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## Morphological and biochemical differentiation in Antarctic krill

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### ABSTRACT

During the February 1981 cruise FIBEX MD-25 between 30–50°E and 61–64°S, hydrography showed the presence of two gyres, confirmed by the geostrophic circulation relative to 1000 m from Levitus climatology, at the borders of these gyres concentrations of highly morphologically differentiated krill were found. Gaussian component analysis of krill samples, pooled by sectors, showed three cohorts of *Euphausia superba* in the western sector and one in the eastern sector. Across the sampling area, *Thysanoessa macrura* and *E. superba* occurred at separate stations. Analysis of cohorts in *T. macrura* separated two size groups in both the western and the eastern sectors. The use of a Differentiation Index (D.I.) [Färber-Lorda, J., 1990. Somatic length relationships and ontogenetic morphometric differentiation of *Euphausia superba* and *Thysanoessa macrura* of the southwest Indian Ocean during summer (February 1981). *Deep-Sea Res.* 37, 1135–1143.], based on somatic lengths, allows studying certain morphological differences within the populations sampled. Morphologically different and bigger males II (D.I. from 2.8 to 3.5) were present only in the southern transect while smaller males I (D.I. from 3.5 to 5.0) were present over the entire area. Biochemical composition of both species showed significant differences among stations for protein, lipids, and carbohydrates. A significant difference in lipid content was found between males I, and males II. For *T. macrura*, percentage of lipid content in mature animals was much higher than that in *E. superba*. The D.I. size distribution showed that when populations of *E. superba* were highly differentiated (corresponding to mature animals) in morphology, lipid content was high, and they were located near a gyre. Differences in morphometry can influence distribution of the species, because different developing stages have different swimming capacities. It is shown that, together with hydrography and trophic conditions, lipid content and morphometry of krill populations, are different but complementary aspects that help to understand krill ecology and distribution.

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### 1. Introduction

Antarctic krill distribution and abundance have been examined by analysis of length–frequency histograms and related to hydrography (Kock and Stein, 1978; Fevolden, 1979; Rakusa-Suszczewski and Stepnik, 1980; Brinton, 1985; Siegel, 1986, 1989; Brinton, 1991). Many papers have been dedicated to this subject and many hypothesis and facts presented, but the way hydrographic or trophic conditions control krill distributions still remain vague. *Euphausia superba*'s adaptability and constant swimming activity (Kils, 1981) aggravate this problem. Nevertheless, some papers have shown that krill distribution and swarming are controlled mostly by hydrographic characteristics and currents (Kock and Stein, 1978; Makarov, 1979; Nasu, 1983; Brinton, 1985; Pakhomov, 2000).

In population studies, the approach commonly utilized is size–class composition analysis, in which histograms show different cohorts or clustered cohorts. However, changing hydrographic or trophic condi-

tions can induce substantial size differences, and given the fact that crustaceans do not have permanent calcified elements (like otoliths in fish), there is presently no reliable method to evaluate age in crustaceans. Ikeda and Dixon (1982) showed that *E. superba* in aquaria shrink in size during fasting, as a survival strategy, thus further complicating population studies in this species.

*Thysanoessa macrura* has rarely been studied; exceptions include larval ecology in the Scotia Sea (Makarov, 1979), and summer and winter distributions (Nordhausen, 1992, 1994). Mayzaud et al. (1985) studied biochemical adaptations in both *E. superba* and *T. macrura*, during the cruise reported here, and concluded that *T. macrura* is omnivorous but with a less diversified diet than that of *E. superba*; biochemical composition was studied by dry weight but no relation was established with local hydrography or animal morphometrics. Clarke (1980, 1985) studied biochemical composition of *E. superba* and found that females loose up to 60% of their lipids during spawning. These papers examined biochemical changes related to maturity, or time of the year. Pond et al. (1995) found variability in lipid content in a spatial study near South Georgia, and site-to-site variability in total lipid and lipid composition that could not be attributed to either size or sex ratio. Mayzaud et al. (1998) studied

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lipids and lipid classes from the same survey in the southern Indian sector of the Antarctic Ocean as the present study, and related that to location, sex, and distribution among organs; stations were grouped according to the different lipid descriptors considered; no relation with trophic descriptors was found.

Färber-Lorda (1986, 1990) demonstrated morphological differentiation in *E. superba* and *T. macrura* in relation to maturity. In *E. superba* a significant difference was found in the slope of the total length versus carapace length among males I, males II, gravid females, spent females, and juveniles. For *T. macrura* for the same allometric relationships significant differences were found between males, females, and juveniles, and between juveniles and adults. A Differentiation Index (D.I.) was proposed, with the purpose of obtaining more accurate information on the age- or stage-composition of the populations sampled, but used only in *E. superba*. Miller (1983) also found a difference in the slope of the regression of total length versus carapace length between males and females. Endo (1989) found allometric differences between males III B and males II A3, showing a shorter carapace in males III B and longer exopodites of thoracic legs and pleopods as well as bigger eyes. Färber-Lorda (1991) performed a multivariate analysis of this species, including morphometric parameters, lipids, and pigment data; he showed sex and development stage related changes, linked to age, and related to factors other than size. Males were grouped as males I and males II, the latter having lower lipid content, a shorter cephalotorax, and a lower D.I. value. The results published by Virtue et al. (1996) showing lower lipid content in mature males agree with Färber-Lorda (1991) in explaining the differences. Virtue et al. (1996) also found high mortality of mature males, and a very low lipid and reserve lipid concentration in IIIB males. They also found a progressive reduction in abundance of reproductive males during seven consecutive Antarctic summers. They hypothesized that a reduced population size is a mechanism that this species employs to survive the Antarctic's winter poor trophic conditions.

### 1.1. Hypothesis

Here, population structure and morphological differences are analyzed, utilizing the Differentiation Index, in an attempt to understand adaptations of the species to hydrographic and trophic conditions in the southwestern sector of the Indian Ocean (see Fig. 1). The working hypothesis is that morphological differences should have a consequence in the distribution of the species, since

krill's different development stages should have different swimming capacities, thus, a spatial study of the D.I. distribution per station, and in relation to hydrography and trophic conditions is necessary to understand their distribution.

Biochemical composition data are presented to help interpret the physiological implications of population structure, and its relation to the species distribution, and the possible consequences of morphometric differences in the distribution and biochemical composition of the species. This seldom-studied region is located in the eastern limit of the Weddell Drift, along the Antarctic Divergence (Simon, 1983, 1986).

## 2. Material and methods

Samples were obtained during the MD 25/FIBEX oceanographic cruise from February 13 to 24, 1981 (Antarctic summer) as part of the BIOMASS program on board of the R.V. Marion Dufresne. Depth of krill location was determined by echo-sounding, and echo-integration was performed during the entire cruise to determine krill biomass in the area. Tows were performed with a RMT net with 5 mm mesh in the net and 2 mm in the cod end. Samples were preserved by freezing at  $-70^{\circ}\text{C}$  (Färber-Lorda, 1990). Stations sampled are shown in Fig. 1. A random sub-samples (according to the size of the catch, between 40 and 110 individuals by station) of the total sample was used for this work, station 1 was not analyzed.

