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Is It the Same Every Summer for the Euphausiids of the Ross Sea?

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Abstract: The pelagic ecosystem in the Ross Sea has one central component that is very important for energy exchanges between upper and lower trophic levels: the Middle Trophic Level. Krill species are the most important and abundant organisms within this level. Several acoustic surveys were conducted in the western Ross Sea over the past 25 years, revealing that Euphausia superba is by far the most abundant species of krill in the Ross Sea during austral summer, and that its core distribution is concentrated in the northern part, bordering the Southern Ocean. Euphausia crystallorophias, the second most abundant krill species, is more concentrated in the central Ross Sea, generally near the coast. Data on krill biomass were collected in December and January from 1994 to 2016 and analyzed together with key environmental parameters by means of two-way ANOVA in order to explain species behavior and identify possible environmental drivers. Temperature and dissolved oxygen influenced the biomass of both species of krill, while other environmental parameters only affected one species. In conclusion, the biomass of both species has varied over the years, possibly due to a complex synergy of environmental drivers.

Keywords: krill; marine acoustics; biomass; spatial distribution; environmental data

1. Introduction

Krill is a fundamental resource in the Ross Sea, sustaining the survival and wellness of many species of marine mammals and birds inhabiting this region [1,2]. Past studies have attempted to deepen our knowledge of the dynamics of the Ross Sea marine ecosystem at various trophic levels [3–5]. However, many aspects need further study. The recent establishment of a Marine Protected Area (MPA) in the Ross Sea and surrounding areas, which has been in effect since 1 December 2017 [6], has made specific studies on these very important animals even more interesting, allowing researchers to compare their population dynamics with those recorded in other areas around the Antarctic continent where specific fisheries are conducted.

Following a pilot survey in 1989–1990, eight acoustic surveys targeting Antarctic krill (Euphausia superba) and crystal krill (Euphausia crystallorophias) in the western Ross Sea were conducted between 1994 and 2016, yielding some intriguing information on the krill populations of the Ross Sea [7–9]. Taking into account ice coverage and krill spatial distribution, it was clearly evident that both E. superba and E. crystallorophias were concentrated around latitude 74° S in November, when ice coverage was quite dense and diffused. The situation differed in December-January when polynyas (ice-free areas) are typically much larger; both species traveled north, but to varying degrees, with E. superba reaching farther north, close to the shelf break than E. crystallorophias. These two species are probably in competition, having similar feeding appendages and a similar diet based primarily on phytoplankton [10,11], but with a non-negligible quota of zooplankton [12,13].
In the Ross Sea, however, *E. superba* appears to prefer water mixing at the shelf break and continental slope, while *E. crystallorophias* generally prefer shallow waters or areas close to ice [8,9], thus reducing overlap and competition for food.

There is evidence that environmental factors can influence krill populations around the Antarctic continent, resulting in changes in their abundance and spatial distribution [4,14]. For instance, phytoplankton blooms originating from ice melting through released algae appear to promote an increase in krill biomass [15,16]. Therefore, krill abundance may be locally favored by low salinity conditions and high chlorophyll *a* concentration, which means ice melting and consequent phytoplankton bloom [1]. Moreover, the ice edge may be a favorable environment for krill due to its high productivity conditions, also providing protection to early developmental stages from predators [17,18]. Other environmental factors, such as dissolved oxygen, especially if considered in conjunction with the general rise in temperature, which reduces the amount of oxygen in the water, with potential consequences for krill swarm formation and relative packing density, could also be important for krill dynamics [19]. This factor may also represent a direct threat to the survival of these species [20].

The Ross Sea has witnessed significant changes in recent years, including an increase in mean summer air temperature and a decrease in shelf water salinity from the 1950s to the present day [21]. On a decadal time scale (1995–2006), these factors affected the formation of Antarctic Bottom Water (AABW) in the western and central Ross Sea [22,23], as well as Ice Shelf Water (ISW) and High Salinity Shelf Water (HSSW). All these changes, and eventually others, may have influenced the behavior of krill.

In this paper, we analyzed Antarctic krill and crystal krill biomass data and satellite environmental data to determine whether recent environmental changes have altered the abundance and distribution of *E. superba* and *E. crystallorophias* in the western Ross Sea. We also investigated the potential ramifications for other levels of the local pelagic food web.

2. Materials and Methods

2.1. Acoustic and Biological Data

This study focuses on the western Ross Sea area (GSA 88.1, Figure 1). A stable presence of *E. superba* and *E. crystallorophias* populations was observed in this region following several acoustic surveys [8,9]. This region approximates a rectangular area delimited by latitudes 69°30′ and 78°6′S (955 km) and longitudes 164°30′E and 175°30′W. This area has been surveyed acoustically eight times since 1989 under different ice coverage conditions. The six surveys selected from the total were all conducted between December and January during the austral summer.

