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Distribution and abundance of krill in various areas of the Southern Ocean: dataset compilation based on samples collected in CHINARE during 2009–2019

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Abstract This study investigates the composition, abundance, and basic biological parameters of krill in Prydz Bay, Antarctic Peninsula and Amundsen Sea by analyzing samples and environmental data from the Chinese National Antarctic Research Expeditions conducted between 2009/2010 and 2019/2020. The predominant krill species observed were *Euphausia superba*, *Euphausia crystallorophias*, and *Thysanoessa macrura*. *T. macrura*, although the most widespread, exhibited the lowest mean abundance (9.96 ind·(1000 m^{-3})) and biomass (0.31 g·(1000 m^{-3})), predominantly found in low-latitude regions of the Amundsen Sea while *E. crystallorophias* was most concentrated in polynyas of Prydz Bay. *E. superba*, with an average abundance of 34.05 ind·(1000 m^{-3}) and biomass of 11.80 g·(1000 m^{-3}), was mainly distributed in the Antarctic Peninsula and Prydz Bay. This study also identified regional variations in mean body length and frequency distributions of krill. The relationship between krill body length and wet weight followed a power-law pattern. Regional differences were observed in the relationship between krill abundance, biomass, and environmental factors with varying correlations. In the Amundsen Sea, no significant correlation was found between krill abundance and environmental factors. Notably, *E. crystallorophias* in Prydz Bay demonstrated a significant positive correlation with chlorophyll *a* concentration, while *T. macrura* abundance and biomass in the Antarctic Peninsula exhibited a significant negative correlation with ice-free days. The findings contribute valuable regional data on krill distribution, abundance, and biomass in the Southern Ocean, serving as foundational information for the conservation of the Southern Ocean ecosystem and Antarctic krill fishery management on a circumpolar scale.

Keywords **Southern Ocean**, **krill**, ***Euphausia superba***, **biomass**, **dataset**

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1 Introduction

The Southern Ocean, constituting 20% of the global ocean area, plays an irreplaceable and crucial role in global heat circulation, nutrient cycling, biogeochemistry, carbon cycling, ocean productivity, and sea-level regulation (Kim and Kim, 2021; Li et al., 2020). Regarded as Earth's last ecological barrier, the Southern Ocean holds profound implications for the future development of humanity.

In the Southern Ocean, krill species are among the most abundant zooplankton groups, with their range extending from coastal waters to the Polar Frontal Zone (PFZ) (Haraldsson and Siegel, 2014). In the Southern Ocean ecosystems and food webs, krill plays a connecting role, not only as a significant predator of lower trophic level organisms such as phytoplankton, but also as the main bait for many higher trophic level animals such as seals, penguins, and fish (Forcada et al., 2012; Panasiuk et al., 2020). The ecological importance of krill has garnered widespread attention due to their critical role in sustaining the Southern Ocean's biodiversity (Cavan et al., 2019; Trinh et al., 2023). Among the krill species, *Euphausia superba* holds the highest biomass in the Southern Ocean, estimated at 0.65×10^{10}–1.00×10^{10} t (Everson, 2001), with medicinal prospects and commercial development value. *Thysanoessa macrura*, widely distributed across the Southern Ocean (Haraldsson and Siegel, 2014), is usually considered as a primary food source for higher trophic levels in regions where biomass of *E. superba* is comparatively lower (Driscoll, 2013), particularly in the lower-latitude waters of the South Pacific. *E. crystallorophias*, a coastal species distributed around the Antarctic, has the ability to outperform *E. superba* in some coastal areas, playing a vital role in the material cycling and energy flow of coastal ecosystems in the Southern Ocean (Sala et al., 2002).

As a globally important fishery resources development object, in recent years, Antarctic krill is facing a series of crises. In addition to fisheries (Meyer, 2012) and other anthropogenic activities, the climate and environmental issues such as rising temperatures, the reduction of sea ice and ocean acidification (Kawaguchi et al., 2013; Sylvester et al., 2021; Veytia et al., 2020), are also further threatening the biomass of Antarctic krill. The rapid warming of the Antarctic region due to global temperature rise has led to a significant reduction in sea ice coverage and density (Eayrs et al., 2021). Sea ice provides a favorable feeding environment and shelter for overwintering krill (Flores et al., 2012). The Atlantic sector, a primary habitat for Antarctic krill, is one of the fastest-warming regions in Antarctic (Vaughan et al., 2003). Since the 1970s, sea ice in the southwestern Atlantic region has rapidly decreased, resulting in a significant decline in krill density and a trend of shifting towards polar high-latitude regions (Atkinson et al., 2004, 2019). Recent studies also indicate that krill exhibits adaptive capabilities, utilizing new refuges to cope with the rapid warming and reduced sea ice in their primary habitats, showcasing a trend of migrating from rapidly changing environments to relatively stable regions (Yang et al., 2021). These findings imply that both the abundance and distribution patterns of krill on an Antarctic scale are likely to undergo changes in the future, emphasizing the necessity for comprehensive research on a large scale.

This paper is based on krill samples collected by Chinese National Antarctic Research Expeditions (CHINARE) using the Isacca-Kidd Mid-water Trawl (IKMT) net during the past decade (2009/2010–2019/2020), investigates the abundance, distribution and basic biological characteristics of different krill species (*E. superba*, *E. crystallorophias* and *T. macrura*) in the Southern Ocean. Additionally, we analyzed the impact of various environmental factors on the abundance and distribution of krill. The aim is to provide foundational information for the conservation of the Southern Ocean ecosystem and the environmental management of krill fisheries on an Antarctic scale.

2 Materials and methods

2.1 Survey sites and time

Sampling was conducted during the 26th to 36th CHINARE from 2009/2010 to 2019/2020, during the Antarctic summer. A total of 54 sampling stations were established for Antarctic krill sample collection. Based on the distribution of these stations, the study area was categorized into three major regions: Prydz Bay (65°E–78°E, 63°S–69°S), the Antarctic Peninsula (42°W–73°W, 59°S–67°S), and the Amundsen Sea (90°W–178°W, 66°S–76°S). The specific survey times and station distributions are detailed in Table 1 and Figure 1.

2.2 Sampling methods and sample processing

Krill was sampled using an IKMT net with a mouth area of 2 m^2 and mesh size of 6 mm at a vessel speed of 3–4 kn. Detailed sampling information, including cable length and maximum sampling depth were documented in Table S1. Temperature-depth (TD) profiles were used in several stations to measure the maximum sampling depth. Based on the records of cable length and sampling depth from these stations, a logarithmic relationship between cable length and maximum water depth was established and used to estimate the sampling depth of other stations (Table S1). The filtered water volume was calculated by multiplying the mouth area of the net by the towing time and ship speed. All collected krill samples were fixed and preserved with a 5% formalin solution on-site and transported back to China for identification, measurement, and analysis.

Initially, *E. superba*, *E. crystallorophias* and *T. macrura* samples from each station were identified and sorted. The identification and analysis of these three krill species were conducted under a dissecting microscope (Nikon SMZ 745T) based on the classification criteria proposed by

Table 1 Duration and coverage of krill survey from 2009/2010 to 2019/2020

Cruise	Station	Year	Survey time	Survey area	
				Longitude	Latitude
S26	A01–A06	2009/2010	2009-12-22–2010-02-25	71°E–75°E	63°S–69°S
S27	B01–B04	2010/2011	2011-01-01–2011-01-16	70°E–74°E	65°S–69°S
S28	C01–C05	2011/2012	2012-01-23–2012-03-01	47°W–73°W	60°S–67°S
S29	D01–D05	2012/2013	2013-02-02–2013-03-02	68°E–78°E	66°S–68°S
S31	E01–E07	2014/2015	2015-02-03–2015-02-28	65°E–74°E	65°S–68°S
S32	F01–F05	2015/2016	2015-12-30–2016-01-12	47°W–60°W	61°S–64°S
S33	G01–G07	2016/2017	2016-12-25–2017-01-11	42°W–58°W	59°S–63°S
S34	H01	2017/2018	2018-03-08	126°W	66°S
S35	I01–I04	2018/2019	2019-01-14–2019-01-18	90°W–105°W	66°S–69°S
S36	J01–J10	2019/2020	2020-01-06–2020-02-06	120°W–178°W	68°S–76°S

