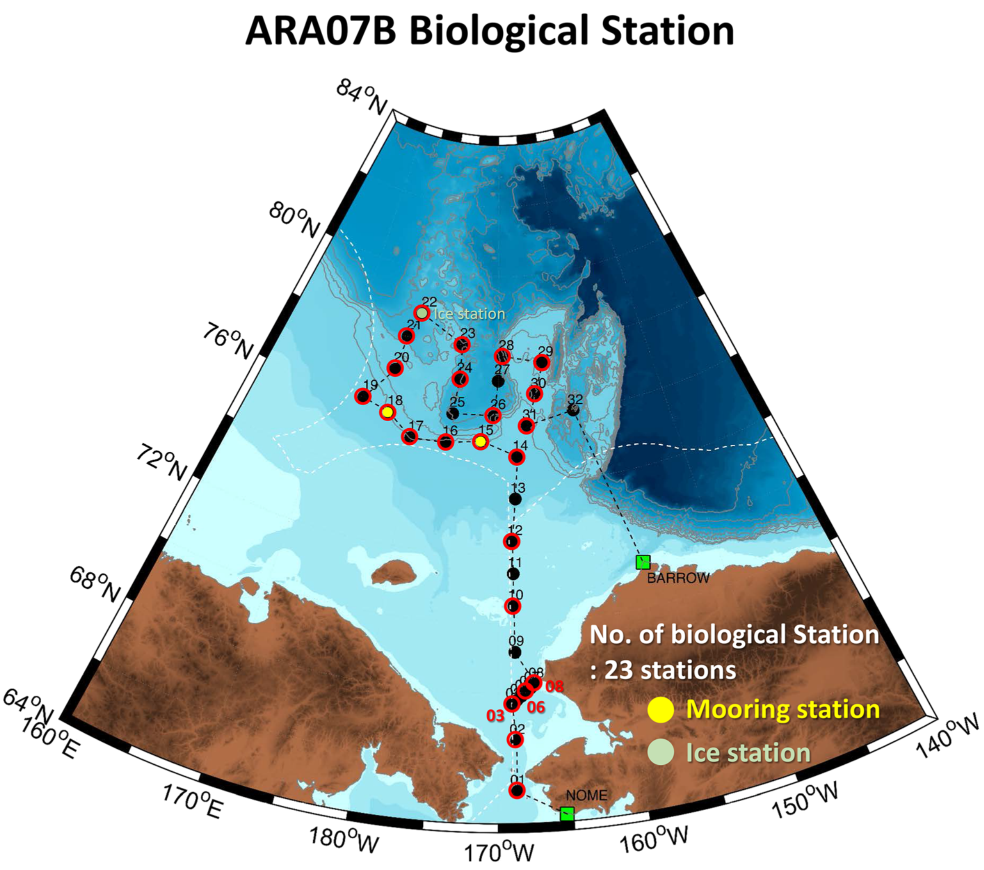

Fig. 1 Sampling stations: Korean icebreaker Araon in the Chukchi Sea of the western Arctic Ocean, encompassing the area from the Mendeleev Ridge to the Chukchi Borderland (including the Chukchi Plateau and Northwind Ridge) during summer from August 5 to 24, 2016

biological and environmental matrices and determine the 10 best combinations of environmental variables to the community patterns, respectively (Xu et al. 2015a).

Linear regression was used to detect the correlations between biological parameters and environmental variables using the software SPSS v22.0 (Xu et al. 2014a).

Results

Environmental conditions

Table S1 shows the average environmental conditions for eight depth ranges. There was clear vertical variability among the eight environmental variables at the eight depths. For example, the average water temperature decreased with increasing depth, whereas the PO_4, $Si(OH)_4$, and $NO_2 + NO_3$ all increased with depth. Chl *a* and NH_4 were highest at 40–50 m and lowest at 100 m.

Species richness and distribution

The distribution and abundance of the 44 ciliate species observed during this cruise are shown in Table S2. According to the γ-diversity in Table 1, 47, 33, 28, 26, 29, 24, 20, and 21 species were recorded at 0–10, 10–20, 20–30, 30–40, 40–50, 50–60, 60–80, and 100 m, respectively.

Rarefied analysis implied that the total species richness (γ-diversity) declined from the surface layer (46.7) to 100 m (20.7), whereas the difference in species richness (β-diversity) decreased from 0 to 60 m and then increased from 60 to 100 m, peaking at 100 m (Table 1). However, the average species richness (α-diversity) had a different pattern, decreasing from 0 to 30 m, increasing from 30 to 60 m with a peak at 40–50 m, and then dropping at 60 m (Table 1).

