Polar Biology
https://doi.org/10.1007/s00300-021-02836-1

ORIGINAL PAPER

Density and distribution of euphausiid larvae in the Scotia Sea in the 2011 summer

Rombolá E.[1,2] · **Franzosi C.**[1] · **Tosonotto G.**[1] · **Vivequin S.**[1] · **Alder V.**[1,2,3] · **Marschoff E.**[1]

Received: 15 October 2019 / Revised: 3 February 2021 / Accepted: 23 February 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

Monitoring of early euphausiid larvae provides valuable information on the mechanisms involved in recruitment to the adult populations. As the Antarctic is undergoing rapid environmental change, these mechanisms are key to ecosystem-based management of the krill fishery. We analyzed the distribution and abundance of early euphausiid larvae (calyptopes I to late furciliae) from 76 plankton samples from surface to 300 m depth in the Atlantic sector in January 2011 in relation with a previous survey and published information. *Thysanoessa macrura* (mean density: 209 ind m^{-2}) dominated the sampling while *Euphausia superba* (mean density: 13.63 ind m^{-2}) and *Euphausia frigida* (mean density: 10.05 ind m^{-2}) were also present. *T. macrura* density increased while *E. superba* experienced a high decrease respect to historical data. Clustering of stations and correspondence analysis showed that the associations of larvae and water masses are in agreement with literature reports, so the differences on the abundance of early larvae are within the observed variability and cannot be attributed to any single factor, suggesting that it is due to more subtle changes such as the stability of the water column and/or vorticity in the fronts.

Keywords Euphausiid larvae · Density · Geographical distribution · Scotia Sea

Introduction

Climate change, through sea ice decline, ocean warming, acidification, and other environmental stressors, such as modifications in circulation patterns, will impact on the abundance, distribution and life cycles of Antarctic krill and other euphausiids (Flores et al. 2012). Under the new conditions generated by climate change, ecosystems will be fundamentally modified (Hoegh-Guldberg and Bruno 2010). Understanding the expected changes and the mechanisms involved is crucial for their conservation and ecosystem-based fisheries management (Flores et al. 2012).

In the Atlantic Sector of the Antarctic, bottom topography and emerged continental masses create a complex environment where six euphausiid species are found*:* *Euphausia superba, Euphausia frigida, Euphausia crystallorophias, Euphausia triacantha, Thysanoessa macrura* and *Thysanoessa vicina*. Their different physiological tolerances (Ross et al 1988; Quetin and Ross 1984, 1989) result in the latitudinal replacement of species (Tattersall 1924; Baker 1965; Ponomareva and Dobryisheva 1978; Marschall and Mizdalzki 1985; Ross et al. 1988; Hofmann et al. 1992) associated with the circumpolar oceanic circulation.

The main oceanographic features of the survey area are the Antarctic Circumpolar Current (ACC), the Weddell-Scotia Confluence (WSC), also known as the secondary front (Deacon 1937, 1979; Makarov and Maslennikov 1981; Makarov et al. 1992) and the northern branch of the Weddell gyre (WS). The nutrient rich Upper Circumpolar Deep Water (UCDW), typical of the ACC (Heywood et al. 2004) defines the southern boundary of the ACC at the Scotia Front (Orsi et al. 1995). This feature, also known as the Southern Boundary (SBACC), is an area of divergence or upwelling, that corresponds to the circumpolar distributions

✉ Rombolá E.
rombola_emilce@hotmail.com

[1] Instituto Antártico Argentino. Dirección Nacional del Antartico, 25 de Mayo 1143, San Martín, Buenos Aires, Argentina

[2] Consejo Nacional de Investigaciones Cientificas Y Técnicas, Buenos Aires, Argentina

[3] Departamento de Ecología, Genética Y Evolución. Facultad de Ciencias Exactas Y Naturales, Universidad de Buenos Aires, Intendente Güiraldes 2160. Ciudad Universitaria. C1428EGA, Buenos Aires, Argentina

Published online: 18 March 2021

of baleen whales, krill and to regions of high phytoplankton biomass (Tynan 1998).

The WSC results from the encounter of water of three different origins, moving at different speeds in the same overall direction and mixing while moving eastwards. (Patterson and Sievers 1980; Whithworth et al. 1994; Thompson and Youngs 2013; Meredith et al. 2015). It begins at the easternmost South Shetland Islands with the injection of water from the Antarctic Coastal Current between the ACC to the north and the northern branch of the Weddell Gyre to the south. The WSC is weakly stratified and the vertical distribution of properties is homogeneous (Patterson and Sievers 1980) with lower salinities, and higher oxygen concentrations than waters adjacent to the north and south (Whithworth et al. 1994). This complex provides a predictable foraging ground for many species, and is of critical importance to the functioning of the Southern Ocean ecosystem (Loeb et al. 2009, 2010; Venables et al. 2012). Large densities of euphausiid larvae have been regularly observed at the WSC during the twentieth century: *E. superba* up to 10^6 ind m^{-3} (Marr 1962; Hempel 1985a); between 100–1000 ind m^{-2} (Makarov and Menshenina 1989), and 2044 ind m^{-2} described during CCAMLR 2000 Survey (Siegel et al. 2004); *T. macrura* with densities between 1000–3000 ind 1000 m^{-3} (Hempel and Marschoff 1980), and up to 7200 ind m^{-2} (Makarov et al. 1992) during seventies and eighties respectively. High interannual variability was also recorded, as summarized by Siegel and Watkins (2016) for *E. superba* in the western Atlantic Sector. In 1981 Antarctic krill was particularly abundant with a mean density of 1.9 10^4 ind m^{-2} and a maximum of 1.8 10^6 calyptopes m^{-2}. The 1981 spawning season was unusual in that krill larval densities were an order of magnitude higher than during 2000 (Siegel et al. 2004). The highest numbers of larvae were recorded in the central Scotia Sea, in the open ocean and along the shelf slopes (Rakusa-Suszczewski 1984; Siegel et al. 2004).

With the exception of those of *E. crystallorophias,* the Euphausiids eggs sink after spawning, reaching different depths at hatching (Marr 1962; Mackintosh 1973; Ponomareva and Dobryisheva 1978; Makarov 1979a). From the first calyptopis onwards, larvae reside in the upper 100 m and, since they do not perform significant diel vertical migrations (Marschoff et al. 1998), their dispersion is due to surface currents alone. While developing, euphausiid larvae in the WSC are carried eastwards reaching the South Sandwich Islands and east of the South Georgia Islands, already mixed with populations carried by the ACC. Thus, the WSC region becomes an important source of *E. superba* recruits in the eastern Scotia Sea.

Warming and freshening of sea water as a result of the climate change process are accompanied by the intensification of the ACC and its poleward migration (Chapman et al 2020). These changes in the extent and disposition of the frontal systems in the Scotia Sea will impact on the early life histories of the euphausiid species.

Our aim is to establish if the interannual variability observed in the densities of early euphausiid larvae in the Scotia Sea might be explained by changes in their distribution patterns, thus reflecting the impact of long term changes.

In the present study we focus on the spatial distribution and abundance of euphausiid larvae in relation to water mass distributions in the WSC and surroundings in 2011 when the densities of *E. superba* were very low in comparison with historical data when *E. superba* densities were very high.

Material and method

From 13th January to 1st February 2011, 76 plankton samples were taken on board of the oceanographic research vessel Puerto Deseado, operated jointly by CONICET, Instituto Antártico Argentino (IAA) and the Argentine Navy. The stations were distributed in seven transects located in the region comprised between 43°30′W and 58°12′ W (Fig. 1). CTD (conductivity, temperature and depth) profiles were obtained using a Seabird CTD 9 profiler. Water masses were identified from the Temperature–Salinity profiles. The plankton net was constructed accordingly to the WP_2 specifications (Tranter 1968) (mesh: 200-µm; 60 cm opening diameter). It was hauled vertically from 300 m back to the surface at 1 ms^{-1} (depth was determined by the length and angle of the wire paid off), projecting the whole track of the net against the vertical to the maximum depth in the haul.

