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Age Structure and Spatial Distribution of *Euphausia superba* Larvae off the Antarctic Peninsula, Southern Ocean

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Abstract: The Antarctic krill, *Euphausia superba* Dana, 1850, is a species forming high biomass and, therefore, playing a major role in the Antarctic marine food web. The age structure and patterns of spatial distribution of *E. superba* larvae in the waters of the Bransfield Strait (Antarctic Sound, Powell Basin), and off the South Orkney Islands, were studied based on data collected through a research survey in January and February 2022. Eggs and larvae (naupliar, calyptopis, and furcilia stages) of *E. superba* were found in these regions. Eggs and nauplii were concentrated in the southern, deep-sea part of the Antarctic Sound and over the northeastern and southwestern slopes of the Powell Basin, while calyptopis and furcilia larvae were concentrated north of the South Orkney Islands. The larvae abundance increased in an easterly direction. Four groups of communities comprising krill larvae at different development stages were identified. These groups were located in two subregions with the border between them running off the South Orkney Islands. The distribution and abundance of *E. superba* larvae showed a clear relationship with environmental conditions, in particular with a combination of such factors as sea surface temperature and chlorophyll *a* concentration.

Keywords: Antarctic krill *Euphausia superba*; eggs; nauplii; calyptopis; furcilia; abundance; distribution; Atlantic sector; Southern Ocean

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1. Introduction

The Antarctic krill, *Euphausia superba* Dana, 1850, (hereafter referred to as krill) is a major link between primary producers and vertebrates (seals, whales, and seabirds) in the food web of the Southern Ocean [1]. It is also an important target species of commercial fisheries [2,3]. Over the past 25 years, the population density of krill in the Atlantic sector has markedly decreased [4–6], and therefore, recovery processes in this species attract increasing research attention. Although pelagic communities in the Atlantic sector of the Southern Ocean have been quite thoroughly studied to date [7–10], there is still little information on the distribution of early development stages of *E. superba* in this region. Previous studies described the relationship between spatial variations in larval aggregations and concentration of adult krill [11,12], the distribution of life-history stages and overlaps of their ranges, and also their relationships with environmental dynamics [13–15]. Krill development passes through a series of successive stages. Fertilized eggs descend from the surface layer to a depth of 1000 m, where nauplii hatch and begin rising back to the surface. During the ascent, the development stages of krill larvae sequentially change from nauplius to metanauplius, calyptopis, and furcilia [11,14].

Significant warming has been observed in the Southern Ocean in recent decades: since 1955, the temperature of the upper ocean layers west of the Antarctic Peninsula has increased by more than 1 °C [16]. The reduction in the sea ice extent and proportion of multi-year sea ice is still ongoing [17,18]. The continuing climate change in the Southern Ocean [19,20] makes pelagic communities adapt to new conditions [21,22]. Since krill larvae are extremely sensitive to environmental factors [23,24], study of their responses to variations in environmental factors is of particular relevance to address the conservation of the species and provide sustainability of krill fishery in the future. In the present study, we assessed the current spatial distribution of krill larvae in the waters off the Antarctic Peninsula (Atlantic sector of the Southern Ocean) and identified the main environmental factors responsible for the distribution and density of various krill larvae stages. The results of the study are expected to be of high practical value for monitoring the current status of the changing Antarctic marine ecosystem.

2. Materials and Methods

The material for this study was collected in January and February 2022 at 23 integrated stations. The study area included the Bransfield Strait, the Antarctic Sound, the Powell Basin of the Weddell Sea, and the waters off the South Orkney Islands. Sampling was carried out using the opening/closing Multinet system [25] (0.25 m^2 aperture) equipped with five 150-µm mesh nets, a WP-2 net [26] with a mesh size of 150 µm, and a Bongo net (505-µm mesh and 0.6 m mouth diameter) [27] (Figure 1). The tows from a 200-m depth to the surface were performed obliquely. The vertical, stratified sampling tows from the bottom (maximum 1000 m) to depths of 500, 500–200, 200–100, 100–50, and 50–0 m were made at a velocity of 0.5–1 m/s. The Bongo net was equipped with a water flow counter (Hydrobios, Germany). A total of 120 plankton samples were collected. Fresh samples, immediately after being hauled aboard and brought to the laboratory, were viewed in a Bogorov counting chamber under a SZX7 binocular microscope (Olympus, Japan) and then fixed with a 4% formalin solution. The development stages of *E. superba* were identified using special identification keys [11,28]. Hydrological measurements of water temperature (T, °C) and salinity (S, psu) were carried out using an OCEAN SEVEN 320 Plus CTD multiparameter probe (Idronaut, Italy), lowered from the surface to the bottom. Chlorophyll *a* (Chl *a*) profiles were measured with a calibrated fluorometer (Seapoint Sensors Inc., Exeter, NH, USA) mounted on the CTD probe. Temperature and salinity within the upper 50 m horizon were referred to as "surface". Mean values of Chl *a* concentration were calculated for the upper 100 m of the water column, which was the estimated average depth of the euphotic zone.