Vertical variations in community structure

The metric multidimensional scaling ordinations based on bootstrap average analyses for the ciliate community structures at three dissimilarity resolutions are shown in Fig. 2. All three community structure patterns were similar along the depth gradient. For example, the increase in samples at 100 m was distinct from that at other depths, and most samples showed lower variance at depths of 50–60 and 60–80 m than at other depths (Fig. 2).

Vertical variations in dispersion measure

Figure 3 shows the average dispersion of the samples at all three dissimilarity resolutions. All three dispersions generally

Table 1 α-, β- and γ-diversity indices of the pelagic ciliate communities at eight layers in the Chukchi Sea and the northern Bering Sea of the western Arctic Ocean during the summer sea ice reduction period (August 5–24, 2016)

Parameters	0–10 m	10–20 m	20–30 m	30–40 m	40–50 m	50–60 m	60–80 m	100 m
α-diversity	8.6	7.3	5.5	6.9	8.4	7.8	4.6	0.8
β-diversity	0.82	0.78	0.80	0.73	0.71	0.67	0.77	0.96
γ-diversity	46.7	32.7	27.8	25.9	28.5	23.7	20.3	20.7

leveled off from the surface layer to 50 m, then dropped sharply until 80 m, and finally peaked at 100 m (Fig. 3). Linear regression showed significant correlations between the dispersions Z_S ($R^2 = 0.539$, $P < 0.05$) and Z_{BC} ($R^2 = 0.484$, $P < 0.05$) and the β-diversity index (Fig. 4).

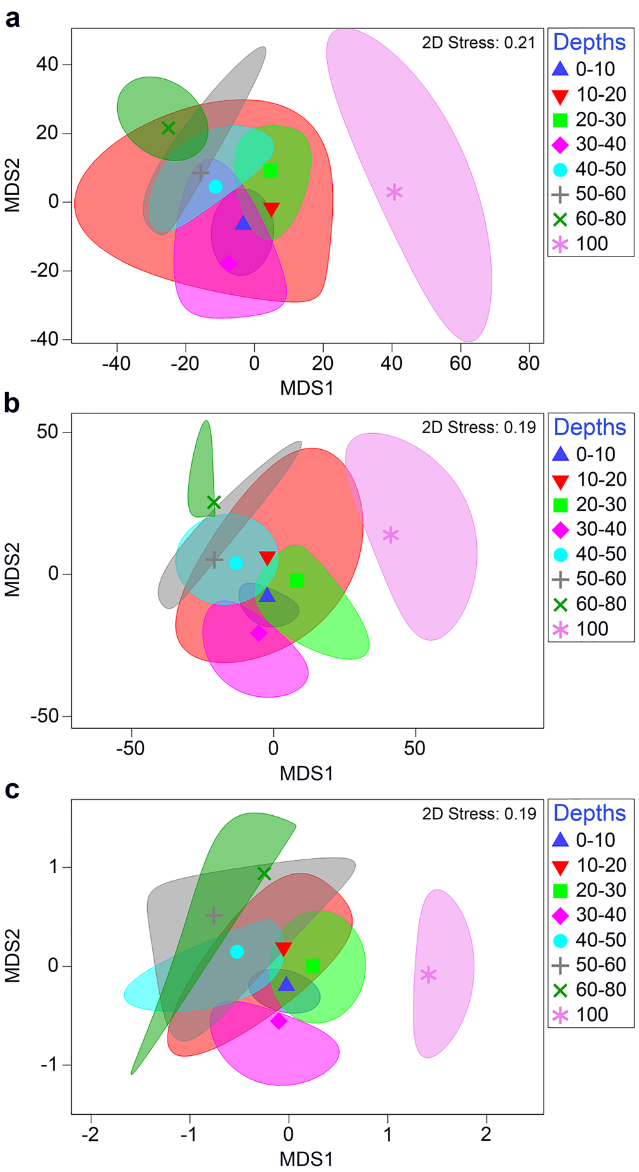

Fig. 2 Metric MDS ordinations based on the analysis of bootstrapped averages, showing the vertical pattern of the pelagic ciliate communities based on Sorensen (a), Bray–Curtis (b), and modified Gower (c) dissimilarity matrices among eight water depths during the study period

Linkage between pelagic ciliate data and environmental variables

The RELATE test demonstrated that the community patterns were significantly correlated with environmental variables at all three dissimilarity resolutions: species composition with a correlation at $P = 0.287$ ($P < 0.05$), community structure with $P = 0.309$ ($P < 0.05$), and individual abundance with $P = 0.363$ ($P < 0.05$).