Acoustic monitoring was carried out every 24 h from 15 to 200 m to obtain a more complete picture of krill abundance in the water column and avoid missing any krill aggregations due to nictemeral movements, which were not particularly significant in the study area [9]. In general, there was no discernible decline in schooling behavior. After noise testing, the vessel’s speed during the survey was generally set between 8 and 9.5 knots, depending mainly on water current and wind intensity conditions. Survey routes deviated from the original plan in the presence of ice.

The dB difference methodology [24,25] was used to identify krill swarms, taking into account specific dB intervals between pairs of available frequencies for the target species, verified with the help of pelagic hauls.

Acoustic density estimates per nautical mile were expressed as nautical area scattering coefficients (NASC; m²/nm²). NASC values at 120 kHz (generally the lead frequency for krill) of swarms identified as *E. superba* or *E. crystallorophias* were used for subsequent abundance calculation using the fluid sphere model [8,26–28]. A density contrast coefficient (g) of 1.0357 and a sound speed contrast coefficient (h) of 1.0279 were taken from the literature [29] and used for the two species; the average tilt angle was set to 15°. Acoustic data acquisition followed CCAMLR guidelines [30]. As regards data processing, the fluid sphere model [28] was applied in all the acoustic surveys carried out in the Ross Sea.
since 1989. This methodology [31–34] for estimating krill biomass has been validated and improved over time.

Figure 1. The Ross Sea, the reference study area.

During acoustic surveys, pelagic hauls were also conducted to aid in the analysis of echograms, to differentiate between target krill swarms and non-target organisms, and to collect length-weight data of krill samples. Hauls along the acoustic survey routes were conducted using a 5 m² Plankton Hamburg Net (HPN) in 1994, 1997, and 2000 [26], while HPRI-1000, a new plankton net designed at the CNR in Ancona (Italy), has been used since 2004 [27]. The net’s mesh size, which was 0.5 mm in 1994, changed to 1 mm from 1997 onwards. The number and position of the hauls were not fixed, depending on target visualization on the echosounder screen and ice coverage. Capture precision, that is, the capture of acoustically identified schools, was enhanced by connecting the echosounder to the SIMRAD ITI trawl positioning and monitoring system. Moreover, during the last two surveys [9], it was possible to plot the depth data flow on the sounder screen; this made it easier to check in real time whether the net was indeed catching the targeted schools, adjusting the depth stratum as necessary. During towing, net opening and trawl depth were displayed in real time on the screen, enabling accurate sampling in correspondence with echo traces. The total catch weight of each species was established after the catch was sorted. Total length, carapace length, weight, diameter of the compound eye, and sex were determined in 100 individuals per species. The length was measured using a gauge to the nearest millimeter, and the weight of each individual was measured with a high-precision scale (0.1 g) equipped with a motion compensation device (PL1020 Marel, Gardabaer, Iceland). In general, trawling was conducted horizontally in the stratum of interest between approximately 15 and 150 m; krill swarms were not very common below this depth. Haul duration was of one hour during the first expeditions and subsequently
shortened to a duration of half an hour which, given the technological improvements in trawling operations, was considered to be sufficient to obtain a good sample for biometric measurements. The average vessel speed during pelagic trawling was 2.5 knots. The length-weight equation was computed using the best fit methodology from the specific graph.

Biomass estimates derived from acoustic surveys are expressed as the mean krill density in tons per square nautical mile per Elementary Statistical Sampling Rectangle (ESSR) [27]. The ESSR method was employed in all the above-cited surveys, given its suitability for the acoustic monitoring of large areas [28]. Consequently, the western Ross Sea was subdivided into rectangular grid cells that were spaced at intervals of 1° in longitude but varied in latitude following the Earth’s curvature variation at the poles, resulting in rectangles with a constant area of 600 nm². Species abundance and biomass were calculated for each rectangle by considering the average NASC value of the portion of acoustic transects that lay within the rectangle. Biomass was estimated by referring to the depth stratum from 15 to 200 m. The first 15 m were excluded in order to account for vessel noise, noise owing to the presence of ice, and near field issues on the basis of the transducer draft.

Table 1 contains additional information on the acoustic surveys considered in this paper.

