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Contributions of Transparent Exopolymer Particles by Specific Phytoplankton Groups in the Cosmonaut Sea, East Antarctic

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Abstract: Transparent exopolymer particles (TEP) play a crucial role in marine carbon cycling. While phytoplankton are known to be the primary contributors to TEP, the impact of changes in phytoplankton community structure on TEP production in natural aquatic environments remains incompletely understood. This study employed multiple linear regression (MLR) modeling to quantify the contributions of two dominant phytoplankton groups, diatoms and haptophytes (primarily *Phaeocystis antarctica*), to TEP production in the surface waters of the Cosmonaut Sea, antarctica during the austral summer. Results demonstrate that in situ TEP production by each group can be estimated by scaling laboratory-derived theoretical values with an environmentally adjusted correction factor (β). These β factors, primarily governed by phytoplankton community structure, reveal taxon-specific discrepancies between field and laboratory TEP production capacities. Notably, temperature, ammonium, and polysaccharide composition act as secondary modifiers of β through indirect physiological effects. This study revealed that when the chlorophyll *a* concentration (Chl *a*) of *P. antarctica* exceeds 0.5 μg/L in the Cosmonaut Sea, its TEP production capacity surpasses that of diatoms at equivalent biomass levels—challenging the paradigm of diatom-dominated TEP contributions. In the research area, *P. antarctica* contributed 14.6 – 82.5% (mean: 48.6 ± 15.4%) to total TEP production, while diatoms contributed 31.0 – 112.0% (mean: 55.1 ± 21.2%; values >100% reflect co-occurring group contributions). This highlights the pivotal role of *P. antarctica* in Southern Ocean carbon cycling and provides mechanistic insights for refining polar carbon budget models.

Keywords: Transparent exopolymer particles, *Phaeocystis antarctica*, Multiple linear regression modeling, Cosmonaut Sea

1 Introduction

Transparent exopolymer particles (TEP), predominantly composed of high-molecular-weight acidic polysaccharides, are a significant component of marine organic matter (Passow, 2002a; Passow, 2002b; Zhou et al., 1998). These gel-like polymers play a crucial role in marine carbon cycling due to their distinctive physicochemical properties, such as high viscosity (Mopper et al., 1995), low density (Engel and Schartau, 1999; Azetsu-Scott and Passow, 2004), and substantial carbon content (Smith et al., 1995). Phytoplankton serve as the primary source of TEP in marine ecosystems (Aluwihare and Repeta, 1999; Radic et al., 2005; Fukao et al., 2010). Numerous studies have documented TEP production across diverse algal taxa, with

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notable contributions from diatoms (Passow and Alldredge, 1994), flagellates (Passow, 2002a; Guo et al., 2022), coccolithophores (Engel et al., 2002), and *Phaeocystis spp.* (Hong et al., 1997; Ramaiah et al., 2001). Diatoms, in particular, have been consistently identified as the most prolific TEP producers (Engel, 1998; Passow, 2002b; Passow, 2002a; Engel, 2004), with phytoplankton-derived polysaccharides accounting for 70-94 % of the extracellular organic carbon pool (Biddanda and Benner, 1997). However, the quantitative contribution of different phytoplankton species to TEP production exhibits considerable variability, influenced by species-specific metabolic traits, physiological status, and ambient environmental conditions (Penna et al., 1999; Staats et al., 2000).

TEP production occurs throughout the various growth phases of phytoplankton, including exponential, stationary, and senescent stages (Fukao et al., 2010). Significant interspecies variability in TEP production capacity has been documented, attributed to differences in growth rates among phytoplankton species (Waite et al., 1995; Engel, 1998; Passow, 2002a). Several environmental parameters regulate TEP production through their effects on phytoplankton, including: (1) light intensity (Hong et al., 1997), (2) CO_2 concentration (Engel, 2002), (3) temperature (Guo et al., 2022), and (4) nutrient and trace metal availability (Kraus, 1997). Additionally, physical factors such as turbulence significantly influence TEP formation dynamics (Passow, 2000). Empirical studies have established exponential relationships between chlorophyll-a (Chl *a*) concentrations and TEP production for specific phytoplankton taxa (Passow and Alldredge, 1995a; Waite et al., 1995; Hong et al., 1997; Passow, 2002a). However, these models are primarily derived from laboratory monoculture experiments or single-species field investigations, while natural marine ecosystems feature complex, multi-species phytoplankton assemblages. Despite significant advances in understanding the environmental controls on TEP production, key gaps remain regarding species-specific TEP production in mixed phytoplankton communities and interactions among coexisting phytoplankton groups. To address these limitations, this study aims to develop a novel methodology to quantify the relative contributions of diverse phytoplankton groups to TEP production in marine ecosystems.

Multiple linear regression (MLR) is a robust statistical method for modeling linear relationships between multiple independent variables and a single dependent variable (DeVore and Kaukis, 2003; Montgomery et al., 2021). This approach is theoretically appropriate for analyzing the association between phytoplankton-

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derived TEP (independent variables) and measured TEP concentrations (dependent variable), given the established role of phytoplankton as primary TEP producers. However, the application of MLR becomes problematic in coastal ecosystems that receive substantial terrestrial inputs, such as riverine discharges and continental shelf exchanges (Li et al., 2018; Ge et al., 2022). In these environments, allochthonous organic matter may constitute a significant portion of TEP pools, challenging the conventional assumption of phytoplankton dominance in TEP production. Consequently, MLR exhibits limited applicability for fitting TEP data in such environments.

The Southern Ocean is a critical component of the global carbon cycle and ranks among the largest oceanic carbon sinks globally (Arteaga et al., 2018). In this region, autochthonous production by phytoplankton is the primary source of organic matter (Arrigo et al., 2008; Arrigo et al., 2015; Lee et al., 2017; Ortega-Retuerta et al., 2017). The Cosmonaut Sea, in particular, features a relatively simple phytoplankton community structure, predominantly consisting of *Phaeocystis antarctica* (*P. antarctica*) and diatoms (Li et al., 2024). This simplified ecosystem is sustained by unique hydrographic conditions, where sea-ice dynamics and water mass properties promote strong vertical stratification and exceptional environmental stability in surface waters (Williams et al., 2010). These distinctive characteristics collectively establish the Cosmonaut Sea an ideal natural laboratory for studing phytoplankton dynamics and their role in carbon sequestration.

This study analyzes TEP and phytoplankton pigment samples collected from the surface layer of the Cosmonaut Sea during the 36th Chinese National Antarctic Research Expedition. By employing MLR modeling on these in situ measurements, we quantitatively evaluate the relative contributions of different phytoplankton functional groups to TEP production in this environmentally homogeneous region. Our investigation focuses on two primary objectives: (1) to resolve a critical gap in understanding the biogeochemical cycling of TEP in Southern Ocean ecosystems by isolating community-structure controls, and (2) to advance the mechanistic understanding of phytoplankton ecological roles in carbon export by establishing direct connections between plankton composition and TEP-driven organic matter production. The findings demonstrate that phytoplankton community structure is the principal regulator of TEP dynamics in this climatically sensitive region, providing a framework for scaling group-specific carbon fluxes.

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2 Materials and methods

2.1 Sampling stations

This study utilized samples collected from the Cosmonaut Sea in East Antarctica during the 36th Chinese Antarctic Research Expedition (CHINARE-36). The sampling locations are illustrated in Figure 1, with detailed information provided in Table 1. Sampling was conducted in surface seawater from December 8, 2019, to January 6, 2020, within the coordinates of 60 °S, 34.97 °E to 70 °S, 70.00 °E. Basic hydrological parameters were obtained using a Sea-Bird SBE 911 CTD. Water samples were collected using a 10 L Niskin bottle. The parameters measured included water temperature, salinity, water depth, photosynthetically active radiation (PAR), nutrients, TEP, and pigments, as detailed in Section 2.2. Furthermore, the study area is influenced by two major current systems: the eastward-flowing Antarctic Circumpolar Current (ACC) and the westward-flowing Antarctic Slope Current (ASC). Specifically, the region west of Cape Ann is affected by the eastern Weddell Gyre (WG) (Williams et al., 2010).

