

Physical-chemical and biological control of the zooplankton community in the Amundsen Sea, Antarctica

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Abstract Zooplankton are critical components of the Southern Ocean ecosystems, acting as trophic links between phytoplankton and higher-level species. The composition, abundance, carbon biomass, and community structure of zooplankton were studied based on samples collected with a Norpac net (330- μ m mesh, 0.5-m² net mouth) during the austral summers of 2017/2018. Three communities in a latitudinal gradient were identified based on both a zooplankton abundance dataset and a biomass dataset. Zooplankton were mainly dominated by small copepods (e.g., *Oithona similis* and *Ctenocalanus citer*) in terms of abundance, while the total zooplankton biomass was dominated by krill (*Euphausia superba* and *Thysanoessa macrura*) and large copepods (e.g., *Calanoides acutus*, *Calanus propinquus*, and *Metridia gerlachei*). Redundancy analysis demonstrated that environmental factors (e.g., temperature, nitrate, dissolved oxygen, ammonium) accounted for more than 40% of the variance in zooplankton abundance/biomass. This indicates that physical processes significantly affect the zooplankton community. Meanwhile, a significant positive correlation was found between the abundance/biomass of zooplankton and that of dominant phytoplankton and ciliates, which suggests trophic links among various plankton functional groups. Our results reveal that both physical processes and biological factors shape the community structure of zooplankton in the Amundsen Sea.

Keywords zooplankton community, abundance, biomass, Amundsen Sea, Southern Ocean

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1 Introduction

The Southern Ocean supports important ecosystem

services like carbon sequestration, fisheries, and tourism (Cavanagh et al., 2021). Zooplankton play central roles in both the structure and function of the Southern Ocean ecosystem as trophic links, transferring carbon from phytoplankton to higher trophic-level species (Johnston et al., 2022). Zooplankton are also pivotal in the biological carbon pump and biogeochemical cycles of the Southern

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Ocean through feeding, fecal pellets, sinking of carcasses and molts, and diel and seasonal vertical migration (Schmidt et al., 2016; Cavan et al., 2019; Manno et al., 2020; Halfter et al., 2021).

Several biotic (e.g., food availability, predation, competition) and abiotic (e.g., sea ice, temperature, currents, nutrients) factors are important in shaping zooplankton communities of the Southern Ocean (Nicol et al., 2000; Atkinson et al., 2004; Hunt et al., 2005). Among these factors, it is widely accepted that bottom-up control (i.e., changes in food availability regulated by sea ice retreat and iron) is one of the most important factors influencing the zooplankton community and marine ecosystems of the Southern Ocean (Arteaga et al., 2020). But top-heavy biomass pyramids in the plankton food web (in which the zooplankton biomass exceeds phytoplankton biomass) are reportedly prevalent in the Southern Ocean, which indicates the importance of top-down processes (Yang et al., 2022). A positive relationship between zooplankton biomass and primary production is found in the global ocean (Hernández-León et al., 2020); however, strong seasonality in both the environment and life cycle of plankton in the polar region would complicate the match/mismatch dynamics between zooplankton and phytoplankton (Vereshchaka et al., 2021). Meanwhile, the correlations between consumers and their diet could also be affected by environmental variables (Hendriks et al., 2021).

The Southern Ocean reportedly suffers from the most rapid regional environmental change, while the rates and directions of the change varied among various sectors (McCormack et al., 2021). Regional warming and loss of ice in the southwest Atlantic sector have caused poleward range shifts of Antarctic krill, the keystone species of the Southern Ocean ecosystem (Atkinson et al., 2019, 2022), though mesozooplankton communities (mainly dominated by copepods in abundance) have shown resilience to long-term climate change (Tarling et al., 2018). Future changes in sea ice, fronts, and temperature are expected to have a significant impact on the zooplankton community and the marine ecosystem (Constable et al., 2014; Rogers et al., 2020). To enhance our understanding of the response of the Southern Ocean ecosystem to climate change, it is imperative to evaluate the effects of biotic and abiotic factors on the zooplankton community (Johnson et al., 2022).

Some physical factors like the Antarctic Circumpolar Current lead to strong physical and ecological connectivity between different sectors of the Southern Ocean (Murphy et al., 2021). A network of Marine Protected Areas and food web models in the Southern Ocean requires circumpolar-scale zooplankton data (Atkinson et al., 2012; Pinkerton et al., 2020). However, detailed quantitative data on zooplankton (i.e., composition, distribution, abundance, biomass) in the western Pacific sector is severely limited (Pinkerton et al., 2020; Yang et al., 2021).

The Amundsen Sea, located in the Pacific sector, is considered one of the most productive areas in the Southern Ocean for the existence of coastal polynyas (Arrigo et al., 2012). Because most zooplankton studies in this area have focused on the neritic region (Wilson et al., 2015; Yang et al., 2019), there is a paucity of zooplankton data for the oceanic and shelf regions. Here, we report on the zooplankton community in the Amundsen Sea during the austral summer of 2018. Integrating physical, chemical, and biological data, we study the biotic and abiotic control of the zooplankton community.

2 Materials and methods

2.1 Sampling

During the 34th Chinese National Antarctic Research Expedition, microplankton (phytoplankton and ciliates) and zooplankton samples were collected in February 2018, from 23 stations in the Amundsen Sea (Figure 1).