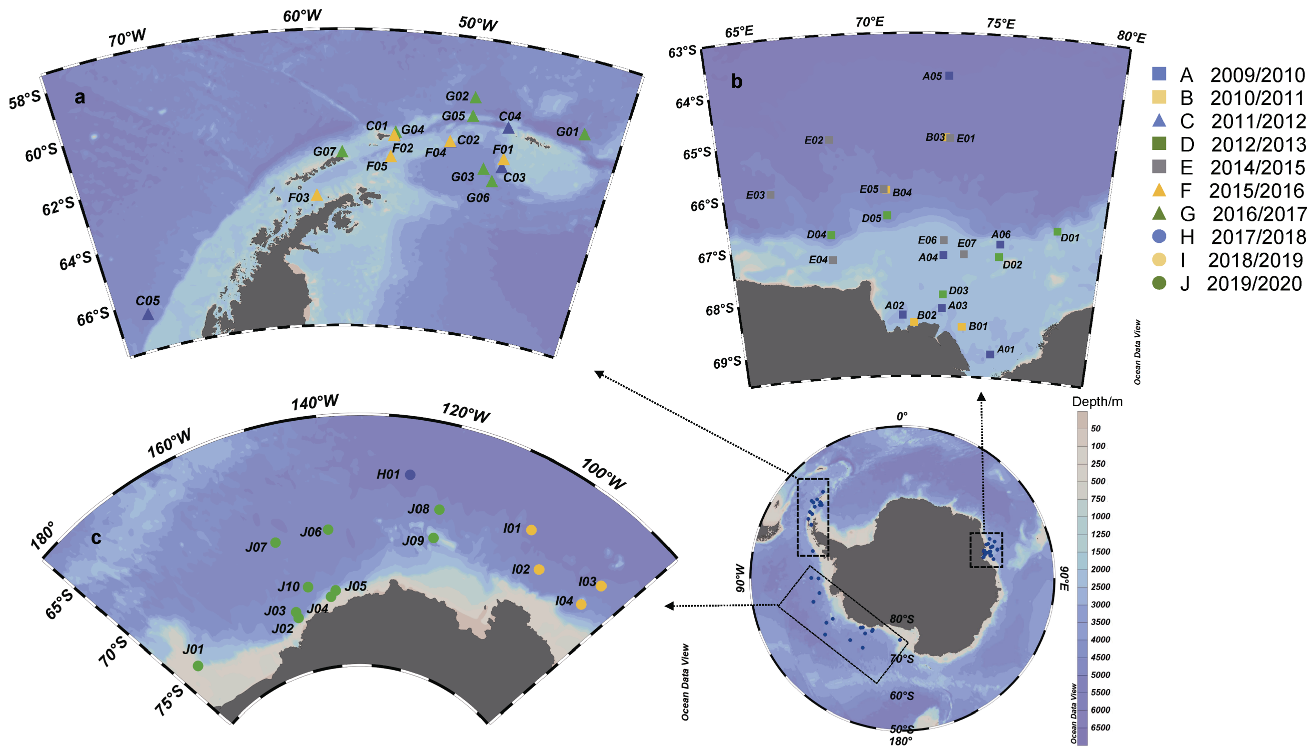

Figure 1 Net sampling stations in the Southern Ocean between 2009/2010 and 2019/2020. **a**, Antarctic Peninsula; **b**, Prydz Bay; **c**, Amundsen Sea.

Makarov and Denys (1980). The krill were categorized as juveniles or adults based on the absence or presence of apparent external characteristics and their body length. Counts were made for both intact and damaged krill samples. For stations with a substantial number of krill samples, 30 juveniles and 30 adults of each krill species were randomly selected for body length and wet weight measurements, as well as gender analysis. For stations with fewer krill samples, measurements and analyses were conducted on all available intact krill. Body length measurements followed the standards set by Mauchline (1980), with a vernier caliper with an accuracy of 0.1 mm. Wet weight measurements were conducted after removing surface moisture using absorbent paper, using an electronic balance with an accuracy of 0.001 g. All the measured adults and a subsample of juveniles (based on the abundance ratio of adults/juveniles in each sample) were used for the length frequency analysis. Gender analysis of adult krill followed the criteria of Makarov and Denys (1980) and was conducted under a dissecting microscope (Nikon SMZ 745T).

2.3 Environmental data

Relevant environmental data utilized in this study were obtained through satellite data channels: Antarctic sea ice data and images were sourced from the National Snow and Ice Data Center at the University of Colorado Boulder (https://nsidc.org/data/g02135/versions/3), with a spatial resolution of 25 km×25 km. Sea surface temperature (SST) data were obtained from NOAA's SST database (https://www.ncei.noaa.gov) with a spatial resolution of 25°×25°. Chlorophyll *a* concentration data were sourced from the Copernicus Marine Environment Monitoring Service's global ocean biogeochemical analysis and forecasting platform (https://data.marine.copernicus.eu) with a spatial resolution of 25°×25°. Due to the limitations of the Antarctic cruise season, the time range for all three environmental data sets was from March to December of the years 2009 to 2020, with a daily time resolution.

2.4 Data processing and statistical analysis

2.4.1 Body length-wet weight relationship

The body length-wet weight relationship for the three krill species was fitted using an allometric equation (Zhan, 1995):

$$W_W = a \times L_B^b$$

where, W_W is wet weight (g), L_B is body length (mm), *a* is the condition factor, reflecting the advantages and disadvantages of the krill's environment, *b* is the allometric factor, which can be used to determine whether the population is in the state of uniform growth. When $b<3$, the growth is called negative allometric; when $b=3$, the growth is called isometric growth; and when $b>3$, the growth is called positive allometric.

2.4.2 Statistical analysis

Regional differences in environmental factors and krill body length were evaluated using one-way analysis of variance (ANOVA). Pearson correlation analysis was employed to assess the correlation between environmental factors and krill abundance and biomass. The regional differences and Pearson correlation analyses were processed using SPSS 19 statistical software. Additionally, Chiplot was used for visualizing the correlation between environmental factors and krill abundance and biomass (https://www.chiplot.online).

3 Results

3.1 Environmental factors

3.1.1 Ice free days

The ice free days (i.e., the number of days the station was not covered by sea ice before sampling, with negative values indicating the days defined as ice free after sampling) at each station are presented in Table 2. Stations in the Antarctic Peninsula exhibited early sea ice retreat, with ice free days exceeding one month on average, significantly higher than those in Prydz Bay (ANOVA, $p<0.001$) and the Amundsen Sea (ANOVA, $p<0.001$). Based on daily sea ice extent images provided by the National Snow and Ice Data Center, and considering the station sampling times and distribution, 42 stations (77.8%) were identified to be in open water or beyond the ice edge during the sampling period, including all stations in the Antarctic Peninsula. In the sampling years of 2009/2010, 2010/2011, and 2019/2020, polynyas were observed in the study area, with some stations in Prydz Bay and the Amundsen Sea located within polynyas.

Table 2 Environmental conditions in various sampling regions of the Southern Ocean

Sea area	Ice free days /d		SST /℃		Chlorophyll *a* /(mg·m^{-3})	
	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
Antarctic Peninsula	33–127	93.9±25.9	–0.3–2.0	0.55±0.53	0.3–2.8	1.13±0.70
Prydz Bay	–16–80	28.5±24.5	–1.8–0.7	–0.55±0.65	0.2–1.8	0.70±0.41
Amundsen Sea	–14–89	22.4±40.8	–1.5–1.0	–0.64±0.97	0.3–0.8	0.39±0.14

3.1.2 Sea surface temperature

The average SST at stations in the study area was –0.23 ℃ (–1.8–2.0 ℃). The highest temperature was recorded at station G07, located near the northern coast of the Antarctic Peninsula, while temperatures at other stations were 1.0 ℃ or below. The lowest temperature occurred at station E07 in the shelf break area of Prydz Bay. There were significant regional differences in SST distribution, with the average temperature in the Antarctic Peninsula (0.55 ℃) significantly higher than that in Prydz Bay (–0.55 ℃) (ANOVA, $p<0.001$) and the Amundsen Sea (–0.64 ℃) (ANOVA, $p<0.01$). However, there was no significant difference in SST between Prydz Bay and the Amundsen Sea ($p = 0.983 > 0.05$), as shown in Table 2.