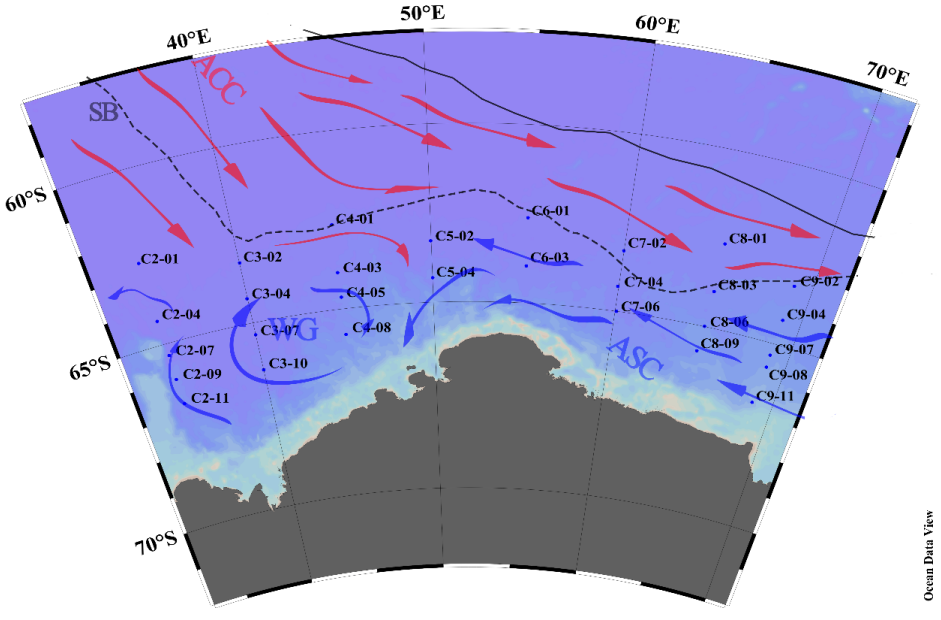

Figure 1: Sampling stations in the Cosmonaut Sea (ACC: Antarctic Circumpolar Current; ASC: Antarctic Slope Current; SB: Southern Boundary; WG: Weddell Gyre)

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111 **Table 1 Detailed information of surface sampling stations in the Cosmonaut Sea**

Station	Date	Longitude (°E)	Latitude (°N)	Sampling depths (m)	Sea ice
C4-01	2019/12/24	45.00	-62.65	0	No
C4-03	2019/12/25	44.98	-63.99	0	No
C4-05	2019/12/25	45.01	-64.68	0	No
C4-08	2019/12/26	45.00	-65.70	0	No
C3-10	2019/12/27	40.00	-66.31	0	No
C3-07	2019/12/28	39.99	-65.33	0	No
C3-04	2019/12/29	39.97	-64.32	0	No
C3-02	2019/12/31	40.01	-63.31	0	No
C2-01	2020/1/1	35.01	-62.66	0	No
C2-04	2020/1/2	34.98	-64.34	0	No
C2-07	2020/1/5	35.03	-65.33	0	No
C2-09	2020/1/6	34.99	-66.01	0	No
C2-11	2020/1/6	35.01	-66.69	0	No
C6-01	2019/12/21	54.94	-62.64	0	No
C6-03	2019/12/22	54.99	-63.98	0	No
C5-04	2019/12/23	50.00	-64.33	0	No
C5-02	2019/12/23	49.98	-63.31	0	No
C9-07	2019/12/8	68.94	-65.32	0	No
C9-08	2019/12/8	68.95	-65.66	0	No
C9-11	2019/12/9	68.79	-66.68	0	No
C9-04	2019/12/11	69.00	-64.32	0	No
C9-02	2019/12/12	69.03	-63.32	0	No
C8-01	2019/12/13	65.00	-62.65	0	No
C8-03	2019/12/14	65.04	-64.01	0	No
C8-06	2019/12/16	65.00	-65.00	0	No
C8-09	2019/12/16	64.91	-65.69	0	No
C7-06	2019/12/18	60.08	-65.00	0	Yes
C7-04	2019/12/19	59.95	-64.31	0	No
C7-02	2019/12/20	59.99	-63.32	0	No

Note: Sea ice concentration data were obtained from remote sensing observations provided by the University of Bremen (available at: https://data.seaice.uni-bremen.de/databrowser/). Of all the sampling stations, only station C7-06 exhibited the presence of sea ice, while all other stations were free of ice during the investigation period.

112 **2.2 Parameter determination**

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2.2.1 Basic parameters

Hydrological parameters including temperature, salinity, and water depth were measured using a Sea-Bird SBE 911 Plus CTD. PAR data were obtained from a PAR sensor integrated with the CTD system.

2.2.2 Nutrients

Seawater samples were filtered through 0.45 μm acetate fiber membranes and subsequently stored at -20 °C until analysis. Nutrient determinations were conducted in accordance with the 'Marine Survey Specification GB/T 12763.4'. Ammonium concentrations were measured on-site using a 7230G spectrophotometer, while the remaining four nutrients were analyzed using a continuous flow nutrient automatic analyzer (Skalar San++, Netherlands). The standard solutions used for analysis were obtained from the Reference Material Center of the Second Institute of Oceanography, Ministry of Natural Resources (GBW 08617-08645). The precision of the measurements for ammonium, nitrate, phosphate, and silicate were 1.2 %, 2.4 %, 2.4 %, and 3.0 %, respectively.

2.2.3 TEP

The method for determining TEP primarily follows the experimental protocol established by Passow and Alldredge (1995b). Approximately 100 mL of seawater samples were collected and filtered through a 25 mm diameter polycarbonate filter membrane with a pore size of 0.4 μm, using a negative pressure of less than 0.02 MPa. Subsequently, 500 μL of 0.02 % Alcian blue (8 GX, pH = 2.5, Sigma) was added for staining, ensuring that the membrane surface was fully immersed for 2 seconds. Excess dye was removed by washing the membrane with deionized water. The membrane sample was then dissolved in 6 mL of 80 % sulfuric acid for 2 hours, during which the test tube was manually agitated 3 to 5 times. Finally, the supernatant was transferred to a 1 cm cuvette, and the absorbance was measured at a wavelength of 787 nm. Each surface station was sampled 2 to 3 times, and the average absorbance value was recorded after subtracting the blank reading from the filter membrane.

The absorbance values were determined using an enhanced calibration method for xanthan gum, as described by Bittar et al. (2018). Initially, a series of xanthan gum standard solutions with varying concentrations were prepared. For each solution, 2 mL was transferred into a test tube, followed by the addition of 500 μL of

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Alcian blue solution for mixing. The mixture was then filtered through a polycarbonate filter membrane. The subsequent steps for dissolving and measuring the membrane samples were conducted in accordance with the procedures used for TEP.

2.2.4 Pigments

Water samples were quantitatively filtered using a Whatman glass fiber filter membrane with a pore size of 0.7 μm. The filtered membrane samples were stored in the dark at -80 °C. Pigments were extracted by adding 3 mL of methanol at -20 °C for 2 hours, followed by ultrasonication in an ice water bath for 30 seconds. The extract was then filtered through a syringe filter (4 mm, 0.45 μm PTFE, Whatman) to remove any debris. The resulting extract was evaporated to dryness under a stream of nitrogen gas and subsequently reconstituted in 300 μL of a methanol-water mixture (19:1, v/v). Analysis of the samples was conducted within 4 hours. Chromatographic analysis was performed using an Acquity UPLC® BEH C18 column (50 mm length, 1.7 μm particle size, 2.1 mm diameter) equipped with a PDA eλ detector and a fluorescence detector (UPLC, Waters Corp., Milford, USA). Qualitative and quantitative analysis of pigments was conducted by comparing the characteristic absorption wavelengths, peak areas, and peak times of pigment standards from the Danish Institute of Water Environment, Denmark. The precision and detection limit of the instrument were 0.26 $mg \cdot m^{-3}$ and 2.2 $mg \cdot m^{-3}$, respectively (It should be noted that the method uses methanol as the solvent to concentrate the sample, and its precision and detection limit may be more than 10 times higher than the original sample). The pigment concentrations obtained using the CHEMTAX software allow for the estimation of Chl *a* contributions from individual phytoplankton groups (Alderkamp et al., 2012; Mackey et al., 1996). Specifically, fucoxanthin is the characteristic pigment associated with diatoms, 19'-hexanoyloxyfucoxanthin with haptophytes (primarily *P. antarctica*), peridinin with dinoflagellates, alloxanthin with cryptophytes and lutein with chlorophytes (Wright et al., 2010).