Table 1. Specific details of the selected acoustic surveys. The EK echosounders are SIMRAD scientific equipment.

| Year (yyyy) | Month (MON) | Vessel | Subarea | Survey Area (km²) | Echosounder | Load Freq (kHz) | Other Available Freq (kHz) | Target Identification Method | TS Model Used | Analysis Depth Range (m) | Time of Day | Survey Design |
|------------|-------------|--------|---------|------------------|-------------|----------------|---------------------------|----------------------------|---------------|--------------------------|-------------|---------------|
| 1994       | Dec         | Italica | 88.1    | 37,200          | BioSonics   | 102            | 38                        | dB difference             | Fluid sphere model         | 15–200       | Day and night           | Parallel transects |
| 1997       | Dec         | Italica | 88.1    | 39,600          | EK500       | 120            | 38, 200                   | dB difference             | Fluid sphere model         | 15–200       | Day and night           | Parallel transects |
| 2000       | Jan         | Italica | 88.1    | 60,600          | EK500       | 120            | 38, 200                   | dB difference             | Fluid sphere model         | 15–200       | Day and night           | Parallel transects |
| 2004       | Jan         | Italica | 88.1    | 50,800          | EK500       | 120            | 38, 200                   | dB difference             | Fluid sphere model         | 15–200       | Day and night           | Parallel transects |
| 2014       | Jan         | Italica | 88.1    | 16,000*         | EK600       | 120            | 38, 200                   | dB difference             | Fluid sphere model         | 15–200       | Day and night           | Parallel transects |
| 2016       | Jan         | Italica | 88.1    | 12,000*         | EK600       | 120            | 38, 200                   | dB difference             | Fluid sphere model         | 15–200       | Day and night           | Parallel transects |

* reduced coverage due to time constraints.

Acoustic data and associated pelagic haul data are stored in a database at the CNR IRBIM in Ancona (Italy) and can be obtained by submitting a request to the scientist responsible for the project.

2.2. Satellite Data

Satellite data were downloaded from the Copernicus Marine Service. Monthly means of temperature [35], salinity, and ice coverage variables at 1° of horizontal resolution for 75 vertical levels were selected and analyzed together with krill biomass data. For temperature and salinity, only superficial levels from the surface to around 200 m were selected for the analyses, since these are the strata monitored by the acoustic survey. An attempt was made to take into account the average values for the entire stratum; the values at 0.5, 97, and 199 m were then analyzed. Also selected were the monthly means of total chlorophyll a, total primary production, dissolved oxygen, and total phytoplankton at a horizontal resolution of 0.25° for 75 vertical levels, with the same depth levels as above. Temperature, salinity, water velocity, and ice coverage data were acquired from the new Mercator Ocean (Toulouse, FR) Global Ocean Ensemble Reanalysis [36]. These data consist of a numerical ocean model constrained with satellite data and in situ observations. The multi-model ensemble approach allows for the estimation of uncertainties in the ocean state. This reanalysis uses altimetry data observations that began in 1993. These data were obtained from the CMCC Global Ocean Physical Reanalysis System (C-GLORS), which simulates the state of the ocean over the past decades [37,38]. Ice coverage data were obtained from the same source as temperature and salinity and were expressed as a percentage of area coverage, i.e., sea ice area fraction (SIC). Total chlorophyll a, total primary production, dissolved oxygen, and total phytoplankton data use the PISCES
biogeochemical model available on the NEMO [39] modeling platform. The forcings used were FREEGLORYS2V4 ocean physics generated at Mercator-Ocean and ERA-Interim [40] atmosphere produced at ECMWF on a daily basis. 3D mean fields were interpolated on a standard regular grid in NetCDF format.

2.3. Statistical Analyses

After preliminary data exploration with the statistical software R [41], biomass data were log-transformed (log_{10}(x + 1), where x is the biomass) since they presented much higher absolute values than satellite environmental data. For each statistical rectangle used to estimate krill biomass, the corresponding environmental parameters were cut inside them by means of R software. This provided the most coherent information in each rectangle. If one of the rectangles lacked data and this was therefore deemed “not available” (=NA), data from that rectangle were discarded. This approach enabled us to compile the most complete dataset possible.

Two-way ANOVA (Analysis of Variance) was used to examine potential correlations between krill biomass and environmental data, based on four main case studies involving the selection of environmental data:

- Environmental data averaged from 0 to 200 m
- Environmental data at surface stratum
- Environmental data at a 97 m stratum
- Environmental data at a 199 m stratum

The selection of three case studies at fixed depths, in addition to the one addressing the entire water column from 0 to 200 m, was intended to determine whether the influence of certain environmental parameters on krill could be localized, preferably at specific depths. Separate ANOVA tests were conducted for each species, and the final reported results are those obtained by retaining only the statistically significant parameters from the first run.

The final models presented in this paper were chosen from a wide number of models. The best available models were identified by using the Q-Q plot technique, one of the well-known and widely used graphical techniques for testing conformity between empirical distribution and the given theoretical distribution [42]. Analyzing ANOVA model residuals to check normality for all groups at once is easier, and particularly useful when there are many groups, as in this case [43,44]. Levene’s test for homogeneity of variances was used to test the hypothesis of equality of group variances [45]. Finally, a post-hoc Tukey’s Honest Significant Difference test [46] was performed to highlight differences over the years.