At each station, 1-L seawater samples were collected from depths of 0 m, 50 m, 100 m, and 200 m using Niskin bottles mounted on a rosette. Samples were preserved in 1% acid Lugol's solution and stored in the dark. In the lab, an aliquot of 27 mL was taken from each sample and placed in an Utermöhl settling chamber for 24 h before the identification and counting of microplankton. Phytoplankton/ciliates were identified to species level where possible. The carbon biomass of each species was determined by multiplying the cell biovolume and the carbon conversion ratio based on previous studies (Menden-Deuer and Lessard, 2000; Sun and Liu, 2003). Meanwhile, seawater samples from depths of 0 m, 50 m, 100 m, and 200 m were also collected to measure dissolved nutrients (nitrate, phosphate, and silicate) and dissolved oxygen (DO) parameters. Seawater samples were filtered through pre-washed GF/F filters, and concentrations of nutrients in the filtrate were determined on a continuous flow analyzer (Skalar Analytical, Netherlands). The DO of seawater was determined using the Winkler titration method. In this study, integrated values from the top 200 m of the water column were used in the following analysis.

Zooplankton samples were collected using a Norpac net (net mouth: 0.5 m², mesh size: 330 μm, towing speed: 1 m·s⁻¹) at 200 m below the surface. Samples were preserved in 5% buffered formalin prior to identification and counting using a dissecting microscope (Nikon SMZ 745T, Japan) in the lab. Large macrozooplankton were picked out and counted in each entire sample, while the remaining zooplankton were counted in aliquots of 1/2–1/128, split with a Folsom plankton splitter to ensure that 500 individuals were counted per sample. Krill (*Euphausia superba* and *Thysanoessa macrura*) and four copepod species (*Calanoides acutus*, *Calanus propinquus*, *Metridia gerlachei*, and *Rhincalanus gigas*) were sorted by

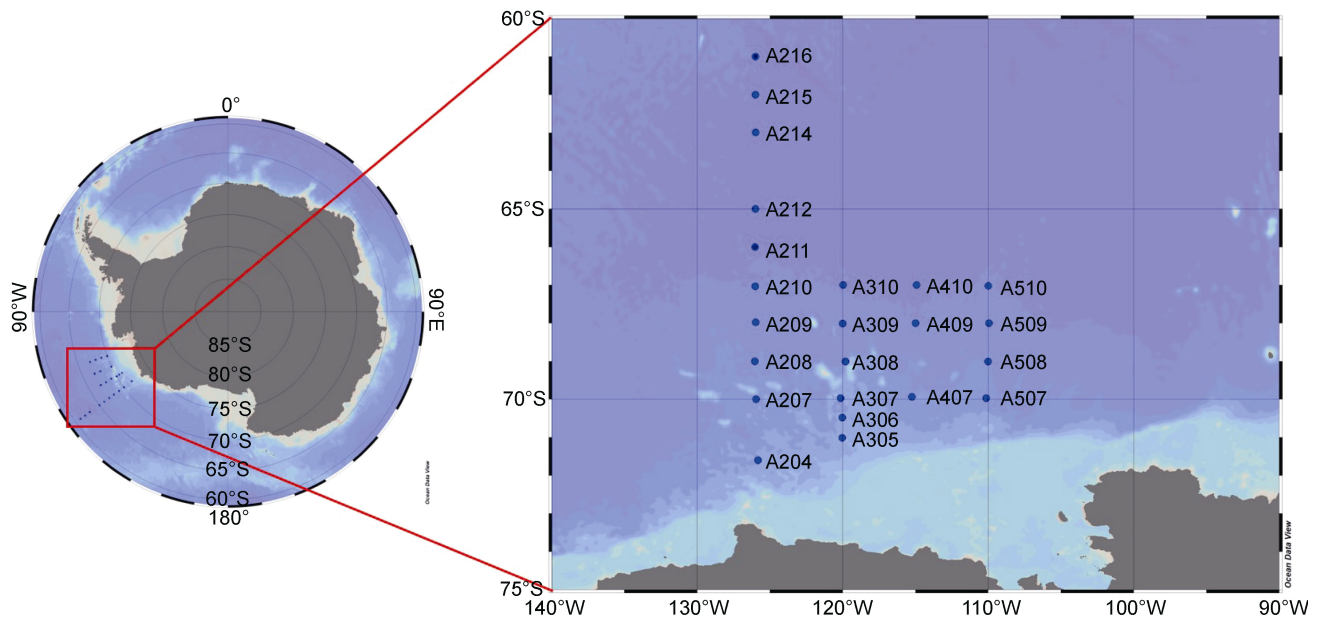


Figure 1 Map of the Amundsen Sea with plankton sampling stations.

developmental stage. The body length (total length) of 30 individuals for each species/developmental stage was recorded in each sample. The carbon biomass of each species was calculated based on interconversion equations for body length, dry mass, and carbon mass that were compiled in previous studies (Atkinson et al., 2012; Bednaršek et al., 2012; Mayzaud and Pakhomov, 2014).

