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Antarctic krill under perennial sea ice in the western Weddell Sea

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Abstract: The results of underwater observations and sampling of krill (*Euphausia superba*) in the western Weddell Sea during the joint Russian-USA Ice Station Weddell-1 Expedition (11 February–9 June 1992) are presented. Krill was sampled from the same large ice floe composed of both 1- and 2-year ice as it drifted northward for a distance of *c.* 700 km. Abundance estimates for krill under this floe were in the range 0.1–6.25 ind m^{-2}. Krill aggregate in areas where rafting of ice floes and formation of new ice occur, or around a protected diving hole. The krill sampled consisted mainly of furcilia 6 and post-larvae which did not belong to the 0+ group originating in this (1991–92) year, but presumably hatched in the summer season of 1990–91 and developed very slowly so that at the end of the following summer season, larval stages were still present in the population. No increase of the mean krill size was observed during 2.5 months of observation. The role of larval advection for the maintenance of krill population in the Weddell Sea is discussed.

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Introduction

Antarctic krill, ***Euphausia superba*** Dana, 1852 is a remarkable euphausiid species which is capable of changing from a cryopelagic mode of life in winter–spring to a pelagic one in summer (Andriashev 1968, Marschall 1988, Smetacek *et al.* 1990). *E. superba* represents one of the most important trophic links between the primary production of the sea ice flora (Garrison *et al.* 1986) and the underlying water column (Smetacek *et al.* 1990). The Atlantic sector (i.e. the Antarctic Peninsula area, the southern Scotia Sea and the northern and the south-eastern parts of the Weddell Sea) supports the largest krill stock in the Antarctic (Mackintosh 1973, Miller & Hampton 1989).

Marr (1962) and Mackintosh (1972, 1973) have proposed that the water masses coming from the western Weddell Sea and flowing to the east (i.e. the Weddell Drift) are an important source of huge krill concentrations found along the Scotia Sea/Weddell Sea boundary. They were thought to transport krill from another zone of abundance, the East Wind drift, or the Coastal Current. Makarov (1972) and Maslennikov & Solyankin (1980) assumed the cyclonic gyre of the Weddell Sea supported a population of *E. superba.* Although it is not yet clear how krill enter the Weddell Gyre from the east, macroscale water circulation pattern in the gyre (Gouretski & Danilov 1993, Orsi *et al.* 1993, Fahrbach *et al.* 1994) together with krill distribution data suggest that krill enter the eastern and the southern limb of the Weddell Gyre (i.e. the Coastal Current) mainly between 20° and 40°E (Latogursky *et al.* 1990).

While drifting with the Coastal Current along the continental slope, krill may live in close contact with sea ice in the spring (O'Brien 1987, Marschall 1988). The Coastal Current zone in the eastern Weddell Sea is an area of krill reproduction, so krill larvae may be fairly abundant along the continental slope of the Weddell Sea in summer (Fevolden 1980, Hempel & Hempel 1983). However, *E. superba* is very scarce on the south-western Weddell Sea shelf (Siegel 1983, 1986, Piatkowski 1987).

In the Weddell Gyre interior, to the east of 20°W, krill are rather dispersed and not abundant (Mackintosh 1973, Endo *et al.* 1986, Marschall 1988, Spiridonov 1992). In the central Weddell Sea (63–67°S, 20–40°W) krill are very scarce or apparently absent (Siegel 1986, Spiridonov 1992). The scarcity of krill in the central Weddell Sea was the reason why Siegel (1986) doubted the importance of the circular drift of *E. superba* in the Weddell Sea as suggested by previous authors.

Up to now very little information has been collected on the occurrence of Antarctic krill in the western Weddell Sea which is covered with perennial sea ice. The joint Russian-USA drifting Ice Station Weddell-1 (ISW-1) operated in the perennial ice there between 72–65°S and 51–53°W in February–June 1992 (Gordon & Lukin 1992). The ice floe on which the ISW was established was composed of 1- and 2-year old ice with thick snow cover and originated from the eastern Weddell Sea (Lukin & Provorkin 1996). The biological programme at the ISW-1 aimed to determine primary and secondary production rates in the pack ice zone (Fritsen *et al.* 1994, Melnikov in press). Additionally, observations on zooplankton and micronekton in the ice-water interface and in the water column were carried out (Menshenina & Melnikov 1995). In this paper we present the observations on the occurrence, behaviour and population composition of *E. superba* living under permanent sea ice in the area of the

Table I. The data on krill collection during the work of ISW-1. UW – underwater sampling with SCUBA, H – collection in the diving hole, *n* – numbers of specimens collected, m^3 – density of krill calculated per unit volume, m^2 - density of krill per unit area in the ice/water interface.

