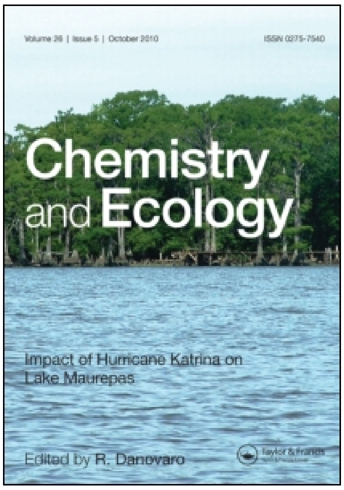

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Spatial–temporal relationships between two euphausiid species in the Ross Sea

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This paper summarizes the results obtained during the Italian marine Antarctic expeditions to the Ross Sea in November and December 1994, December 1997, and January 2000. The distribution and abundance of the two krill species (*Euphausia superba* and *Euphausia crystallorophias*) are shown in relation to the degree of ice cover, and a potential mechanism is presented that allows the coexistence of the two similar species in the same region. The surveys indicate that the northern and north-western areas of the Ross Sea are largely dominated by *Euphausia superba*, while the southern and south-western areas are dominated by *Euphausia crystallorophias*. The two krill populations show some overlap in the central part of the Ross Sea, where the distribution of the two species appears related to the ice cover. The biomass centroids of the two krill species seem to move northward associated with the ice edge retreat in summer. The centroid of the *Euphausia superba* biomass moves much faster and further than that of *Euphausia crystallorophias* and reaches ice-free waters at the edge of the Ross Sea in summer. This suggests that the spatial extent of the *Euphausia superba* population may extend beyond the Ross Sea, and a portion of this population may spread into the ocean waters starting in early January. In contrast, the *Euphausia crystallorophias* population appears to be restricted to the Ross Sea.

Keywords: *Euphausia superba*; *Euphausia crystallorophias*; Ross Sea; Echosurvey; Biomass; Polynya ice edge

1. Introduction

In the Southern Ocean, the name *Euphausia superba* is almost a synonym for krill. However, in the Ross Sea (figure 1a), probably because of the particular geographical distribution, two krill species, closely related genetically [1, 2] and similar in behaviour [3], dominate the biomass and play a central role in the pelagic ecosystem: *Euphausia superba* (*E. superba*) and *Euphausia crystallorophias* (*E. crystallorophias*). The two species are probably in competition. They have similar feeding appendages [4], and both feed on phytoplankton [5–8], though they may have different food preferences [9].

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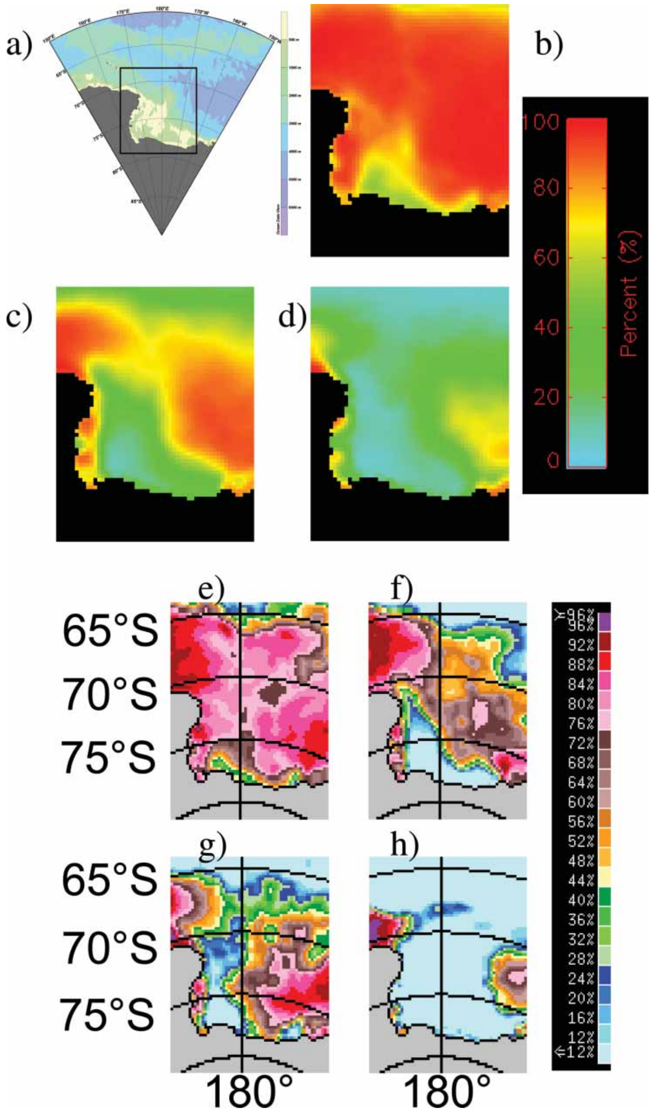

Figure 1. (a) Map of the study area (Ross Sea, the shelf area inside the black square). (b, c, d) Climatologic monthly sea-ice concentrations for November, December, and January, respectively; (e, f, g, h) sea-ice concentrations for November 1994, December 1994, December 1997, and January 2000, respectively.

The current scientific opinion is that *E. superba* prefers turbulent environment habitats such as continental slopes, where marine currents mix, and it is seldom found in shallow waters or close to ice, such as the Ross Ice shelf, in which the smaller *E. crystallorophias* predominates [6, 10]. However, many important questions remain. What are the boundaries of the two krill populations? How are the biomasses of the two krill populations distributed within their boundaries, and how great is their degree of overlap? What are the spatial and temporal relationships between the distributions of the two krill populations and that of both sea ice and phytoplankton? The importance of dispersion and dispersion rate in the interactions of two competing species in spatially heterogeneous environments is well known [11, 12]. The aim of this study is to answer some of those questions and thus to gain a deeper understanding on mechanisms that allow the coexistence of the two krill species in an area where the physical, chemical, and biological parameters are particularly variable due to the ice dynamics [13, 14]. This problem is important not only in ecology, but also in the future management of krill fisheries in the Ross Sea.