Samples were fixed in 2% seawater formaline, buffered with borax. Euphausiids were sorted to species and stage and counted under a Wild M8 stereomicroscope. When necessary, a Motoda plankton splitter (Motoda 1959) was used for subsampling. All larvae were identified to species and staged as calyptopes (CI–CIII) and furciliae (FI–FIV pooled as early furciliae, EF; the remaining as late furciliae, LF) using keys and figures published by Pertzova (1976); Makarov (1979a); Marschoff (1996) and Gallotti (2013). Results were expressed as densities (number of individuals per square meter) for each combination of species and stage, Three clusters were constructed applying the hierarchical agglomerative clustering method with the PRIMER software (Clarke and Gorley 2015). One was based on the standardized temperature and salinity measured at 10 m, 50 m and 100 m (environmental cluster) and the other was based on the log transformed densities of euphausiid larvae (taxa cluster) data. The Bray–Curtis coefficient and distance linkage group average were used to obtain dendrograms.

The water masses identified from the temperature and salinity profiles were used to identify the stations belonging to each water mass. The association between the two clusters

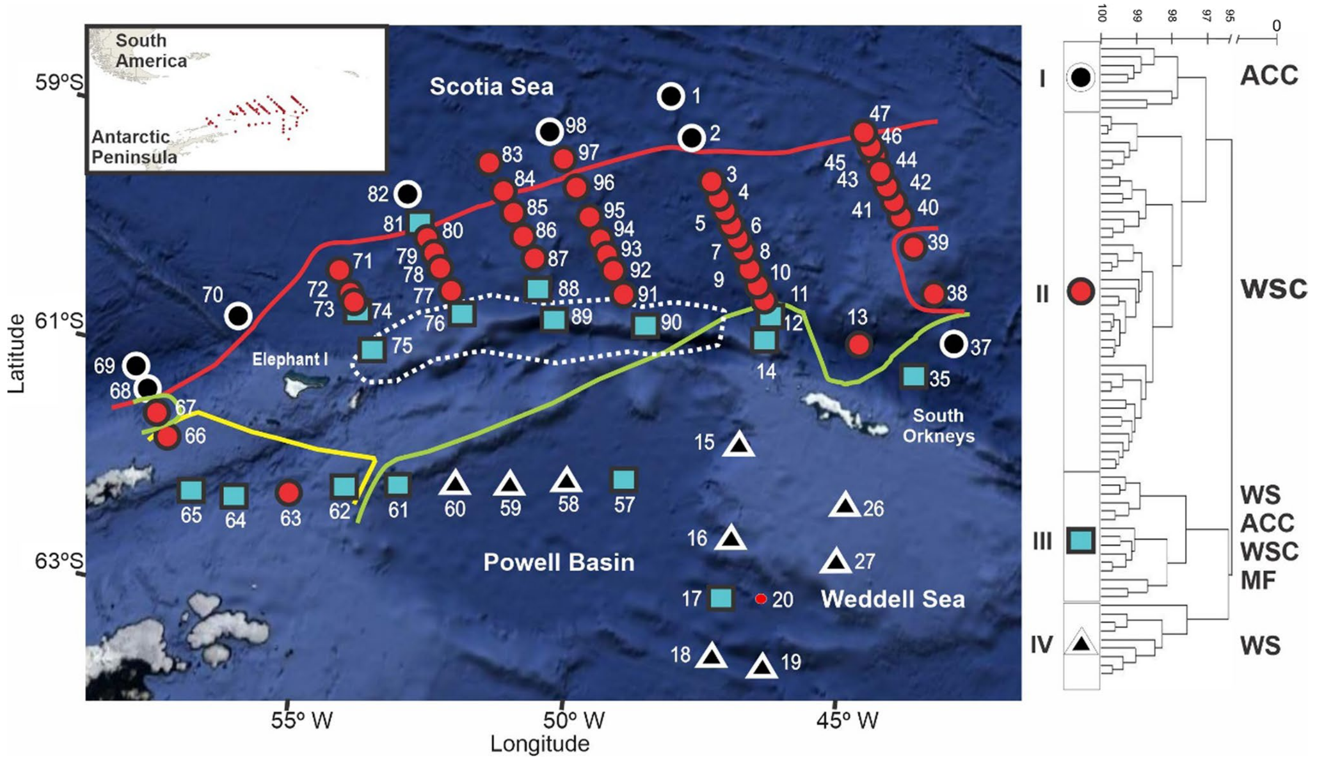

Fig. 1 Position of the stations and main oceanographic features in the Southern Scotia Sea region during austral summer 2011. Cluster analysis based on temperature and salinity). No CTD data were obtained on station 20. Red line: Scotia Front; yellow line boundary of Peninsula waters; broken white line: Hesperides trench; green line: Weddell Front; *MF* Mar de la Flota, *WS* Weddell Sea. Stations are colored accordingly to numbered cluster groups

classifications from 2011 and the water masses were tested with a G-test.

The correspondence analysis for the 2011 data was performed accordingly to Lebart et al. (1979) obtaining the position of stations and taxa on the correspondence axes. The PERMANOVA (Permutational Multivariate Analysis of Variance), (Morrison 1976) was applied to the coordinates on the correspondence axes (derived from larvae data) of the stations grouped by water masses.

Results

Oceanographic setting

Besides the Antarctic Surface Water and Winter Water the analysis of CTD data along the meridional sections shown in Fig. 1 revealed the presence of Weddell Sea (WS), Antarctic Circumpolar Current (ACC), Antarctic Peninsula (Mar de la Flota/Bransfield Strait, MF) and Weddell-Scotia Confluence (WSC) waters. The position of the 27.7 kg m^{-3} isopycnal surface observed in January 2011 was within the described limits. Thus, each station was ascribed to one of the four water masses identified.

The local values of temperature remain well within the physiological limits of euphausiid larvae, as they were experimentally determined (Ikeda 1984; Ross et al. 1988; Quetin and Ross 1989) between 0 ºC and 2 ºC, temperatures seen at the surface during the austral summer.

The region of the ACC was characterized by the presence of UCDW identified by deep maxima of temperature and salinity (1.8–2 °C and 34.6–34.7), defining the 27.7 kgm^{-3} potential density anomaly surface. This surface becomes shallower from north to south, from 600 m in the ACC to less than 200 m in the Weddell Sea. The southern limit of the ACC is marked by the deepening of the isotherms at the Scotia Front. Two stations (N° 38 and 39), located in the easternmost section, with properties close to those of the northern extreme of the section were considered as pertaining to the ACC.

From the comparison with historic datasets, the 1995 sampling year (Marschoff et al. 1998) results that the oceanographic conditions during the cruise presented lower salinity in the Confluence region, probably as a result of greater influx of fresh water from ice melting in the Weddell Sea as shown in the T–S graphs presented in Fig. 2 (limited to the stations in the region of overlapping in the 1995 and 2011 surveys).

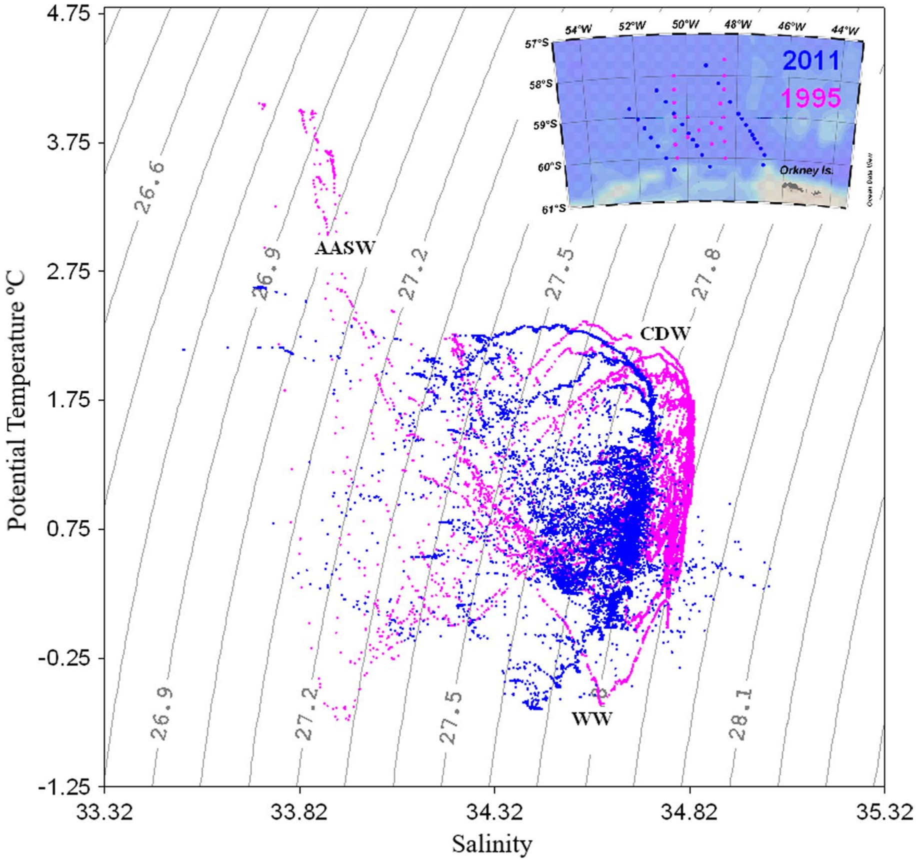

Fig. 2 T-S diagram showing the change (dilution) observed between 1995 (red) and 2011 (blue). AASW (Antarctic Surface Water), *CDW* Circumpolar Deep Water, *WW* Winter Water. Upper right corner: position of the stations of the cruises