Sta	date	long S	lat S	method	depth m	*n*	m^3	m^2
1	25.02	71°24'	52°59'	UW	0	25	10.4	2.1
	25.02			UW	5	0	0	-
2	29.02	71°23'	53°11'	UW	0	75	31.2	6.2
3	01.03	71°22'	53°12'	UW	0	21	8.7	1.7
	01.03			UW	5	29	12.1	-
4	04.03	71°20'	53°13'	UW	0	2	0.8	0.2
5	06.03	71°07'	53°39'	UW	0	1	0.4	0.1
6	11.03	70°59'	53°39'	UW	0	3	1.2	0.3
	11.03			UW	5	0	0	-
7	15.03	70°41'	53°37'	UW	0	3	1.2	0.3
	18.03	70°28'	53°27'	H	0	21	-	-
	19.03	70°25'	53°29'	H	0	276	-	-
8	24.03	69°54'	53°38'	UW	0	3	1.2	0.3
	24.03			UW	5	11	4.6	-
	27.03	69°39'	53°46'	H	0	2	-	-
9	02.04	68°56'	53°30'	UW	0	6	2.4	0.6
	02.04			H	0	39	-	-
10	06.04	68°53'	53°32'	UW	0	17	7.0	0.7
	06.04			UW	5	0	0	-
	09.04	68°42'	53°33'	H	0	175	-	-
11	11.04	68°34'	53°38'	UW	0	9	3.6	0.9
12	15.04	68°37'	53°18'	UW	0	0	0	0
13	20.04	68°21'	53°04'	UW	0	129	53.7	10.7
14	21.04	68°20'	53°00'	UW	0	47	10.6	3.9
15	23.04	68°20'	52°56'	UW	0	105	43.7	8.7
	09.05	67°40'	53°16'	H	0	2	-	-
	11.05	67°29'	53°11'	H	0	15	-	-

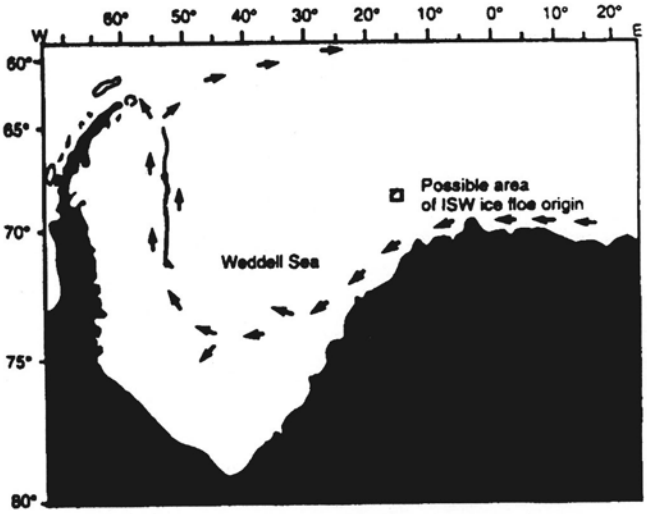

Fig. 1. The ISW-1 drift track shown by the line; a portion between two circles shows the part of the ISW track where observations on Antarctic krill have been performed. The area of possible origin of the ISW ice floe is shown by a box. Arrows show a generalized direction of the Coastal Current in the Weddell Sea (according to Fahrbach *et al.* 1994) partly coincided with the direction of sea ice drift (according to Kottmeier *et al.* 1992).

ISW drift. These data provide new information on krill distribution, advection and growth conditions in the western rim of the Weddell Gyre.

Materials and methods

The cryopelagic fauna was sampled from the ISW ice floe (ice thickness 1.5–2 m) using SCUBA, as a rule, close to midday (maximum light intensity under-ice). Dives at Sts 1–12 were carried out through a hole protected by a tent, at Sts 13–15 they were performed under newly-formed ice in a lead (Table I). During all dives, a 50 m rope marked at each 1 m was stretched on the undersurface of ice in the direction of ice drift. Rather smoothed under-ice relief (although with hummocks) made this possible. Samples were collected by hauling a net (mesh size 180 μm, 40 x 20 cm rectangular frame) in front of a diver with a speed *c.* 20 cm s^{-1} for a distance 30 m along the marked rope (0 m tows). Immediately after completing a tow the net was closed in the water. The sampling in the ice/water interface was complemented with additional horizontal tows at a depth of 5 m using the same net. The volume filtered was roughly calculated by multiplying the mouth area by the distance towed; current velocities were not taken into account. Apart from underwater sampling, krill were collected from the surface in the diving hole using a dip net. Samples were preserved in 4% formalin. Video recording was also undertaken during the dives although not specially to record krill. Videofilms were watched at the ice station and repeatedly at the home institute and used for verifying the data on the size of krill and diver's observations on the size and distribution of krill groups.