2.3 Data processing

2.3.1 Multiple linear regression (MLR) fitting

The TEP release by each phytoplankton group follows a power law function as described in Eq. (1) (Hong et al., 1997; Passow, 2002b):

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$$TEP = A(Chl\ a)^B \quad (1)$$

In this equation, A quantifies the initial TEP production potential of phytoplankton, which varies significantly depending on group composition and physiological status. Higher A values correspond to greater TEP release capacity during early growth phases. Previous studies have established that TEP production efficiency typically declines as bloom progress (Waite et al., 1995; Passow, 2002b). The coefficient B, consistently observed to be <1, reflects a density-dependent inhibition effect on TEP production. The A and B coefficients of various phytoplankton groups generally exhibit significant variability, influenced by factors such as nutrient availability (Schartau et al., 2007), CO_2 concentration (Engel, 2002), light conditions, and the dynamics of microbial communities (Hong et al., 1997). Theoretical A and B values are generally higher than those observed in natural aquatic environments. However, obtaining representative phytoplankton groups from the Cosmonaut Sea has proven challenging. Current data only provide A and B coefficients for haptophytes, diatoms, and dinoflagellates under mesoscale and in situ bloom conditions (Table 2). Compared to the multi-algae environment, the results presented in Table 2 offer the most accurate available approximation of theoretical A and B values for major phytoplankton groups. Consequently, we utilized these values as the theoretical foundation for subsequent fitting analyses.

Table 2 The relationship between TEP and Chl *a* during the mesocosm blooms (1400liter) and in situ blooms: $TEP = A(Chl\ a)^B$ in μg Xeq L^{-1} and in μg L^{-1}

Groups (Species)	Sample site	A	B	Reference
Dinoflagellates	Mesocosm 95	163	0.56	Passow, 2002a
Haptophytes (*P. antarctica*)	Mesocosm 96	106	0.76	Passow, 2002a
Diatoms	Baltic Sea	282	0.33	Engel, 1998

Researches have established that biological processes are the primary driver of TEP production in marine systems (Passow, 2002b). However, field observations reveal that environmental factors can substantially alter TEP release dynamics across different phytoplankton taxa, resulting in substantial spatial and temporal variability in TEP content (Engel et al., 2017). To quantitatively assess taxon-specific TEP contributions under natural conditions, we propose an environmental correction factor (β), representing the ratio of TEP released by phytoplankton in the natural environment to the theoretical value. Thus, in situ TEP production

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can be expressed as the theoretical value multiplied by β. The following prerequisites must be fulfilled for the model to function effectively: First, TEP are predominantly produced through biological processes, and the contribution of non-biological processes is negligible, which has been already confirmed in the results of correlation analysis in Part 3.2. Second, there should be no significant alterations in the structure of the phytoplankton community at the marine stations, ensuring that the dominant algal groups remain consistent. Third, haptophytes, diatoms and dinoflagellates are the principal contributors to TEP, while contributions from other algal groups are minimal. Environmental factors such as water temperature and light primarily exert indirect influences on TEP production by affecting phytoplankton growth. Given the minimal spatial variation in surface water temperature (Δ T < 2.3 °C), uniform non-limiting nutrient conditions (N/P $\approx$ 16), and consistent PAR levels across stations, environmental parameters exerted negligible direct physiological impacts on phytoplankton TEP production. Consistent with regional microbial biomass observations (Han et al., 2022), surface waters in our study area exhibited characteristically low abundances of picoeukaryotes and prokaryotic cells. Given the homogeneity of environmental forcing and minimal microbial interference in the study area, phytoplankton community structure is identified as the primary direct driver of TEP production in the Cosmonaut Sea surface waters during austral summer. Finally, we present the formula Eq. (2) for TEP content derived from MLR analysis.

$$TEP = \sum_i(\beta_i\, TEP_i) + \varepsilon \quad (2)$$

where β_i represents the correction factors for haptophytes (β_{Hapt}), diatoms (β_{Diat}), and dinoflagellates (β_{Dino}), respectively. TEP_i denotes the theoretical concentration of TEP released by haptophytes, diatoms, and dinoflagellates. ε represents the residual term, encompassing the total TEP contribution from other phytoplankton groups beyond haptophytes, diatoms, and dinoflagellates, as well as the random variation that the model does not account for.

The objective of MLR is to identify a set of correction factor (β) that minimizes the discrepancy between the predicted TEP values generated by the model and the actual observed values. This is typically accomplished by minimizing the sum of the squared residuals, a technique known as the least squares method. In this study, the theoretical TEP content released by haptophytes, diatoms, and dinoflagellates (independent variables) was calculated separately. Subsequently, a fitting procedure was conducted to correlate these theoretical

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values with the actual TEP content (dependent variable) using Matlab software (R2019a), with the specific modeling and calculation processes detailed in Supporting Information. The fitting coefficients and other relevant results were subsequently reported based on the fitting outcomes.

2.3.2 Percentage of meltwater

In polar environments, the melting of sea ice can significantly impact marine ecosystems. This study evaluates the effect of sea ice melting on the structure of phytoplankton communities by calculating the percentage of meltwater (MW%) using Eq. (3) (Rivaro et al., 2014):

$$MW\% = \left(1 - \frac{So-6}{Sd-6}\right) \times 100 \quad (3)$$

Here, So represents the salinity of the surface water, while Sd denotes the salinity of the deep water at the same station unaffected by the dilution from melting ice (in this paper, d=300 m). It is also assumed that the average salinity of sea ice is 6 (Ackley et al., 1979).

2.3.3 Correlation analysis and visualization

This study employs IBM SPSS Statistics (Version 22, https://www.ibm.com/analytics/spss-statistics-software) for statistical analysis and uses Ocean Data View (Version 5.1.7, http://odv.awi.de) and Origin (OriginPro Version 2022, https://www.originlab.com) for data visualization.

3 Results

3.1 Surface hydrographic variability in the Cosmonaut Sea

The results for key parameters in the surface layer of the Cosmonaut Sea are summarized in Table 3, with their spatial distributions illustrated in Figure 2. The mean surface water temperature was -0.62 ± 0.58 °C, with lower values in coastal regions and higher values offshore. Notably, the western sector of Cape Ann exhibited warmer waters compared to the eastern sector. The average salinity was 33.76 ± 0.19 ‰, with elevated values observed east of Cape Ann. Generally, salinity was higher near the coast compared to offshore, except in the nearshore area west of Cape Ann, where no significant salinity increase was detected. The MW% exceeded 2 % at most stations (excluding C9-11), indicating a substantial influence of ice melt. PAR levels

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241 were higher west of Cape Ann compared to eastern areas, though no distinct overall pattern was evident.
242 Nutrient distributions exhibited considerable variability: Silicate, phosphate and nitrate showed similar
243 spatial trends, with higher concentrations in coastal zone and lower values offshore. In contrast, nitrite
244 exhibited an inverse distribution, with lower concentrations near the coast and higher values offshore.
245 Ammonium levels were lower in waters west of Cape Ann compared to eastern regions.