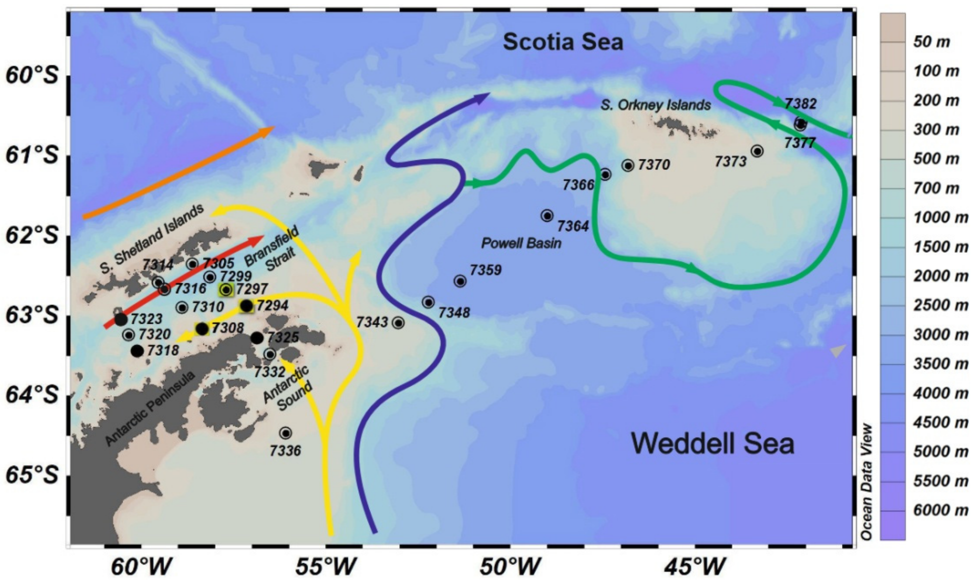

Figure 1. The sampling stations and the major currents in the study area. Orange line is the Antarctic Circumpolar Current (ACC); red line, the Bransfield Current (BC); yellow line, the Antarctic Coastal Current (ACoC); blue line, the Antarctic Slope Front (ASF); green line, the Weddell Front (WF). Plankton nets used at the stations are designated as follows: ⦿—Multinet, ●—Bongo, and •—WP-2.

Statistical analysis was carried out using the PRIMER v. 6 software package [29]. For data processing, a matrix of larvae similarity of samples was calculated on the basis of the Bray–Curtis dissimilarity index. Number of larvae at different development stages per 1 m^3 of water was used as initial data. To assess the reliability of clustering results, a SIMPROF permutation test was performed (with a number of repetitions of 999, $p = 0.05$). In addition, effects of environmental parameters (water temperature, salinity, and Chl *a*) on the age structure of krill larvae were analyzed by BEST (BIOENV analysis) relating the larvae abundance matrix to the Euclidean distance matrix of environmental parameters. The BEST procedure selects the subset of abiotic variables that maximizes the rank correlation (ρ) between the biotic and abiotic (dis)similarity matrices [30]. The Spearman's rank correlation analysis was performed to show correlations between abundance and hydrological variables in order to identify the variables most responsible for their distribution between the stations (run in PAST ver. 4.05). The maps of the sampling area and spatial distribution of krill larvae abundance were composed using the Ocean Data View v. 5 software.

3. Results

The highest sea surface temperature (SST) values (with a maximum of 1.8 °C) were recorded from the waters northeast of the South Orkney Islands and in the Bransfield Strait off the South Shetland Islands; medium values were in the middle of the Bransfield Strait and in the Powell Basin; the lowest values, in the Antarctic Sound and in the waters off the Antarctic Peninsula, where one extreme temperature minimum (stn. 7336) was recorded (Figure 2A). The highest sea surface salinity (SSS) values were recorded from the areas in the middle of the Bransfield Strait and in the Antarctic Sound; medium values were in the Powell Basin and northeast of the South Orkney Islands; the lowest values were in the Bransfield Strait off the South Shetland Islands and off the Antarctic Peninsula (Figure 2B). The distribution of mean Chl *a* concentrations is shown in Figure 2C.