3. Results

Figures 2 and 3 depict Antarctic krill and crystal krill biomass, respectively, estimated acoustically for the ESSR covered by the six surveys held in the western Ross Sea. The bathymetry reference for these figures is [47], while the land is based on [48].
Figure 2. The estimated biomass density of Antarctic krill in the western Ross Sea based on six selected acoustic surveys.
Figure 3. The estimated biomass density of crystal krill in the western Ross Sea based on six selected acoustic surveys.

![E. crystallorophias - 1994](image)

![E. crystallorophias - 1997](image)

![E. crystallorophias - 2000](image)

![E. crystallorophias - 2004](image)

![E. crystallorophias - 2014](image)

![E. crystallorophias - 2016](image)
3.1. Mean Environmental Data in the Water Column Relevant for Krill Biomass Estimation (0–200 m)

The ANOVA results for *E. crystallorophias*, leaving the significant environmental parameters, are reported in Table 2, while the residuals’ histograms and QQ plots are shown in Figure 4.

Table 2. Two-way ANOVA for *E. crystallorophias* and averaged environmental parameters.

| Parameters       | Df | Sum Sq | Mean Sq | f-Value | p-Value | Signif. |
|------------------|----|--------|---------|---------|---------|---------|
| Month            | 1  | 0.00   | 0.00    | 0.01    | 0.926   |         |
| Year             | 4  | 5.62   | 1.41    | 6.95    | 0.000   | ***     |
| Ice              | 1  | 4.37   | 4.37    | 21.61   | 0.000   | ***     |
| Salinity         | 1  | 1.79   | 1.79    | 8.85    | 0.003   | **      |
| Water velocity   | 1  | 1.00   | 1.00    | 4.94    | 0.027   | *       |
| Dissolved oxygen | 1  | 3.04   | 3.04    | 15.02   | 0.000   | ***     |
| Phytoplankton    | 1  | 1.33   | 1.33    | 6.59    | 0.011   | *       |
| Residuals        | 282| 56.98  | 0.20    | -       | -       |         |

Signif. codes: ‘***’ p < 0.001 ‘**’ p < 0.01 ‘*’ p < 0.05.

Figure 4. (a) Histogram of the residuals for the *E. crystallorophias* biomass case study and environmental values averaged between 0 and 200 m; (b) QQ plot of the residuals.

The ANOVA results for *E. superba*, including only the significant environmental parameters, are reported in Table 3; residuals’ histograms and QQ plots are shown in Figure 5.

Table 3. Two-way ANOVA for *E. superba* and averaged environmental parameters.

| Parameters       | Df | Sum Sq | Mean Sq | f-Value | p-Value | Signif. |
|------------------|----|--------|---------|---------|---------|---------|
| Month            | 1  | 25.47  | 25.47   | 62.42   | 0.000   | ***     |
| Year             | 4  | 17.72  | 4.43    | 10.86   | 0.000   | ***     |
| Salinity         | 1  | 3.22   | 3.22    | 7.88    | 0.005   | **      |
| Water velocity   | 1  | 3.78   | 3.78    | 9.27    | 0.003   | **      |
| Chlorophyll *a*  | 1  | 13.39  | 13.39   | 32.83   | 0.000   | ***     |
| Dissolved oxygen | 1  | 34.37  | 34.37   | 84.22   | 0.000   | ***     |
| Residuals        | 283| 115.47 | 0.41    | -       | -       |         |

Signif. codes: ‘***’ p < 0.001 ‘**’ p < 0.01.
To summarize the most important results, crystal krill biomass presented highly statistically significant correlations with the survey year, ice coverage, and dissolved oxygen, whereas significant correlations were found with salinity. Antarctic krill showed highly significant correlations with the survey month, survey year, chlorophyll \(a\) concentration, and dissolved oxygen, whereas significant correlations were found with salinity and water velocity. This indicates that both species are sensitive to dissolved oxygen levels and that their biomass has altered over the years. As regards crystal krill, ice coverage also seems to be important, while the \(E.\ superba\) biomass has a significant association with chlorophyll \(a\) concentration and the survey month.

### 3.2. Environmental Data at the Surface Layer (0.5 m)

The \(E.\ crystallorophias\) ANOVA results for this case study are reported in Table 4, while the residuals’ histograms and QQ plot are reported in Figure 6.