Measurements were: Total Length: from the eyestalk to end of sixth abdominal segment; carapace length: from eyestalk to posterior end of carapace; and Abdominal Length: the difference between total length and carapace length. *N* values for each station do not reflect natural abundance, but are the number of individuals measured per station or sector. Total lengths were obtained by transformation of the initial measurement to the reference measurement (Färber-Lorda, 1986) recommended by the BIOMASS Handbook No. 4, (from the eyestalk to the end of the uropod, setae not included) (Mauchline, 1980). Sex determination was made according to Färber-Lorda (1991) on thawing animals.

Frequency diagrams were plotted for each station and for two discrete hydrographic areas. The Bhattacharya's (1967) method and the DILOG program (Reys, pers. comm.) were used to discriminate plurimodal distributions. In this method, the difference between the logarithm of the frequency of one size class, and the logarithm of the frequency of the next size class (*Y*) is plotted against the greater size class (*X*), lines are traced between succeeding points. Lines traced

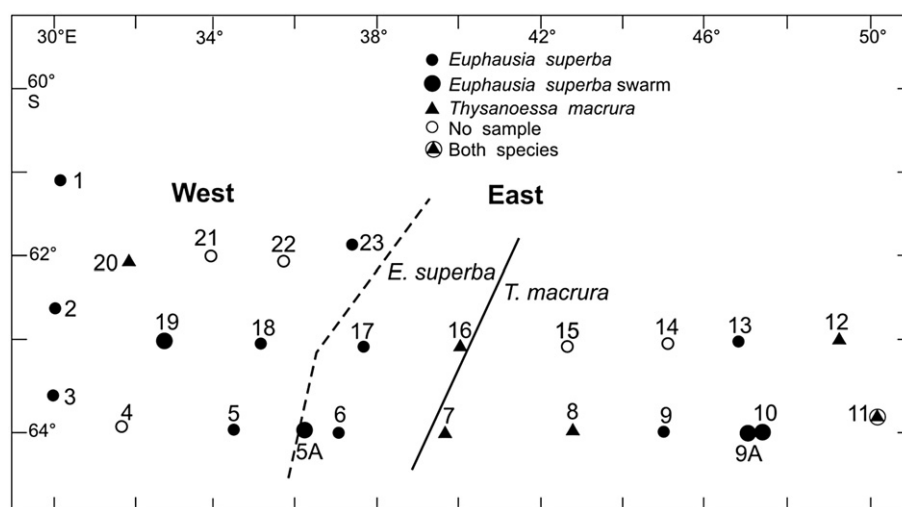


Fig. 1. Stations sampled during the cruise, with their position. The west and east sectors are indicated. Note the different classifications for both species.

with an angle greater than 90° to the X-axis, define a mode or cohort. Morphological differences between stations were assessed using the Differentiation Index (D.I.), which provides a measure of morphological differentiation among the animals, (Färber-Lorda, 1990), as follows:

$$D.I. = \frac{TL}{(AL - CL)}$$

where, D.I. is the Differentiation Index, TL is the Total Length, and AL is the Abdominal Length.

A small D.I. (2.8–3.5) is considered as males II (Färber-Lorda, 1986, 1990, 1991), as these males have a shorter carapace than males I (D.I. from 3.5 to ~5.0). Females have the highest D.I. (~5.0 to 8.3) and juveniles have an intermediate value. Färber-Lorda (1991) used this index and other allometric variables to establish age by multivariate analysis. For *E. superba* the frequency diagram was plotted for each station.

Biochemical composition was performed on the animals measured, as described by Mayzaud et al. (1985), and Färber-Lorda (1986, 1991). The wet weight for each animal was obtained from the length–weight relationships, calculated for each station (Färber-Lorda, 1994). For lipids, the wet weight was obtained in an analytical balance (Färber-Lorda, 1991). Biochemical analyses and measurements were performed within one year after the samples were obtained. Chitin was analyzed as described in Färber-Lorda (1986). From the protein extract, samples were submitted to alkaline hydrolysis in NaOH 1 N at 100 °C for 6 h. They were subsequently filtered on pre-weighed FGC filters, washed with distilled water and acetone for delipidation and dried at 60 °C until constant weight was obtained; chitin values were obtained by change in weight. Water content was obtained by heating thawed animals at 50 °C for 72 h; calculating weight difference. Ash was obtained from weight difference after burning at 450 °C for 12 h.

ANOVA and Kruskal–Wallis analyses were performed on the data with an alpha = 0.05.

Hydrographic data were obtained from the Museum National d'Histoire Naturelle (Gamberoni et al., 1981), and from Simon (1983). Chlorophyll a data for each station were obtained from G. Jacques (Banyuls, France). Chlorophyll determinations were performed at six depth levels within the euphotic zone. Lipid data were plotted over density (sigma-t) profiles to examine the relation between hydrography and the physiological condition of the animals of both species.

### 2.1. Geostrophic velocity

Before the geostrophic velocity calculation, the observed temperature and salinity were objectively mapped to remove small-scale variability. A standard objective-mapping interpolation was used with a classical Gaussian correlation function with relative errors of 0.1, and 1.0° for the horizontal length scale. The surface pattern of geostrophic circulation was obtained by standard geostrophic analysis (e.g. Pond and Pickard, 1983), and relative to a level of no motion of 1000 m. In order to extrapolate the observed circulation pattern we used the hydrographic climatology of Levitus for February obtained from NOAA-NESDIS–National Oceanographic Data Center (<http://www.nodc.noaa.gov/OC5/WOAO1>), and used a similar geostrophic calculation described above. As Levitus data have a 1/4° of horizontal resolution, we calculated the geostrophic velocities directly from the original temperature and salinity fields, using the same reference level.

## 3. Results

### 3.1. Hydrography and chlorophyll

Temperature at 50 m (Fig. 2a) data shows alternating plumes of water with temperatures above and below zero at ~80 mile intervals