2.2 Statistical analyses

The zooplankton community structure at the sampling stations was analyzed based on abundance datasets and biomass datasets. Zooplankton abundance or biomass data were square-root transformed and subjected to a Q-type cluster analysis (to investigate zooplankton assemblages at all sampling stations) based on Bray–Curtis similarity and group average linkage classification. The relationship between the dominant zooplankton species (in terms of both abundance and biomass) and environmental factors was estimated using redundancy analysis (RDA). Environmental parameters included temperature, salinity, chlorophyll *a* (Chl *a*), dissolved oxygen (DO), $\text{NO}_3\text{-N}$, $\text{SiO}_3\text{-Si}$, $\text{NH}_4\text{-N}$, $\text{NO}_2\text{-N}$, and $\text{PO}_4\text{-P}$. Chl-*a* data were provided by the Second Institute of Oceanography, Ministry of Natural Resources, China. Pearson's correlation analysis was performed to examine the relationships among the abundance/biomass of dominant zooplankton species/groups and that of phytoplankton and ciliates. Statistical analyses were performed using Canoco 5.0 (ter Braak and Smilauer, 1998) and the R version 4.2.2 (Ihaka and Gentleman, 1996). Abundance and biomass distribution maps of phytoplankton, ciliates, and zooplankton were produced using ArcGIS Version 10.0 (Law and Collins, 2013).

3 Results and discussion

3.1 Abundance and biomass of phytoplankton and ciliates

Phytoplankton abundance varied between $35.49 \text{ cell}\cdot\text{mL}^{-1}$ and $226.43 \text{ cell}\cdot\text{mL}^{-1}$, while the total biomass of phytoplankton ranged from $16.23 \text{ mg C}\cdot\text{m}^{-3}$ to $93.52 \text{ mg C}\cdot\text{m}^{-3}$ (Figures 2a, 2d). These values were similar to those of previous studies conducted in the marginal sea ice zone and oceanic area of the Amundsen Sea (Lee et al., 2013). Diatoms, mainly composed of *Chaetoceros* spp., *Fragilaria* spp., and *Nitzschia* spp., contributed to the top 85% of both phytoplankton abundance and biomass in each station (Figures 2a, 2d). Total ciliate abundance and biomass ranged within $0.99\text{--}3.42 \text{ ind}\cdot\text{mL}^{-1}$ and $2.01\text{--}9.97 \text{ mg C}\cdot\text{m}^{-3}$, respectively (Figures 2b, 2e). Shell-less ciliates represented more than 50% of the total abundance and biomass of ciliates at most of the stations (Figure 2b, 2e).

3.2 Zooplankton community structure and dominant species in the Amundsen Sea

In this study, 35 zooplankton species were identified, and 15 of these species made a major contribution (>90%) to the total abundance and biomass in any sample (Table 1). Total zooplankton abundance ranged from $11.02 \text{ ind}\cdot\text{m}^{-3}$ to $1081.1 \text{ ind}\cdot\text{m}^{-3}$, while total zooplankton biomass ranged from $0.71 \text{ mg C}\cdot\text{m}^{-3}$ to $57.94 \text{ mg C}\cdot\text{m}^{-3}$.

In accordance with previous studies conducted in Prydz Bay, Scotia Sea, Amundsen Sea, Ross Sea, and other regions of the Southern Ocean (Ward et al., 2012; Lee et al., 2013; Stevens et al., 2015; Bonello et al., 2020; Granata et

al., 2022; Grillo et al., 2022), the zooplankton community was mainly dominated by an abundance of small copepods like *Oithona similis* and *Ctenocalanus citer*, whereas the total zooplankton biomass was mainly made up of krill (*Euphausia superba* and *Thysanoessa macrura*) and large copepods such as *Calanoides acutus*, *Calanus propinquus*, and *Metridia gerlachei* (Figure 3, Table 1).

Cluster analysis identified three groups (A, B, and C) based on zooplankton abundance data (Figure 3a). Group A, represented by four stations, was located near the shelf regions, while Group B included 16 stations and Group C included three stations located in the northern regions of the sampling area (Figure 3a). A similar zooplankton community structure pattern in the latitudinal gradient was also found based on biomass data. Group A was represented

by two stations located near the shelf regions, while Group B comprised 15 stations, and group C comprised six stations located in the northern regions of the sampling area (Figure 3b). The northern group (Group A) showed a relatively lower total mean abundance ($36.03 \text{ ind}\cdot\text{m}^{-3}$) and biomass ($1.75 \text{ mg C}\cdot\text{m}^{-3}$) compared with the middle group (Group B, abundance: $420.29 \text{ ind}\cdot\text{m}^{-3}$, biomass: $9.80 \text{ mg C}\cdot\text{m}^{-3}$) and southern group (Group C, abundance: $399.26 \text{ ind}\cdot\text{m}^{-3}$, biomass: $40.17 \text{ mg C}\cdot\text{m}^{-3}$, Table 1). *Ctenocalanus citer*, *O. similis*, and *M. gerlachei* made up more than 60% of the total abundance in Group A, while *P. antarctica*, *M. gerlachei*, and *C. acutus* represented nearly 80% of the total biomass in Group A (Table 1). The abundances of the middle group (Group B) and southern group (Group C) were dominated by *O. similis*, *C. citer*, *C.*