The age structure and abundance of krill larvae differed between the waters off the Antarctic Peninsula and off the South Orkney Islands coast. The maxima of abundance of krill eggs and larvae (2300 ind./m^3) were recorded from three areas: the Antarctic Sound, the Powell Basin, and the waters northeast of the South Orkney Islands. The minimum abundance values of krill eggs and larvae (1.3 ind./m^3) were in the Bransfield Strait and off the Antarctic Peninsula, with their concentration increasing 3–5-fold from the coast to the middle of the Bransfield Strait (Figure 3A). Krill eggs and nauplii were concentrated in three areas: the southern Antarctic Sound and over the southwestern and northeastern slopes of the Powell Basin (Figure 3A). Krill larvae in calyptopis and furcilia stages were concentrated at a maximum abundance northeast of the South Orkney Islands. In general, the krill larvae abundance increased in an easterly direction. In the waters off the Antarctic Peninsula and in the Powell Basin, the major proportion (%) of krill larvae was formed by eggs and nauplii, while east of this area, in the waters off the South Orkney Islands, calyptopis and furcilia larvae accounted for a maximum proportion (Figure 3B).

The age structure and vertical distribution pattern of *E. superba* larvae are shown in Figure 4. The maximum values of average abundance of krill eggs and nauplii were observed in the relatively warm surface (0–50 m) layer in the warm Antarctic Surface Water (AASW) (Figure 4F). Relatively high concentrations of krill eggs and nauplii were recorded from the deep-sea (500–800 m) layer in the cool and saline Transitional Zonal Water with Weddell Sea influence (TWW) and Shelf Water (SW) (Figure 4D,E). The maximum concentrations of calyptopis and furcilia larvae were recorded from the warmer 0–100 m layer in the AASW (Figure 4G). Highly abundant krill eggs and larvae were observed in the surface water, where they co-occurred with blooming phytoplankton (visually in samples).

