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Abundance, sizes and developmental stages of larval krill, *Euphausia superba*, during winter in ice-covered seas west of the Antarctic Peninsula

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Larval krill were sampled west of the Antarctic Peninsula during three winter cruises: September 1991, June 1993 and September 1993. Larval abundances were estimated from net catches and compared directly to visual counts (made by a SCUBA diver) of larvae occupying the ice habitat at the same sampling stations. The number of larvae per square meter sampled with nets was more often greater than that observed by the diver, irrespective of the sampling period. However, comparisons of larval abundance within sampling periods were not statistically significant. Larval krill collected by divers were significantly larger than those collected with nets for each of the three cruises. The stage composition of larval krill also depended on the collection method: net-collected samples contained a disproportionately high number of early furcilia larvae in June 1993 (early winter), and a disproportionately low number of early juveniles during September 1991 and 1993 (late winter). These results lead us to suggest that larval/juvenile krill occupy both the water column and sea ice habitat during the austral winter, and that there are often differences in the sizes and developmental stages of the two groups. For larval krill that occupied the sea ice habitat, aggregations were larger and more numerous during late winter than in early winter. In addition, larvae within aggregations occupied structurally complex microhabitats, provided by over-rafted ice floes, more often than they occupied smooth, downward-facing ice surfaces where ice was not over-rafted.

INTRODUCTION

Larval krill have been observed to occupy the underside of annual sea ice in the Southern Ocean during winter and are known to feed on ice-associated biota (Garrison *et al.*, 1986; Kottmeier and Sullivan, 1987; Quetin and Ross, 1988; Stretch *et al.*, 1988; Hamner *et al.*, 1989; Daly, 1990; Daly and Macaulay, 1991; Ross and Quetin, 1991; Quetin *et al.*, 1994; Frazer, 1996; Frazer *et al.*, 1997a). Early observations of krill under sea ice were qualitative and the evidence for the importance of sea ice to the development of larval krill was based on their physiological requirements. On physiological grounds, Ross and Quetin suggested that larval krill are obligatory inhabitants of the under-ice habitat and depend on ice-associated biota for winter survival (Ross and Quetin, 1991). In addition, from direct observations of larval krill under sea ice, Hamner *et al.* suggested that sea ice facilitates the aggregation of larval krill, providing a mechanism for school formation (Hamner *et al.*, 1989).

Quantitative observations of krill larvae beneath ice at different times during the seasonal advance and retreat of sea ice or between winters are lacking. Quantitative observations and collections of krill in austral winter are problematic because of the close association of larval krill with sea ice surfaces, and the relative partitioning of larvae between the ice habitat and the water column below the ice is not yet known [cf. (Smetacek *et al.*, 1990)]. Direct counts of larval krill by divers indicate that krill can be numerous under the ice, particularly in late winter (Menshenina and Melnikov, 1995; Quetin *et al.*, 1996; Frazer *et al.*, 1997a). However, larval krill are also captured with nets from the water column in this same habitat type (Guzman, 1983; Daly and Macaulay, 1991). No direct comparisons of these abundance estimates and/or the two methods have been made, although Quetin *et al.* (Quetin *et al.*, 1992) and Frazer *et al.* (Frazer *et al.*, 1997a) suggested that nets may undersample larvae in ice-covered seas.

This study compares the abundance, sizes and developmental stages of krill larvae as estimated by divers and from net tows during three cruises west of the Antarctic Peninsula in winter. Comparisons of size– and stage–frequency distributions for net-collected and diver-collected samples were used to test a prediction that early-stage furcilia are absent from the ice habitat. Additional data on the orientation of larval krill to the structure of the ice habitat were analyzed to understand fine-scale spatial heterogeneity of larval distributions.