3.1.3 Chlorophyll *a* concentration

There were significant differences in chlorophyll *a* concentration among stations in the study area, ranging from 0.2 to 2.8 mg·m^{-3}, with an average of 0.75 mg·m^{-3}. The highest chlorophyll *a* concentration occurred in the Antarctic Peninsula area, with an average of 1.13 mg·m^{-3}. Stations with chlorophyll *a* concentrations exceeding 2 mg·m^{-3} (C01, F02 and F03) were all located in the Antarctic Peninsula. Prydz Bay followed the Antarctic Peninsula with an average chlorophyll *a* concentration of 0.70 mg·m^{-3}, showing a correlation between chlorophyll *a* concentration and latitude (Pearson, $p<0.01$), with a trend of lower concentrations in deep-sea areas and higher concentrations in coastal areas. The Amundsen Sea exhibited significantly lower chlorophyll *a* concentrations compared to the Antarctic Peninsula (ANOVA, $p<0.01$) and Prydz Bay (ANOVA, $p<0.05$), with an average of 0.39 mg·m^{-3}. Chlorophyll *a* concentrations at all stations in the Amundsen Sea were below 1.0 mg·m^{-3} and increased with higher latitudes (Pearson, $p<0.01$).

3.2 Krill abundance, biomass, and distribution

The krill samples in the surveyed area primarily consisted of three species: *E. superba*, *E. crystallorophias*, and *T. macrura*. Additionally, a small number of *Euphausia triacantha* were discovered at station I04 in the Amundsen Sea in 2018/2019. Of the 54 sampling stations, only 2 stations (D02 and G04) did not collect krill and 4 stations collected krill larvae, of which 1 and 34 individuals of FVI stage of *T. macrura* were collected respectively at stations G01 and G02 in the Antarctic Peninsula in 2016/2017, one individual of CIII stage of *T. macrura* was collected at stations I01 and I03 in the Amundsen Sea in 2018/2019, and 12 individuals of FVI stage of *E. superba* were collected at station J10 in the Amundsen Sea in 2019/2020. The remaining stations were composed of late-stage larvae (including juveniles and adults). Krill distribution in the surveyed area exhibited a patchy pattern, as illustrated in Figure 2.

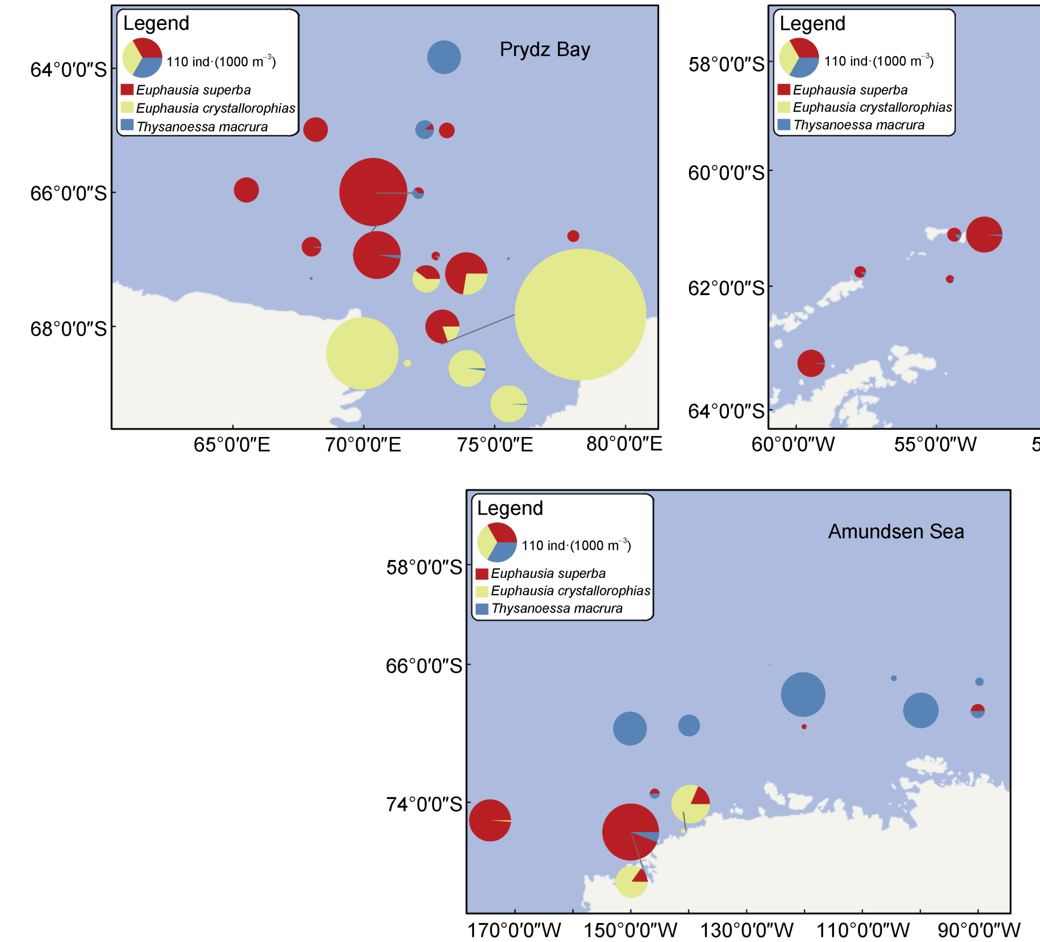

Figure 2 Spatial distribution of Antarctic krill abundance and species proportions in various sampling regions of the Southern Ocean.

E. superba exhibited a widespread distribution, appearing at 37 stations, with a predominant presence in Prydz Bay (41.7%) and the Antarctic Peninsula (38.7%). The average abundance was 34.05 ind·(1000 m^{-3}), ranging from 0 to 433.45 ind·(1000 m^{-3}), and the average biomass was 11.80 g·(1000 m^{-3}), ranging from 0 to 232.26 g·(1000 m^{-3}). High abundance stations were mainly situated in deep-sea areas, with three stations exceeding 200 ind·(1000 m^{-3}): station C04 in the Antarctic Peninsula (433.45 ind·(1000 m^{-3})), station E05 in Prydz Bay (306.55 ind·(1000 m^{-3})), and station J03 in the Amundsen Sea (203.64 ind·(1000 m^{-3})). However, the majority of stations had abundance and biomass below 50.00 ind·(1000 m^{-3}) and 20.00 g·(1000 m^{-3}), respectively.

E. crystallorophias had a limited distribution, appearing at only 13 stations, with 92.5% located in shallow waters (⩽1000 m) of Prydz Bay, and the remaining stations in the nearshore areas of the Amundsen Sea. *E. crystallorophias* were not collected in the Antarctic Peninsula. The average abundance was 35.03 ind·(1000 m^{-3}), ranging from 0 to 1144.57 ind·(1000 m^{-3}), and the average biomass was 2.75 g·(1000 m^{-3}), ranging from 0 to 95.53 g·(1000 m^{-3}). There were significant differences in abundance and biomass among stations, with the majority having values below 100.00 ind·(1000 m^{-3}) and 20.00 g·(1000 m^{-3}), respectively. Two stations, A03 (1144.56 ind·(1000 m^{-3}))

and A02 (345.83 ind·(1000 m^{-3})), both located near the coast of Prydz Bay, had abundance values exceeding 300.00 ind·(1000 m^{-3}).

T. macrura had the broadest distribution, appearing at 41 stations, mainly in the low-latitude regions of the Amundsen Sea (65.8%). The average abundance was 9.96 ind·(1000 m^{-3}), ranging from 0 to 132.68 ind·(1000 m^{-3}), and the average biomass was 0.31 g·(1000 m^{-3}), ranging from 0 to 5.72 g·(1000 m^{-3}). The three highest abundance values were all in the Amundsen Sea between 68°S and 70°S, specifically at stations J08 (132.68 ind·(1000 m^{-3})), I02 (83.99 ind·(1000 m^{-3})), and J07 (76.15 ind·(1000 m^{-3})).

The composition of krill in the three regions varies markedly, Prydz Bay was dominated by *E. crystallorophias* and *E. superba*, with *T. macrura* contributing less. The average abundance of *E. crystallorophias* was 79.51 ind·(1000 m^{-3}), and that of *E. superba* was 34.86 ind·(1000 m^{-3}), together accounting for over 95% of total krill abundance. The main distribution areas for the three krill species in the region were the nearshore, shelf, and deep-sea areas. The Antarctic Peninsula was dominated by *E. superba*, with an average abundance of 41.82 ind·(1000 m^{-3}), constituting over 90% of the krill population, and no *E. crystallorophias* were found. The Amundsen Sea was primarily occupied by *T. macrura* and Antarctic krill, accounting for 42.12% and 41.30%, respectively, with *E. crystallorophias* only found at two nearshore stations.