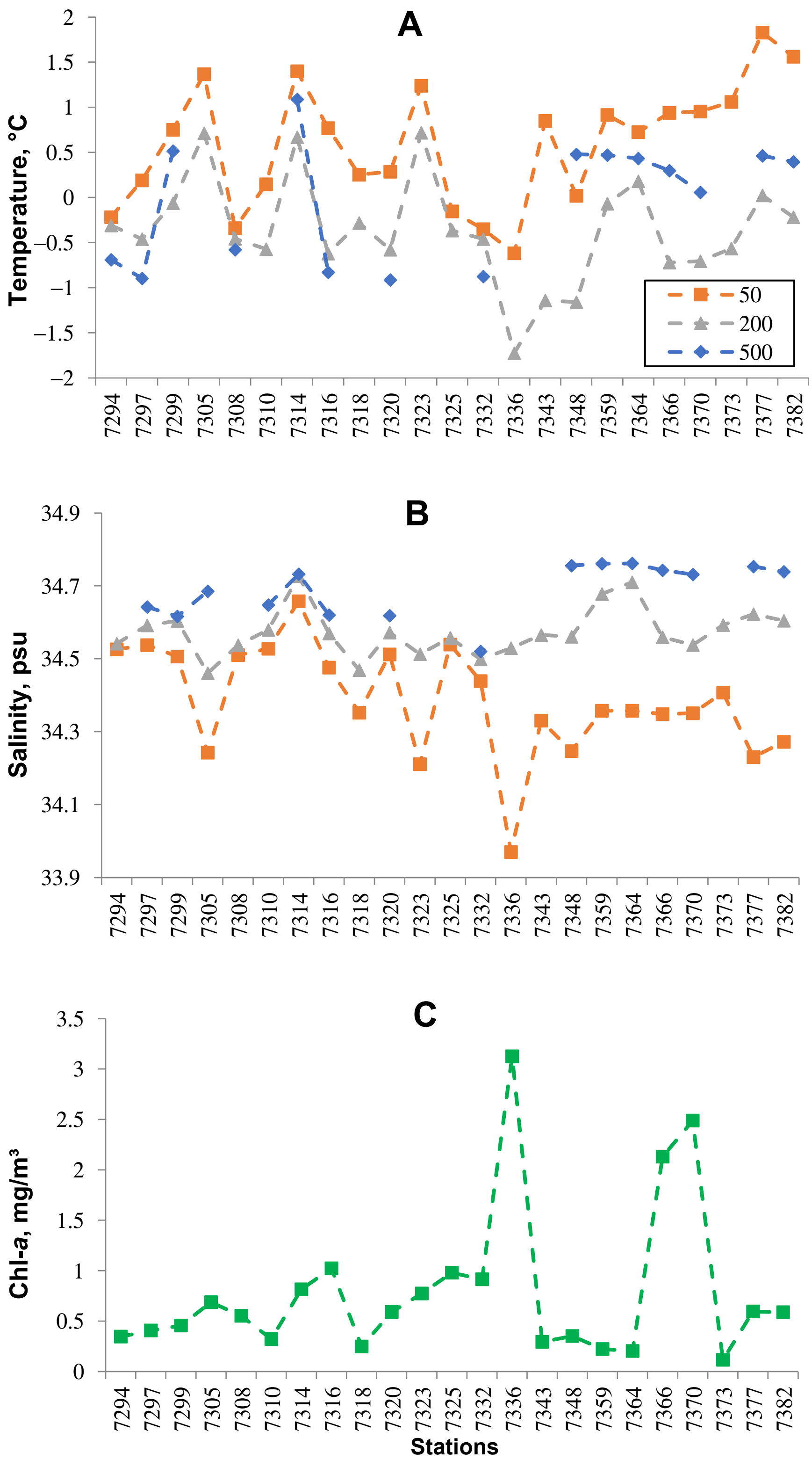

Figure 2. Mean values of water temperature (**A**), salinity (**B**) at the surface (to 50 m), in the 200-m layer, and in the 500-m layers, and also mean values of chlorophyll *a* (**C**) concentrations (mg/m^3) at stations sampled during January and February 2022.