In addition to direct observations during dives, a video camera was installed at a depth of *c.* 3 m from the average level of the ice undersurface on the shelf-like ice ledge (originating from both ice melting and washing by the currents) and operated from the diving tent on 17–19 March. The field of view of the camera was 5 x 1 m.

The larvae of *E. superba* collected were identified to a larval stage according to Makarov (1980) and Makarov *et al.* (1986). Their carapace length (CL) was measured from the tip of rostrum along the dorsal mid-line. Total length (TL) was measured from the anterior edge of eye to the end of telson in several specimens (furcilia 6 – post-larvae) in order to obtain a regression of the CL to TL.

Results

Krill abundance, microdistribution and behaviour

The areas where krill were observed during the ISW drift are shown in Fig. 1. The data on the stations where krill were collected using SCUBA along with estimates of krill density per unit of ice surface or per unit of water volume and the data on krill collection in the diving hole are presented in Table I. The data on krill collected in the hole were not used for calculation of any indices of abundance.

During the first dives in late February, a number of solitary krill and small krill groups, i.e. swarms and schools, occurred close to the undersurface of the ice (0–30 cm). The difference between swarms and schools lies in their polarization: a swarm is a non-polarized group, while in a school all animals have similar orientation (Hamner 1984). The horizontal dimension of the groups did not exceed 0.5–1 m (estimates by eye). The density of animals in these groups reached 100 ind m^{-3} assuming an average 20 cm distance between krill individuals. Most krill schools occurred in the areas of ridges or under-ice hummocks on the side opposite to a current direction. Krill behaviour in the schools was very calm, and the animals seemed to orientate towards the current. Krill swarms were not observed to be associated with any particular form of microrelief of the ice undersurface. Dense swarms and schools were not met on a standard hauling track where either solitary specimens or krill in small groups was sampled. During sampling, krill slowly sank down in front of the diver, thus partly escaping capture.

Catches in the 0 m level between 25 February–1 March yielded average abundance of 3.3 ind m^{-2} (s d = 2.0). At the depth 5 m during this period krill were recorded only on 1 March (Table I). The weather during dives in February was rather calm and the ISW floe drifted to the north at an average speed 4.8 km day^{-1} (Lukin & Provorkin 1996).

After 1 March the velocity of ice drift increased averaging in March 8.3 km day^{-1} (Lukin & Provorkin 1996). From 4 March krill became scarce near the bottom surface of ice but a few metres below krill were observed more frequently. With the video camera, it was possible to observe that during a strong drift of the ISW ice floe on 17–19 March (the under-ice current velocity of *c.* 20–30 cm s^{-1}), all animals (including krill) in the upper 3–4 m were either advected passively or swam in a disorderly fashion. They usually disappeared out of the camera's view within a few minutes. Some krill seemed to remain on the undersurface of ice. The density of krill passing in front of the camera was estimated to be *c.* 3–5 ind m^{-2}. The average abundance for the 0 m catches obtained between 4 March–2 April was 0.3 ind m^{-2}(s d = 1.5) or 0.96 ind m^{-3} (s d = 0.32). However, in the tows at 5 m on 24 March, krill abundance reached the higher values of 4.6 ind m^{-3}.

In early April, there was an increase in krill abundance at the ice–water interface (Table I). However, krill was most abundant near the undersurface of young ice in a frozen lead on 20–23 April (mean 7.8 ind m^{-2}, s d = 2.85). The ice drift during these dives was rather slow (*c.* 1 km day^{-1}).

Some observations were made on the moulting behavior of krill. On 29 February many light-coloured individuals were sampled, while from 1–4 March, a large number of moult casts were observed suspended in the water. The moult casts were not recorded again until 24 March, when they were present in the surface catch along with few krill. Underwater observations on feeding showed that krill swarms scraped algae off the walls in channels originating from ice fracturing, ridging and rafting.