METHOD

Study area

Samples were collected from ice-covered seas west of the Antarctic Peninsula during September 1991, June 1993 and September 1993 (Figure 1). Diver- and net-collected samples at any particular station were generally within 5 km of each other. During September 1991 and June 1993, sampling was restricted to a relatively small area offshore of Adelaide Island over the continental shelf. During September 1993, a mesoscale survey was conducted between Anvers Island and Marguerite Bay; this area is in the center of the Peninsula grid (Waters and Smith, 1992) of the Palmer Long-Term Ecological Research (LTER) site. Palmer LTER sampling stations are primarily over the continental shelf, although a few are over the slope.

Diver-collected samples

Quantitative visual census

Larval krill associated with annual sea ice were censused visually with SCUBA. At each sampling station (Figure 1), larvae were censused along 2-m wide by 30-m long transects to a depth of 3 m below the nearest ice surface. Usually, three replicate transects at each sampling station were completed during a single 30- to 60-min dive. Additional details and discussion of the method have been reported by Frazer *et al.* (Frazer *et al.*, 1997a). Larval

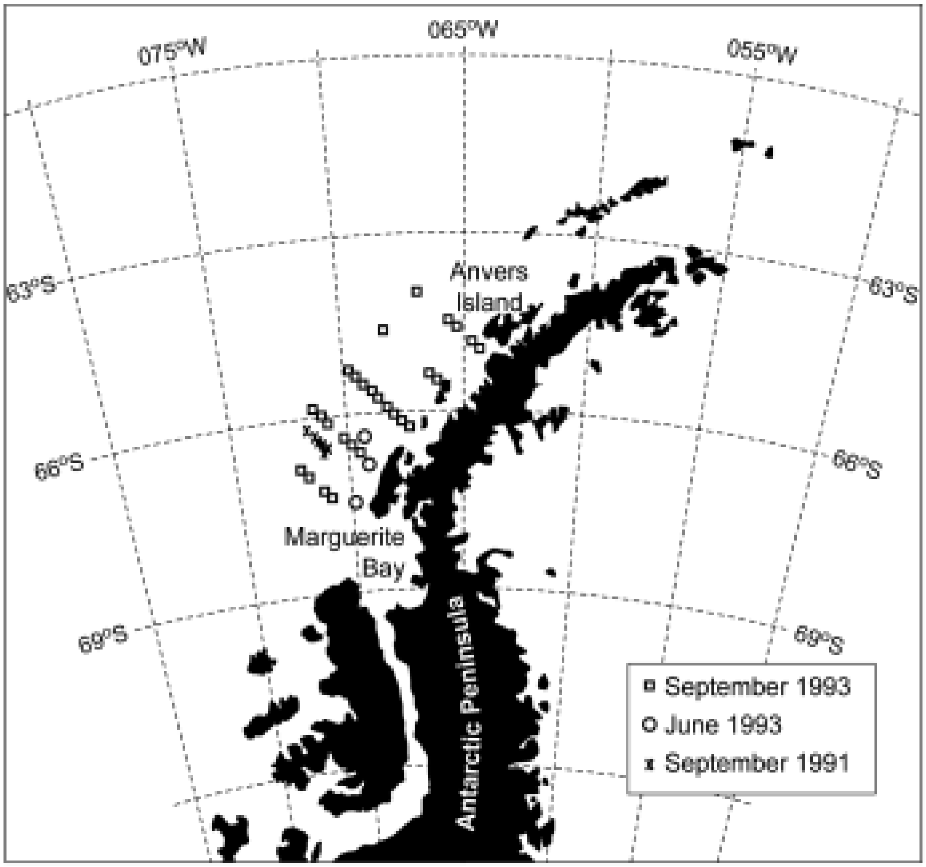

Fig. 1. Sampling stations occupied during September 1991 (X), June 1993 (○) and September 1993 (□). All sampling was conducted west of the Antarctic Peninsula in a region between Anvers Island and Marguerite Bay.

abundances were calculated as the number of individuals per square meter and are reported here as the mean of replicate transect counts at each sampling station.