246

247 **Table 3 The range and mean values of key parameters in the surface layer of the Cosmonaut Sea.**

Parameter	Range	Average	± SD, N
Temp [°C]	-1.83 — 0.42	-0.62	0.58, 29
Salinity [‰]	33.27 — 34.17	33.76	0.19, 29
Silicate [μmol L^{-1}]	18.75 — 62.64	31.14	9.47, 29
Phosphate [μmol L^{-1}]	0.91 — 2.23	1.29	0.30, 29
Nitrate [μmol L^{-1}]	13.85 — 44.21	21.42	6.53, 29
Nitrite [μmol L^{-1}]	0.09 — 0.60	0.24	0.12, 29
Ammonium [μmol L^{-1}]	0.13 — 1.10	0.41	0.25, 29
PAR [E m^{-2} d^{-1}]	22.15 — 44.50	33.36	6.77, 29
MW%	1.6 — 5.0	3.2	0.7, 27
TEP [μg Xeq L^{-1}]	2.07 — 38.99	16.58	10.19, 29
Haptophytes [μg L^{-1}]	ND* — 1.29	0.31	0.31, 27
Diatoms [μg L^{-1}]	0.01 — 0.60	0.17	0.13, 27
Dinoflagellates [μg L^{-1}]	ND — 0.32	0.08	0.08, 27
Chlorophytes [μg L^{-1}]	ND — 0.10	0.02	0.03, 27
Cryptophytes [μg L^{-1}]	ND — 0.24	0.07	0.01, 27
Chl *a* [μg L^{-1}]	0.01 — 1.72	0.66	0.50, 27

*ND (Not Detected), which can be calculated by 0.

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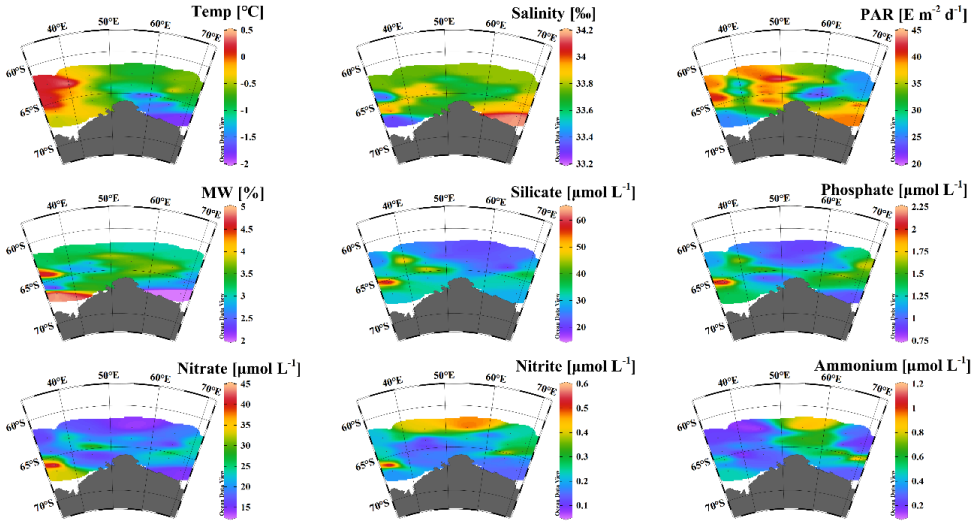

Figure 2 Distribution of hydrographic parameters in the surface layer of the Cosmonaut Sea

3.2 Distribution of TEP and Chl *a* in different phytoplankton groups

Figure 3 illustrates the spatial distributions of TEP and Chl *a*. The mean TEP concentration was 16.58 ± 10.19 µg Xeq L^{-1}, while the mean Chl *a* concentration was 0.66 ± 0.50 µg L^{-1}. Both parameters exhibited distinct spatial heterogeneity across Cape Ann waters, with elevated values in the WG region and significantly lower concentrations in eastern waters. The highest TEP concentration was recorded at station C3-07, while the peak Chl *a* was observed at station C4-03. Phytoplankton community composition analysis revealed that haptophytes dominated the phytoplankton community (mean concentration: 0.31 ± 0.31 µg L^{-1}), followed by diatoms and dinoflagellates. Cryptophytes and chlorophytes maintained consistently low abundances throughout the study area. As depicted in Figure 4, the relative abundance of the dominant phytoplankton groups followed the order: haptophytes > diatoms > dinoflagellates > other groups.

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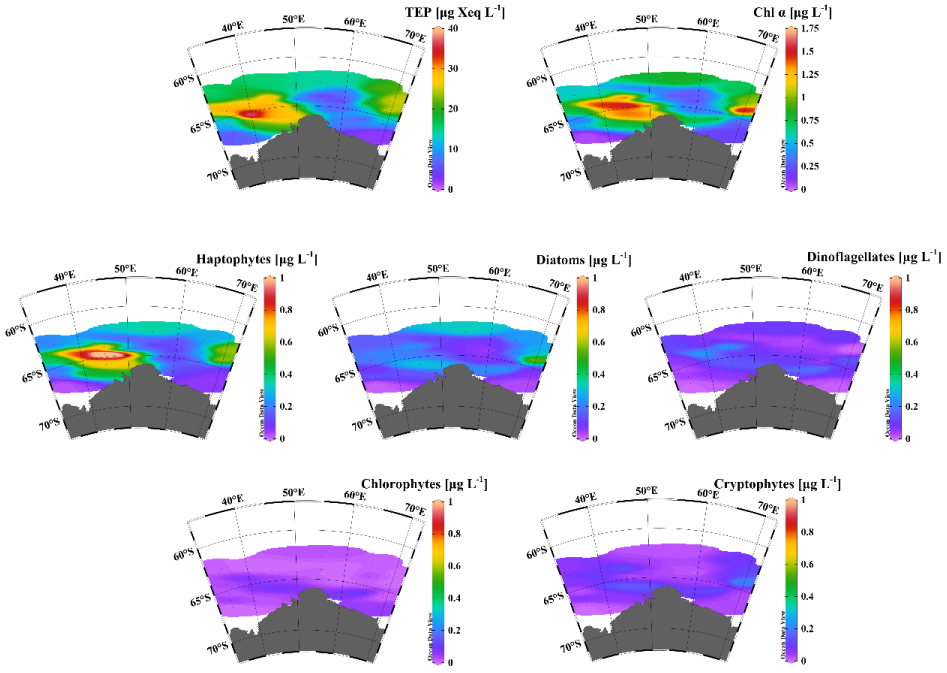

Figure 3 Distribution of TEP and phytoplankton biomass (Chl *a*) in the surface layer of the Cosmonaut Sea

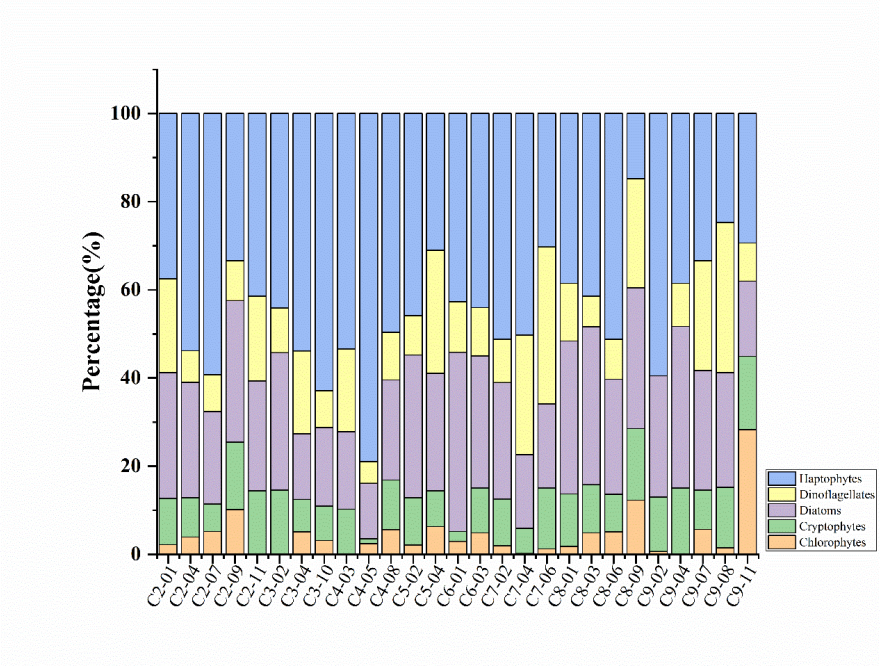

Figure 4 Phytoplankton population percentage in the surface layer of the Cosmonaut Sea