The BIOENV analysis showed that the vertical change in community patterns in species composition/occurrence and community structure were driven by the combination of PO_4 and sum of $NO_3 + NO_2$ and that individual abundance was shaped by ammonia and chlorophyll *a* (Table 2).

Univariate correlation analyses revealed that the dispersion index based on both species composition (Z_S) and community structure (Z_{BC}) was remarkably positively related to the nutrients $NO_2 + NO_3$ and SiO_2 but negatively correlated with the DO concentration and Chl *a* ($P < 0.05$), similar to the β-diversity measure (Table 2). The dispersion index calculated from the modified Gower dissimilarity matrix was significantly correlated with the nutrient NH_4 (Table 3).

Discussion

Many studies have shown that multivariate dispersion can be used as a measure of β-diversity, but decisions about how data are transformed before analysis and how dissimilarity measures are chosen are crucial to the results (e.g., Ellingsen and Gray 2002; Anderson et al. 2006; Xu et al. 2015a). In this study, we used three different dissimilarity measures to evaluate the weights of compositional occurrence and relative abundance. For species composition, community structure, and abundance with an order of magnitude change, the dispersion of ciliate communities showed clear vertical variation along the depth gradient. The correlation analysis revealed that the vertical shift in community pattern at all three dissimilarity resolutions was mainly driven by nutrients (PO_4, NH_4, and $NO_2 + NO_3$), alone or in combination with temperature and salinity. Otherwise, all of the dispersion measures based on the three dissimilarity matrices were significantly correlated with the sum of $NO_2 + NO_3$ or NH_4. This implies that