#### Table 4. Two-way ANOVA for \(E.\ crystallorophias\) and environmental parameters at the surface layer (0.5 m).

| Parameters     | Df | Sum Sq | Mean Sq | \(f\)-Value | \(p\)-Value | Signif. |
|----------------|----|--------|---------|-------------|-------------|---------|
| Month          | 1  | 0.40   | 0.40    | 2.01        | 0.158       |         |
| Year           | 3  | 2.75   | 0.92    | 4.62        | 0.004       | **      |
| Ice            | 1  | 0.78   | 0.78    | 3.95        | 0.048       | *       |
| Temperature    | 1  | 8.51   | 8.51    | 42.93       | 0.000       | ***     |
| Water velocity | 1  | 0.97   | 0.97    | 4.87        | 0.028       | *       |
| Chlorophyll \(a\) | 1  | 1.95   | 1.95    | 9.81        | 0.002       | **      |
| Phytoplankton  | 1  | 0.84   | 0.84    | 4.23        | 0.041       | *       |
| Residuals      | 206| 40.84  | 0.20    | -           | -           |         |

Signif. codes: ‘***’ \(p < 0.001\) ‘**’ \(p < 0.01\) ‘*’ \(p < 0.05\).
Figure 6. (a) Histogram of the residuals for the *E. crystallorophias* biomass case study and environmental values at 0.5 m; (b) QQ plot of the residuals.

The *E. superba* ANOVA results analyzed together with environmental parameters at the surface layer are reported in Table 5; residuals’ histograms and QQ plots are shown in Figure 7.

Table 5. Two-way ANOVA for *E. superba* and environmental parameters at the surface layer (0.5 m).

| Parameters     | Df | Sum Sq | Mean Sq | f-Value | p-Value | Signif. |
|----------------|----|--------|---------|---------|---------|---------|
| Month          | 1  | 16.39  | 16.39   | 36.03   | 0.000   | ***     |
| Year           | 3  | 13.57  | 4.52    | 9.94    | 0.000   | ***     |
| Temperature    | 1  | 18.66  | 18.66   | 41.01   | 0.000   | ***     |
| Salinity       | 1  | 4.03   | 4.03    | 8.86    | 0.003   | **      |
| Water velocity | 1  | 1.33   | 1.33    | 2.91    | 0.089   |         |
| Residuals      | 208| 94.65  | 0.46    | -       | -       |         |

Signif. codes: **** *p < 0.001 ** *p < 0.01.

Figure 7. (a) Histogram of the residuals for the *E. superba* biomass case study and environmental values at 0.5 m; (b) QQ plot of the residuals.
Crystal krill biomass presented highly significant connections with temperature and significant correlations with the survey year and chlorophyll $a$ concentration. Antarctic krill exhibited highly significant connections with the survey month, survey year, and temperature, while a significant correlation was found with salinity. At the surface layer, both species were shown to be influenced by temperature, with Antarctic krill biomass being the only one to also vary in accordance with the survey year and month, as was the case for averaged environmental parameters throughout the water column.

### 3.3. Environmental Data at the 97 m Layer

The ANOVA results for the *E. crystallorophias* case study are reported in Table 6, while the histograms and QQ plots depicting residuals are reported in Figure 8.

**Table 6.** Two-way ANOVA for *E. crystallorophias* and environmental parameters at the 97 m layer.

| Parameters       | Df | Sum Sq | Mean Sq | f-Value | p-Value | Signif. |
|------------------|----|--------|---------|---------|---------|---------|
| Month            | 1  | 0.40   | 0.40    | 2.13    | 0.146   |         |
| Year             | 3  | 2.75   | 0.92    | 4.90    | 0.003   | **      |
| Ice              | 1  | 0.78   | 0.78    | 4.20    | 0.042   | *       |
| Temperature      | 1  | 4.44   | 4.44    | 23.76   | 0.000   | ***     |
| Water velocity   | 1  | 1.35   | 1.35    | 7.25    | 0.008   | **      |
| Chlorophyll $a$  | 1  | 1.66   | 1.66    | 8.92    | 0.003   | **      |
| Dissolved oxygen | 1  | 7.18   | 7.18    | 38.46   | 0.000   | ***     |
| Residuals        | 206| 38.47  | 0.19    | -       | -       |

Signif. codes: ‘***’ $p < 0.001$ ‘**’ $p < 0.01$ ‘*’ $p < 0.05$.

**Figure 8.** (a) Histogram of the residuals for the *E. crystallorophias* biomass case study and environmental values at 97 m; (b) QQ plot of the residuals.

The *E. superba* ANOVA results analyzed together with environmental parameters at the 97 m layer are reported in Table 7; residuals’ histograms and QQ plots are shown in Figure 9.
At around 100 m depth, the factors that seem to exert the biggest influence are temperature and dissolved oxygen. \( E. \) \textit{crystallorophias} and \( E. \) \textit{superba} exhibited highly significant correlations with the survey month and year, temperature, chlorophyll \( a \) concentration, and dissolved oxygen. At around 100 m depth, the factors that seem to exert the biggest influence are temperature and dissolved oxygen. \( E. \) \textit{crystallorophias} and \( E. \) \textit{superba} were found to be the survey year, water velocity, and environmental parameters at the 199 m layer. Other significant correlations for \( E. \) \textit{crystallorophias} were found to be the survey year, water velocity, and environmental parameters at the 97 m layer.