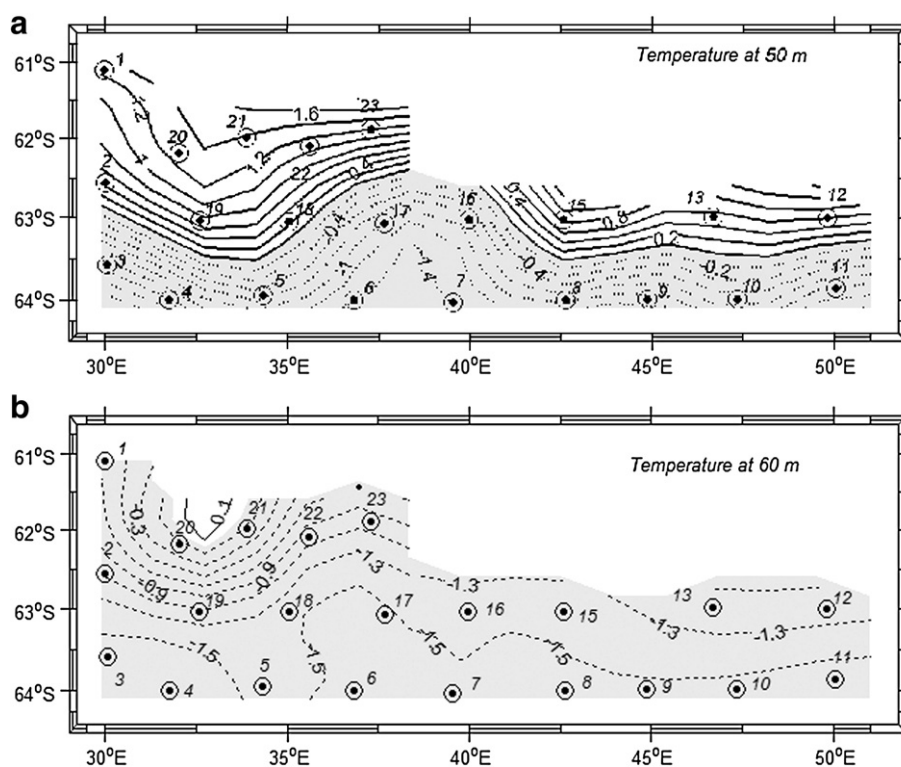


Fig. 2. a) Isotherms at 50 m for the FIBEX MD 25 cruise. Broken lines represent below zero temperatures. b) Isotherms at 60 m for FIBEX MD 25 cruise.

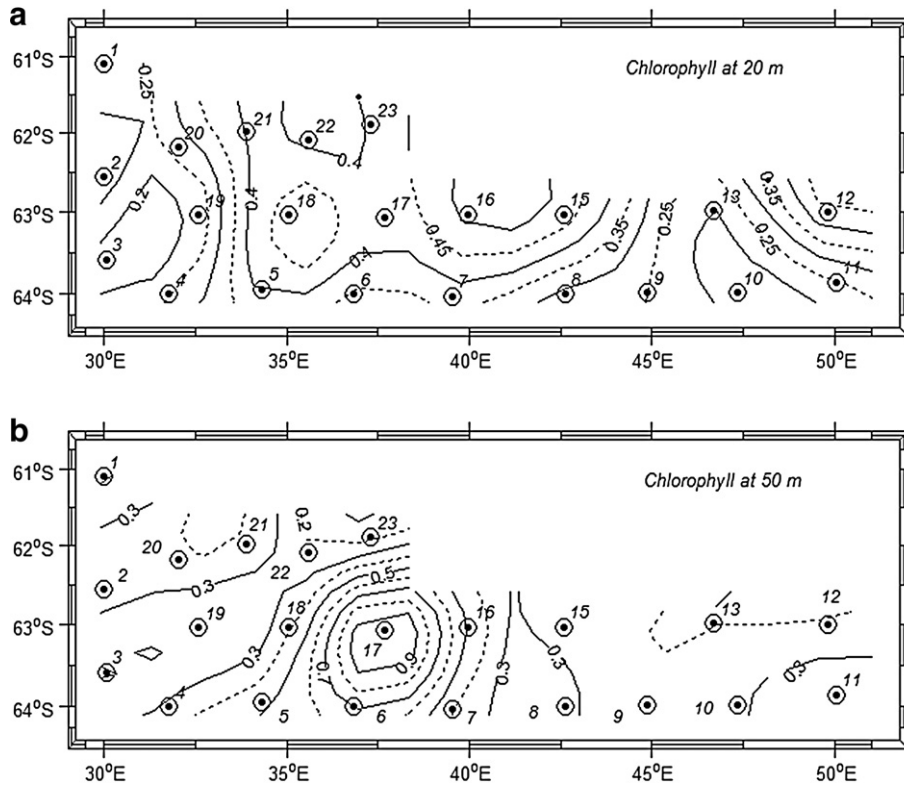


Fig. 3. a) Chlorophyll isopleths at 20 m depth. b) Chlorophyll isopleths at 50 m depth.

along the southernmost east–west transect suggesting the presence of two gyres one in the east and one in the west. One of the colder plumes encompassed the 63°S transect and was evident at 60 m

(Fig. 2b). Chlorophyll at 20 and 50 m showed its highest values around stations 17 and 18 (Fig. 3a and b), and higher values in both eastern and western gyres, being higher in the western one.

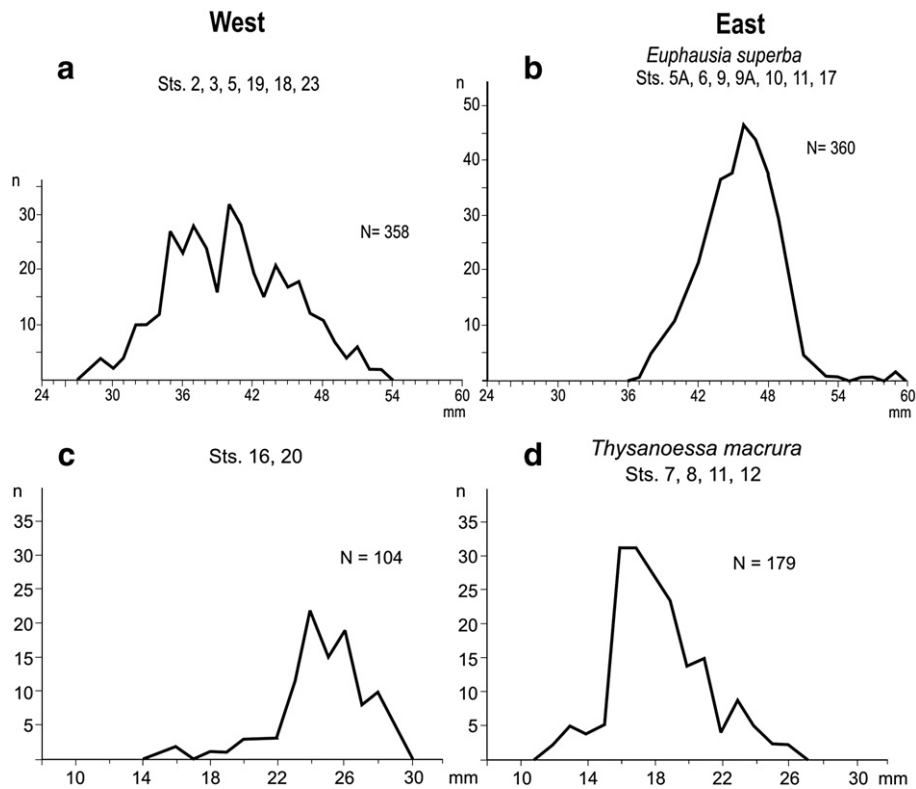


Fig. 4. a), b). Class size distribution of *Euphausia superba* by sector. c), d). Class size distribution of *Thysanoessa macrura* by sector.