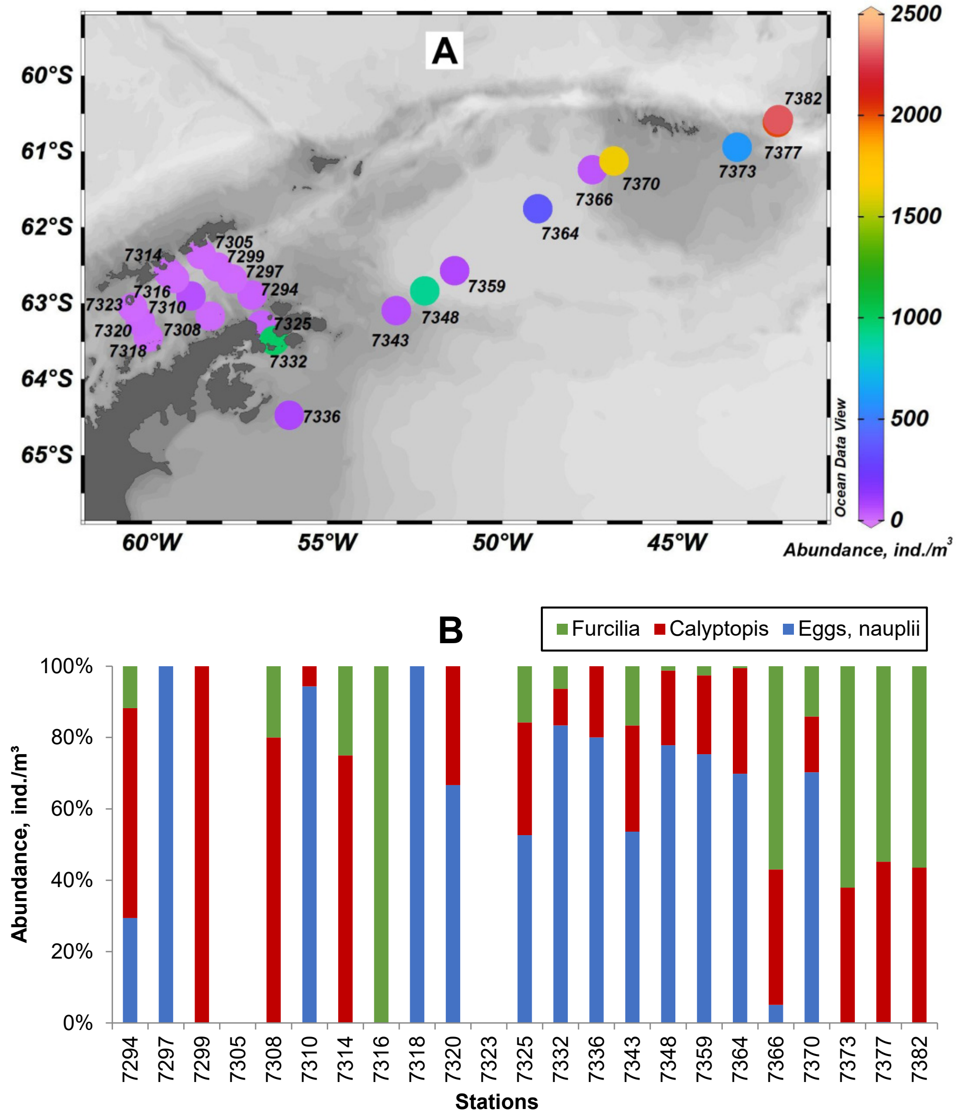

Figure 3. Spatial distribution of total abundance ((**A**) ind./m^3) and contribution ((**B**) %) of *Euphausia superba* eggs and larvae at different development stages in January and February 2022.

Four significant groups of stations were identified (SIMPROF R = 0.73, p = 0.05%) (Figure 5A). Group A was mainly confined to the waters of the Bransfield Strait and Powell Basin (Figure 5B), characterized by high values of SSS and Chl *a* concentration. Group B tended to the waters off the South Orkney Islands that had high values of SST, water temperature at depths of 200 and 500 m, and salinity at 200 and 500 m. Group C was mainly located in the waters of the Antarctic Sound and Powell Basin with low temperatures at 200 m, a low SSS, and a high Chl *a* concentration; Group D was confined to the Bransfield Strait (Figure 5B) with low values of SST, temperature at 200 and 500 m, a low SSS, salinity at 200 and 500 m, and a low mean Chl *a* concentration in 0–100 m.

Differences in the spatial dominance of eggs and larvae at different development stages were observed between the identified groups of stations. The groups A, C, and D were dominated by krill eggs and nauplii (first subregion); the group B, by larvae of calyptopis and furcilia stages (second subregion). The border between the subregions ran near the South Orkney coast.

The Spearman's rank correlation analysis indicated that SST was the most important factor determining the distribution of the different development stages of krill larvae ($\rho = 0.307$, $p < 0.05$). A higher correlation coefficient was obtained with a combination of SST and Chl *a* concentration ($\rho = 0.369$, $p < 0.05$) (Table 1). The abundance of krill eggs and nauplii positively correlated with Chl *a* concentration and salinity at 500 m and negatively correlated with the other factors. The abundance of both calyptopis and furcilia larvae significantly positively correlated with SST and temperature at 500 m, as well as with salinity at 200 and 500 m, and negatively correlated with SSS, temperature at 200 m, and Chl *a* concentration. The abundance of furcilia larvae proved to be closely related with that of calyptopis larvae (Table 2).