South of the Scotia Front the WSC region was vertically homogeneous, its southern limit was defined by the Weddell Front. Within the WSC region, the vertical profiles in the Hesperides Trench were even more homogenous. The Weddell front was marked by the deepening of the isotherms and the isopycnal surface of 27.7 kg m^{-3} reaching 200 m; the Weddell region (northern branch of the Weddell gyre in our study) was characterized by the subsurface minimum temperature.

Finally, close to the Antarctic Peninsula we found the slope front defining the MF region, identified by the change in the slope of the isopycnal lines and the intrusion of the 0 °C isotherm to the west. This region is characterized by the influence of the cold and fresher shelf water.

Local eddies or meanders were found at Stations: 83 (ACC); 71, 93, 91, 13 (WSC), 61, 14 and 35 (Weddell), but only at station 71 reached the surface. The cluster constructed with the salinity and temperature parameters yielded four groups (Fig. 1):

Group 1: associated with the ACC in the Scotia Sea
Group 2: stations in the WSC,
Group 3: southern WSC including the Hesperides Trench
Group 4: Weddell Sea.

Distribution of larvae

Larvae of *E. superba, E. frigida* and *T. macrura* were present in the sampling; their relative densities and spatial distributions are presented in Fig. 3. *T. macrura* was the most abundant (87.2% of the total), with all larval stages present; larvae of *E. superba* (5.74%) were at calyptopes stages. Larvae of *E. frigida* (5.77% of the total calyptopes); where first calyptopes represented 86.26% of total larvae and the remaining early furciliae (Fig. 3).

Thysanoessa macrura was caught in all samples but one, with a mean density of 210 ind m^{-2} and mean densities of 36, 17 and 9 ind m^{-2} for first to third calyptopis and 39 and 107 ind m^{-2} for early and late furciliae. *E. superba* calyptopes, were present in 72% of the samples with a mean density of 14 ind m^{-2}. It was practically absent in the South Orkneys plateau and the South Shetlands. Most of the positive stations (62%) were in the WSC region (Fig. 3). *E. frigida* calyptopes were also present in 72% of the samples, showing a more northerly distribution with a mean density of 16 ind m^{-2}. The largest densities were in the NW Scotia Sea. It was not found in the South Orkneys plateau and the Hespérides Trench and only low densities were estimated from the Weddell Sea (Fig. 3).

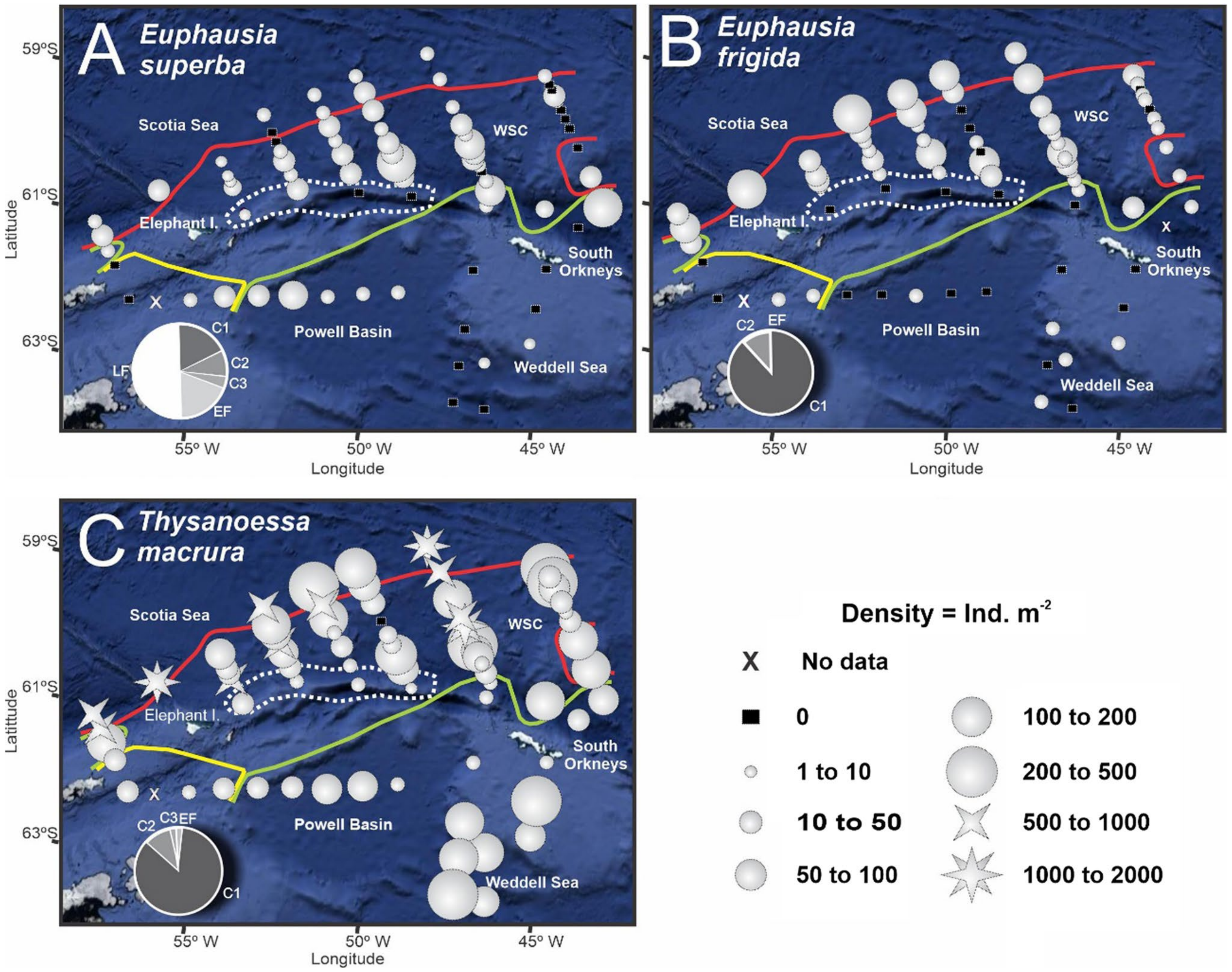

Fig. 3 Spatial distribution of *Euphausia frigida, E. superba*, and *Thysanoessa macrura* in the studied area during austral summer 2011. The proportions of larval stages of each species are included in the lower left corner

The log transformed densities of each combination of species and stages yielded the dendrogram shown in Fig. 4. Six groups were recognized:

Group 1: most of the larvae were *T. macrura* with relative densities below 1 ind m^{-2}, low densities of *E. frigida* and very low of *E. superba* were found.
Group 2: most of the stations lie in the WSC; *E. superba* was the dominant
Group 3: low densities of *T. macrura* and a few stations with relatively high densities of *E. superba* (above 1.5 ind m^{-2}), also in the WSC, Weddell Sea and South Shetland.
Group 4: 45% of the samples were in this group. The three species were present, reaching the highest relative densities; most of the stations were located in the WSC and the Scotia Sea
Group 5: only low densities of *T. macrura* with half of the stations from WSC waters
Group 6: very low densities of all species mainly from WSC waters

Each station pertains to one of the four groups obtained with the environmental data and to one of the six groups from the stages and species data and were identified as belonging to one of the four water masses, allowing to test their associations applying the G statistic. The association between cluster classifications was significant (*G-test* $G = 50.76$, $\upsilon = 15$, $p < 0.00001$). The stages and species groups were also significantly associated with the classification of the stations based on the water masses derived from the analysis of the stations profiles (*G-test*, $G = 35.69$, $\upsilon = 20$, $p < 0.002$).