Size– and stage–frequency distributions

Larval krill collected for analyses of size distribution and stage frequency were collected at sampling stations corresponding to those for diver censuses (Figure 1). Collections were made either on the census dive or on subsequent dives at the same station. Larval krill were captured by divers with hand-held aquarium nets (mesh size ~680 μm), and collections were taken from discrete patches of larvae (generally >100 individuals). All of the larval krill, or a random subsample (minimum number = 88) from each collection, were staged according to Fraser (Fraser, 1936), and measured under a dissecting microscope for total length (TL; tip of the rostrum to the end of the uropod) to the nearest 0.1 mm. Measurements were recorded from fresh specimens, as well as animals preserved in 10% buffered formalin.

Characterization of patch structure

Locations of discrete aggregations of larval krill (>2 larvae) associated with sea ice were recorded to the nearest 1 m along each 30-m transect, and the numbers of individuals within each aggregation estimated as part of the *in situ* census method described above. The spatial orientation of the ice surface(s) occupied by larval krill within each aggregation was recorded (see Figure 2).

In some instances, larval krill within an aggregation did not exhibit an obvious orientation to any ice surface, although individuals within the group were generally <0.3 m from one or more ice surfaces. Isolated individuals (89 total observations; not included in subsequent analyses) and small clusters of larval krill (<10 individuals) in close proximity, but without obvious orientation to one another, were sometimes observed swimming in the water column <1 m from overlying sea ice. No larger aggregations (>10 individuals) of larval krill were observed swimming in a directed manner below sea ice, i.e. no polarized schools were seen [cf. (Hamner *et al.*, 1989)]. Discrete patches of larvae were categorized as very small (<10 larvae), small (tens of larvae), medium (hundreds of larvae) or large (thousands of larvae). A very large aggregation of larval krill (>10 000 individuals) was observed on only one occasion (September 1991). This observation was placed into the 'large aggregation' category for subsequent analyses.

Net sampling

Collection of larval krill

Oblique tows, with nets attached to rectangular frames, were generally made to 300 m (Table I). All tows in

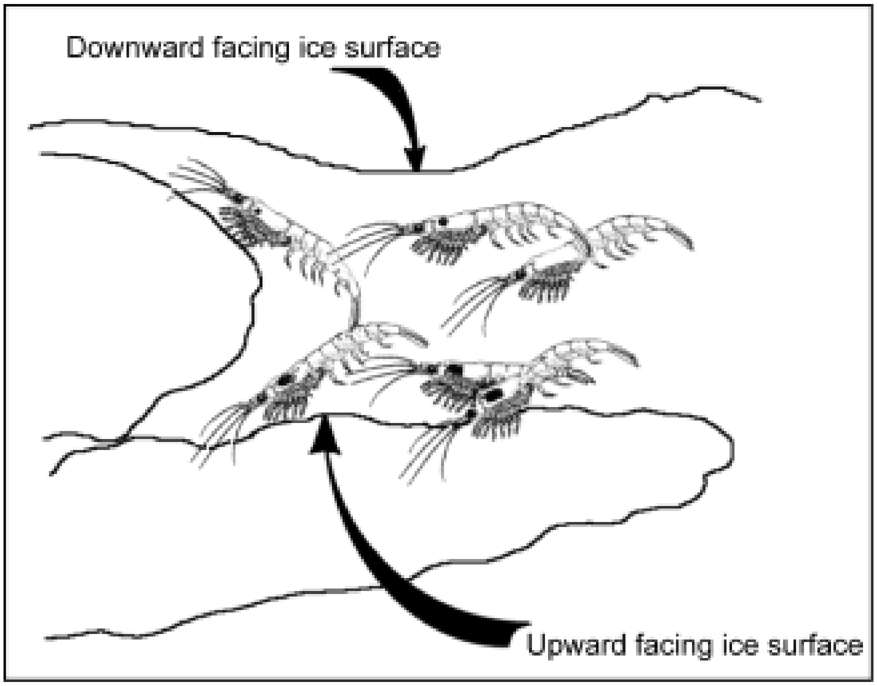

Fig. 2. Aggregations of larval krill (late-stage furcilia are depicted here) tend to occupy upward-facing ice surfaces and/or more structurally complex habitats (see the text) that occur, for example, when pans of sea ice are over-rafted. Note that krill do not generally occupy downward-facing ice surfaces, particularly if there is no additional structural character to the ice.