Until 1989, the scientific opinion was that the Ross Sea was inhabited almost exclusively by *E. crystallorophias* [10]. The six acoustic surveys carried out within the PNRA projects from 1989 to 2004 have shown that the most abundant krill species is in fact *E. superba* [15], with an average biomass of about 2 million tonnes, which is about 10–15 times that of *E. crystallorophias*. Both species are eaten by predators, but only *E. superba* is used for human food. There are no fisheries for *E. superba* at present in the Ross Sea, but this could change in the near future, altering the strategies of coexistence between the two krill species with completely unforeseeable effects.

The spatial scale chosen for this study is the region of the Ross Sea where the environmental gradients have their maximum values from November to January (figures 1b–d). Data on this region come from four large-scale surveys carried out from 1994 to 2000 in very different ice coverage situations (from 5% to 90%).

This paper firstly describes the methods used for the acoustic surveys, then presents new data on the sea ice dynamics and spatial distributions of krill—focusing on key differences between the two krill species—and finally provides a possible mechanism which allows the coexistence of these two species in the Ross Sea.

2. Material and methods

The data presented in the paper relate to the region of the Ross Sea, where the temporal variability in the water column associated with ice-edge melting and recession is particularly strong [14]. The region is a rectangle delimited by latitude 69° 30′ and 78° 06′ S (955 km) and by longitude 164° 30′ E and 175° 30′ W (extending 460 km at the southern end, and 762 km at the northern end). It was surveyed acoustically four times in different conditions of ice cover, twice in 1994, and once each in 1997 and 2000. The first survey was conducted from 9 November to 10 December 1994, behind an icebreaker, in conditions of almost 100% ice cover (figure 1e). The second survey was carried out from 17 to 28 December 1994 in conditions of partial ice cover (figure 1f). In both surveys, acoustic data were collected using a BioSonics 102 scientific echosounder, operating at 38 and 120 kHz, and a dual beam echosignal processor, running on a personal computer [15]. The 1997 survey was conducted from 7 December to 5 January in conditions of partial (figure 1g) ice-cover and the 2000 survey from 16 January to 7 February in almost ice-free waters (figure 1h). In the last two surveys, acoustic measurements were carried out using a Simrad three-frequency echosounder (38 and 120 kHz split-beam transducers and 200 kHz single beam transducer). Data were recorded and processed on an HP9000/715 workstation with BI 500 software. All the above acoustic equipments were calibrated in Italy before, and after, each expedition according to the method described by MacLennan and Simmonds [16].

The three-frequency method was applied for recognition of *E. superba* and *E. crystallorophias* swarms [17]. On the basis of this method, the probability of correct classification of an unknown swarm is estimated at >0.90. About 91% of the *E. superba* swarms and 97% of *E. crystallorophias* swarms sampled by the net during the four expeditions were identified correctly by this method.

The mean length of the two species was determined from hauls. Hauls were carried out along the routes of the four surveys, using a 5 m^2 Plankton Hamburg Net (HPN) with a 500 μm (1994) or 1000 μm (1997, 2000) mesh size. The number and position of the hauls were different in the four surveys because of the difference in ice cover. During the two 1994 surveys, 23 hauls each of 60 min duration were carried out: eight in the first survey and 15 in the second survey [15]. During the 1997 and 2000 surveys, 35 hauls of 60 min duration and 63 hauls of 30 min duration were conducted, respectively [18, 19]. At each sampling site, euphausiids were identified and counted. If the catch was large, the mean length of each species was determined from a random sub-sample of 100 individuals. Otherwise, the mean lengths were determined from measurements of all the individuals.