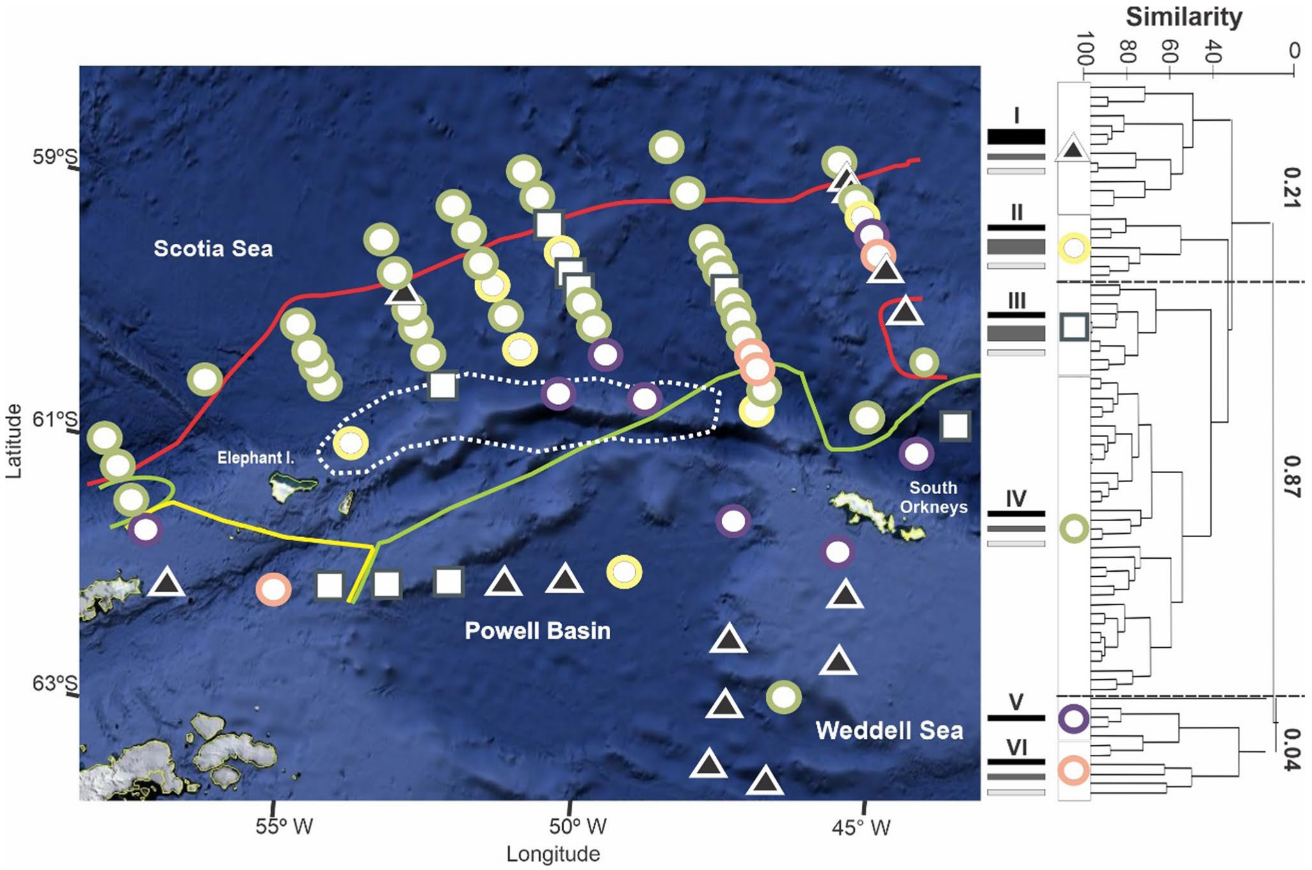

Fig. 4 Position of the stations and main oceanographic features in the Scotia Sea region during austral summer 2011. Cluster analysis based on euphausiid larvae log densities. Oceanographic features as in Fig. 1 Stations are colored according to cluster groups. The mean relative densities (ind m^{-2}) are indicated in each group. Black bars: *Thysanoessa macrura*; dark gray: *Euphausia superba;* light gray*: Euphausia frigida*; thickness proportional to the relative abundances within each group

Correspondence analysis conducted on the densities of the stages observed at each station resulted in three axes explaining 82.84% of the total variability (40%, 27% and 16% respectively). The first two axes are represented in Fig. 5 showing the positions of the larvae and the stations (indicated by their water mass). *E. superba* appeared associated with the WSC and Weddell Sea, *E. frigida* with the ACC and *T. macrura* more widely distributed.

The coordinates of the stations on the correspondence axes were tested for associations with the variables observed at each station. Stations were grouped by water mass and their correspondence coordinates on the first three axes tested by PERMANOVA (1000 permutations) finding that the coordinates on the three axes were significant ($\lambda_1 = 0.477$, $p = 0.0001$); $\lambda_2 = 0.876$, $p = 0.0025$): $\lambda_3 = 0.975$, $p = 0.0129$).Table 1 shows the means of the position of the water masses on the first three correspondence axes (Table 1a) and the Mahalanobis distances between them (Table 1b). Associated probabilities were obtained simultaneously with the PERMANOVA.

Discussion

Oceanographic setting

The freshening observed in waters of the WSC (Fig. 2), has been discussed by Dotto et al (2016). Based on hydrographic data from the period 1960–2010s, they showed freshening and lightening of the deep water masses at the western extreme of the WSC. This process is probably caused by large freshwater inputs originating from the western shelf of the Weddell Sea, where the basal melting of the Larsen Ice Shelves system at the eastern Antarctic Peninsula (Rignot et al. 2013) produced large freshwater inputs between 2003 and 2008.

Since the 1970s the westerly winds increased by 20% and the temperature of the ACC by 0.5 °C between 300 m to 1000 m (Turner et al. 2009), but the transport by the ACC has not augmented (Boning et al. 2008). The response to increased wind stress seems to be a change in

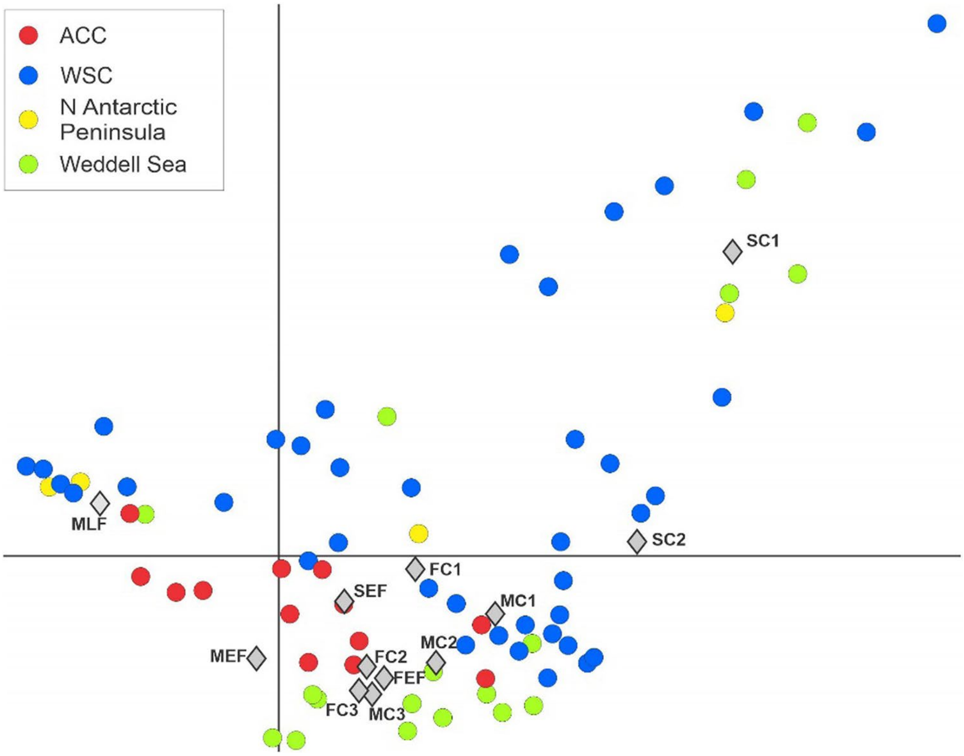

Fig. 5 Distribution of stations/water masses, species and stages on the first two correspondence axes obtained from the densities observed at each station in summer 2011. *SC1 Euphausia superba* calyptopis 1, *SC2 E. superba* calyptopis 2, *FC1 Euphausia frigida* calyptopis 1, *FC2 E. frigida* calyptopis 2, *FCIII E. frigida* calyptopis III, *FEF E. frigida* early furciliae, *MC1 Thysanoessa macrura* calyptopis 1, *MC2 T. macrura* calyptopis: 2, *MC3 T. macrura* calyptopis 3, *MEF T. macrura* early furciliae, *MLF T. macrura* late furciliae