### 3.4. Environmental Data at the 199 m Layer

The ANOVA results for the \( E. \) \textit{crystallorophias} case study are reported in Table 8, while the residuals’ histograms and QQ plot are depicted in Figure 10.

### Table 7. Two-way ANOVA for \( E. \) \textit{superba} and environmental parameters at the 97 m layer.

| Parameters          | Df | Sum Sq | Mean Sq | f-Value | p-Value | Signif. |
|---------------------|----|--------|---------|---------|---------|---------|
| Month               | 1  | 16.39  | 16.39   | 41.83   | 0.000   | ***     |
| Year                | 3  | 13.57  | 4.52    | 11.54   | 0.000   | ***     |
| Temperature         | 1  | 6.84   | 6.84    | 17.46   | 0.000   | ***     |
| Water velocity      | 1  | 1.61   | 1.61    | 4.11    | 0.044   | *       |
| Chlorophyll \( a \) | 1  | 5.59   | 5.59    | 14.26   | 0.000   | ***     |
| Dissolved oxygen    | 1  | 23.49  | 23.49   | 59.93   | 0.000   | ***     |
| Residuals           | 207| 81.14  | 0.39    | -       | -       | -       |

Signif. codes: *** \( p < 0.001 \) ** \( p < 0.01 \) * \( p < 0.05 \).

### Figure 9. (a) Histogram of the residuals for the \( E. \) \textit{superba} biomass case study and environmental values at 97 m; (b) QQ plot of the residuals.

Temperature and dissolved oxygen were found to be highly significant for the \( E. \) \textit{crystallorophias} biomass. \( E. \) \textit{superba} exhibited highly significant correlations with the survey month and year, temperature, chlorophyll \( a \) concentration, and dissolved oxygen. At around 100 m depth, the factors that seem to exert the biggest influence are temperature and dissolved oxygen for both species. \( E. \) \textit{superba} presented a highly significant connection with chlorophyll \( a \) concentration, survey month, and survey year. Other significant correlations for \( E. \) \textit{crystallorophias} were found to be the survey year, water velocity, and chlorophyll concentration.

### Table 8. Two-way ANOVA for \( E. \) \textit{crystallorophias} and environmental parameters at the 199 m layer.

| Parameters          | Df | Sum Sq | Mean Sq | f-Value | p-Value | Signif. |
|---------------------|----|--------|---------|---------|---------|---------|
| Month               | 1  | 0.42   | 0.42    | 2.39    | 0.123   | **      |
| Year                | 3  | 2.65   | 0.88    | 5.01    | 0.002   | **      |
| Ice                 | 1  | 0.80   | 0.80    | 4.56    | 0.034   | *       |
| Temperature         | 1  | 10.02  | 10.02   | 56.80   | 0.000   | ***     |
| Salinity            | 1  | 1.88   | 1.88    | 10.67   | 0.001   | **      |
| Water velocity      | 1  | 0.82   | 0.82    | 4.67    | 0.032   | *       |
| Chlorophyll \( a \) | 1  | 1.73   | 1.73    | 9.78    | 0.002   | **      |
| Phytoplankton       | 1  | 2.77   | 2.77    | 15.70   | 0.000   | ***     |
| Residuals           | 202| 35.63  | 0.18    | -       | -       | -       |

Signif. codes: **** \( p < 0.001 \) *** \( p < 0.01 \) ** \( p < 0.05 \).
The ANOVA results for *E. superba* analyzed together with environmental parameters at the 199 m layer are reported in Table 9; residuals’ histograms and QQ plots are shown in Figure 11.

Table 9. Two-way ANOVA for *E. superba* and environmental parameters at the 199 m layer.

| Parameters          | Df | Sum Sq | Mean Sq | f-Value | p-Value | Signif. |
|---------------------|----|--------|---------|---------|---------|---------|
| Month               | 1  | 16.78  | 16.78   | 42.07   | 0.000   | ***     |
| Year                | 3  | 12.90  | 4.30    | 10.78   | 0.000   | ***     |
| Temperature         | 1  | 26.46  | 26.46   | 66.36   | 0.000   | ***     |
| Chlorophyll a       | 1  | 3.26   | 3.26    | 8.17    | 0.005   | **      |
| Dissolved oxygen    | 1  | 2.54   | 2.54    | 6.37    | 0.012   | *       |
| Residuals           | 205| 81.74  | 0.40    | -       | -       | -       |

Signif. codes: ‘***’ *p* < 0.001; ‘**’ *p* < 0.01; ‘*’ *p* < 0.05.