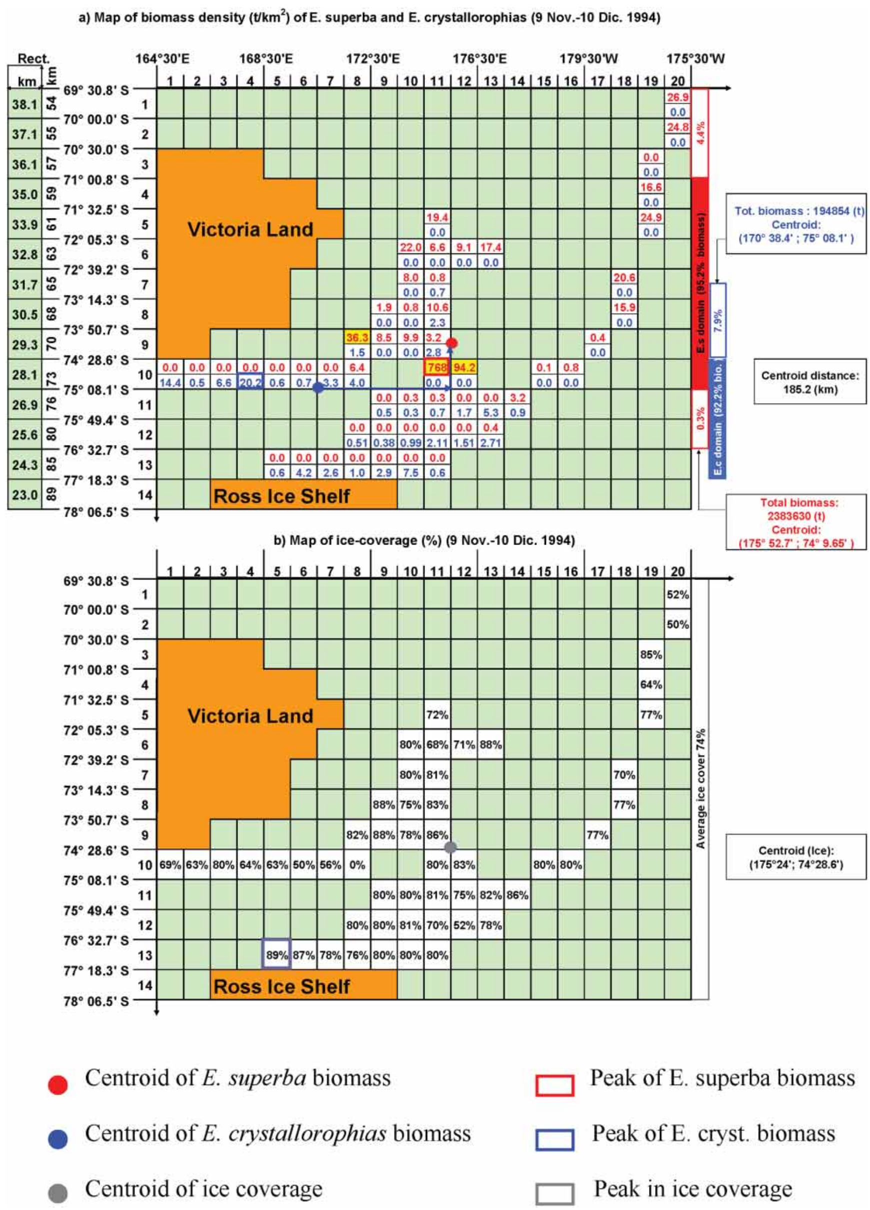

Figure 2. (a) Map of krill biomass distributions found during the first survey (9 November to 10 December 1994) of the X Italian Antarctic Expedition to the Ross Sea. The yellow rectangles (3) represent krill concentration areas. (b) Map showing ice coverage (expressed in percentage) in the studied area, in the period of the survey.

The biomass of the two krill species was calculated at 120 kHz from the mean volume backscattering strength, using the weight/length relationships of each species [20, 21] and the backscattering cross-sectional area of krill [22]. The geographic distribution of biomass was estimated for each species using the Elementary Statistical Sampling Rectangle (ESSR) method of MacLennan and Simmonds [16]. The surveyed area was transformed into a lattice of rectangles of constant area (600 square nautical miles or about 2058 km^2), spaced 1° in longitude and with variable intervals in latitude (figures 2–5). The area under examination was filled with 220 rectangles. The number of sampled rectangles was 53 (23%) in November

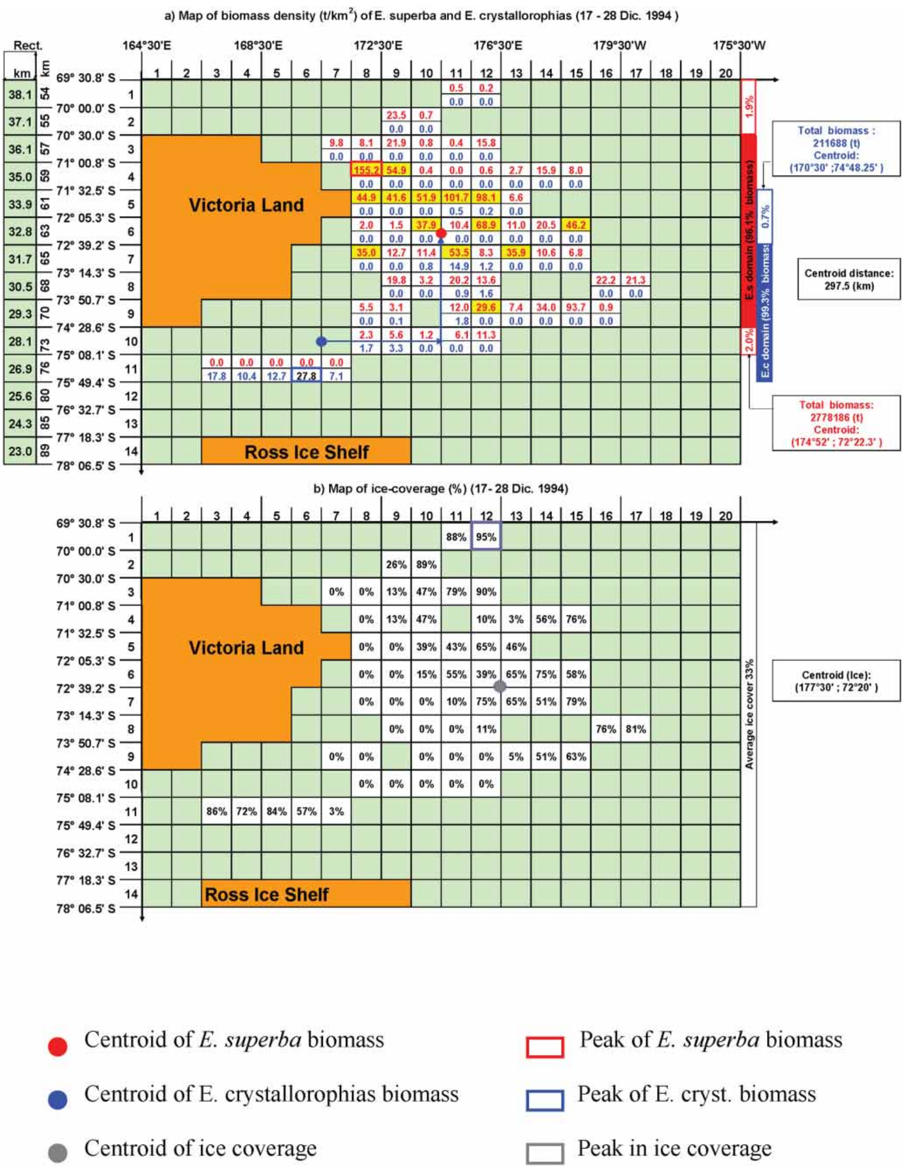

Figure 3. (a) Map of krill biomass distributions found during the second survey (17–28 December 1994) of the X Italian Antarctic Expedition in the Ross Sea. The yellow rectangles (14) represent krill concentration areas. (b) Map showing ice coverage (expressed in percentage) in the studied area, during the survey.