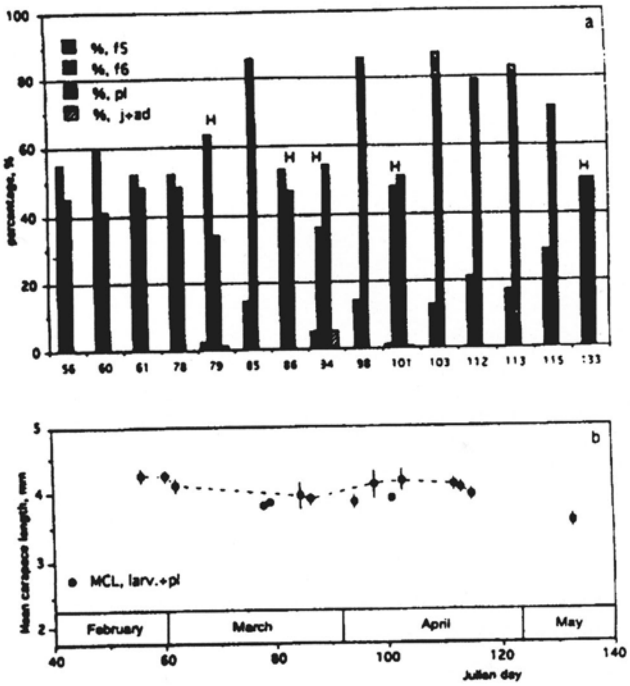

Fig. 2. a. Changes of developmental stage composition. H indicates the sample from the hole. **b.** change in size, CL - mean carapace length of *Euphasia superba*. Bars indicate confidence limits (P<0.01) for the averages (the absence of bars means the confidence limits are smaller than the diameter of dots); the broken line connects the points for underwater (0 m) samples. Other points are the samples from the hole.

Developmental stage and size composition of krill

The krill caught either underwater or in the hole consisted mostly of late stages of furciliae (F 5–6) and small-sized post-larvae. At the start of the observations, the composition of the samples of 25 and 29 February was similar (consisting of only F6 and post-larvae with a slight dominance of the former). In early March, the percentage of F6 decreased (Fig. 2a). From late March, F6 did not exceed 30% of the underwater samples while post-larvae distinctly dominated (Fig. 2a). Adult krill were recorded in the SCUBA samples only once (Sta 6, 11 March). The composition of the krill collected in the diving hole was different. Only in these samples, F5 were found along with occasional adult krill. F6 dominated in the hole samples in March while in April–May the dominance shifted to post-larvae (Fig. 2b).

The regression of the total length (TL) to the carapace length (CL) was calculated (TL = 3.59 CL – 0.9; r^2 = 0.799, n = 13). Using this equation the mean TL of krill sampled was estimated to be in the range 11.8–14.4 mm (Table II). Underwater observations and video confirmed that the size composition of krill under-ice was rather homogeneous, in the range of 10–15 mm.

The krill sampled between 25 February–1 March were larger than krill caught during the following months (Table II, Fig. 2b). F6 from these summer samples were larger than

Table II. Size data on krill collected during the ISW programme. F6 - furcilia 6, PL - post-larvae, Σ - mean for total sample, CL - mean carapace length, Conf - confidence limites for mean carapace length ($P<0.01$), TL - mean total length calculated from equation TL = 3.59 CL - 0.9, n - number of specimens measured.

		F6				PL				Σ
Sts.	date	CL	Conf	TL	n	CL	Conf	TL	n	TL
0 m										
1	25.02	4.04	0.12	13.6	10	4.39	0.13	14.9	18	14.4
2	29.02	4.13	0.09	13.9	45	4.45	0.09	15.1	31	14.4
3	1.03	4.0	0.13	13.5	11	4.21	0.14	14.2	10	13.8
8	24.03	-	-	-	0	3.96	0.26	13.3	5	13.3
10	6.05	-	-	-	0	4.22	0.22	14.2	6	13.8
11	11.04	-	-	-	0	4.23	0.15	14.3	7	14.1
13	20.04	3.74	0.12	12.5	27	4.16	0.09	14.0	102	13.7
14	21.04	3.77	0.2	12.6	8	4.16	0.09	14.0	39	13.8
15	23.04	3.61	0.11	12.1	27	4.06	0.08	13.7	66	13.4
Hole	18.03	3.64	0.11	12.2	11	3.92	0.28	13.2	10	12.6
	19.03	3.75	0.04	12.6	174	4.06	0.06	13.7	94	12.9
	25.03	3.75	0.12	12.6	17	4.0	0.1	13.5	15	13.0
	2.04	3.75	0.12	12.6	14	4.0	0.1	13.5	21	12.8
	9.04	3.72	0.06	12.5	83	4.07	0.05	13.7	89	13.0
	11.05	3.42	0.08	11.4	7	3.65	0.07	12.2	7	11.8

krill at the same stage caught later. The mean carapace length (CL) of F6 in late February was not significantly different from that of post-larvae in autumn. From mid-March to late April, no significant changes in the mean CL of the krill sampled were observed (Table II, Fig. 2a). The last sample from the diving hole (11 May) included even smaller krill than in April (Fig. 2a).