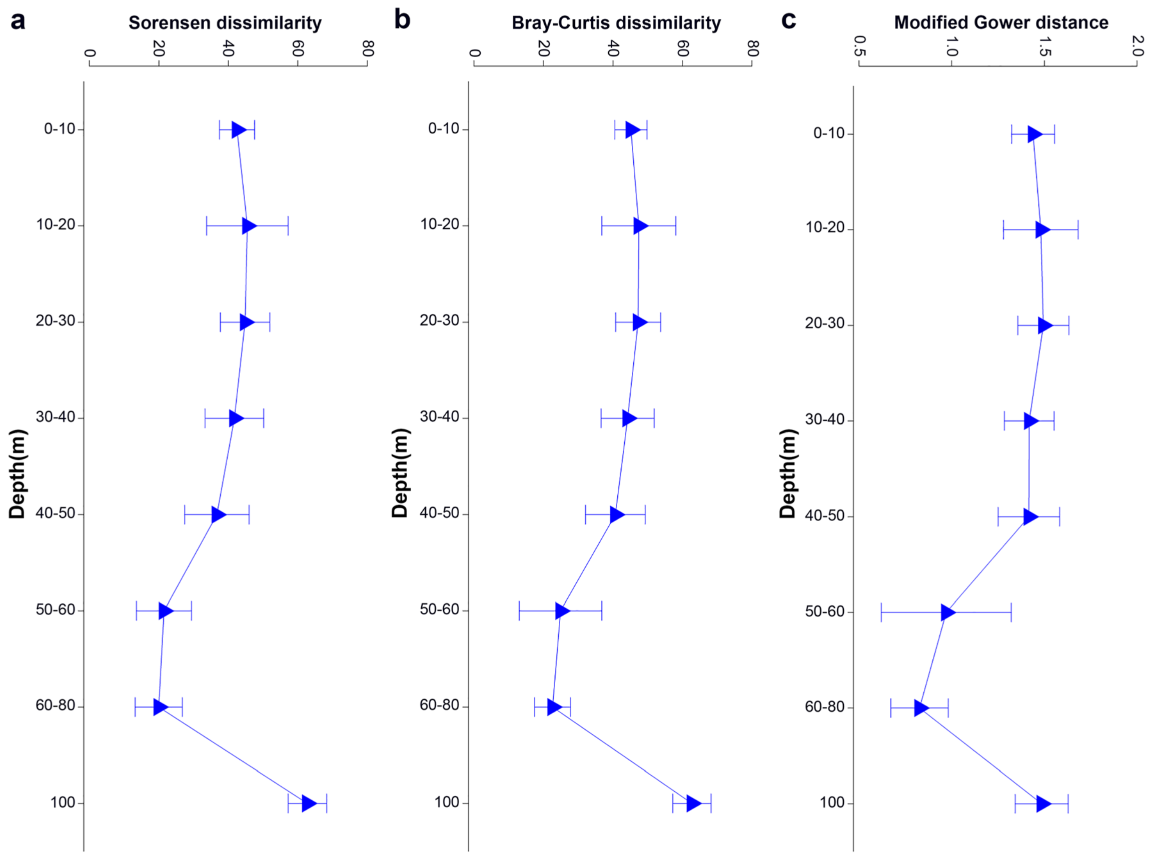

Fig. 3 Vertical variations in multivariate dispersions of the pelagic ciliate communities based on Sorensen (a), Bray–Curtis (b), and modified Gower (c) dissimilarity matrices among eight water depths during the study period

the dispersion measures reflect the environmental heterogeneity in different water layers. For example, the highest average dispersion measure occurred at 100-m depth, and the lowest was found at 60–80 m. This means that the dispersion of the phytoplankton communities can be used to assess vertical heterogeneity in marine ecosystems.

Here, we used three different dissimilarity measures to assess vertical heterogeneity of water columns in the Pacific Arctic Ocean. The dispersion measures at both community structure and species composition resolutions (i.e., z_S and z_{BC}, respectively) were significantly correlated with the traditional β-diversity index and reflected the heterogeneity in water quality status among different layers. This finding was consistent with Anderson et al. (2006), who proposed that the β-diversity can be measured as the average distance from each sample to the group centroid based on an appropriate dissimilarity measure. Otherwise, the dispersions of compositional pattern and community structure exhibit significant correspondence to the traditional β-diversity index and are significantly correlated with the concentrations of nutrients and Chl *a*. These findings suggest that the distribution patterns

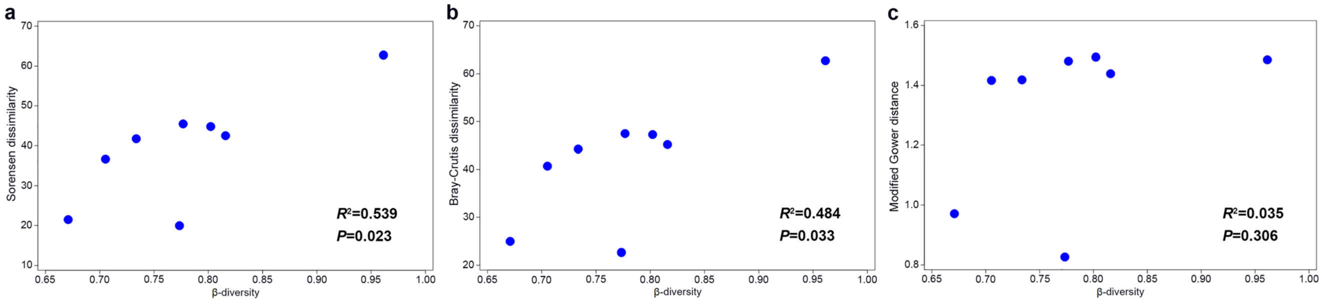

Fig. 4 Linear relationships between the dispersion measures of the pelagic ciliate communities based on Sorensen (a), Bray–Curtis (b), and modified Gower (c) dissimilarity matrices and β-diversity index among eight water depths during the study period

Table 2 Summary of results from biota-environment (BIOENV) analysis showing the 10 best matches of environmental variables with spatial variations in the pelagic ciliate species composition, community structure, and community pattern in abundance at eight layers in the water column during the study period