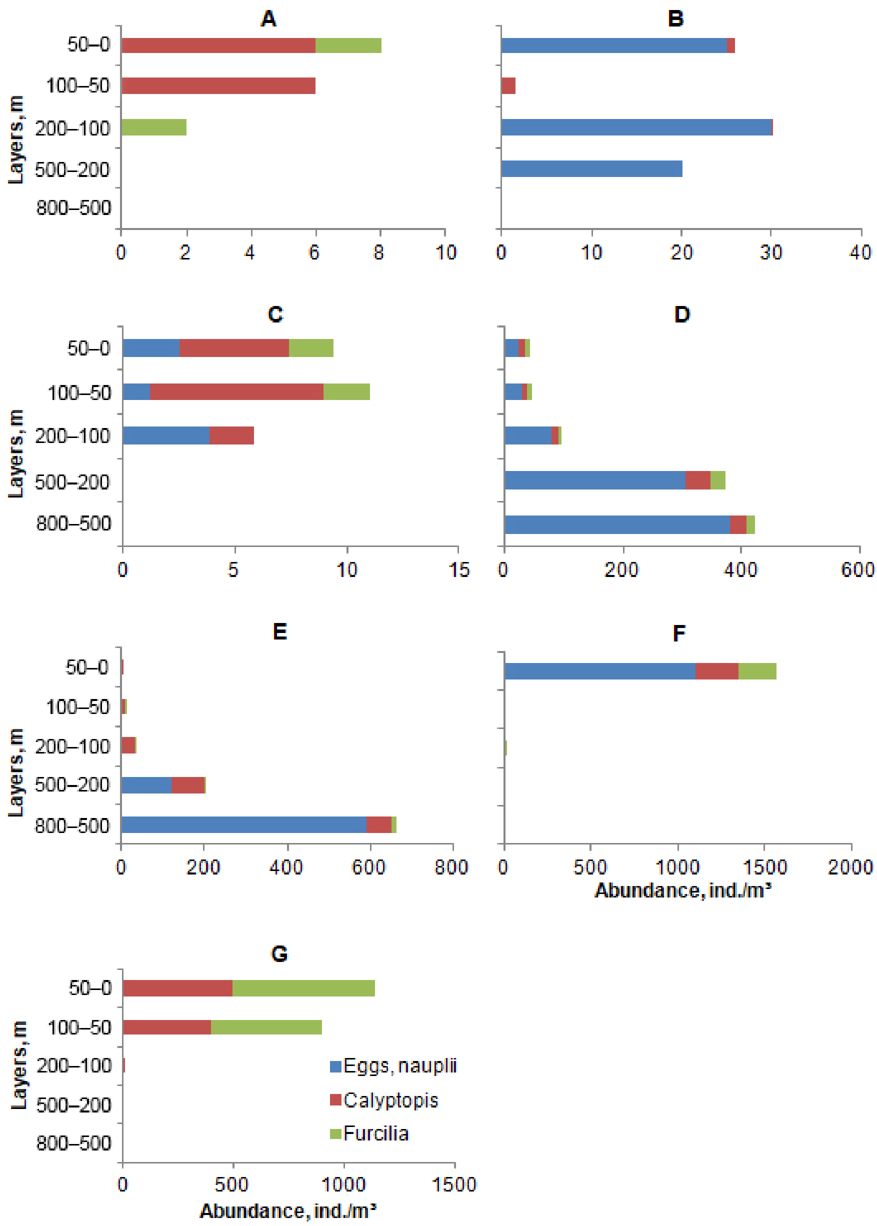

Figure 4. Vertical distribution of average abundances of *Euphausia superba* eggs and larvae (ind./m^3) in the study area: (**A**) in the Bransfield Strait off the South Shetland Islands; (**B**) in the middle of the Bransfield Strait; (**C**) in the Bransfield Strait off the Antarctic Peninsula; (**D**) in the deep-sea waters of the Antarctic Sound; (**E**) over the southwestern slope of the Powell Basin; (**F**) over the northeastern slope of the Powell Basin; (**G**) northeast of the South Orkney Islands.

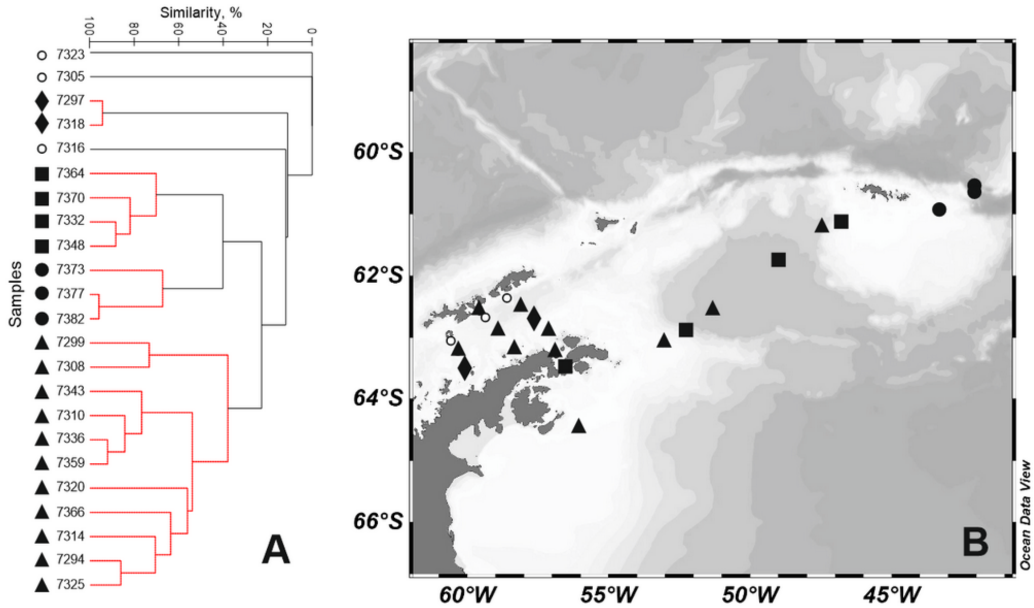

Figure 5. Dendrogram of stations resulting from a cluster analysis based on the abundances of *Euphausia superba* eggs and larvae at different development stages (**A**); geographical distributions of the identified groups of stations (**B**). Groups are as follows: ▲—A, •—B, ■—C, ♦—D, ○—no groups.