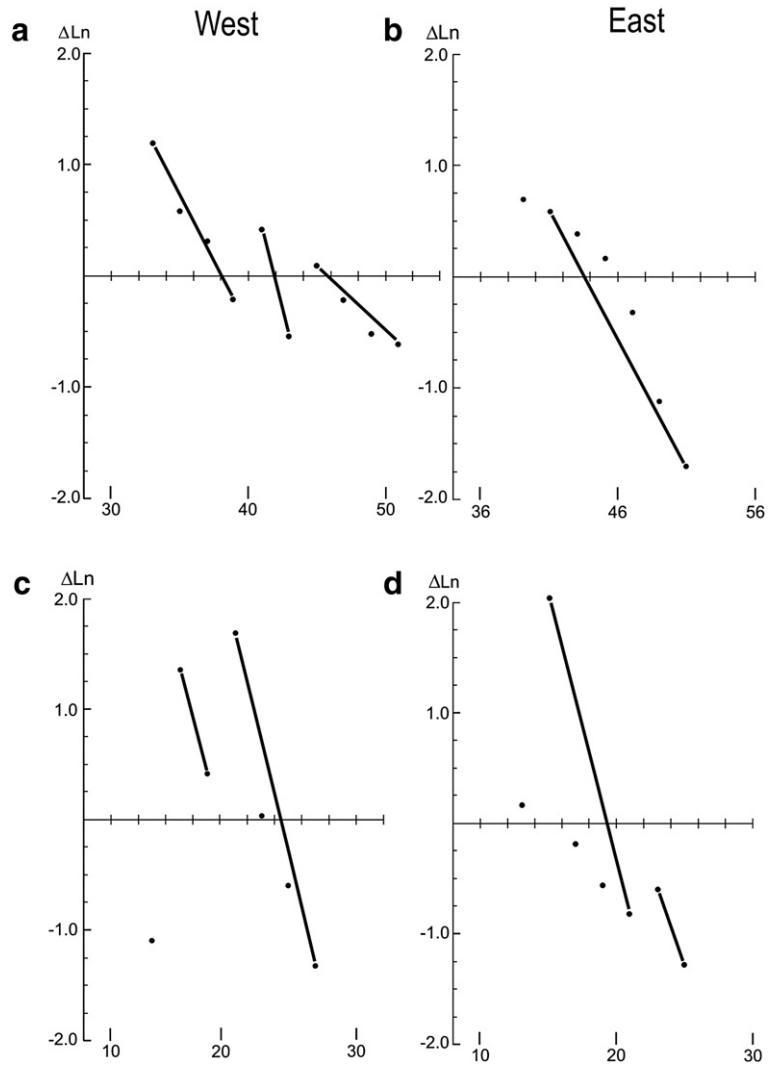


Fig. 5. a) Bhattacharya's (1967) test for the eastern populations of *Euphausia superba*. b) Bhattacharya's (1967) test for the western populations of *Euphausia superba*. c) Bhattacharya's (1967) test for the eastern populations of *Thysanoessa macrura*. d) Bhattacharya's (1967) test for the western populations of *Thysanoessa macrura*.

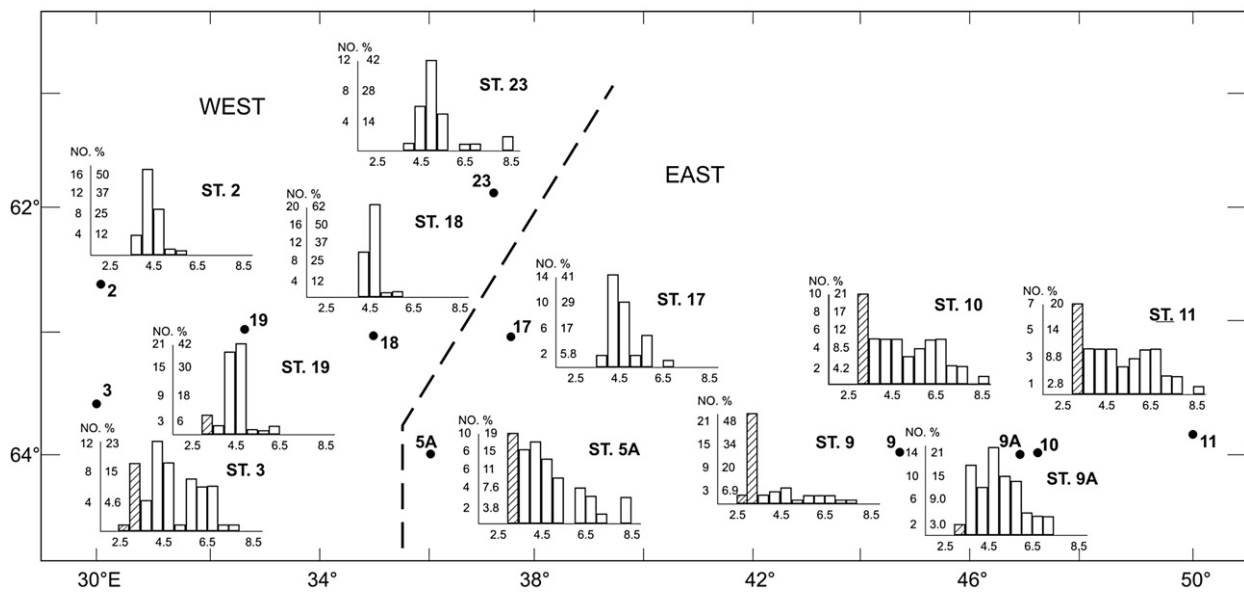


Fig. 6. Differentiation Index (D.I.) histograms for *Euphausia superba*'s sampled populations. Shaded histograms correspond to males II individuals, dots show the geographic position of the stations.