Table 1 (**a**) Means $*10^4$ of the position of the water masses on the space of the first three correspondence axes derived from the densities of larvae and number of observations in each group. (**b**) *Mahalanobis distances* between the means of water masses in the upper half of the matrix; their probabilities in the lower (in bold those significant)

A	N	First axes	Second axes	Third axes	B	WSC	ACC	WS	MF
WSC	40	0.005	0.003	0.002	WSC	0	2.60	4.27	1.17
ACC	14	0.001	−0.002	−0.0001	ACC	**0.0002**	0	1.17	1.43
WS	18	0.005	−0.001	−0.003	WS	**0.0001**	**0.0358**	0	3.46
MF	4	0.001	0.004	−0.001	MF	0.2461	0.2298	**0.0164**	0

Probabilities calculated from 10,000 permutations (B). *WSC* Weddell-Scotia Confluence, *ACC* Antarctic Circumpolar Current, *WS* Weddell Sea, *MF* Mar de la Flota

eddy activity (Hallberg and Gnanadesikan 2006; Meredith and Hogg 2006).

While the position of frontal zones and the general disposition of water masses remained constant, these circulation changes might influence the reproductive processes of euphausiids (Siegel and Watkins 2016; Meyer et al. 2020).

Variability of Euphausiid larvae densities

A previous study (Rombolá et al. 2019) reported the high variability in the densities of euphausiid larvae in three recent cruises compared with historical results, discussing possible sources. This comparison of the densities obtained in 2011 with those from 1981 and 1995 demonstrate the increase in *T. macrura* and the reduction in *E. superba,* which was even less abundant than *E. frigida.* Similar changes in the predominant species were also observed by Panasiuk-Chodnicka at Admiralty Bay in the 2008–2009 season (SC-CAMLR XXXIII 2014; Annex 6 paragraph 6.8). Present analysis shows that, in 2011 the distributions of larvae were closely related with the water masses as demonstrated by the G tests applied to the clusters obtained with larval densities and properties of the water masses identified from CTD results. The same relations were observed in 1981 on a dataset obtained in a previous cruise in the same region (Marschoff 1985, 1996).

For comparison with present results, Fig. 6 shows the species-stage cluster of the log transformed densities of the 1981 dataset. The four groups derived from the larval

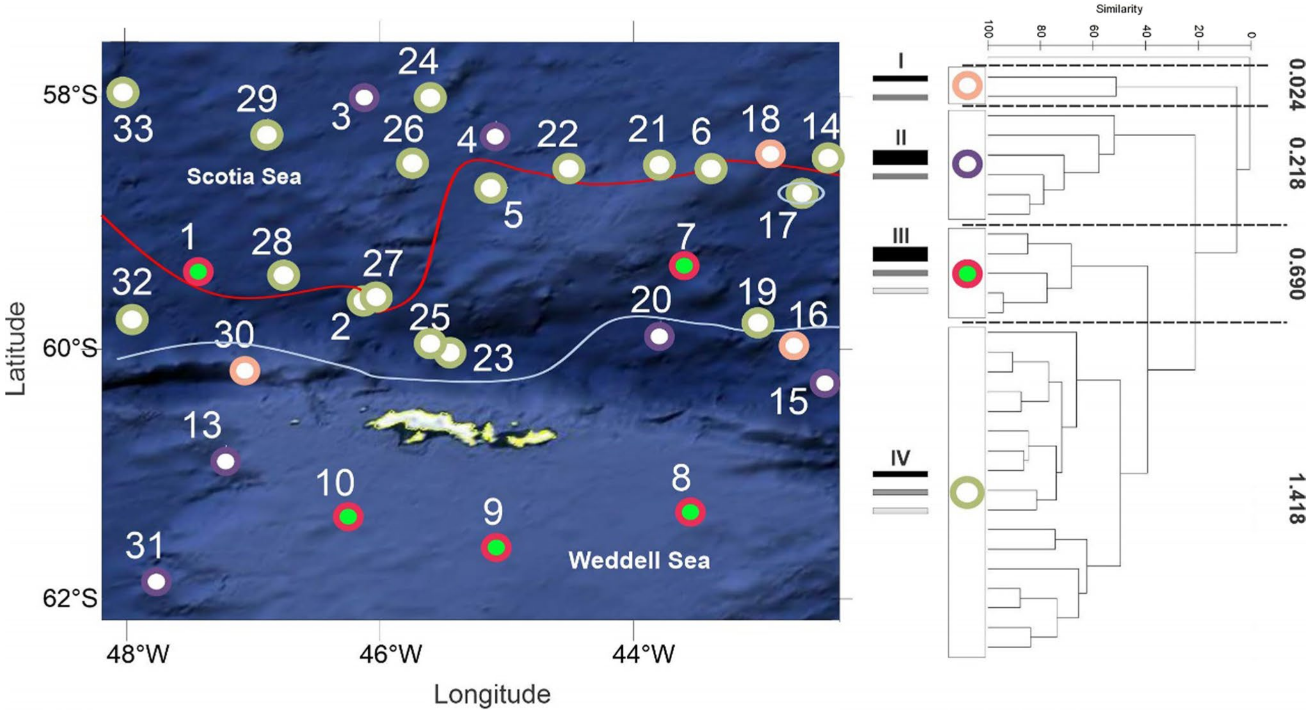

Fig. 6 Position of the stations and main oceanographic features in the Southern Scotia Sea region during austral summer 1981. Cluster analysis based on euphausiid larvae log densities. Cluster features as in Fig. 4

composition at each station also correspond to their position in relation with fronts.

The close relation of larval populations with the distribution of water masses is also demonstrated by the PERMANOVA analysis which was able to identify the stations belonging to different water masses from the larvae caught.

Both, in 2011 (Fig. 5) and 1981 (Marschoff 1996), the correspondence axes were related with the same characteristics of water and larval populations (salinity and age).

Thus, in spite of the large differences in densities, the distribution of the catches during the 2011 survey are associated with the distribution of water masses as observed in 1981.

In 2011 the most abundant euphausiid was *T. macrura,* the most ubiquitous species in the area (Makarov 1979b; Nordhausen 1992; Fisher et al. 2004). It was widely distributed, covering the largest area, including the Scotia Sea, the WSC and the Northern Weddell Sea, being more abundant in the ACC (Makarov 1979b; Hempel and Marschoff 1980; Hempel 1981; Nordhausen 1992; Haraldsson and Siegel 2014). Due to its early spawning *T. macrura* was found in all stages, up to late furciliae; and was recorded in virtually all stations, densities increased considerably in relation with the historic cruises analyzed. At a number of stations to the south of the South Orkney Islands, calyptopes densities were low with few early furciliae. Late furciliae were found in the ACC and in the WSC in high densities (more than 1000 ind m^{-2}).