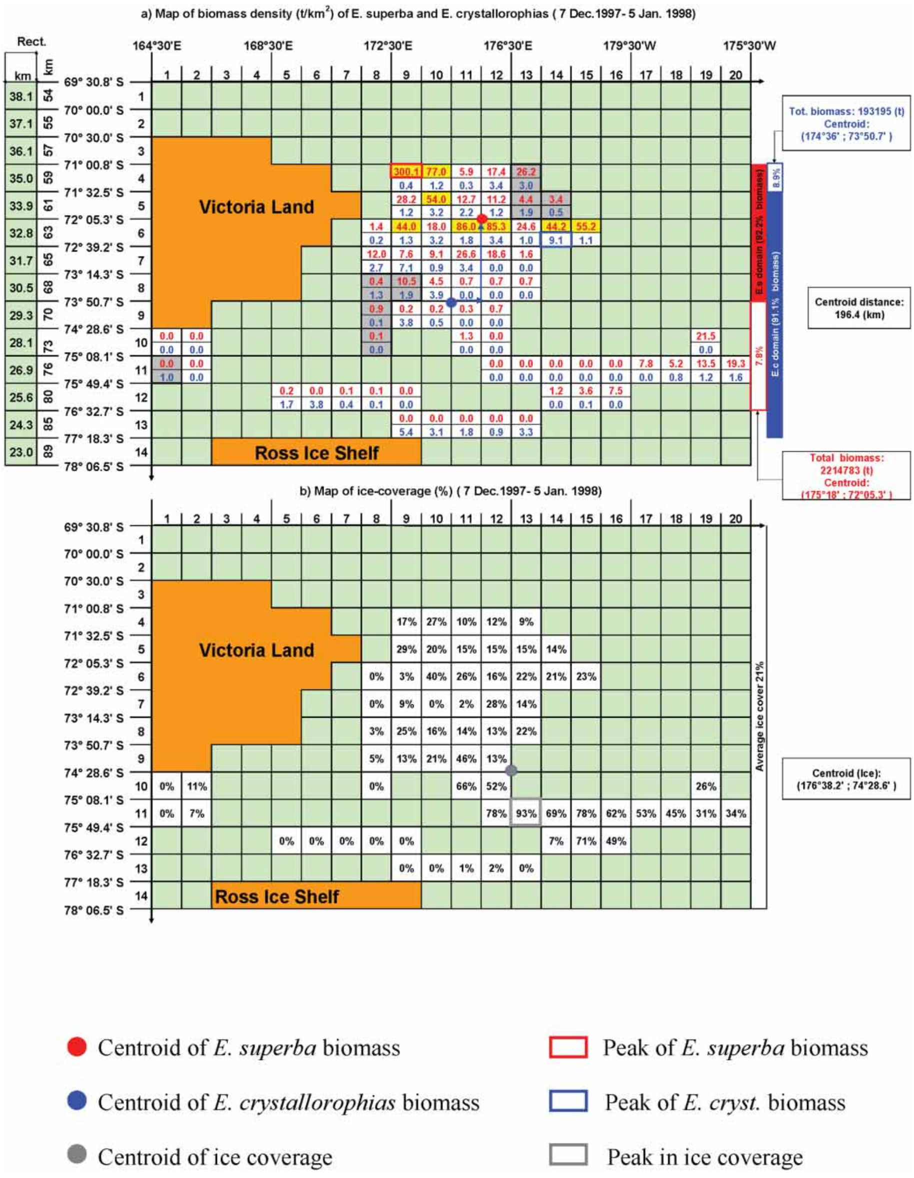

Figure 4. (a) Map of krill biomass distributions found during the XIII Italian Antarctic Expedition in the Ross Sea (7 December to 5 January 1997). The yellow rectangles (8) represent krill concentration areas. Rectangles with juveniles of *E. superba* and *E. crystallorophias* are highlighted in grey. (b) Map showing ice coverage (expressed as a percentage) in the studied area, in the period of the survey.

1994, 62 (27%) in December 1994, 66 (29%) in December 1997, and 101 (44%) in January 2000. The distance travelled in each rectangle was 46–65 km. It is assumed that the measured krill densities in each rectangle are representative of the rectangle within which they were collected. The rectangles of biomass above 60 000 t (or average density above 29.2 t km^{-2}) are regarded as krill concentration rectangles (yellow rectangles in figures 2–5). An aggregate of rectangles containing at least 90% of the total biomass of one krill species was called the domain of that species. The southern and northern borders of the domain were called species boundaries.