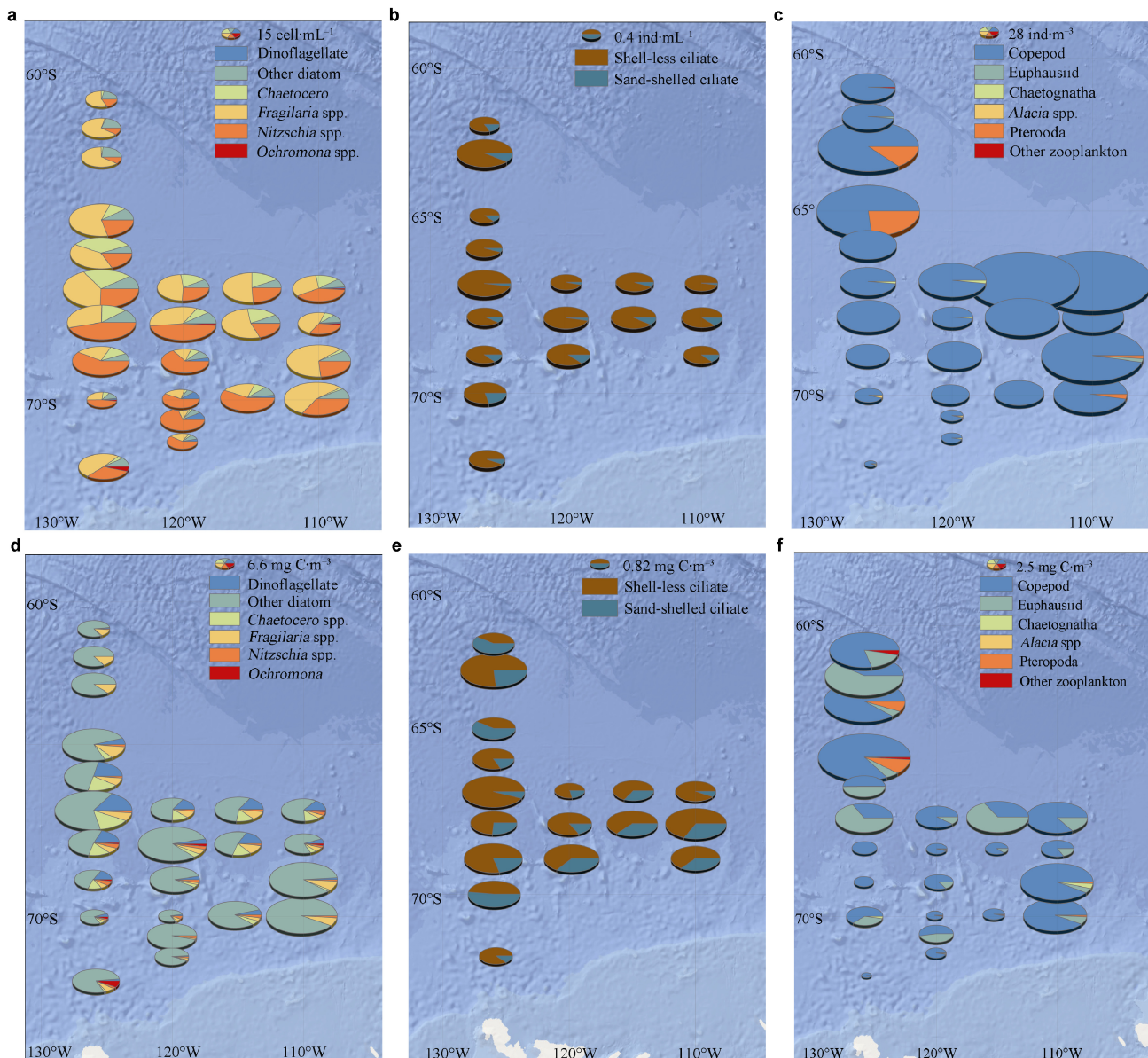
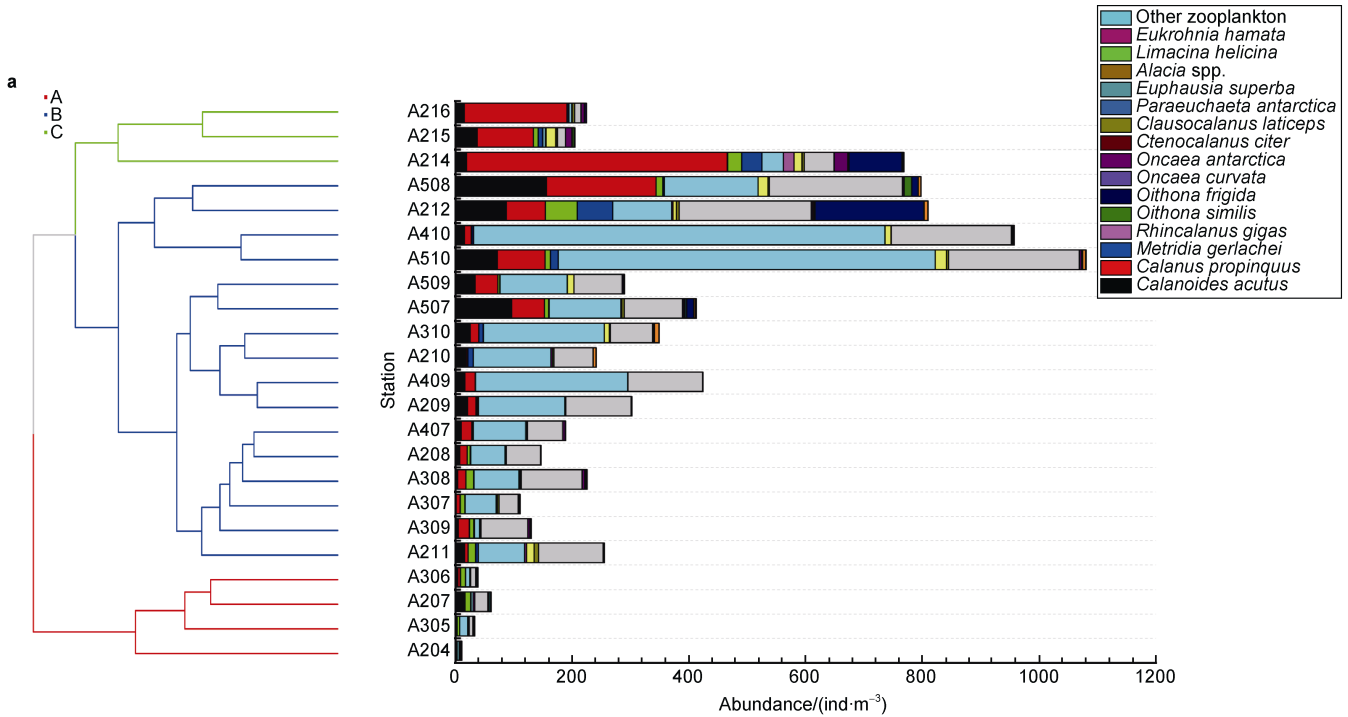