Euphausia frigida is a typical species of the ACC, being more abundant in the Drake Passage to the north of the South Shetland Islands (John 1936; Makarov 1977; Loeb and Shulenberger 1987). Spawning is reported to begin in August, extending to April (Menshenina 1989). As in other studies, (Hempel and Marschoff 1980; Hempel 1981; Hempel and Hempel 1982; Makarov and Menshenina 1989; Fedotov 1992), CI dominated our sampling, with early furciliae present in a few samples. As described by Makarov et al. (1992), *E. frigida* larvae declined markedly to the south, in the easternmost part of the Weddell Gyre, but, even though in low quantities, it was found in the northern Weddell Sea (Hempel and Hempel 1982). The unusual finding of *E. frigida* south in the Weddell Sea (62.49 S; 45.99 W) on 15th January 2011, might be due to the meanders detected in the area.

Euphausia superba was abundant in the WSC (Hempel 1981; Hempel and Hempel 1982; Siegel 2000; Siegel et al. 2004, 2013; Gao et al. 2013; Loeb and Santora 2015). CI was the dominant stage in the WSC with increasing numbers toward the eastern Scotia Sea. In the present study, it was recorded in the western Weddell Sea, in agreement with the reported distribution summarized by Siegel and Watkins (2016), but not with their densities, as their review reported very high values such as 20 × 10^{3} ind m^{-2} in the western

Atlantic sector in 1981 in contrast with the very low density of 14 ind m^{-2} in this cruise. More recently, Gao et al. (2013) reported an average density of 1.173 ind m^{-2} of calyptopes with relative abundance of 99.81% east of Elephant Island.

Only few early furciliae of *E. superba* were found in the 2011 sampling, a result already reported for the area in January and early February (Hempel and Hempel 1978; Brinton and Towsend 1984; Hempel 1985a, b; Marschoff 1996; Siegel et al. 2013). North of the Antarctic Peninsula (the westernmost area surveyed in our cruise), Setubal Pires (1986) reported that in 1983 *E. superba* was present in 50% of the stations CI being the dominant stage with 21.83% of the total larvae at stations north of Elephant Island in contrast with 3.75% in the same area in the present study. These larvae are carried westwards by the ACC mixing with larvae from the WSC and Scotia Sea (Siegel and Watkins 2016).

In the comparison of their overall distributions among water masses in 1981 and 2011, Table 2 shows that, in both years, *E. superba* densities were similar in the ACC and in the WSC. *E. frigida* maintained their maximum densities in the ACC and *T. macrura,* evenly distributed in 1981 increased significantly in 2011.

In 2011 we found very low densities north of the Antarctic Peninsula; 33.54 ind m^{-2} to the east and the maximum density in the WSC (166 ind m^{-2} and relative abundance of 16.54%). Dietrich et al. 2014, also in January 2011 around Elephant Island, found 35% of the positive samples with *E. superba* calyptopes, and 17% with furciliae, while *T. macrura* was the most abundant, with 98% of occurrence in the positive stations. In a survey conducted in January 2011 in waters off the Western Antarctic Peninsula, Siegel et al. (2013) found a mean density of larvae in the northern stations of 15.2 ind m^{-2}, dominated by early calyptopes stages. Higher densities of CI were found far south in the area of the Bellingshausen gyre. This suggests that in the summer 2010–2011 *E. superba* larvae were not reaching the South Shetland Islands and the ACC.

Table 2 Means of the logarithm of the densities of euphausiid early larvae in the water masses in 2011 and 1981

Water masses	*N*	(Marschoff 1985)	*N*	(present study)
T. macrura				
WSC	13	8.52 (6.29)	40	7.78 (4.98)
ACC	8	6.24 (3.70)	14	20.01 (4.29)
WS	10	5.15 (4.41)	18	8.39 (5.01)
E. superba				
WSC	13	16.23 (8.07)	40	2.23 (1.70)
ACC	8	16.78 (11.44)	14	1.96 (1.20)
WS	10	7.6 (10.06)	18	1.26 (1.52)
E. frigida				
WSC	13	1.92 (2.06)	40	1.87 (1.51)
ACC	8	2.22 (2.43)	14	5.63 (3.16)
WS	10	0	18	0.65 (0.91)

Standard deviations in brackets. *ACC* Antarctic Circumpolar Current, *WSC* Weddell – Scotia Confluence, *WS* Weddel Sea, *N* number of samples

A possible explanation, largely speculative, is based on the mechanisms involved in the coupling of biological and oceanographic processes involved after spawning occurs.

Given the depths reached by the eggs of the euphausiid species, Marschoff (1996) proposed that, as the eggs and nauplii of *E. superba* hatch deeper than those of *T. macrura* and *E. frigida,* they will be more dependent on the development of divergences facilitating the developmental ascent process by the increase in vertical transport. Eggs of *T. macrura* and *E. frigida*, not reaching depths below 800 m, will not depend on vertical transport. This difference in the hatching depths implies that, *E. superba* will reach surface waters in one or both sides of the fronts, while *T. macrura* and *E. frigida* will be retained in eddies formed at the fronts.

The overall impact of climate change on *E. superba* was analyzed by Flores et al. (2012) and revised by Meyer et al. (2020), identifying the high priority to be given to research on the recruitment process to obtain a mechanistic understanding of the factors leading to successful spawning and survival of early larvae, in order to advice fisheries management on the benefits of incorporating uncertainty surrounding key aspects of krill ecology into management decisions (Meyer et al. 2020). There is strong evidence that krill is sensitive to climatic modes such as the SAM and the ENSO (Saba et al. 2014; Loeb and Santora 2015) and that climatic conditions in the SW Atlantic have become increasingly unfavorable for recruitment (Meyer et al. 2020).

Thus, the increase in *T. macrura* and *E. frigida* larvae and the reduction in *E. superba* observed in 2011 would be explained by a reduction in vertical transport resulting from increased stability of the water column and eddy activity resulting from these changes that might be attributed to climate change. On the other hand, the low densities observed in *E superba* larvae abundance in 2011 could be explained as the result of the dynamic equilibrium of many highly variable factors; as the larvae observed in a determined area is the result of the origin and history of the water masses rather than the direct result of actual hydrological characteristics (Marschoff 1996; Stupnikova et al. 2018), and no single environmental factor shows a predictable relationship with krill density (Weber et al. 1986; Rombolá et al. 2019).

Short term variability was observed by Brinton et al. (1986) who found average larval densities of 35 ind m^{-2} in the Scotia Sea during summer 1984. The CCAMLR 2000 survey yielded a mean density of larvae in the western Scotia Sea of 2044 ind m^{-2} (Siegel et al. 2004), and even higher densities were recorded during Fibex 1981 (Rakusa-Suszczewski 1984). We also have recorded higher densities than in 2011 in the 2014 season, but also a very poor summer in January 2012 (Rombolá et al. 2019). Discerning whether changes are due to long term phenomena or just the response to short term fluctuations in oceanographic conditions requires the of monitoring of early larvae populations and environmental variables during an extended period. In this study we present methods to observe the relation between the larval and the water masses distributions as a contribution to the interpretation of the time series required to identify changes due to short term variability against a background of large global processes such as those derived from climate change.

Further research is needed, obtaining oceanographic information specifically designed to study the processes associated with the developmental ascent of early larvae in order to elucidate possible causes of the observed variability.

Acknowledgements We wish to thank members of Puerto Deseado Oceanographic vessel and scientists from Instituto Antártico Argentino for their logistic help during the campaign. The financial support was partially covered by PICTO 118-2010 (Agencia Nacional de Promoción Científica y Tecnológica) and Instituto Antártico Argentino, the Dirección Nacional del Antártico provided the logistic support of the campaign. We wish to thank reviewer #3 M Hamame and the other anonymous referees for comments that greatly improved the paper.

Author contributions All authors made contributions to the present work. The conception of the study was designed by EM. Material preparation and data collection were performed by ER, EM, SV and CF. Data analysis were performed by EM and ER. Figures were designed by CF and VA; GT made de oceanographic analysis from the CTD data. Logistic support for the campaign by SV. ER and EM wrote the manuscript, which was revised by all authors. All authors read and approved the final manuscript.

Declarations

Conflict of interest The authors declare that no conflicts of interest exist. Procedures used in this study comply with the current laws for working in Antarctica. Permission to work was granted by the Environmental Management and Tourism Program of the Dirección Nacional del Antártico (DNA), Argentina.