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3.2 Analysis of relationships

The results of the correlation analysis (Figure 5) indicate that silicate levels are positively correlated with both phosphate and nitrate concentrations ($r = 0.81$, $p < 0.01$; $r = 0.62$, $p < 0.01$), while phosphate is also positively correlated with nitrate ($r = 0.66$, $p < 0.01$). Salinity exhibits a negative correlation with MW% ($r = -0.995$, $p < 0.01$). Furthermore, TEP shows positive correlations with all phytoplankton populations (haptophytes: $r = 0.86$, $p < 0.01$; diatoms: $r = 0.67$, $p < 0.01$; dinoflagellates: $r = 0.48$, $p < 0.05$; cryptophytes: $r = 0.60$, $p < 0.01$), except for chlorophytes. Additionally, TEP is negatively correlated with ammonium levels ($r = -0.50$, $p < 0.05$) and positively correlated with temperature ($r = 0.54$, $p < 0.01$).

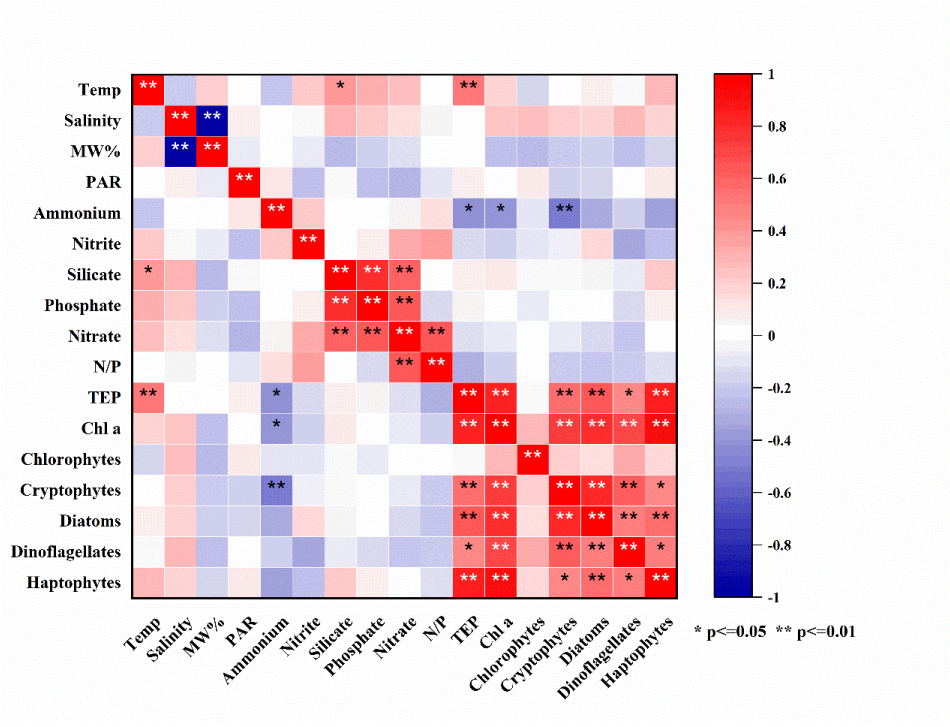

Figure 5 Heatmap of correlations among various parameters

3.3 Results of MLR fitting

Five stations (C7-04, C7-06, C8-09, C9-08, and C9-11) exhibited anomalous phytoplankton community compositions that significantly deviated from both other stations and our initial ecological assumptions (detailed in Supporting Information). Consequently, these outlier stations were excluded from subsequent

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model fitting analyses. The regression results are summarized in Table 4. The initial MLR model yielded a non-significant intercept (ε) of -1.14 (p = 0.77), with correction coefficients of β_{Hapt} = 0.189 (p < 0.01), β_{Diat} = 0.061 (p > 0.05), and β_{Dino} = 0.032 (p > 0.05). While the model explained 83.1% of the variance in TEP production (R^2 = 0.83), the non-significant coefficients for β_{Diat} and β_{Dino}, along with the marginal significance of the intercept term, indicated potential for model refinement. Through stepwise model optimization, we constrained ε to zero and excluded β_{Dino}. The final optimized model demonstrated improved statistical performance, with significant β_{Hapt} (0.201, p < 0.01) and β_{Diat} (0.058, p < 0.01), with maintaining high explanatory power (R^2 = 0.82). The final results robustly quantify the differential contributions of phytoplankton groups to TEP production in Cosmonaut Sea surface waters, establishing haptophytes as primary contributors, followed by diatoms, while dinoflagellate showed no statistically significant contribution.

Table 4 Results of MLR fitting

Fitting result	Initial fitting			Final fitting		
	Value	SE	p	Value	SE	p
$\boldsymbol{\beta_{Hapt}}$	0.189	0.041	0.0002	0.201	0.034	0.00001
$\boldsymbol{\beta_{Diat}}$	0.061	0.032	0.07	0.058	0.012	0.0001
$\boldsymbol{\beta_{Dino}}$	0.032	0.055	0.57	/	/	/
$\boldsymbol{\varepsilon}$	-1.143	3.792	0.77	/	/	/
R^2		0.83			0.82	

Note: SE represents the standard error of the statistic; p < 0.05 indicates statistically significant, while p > 0.05 indicates non-significant; R^2 denotes the coefficient of determination, with higher values indicating greater explanatory power of the model

4 Discussion

4.1 The effect of phytoplankton on the distribution of TEP

As shown in Figure 3, both TEP and Chl *a* show significant enrichment in the WG region and at hydrographic frontal zones marking water mass convergence. A strong positive correlation was observed between TEP and Chl *a* (r = 0.89, p < 0.01), indicating that phytoplankton are the predominant source of TEP (Passow, 2002a; Passow, 2002b). The WG region is characterized by upwelling and hosts a persistent polynya known as the

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sensible heat polynya (Williams et al., 2010; Geddes and Moore, 2007). This polynya enhances vertical nutrient flux from subsurface layers (Zhan et al., 2023) and contributes to a reduction in mixed layer depth (Xue et al., 2023). The shallower mixed layer facilitates light availability for phytoplankton in the photic zone (Le Grix et al., 2021; Noh et al., 2022), thereby stimulating phytoplankton blooms and increasing their abundance in the WG region. The ACC is primarily comprised of Circumpolar Deep Water (CDW), which originates in the North Atlantic and undergoes eastward transport around Antarctica (Pakhomov, 2000). CDW is characterized by elevated heat content and enhanced nutrient concentrations (Martinson, 2012; Williams et al., 2010). Moreover, the frontal zone between the ACC and ASC frequently exhibits divergent upwelling features (Park et al., 1998; Williams et al., 2010). This upwelling process increases nutrient availability within the convergence zone, stimulating phytoplankton proliferation. The subsequent phytoplankton blooms enhance TEP release, leading to elevated TEP concentrations in these regions.

Previous studies have demonstrated that extracellular polymer production is regulated by nitrogen and phosphorus availability (Guerrini et al., 2000; Magaletti et al., 2004; Li et al., 2020). Under low nitrogen conditions, nutrient depletion in algal cells can induce physiological stress, leading to increased secretion of extracellular substances (Granum et al., 2002; Yang et al., 2010; Staats et al., 2000; Barcelos et al., 2020). As shown in Table 3, nitrate concentrations exceeded 10 μmol L^{-1}, while phosphate concentrations were above 0.3 μmol L^{-1}, indicating no nutrient limitation (Moore et al., 2013). The Redfield ratio (C:N:P = 106:16:1) serves as a fundamental reference for evaluating nutrient limitation in marine systems (Redfield, 1958; Tanioka et al., 2022). To evaluate potential nutrient limitations, we calculated the nitrogen-to-phosphorus (N/P) ratio from available nutrient data (Figure 6). The results reveal that most surface waters in the Cosmonaut Sea are not nitrogen-limited, with N/P ratios primarily ranging between 15–16. Additionally, correlation analysis (Figure 4) revealed no significant relationship between N/P ratios and TEP or phytoplankton biomass, suggesting that nutrient availability does not exert a primary limiting effect on phytoplankton growth in this region.