Figure 2 Abundance (a, b, c) and biomass (d, e, f) of dominant phytoplankton taxa/groups (a, d), dominant ciliate groups (b, e), and dominant zooplankton groups (c, f) in the top 200 m of the water column.

Table 1 Mean abundance and mean carbon biomass of identified species with >90% total abundance/biomass of zooplankton in each group based on cluster analysis (Figure 3)

	Abundance/(ind·m ⁻³)			Biomass/(mg C·m ⁻³)		
	Group A	Group B	Group C	Group A	Group B	Group C
<i>Calanoides acutus</i>	5.11	36.29	23.47	0.19	1.32	10.60
<i>Calanus propinquus</i>	2.05	35.83	240.32	0.11	0.70	11.46
<i>Metridia gerlachei</i>	6.02	8.49	10.56	0.26	0.38	0.92
<i>Rhincalanus gigas</i>	0.29	6.8	15.15	0.14	1.98	6.86
<i>Oithona similis</i>	7.1	185.58	15.57	0.05	0.95	0.39
<i>Oithona frigida</i>	1.57	1.04	6.72	0.01	0.007	0.03
<i>Oncaea curvate</i>	0.54	6.04	11.41	0.002	0.01	0.02
<i>Oncaea antarctica</i>	0.07	1.72	2.24	0.0002	0.003	0.008
<i>Ctenocalanus citer</i>	9.6	118.28	25.49	0.02	0.55	0.63
<i>Clausocalanus laticeps</i>	0.54	1.88	13.12	0.004	0.01	0.07
<i>Paraeuchaeta antarctica</i>	0.85	0.45	0.64	0.86	0.31	0.91
<i>Euphausia superba</i>	0.09	1.24	1.82	0.03	3.41	6.09
<i>Alacia</i> spp.	0.99	0.31	0.05	0.0003	0.008	0.009
<i>Limacina helicina</i>	0.005	13.20	30.36	0.01	0.0003	1.36
<i>Eukrohnia hamata</i>	0.72	2.65	0.77	0.02	0.05	0.23
Other zooplankton	0.48	0.49	1.57	0.03	0.11	0.57