3.3 Krill developmental stage composition

Due to the limited occurrence and low quantity of krill larvae at only four stations, this study categorizes krill into two developmental stages: juvenile stage and adult stage. Figure 3 illustrates the proportional representation of the developmental stages of three krill species across different regions. *E. superba*, *E. crystallorophias*, and *T. macrura* are predominantly in the adult stage in all regions, with a lower proportion in the juvenile stage. Specifically, for *E. superba*, the percentage of adult was 70.7% in Prydz Bay, 79.3% in the Antarctic Peninsula and 90.1% in the Amundsen Sea. Similarly, *E. crystallorophias* in the Amundsen Sea shows a higher adult proportion (91.2%) compared to that of Prydz Bay (74.6%). In contrast, *T. macrura* exhibits an inverse pattern, with a lower adult proportion (79.3%) in the Amundsen Sea compared to that of Prydz Bay (93.3%) and the Antarctic Peninsula (96.2%).

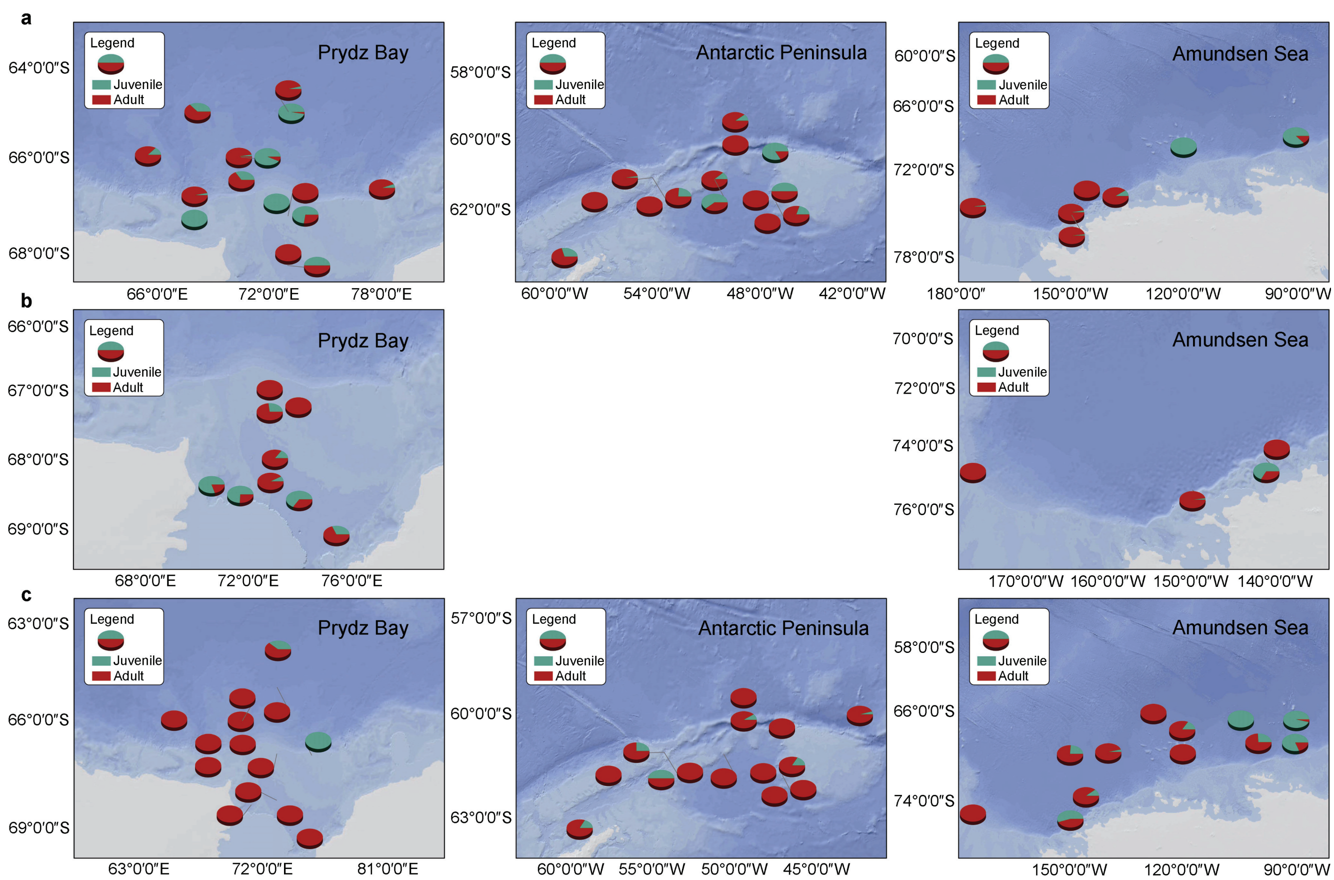

Figure 3 Percentage of developmental stages of *E. superba* (**a**), *E. crystallorophias* (**b**) and *T. macrura* (**c**).

3.4 Krill length and wet weight

3.4.1 Length range and wet weight

Table 3 presents the length range and mean values for the three krill species. The length range and mean length of *E. superba* are 13.2–57.7 mm and 34.44 mm, respectively, with a wet weight range of 0.007–1.362 g and a mean wet weight of 0.327 g. *E. crystallorophias* has a length range of 12.6–34.9 mm, a mean length of 24.50 mm, a wet weight range of 0.008–0.267 g, and a mean wet weight of 0.080 g. *T. macrura* has a length range of 11.0–30.4 mm, a mean length of 17.87 mm, a wet weight range of 0.005–0.146 g, and a mean wet weight of 0.0333 g. ANOVA variance analysis indicates that in the Amundsen Sea, the adult length of *E. superba* is significantly lower than those in Prydz Bay and the Antarctic Peninsula (p<0.05). There is no significant difference in juvenile length between regions (p>0.05). For *E. crystallorophias*, both juvenile and adult lengths exhibit consistent differences, with a significant variation between Prydz Bay and the Amundsen Sea (p< 0.01). However, there is no significant difference in length among regions for *E. crystallorophias*.

Table 3 Ranges and mean values for krill length in various sampling regions of the Southern Ocean

Species	Stages	Prydz Bay			Antarctic Peninsula			Amundsen Sea		
		n	Range/mm	Mean±SD/mm	*n*	Range/mm	Mean±SD/mm	*n*	Range/mm	Mean±SD/mm
E. superba	J	220	13.9–27.9	23.1±2.88	145	13.2–28.0	23.1±3.84	42	16.0–27.7	22.6±3.19
	A	299	28.0–55.2	41.9±7.11	290	27.7–57.7	41.3±7.41	130	24.6–52.6	38.0±5.16
E. crystallorophias	J	132	13.9–23.9	19.1±2.06	0	N.A.	N.A.	14	12.6–22.3	19.4±2.78
	A	222	19.6–34.9	26.8±3.08	0	N.A.	N.A.	78	20.8–34.1	27.9±3.95
T. macrura	J	31	12.4–16.3	14.6±1.01	5	13.7–16.0	15.2±0.89	65	11.0–16.2	13.9±1.19
	A	146	12.7–26.8	18.2±2.81	133	13.2–30.1	18.6±2.58	175	14.2–30.4	19.2±3.24

Notes: *n*=total number of krill measured in all stations of each sampling region; J=juvenile; A=adult.

3.4.2 Length frequency distribution

The length frequency distribution of the three krill species is depicted in Figures 4a, 4c and 4e. There are significant differences in the length frequency distribution of krill among different regions. The length frequency distribution of *E. superba* (Figure 4a) in Prydz Bay exhibits a typical multimodal pattern, with two dominant length groups at 20–26 mm and 42–48 mm. In the Antarctic Peninsula, a multimodal pattern is also observed, but with a more evenly distributed frequency of length groups. In the Amundsen Sea, there is significant variation in length group frequencies, with a lower proportion of length groups below 28 mm (typically indicative of juvenile Antarctic krill). The length frequency distribution of *E. crystallorophias* (Figure 4c) is similar to *E. superba*, with a multimodal pattern in Prydz Bay and the Amundsen Sea. However, in Prydz Bay, the distribution is more even, while in the Amundsen Sea, there is significant variation in length group frequencies, and the proportion of juvenile length groups is low. The length frequency distribution of *T. macrura* (Figure 4e) is unimodal in all three regions. In the Amundsen Sea, the length group range is the largest (11–31 mm), and the proportion of juvenile length groups is higher compared to the other two regions.