Table 1. Correlation coefficients inferred from the BEST analysis of relationships between the distribution and age structure of *Euphausia superba* and the environmental parameters such as water temperature (T, °C), salinity (S, psu), and chlorophyll *a* concentration (Chl *a*, mg/m^3).

Environmental Factors	ρ	Mean ± SD			
		Group A	**Group B**	**Group C**	**Group D**
SST, °C	0.307	0.36 ± 0.65	1.48 ± 0.39	0.34 ± 0.61	0.22 ± 0.04
200 m T, °C	0.096	–0.48 ± 0.61	–0.25 ± 0.30	–0.54 ± 0.56	–0.37 ± 0.13
500 m T, °C	0.089	0.03 ± 0.75	0.43 ± 0.05	0.02 ± 0.63	–0.90 ± 0.07
SSS, psu	0.101	34.43 ± 0.18	34.30 ± 0.09	34.35 ± 0.08	34.44 ± 0.13
200 m S, psu	0.093	34.59 ± 0.06	34.61 ± 0.02	34.58 ± 0.09	34.53 ± 0.09
500 m S, psu	0.081	34.69 ± 0.07	34.75 ± 0.01	34.69 ± 0.12	34.64 ± 0.03
Chl a, mg/m^3	0.163	0.89 ± 0.91	0.43 ± 0.27	0.99 ± 1.05	0.33 ± 0.11
BEST combination of factors (SST and Chl *a*)	0.369				

Table 2. Spearman's rank correlations between the abundances of different development stages of *Euphausia superba* and the environmental factors ($p < 0.05$).

	SST	SSS	200 m T	200 m S	500 m T	500 m S	Chl *a*	E and N	C	F
E and N	–0.38	–0.16	–0.44	–0.02	–0.08	0.29	0.36	1		
C	0.22	–0.32	–0.20	0.37	0.41	0.57	–0.09	0.58	1	
F	0.33	–0.18	–0.16	0.26	0.23	0.44	–0.06	0.32	0.86	1

Notes: T is water temperature (°C); S, water salinity (psu); Chl *a*, chlorophyll *a* concentration (mg/m^3); E and N, eggs and nauplii; C, calyptopis; F, furcilia.

4. Discussion and Conclusions

The pattern of the major currents in the study area was described earlier in the literature [31–33]. In the Bransfield Strait, a multidirectional (two jets) system of currents is observed: the continuation of the cold Antarctic Coastal Current (ACoC) flowing southwest and carrying the relatively cool and saline Transitional Zonal Water with Weddell Sea influence (TWW), and the warm Bransfield Current (BC) directed southeast along the South Shetland Islands and carrying the worm Transitional Zonal Water with Bellingshausen

Sea influence (TBW) [34–36]. The Weddell Surface Water spreading zone is located in the Antarctic Sound [37], where the northward TWW is flowing in the southern, deep-sea part of the strait. A current of the very cold (close to freezing) temperatures (–1.9 °C), Shelf Water (SW) is running south of the Antarctic Sound [38]. There are three northward currents in the Powell Basin: the ACoC, the Antarctic Slope Front (ASF), and the Weddell Front (WF), where the surface layer is occupied by the warm Antarctic Surface Water (AASW), with the Warm Deep Water (WDW) located below [39]. In the region off the South Orkney Islands, the Antarctic Circumpolar Current (ACC) and the Weddell Sea water interact [40].

The results we obtained characterize the known patterns of spatial distribution of krill eggs and larvae, which have not changed in general. However, the average value of krill larvae abundance in our study was 3–5-fold lower than those reported by other researchers [13,14,41,42]. It is probable that the low abundance of krill eggs and larvae that we observed in 2022 coincided in time with a period between high krill abundance waves. Effects of various currents determine the pattern of distribution of krill eggs and larvae that are transported by the longitudinal component of the currents from deep horizons of deep-sea waters to the divergence zones, where local density maxima of krill juveniles are formed. The krill distribution is associated with the action of vortex currents near the surface in the mixing zone of the Weddell Sea and ACC waters and in the gyres and shadow zones off the South Orkney Islands [11,43]. In our study, the concentration of krill eggs and larvae increased 5-fold in the direction from the coast towards the middle of the Bransfield Strait, in the zone where the warm BC water is mixed with the cold and saline ACoC water.