Notably, ammonium (NH_4^+) shows a negative correlation with TEP, cryptophytes, diatoms, and haptophytes, indicating that under nutrient-replete conditions, ammonium assimilation may stimulate the growth of these phytoplankton groups, thereby enhancing TEP production. This pattern likely reflects the preferential uptake

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of ammonium over nitrate by phytoplankton (Karasiewicz et al., 2018; Xu et al., 2022). In particular, haptophytes exhibit greater ammonium uptake efficiency compared to diatoms (Tungaraza et al., 2003), which explains their elevated abundance in the study area (Figure 4). Additionally, MW% data from the region (Figure 2) reveal that the surface layer of the Cosmonaut Sea is affected by meltwater input (MW% > 2%), which may enhance water column stratification and potentially favor phytoplankton growth (Massolo et al., 2009; Rivaro et al., 2014). However, the absence of significant correlation between MW% and phytoplankton abundance suggests that meltwater does not act as a primary limiting factor for phytoplankton growth. In summary, nutrient availability in both the WG region and the water mass convergence zone remains non-limiting, while favorable light conditions further promote phytoplankton proliferation and the subsequent release of substantial TEP quantities.

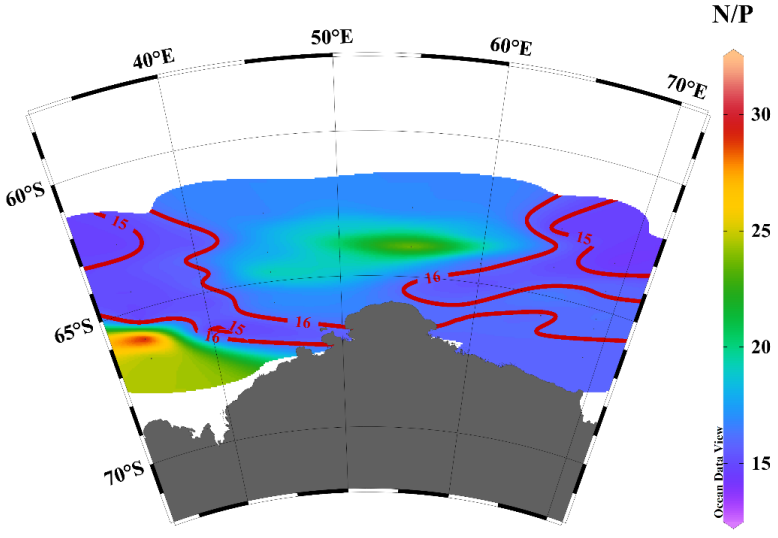

Figure 6 The ratio of N/P in the surface layer of the Cosmonaut Sea (N/P = (Ammonium+ Nitrite+ Nitrate)/ Phosphate. The red solid line (N/P = 16) denotes the nutrient limitation threshold, and N/P < 16 indicates nitrogen limitation)

4.2 The effects of temperature, ammonium and polysaccharide components on the correction coefficient

The regression fitting yielded R^2 values of 0.83 and 0.82, respectively, indicating robust explanatory power of the models. These results demonstrate that the selected independent variables significantly predict the

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dependent variable, supporting our hypothesis regarding the linear relationship between TEP concentration and theoretical TEP production by individual phytoplankton groups. Statistical analysis revealed significant correction coefficients for haptophytes (β_{Hapt}) and diatoms (β_{Diat}), with p-values < 0.05, confirming their substantial contribution to TEP content. In contrast, non-significant p-values (p > 0.05) were obtained for both dinoflagellates (β_{Dino}) and the intercept term (ε), suggesting their negligible effects on the model. The final simplified linear regression model Eq. (3) can be expressed as:

$$TEP = 0.201TEP_{Hapt} + 0.058TEP_{Diat} \quad (3)$$

The regression analysis revealed that β_{Diat} was lower than β_{Hapt}, indicating greater deviation from theoretical TEP values for diatoms. This suggests that diatom-associated TEP production is more sensitive to environmental variability compared to haptophytes. Although numerous environmental factors including light intensity, photoperiod, and spectral quality are known to regulate algal extracellular polysaccharide secretion in a species-specific manner (Price et al., 1998; Otero and Vincenzini, 2003; You and Barnett, 2004), our correlation analyses showed no significant relationship between PAR and either TEP or phytoplankton biomass. This finding suggests that light conditions do not constitute a primary controlling factor in our study region.

Microalgal extracellular polymer synthesis is regulated by temperature, as the enzymatic processes involved often possess different thermal optima compared to those controlling microbial growth (Barcelos et al., 2020). Polar diatoms adapt to subzero temperatures (-4 °C) by upregulating carbohydrate metabolism enzymes, thereby increasing extracellular polymer production to maintain cellular protection (Aslam et al., 2018). However, at elevated temperatures, these enzymatic activities may become less efficient, potentially reducing diatom contributions to TEP formation. In our study region, where surface water temperatures consistently remain above -4 °C, warming conditions could reduce the efficiency of diatom-mediated TEP synthesis. In contrast, haptophytes, exhibiting greater thermal adaptation to warmer waters (Van Rijssel et al., 2000; Cheng et al., 2023), display less temperature-dependent variation in TEP production, explaining their higher correction coefficient relative to diatoms. It should be noted that although water temperature exhibited limited spatial variability across the study area ($\Delta T < 2.3^{\circ}$ C), it served as a uniform background driver that systematically modulated the competitive balance between diatoms and haptophytes. The higher β

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coefficient for haptophytes (0.201 vs. 0.058 for diatoms) suggests that even within this narrow thermal range, the ambient temperature near 0°C favored haptophytes in TEP production efficiency. This mechanism operates homogeneously across the region rather than generating spatial contrasts. The apparent positive correlation between temperature and TEP ($r = 0.54$, $p < 0.01$) likely stems from co-variation with biological processes. When phytoplankton biomass is accounted for, the direct effect of the narrow temperature range (< 2.3°C) on TEP is likely negligible, as confirmed by the dominance of community structure effects in the MLR model.

Nutrient availability significantly regulates phytoplankton extracellular polymer production. As established earlier, the surface waters of the Cosmonaut Sea exhibit no-limiting nutrient conditions. Of particular ecological relevance, haptophytes demonstrate enhanced ammonium assimilation efficiency compared to diatoms, a physiological advantage contributing to their numerical dominance. The substantial proliferation of haptophytes can induce cyst formation (Hamm, 2000), a process with dual ecological implications: these cysts may provide microhabitats for other algal species (Rousseau et al., 1994; Hamm and Rousseau, 2003), yet simultaneously harbor symbiotic Vibrio bacteria (Cho et al., 2017). These associated Vibrio species possess laminarinase-producing capabilities (Alderkamp et al., 2007b), potentially compromising polysaccharide synthesis through laminarin degradation. Furthermore, Vibrio bacteria exhibit significant algicidal activity (Dungca-Santos et al., 2019) and demonstrate competitive inhibition against diatoms and other phytoplankton groups (Liu et al., 2008). Ammonium concentration appears to be a critical regulator of Vibrio-phytoplankton population dynamics (Xu et al., 2022). Consequently, elevated ammonium levels may stimulate Vibrio proliferation, leading to suppressed diatom metabolic activity. This intricate trophic interaction network likely explains the observed differential regression coefficients between diatoms (lower) and haptophytes (higher).