3.4.3 Body length-wet weight relationship

Figures 4b, 4d and 4f show the length-wet weight relationships for *E. superba*, *E. crystallorophias*, and *T. macrura*, respectively. The length-wet weight relationships for all three krill species follow a typical power-law relationship. The growth exponent (b-value) for *E. superba* is highest in Prydz Bay (3.317), and exceeds 3 in all regions, indicating positive allometric. For *E. crystallorophias*, the b-values in Prydz Bay and the Amundsen Sea are 3.772 and 3.452, respectively, both indicating positive allometric. *T. macrura* has the highest b-value on the Antarctic Peninsula (3.211), showing positive allometric. In Prydz Bay, the b-value approaches 3, indicating isometric growth, while in the Amundsen Sea, the growth factor is less than 3, indicating negative allometric.

3.5 Correlation between krill abundance/biomass and environmental factors

Correlation analyses between krill abundance/biomass and environmental factors in different regions are depicted in Figure 5. In Prydz Bay (Figure 5a), total krill abundance, *E. crystallorophias* abundance, and biomass are positively correlated with chlorophyll *a* concentration (Pearson, p< 0.05), and total krill biomass is positively correlated with SST (Pearson, p<0.05). In the Antarctic Peninsula (Figure 5b), abundance and biomass of *T. macrura* are negatively correlated with ice free days (Pearson, p<0.05). In the Amundsen Sea (Figure 5c), there is no significant correlation between krill abundance/biomass and environmental factors (SST, chlorophyll *a* concentration, and ice free days) (Pearson, p>0.05).

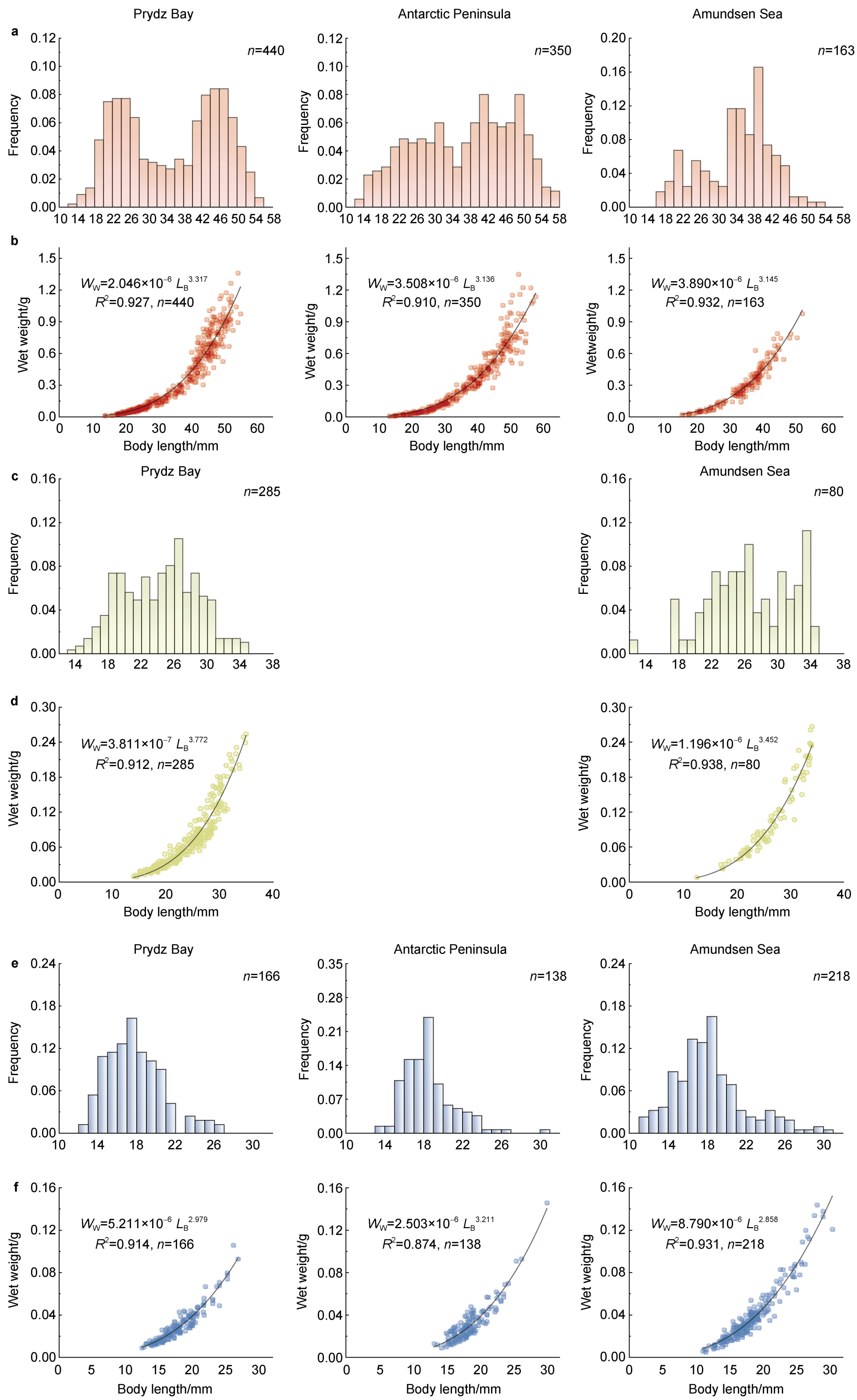

Figure 4 Body length frequency (**a**, **c**, **e**) and length-wet weight relationships (**b**, **d**, **f**) of *E. superba* (**a**, **b**), *E. crystallorophias* (**c**, **d**) and *T. macrura* (**e**, **f**).