Discussion

Krill aggregation pattern and abundance under-ice

Krill larvae younger than F4 have not been reported to form any type of aggregation but pieces of floating ice may stimulate a behavioural transition from isolated individuals to swarms and, then, to small site-specific schools consisting mostly of F5 and F6 (Hamner *et al.* 1989). In the western Weddell Sea under perennial sea ice the aggregation pattern of larval and early postlarval krill was not very complex, i.e. either solitary krill or small swarms and schools were observed. This pattern is simpler than those described for adult krill under-ice in spring where various types of krill groups have been observed (Spiridonov *et al.* 1985, O'Brien 1987, Marschall 1988, Bergström *et al.* 1990) thus resembling the situation in the krill larval population on the west side of Antarctic Peninsula in early winter (Frazer *et al.* in press). Following the ontogenetic approach of Hamner *et al.* (1989) we might consider the microdistribution pattern observed as rather early stages of schooling development.

Our estimates of F6 and post-larvae abundance under large ice floes composed of both 1- and 2-year ice were in the range 0.1–6.25 ind m^{-2} (Table I). This is an underestimate both because of the escape reaction of krill and since compact and dense swarms and schools of krill were not sampled. However, visual observations and video show that this underestimate is probably less than one order of magnitude. Previous researchers who assessed krill abundance in the ice/water interface used estimates from video (Marschall 1988) and visual counts along transects (Frazer *et al.* in press). These methods appear to give more accurate estimates of krill abundance than net sampling because they cover a more extensive area, do not scare away the animals as much, and can assess krill abundance in areas with a complicated under-ice relief which are inaccessible for net sampling. Nevertheless, under old ice with a smooth under-ice relief, net sampling seems an acceptable technique which also allows a simultaneous collection of other species of the cryophylic fauna (Menshenina & Melnikov 1995) and the assesment of the size composition of krill.

Our figures for krill density approach the estimate of Marschall (1988) for juvenile and adult krill under large old ice floes in the south-eastern Weddell Sea (0.1–21 ind m^{-3}). With regard to overwintering furciliae, similar values (*c.* 2 ind m^{-2}) are reported by Frazer *et al.* (in press) for the the Antarctic Peninsula region in early winter.

The formation of young ice appears to attract krill which aggregate there, as demonstrated by sampling on 20–23 April, and a regular occurence of krill in the ice hole (Table I). Bergström *et al.* (1990) mentioned that in the northern Weddell Sea in spring, the smoothly undulated undersurface of old floes with thick snow cover were almost devoid of krill which were usually present under the thin ice of re-frozen leads.

When comparing the composition of krill collected at the ISW, it is easy to see a difference between the underwater samples (which are rather uniform consisting of F6 and post-larvae) and the samples taken from the hole which are more diverse and include a few adults and F5 (Fig. 2a). Adult krill being good swimmers (Hamner *et al.* 1983, Kils 1983), could have avoided the ISW floe which was rather uniform and smoothly surfaced, but were attracted to the hole as a form of "lead". These observations show that the human requirements for sea ice as a platform for a station are not the same as krill requirements for sea ice as a habitat!

Wind-induced velocity beneath sea ice is probably also an important factor influencing krill behaviour and microdistribution. When the velocity of ice drift increased (after 1 March), krill schools and swarms may have been dispersed by the strong current in the uppermost part of the water column. This resulted in low catches of krill in the ice/water interface (Table I). The schools of small krill were often observed in the area of under-ice hummocks and ridges, i.e. probably in hydrodynamically calm zones. Similar microdistribution and behaviour of hyperiid amphipods were observed under pack ice in the Arctic (Melnikov 1984).

Krill development and growth

Throughout the area of *E. superba* distribution, the dominance of late furcilia and early post-larvae in February–April has not been recorded previously. *E. superba* is a summer–autumnal spawner and its complete larval development in late summer–autumn takes *c.* 4.5 months (for reviews see Menshenina & Spiridonov 1991, Spiridonov 1995). The composition of the population that was observed in the western Weddell Sea in February–April, was typical for late winter–early spring elsewhere (Marr 1962, Daly 1990, Spiridonov 1992). The late furciliae and post-larvae studied certainly could not belong to the 0+ group originating in this (1991–92) year. They must have been born in the summer season of 1990–91, developed very slowly and overwintered (like *E. crystallorophias* – see Makarov *et al.* 1990) at mid-furcilia stages so that at the end of the following summer season, larval stages were still present in the population.

For krill furcilia 3–6 in winter, Daly (1990) estimated an intermoult period to be *c.* 20 days. Assuming one intermoult period to correspond to a larval stage duration, even these developmental rates seem to be too high to explain minor changes in the stage composition of krill from late February–May. Moreover, the moulting event observed on 24 March was not associated with apparent changes of the F6/post-larvae ratio in the following days while after moulting on 29 February, only a small decrease of the F6 percentage was observed. However, a furcilia stage in Euphausiacea sometimes contains several instars which may be the case for *E. superba* (Menshenina 1988), especially under poor feeding conditions. The presence of several instars at late furcilia stages with nearly zero growth during the moults might explain the observed temporal changes in developmental stage composition of krill in the western Weddell Sea.