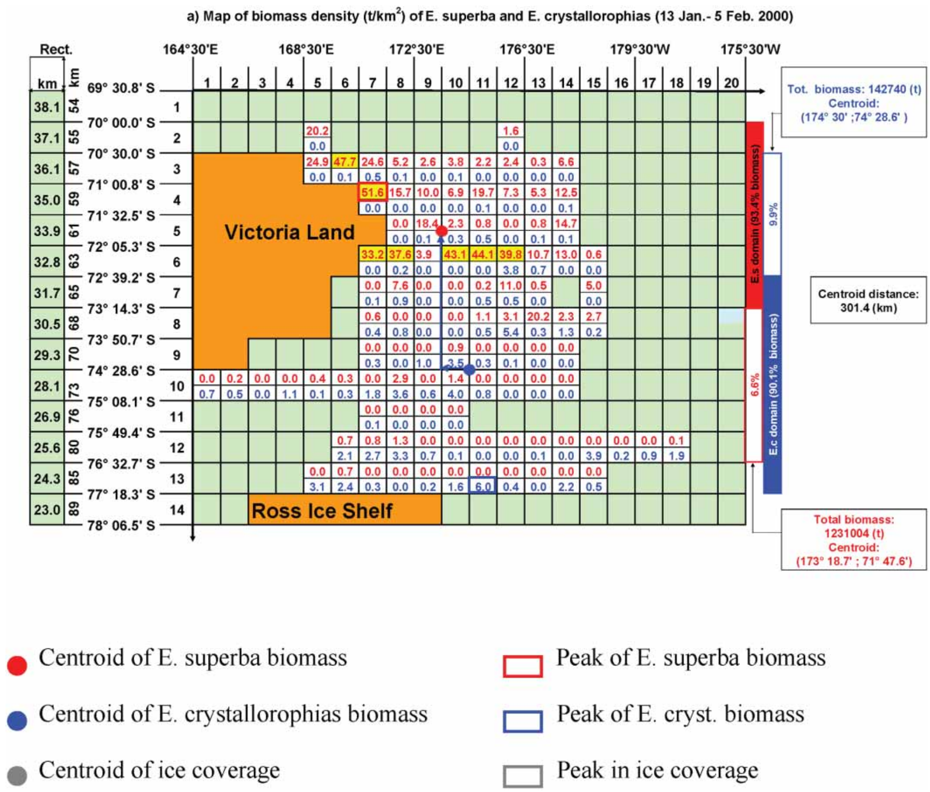

Figure 5. Map for assessing krill biomass density by rectangles during the XV Italian Antarctic Expedition in the Ross Sea (16 January to 7 February 2000). The yellow rectangles (7) represent krill concentration areas.

Data on ice cover in the studied area were recorded by an observer from the flying bridge on the vessel, for each mile during the surveys (figures 2b, 3b, and 4b). Ice-cover data on the entire area in the month of the survey were obtained by Nimbus-7 SMMR and DMSP SSM/I Passive Microwave Data [23]. Sea ice-cover images were downloaded from the National Snow and Ice Data Center (figures 1e–h).

Two types of measurements were calculated from the sampled rectangles in the lattice [24]:

- the positions of the centroids were calculated to represent the spatial distributions of the biomass and ice cover;
- the distances, and the change in distances, between the centroid positions were calculated to represent the difference in the spatial biomass distribution between the two species over time.

The centroid is the point of balance of the biomasses (or of the ice cover values) in the surveyed area. It has two components (X_c, Y_c), denoting the column and row positions of balance of the biomasses. The two numbers are expressible by:

$$X_c = \frac{\sum_j \sum_i x_i B_{i,j}}{B};\ Y_c = \frac{\sum_i \sum_j y_j B_{i,j}}{B};\ i = 1, 2, \ldots, 20\ \text{(column)};\ j = 1, 2, \ldots 14,\ \text{(row)},$$

where $B_{i,j}$ is the biomass in the rectangle (i, j), B is the total biomass in the surveyed area, and (x_i, y_j) are the coordinates of the centre of the rectangle (i, j).

The centroid is determined only by the mutual locations of the rectangles and their biomasses. When the set of biomasses is in motion, the centroid is also in motion. Therefore, the spatial biomass patterns and movements can be studied using the centroid techniques.

In this paper, the coordinates of the centroids are expressed in terms of longitude (x-axis, increasing from 164° 30′ E and 175° 30′ W) and latitude (y-axis increasing from 69° 30′ S (0 km) and 78° 06′ S (955 km)), while the distances and the changes of distances in the distribution of centroids are expressed in terms of kilometres. Three distances are calculated: along latitude, along longitude, and in total.

3. Results

3.1 *Ice dynamics in the region during the periods under examination*

While krill swarm formation is caused primarily by social behaviour, the aggregation of many swarms in certain areas must be connected with factors of a more global nature. It seems that in the area under examination, an important factor causing uneven spatial distribution of krill is the ice dynamics. The surveys from November to February, although carried out in different years, allow us to reconstruct the dynamics of the ice-edge retreat.

As shown by the monthly average ice cover images produced by the National Snow and Ice Data Center from Nimbus-7 SMMR and DMSP SSM/I data set (November 1978 through December 2003 [25]), in November the southern Ross Sea polynya widens slowly around Ross Island and along the western part of the Ross Ice Shelf (the southern boundary of figure 1b) and spreads northward. In December, a noticeable ice edge, thickened by ice pieces transported by wind, develops around latitude 75° S (figure 1c). This ice edge, and consequently the polynya, moves steadily northwards from 75° S to 70° S until the polynya encounters the circumpolar ice edge and joins with the whole Southern Ocean (figure 1d). The patterns of sea ice cover during the four surveys generally followed the climatological averages but with some differences. In November 1994, the sea-ice concentration (figure 1e) was very similar to the average (figure 1b). In December 1994 (figure 1f) and 1997 (figure 1g), the sea-ice cover was again quite similar to the average (figure 1c) but with a wider polynya in 1994. In January 2000 (figure 1h), the Ross Sea was almost completely ice-free, with a sea ice cover considerably lower than the average (figure 1d).

The polynya progresses northwards much faster between longitude 170° 30′ and 178° 30′ E than it does to the east or the west. Therefore, the temporal variability in the vertical structure of the water column, associated with ice melting, is much stronger in the central areas of the region under examination than in the east and west boundary regions. Moreover, the discontinuous progression of the polynya ice front northwards from November to January leads to a strong spatial and temporal variability in the light and algae released in the water column [14], which probably explained the krill concentrations and movements. What makes these concentrations interesting is that their areas of occurrence and movements are different in the two krill populations.

3.2 *Dynamics of krill populations*

3.2.1 November 1994. The spatial distribution of the biomass of the two krill species in relation to the ice cover in November 1994 is shown in figures 1e and 2a and b. The mean ice-cover percentage in the areas surveyed was 74%. The total biomass (tables 1 and 2) of

Table 1. Most significant parameters related to biomass distribution of *E. superba*, *E. crystallorophias*, and ice coverage during the surveys.