The carbohydrate pool of Southern Ocean diatoms is predominantly composed of glucose, which constitutes a major fraction of total carbohydrates (Alderkamp et al., 2007a; van Oijen et al., 2003). As a simple monosaccharide, glucose lacks sulfate ester groups ($R\text{-}OSO_3^-$) (Zhou et al., 1998). In contrast, haptophyte-derived polysaccharides (e.g., fucoidan) typically contain elevated concentrations of these anionic functional groups, which facilitate ionic bond formation (Smith et al., 1995; Van Boekel et al., 1992). This structural

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difference confers greater resistance to microbial degradation on haptophyte polysaccharides compared to diatom-derived compounds. Consequently, diatom-associated TEP exhibits reduced persistence in the marine environment, explaining the observed lower correction coefficient for diatoms relative to haptophytes in our analysis.

4.3 The contribution of different phytoplankton groups to TEP

Laboratory-controlled experiments demonstrate a positive correlation between group-specific TEP production and Chl *a* concentrations. As illustrated in Figure 7(a), diatoms consistently exhibit higher TEP release rates than haptophytes, corroborating previous findings that diatoms contribute more substantially to TEP production per unit biomass than haptophytes (Passow, 2002a; Passow, 2002b). However, our field observations reveal a contrasting pattern when correction coefficients are applied: the TEP production dynamics between these phytoplankton groups show distinct biomass-dependent trends. At equivalent biomass levels (represented by Chl *a* below 0.5 μg L^{-1}), diatoms maintain their characteristic elevated TEP production compared to haptophytes. This relationship undergoes a marked reversal at higher biomass concentrations (Chl *a* > 0.5 μg L^{-1}), where haptophytes demonstrating significantly greater TEP release than diatoms, as shown in Figure 7(b).

To quantitatively assess these contributions, we derived corrected TEP values (designated TEP_d-Hapt and TEP_d-Diat) by applying group-specific correction coefficients to theoretical TEP contents. Comparative analysis of these corrected values with measured TEP concentrations (Figure 8) reveals a clear ecological transition: in haptophyte-dominated waters, diatoms contribute more substantially to TEP pools at low phytoplankton biomass (Chl *a* < 0.5 μg L^{-1}), while haptophytes emerge as the dominant TEP producers at higher biomass levels.

Existing literature has established both diatoms (Mari and Burd, 1998; Fukao et al., 2010) and haptophytes (Hong et al., 1997) as important sources of TEP, with diatoms generally considered the predominant contributors (Alldredge et al., 1993; Ramaiah et al., 2001; Azetsu-Scott and Passow, 2004). However, our findings demonstrate that phytoplankton contributions to TEP production exhibit strong dependence on interspecific variations in Chl *a* content among dominant groups. This biomass-dependent variation in TEP

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production may be attributed to competitive interactions between phytoplankton groups, consistent with previous ecological observations (Liu et al., 2008).

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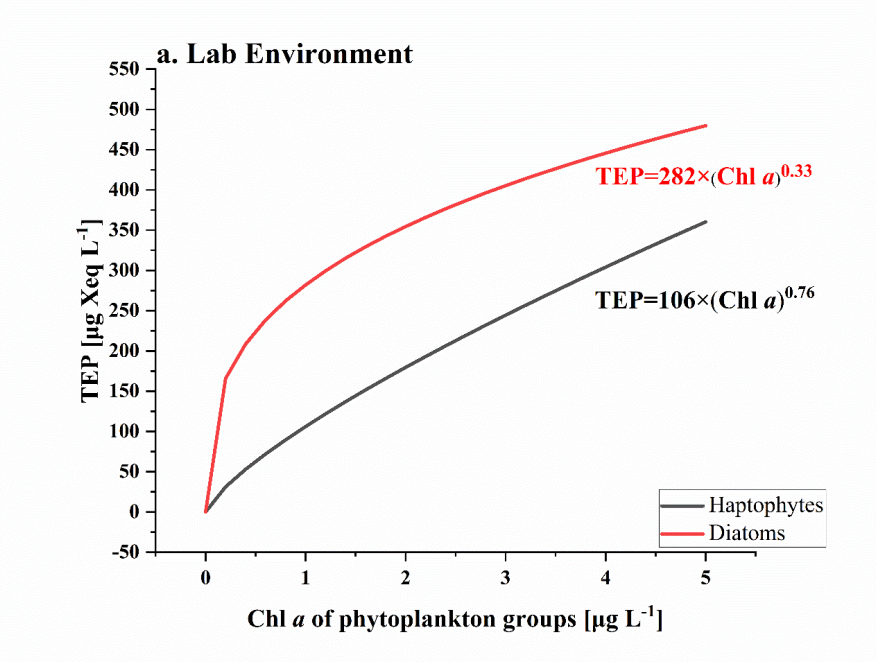

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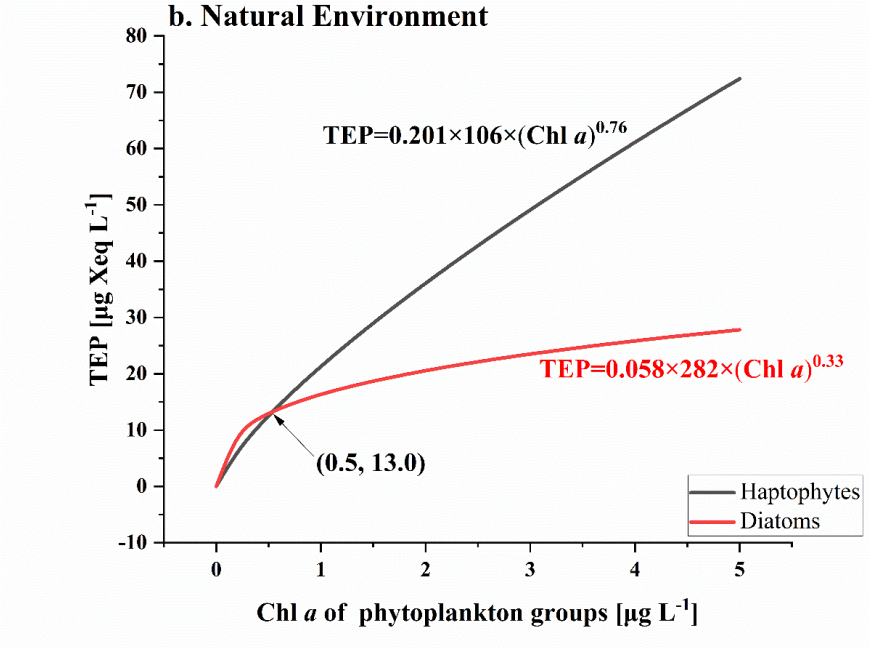

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428 **Figure 7 The release of TEP by haptophytes and diatoms at varying concentrations of Chl *a* (a. laboratory**
429 **environment, with the empirical formula is derived from Passow (2002b) ; b. natural environment)**

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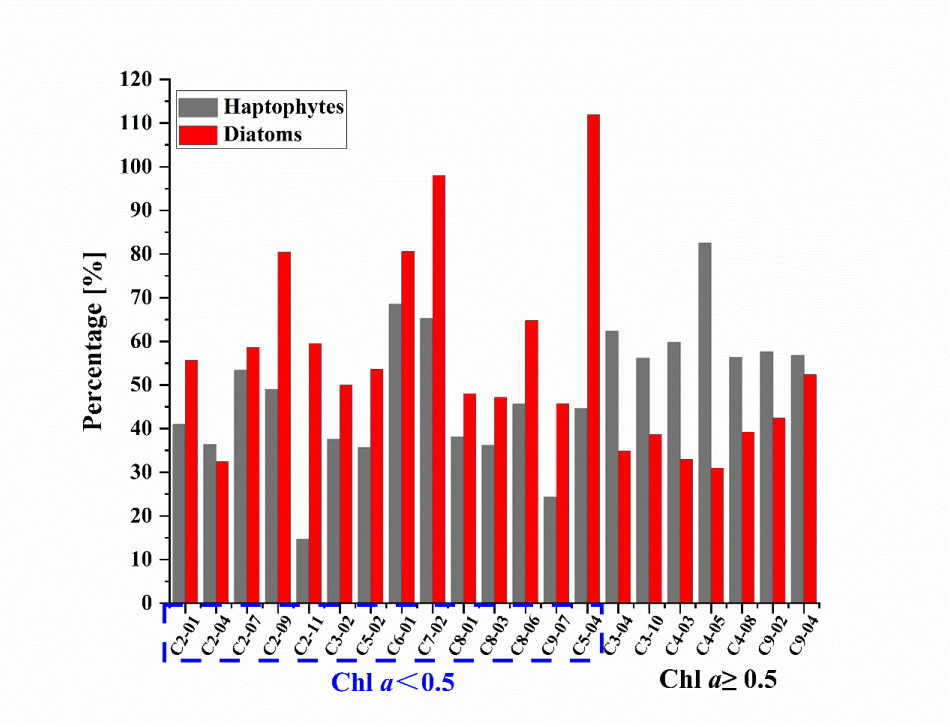