The lack of evidence for an apparent growth of young krill (in the sense of Mackintosh (1972)), during the ISW work may be explained, of course, by assuming two different cohorts sampled correspondingly from late February until early March and in mid-March and April. This means that the cohort of larger animals sampled in late February could be dispersed by the increasing under-ice current velocity and replaced by smaller krill during the first half of March. However, even if this was the case, the absence of changes in krill carapace length during March–April indicated a very weak growth at least at that time.

The negligible growth of krill late furciliae and post-larvae under perennial sea ice was probably caused by specific feeding conditions in the western Weddell Sea. Since chlorophyl *a* concentration in the water column did not exceed 0.1 $\mu g\ l^{-1}$ (Melnikov in press) the principal food available for the young krill in the area studied was the organic matter produced by ice algae, although the possibility of carnivorous feeding also should not be excluded. Chlorophyll *a* concentration in the bottom ice layer was in the range 6–9 $\mu g\ l^{-1}$ (Melnikov in press) while net algal production in the second-year ice reached 57 mg C $m^{-2} day^{-1}$ (Fritsen *et al.* 1994). However, a pronounced algal-microbial film was not observed on the undersurface of ice. A brine and sea water exchange, which was studied at the ISW (Fritsen *et al.* 1994, Melnikov 1995) may be one of the dominant mechanism of organic carbon flow from ice. If there is no algal-microbial film on the undersurface of ice, krill must search for the algal material drained from ice with brine or for newly-formed "outcrops" (caused by ice fracturing and rafting) which expose algae-rich ice strata. Moreover, the ability of krill larvae to recover algae from sea ice may be limited by ice structure and texture. Laboratory observations on krill larvae behavior in May 1996 (the cruise ANTARKTIS XIII/4 of R/V "*Polarstern*" in the Weddell Sea) did not reveal any contacts between early furciliae and ice pieces which contained diatoms but lacked algal films (Spiridonov, unpublished). The areas of the brine drainage and "outcrops" with available algal material may be patchy and require energy expenditure to search for them. As Daly (1990) pointed out: "The POC measured in ice cores may not adequately describe what is available to consumers foraging along the sea-ice interface".

Advection of krill within the western rim of the Weddell Gyre

Krill spawning is hardly possible in ice-covered waters because the final stages of oocyte maturation require feeding by krill females on phytoplankton in the water column (Spiridonov 1995). Therefore, the furciliae and post-larvae of the 1990–91 generation which were observed in the western Weddell Sea in summer 1992 could not be krill of local origin that remained in the area.

The south-eastern Weddell Sea along with adjacent waters of the Lazarev Sea were for a long time considered as the major area of krill reproduction in the high latitudes of the Atlantic sector (Fevolden 1980, Hempel & Hempel 1983, Siegel 1983, Makarov & Menshenina 1989). Krill larvae are subject to the advection with the Coastal Current along the continental slope to the west (Hempel & Hempel 1983). Beginning from 35–40°W, the larvae may be transported to the north following the retroflection of the Coastal Current (Fahrbach *et al.* 1994).

Krill furciliae which have hatched in the south-eastern Weddell Sea, may reach the starting point of the ISW drift either by being advected by currents or following the ice drift. Very rough estimates based on instrumental measurements of current velocities (3.5–6 km day^{-1}; Fahrbach *et al.* 1994) and the velocities of ice drift (8.6–17.2 km day^{-1}; Kottmeier *et al.* 1992) show that as passive drifters, krill larvae may cover the distance from Kapp Norwegia to the western slope of the Antarctic Peninsula in 8–12 months.

Regardless of the source of krill transported by the western rim of the Weddell Gyre, this transport itself may be a regular event. Siegel (1986) mentioned the occurrence of krill juveniles ("Eiskrill") in the north-western Weddell Sea (as small as 18 mm in length in autumn) and suggested that this group could originate from the south-eastern Weddell Sea. The presence of these small juveniles in the north-western Weddell Sea in other autumn seasons was confirmed by Daly & Macaulay (1991). The transport of small juveniles to the northern Weddell Sea probably reaches a maximum in autumn (which is determined by a short spawning season in the place of this group's origin – see Spiridonov 1995) as suggested by Makarov (1973). The transport of krill within the Weddell Gyre appears to be circular although the conditions in the western Weddell Sea are far from the optimum for the krill population transported. The relative contribution of the circular drift of *E. superba* in the Weddell Gyre to the maintenance of huge krill concentrations in the northern Weddell-southern Scotia Sea has still to be evaluated. It may vary annually, depending, in particular on ice conditions in the southern Weddell Sea which have multiple effects on krill reproductive timing and development of the larval population.