			November 1994	December 1994	December 1997	January 2000
Ross Sea	Covered area (km^2)		109 071	129 650	135 824	207 852
	Sampled (km)		2956	3030	3506	4754
E. superba	Centroids	Longitude (E)	175° 52.7′	174° 52′	174° 18′	173° 18′
		Latitude (S)	74° 09.6′	72° 22.3′	72° 05.3′	71° 47.6′
	North front	Latitude (S)	≥71° 00′	≥70° 30′	≥71° 00′	≥70° 00′
	South front	Latitude (S)	75° 08′	74° 28′	73° 50.7′	73° 14′
E. superba concentrations	Area (percentage of covered area)		5.7	22.6	12.0	6.9
E. crystallorophias	Centroids	Longitude (E)	170° 38.4′	170° 30′	174° 36′	174° 30′
		Latitude (S)	75° 08.1′	74° 48.2′	73° 50.7′	74° 28.6′
	North front	Latitude (S)	74° 28.6′	72° 39.2′	71° 32.5′	74° 28.6′
	South front	Latitude (S)	77° 18.3′	≤75° 49.4′	77° 18.3′	77° 18′
Distance *E. superba* vs. *E. crystallorophias* centroids (km)		Longitude	147.2	114.2	21.3	–35.2
		Latitude	–108.2	–270.6	–195.1	–299.2
		Total	185.4	297.5	196.4	301.4
Breadth of overlapping strip (km)			73	203	256	65
Ice	Centroids	Longitude	175° 24′	177° 30′	176° 38.2′	
		Latitude	74° 28.6′	72° 20.0′	74° 28.6′	No ice
	Mean coverage (%)		74	33	21	
E. superba	Mean length (mm)		42.51	42.36	36.63	44.83
	Biomass (t)		2 383 630	2 778 186	2 214 783	1 231 004
	Mean density (t km^{-2})		21.9	21.4	16.3	11.0
E. superba concentrations	Biomass (percentage of total *E. superba* biomass)		77.6	66.7	69.0	49.7
	Mean density (t km^{-2})		297.5	63.2	93.8	42.7
	Maximum density (t km^{-2})		767.8	155.2	300.1	51.6
E. crystallorophias	Mean length (mm)		25.58	26.8	17.02	20.39
	Biomass (t)		194 855	210 248	193 195	142 740
	Mean density (t km^{-2})		1.8	1.6	1.4	0.7

E. superba was estimated as 2.4 million tonnes (mean density: 21.9 t km^{-2}), which is almost 11 times higher than the biomass of *E. crystallorophias* at 0.2 million tonnes (mean density: 1.8 t km^{-2}). More than 95% of *E. superba* biomass was distributed between latitude 71° 00′ S (northern species boundary) and 75° 08′ S (southern species boundary) and longitude 171° E and 177° 30′ W (tables 1 and 2). Three rectangles had high concentrations of *E. superba* (figure 2a), containing 77.6% of the total *E. superba* biomass while representing only 5.7% of the surveyed area. The centroid of *E. superba* biomass (latitude 74° 09.6′ S; longitude 175° 53′ E) was 108 km north of its southern species boundary (table 1) and close to the three rectangles of highest concentrations.

E. crystallorophias mainly occurred in the areas south of latitude 74° 28.6′ S (northern species boundary) (table 2). This area included 58.5% of the surveyed region and contained 92.1% of the *E. crystallorophias* biomass. The centroid of the *E. crystallorophias* population (latitude 75° 08.1′ S; longitude 170° 38.4′ E) was close to its northern border. It was 108 km south and 147 km east of the centroid of the *E. superba* population (table 1). Even though the domains of the two krill species slightly overlapped (table 2), their centroids were separated by 185 km. In November 1994, the catch of both species comprised only adults. From all samples, the average *E. superba* length was 42.51 mm TL (range 42.4–45.0 mm), and the average *E. crystallorophias* length was 25.58 mm TL (range 25–30 mm).

Table 2. Distributions in abundance per latitude of the two species of Euphausiids.

	November 1994			December 1994			December 1997			January 2000		
Lat	**% E. s.**	**% E. c.**	**% Ice**	**% E. s.**	**% E. c.**	**% Ice**	**% E. s.**	**% E. c.**	**% Ice**	**% E. s.**	**% E. c.**	**% Ice**
69° 30.8' 70° 00.0'	2.3	0.0	52	0.1	0.0	**92**	---------	---------	---------	---------	---------	---------
70° 00.0' 70° 30.0'	2.1	0.0	50	1.8	0.0	58	---------	---------	---------	3.6	0.1	0
70° 30.0' 71° 00.8'	0.0	0.0	85	4.2	0.0	38	---------	---------	---------	20.1	1.2	0
71° 00.8' 71° 32.5	1.4	0.0	64	17.6	0.0	29	**39.6**	8.9	15	21.6	0.3	0
71° 32.5' 72° 05.3'	3.8	0.0	75	**25.5**	0.7	32	10.6	10.8	18	6.2	1.4	0
72° 05.3' 72° 39.2	4.8	0.0	77	14.7	0.0	38	33.3	**22.3**	19	**37.8**	6.9	0
72° 39.2 73° 14.3'	2.5	0.8	77	12.9	16.4	35	7.0	15.0	9	4.1	2.9	0
73° 14.3' 73° 50.7'	2.5	2.5	81	7.4	2.4	28	1.6	7.5	15	5.0	12.7	0
73° 50.7' 74° 28.6'	5.0	4.6	**82**	13.8	1.9	15	0.2	4.7	20	0.2	7.6	0
74° 28.6' 75° 08.1'	**75.1**	**53.2**	64	2.0	4.8	0	2.1	4.0	26	0.9	19.6	0
75° 08.1' 75° 49.4	0.3	9.9	81	0.0	**73.7**	60	4.3	4.9	**50**	0.0	0.2	0
75° 49.4 76° 32.7	0.0	8.7	74	---------	---------	---------	1.2	6.5	16	0.5	22.9	0
76° 32.7 77° 18.3	0.0	20.5	81	---------	---------	---------	0.0	15.4	0	0.1	**24.2**	0
77° 18.3 78° 06.5	---------	---------	---------	---------	---------	---------	---------	---------	---------	---------	---------	---------
Total Biomass	**100.0%** **2383631 t**	**100.0%** **194854.2 t**		**100.0%** **2778186 t**	**100.0%** **211688 t**		**100.0%** **2214783.3 t**	**100.0%** **193196 t**		**100.0%** **1231005 t**	**100.0%** **142740 t**	

Note: Centroids for *E. superba*, *E. crystallorophias*, and ice coverage are represented by grey rectangles.