Figure 10. (a) Histogram of the residuals for the *E. crystallorophias* biomass case study and environmental values at 199 m; (b) QQ plot of the residuals.

Figure 11. (a) Histogram of the residuals for the *E. superba* biomass case study and environmental values at 199 m; (b) QQ plot of the residuals.
Temperature and phytoplankton correlations with the *E. crystallorophias* biomass were found to be highly significant. *E. superba* showed highly significant associations with the survey month, survey year, and temperature. At a depth of 200 m, temperature appears to influence both species. Phytoplankton concentration seems to be important for crystal krill, while the survey month and year influence Antarctic krill. Other significant connections were found with the survey year and chlorophyll *a* concentration for *E. crystallorophias*, as well as chlorophyll concentration in the case of *E. superba*.

All the above results, limited to highly significant correlations, are summarized in Table 10.

**Table 10.** Summary of highly significant correlations between the two krill species and environmental parameters for each case study.

| Species | Depth Stratum 0–200 m               | Depth Stratum 0.5 m            | Depth Stratum 97 m           | Depth Stratum 199 m     |
|---------|------------------------------------|--------------------------------|-----------------------------|-------------------------|
| E. crys. | survey year, ice, oxygen           | temperature                    | temperature, oxygen         | temperature, phytoplankton |
| E. sup.  | survey month, survey year, chlorophyll *a*, oxygen | survey month, survey year, temperature | survey month, survey year, temperature, chlorophyll *a*, oxygen | survey month, survey year, temperature |

The results of Levene’s test and the Tukey test for each of the above case studies can be found in the Supplementary Materials.

### 4. Discussion

Crystal krill yielded very different results when environmental average values from 0 to 200 m were compared to values at fixed depth strata. In the former case, the most significant correlations involve the survey year, ice coverage, and dissolved oxygen. However, when fixed depth strata are considered, the variable most strongly correlated with krill biomass is temperature, followed by dissolved oxygen at a depth of 100 m and total phytoplankton concentration at a depth of 200 m. The correlation between the survey year and crystal krill biomass in the western Ross Sea suggests that the biomass has varied significantly across the years in which the surveys were conducted. Previous studies have revealed a correlation between *E. crystallorophias* biomass and ice coverage [9,49], as this species prefers to inhabit coastal and ice-covered areas and should be sensitive to ice dynamics. The relationship between crystal krill and sea ice can be explained by the availability of food and the desire to protect eggs and early life stages [50–52].

As regards the synergistic relationship between temperature and dissolved oxygen, we have already mentioned a general rise in water temperature in the Ross Sea, which would result in a decrease in the water’s oxygen concentration. This may have a deleterious impact on krill swarm formation and relative density [19], posing a potential threat to these species’ survival rate [20]. Based on our results, this synergistic effect on crystal krill should be stronger at a depth of around 100 m. In all fixed strata analyses, the temperature is by far the most prominent environmental parameter with significant connections in the case of crystal krill. This factor may be related to the importance of temperature in the regulation of krill metabolism [53]. Some experiments [54] demonstrated that food and oxygen demands tend to increase as temperatures rise, with a possible subtraction of energy from other activities, such as reproduction, in a global warming scenario such as the one we are helping to create. Temperature is also important for the stabilization of ice coverage, given that ice is important as a reserve of food and shelter for the protection of krill larvae [55–58]. Moreover, ice-free areas often demonstrate the predominance of krill rivals such as *Salpa thompsonii* [57]. Optimal summer temperatures seem to differ for these two krill species, with *E. superba* preferring higher temperatures at the shelf break in the northern part of the Ross Sea and *E. crystallorophias* preferring the shallower depths and colder temperatures of the south-western neritic part [8,9,50]. At least during the austral summer, this factor
contributes to the spatial separation of these species and significantly reduces competition for food. The link between crystal krill abundance and phytoplankton has already been the subject of prior research [1,9]; however, the significance of its availability at greater depths (200 m), as demonstrated in this study, may not be as well documented. As also reported in other Antarctic areas [58], our data revealed that this species is quite abundant even at 100 m or more. For this reason, crystal krill at depths between 100–200 m could be quite influenced by the availability of phytoplankton in these or neighboring strata above.