**Table 1**  
Biochemical composition of *E. superba* (% of wet weight  $\pm$  variance, *n* in brackets).

Station	Water	Proteins	Lipids	Carbohydrates	Ash	Chitin	Total
2	77.96 $\pm$ 1.13 (5)	12.78 $\pm$ 2.25 (11)	3.09 $\pm$ 0.41 (10) (267–594 mg)	0.32 $\pm$ 0.03 (10)	2.87 $\pm$ 0.08 (3)	0.85 $\pm$ 0.08 (5)	97.87
3	80.97 $\pm$ 0.16 (10)	12.81 $\pm$ 3.52 (10)	3.44 $\pm$ 1.45 (10) (339–1248 mg)	0.47 $\pm$ 0.10 (10)	2.76 $\pm$ 0.17 (3)	0.66 $\pm$ 0.10 (4)	101.11
5	–	13.14 $\pm$ 3.11 (8)	2.49 $\pm$ 0.76 (5) (274–888 mg)	0.58 $\pm$ 0.12 (5)	–	0.79 $\pm$ 0.18 (5)	–
5A	77.78 $\pm$ 1.38 (15)	13.13 $\pm$ 2.88 (15)	2.15 $\pm$ 0.50 (13) (357–955 mg)	0.43 $\pm$ 0.14 (10)	3.25 $\pm$ 0.22 (3)	0.82 $\pm$ 0.17 (9)	97.56
6	–	13.77 $\pm$ 2.14 (5)	1.48 $\pm$ 0.60 (5) (612–967 mg)	0.53 $\pm$ 0.17 (5)	–	0.83 $\pm$ 0.17 (5)	–
9	80.45 $\pm$ 2.42 (5)	13.66 $\pm$ 4.47 (14)	2.15 $\pm$ 0.70 (10) (589–1072 mg)	0.44 $\pm$ 0.04 (10)	2.76 $\pm$ 0.38 (5)	0.88 $\pm$ 0.12 (8)	100.34
9A	80.39 $\pm$ 2.21 (7)	11.90 $\pm$ 2.26 (10)	3.44 $\pm$ 1.45 (10) (525–964 mg)	0.37 $\pm$ 0.06 (10)	2.93 $\pm$ 0.31 (7)	1.60 $\pm$ 0.31 (5)	100.63
10	78.35 $\pm$ 1.61 (6)	12.90 $\pm$ 3.28 (10)	3.24 $\pm$ 0.90 (10) (628–1834 mg)	0.44 $\pm$ 0.07 (10)	2.99 $\pm$ 0.17 (5)	0.95 $\pm$ 0.11 (7)	98.87
11	79.91 $\pm$ 1.72 (5)	12.79 $\pm$ 3.50 (10)	2.01 $\pm$ 0.51 (10) (494–1278 mg)	0.50 $\pm$ 0.05 (10)	3.03 $\pm$ 0.19 (5)	1.13 $\pm$ 0.26 (7)	99.37
17	73.53 $\pm$ 1.91 (15)	14.84 $\pm$ 1.83 (16)	3.41 $\pm$ 2.13 (15) (685–1210 mg)	0.34 $\pm$ 0.06 (10)	2.83 $\pm$ 0.42 (5)	1.21 $\pm$ 0.26 (7)	96.16
18	79.99 $\pm$ 0.99 (15)	14.38 $\pm$ 1.47 (16)	2.85 $\pm$ 0.84 (13) (171–449 mg)	0.44 $\pm$ 0.09 (9)	2.46 $\pm$ 0.46 (6)	1.25 $\pm$ 0.46 (6)	101.37
19	75.24 $\pm$ 1.34 (15)	12.71 $\pm$ 1.91 (38)	3.66 $\pm$ 1.06 (36) (250–994 mg)	0.38 $\pm$ 0.06 (10)	3.42 $\pm$ 0.41 (16)	1.32 $\pm$ 0.44 (7)	96.73
23	77.13 $\pm$ 5.96 (15)	13.52 $\pm$ 5.44 (14)	2.73 $\pm$ 1.39 (14) (155–645 mg)	0.33 $\pm$ 0.06 (10)	3.31 $\pm$ 0.48 (5)	0.96 $\pm$ 0.39 (8)	97.98

In brackets the range of wet weights of the animals utilized for lipids.

### 3.2. Euphausiid distribution

#### 3.2.1. *E. superba*

Caught at 13 of 23 stations, catches from swarms were obtained at stations 5A, 9A, 10 and 19. Stations were divided into eastern (5A, 6, 9, 9A, 10, 11, 17) and western (2, 3, 5, 18, 19, 23) sectors, according to the size classes found, and the hydrography of the area. Fig. 4a and b shows the size-class distribution for these two areas. In the western sector, the peak at ~44–46 mm nearly coincided with the peak of the eastern sector. It is noteworthy that in the eastern sector, only a very small proportion of the large (>54 mm) animals were found, and all were females; the biggest male measured 52 mm.

The sex ratio was highly variable among stations. Subadults and juveniles dominated western stations, and in some cases there were only juveniles (e.g., 2 and 18). At stations 5A, 9 and 11, males (both I and II) made up most of the sample. A majority of individuals showing a regression of external sexual characteristics was seen at station 17.

#### 3.2.2. *T. macrura*

Apparently, the distribution of *T. macrura* was opposite to that of *E. superba*. It was found at only six stations (Fig. 1). A catch on a small swarm was obtained only at station 8. At the eastern sector Sts. 7, 8, 11, and 12 (Fig. 4c, d), subadults and juveniles were largely dominant, (peaks at 17 and 18 mm). The western sector showed peaks at 24 and 26 mm. The first group was comprised of subadults, and the second of adults. Bigger individuals were present at station 16, with a peak between 23 and 26 mm, and a small proportion of subadults and juveniles. Both species were caught in the same trawl only at St. 11. Mature adult females dominated station 20. When the stations were plotted as east or west sectors, (Fig. 4c, d), the separation into two groups was less clear. In the eastern sector, a large peak was found at 15 mm, and a smaller one at 23 mm. In the western sector, most animals were adults (peaks at 24 and 26 mm), and females, with a few small animals (15–20 mm).

### 3.3. Bhattacharya's test

In order to separate different cohorts, Bhattacharya's (1967) test was used to discriminate plurimodal distributions. Fig. 5a shows that

for *E. superba*, the eastern sector had only one cohort, indicating a uniform population. On the other hand the western sector had three predominant cohorts (Fig. 5b). For *T. macrura* we found two cohorts for both sectors (Fig. 5c and d). Even if this method is considered as somewhat subjective, it appears that cohort mixing had occurred mostly in the western sector.

### 3.4. Differentiation Index

We did not analyze the D.I. in *T. macrura* because it is correlated with size (Färber-Lorda, 1986, 1990). However, for *E. superba*, most males II (with small D.I.) were present in the most southern transect (Fig. 6). Only few animals with small D.I. (8% at St. 19) were found in the other transects, near a cold water plume that extended into the 63°S transect. At station 9 the D.I. size-class distribution showed that males II were dominant, indicating a mature population. At station 11 females showed the highest D.I., and most had an empty spermatophore still attached.

### 3.5. Biochemical composition

Each species is described separately. All biochemistry data were arc sin transformed.

#### 3.5.1. *E. superba*

The biochemical composition per station is given in Table 1. We analyzed between 5 and 36 individuals per station for proteins and carbohydrates. In general, lipids showed low and variable mean values, from 1.48 (ST. 6) to 3.66% (ST. 19) on wet weight basis. Much variability occurred within stations, with variances between 13.26 and 62.46% of the station's mean. A significant difference was found among the stations sampled for lipids ( $H_{16}^2 = 47.3$ ,  $P < 0.01$ ). Proteins were also variable within stations, though less so than lipids, from 10.22 to 40.24%

**Table 2**  
Lipid content of males of *E. superba* (% of wet weight  $\pm$  variance).

Males I	2.29 $\pm$ 0.75 (29) (515–1023 mg, range of wet weight)
Males II	1.56 $\pm$ 0.42 (14) (636–1247 mg, range of wet weight)