3.2.2 December 1994. The average densities of both krill species found in December 1994 (mean *E. superba* density: 21.4 t km^{-2}, mean *E. crystallorophias* density: 1.6 t km^{-2}) were approximately the same as those 1 month before (tables 1 and 2). However, their spatial patterns, as well as the extension (33%) and distribution of ice cover, had changed dramatically (figures 1f and 3a and b). The rectangles containing high *E. superba* concentrations had increased in number from three to 14, decreased in average density (table 1), and moved to the north-west. The domain of *E. superba*, containing about 96% of the biomass, was delimited by latitude 74° 28′ (southern species boundary); 70° 30′ (northern species boundary) and by longitude 170° 30′ E; 178° W (tables 1 and 2). The centroid of *E. superba* biomass was located in the centre of the domain and surrounded by rectangles of high concentrations (latitude 72° 22.3′ S; longitude 174° 52′ E; see table 1). The *E. crystallorophias* biomass was found mainly between latitude 72° 39.2′ S (northern species boundary) and 75° 49.4′ S (southern species boundary). This indicates that the domain of *E. crystallorophias* had extended northward and that its degree of overlap with the southern side of *E. superba* domain had increased concomitant with a reduction in ice cover (table 2). However, the centroid of *E. crystallorophias* biomass (latitude 74° 48.2′ S and longitude 170° 30′ E) had moved only very slightly with respect to the previous period, although its distance from the *E. superba* centroid had increased to about 297 km (table 1). In December 1994, the average *E. superba* length was similar to that found 1 month earlier (42.36 mm TL), but the range of length distribution (34.9–46.8 mm) had increased due to the presence of juvenile krill. However, the number of small krill was too low to identify any juvenile or sub-adult age group. The average length of *E. crystallorophias* of 26.8 mm was similar to that in November (table 1), but the number of individuals caught was too low to calculate even the size range.

3.2.3 December 1997. The spatial distributions of the biomass of the two krill species and of the ice cover in December 1997 are given in figures 4a and b. The ice cover (21%, figures 1g and 4b) was less extensive and had a different distribution to that in December 1994. The total biomass (table 1) of *E. superba* was estimated to be 2.2 million tonnes (average density 16.3 t km^{-2}). It was 11 times higher than the *E. crystallorophias* biomass of about 0.2 million tonnes (mean density of 1.4 t km^{-2}). The krill population sampled in this survey was characterized by a consistent number of juveniles of both species [18]. The average *E. superba* length in December 1997 was 36.63 mm TL (13.5% lower than in December 1994; table 1). The juveniles of *E. superba* (19.24 mm TL) represented 19.2% of the net samples. They were found between latitude 73° and 75° S and longitude 171° 30′ and 173° 30′ E, within the domain of the *E. crystallorophias* population, and between latitude 71° and 72° S and longitude 176° 30′ and 178° 30′ E, in the continental slope (figure 4a). The average length of *E. crystallorophias* was 17.02 mm TL (35.70% lower than in December 1994). The juveniles of *E. crystallorophias* represented 30% of the net samples. They were found, both in areas very close to ones of juveniles of *E. superba* and in a small area, in front of Terranova Bay, between latitude 75° and 75° 30′ and longitude 164° 30′ and 165° 30′. The areas containing more than 90% of total *E. superba* biomass extended in latitude from 71° 00′ S (northern species boundary) to 73° 50′ 7 S (southern species boundary) and in longitude from 171° to 179° E (table 1). There were eight rectangles of *E. superba* concentrations, all situated north of latitude 72° 39′ S, which represented 12% of the sampled area and contained 69% of the total *E. superba* biomass. The centroid of *E. superba* biomass (latitude 72° 05.3′ S; longitude 175° 18′ E; see table 1) was shifted slightly to the northeast of that obtained in December 1994 (table 1). Over half (57%) of the *E. crystallorophias* biomass was found between latitude 71° and 73° S, mixed with *E. superba* biomass. The remaining 43% was distributed between 73° and 77° S, in rectangles with very few *E. superba*. Although the domains of the two krill populations overlapped to a large extent in this survey, the centroids were still far apart. The *E. crystallorophias* centroid was found 196 km to the southeast of the *E. superba* centroid (table 1). Comparison between these results and those obtained under similar ice conditions in December 1994 indicates that the southern boundary of *E. superba* biomass moved northward in December 1997, but its centroid remained similar to that found in 1994 (tables 1 and 2). In contrast, in December 1997, the northern *E. crystallorophias* boundary was much further north, the biomass centroid had moved to the northeast, and the portion of *E. crystallorophias* biomass found within the *E. superba* domain was much higher than in December 1994. It is possible that krill distribution is influenced by age structure, and the consistent number of juveniles of both species, found in December 1997, had facilitated their mixing.

3.2.4 January 2000. Figure 5 represents the spatial distributions of the two krill populations in January 2000, when the waters of Ross Sea were virtually ice-free (figure 1h). The total *E. superba* biomass (tables 1 and 2) was estimated to be 1.2 million tonnes (average density 11 t km^{-2}), 8.6 times higher than *E. crystallorophias* biomass of 0.14 million tonnes (average density 0.7 t km^{-2}). In ice-free conditions, the domain of *E. superba* comprising 93.4% of the biomass was distributed in an area between latitude 70° 00′ S (northern species boundary) and 73° 14′ S (southern species boundary). There were seven rectangles of high *E. superba* concentrations representing 6.9% of the sampled area and containing 49.7% of the total *E. superba* biomass. The centroid of *E. superba* biomass (latitude 71° 47.6′ S; longitude 173° 18′ E) was found at the most north-western position of all previous surveys. The domain of *E. crystallorophias*, containing more than 90% of biomass, was delimited by latitude 72° 39′ S (northern species boundary) and 77° 18′ S (southern species boundary). The areas south of latitude 73° 14′ S were dominated by the *E. crystallorophias* population. They contained 87.2% of *E. crystallorophias* biomass and only 6.6% of *E. superba* biomass. The centroid of *E. crystallorophias* biomass (latitude 74° 28.6′ S; longitude 174° 30′ E) was located more than 300 km south of the *E. superba* centroid. This is the largest distance between centroids in all the surveys, albeit similar to the distance in December 1994 (tables 1 and 2). It seems that in ice-free conditions, the *E. superba* biomass distribution may extend northwards beyond the edge of the Ross Sea in parallel with the progression and melting of the sea-ice. In contrast, most of the *E. crystallorophias* biomass remains confined within the southern part of the Ross Sea in all ice-cover situations. The average *E. superba* length in January 2000 was 44.8 mm TL (range 32.2–54.5 mm), but the number of small krill was too low to identify any juvenile or sub-adult age group. The average length of *E. crystallorophias* was 20.4 mm TL (range 7.9–40.41 mm). The number of juveniles represented 35.9%, and the number of sub-adults 31.5% of all the catches [19].