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References

Andriashev, A.P. 1968. The problem of the life community associated with the Antarctic fast ice. *In Symposium on Antarctic oceanography* (Santiago, 1966). Cambridge: SCAR, 147-155.

Bergström, B.I., Hempel, G., Marschall, H-P., North A., Siegel V. & Strömberg, J-O. 1990. Spring distribution, size composition and behavior of krill *Euphausia superba* in the western Weddell Sea. *Polar Record*, 26, 85-89.

Daly, K. 1990. Overwintering development, growth and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. *Limnology and Oceanography*, 35, 1564-1576.

Daly, K. & Macaulay, M. 1991. Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the antarctic marginal ice zone. *Marine Ecology Progress Series*, 79, 37-66.

Endo, Y., Imaseki, T. & Komaki, Y. 1986. Biomass and population structure of Antarctic krill *(Euphausia superba)* collected during SIBEX II Cruise of R.V. "*Kaio-Maru*". *Memoirs of National Institute of Polar Research, Tokyo, Special Issue*, 44, 107-117.

Fahrbach, E., Rohardt, G., Schröder M. & Strass, V. 1994. Transport and structure of the Weddell Gyre. *Annalae Geophysicae*, 12, 840-855.

Fevolden, S. 1980. Krill off Bouvetöya and in the southern Weddell with a description of larval stages of *Euphausia crystalloroph.* *Sarsia*, 65, 149-162.

Frazer, T.K., Quetin L.B. & Ross R.M. In press. Abundance distribution of larval krill, *Euphausia superba*, associated with an sea ice in winter. *In* Battaglia, B., Valencia, J. & Walton, D.W *eds. Antarctic communities: species, structure and survi* Cambridge: Cambridge University Press.

Fritsen, C.H., Lytle, V.I., Ackley, S.F. & Sullivan, C.W. 1994. Aut bloom of Antarctic pack ice algae. *Science*, 266, 782-784.

Garrison, D.L., Sullivan, C.W. & Ackley, S.F. 1986. Sea ice micro communities in Antarctic. *BioScience*, 36, 243-250.

Gordon, & Lukin, V. 1992. Ice Station Weddell #1. *Antarctic Jour of the US*, 27 (5), 97-99.

Gouretski, V.V. & Danilov, A.I. 1993. Weddell Gyre: structure of eastern boundary. *Deep-Sea Research*, 40, 561-582.

Hamner, W.M. 1984. Aspects of schooling in *Euphausia supe* *Journal of Crustacean Biology*, 4 (Spec.1), 67-74.

Hamner, W.M., Hamner, P.P. & Obst, B.S. 1989. Field observatio the ontogeny of schooling of *Euphausia superba* furciliae an relationship to ice in Antarctic waters. *Limnology and Oceanogra* 34, 451-456.

Hamner, W.M., Hamner, P.P., Strand, S.W. & Gilmer, R.W. 19 Behaviour of Antarctic krill, *Euphausia superba*: chemorecept. feeding, schooling and molting. *Science*, 220, 433-435.

Hempel, I. & Hempel, G. 1983. Distribution of euphausiid larvae in southern Weddell Sea. *Meeresforschung*, 29, 253-266.

Kils, U. 1983. Swimming and feeding of Antarctic krill, *Eupha.* *superba* - some outstanding energetics and dynamics, some un morphological details. *In* Schnack, S.B., *ed. On the biology of* Euphausia superba. *Berichte zur Polarforschung*, 4, 130-155.

Kottmeier, C., Frieden, O.J. & Roth, R. 1992. Wind forcing and motion in the Weddell Sea region. *Journal of Geophysical Resea* 97, 20373-20383.

Latogursky, V.I., Maklygin, L.G., Fedotov, A.S., Makarov, R.R. Solyankin, E.V. 1990. Distribution and pecularities of *Eupha.* *superba* Dana population structure in the area of the Weddell Gyre adjacent waters. *In* Danilov, A.I., Makarov, R.R. & Solyankin, E *eds. Investigations of the Weddell Gyre. Oceanographic condi and pecularities of development of plankton communities.* Mos VNIRO Publication, 183-206 [in Russian].

Lukin, V. & Provorkin, A. In press. Peculiarities of the large-scale ice dynamics withiSn the Weddell Gyre. *In* Melnikov, I.A., *Biology of the Western Weddell Sea*. Moscow: Nauka. [in Russi

Mackintosh, N.A. 1972. Life cycle of Antarctic krill in relation to ice water conditions. *Discovery Reports*, 36, 1-94.

Mackintosh, N.A. 1973. Distribution of post-larval krill in the Anta *Discovery Reports*, 36, 95-156.