We observed a close relationship of distribution and abundance of krill larvae at different development stages with a certain combination of abiotic environmental factors, in particular, SST and Chl *a* concentration, and also found that larvae tended to the areas characterized by such a combination. The circulation of water masses within the region is also an important factor affecting the dynamics of this relationship. The study area was influenced by the warm and saline water of the ACC southern jet in the west [44] and the colder and freshened water of the Weddell Sea and the associated fronts in the east [45]. In the Antarctic Sound and over the Powell Basin slope, influenced by the cold (−0.5 to −1.5 °C), saline (34.5 psu), and chlorophyll *a*-rich (up to 2.5 mg/m^3) waters carried by the ACoC, we recorded the maximum concentrations of krill eggs and nauplii having the Weddell Sea origin. This distribution can be explained by the transport of eggs and nauplii from the shelf to the slope in a northeasterly direction through the Weddell Gyre [46]. As in our studies, Gao et al. [13] reported an abundance of krill larvae at early development stages in areas with high Chl *a* concentration. The timing of spawning and conditions for subsequent larval development (temperature and food type) have important ecological implications for the success of recruitment in the krill populations [47]. The presence of krill eggs in the study area indicated a late spawning season in 2022, which probably occurred in the Weddell Sea in early February. Thus, the surface layer of the warm and freshened AASW off the South Orkney Islands was dominated by calyptopis and furcilia larvae that are indicators of spring/early summer krill spawning [48,49]. There is a great deal of uncertainty as to whether krill larvae survive the upcoming winter due to late spawning, which may eventually become a cause of low krill recruitment in the following year, since the growth and survival rates of krill larvae decrease at sub-zero water temperatures [23]. As the distribution of maximum concentrations of *E. superba* larvae in the study area shows, the age of larvae increases in the west to east direction. An assumption can be made that the early spawning in krill occurred east of the Antarctic Peninsula, in the waters of the South Orkney Islands.

On the basis of the distribution pattern of krill larvae, the study area can be divided into two subregions. In the waters between the Antarctic Peninsula and southwest of the South Orkney Islands, the age structure of krill larvae was mainly composed of eggs and nauplii, while northeast of the South Orkney Islands, it was dominated by calyptopis and furcilia. Aggregations of krill larvae found in the waters of the South Orkney Islands were more mature and more abundant than those of larvae in the shelf waters off the

Antarctic Peninsula. As in our study, Makarov and Menshenina [50], Gao et al. [13], and Spiridonov et al. [42] found that krill eggs and early larvae are present in the waters of the South Orkney Islands, and in summer these can be transported by the western branch of the Weddell Gyre [46] and be mixed with the group of late larvae transported by the water of the southern ACC jet [51]. In previous studies, eggs and larvae of Antarctic krill were found in the northwestern Weddell Sea [15,43,46], over the shelf slope of the Antarctic Peninsula [14,41,42,45,49], in the waters of the South Orkney Islands, and in the Scotia Sea [11,13,50] during the southern summer until late autumn and the early southern winter (May and June) [48,52]; differences in the development stages of krill larvae were often recorded from these regions.

Krill eggs and larvae are known to inhabit different depths and drift in various directions and, therefore, their aggregations are differentiated in space [43]. According to our observations, krill eggs and nauplii tended to deep-sea layers (up to 800 m), while calyptopis and furcilia larvae tended to the surface layers. The distribution and abundance of krill eggs and nauplii positively correlated with high Chl *a* concentrations, and with salinity at 500 m, whereas the abundance of krill calyptopis and furcilia larvae positively correlated with above-zero SST. In addition to above-zero water temperatures, a high phytoplankton concentration can also contribute to the development of krill larvae [23,47,53,54]. We observed krill eggs and nauplii in the surface (0–50 m) layer, above the layer of high phytoplankton concentration (visually in samples) 50–100 m, whereas the distribution of calyptopis and furcilia larvae found in the 0–50 and 50–100 m layers overlapped with the maximum microalgae concentration (visually in samples).

The climate change that has been observed in the Southern Ocean in recent decades may be both part of a natural systemic process [7,55,56] and a negative trend for the Southern Ocean ecosystem [22,57,58]. The Antarctic krill, *E. superba*, needs further study at all life-history stages for monitoring the actual status of the changing Southern Ocean ecosystem and its biological resources.

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