Discussion and conclusions

The Ross Sea was surveyed four times in different conditions of ice cover. In November 1994, the survey was conducted in waters fully covered by ice. In December 1994 and 1997, the surveys were carried out in conditions of partial ice cover. In contrast, the January 2000 survey was conducted in ice-free waters.

On the basis of the results of the four surveys, it is clear that the northern and north-western areas of the Ross Sea seem particularly suitable for the *E. superba* population, the southern and south-western areas for the *E. crystallorophias* population, while in the central area of the Ross Sea, there is a variation in the two species related with ice cover and perhaps with their age structure. This general distribution seems consistent with that for phytoplanktonic communities of the Ross Sea, with diatoms dominating to the north and west and *Phaeocystis* spp. to the south along the ice shelf [26, 27]. This distribution is probably also reflected in the different diets of the two krill species, as suggested by their biochemical composition [9].

However, the domains of the two species, as well as the biomass patterns within them, are not static, but change in extension, position, and level from the beginning of November to the end of January. The following observations on the dynamics of the spatial distributions of the two krill populations can be made:

- Fifty (January 2000) to 78% (November 1994) of *E. superba* biomass was found in rectangles of swarm concentrations (density $> 29.2\,\mathrm{t\,km^{-2}}$), which represented 23% (January 2000) to 6% (November 1994) of the covered areas. The peak of biomass density in these rectangles varied from $767.7\,\mathrm{t\,km^{-2}}$ (November 1994) to $51.6\,\mathrm{t\,km^{-2}}$ (January 2000).
- In all four surveys, the centroids of *E. superba* biomasses were located to the north-west of the centroids of the *E. crystallorophias* biomasses. The distances between the centroids of the two krill species varied from 185 km (November 1994) to 301 km (January 2000).
- The southern species boundary of *E. superba* domain varied from 75° 08′ S (November 1994) to 73° 14′ S (January 2000), the northern species boundary of *E. crystallorophias* domain from 74° 28′ S (November 1994) to 71° 32′ S (December 1997).
- The domains of the two krill species overlapped within strips, delimited by the southern species boundary of *E. superba* and northern species boundary of *E. crystallorophias*, varying in breadth from 73–65 km (November 1994–January 2000) to 203–256 km (December 1994–December 1997).

There was a relationship between krill and ice-cover distributions. The progressive movement northward of the ice edge from November to January seems to influence the apparent movement of both krill species as measured by their biomass centroids. However, the centroid of the *E. superba* biomass moved differently with respect to that of the *E. crystallorophias* biomass. The *E. superba* centroid moved almost 265 km from latitude 74° 09′ S to an area close to the Ross Sea border (around 71° 41′ S). The *E. crystallorophias* centroid moved northeast, had a maximum displacement of 141 km to the north, and did not extend north of 73° 50′ S. This suggests that portions of the Ross Sea population of *E. superba* may spread into the open ocean waters of the Southern Ocean beginning in January. On the other hand, the *E. crystallorophias* population seems to be confined within the Ross Sea.

The domain of the two krill species moved synchronously with their centroids. In the areas located on the northern side of the *E. superba* centroid, *E. crystallorophias* was seldom found, while on the southern side of the *E. crystallorophias* centroid, *E. superba* was virtually absent. In a strip between the centroids, the two species were found moderately mixed. However, the breadth of this strip seemed to be related to the percentage ice cover and perhaps with the age structure of the two populations.

The rectangles of *E. superba* concentrations were located around the biomass centroid, but the density in these areas was found to decrease with increasing ice cover. It is possible that *E. superba* finds some reference points in the ice edge that would cause swarms to stop and congregate. However, in similar ice conditions, *E. crystallorophias* does not form such concentrations.

All the results seem to indicate that the two krill populations occupy only partially overlapping domains, move at different spatial scales, and react differently to ice cover. Thus, it seems that the two krill populations generally tend to be confined to separate areas and to avoid substantial mixing through migration. This mechanism is probably activated by some external biological and physical factors caused by ice melting and retreating, but may also include some active internal factors such as inter-specific competition and age effects.

Effects such as fisheries on *E. superba* and climate change could alter those external and internal factors, cause large and unpredictable changes in the distribution and abundance of the two krill species, and hence have direct consequences for predators which feed them.

Changes in patterns of ice melt and ice cover could affect the spatial distribution and abundance of both krill species. Direct removal of parts of *E. superba* population could facilitate the tendency of *E. crystallorophias* population to enlarge its domain to the northern parts of Ross Sea.

In conclusion, an attempt was made to describe krill biomass distribution in relation with ice cover and to produce some evidence on the segregation of the two krill species. Only the 'mechanical side' of the problem has been discussed. Moreover, the acoustic surveys in the Ross Sea occurred in different environmental conditions, and consequently different sampling strategies in the four surveys were used. These may have introduced some bias into the estimation of biomasses and their spatial distributions, but these are very difficult to evaluate.

Further experimental and theoretical work is necessary to understand the physical, biological, and behavioural factors that govern the spatial distributions of the two krill species, how those distributions at krill trophic level influence the trophic level above and are influenced by the trophic level below, and how much the fluctuations of the biomasses and their spatial distributions depend on seasons, years, environmental conditions, and unusual events.

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