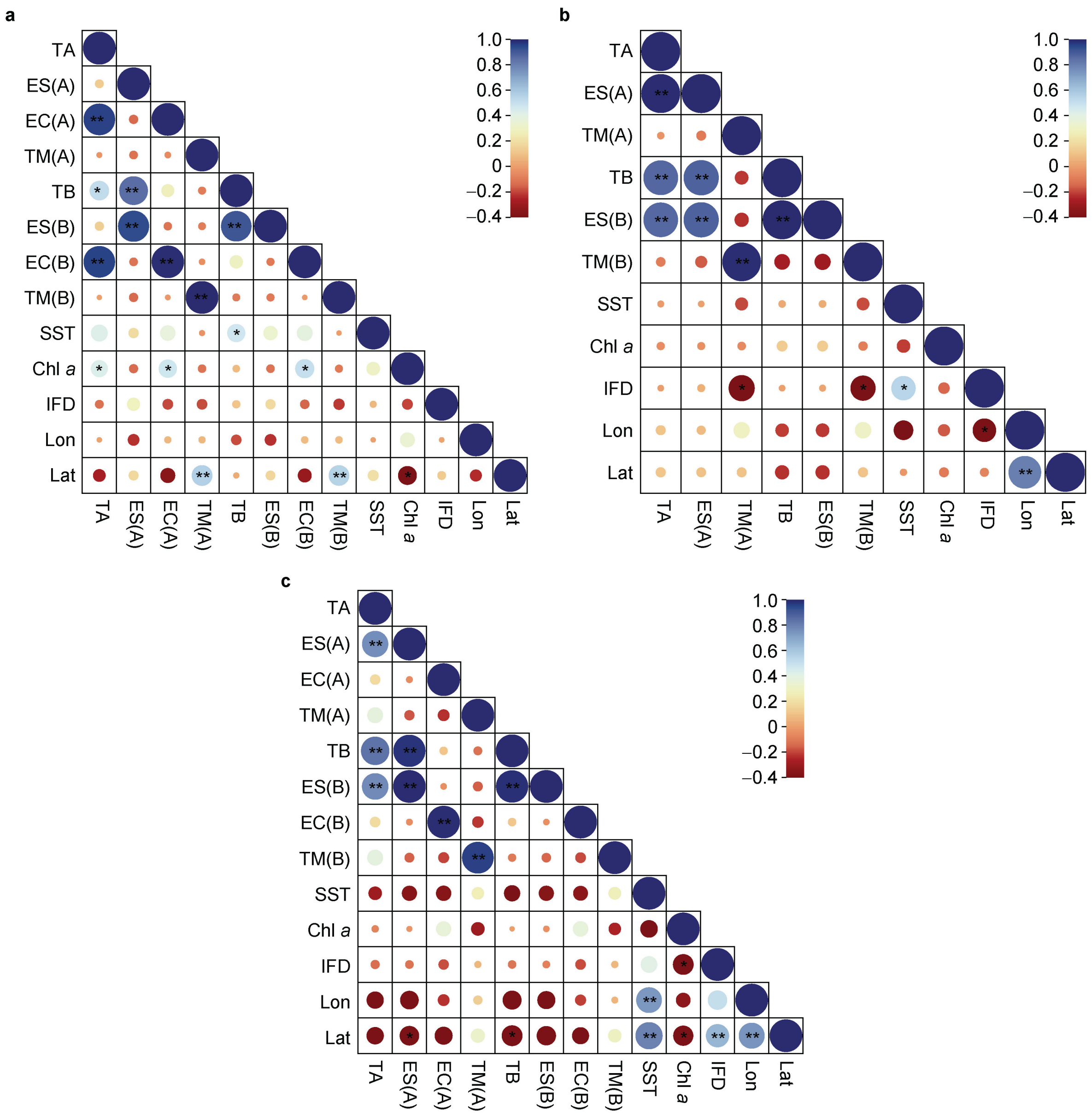

Figure 5 Pearson correlation coefficients between krill abundance, biomass, and environment factors in Prydz Bay (**a**), the Antarctic Peninsula (**b**) and the Amundsen Sea (**c**) . * $p<0.05$, ** $p<0.01$. TA, total abundance; ES(A), *E. superba* abundance; EC(A), *E. crystallorophias* abundance; TM(A), *T. macrura* abundance; TB, total biomass; ES(B), *E. superba* biomass; EC(B), *E. crystallorophias* biomass; TM(B), *T. macrura* biomass; SST, sea surface temperature; Chl *a*, chlorophyll *a*; IFD, ice free days; Lon, longitude; Lat, latitude.

4 Discussion

4.1 Abundance and distribution patterns of krill in the Southern Ocean

Extensive research data since the early 20th century's "Discovery" expedition have revealed an asymmetric circumpolar distribution pattern of *E. superba*, with its highest abundance observed in the South Atlantic, followed by the South Indian Ocean and its lowest abundance in the South Pacific (Atkinson et al., 2004, 2008). In the present study, both catch frequency and mean abundance results revealed higher values of *E. superba* in the Antarctic Peninsula region of the South Atlantic compared to the Prydz Bay in the Southern Indian Ocean. Additionally, lower values were observed in the Amundsen Sea within the South Pacific Ocean waters, which is consistent with previous findings (Table 4). Although *E. superba* populations are lower in Prydz Bay and the Amundsen Sea, both regions have high abundance points that exceed 200 ind·(1000 m^{-3}) (Figure 2), which is higher than the abundance values of 83.4% of the krill sites in the KRILLBASE database (Atkinson et al., 2017), possibly related to the patchy distribution of krill. In addition to regional differences, the interannual variation in *E. superba*

Table 4 Fishing frequency and mean abundance of krill in the Southern Ocean

Sea area	Year	*E. superba*		*E.crystallorophias*		*T. macrura*	
		Captured frequency	Mean abundance /[ind·(1000 m^{-3})]	Captured frequency	Mean abundance /[ind·(1000 m^{-3})]	Captured frequency	Mean abundance /[ind·(1000 m^{-3})]
Prydz Bay	2009/2010	33.3%	3.65	66.7%	268.26	83.3%	13.51
	2010/2011	50.0%	1.46	50.0%	26.90	75.0%	7.10
	2012/2013	80.0%	48.75	20.0%	3.01	40.0%	0.88
	2014/2015	100%	70.77	28.6%	4.73	57.1%	0.31
	Average	68.2%	34.86	40.9%	79.51	63.6%	5.28
Antarctic Peninsula	2011/2012	100%	115.81	N.A.	N.A.	100%	3.61
	2015/2016	100%	17.11	N.A.	N.A.	80.0%	7.13
	2016/2017	71.4%	6.61	N.A.	N.A.	85.7%	2.06
	Average	88.2%	41.82	N.A.	N.A.	88.2%	4.01
Amundsen Sea	2017/2018	N.A.	N.A.	N.A.	N.A.	100%	0.10
	2018/2019	20.0%	1.33	N.A.	N.A.	100%	24.38
	2019/2020	60.0%	35.43	40.0%	14.21	70.0%	25.63
	Average	46.7%	24.06	26.7%	9.48	80.0%	23.59

abundance is significant, especially in the Antarctic Peninsula region, where the highest annual average abundance (115.81 ind·(1000 m^{-3}), 2011/2012) differs by nearly two orders of magnitude from the lowest annual average abundance (6.61 ind·(1000 m^{-3}), 2016/2017). In comparison with previous data, which collected aboard Palmer Station LTER annual cruises off the western Antarctic Peninsula, from 1993 to 2008, the mean annual abundance of *E. superba* in the Antarctic Peninsula fluctuated in an uncontrolled manner between 7.97 and 433.64 ind·(1000 m^{-3}), again with a difference of two orders of magnitude (Trinh et al., 2023).

In this study, *E. crystallorophias* in Prydz Bay, whether in juvenile or adult stages, is found in nearshore areas shallower than 1000 m, further confirms the nearshore distribution characteristic of *E. crystallorophias* (Yang et al., 2010). Based on sea ice imagery (Figure S1), we observed the presence of polynyas in Prydz Bay during the sampling periods of 2009/2010, 2010/2011, and 2019/2020, as well as in the Amundsen Sea in 2019/2020. These polynyas often remain ice free from November to March during the Antarctic summer (MacDonald et al., 2023), with adequate light and supply of dissolved iron providing favorable conditions for the abundant growth of phytoplankton, making crucial habitats for *E. crystallorophias* (Falk-Petersen et al., 2000; La et al., 2015a). This bottom-up process also explains the higher abundance of *E. crystallorophias* when polynyas are present, both in this study and in previous studies (Yang et al., 2011).

T. macrura is one of the most widely distributed krill species in the Southern Ocean (Haraldsson and Siegel, 2014). It is an omnivorous species with rich long-chain fatty acids (Mayzaud et al., 2003), providing energy for its growth and development during food scarcity. Compared to other krill species, the weak dependence on spring phytoplankton and strong tolerance to temperature (Driscoll, 2013) contribute to the widespread distribution of *T. macrura*. In this study, *T. macrura* is the most widely distributed but least abundant species among the three krill species. Meanwhile, due to their shorter body length, *T. macrura* may exhibit strong escape behavior relative to the other two krill species, potentially leading to an underestimation of its abundance results.

4.2 Developmental stage and length-weight relationships of *E. superba*, *E. crystallorophias* and *T. macrura*

Krill samples at 92.60% of stations in this study were exclusively juveniles and adults, with no larvae present. The larger mesh size of IKMT may be the reason for the increased probability of larval escape. The developmental stage composition of the three krill species is similar, with adults dominating in all regions, although a small proportion of juveniles is present. To some extent the proportion of juveniles can indicate the population recruitment strength (Wang et al., 1993). Krill developmental stage composition reveals that *E. superba* in Prydz Bay and the Antarctic Peninsula has a higher proportion of juveniles (Age less than 1+) compared to the Amundsen Sea, indicating stronger population recruitment. *E. crystallorophias* also shows stronger population recruitment in Prydz Bay, while *T. macrura* exhibits the opposite pattern, with stronger population recruitment in the Amundsen Sea and weaker recruitment in Prydz Bay and the Antarctic Peninsula (Figure 3). The strength of population recruitment in krill is related to the survival rate of larvae. Studies suggest that krill spawning in higher productivity areas is more successful due to the higher lipid content of eggs produced in high-productivity regions, leading to higher survival rates in times of food scarcity (Bernard et al., 2022).

As shown in Table 2, chlorophyll *a* concentrations in the Antarctic Peninsula and Prydz Bay during the sampling period are significantly higher than that in the Amundsen Sea, indicating higher productivity conducive to embryo survival and larval development. The unique lipid composition of *T. macrura* makes it less dependent on chlorophyll *a* (Siegel and Leob, 1995), explaining its widespread distribution in high-latitude regions with fewer competitors, contributing to its higher population recruitment strength.