Figure 8 Differences in the contribution of haptophytes and diatoms to TEP production in the surface layer of the Cosmonaut Sea

Biomass-corrected TEP concentrations derived from haptophytes and diatoms are presented in Figure 9(a) and 9(b), respectively. In the surface waters of the Cosmonaut Sea, haptophyte-derived TEP concentrations ranged from 0.9 to 28.0 μg Xeq L^{-1}, while diatom-derived TEP ranged from 2.8-11.4 μg Xeq L^{-1}. These observed TEP concentration ranges align well with established empirical relationships describing phytoplankton abundance and TEP production capacity (Berman and Viner-Mozzini, 2001; Passow, 2002a; Passow, 2002b). When integrated with phytoplankton distribution patterns shown in Figure 3, these results suggest that both haptophytes and diatoms likely experienced bloom conditions in the WG region and water mass convergence zones, leading to enhanced TEP production. Notably, the spatial distribution of haptophyte-derived TEP closely corresponds to the measured bulk TEP concentrations (Figure 3), with the highest values concentrated in the WG region and frontal convergence zones. In contrast, diatom-derived TEP displayed a more homogeneous spatial distribution, with peak concentrations occurring in areas distinct

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from haptophyte-dominated regions. This spatial differentiation may reflect competitive interactions between phytoplankton groups (Liu et al., 2008).

The relative contributions of different phytoplankton groups to TEP production are presented in Figure 9(c) and 9(d). Assuming TEP originates predominantly from haptophytes and diatoms, their cumulative contributions should approximate 100% of total TEP. Our results confirm this theoretical expectation in the WG region and water mass convergence zones, where the cumulative contributions of these two groups approach 100%, establishing their predominance in TEP production in these areas. A notable exception occurs at station C6-03, where the calculated contribution exceeds 100%. This discrepancy likely reflects the exceptionally low measured TEP concentration (3.55 μg Xeq L^{-1}), which approaches both the methodological detection limit (2.45 μg Xeq L^{-1} for colorimetric determination) and the measurement uncertainty range (± 2.27 μg Xeq L^{-1}). Excluding this outlier, our data show that haptophytes contribute 14.6 – 82.5% (mean: 48.6 ± 15.4%) of total TEP, while diatoms account for 31.0 – 112.0% (mean: 55.1 ± 21.2%). The comparable magnitude of contributions from both phytoplankton groups underscores the previously underestimated importance of haptophytes in TEP production. These findings highlight the crucial role of haptophytes in Southern Ocean carbon cycling processes, prompting a necessary reassessment of their ecological significance in the marine ecosystem.

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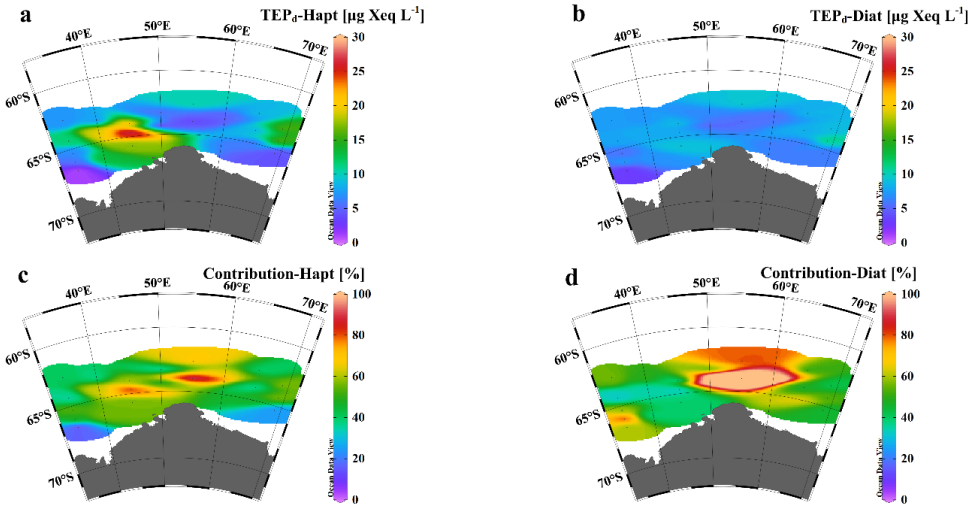

Figure 9 Contribution of haptophytes and diatoms to TEP (a and b represent the biomass-corrected TEP concentrations derived from haptophytes and diatoms, respectively; c and d depict the relative contributions of haptophytes and diatoms to TEP, respectively.)

5 Conclusion

This study analyzed surface water samples from the Cosmonaut Sea, measuring TEP, Chl *a* and key environmental parameters to characterize TEP distribution. The observed spatial heterogeneity in TEP distribution was predominantly driven by phytoplankton community structure. Our MLR model quantified group-specific TEP contributions through environmentally adjusted correction factors (β), revealing significantly higher β for haptophytes (0.201) than diatoms (0.058). This discrepancy reflects group-specific physiological responses to ambient conditions, where temperature, ammonium, and polysaccharide composition indirectly regulate TEP production efficiency via community dynamics. Quantitative analysis demonstrated that haptophytes contributed 14.6 – 82.5% (mean 48.6 ± 15.4%) of total TEP, while diatoms accounted for 31.0 – 112.0% (mean 55.1 ± 21.2%). Critically, we establish a new paradigm that diatoms dominate TEP production when *P. antarctica* Chl *a* < 0.5 μg L^{-1}, while haptophytes emerge as the predominant TEP producers at elevated biomass. This biomass-dependent inversion, undocumented in laboratory studies, highlights the necessity of in situ community-level assessments.

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These results recalibrate our understanding of polar carbon cycling by revealing the pivotal role of *P. antarctica* in Southern Ocean biogeochemistry. While this study provides critical insights, several limitations should be acknowledged: First, the exclusive focus on surface waters during austral summer precludes assessment of seasonal variability or vertical flux dynamics. Second, while our MLR model effectively captured phytoplankton-driven TEP production, it inherently simplified the potential contributions of abiotic processes and bacterial remineralization.

To address these limitations and advance the field, we propose four key research priorities:

(i) Comprehensive multi-seasonal sampling across water column depths to characterize full phenological patterns of TEP production and export;

(ii) Controlled mechanistic experiments to quantify how environmental parameters (temperature, nutrients, light) modulate taxon-specific β factors;

(iii) Application of metatranscriptomic approaches to identify genetic markers of TEP synthesis and their expression patterns in natural phytoplankton assemblages;

(iv) Systematic quantification of bacterial TEP degradation rates in polar surface waters to constrain this potentially important sink term.

Data availability statement

All data generated or analyzed during this study are included in this published article and its supplementary materials. The supplement related to this article is available online at https://doi.org/10.5281/zenodo.16020210.

Author contribution

SYX is responsible for research design, data analysis, and manuscript writing. JH contributed to research design, data verification, and manuscript revision. JZ, DL, HFZ, XFY, CZ, PSY, CFZ, and KYT participated in data provision, sample collection, and manuscript editing. GJF, JMP, and MC provided technical and financial support.

Competing interests

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503 The contact author has declared that none of the authors has any competing interests.

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