References

Boning CW, Dispert A, Visbeck M, Rintoul SR, Schwarzkopf FU (2008) The response of the Antarctic Circumpolar Current to recent climate change. Nat Geosci 1:864–869. https://doi.org/10.1038/ngeo362

Brinton E, Towsend A (1984) Regional relationship between development and growth in larvae of Antarctic krill, *Euphausia superba*, from field samples. J Crustacean Biol 5:224–246

Brinton E, Huntley M, Townsend AW (1986) Larvae of *Euphausia superba* in the Scotia Sea and Bransfield Strait in March 1984 – development and abundance compared with 1981 larvae. Polar Biol 5:221–234

Clarke KR, Gorley RN (2015) PRIMER v7: user manual/tutorial. Plymouth: PRIMER-E. http://updates.primer-e.com/primer7/manuals/User_manual_v7a.pdf

Chapman CC, Lea MA, Meyer A, Sallée JB, Hindell M (2020) Defining Southern Ocean fronts and their influence on biological and physical processes in a changing climate. Nat Clim Change. https://doi.org/10.1038/s41558-020-0705-4

de Baker AC (1965) The latitudinal distribution of *Euphausia* species in the surface waters of the Indian ocean. Dis Rep 33:309–334

Deacon GER (1937) The hydrology of the southern ocean. Discovery Rep 15, Cambridge Univ. Press

Deacon GER (1979) The Weddell Gyre. Deep Sea Res 26:981–998

Dietrich K, Brooks C, Bystrom I, Driscoll R, Ferm N, Hinke J, Janssen M, Lombard D, Pesce A, Romain S,Thoresen L, van Cise A (2014) Distribution and catch rates of zooplankton around the South Shetland Islands, Antarctica. In: Walsh JG (ed) AMLR 2010–11 Field Season Report. NOAA-TM-NMFS-SWFSC-524: 18–27

Dotto TS, Kerr R, Mata MM, Garcia CAE (2016) Multidecadal freshening and lightening in the deep waters of the Bransfield Strait, Antarctica. J Geophys Res Oceans 121:1–16. https://doi.org/10.1002//2015JC011228

Fedotov AS (1992) Winter distribution of Euphausiid larvae in the Convergence Zone of the Antarctic Circumpolar Current and Weddell Sea Waters. Oceanology 32:191–196

Fisher EC, Kaufmann RS, Smith KL Jr (2004) Variability of epipelagic macrozooplankton/micronekton community structure in the NW Weddell Sea, Antarctica (1995–1996). Mar Biol 144:345–360. https://doi.org/10.1007/s00227-003-1177-6

Flores H, Atkinson A, Kawaguchi S, Krafft BA, Milinevsky G, Nicol S, Reiss C, Tarling GA, Werner R, Bravo Rebolledo E, Cirelli V, Cuzin-Roudy J, Fielding S, Groeneveld JJ, Haraldsson LA, Marschoff E, Meyer B, Pakhomov EA, Rombolá E, Schmidt K, Siegel V, Teschke M, Tonkes H, Toullec JY, Trathan PN, Tremblay N, Van de Putte AP, van Franeker JA, Werner T (2012) Impact of climate change on Antarctic krill. Mar Ecol Prog Ser 458:1–19. https://doi.org/10.3354/meps09831

Gao G, Xu Z, Huang H, Chen X, Feng Ch, Li L (2013) Geographical distribution and age composition of *Euphausia superba* larvae (Crustacea:Euphausiacea) in the South Shetland Islands region and southern Scotia Sea in relation to environmental conditions. Acta Oceanol Sin. https://doi.org/10.1007/s13131-013-0378-1

Gallotti DS (2013) Distribución de larvas de eufausiáceos en el extremo sur del Océano Atlántico. Tesis doctoral. Universidad de Buenos Aires 198 pp. http://digital.bl.fcen.uba.ar/download/tesis/tesis_n5390_Gallotti.pdf.

Hallberg R, Gnanadesikan A (2006) The role of Eddies in determining the structure and response of the wind-driven Southern Hemisphere overturning: results from the modeling Eddies in the Southern Ocean (MESO) project. J Phys Oceanogr. https://doi.org/10.1175/JPO2980.1

Haraldsson M, Siegel V (2014) Seasonal distribution and life history of *Thysanoessa macrura* (Euphausiacea Crustacea) in high latitude waters of the Lazarev Sea, Antarctica. Mar Ecol Prog Ser 495:105–118. https://doi.org/10.3354/meps10553

Hempel I, Hempel G (1978) Distribution of euphausiid larvae in the southern Weddell Sea. Meeresforsch 29:253–266

Hempel I, Marschoff E (1980) Euphausiid larvae in the Atlantic Sector of the Southern Ocean. Meeresforsch 28:32–47

Hempel I (1981) Euphausiid larvae in the Scotia Sea and adjacent waters in summer 1977/78. Meeresforch 29:53–59

Hempel I, Hempel G (1982) Distribution of euphausiid larvae in the southern Weddell Sea. Meeresforsch 29:253–266

Hempel I (1985a) Variation in Geographical Distribution and Abundance of Larvae of Antarctic Krill, *Euphausia superba*, in the Southern Atlantic Ocean. In: Condy PR, Laws RM, Siegfried WR (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, Heidelberg, pp 304–307

Hempel I (1985b) Vertical distribution of Larvae of Antarctic Krill, *Euphausia superba*. In: Condy PR, Laws RM, Siegfried WR (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, Heidelberg, pp 308–310

Heywood K, Naveira Garabato A, Stevens D, Muench M (2004) On the fate of the Antarctic Slope Front and the origin of the Weddell Front. J of Geophys Res 109(C06021):1–13. https://doi.org/10.1029/2003JC002053

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the World's. Marine Ecosyst Sci 328:1523–1528. https://doi.org/10.1126/science.1189930

Hofmann EE, Capella JE, Ross RM, Quetin LB (1992) Models of the early life history of *Euphausia superba*. Part I. Time and temperature dependence during the descent-ascent cycle. Deep Sea Res 39:1177–1200

Ikeda T (1984) Development of thelarvae of the Antarctic krill *(Euphausia superba* Dana) observed in the laboratory. J Exp Mar Biol Ecol 75:107–117

John DD (1936) The Southern species of the genus *Euphausia*. Discovery Rep 14:193–324

Lebart L, Morineau A, Fenelon JP (1979) Traitement des données statistiques. Dunod, Methodes et Programmes Paris, p 441

Loeb VJ, Shulenberger E (1987) Vertical Distributions and relations of euphausiid populations off Elephant Island, March 1984. Polar Biol 7:363–373

Loeb VJ, Hofmann EE, Klinck JM, Holm-Hansen O, White WB (2009) ENSO and variability of the Antarctic Peninsula pelagic marine ecosystem. Antarct Sci 21:135–148. https://doi.org/10.1017/S0954102008001636

Loeb V, Hofmann EE, Klinck JM, Holm-Hansen O (2010) Hydrographic control of the marine ecosystem in the South Shetland-Elephant Island and Bransfield Strait region. Deep Sea Res II:519–542. https://doi.org/10.1016/j.dsr2.2009.10.004

Loeb V, Santora J (2015) Climate variability and spatio temporal dynamics of five Southern Ocean krill species. Prog Oceanogr 134:93–122. https://doi.org/10.1016/j.pocean.2015.01.002

Mackintosh NA (1973) Distribution of post-larval krill in the Antarctic. Discovery Rep 36:95–156

Makarov RR (1977) Larvae distribution and some aspects of the ecology of *Euphausia frigida* (Crustacea, Euphausiacea)in the South Scotia region. Okeanologiya 17:324–334

Makarov RR (1979a) Estadios larvales tempranos de los eufausiáceos antárticos. Zool Zhur 58:314–327

Makarov RR (1979b) Larval distribution and reproductive ecology of *Thysanoessa macrura* (Crustacea: Euphausiacea) in the Scotia Sea. Mar Biol 52:377–386

Makarov RR, Maslennikov VV (1981) Ecology of larval development of the Crustacean *Euphausia superba*. Change in dominant larvae forms as a function of environmental conditions. Mar Ecol Prog Ser 4:265–271

Makarov RR, Menshenina LL (1989) On the distribution of Euphausiid larvae in Antarctic waters. Oceanology 29:623–627

Makarov RR, Menshenina LL, Solyankin YV (1992) Euphausiid larvae in the Eastern Zone of the Weddell Gyre. Oceanology 32:186–190