The body length frequency distribution of *E. superba* and *E. crystallorophias* is similar to that of most krill species (e.g., *Euphausia frigida*, *Euphausia triacantha*), displaying a multimodal distribution (Taki et al., 2008). In contrast, *T. macrura* exhibits a unimodal body length frequency distribution in all regions, consistent with previous studies on the body length distribution of *T. macrura* (Nordhausen, 1994). The unique unimodal body length frequency distribution of *T. macrura* indicates that its life history characteristics, such as population recruitment, spawning time, life history cycle, growth rate, and maximum size, may differ significantly from the other two Southern Ocean krill species. For example, Driscoll's study indicated that the population recruitment and loss of *T. macrura* due to death, advection transport, or other behaviors occurs continuously, instead of discretely (Driscoll, 2013). The omnivorous nature, temperature adaptability, and special lipid composition suggest that *T. macrura* may be more plastic than *E. superba* (Driscoll, 2013). However, current research on krill species is mostly focused on *E. superba*. In the face of ongoing rapid environmental changes, further research on *T. macrura* is needed to understand the impact of climate change on the Antarctic ecosystem.

The length-weight relationship (allometric growth model) has significant biological implications for estimating krill biomass using acoustic survey data when direct measurement tools are unavailable. Table 5 presents previous research results on the length-weight relationships of *E. superba*, *E. crystallorophias*, and *T. macrura*. The majority of krill species exhibit positive allometric growth (b>3), consistent with the findings of this study. Morphological characteristics of krill are influenced by environmental factors, gender, and developmental stage. These morphological differences can introduce considerable errors in biomass estimation, making it challenging to assess the accuracy of the models used (Ashjian et al., 2003). To enhance the applicability of the models, it is crucial to collect length-weight relationships of krill at different developmental stages in various regions and seasons, facilitating the conservation of polar ecosystems and the management of current and future fisheries.

Table 5 Length-weight relationship for euphausiids in the Southern Ocean

Species	Stage	Area	Time	Length range/mm	W_D or W_W	b	Reference
E. superba	J	Northern Weddell Sea	Aug/Oct 2013	7–22	W_W	3.06	Schaafsma et al. (2022)
	All	Lazarev Sea	Dec/Feb 2014/2015	19–49	W_W	2.90	Schaafsma et al. (2022)
	Adult	Ross Sea	Jan 2014	22–52	W_W	3.13	Leonori et al. (2017)
	N.A.	Weddell Sea	Feb 1981	N.A.	W_D	3.45	Siegel (1986)
	N.A.	Antarctic Peninsula	May/Jun 1986	N.A.	W_D	3.45	Siegel (1986)
	Adult	N.A.	Jan/Feb 1977/1978	28–58	W_D	3.76	Kils (1979)
E. crystallorophias	M	Admiralty Bay	Dec/Feb 1978/1979	N.A.	W_W	2.79	Rakusa-Suszczewski and Stepnik (1980)
	F	Admiralty Bay	Dec/Feb 1978/1979	N.A.	W_W	3.04	Rakusa-Suszczewski and Stepnik (1980)
	All	Amundsen Sea	Jan 2011	13–36	W_W	3.53	La et al. (2015b)
T. amacrura	All	Admiralty Bay	Dec/Feb 1978/1979	11–28	W_W	3.06	Rakusa-Suszczewski and Stepnik (1980)
	All	Northern Weddell Sea	Aug/Oct 2013	9–26	W_W	3.30	Schaafsma et al. (2022)
	All	Southwest Indian Ocean	Feb 1981	9–22	W_W	3.72	Färber-Lorda (1994)

Notes: $W = a \times L^b$ for weight (in mg) and body length (in mm) (a is the condition factor, b is the allometric factor); W_W, wet weight; W_D, dry weight; M, males; F, females; J, juvenile.

4.3 Regional variations in the correlation between krill abundance, distribution, and environmental factors

Various environmental factors in the Southern Ocean, such as temperature, salinity, sea ice, circulation, and chlorophyll, significantly influence the abundance and distribution of krill (Ichii et al., 2023; Michael et al., 2021; Trathan et al., 2003; Veytia et al., 2020). In this study, there are regional differences in the relationship between krill abundance, biomass, and environmental factors. Specifically, the abundance and biomass of *T. macrura* in the Antarctic Peninsula are negatively correlated only with the number of ice free days, while the abundance and biomass of *E. crystallorophias* in Prydz Bay are positively correlated with chlorophyll *a* concentration. In the Amundsen Sea, there is no significant correlation between krill abundance and environmental factors (Figure 5).

Sea ice is closely tied to all stages of the krill life cycle and is regarded as one of the most important environmental factors influencing krill distribution (Flores et al., 2012;

Vallet et al., 2011). In addition to sea ice extent and density, ice free days (i.e. length of time without an ice cover) are one of the most relevant environmental variables for mesoplankton distribution patterns (Swadling et al., 2010). Following the concept of ice free days as an environmental parameter in the present study, *T. macrura* abundance and biomass were found to be negatively correlated with the number of ice free days on the Antarctic Peninsula. This indicates that areas with retreating ice edge and high primary production are the hotspots of most Southern Ocean zooplankton species during summer, although *T. macrura* was reported to feed more omnivorously compared with *E. superba* (Yang et al., 2021). In Prydz Bay, the highest abundance of *E. crystallorophias* occurs at sites with the highest chlorophyll concentration, indicating a favorable feeding environment that ensures the energy needed for krill growth and development.

Krill is a circumpolar species with a crucial role in ecosystems and food webs, as well as significant commercial value, emphasizing its biological importance for research. The challenging task of collection is hindered by the harsh environment and high transportation costs in the Southern Ocean, leading to temporal and spatial data gaps, especially in the Amundsen Sea region, which remains ice-covered almost throughout the year. Utilizing biological samples gathered over the past decade, our study focused on the abundance, distribution, and fundamental biological traits of krill in three key areas of the Southern Ocean. This research work supplements the limited information available in the KRILLBASE database regarding *E. crystallorophias* and *T. macrura*, while also filling crucial data gaps in the Amundsen Sea region. Climate change poses a potential threat, as alterations in krill habitat conditions can impact krill physiology, subsequently influencing krill dynamics across different levels and scales (Kawaguchi et al., 2024). Recent years have witnessed rapid environmental changes and shifts in krill distribution patterns, underscoring the critical need to investigate the specific mechanisms underlying the interaction between krill and its environment. Our findings reveal that sea ice and chlorophyll concentrations significantly influence krill abundance and distribution, albeit with regional variations in the relationship between the two factors. This study provides essential insights for ecosystem conservation and the sustainable management of krill fisheries on a circumpolar scale.

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Supplementary Table and Figure