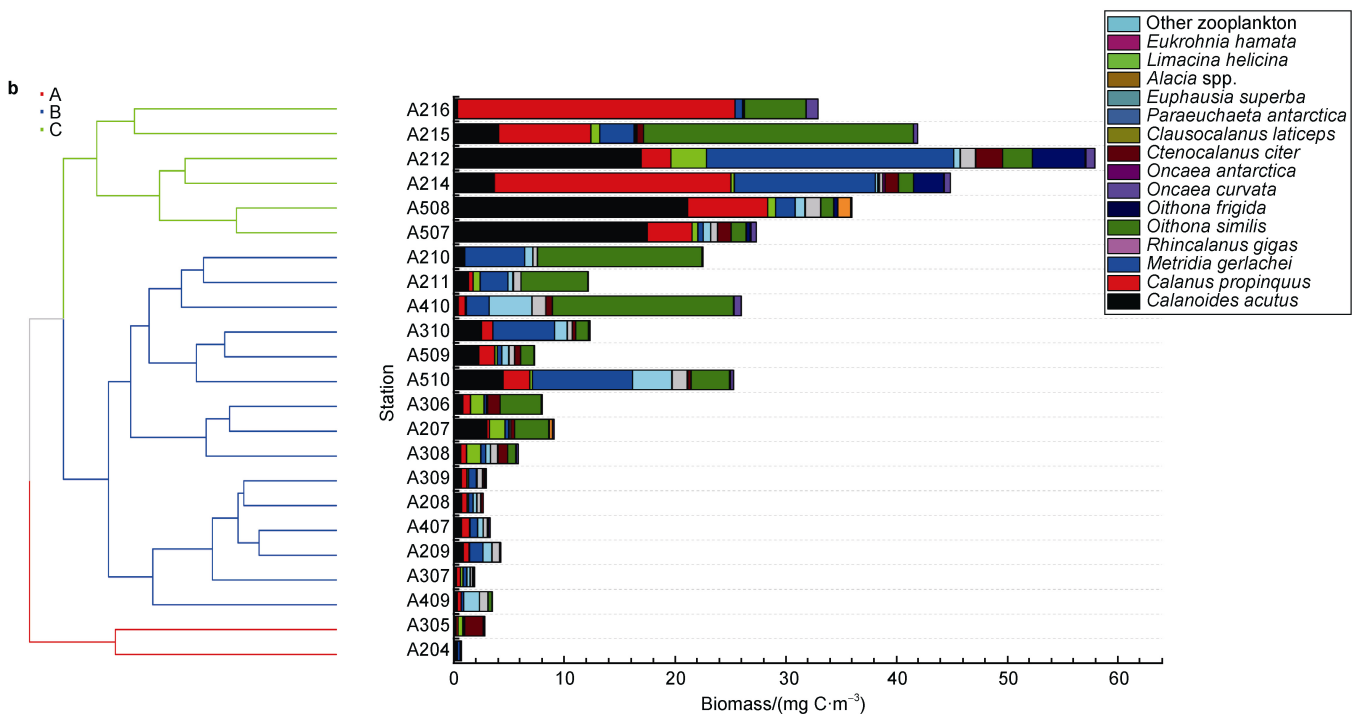


Figure 3 Cluster analysis performed on abundance datasets (a) and biomass datasets (b) of all stations. Composition of dominant zooplankton species to total abundance (a) and total biomass (b) of each station is shown in the right panel.

acutus, *C. propinquus*, and *Limacina helicina*, whereas the biomass of these two groups mainly consisted of *C. acutus*, *C. propinquus*, *R. gigas*, and *E. superba* (Table 1). A significant positive correlation was found between total zooplankton abundance and biomass ($p=0.001$, Pearson correlation). Coherent temporal synchrony in both zooplankton biomass and abundance patterns was proven based on a worldwide comparison (Batchelder et al., 2012). Although results similar to those of cluster analysis were found using abundance data and biomass data, more information could be obtained when both datasets were combined (Figure 3). With the increasing demand for zooplankton biomass data in food web models and carbon budget analysis (Hill et al., 2021), some datasets have been compiled for the global ocean and the Southern Ocean (Moriarty and O'Brien 2013; Yang et al., 2022).

3.3 Biotic and abiotic factors affecting the zooplankton community

Various abiotic factors, including temperature, depth, Chl *a*, sea ice, and nutrient concentrations, have great impacts on zooplankton communities of the Southern Ocean (Swadling et al., 2010; Tarling et al., 2018; Ward et al., 2018; Electronic Supplementary Material [ESM]). Meanwhile, some functional traits (e.g., diel vertical migration patterns and feeding strategies) of dominant zooplankton species could also affect the zooplankton community structure (Guglielmo et al., 2011). The results of the RDA analysis based on both zooplankton abundance

and biomass are shown in Figure 4. The first axis explained 49.3% of the variance in the species abundance data and 31.1% of the variance in the species biomass data (Figure 4). The Monte Carlo permutation test revealed that salinity ($p=0.008$), $\text{NH}_4\text{-N}$ ($p=0.012$), and $\text{NO}_2\text{-N}$ ($p=0.016$) significantly affected the abundance of the zooplankton community (i.e., accounted for more than 54% of the variance in zooplankton abundance), while temperature ($p=0.002$) and DO ($p=0.048$) explained 35.4% of the variance in zooplankton biomass.

The abundance and biomass of total zooplankton and most of the dominant species showed a positive correlation with those of phytoplankton and ciliates (Figures 5 and 6). Zooplankton mainly consumed phytoplankton during the austral summer (Pasternak and Schnack-Schiel, 2001), though protozoans were also considered an important food source for some dominant species like *E. superba* and copepods, especially in regions with lower phytoplankton concentrations (Schmidt et al., 2006; Yang et al., 2013). Though the bottom-up process was considered the main control of the plankton food web in the Southern Ocean (Yang et al., 2011), the preference for ciliates by some zooplankton may also impact the biomass of ciliates and phytoplankton (Yang et al., 2019). Previous studies in the Amundsen Sea have shown that a significant proportion of the phytoplankton production (34% during the peak of the bloom and >80% after the bloom) was grazed on by microzooplankton (Yang et al., 2019). Meanwhile, only a small proportion of primary production may be available for vertical carbon export and direct consumption by zooplankton