Marr JWS (1962) The natural history and geography of the Antarctic Krill *Euphausia superba*. Discovery Rep 32:33–464

Marschall S, Mizdalzki E (1985) Euphausiid larvae in plankton samples from the vicinity of the Antarctic Peninsula, february 1982. Ber Polarforsch 21, 47 pp

Marschoff ER (1985) Profile analysis of *Euphausia superba* larvae vertical distribution in the Scotia Sea, related to time factor. Polar Biol 5:35–41. https://doi.org/10.1007/BF00446043

Marschoff ER (1996) Estrategias reproductivas de las especies de eufausiáceos australes como mecanismo regulador de la distribución. Universidad de Buenos Aires, Tesis doctoral

Marschoff E, Calcagno J, Amieiro P (1998) Diel variation in catches of Euphausia superba Dana 1854 early larvae: vertical migration or avoidance reaction? J Exp Mar Biol Ecol 228:107–115. https://doi.org/10.1016/S0022-0981(98)00012-4

Menshenina LL (1989) Dates of spawning of Antarctic euphausiids. SC-CAMLR-VIII/BG 24

Meredith MP, Hogg AM (2006) Circumpolar response of Southern Ocean eddy activity to a change in the Southern Annular Mode. Geophys Res Lett 33:L16608. https://doi.org/10.1029/2006GL026499

Meredith M, Meijers A, Naveira Garabato A, Brown P, Venables H, Abrahamsen P, Jullion L, Messias MJ (2015) Circulation, retention, and mixing of waters within the Weddell-Scotia Confluence, Southern Ocean: the role of stratified Taylor columns. J Geophys Res Oceans. https://doi.org/10.1002/2014JC010462

Meyer B, Atkinson A, Bernard KS, Brierley AS, Driscoll R, Hill SL, Marschoff E, Maschette D, Perry FA, Reiss CS, Rombolá E, Tarling GA, Thorpe SE, Trathan PN, Zhu G, Kawaguchi S (2020) Successful ecosystem-based management of Antarctic krill should address uncertainties in krill recruitment, behaviour and ecological adaptation. Commun Earth Environ 1:28. https://doi.org/10.1038/s43247-020-00026-1

Morrison DF (1976) Multivariate statistical methods. Mc Graw Hill series in probability and statistics, Kogakusha, Tokyo, p 415

Motoda S (1959) Devices of simple plankton apparatus. Mem Fac Fish, Hokkaido Univ, 7: 73–94. http://hdl.handle.net/2115/21829. http://hdl.handle.net/2115/21829.

Nordhausen W (1992) Distribution and growth of larval and adult *Thysanoessa macrura* (Euphausiacea) in the Bransfield Strait region, Antarctica. Mar Ecol Prog Ser 83:185–196

Orsi AH, Whitworth T, Nowlin WD (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. Deep Sea Res I 42:641–673. https://doi.org/10.1016/0967-0637(95)00021-W

Patterson SL, Sievers HA (1980) The Weddell-Scotia Confluence. J of Phys Oceanog 10:1584–1610

Pertzova KN (1976) Larvae of Euphausiacea of the Antarctica Trudy. Inst Okeanol 105:147–170 (**in Russian**)

Ponomareva LA, Drobyisheva TV (1978) Euphausiids of the Australian-New Zealand region and nearby waters of Subantarctic. Akad Nauk SSSR 112:111–117 (**in Russian**)

Quetin LB, Ross RM (1984) Depth distribution of developing *Euphausia superba* embryos, predicted from sinking rates. Mar Biol 79:47–56

Quetin LB, Ross RM (1989) Effects of oxygen, temperature and age on the metabolic rate of the embryos and early larval stages of the Antarctic krill *Euphausia superba* Dana. J Exp Mar Biol Ecol 125:43–62

Rakusa-Suszczewski S (1984) Krill larvae in the Atlantic sector of the Southern Ocean during FIBEX 1981. Polar Biol 3:141–147

Rignot ES, Jacobs S, Mouginot J, Scheuchl B (2013) Ice-shelf melting around Antarctica. Science 341:266–270. https://doi.org/10.1126/science.123579

Rombolá EF, Franzosi CA, Tosonotto GV, Alder VA, Marschoff ER (2019) Variability of euphausiid larvae densities during summer seasons 2011, 2012 and 2014 in the Atlantic sector of the Antarctic. Polar Sci 19:86–93. https://doi.org/10.1016/j.polar.2018.11.004

Ross RM, Quetin LB, Kirsch E (1988) Effect of temperature on developmental times and survival of early larval stages of Euphausia superba Dana. J Exp Mar Biol Ecol 121:55–71

Saba GK, Fraser WR, Saba VS, Iannuzzi RA, Coleman KE, Doney SC, Ducklow HW, Martinson DG, Miles TN, Patterson-Fraser DL, Stammerjohn SH, Steinberg DK, Schofield OM (2014) Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. Nat Commun 5:4318. https://doi.org/10.1038/ncomms5318

SC-CAMLR (2014) Report of the working group on ecosystem monitoring and management. In: Report of the Thirty-three Meeting of the Scientific Committee (SC-CAMLR-XXXVI), Annex 6. CCAMLR, Hobart, Australia.

Setubal Pires AM (1986) Vertical distribution of Euphausiid Larvae (Crustacea) in the Brandfield Strait during the first Brazilian Antarctic Expedition (Summer 1982/83). An Acad Brasil Cienc 58:43–51

Siegel V (2000) Krill (Euphausiacea) life history and aspects of population dynamics. Can J Fish Aquat Sci 57:130–150. https://doi.org/10.1139/f00-183

Siegel V, Kawaguchi S, Ward P, Litvinov F, Sushin V, Loeb V, Watkins J (2004) Krill demography and large-scale distribution in the southwest Atlantic during January/February 2000. Deep Sea Res II 51:1253–1273. https://doi.org/10.1016/j.dsr2.2004.06.013

Siegel V, Reiss CS, Dietrich KS, Haraldsson M, Rohardt G (2013) Distribution and abundance of Antarctic krill (*Euphausia superba*) along the Antarctic Peninsula. Deep Sea Res I:63–74. https://doi.org/10.1016/j.dsr.2013.02.005

Siegel V, Watkins JL (2016) Distribution biomass and demography of Antarctic krill Euphausia superba. In: Siegel V (ed) Biology and Ecology of Antarctic Krill. Springer, Cham

Stupnikova AN, Tarakanov RY, Kulagin DN, Vereshchaka AL (2018) Factors maintaining the identity of mesoplankton communities: cool evidence from the Drake Passage. Hydrobiologia 809:221–232. https://doi.org/10.1007/s10750-017-3474-y

Tattersall WM (1924) Crustacea VIII: Euphausiacea. British Antarctic (Terra Nova) Expedition 1910. Nat Hist Rep Zoology 1:1–36

Thompson AF, Youngs MK (2013) Surface exchange between the Weddell and Scotia Seas. Geophys Res Lett 40:5990–5995. https://doi.org/10.1002/2013GL058114

Tranter DJ (1968) Smaller meso zooplankton. Report of Working Party N 2. In: Standarization of zooplankton sampling methods at sea. Zooplankton Sampling, Unesco

Tynan CT (1998) Ecological importance of the Southern Boundary of the Antarctic Circumpolar Current. Nature 392:708–710

Turner J, Bindschadler RA, Convey P, Di Prisco G, Fahrbach E, Gutt J, Hodgson DA, Mayewski PA, Summerhayes CP (2009) Antarctic climate change and the environment. SCAR, Cambridge, UK

Whitworth T III, Nowlin WD Jr, Orsi AH, Locarnini RA, Smith SG (1994) Weddell Sea shelf water in the Bransfield Strait and Weddell-Scotia Confluence. Deep Sea Res I 41:629–641

Venables H, Meredith M, Atkinson A, Ward P (2012) Fronts and Habitat zones in the Scotia Sea. Deep Sea Res II 59–60:14–24. https://doi.org/10.1016/j.dsr2.2011.08.012

Weber LH, El-Sayed SZ, Hampton I (1986) The variance spectra of phytoplankton, krill and water temperature in the Antarctic Ocean south of Africa. Deep Sea Res 33:1327–1343

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.