Table S1 Krill abundance and pelagic information by station

Cruise	Station	Time	Rope length/m	Estimated sampling depth/m	Longitude	Latitude	Abundance/[ind·(1000 m^{-3})]		
							E. superba	*E. crystallorophias*	*T. macrura*
S26	A01	2009-12-22	250	101.64*	75.38°E	69.08°S	0	88.918	0.935
S26	A02	2009-12-23	250	60.97*	71.12°E	68.38°S	0	345.835	1.182
S26	A03	2009-12-25	250	58.11*	72.96°E	68.25°S	2.08	1144.57	3.432
S26	A04	2009-12-25	250	65.14*	72.99°E	67.25°S	19.85	30.238	0
S26	A05	2009-12-27	250	77.44	73.07°E	63.81°S	0	0	75.026
S26	A06	2010-02-25	250	77.44	75.52°E	67.01°S	0	0	0.51
S27	B01	2011-01-01	250	77.44	73.94°E	68.59°S	0	87.936	2.068
S27	B02	2011-01-02	250	77.44	71.66°E	68.52°S	0	3.675	0
S27	B03	2011-01-06	250	77.44	73.00°E	65.01°S	2.571	0	20.467
S27	B04	2011-01-16	250	77.44	70.48°E	66.01°S	3.274	0	5.87
S28	C01	2012-01-23	250	77.44	54.35°W	61.12°S	85.043	0	1.273
S28	C02	2012-01-24	150	23.68	50.73°W	61.18°S	16.442	0	11.083
S28	C03	2012-01-27	150	23.68	47.17°W	61.80°S	1.129	0	2.935
S28	C04	2012-01-28	250	77.44	47.20°W	60.38°S	433.45	0	2.361
S28	C05	2012-03-01	120	N.A.	73.01°W	66.48°S	42.976	0	0.397
S29	D01	2013-02-02	150	23.68	78.00°E	66.67°S	9.345	0	0
S29	D02	2013-02-12	150	23.68	75.50°E	67.25°S	0	0	0
S29	D03	2013-02-16	150	23.68	73.00°E	68.00°S	61.639	15.042	0
S29	D04	2013-03-02	200	53.96	68.00°E	66.83°S	25.04	0	0.712
S29	D05	2013-03-02	200	53.96	70.50°E	66.50°S	147.75	0	3.679
S31	E01	2015-02-03	200	53.96	73.17°E	65.02°S	16.311	0	0
S31	E02	2015-02-05	300	96.63	68.16°E	65.01°S	40.197	0	0
S31	E03	2015-02-06	300	96.63	65.51°E	65.96°S	41.423	0	0.185
S31	E04	2015-02-07	200	53.96	67.99°E	67.30°S	0.112	0	0.337
S31	E05	2015-02-08	300	96.63	70.36°E	66.00°S	306.55	0	1.223
S31	E06	2015-02-09	300	96.63	72.99°E	66.97°S	4.251	0.115	0.46
S31	E07	2015-02-28	300	96.63	73.91°E	67.23°S	86.533	32.988	0
S32	F01	2015-12-30	180	42.87	47.14°W	61.51°S	0.264	0	33.059
S32	F02	2016-01-02	200	53.96	54.37°W	61.13°S	11.372	0	1.587
S32	F03	2016-01-04	250	77.44	59.47°W	63.26°S	49.29	0	0.694
S32	F04	2016-01-11	200	53.96	50.75°W	61.17°S	20.629	0	0
S32	F05	2016-01-12	250	77.44	54.52°W	61.88°S	4.011	0	0.309
S33	G01	2016-12-25	250	77.44	42.48°W	60.00°S	0	0	4.525
S33	G02	2016-12-27	250	77.44	49.53°W	59.50°S	1.954	0	3.805
S33	G03	2016-12-28	250	77.44	48.34°W	61.97°S	12.856	0	2.057
S33	G04	2016-12-30	250	77.44	54.29°W	61.01°S	0	0	0
S33	G05	2016-12-31	250	77.44	49.52°W	60.16°S	1.131	0	1.131
S33	G06	2017-01-02	280	89.37	47.65°W	62.35°S	22.215	0	1.851
S33	G07	2017-01-11	250	77.44	57.72°W	61.76°S	8.125	0	1.028
S34	H01	2018-03-08	250	77.44	126.02°W	66.00°S	0	0	0.103
S35	I01	2019-01-14	200	53.96	104.58°W	66.95°S	0	0	2.228

Continued

Cruise	Station	Time	Rope length/m	Estimated sampling depth/m	Longitude	Latitude	Abundance/[ind·(1000 m^{-3})]		
							E. superba	*E. crystallorophias*	*T. macrura*
S35	I02	2019-01-16	200	53.96	99.89°W	69.02°S	0	0	83.993
S35	I03	2019-01-18	200	53.96	89.79°W	67.18°S	0	0	4.628
S35	I04	2019-01-18	500	150.40	90.07°W	69.06°S	6.653	0	6.653
S36	J01	2020-01-06	250	55.84*	177.87°W	74.83°S	116.73	1.2	0.171
S36	J02	2020-01-10	180	56.93*	149.90°W	75.42°S	10.429	58.192	0
S36	J03	2020-01-11	250	77.44	150.05°W	75.00°S	203.64	0	12.513
S36	J04	2020-01-14	250	96.50*	140.95°W	74.46°S	0	1.543	0
S36	J05	2020-01-14	150	23.68	139.68°W	74.08°S	18.513	81.21	0
S36	J06	2020-01-16	150	24.30*	139.94°W	69.93°S	0	0	31.346
S36	J07	2020-01-17	150	29.86*	150.15°W	70.11°S	0	0	76.155
S36	J08	2020-01-22	250	56.07*	120.22°W	68.02°S	0	0	132.675
S36	J09	2020-01-22	250	77.44	120.05°W	70.00°S	1.543	0	0.171
S36	J10	2020-02-06	250	75.68*	145.89°W	73.58°S	3.428	0	3.257

Note: * data from Temperature Depth Recorder (ALEC, Japan).

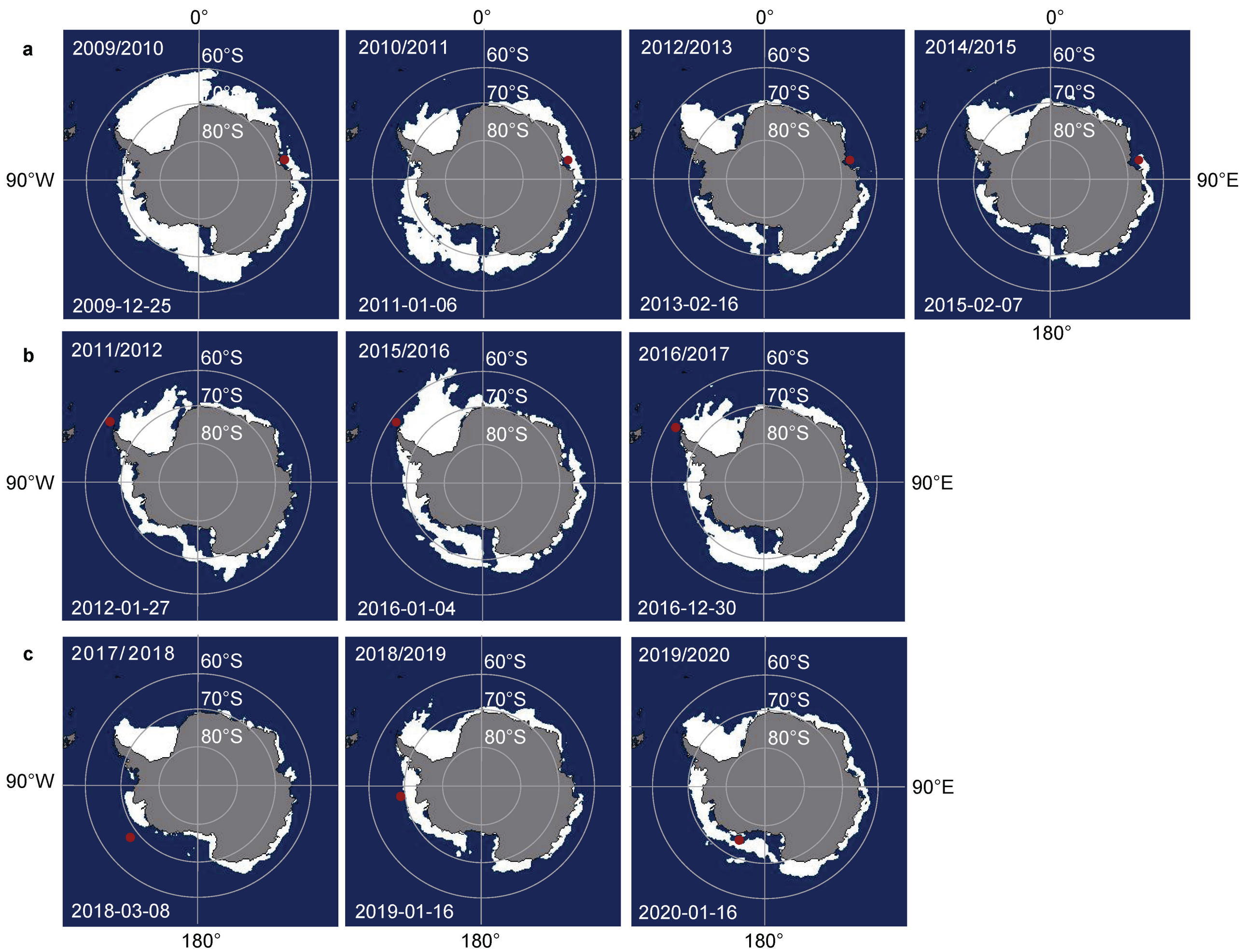

Figure S1 Sea ice conditions during the sampling period 2009/2010–2019/2020. **a**, Prydz Bay; **b**, Antarctic Peninsula; **c**, Amundsen Sea. Red dots are sampling areas.