In the ANOVA results, Antarctic krill presented a main difference with respect to crystal krill: the survey month and survey year had significant correlations with biomass in all case studies. This factor highlights the considerable variability of Antarctic krill biomass over the years, as well as a major difference between the situation in December, when ice is denser, and January, when most of the area is typically ice-free. The different levels of abundance and spatial distribution of Antarctic krill between December and January, as discussed in this paper, were also reported in previous studies [8,9]. In fact, a comparison of the beginning of austral summer with full summer reveals quite a diverse picture for these creatures, with the bulk of Antarctic krill distribution shifting northwards throughout the summer period. Even in the case of Antarctic krill, temperature appears to be a highly significant parameter for similar reasons as those reported for crystal krill; analogous considerations may also be made in this case, but taking into account these two species’ different preferences. Another, less-studied phenomenon connected to the rise in temperature and consequent increase in ice melting, is the stranded Antarctic krill individuals found in certain regions of Antarctica, such as Potter Cove [59], where the creatures’ guts were found to be full of particles suspended in the floods originating from melted ice. The latter is another example of the importance of a balance between temperature, ice presence, and marine organisms in Antarctic ecosystems. A significant association between E. superba biomass and dissolved oxygen was observed in the average values of the first 200 m and the 100 m depth strata. This factor reinforces the notion that both these krill species are sensitive to the same environmental parameters, despite their different preference ranges, as observed for temperature. Similarly, chlorophyll a concentration had an impact on Antarctic krill biomass when environmental parameters were averaged from 0 to 200 m and 100 m depth strata. This element highlights the trophic factor’s importance for Antarctic krill, particularly the availability of phytoplankton [60,61], in addition to boosting krill recruitment [62]. The ANOVA results suggest that the 100 m depth stratum has the highest phytoplankton concentration. Looking at the CTD profiles reported in [63], which were performed at the positions of pelagic hauls during the 2004 acoustic survey in the western Ross Sea, a peak in fluorescence can be seen at a 40–50 m depth, and in one case, even deeper. This suggests that chlorophyll concentration in these depth strata could exert a relevant influence on Antarctic krill. In any case, the analyses of fluorescence data from CTD sampling should be improved in order to support this hypothesis. Some authors also discovered an increase in Antarctic krill lipid reserves in conjunction with increasing levels of chlorophyll a concentration, estimated from remote sensing data collection and a decrease in sea surface temperature [11]. The present results showed significant associations between Antarctic krill biomass, chlorophyll a concentration, and temperature at a depth of 100 m, suggesting that something similar to the reported instance could also have happened in our study.

This paper demonstrates that acoustic estimations of krill biomass combined with satellite-derived environmental data can provide intriguing insights into the environmental variables that exert an influence on krill and, consequently, the Ross Sea’s local pelagic ecosystem. These preliminary results may provide an avenue for expanding our understanding of the spatial and temporal variations of krill biomass in the Ross Sea. The inclusion of krill spatial distribution and data on krill recruitment and krill predators should improve the precision of these conclusions.
5. Conclusions

The analyses in this paper have highlighted the importance of certain environmental parameters for Antarctic krill and crystal krill biomass and demonstrated that the levels of these stocks vary significantly from one summer to another. Temperature and dissolved oxygen are some of the parameters that are common to both species, and although chlorophyll a concentration was shown to be important for *E. superba*, ice coverage is a critical factor for *E. crystallorophias*. These preliminary analyses should be explored further in order to understand the complex intricate links between krill and the environment in the Ross Sea.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14060433/s1, Table S1: Levene’s Test of Homogeneity of Variance (center = mean) for all *E. crystallorophias* case studies; Table S2: Levene’s Test of Homogeneity of Variance (center = mean) for all *E. superba* case studies; Table S3: Tukey multiple comparisons of means with a 95% family-wise confidence level for *E. crystallorophias* and averaged environmental parameters; Table S4: Tukey multiple comparisons of means with a 95% family-wise confidence level for *E. crystallorophias* and environmental parameters at 0.5 m; Table S5: Tukey multiple comparisons of means with a 95% family-wise confidence level for *E. superba* and environmental parameters at 97 m; Table S6: Tukey multiple comparisons of means with a 95% family-wise confidence level for *E. crystallorophias* and environmental parameters at 199 m; Table S7: Tukey multiple comparisons of means with a 95% family-wise confidence level for *E. crystallorophias* and averaged environmental parameters at 0.5 m; Table S8: Tukey multiple comparisons of means with a 95% family-wise confidence level for *E. superba* and environmental parameters at 199 m; Table S9: Tukey multiple comparisons of means with a 95% family-wise confidence level for *E. superba* and averaged environmental parameters at 0.5 m; Table S10: Tukey multiple comparisons of means with a 95% family-wise confidence level for *E. superba* and environmental parameters at 97 m; Table S11: Tukey multiple comparisons of means with a 95% family-wise confidence level for *E. superba* and environmental parameters at 199 m.

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Data Availability Statement: Survey data are available on request. Satellite environmental data presented in this study are freely accessible via the search engine at https://resources.marine.copernicus.eu/products (access on 25 March 2022).

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