Rank	Species composition		Community structure		Variation in abundance	
	P value	Env-var	*P* value	Env-var	*P* value	Env-var
1	0.236	T, PO_4, $NO_2 + NO_3$	0.260	T, PO_4, $NO_2 + NO_3$	0.395	NH_4, Chl *a*
2	0.229	T, PO_4, $NO_2 + NO_3$, SiO_2	0.249	T, $NO_2 + NO_3$	0.393	T, Sal, $NO_2 + NO_3$, Chl *a*
3	0.226	T, $NO_2 + NO_3$, SiO_2	0.248	T, PO_4, $NO_2 + NO_3$, SiO_2	0.392	T, Sal, $NO_2 + NO_3$, NH_4, Chl *a*
4	0.225	T, $NO_2 + NO_3$	0.247	T, DO, PO_4, $NO_2 + NO_3$	0.390	Sal, NH_4, Chl *a*
5	0.224	T, DO, PO_4	0.246	T, Sal, PO_4, $NO_2 + NO_3$	0.388	T, DO, $NO_2 + NO_3$, NH_4, Chl *a*
6	0.224	T, DO, PO_4, $NO_2 + NO_3$	0.245	T, $NO_2 + NO_3$, SiO_2	0.387	T, DO, $NO_2 + NO_3$, Chl *a*
7	0.223	T, Sal, DO, PO_4, $NO_2 + NO_3$	0.244	T, Sal, DO, PO_4, $NO_2 + NO_3$	0.384	T, Sal, DO, $NO_2 + NO_3$, Chl *a*
8	0.220	T, PO_4, SiO_2	0.242	T, PO_4, SiO_2	0.383	T, $NO_2 + NO_3$, NH_4, Chl *a*
9	0.219	T, DO, PO_4, $NO_2 + NO_3$, SiO_2	0.240	T, DO, $NO_2 + NO_3$	0.382	T, Sal, $NO_2 + NO_3$, SiO_2, Chl *a*
10	0.218	T, Sal, PO_4, $NO_2 + NO_3$, SiO_2	0.239	T, Sal, $NO_2 + NO_3$	0.380	Sal, $NO_2 + NO_3$, NH_4, Chl *a*

P, Spearman correlation coefficient, *Env-var* environmental variables, *T* temperature (°C), *Sal* salinity, *DO* dissolve oxygen (ug/L), *PO_4* soluble active phosphate (umol/L), *NO_3* nitrate (umol/L), *NO_2* nitrite (umol/L), *NH_4* ammonium (umol/L), *Chl a* chlorophyll *a* (ug/L)

of both species composition and community structure may be used as a broad β-diversity index to indicate environmental heterogeneity in marine ecosystems.

Note that the community pattern at the modified Gower dissimilarity resolution was significantly correlated with the other two dissimilarity resolutions. This suggests that the dispersion of pelagic ciliates is shaped by both compositional occurrence and abundance. Furthermore, the dispersion measure ($\mathcal{Z}_{MG}$) based on this dissimilarity matrix was strongly positively related to NH_4, but negatively related to the other nutrients. Therefore, we suggest that the dispersions at a modified Gower dissimilarity resolution can also be considered a broad β-diversity measure.

Table 3 Correlations between dispersion measures based on Sorensen ($\mathcal{Z}_S$), Bray–Curtis ($\mathcal{Z}_{BC}$), and modified Gower ($\mathcal{Z}_{MG}$) dissimilarity with β-diversity and environmental variables

Parameters	$\mathcal{Z}_S$	$\mathcal{Z}_{BC}$	$\mathcal{Z}_{MG}$	β-diversity
Temp	0.029	0.075	0.486	−0.396
Sal	−0.523	−0.528	−0.558	−0.291
DO	−0.417	−0.384	−0.012	−0.551
PO_4	0.279	0.250	−0.107	0.458
$NO_2 + NO_3$	0.096	0.072	−0.240	0.303
NH_4	0.072	0.116	0.403	0.439
SiO_2	0.202	0.179	−0.129	0.335
Chl *a*	−0.305	−0.260	0.096	−0.787

Temp temperature (°C), *Sal* salinity, *DO* dissolve oxygen (ug/L), *PO_4* soluble active phosphate (umol/L), *NO_3* nitrate (umol/L), *NO_2* nitrite (umol/L), *NH_4* ammonium (umol/L), *Chl a* chlorophyll *a* (ug/L)

Conclusions

In summary, the phytoplankton community showed gradient heterogeneity in community structure, species composition, and species abundance across the eight water layers. Multivariate analytical methods showed that the community dispersion was mainly driven by species occurrence and cell numbers. The Mantel analysis showed that the spatial changes in community structure, species abundance, and species composition were significantly correlated with the changes in environmental variables. The dispersion measures at both numerical resolutions showed a close linear relationship with the traditional β-diversity index, but the three resolutions were found to be remarkably related to nutrients. This means that the dispersion measure of pelagic ciliate communities can be applied to monitor the environmental heterogeneity of marine ecosystems.

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