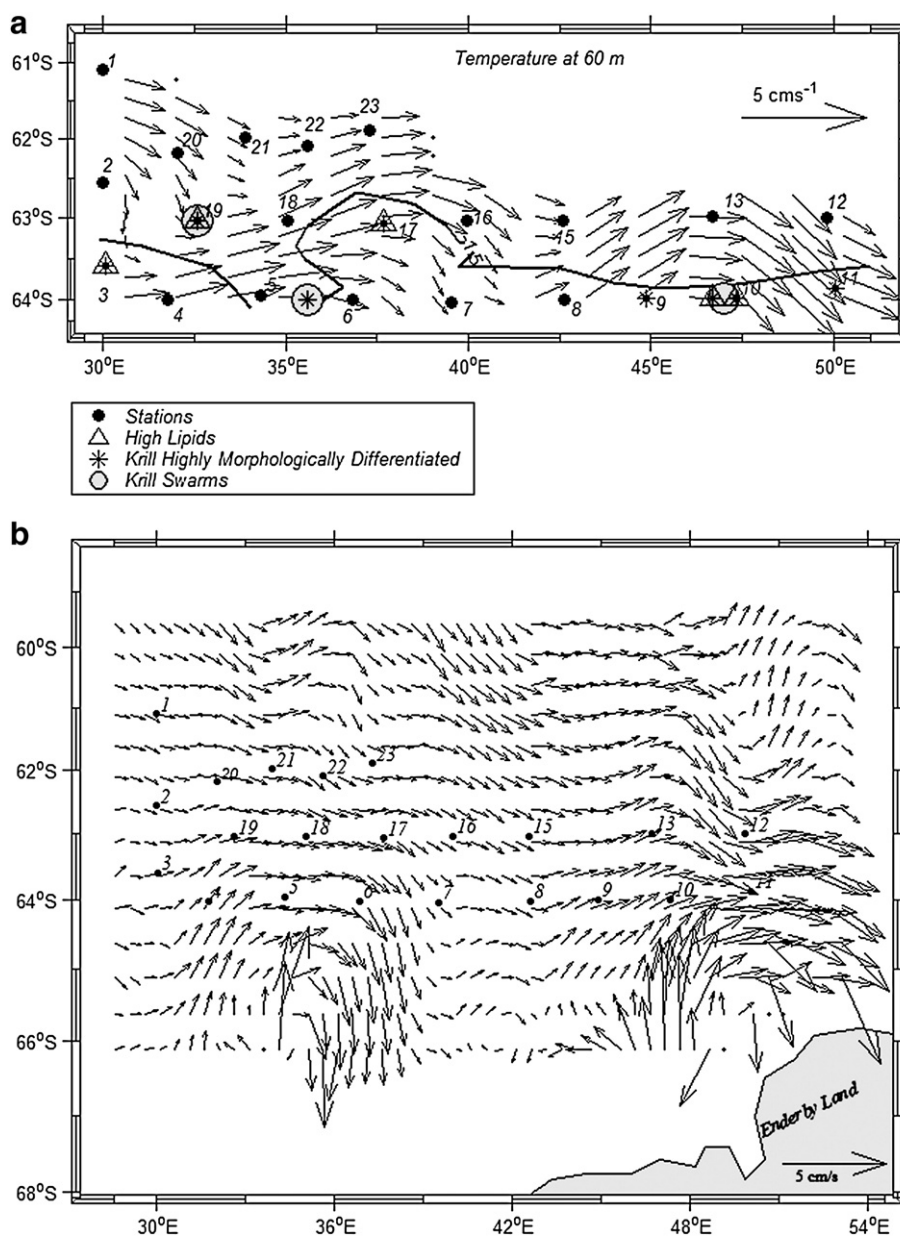
**Table 3**  
Biochemical composition of *T. macrura* (% of wet weight ± variance).

Station	Water	Proteins	Lipids	Carbohydrates	Ash	Chitin	Total
7	72.56 ± 4.56 (5)	15.04 ± 2.11 (15)	2.25 ± 0.72 (10) (29.7–89.4 mg)	0.42 ± 0.04 (10)	4.06 ± 0.60 (5)	4.97 ± 1.52 (5)	99.30
8	72.40 ± 3.48 (13)	14.38 ± 2.43 (16)	2.25 ± 1.05 (10) (17.3–39.3 mg)	0.61 ± 0.08 (10)	4.40 ± 1.14 (6)	6.27 ± 0.48 (6)	98.93
11	75.03 ± 5.60 (5)	13.07 ± 0.93 (15)	2.88 ± 1.91 (10) (20.5–46.7 mg)	0.38 ± 0.05 (10)	3.84 ± 0.63 (5)	5.76 ± 0.52 (6)	101.10
12	76.35 ± 1.67 (5)	12.49 ± 1.19 (14)	3.55 ± 1.92 (9) (28.5–59.6 mg)	0.62 ± 0.10 (10)	2.33 ± 0.18 (5)	4.86 ± 1.44 (6)	100.20
16	76.93 ± 3.53 (5)	13.27 ± 1.87 (12)	3.34 ± 1.73 (10) (57.3–109.69 mg)	0.35 ± 0.04 (10)	2.62 ± 0.32 (5)	3.81 ± 0.90 (6)	100.32
20	71.62 ± 2.41 (5)	10.78 ± 1.69 (11)	8.53 ± 2.68 (10) (78.68–155 mg)	0.33 ± 0.03 (10)	4.14 ± 0.78 (5)	2.89 ± 1.30 (5)	98.29

In brackets the range wet weights of the animals utilized for lipids.

of the station's mean. Significant differences in protein were found among stations sampled ( $H_{177}^{12} = 33.1, P < 0.001$ ). Carbohydrates constituted the smallest fraction (0.32 to 0.58%), but significant differences

were found among stations ( $H_{119}^{12} = 489.3, P < 0.001$ ). An ANOVA on the chitin data, showed significant differences ( $F_{20}^{12} = 3.69, P < 0.001$ ); chitin values were between 1.60 and 0.66%. Ash in this species showed means



**Fig. 7.** a) Geostrophic circulation relative to 1000 m in the sampled area and the isotherm of  $-1.5^{\circ}\text{C}$  at 60 m depth, obtained during the MD-25 FIBEX cruise. Stations of *Euphausia superba* samples with high lipids, high morphological differentiation and *E. superba* swarms are marked in the figure. b) Geostrophic circulation relative to 1000 m from Levitus Climatology during February. Two gyres are presented in the area.