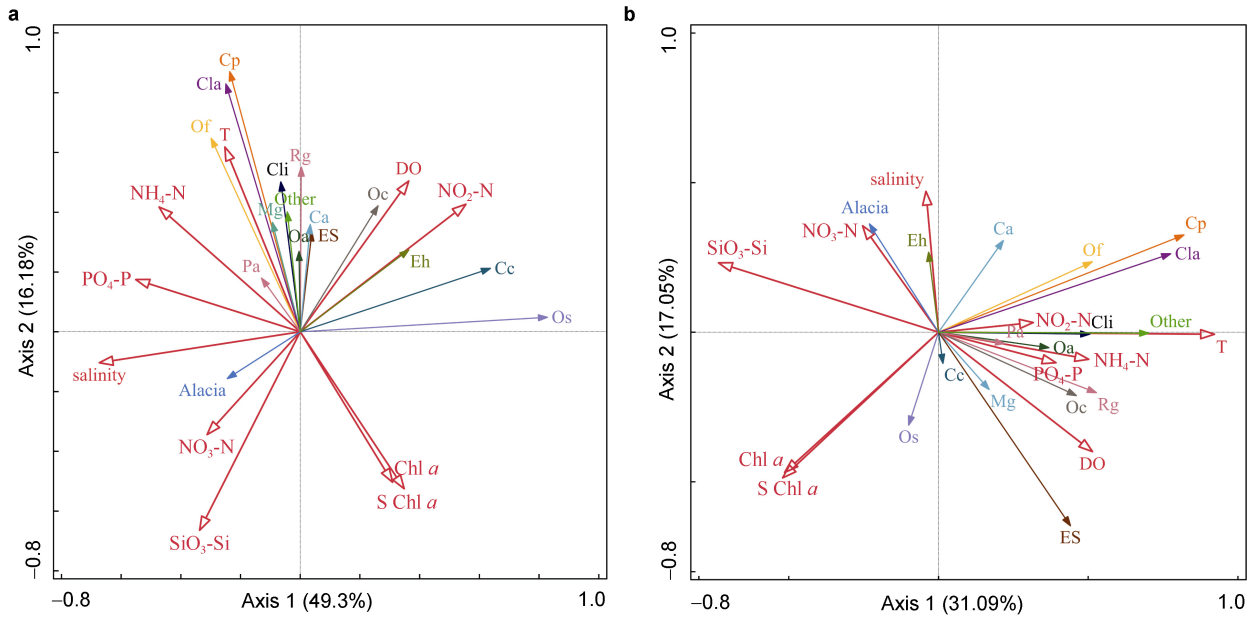


Figure 4 Redundancy analysis (RDA) ordination diagram showing the relationship between dominant zooplankton species and environmental factors based on abundance data (a) and biomass data (b). Cp: *Calanus propinquus*; Mg: *Metridia gerlachei*; Cli: *Clione limacina*; Rg: *Rhincalanus gigas*; Oa: *Oncaea antarctica*; Ca: *Calanoides acutus*; Es: *Euphausia superba*; Oc: *Oncaea curvata*; Eh: *Eukrohnia hamata*; Cc: *Ctenocalanus citer*; Os: *Oithona similis*; Pa: *Paraeuchaeta antarctica*; Of: *Oithona frigida*; Cla: *Clausocalanus laticeps*; Alacia: *Alacia* spp.; DO: dissolved oxygen; T: temperature; S Chl-*a*: surface Chl *a*, Chl-*a*: average chl *a* integrated in the top 200 m of the water column.

like krill and copepods (Yang et al., 2016). Field experiments have also illustrated that the grazing impact of three dominant copepods (*R. gigas*, *M. gerlachei*, and *C. acutus*) on phytoplankton is equivalent to approximately 3% of the phytoplankton standing stock and 4% of the daily primary production (Lee et al., 2013). Daily carbon rations (lower than 10%), which are barely enough to cover the basic metabolic demands of zooplankton, indicate that these dominant copepod species may rely on food sources other than phytoplankton. Microzooplankton likely make a substantial contribution to mesozooplankton diets in the

polynya and adjacent sea ice zone of the Amundsen Sea (Yang et al., 2019). Through trophic cascade effects, mesozooplankton can reduce the grazing pressure of microzooplankton on phytoplankton and regulate carbon and energy transfer in the plankton food webs (Yang et al., 2019).

3.4 Perspectives for spatial protection planning

In the context of climate change and its direct impact on marine ecosystems of the Southern Ocean, nine Marine Protected Area planning domains were defined by the

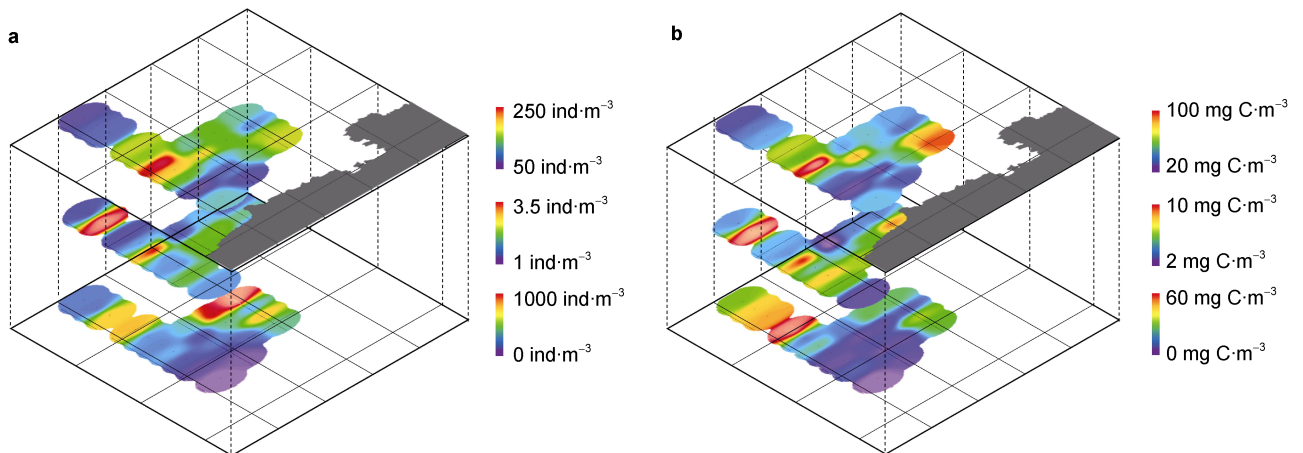


Figure 5 Abundance (a) and biomass (b) of phytoplankton (top panel), ciliates (middle panel) and zooplankton (bottom panel) in each station (integrated in the top 200 m of the water column).