Makarov, R.R. 1972. Life cycle and pecularities of distributio *Euphausia superba* Dana. *Trudy VNIRO*, 77, 85-92 [in Russia

Makarov, R.R. 1973. Peculiarities of the autumnal state of the popul of *Euphausia superba*. *Okeanologia*, 13, 334-338 [in Russian]

Makarov, R.R. 1980. Larval development of the Antarctic euphaus *BIOMASS Handbook*, 3, 1-13.

Makarov, R.R. & Menshenina, L.L. 1989. On the distributio euphausiid larvae in the Antarctic waters. *Oceanology*, 29, 623-

Makarov, R.R., Menshenina, L.L. & Spiridonov, V.A. 1986. *Metho recommendations to the study of Antarctic euphausiid la* Moscow: VNIRO Publication, 104 pp. [in Russian].

Makarov, R.R., Menshenina, L.L., Timonin, V.P. & Shurunov, 1990. Larval ecology and reproduction of Euphausiidae in the Sea. *Biologia Moria*, 1990(No3), 38-45 [in Russian].

Marr, J.W.S. 1962. The natural history and geography of Antarctic *(Euphausia superba* Dana). *Discovery Reports*, 52, 33-464.

Marschall, H-P. 1988. The overwintering strategy of Antarctic under the pack ice of the Weddell Sea. *Polar Biology*, 9, 129-1

Maslennikov, V.V. & Solyankin, E.V. 1980. Role of water dynamics in the maintenance of an *Euphausia superba* population in the Weddell Sea. *Oceanology*, 20, 192-195.

Melnikov, I.A. 1984. On the peculiarities of distribution and behavior of the common species of cryopelagic fauna under the drifting Arctic ice. *Zoologicheskiy Zhurnal*, 63, 86-89 [in Russian].

Melnikov, I.A. 1995. An *in situ* experimental study of Antarctic young sea ice formation on an Antarctic lead. *Journal of Geophysical Research*, 100(C3), 4673-4680.

Melnikov, I.A. In press. Ecology of the western Weddell Sea. *In* Battaglia, B., Valencia, J. & Walton, D.W.H., *eds. Antarctic communities: species, structure and survival*. Cambridge: Cambridge University Press.

Menshenina, L.L. 1988. *Early ontogenesis and ecology of the Antarctic euphausiid larvae*. PhD Thesis, P.P. Shirshov Institute of Oceanology, Moscow, 23 pp. [in Russian].

Menshenina, L.L. & Melnikov, I.A. 1995. Under-ice zooplankton of the western Weddell Sea. *Proceedings of NIPR Symposiums on Polar Biology*, 8, 126-138.

Menshenina, L.L. & Spiridonov, V.A. 1991. Rates of larval development of the Antarctic euphausiid species. *Oceanology*, 31, 621-627.

Miller, D.G.M. & Hampton, I. 1989. Biology and ecology of Antarctic krill *(Euphausia superba* Dana): A review. *BIOMASS Scientific Series*, 9, 1-166.

O'Brien, D.P. 1987. Direct observations of the behavior of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic spring of 1985. *Journal of Crustacean Biology*, 7, 437-448.

Orsi, A.H., Nowlin Jr., W.D. & Whitworth III, T. 1993. On the circulation and stratification of the Weddell Gyre. *Deep-Sea Research*, 40, 172-203.

Piatkowski, U. 1987. Zoogeographische Untersuchungen und Gemeindschaftanalysen an antarktischen Makroplankton. *Berichte zur Polarforschung*, 34, 1-150.

Siegel, V. 1983. Investigations of krill (*Euphausia superba*) in the southern Weddell Sea. *Meeresforschung*, 29, 244-252.

Siegel, V. 1986: Untersuchungen zur Biologie des antarctischen Krill, *Euphausia superba*, im Bereich der Bransfield Strasse und angrenzender Gebiete. *Mitteilungen des Instituts für Seefisherei Hamburg*, 38, 1-244.

Smetacek, V., Scharek, R. & Nöthig, E-M. 1990. Seasonal and regional variation in the pelagial and its relationship to the life history of krill. *In* Kerry, K.B. & Hempel, G., *eds. Antarctic ecosystems. Ecological change and conservation*. Berlin: Springer Verlag, 103-114.

Spiridonov, V.A. 1992. Distribution and biological properties of the Antarctic krill *Euphausia superba* Dana during Winter Weddell Gyre Study (WWGS) 1989. *Proceedings of NIPR Symposium on Polar Biology*, 5, 55-64.

Spiridonov, V.A., 1995. Spatial and temporal variability of reproductive timing of Antarctic krill, *Euphausia superba* Dana. *Polar Biology*, 15, 161-174.

Spiridonov, V.A., Gruzov, E.N. & Pushkin, A.F. 1985. Investigations of schools of Antarctic krill, *Euphausia superba* under-ice. *Zoologicheskiy Zhurnal*, 64, 1655-1661 [in Russian].