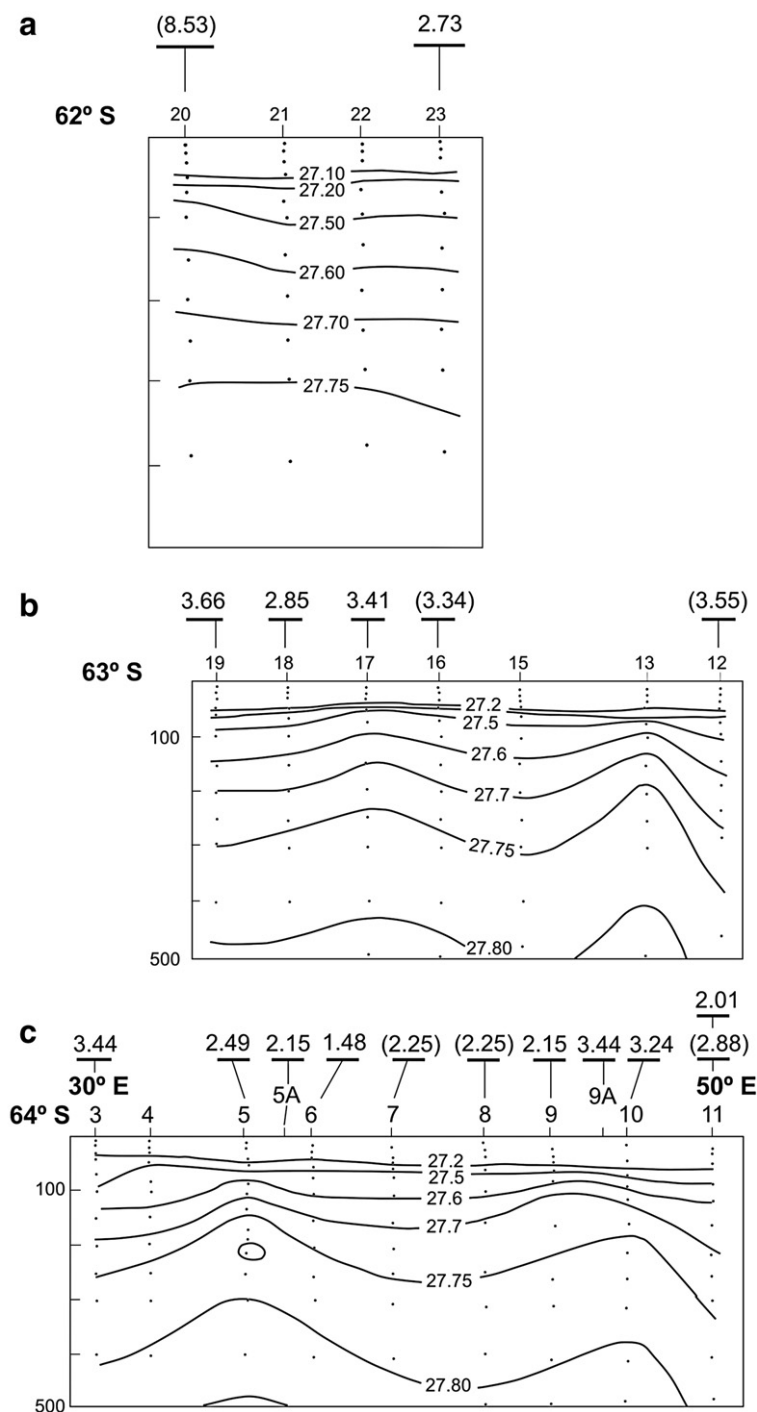


Fig. 8. Mean lipid content in percentage of wet weight for each station of both species, plotted over density ( $\sigma\text{-t}$ ) profiles of the three transects (from Simon, 1983, redrawn from Färber-Lorda, 1994). The values for *T. macrura* are in brackets.

between 2.46% and 3.42%, and significant differences existed among stations ( $F_{46}^{10} = 3.41$ ,  $P = 0.002$ , stations 5 and 6 were not analyzed). Putting together all lipid values for males I and males II, for all stations, we found a significant difference between these two groups ( $t = 3.66$ ,  $df = 41$ ,  $P = 0.004$ ). Results are presented in Table 2.

### 3.5.2. *T. macrura*

For this species, biochemical composition was quite different; at least in mature animals, it had more lipids. The biochemical composition is presented in Table 3. Lipids showed a significant difference among stations ( $H_{39}^5 = 24.3$ ,  $P < 0.001$ ). For proteins, values were higher than those found for *E. superba* (10.78 to 15.04%); it is important to notice that

most of the animals were juveniles or subadults. Significant differences were found among stations for protein ( $H_{83}^2 = 29.8$ ,  $P < 0.001$ ) and carbohydrates ( $H_{70}^2 = 44.48$ ,  $P < 0.001$ ). Values for chitin were higher than in *E. superba* (2.89 to 6.27), a significant difference was found among the stations ( $F_{28}^2 = 4.80$ ,  $P = 0.002$ ). The animals also differ among stations with regard to ash ( $F_{26}^2 = 10.37$ ,  $P = 0.001$ ).

### 3.6. Global analyses

Fig. 7 shows the geostrophic velocities over temperature at 60 m depth, it is clear the coincidence of the  $-1.5\text{ }^\circ\text{C}$  (depth of the bottom of the thermocline) isotherm with higher concentrations of euphausiids

and/or individuals with higher lipid content; with the exception of station 5A, where a dominance of males was found, in all other stations where swarms of krill were sampled, the animals showed a higher lipid content and high morphological differentiation (bimodal distribution of D.I. see Figs. 6 and 8). Also, there is a good agreement with the circulation proposed by other authors with these results (see Fig. 7a); the Levitus Climatology during February confirms the presence of two gyres. The results for lipids by station were plotted for both species, over the density ( $\sigma\text{-t}$ ) isopleths (from Simon, 1983), a coincidence of what seemed to be a domed hydrographic structure with high lipid content was found (Fig. 8).

#### 4. Discussion

The hydrographic structure of the area showed the presence of two gyres, this matches the findings of Treshnikov (1964), and Maslennikov et al. (1986) who worked in the same area, in which our sampling took place. Higher productivity areas correspond to the eastern and western gyres. In the west, it is expected that the Weddell Drift brings colder waters, forming cells of colder, and oxygen rich waters at less than 300 m depth with higher silicates (Simon, 1983, 1986); opposite wind directions were found along the 63° and 64° (Simon, 1983, 1986) transects; thus, it is supposed that sampling took place around the Antarctic Divergence. Water temperature in the gyre was lower in the southernmost transect. Pakhomov (2000) described the circulation of water north of the Cosmonaut Sea (south of our sampling area) and assumed, according to other authors (Treshnikov, 1964; Maslennikov et al., 1986; Bibik et al., 1988) that waters move eastwards at around 64°S. Around 50°E, waters turn south and move westward along the coast and are partially deflected northward at ~30°E, forming cells separated by around 80 miles, this is confirmed by our geostrophic velocities shown in Fig. 7a. To understand the observed circulation pattern we used the hydrographic climatology of Levitus for February; this helps explain water circulation in our sampling area, a wider area is shown in Fig. 7b, in which we observe that, the sampled area is part of two gyres, in its northern extreme and greatly influences the FIBEX MD 25 area. A sharp decrease in temperature occurred between 50 and 60 m depth (Fig. 2a and b) in the entire area. There was an apparent coincidence of low temperature high nutrient concentration (Fig. 3a and b, and Simon, 1983, 1986) with concentrations of large *E. superba*, markedly differentiated in morphology, and with high lipid content. It is important to mention that the oxygen minimum was shallower in these stations, thus, also rising the oxygen maximum (Simon 1983, 1986).

A more complex animal class size structure was found in the western sector, with probable mixing of different populations, brought by the Weddell Drift, as shown by the Bhattacharya's (1967) test. In general, we found more adults along the 64°S transect; on the 63°S transect there were adults only at stations 17 and 19.

All the *E. superba* stations near the  $-1.5$  °C isotherm at 60 m, showed higher krill lipid content and/or highly differentiated animals and/or were concentrated on swarms (see Fig. 7). Females had higher lipid content (see Fig. 8) at the swarming stations 9A and 10, near the extremes of the eastern Gyre, and near the  $-1.5$  isotherm; though, lower than what had been previously found by other authors for other areas (Raymont et al., 1971; Ferguson and Raymont, 1974; Clarke, 1980, 1985; Reinhardt and Van Vleet, 1986; Pond et al., 1995). The cruise took place during *E. superba*'s spawning season (February), sex ratio was variable among stations. Comparing lipid content of spawned females and mature females of the same size, a loss of up to 55% of lipids in females, during spawning, was calculated. Males II also have lower lipid content than coexisting males I, females, or juveniles. Virtue et al. (1996) showed that krill might die after fecundation, which probably is related to the low lipid content found in males II. Our lipids study (see Table 2) showed significant differences between males I (mostly immature) and males II (mature), being lower for the later. Färber-Lorda (1990, 1991) found that mature males I and II are morphologi-

cally different. Large males (>55 mm) were not found during the present cruise (we assume that they had died), also, all male II individuals had very low lipid content ( $1.56 \pm 0.42\%$ ), and fecundation had recently occurred in the sampled area; nevertheless, some stations were found with a predominance of males (Sts. 9, 6, 5A and 11), which apparently does not support the, die-after-fecundation hypothesis.