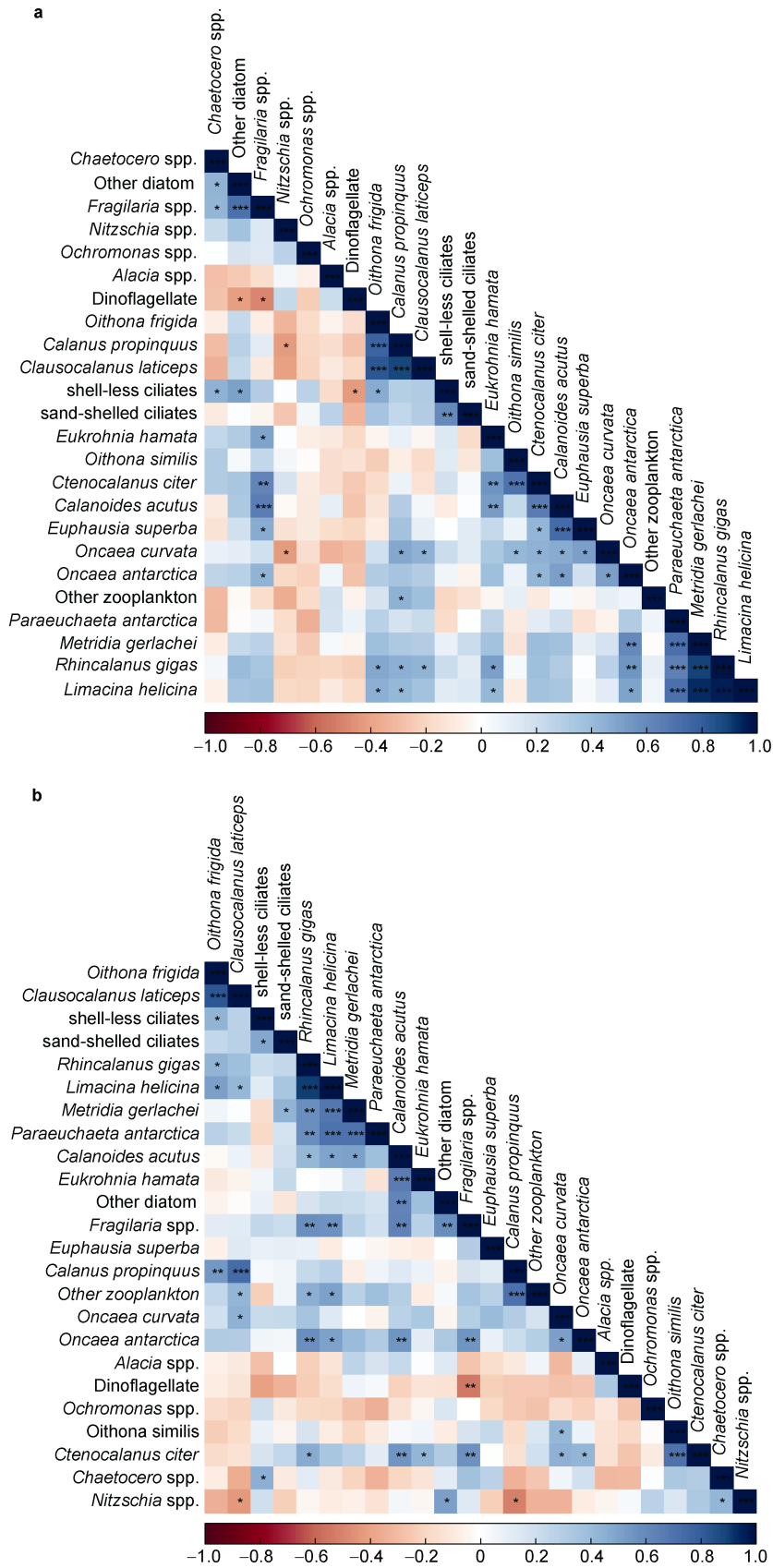


Figure 6 Pearson correlation coefficients among dominant phytoplankton, ciliates, and zooplankton taxa/groups based on abundance datasets (a) and biomass datasets (b). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Commission for the Conservation of Antarctic Marine Living Resources. The Amundsen Sea is remotely located from any nation's permanent research station on the Antarctic continent and has been visited infrequently. The extent of ice coverage in the Bellingshansen/Amundsen Seas sector has been declining overall (Parkinson, 2019). The melting of glaciers and loss of ice in the Amundsen Sea may profoundly alter zooplankton, in terms of species composition, distribution, biomass, and the roles they play in the food web and marine ecosystems. Whether this will provide improved or worsened conditions for primary production and, consequently, higher trophic levels remains unclear as little is known about these ecosystems (Lee et al., 2012). The species composition, abundance, and biomass of the zooplankton community and relationships with biotic/abiotic factors reported in this study have added to the few previous studies conducted nearby (Wilson et al., 2015). Therefore, our results provide some baseline knowledge for the biogeochemical, carbon budget, and food web studies of the Amundsen Sea as it undergoes rapid warming and ice loss.

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