For *T. macrura*, which start spawning in September (Makarov, 1979), some mature females were found in the northern transect. Small immature animals were found along the other transects. A clear bimodal distribution was found along the 63°S transect. At Sts. 16 and 20, larger animals and smaller proportions of the smaller size class of immature animals were found. Nordhausen (1992) assumed a single spring spawning period in the Bransfield Strait region for *T. macrura*. *T. macrura* showed high lipid variability among stations, from 2.25% to 8.53%, but within each station the variability was lower, which is probably related to the smaller size of this species. In the present study, high lipid content was found in adult females, almost three times higher than subadult animals. This condition was also described by Mayzaud et al. (1985), and Mayzaud et al. (1998). Reinhardt and Van Vleet (1986) found, in pooled samples, an equivalent value for *T. macrura* lipids, by dry weight, Falk-Petersen et al. (1999) found that values depended on animal size. In this work, bigger animals showed the highest lipid content (like at station 20). A highest coefficient of condition was also found at the adult dominated stations (Sts. 16 and 20) (Färber-Lorda, 1994), thus showing a greatest growth in weight related to size. Lipids plotted by stations for both species, over the density ( $\sigma\text{-t}$ ) isopleths (from Simon, 1983) (Fig. 8), show a geographic coincidence of rising isopycnets, with probable upwelling, with higher lipid mean values (except for station 5A, which had a strong male dominance), also higher silicates values were found in these stations (Simon, 1983, 1986), it is probable that these favorable conditions were responsible for the higher lipids found.

An inverse distribution of *E. superba* and *T. macrura* was found across the surveyed area; only station 11 had both species. Nordhausen (1992) found that *T. macrura* was uniformly distributed across the Gerlache Strait, the Grandidier Channel, and the Crystal Strait, and that this species occupied a deeper stratum than *E. superba*.

The D.I. helps to understand population composition, and to separate cohorts. Bargmann (1937), John (1936), Makarov and Denys (1979), Mauchline (1980), Siegel (1982), Färber-Lorda (1986, 1990, 1991, 1994) have found sexual dimorphism in *E. superba*, especially in somatic length relationships. Siegel (1982) attributes this dimorphism to stages of sexual maturity, and finds greater variability among larger males in the relationship between carapace and total length. Endo (1989) found that *E. superba* males III B had longer exopodites in the thoracic legs and longer pleopods, shorter carapace and bigger eyes. He hypothesized that they are better swimmers, and more active than females in the fecundation process, Färber-Lorda (1991) also found by multivariate analysis that males II have longer abdomen, shorter carapace, and bigger eyes, as well as lower lipid content. The strong dominance of males in our stations just besides krill concentrations or within concentrations might be related to the different swimming capacities of males and females. The two species differ significantly in the slopes of length versus weight relationships during the same cruise (Färber-Lorda, 1994), which probably reflects different growth rates for both species during Antarctic summer. Falk-Petersen et al. (2000) showed, according with their lipidic composition information, that *T. macrura* reproduction season starts earlier, when there is not yet a phytoplankton "bloom", whereas that of *E. superba* starts during the phytoplankton "bloom", thus *T. macrura* is dedicating more energy to growth than *E. superba*, which might explain this growth rate difference between the two species (Färber-Lorda, 1994), and the higher lipid content of adult *T. macrura*. Mayzaud et al. (1998) studied the same area, measuring total lipids, and lipid classes in relation to geographical location, sexual maturity, and distribution among organs. They assumed that animal morphology was not different among stations, and they considered only one length-weight

relationship for all animals. Färber-Lorda (1994), showed a significant difference for the slope of the length–weight relationship for each of the same stations, showing that morphological differences among stations were more important than sex, or stage differences.

It is interesting to note that the Mayzaud et al. (1998) classification of stations by means of lipid percentage, independently of the sex, separates two groups that, according to our data, are (1) male dominated stations (Sts. 5, 6, 5A, 9, and 11) with low lipid content, and (2) those with high lipid content, mostly stations with female or subadult predominance (Sts 2, 3, 9A, 10, 17, 18, 19, and 23); thus showing the importance of population structure. They also grouped stations based on proximity analysis. This showed that stations placed near a Front (see Fig. 7) (with the exception of St. 9A; Sts 23, 17, 19, and 10, from their Fig. 5) and/or were female dominated, presented a higher reserve lipid content, related to better trophic conditions. At South Georgia, Pond et al. (1995), found that there is great variability in *E. superba* lipid content between stations. With more stations sampled we found the same variability. We also show that males II play an important role in the population structure, and mean lipid content per station. Pond et al. (1995) found that the variability was mostly, but not entirely, dependant on location, and population structure. Males had lower lipid content, possibly resulting from mobilization of material for spermatophore production and attachment. Pond et al. (1995) showed, in general, higher lipid values on a coastal area than our values on oceanic waters. Färber-Lorda et al. (2004) showed that for *Euphausia lamelligera*, a tropical euphausiid, lipid content changes in relation to wind regime, which alters trophic conditions in the area of the Gulf of Tehuantepec.

For mature populations of *E. superba*, D.I. size-class distribution is more scattered, and in many cases histograms are clearly separated between males and females. A more detailed study of the relation between sexual maturity and the D.I. will probably be of help in obtaining better information from this index. In Fig. 7, we observe a coincidence of higher lipid content, and highly morphologically differentiated animals in both gyres. Morphological differences and lipid content can be good descriptors of maturity. Morphometry, biochemical composition, and population structure are only some of the factors influencing or describing populations. Here we showed that along with hydrography, krill distribution, and its relation with trophic conditions can be explained in relation to morphometry of populations.

One important purpose of this paper is to stress the importance of considering different factors and variables contributing to the understanding of krill ecology and distribution. A longer term study will certainly give better results, but it is important to notice that, in population studies, it is convenient to analyze these variables together, as different, but complementary, descriptors of the environment.

## 5. Conclusion

Hydrography of the area is conditioning the distribution of both species, and their biochemical composition, since gyres are helping krill to stay in a more productive area, and are also helping in their retention in those areas. Morphological differences are shown and its distribution is apparently related to different swimming capacities of different developing stages. The distribution patterns of the populations and their biochemical composition are the result of a complex combination of population's structures, together with hydrographic conditions, swimming performance of the species, and trophic conditions. A more detailed study of the relationship between morphometry, developing stages, and sexual maturity is necessary to understand *E. superba*'s ontogenetic morphological differentiation.

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