Table I: Summary of cruises, dates and locations where quantitative sampling was conducted

Cruise	Diver-collected data				Net-collected data				
	Date	Lat. (°S)	Long. (°W)	Larvae per (m^2)	Date	Lat. (°S)	Long. (°W)	Larvae per (m^2)	Notes
WCIV	17 Sept 91	66.1833	071.7	18.21	17 Sept 91	66.182	071.680	260.50	5
WCIV	18 Sept 91	66.317	071.383	6.19	18 Sept 91	66.317	071.390	162.50	5
WCIV	19 Sept 91	66.450	071.1	14.4	20 Sept 91	66.468	071.112	12.38	4
WCIV	22 Sept 91	66.667	071.083	2.99	24 Sept 91	66.599	071.086	38.92	4
WCIV	22 Sept 91	66.517	070.917	20.4	21 Sept 91	66.529	070.925	15.92	4
WCIV	26 Sept 91	66.400	071.283	95.62	26 Sept 91	66.396	071.280	3.54	4
WCV	08 June 93	67.45	069.867	1.57	08 June 93	66.442	069.287	0.00	2
WCV	13 June 93	66.853	069.183	0.02	12 June 93	66.778	069.286	32.50	2
WCV	17 June 93	66.43	069.283	4.52	15 June 93	67.421	069.892	15.00	3
LTER93C	21 Sept 93	67.380	070.907	46.02	NO NET COLLECTION			N/A	
LTER93C	21 Sept 93	67.248	071.221	19.08	NO NET COLLECTION			N/A	
LTER93C	22 Sept 93	66.982	071.838	12.80	NO NET COLLECTION			N/A	
LTER93C	22 Sept 93	66.848	072.142	42.17	NO NET COLLECTION			N/A	
LTER93C	17 Sept 93	66.634	069.555	5.76	17 Sept 93	66.641	069.570	2.46	1
LTER93C	16 Sept 93	66.505	069.867	0.74	16 Sept 93	66.516	069.889	24.82	1
LTER93C	16 Sept 93	66.375	730.175	14.40	16 Sept 93	66.390	070.200	12.17	1
LTER93C	15 Sept 93	66.245	070.481	1.17	NO NET COLLECTION			N/A	
LTER93C	15 Sept 93	66.114	070.783	6.49	15 Sept 93	66.104	070.769	12.17	1
LTER93C	14 Sept 93	66.982	071.082	1.81	15 Sept 93	65.968	071.067	1.91	1
LTER93C	14 Sept 93	66.850	071.337	1.25	14 Sept 93	65.836	071.358	8.36	1
LTER93C	30 Aug 93	63.966	066.856	7.99	30 Aug 93	63.955	066.834	29.04	1
LTER93C	01 Sept 93	64.575	065.341	45.69	01 Sept 93	64.581	065.330	21.44	1
LTER93C	01 Sept 93	64.455	065.650	37.1	01 Sept 93	64.461	065.626	22.25	1
LTER93C	03 Sept 93	64.815	064.717	21.78	03 Sept 93	64.807	064.715	144.99	1
LTER93C	04 Sept 93	64.610	068.239	13.12	04 Sept 93	64.613	068.308	2.53	1
LTER93C	07 Sept 93	65.357	066.464	11.04	07 Sept 93	65.348	066.452	50.05	1
LTER93C	08 Sept 93	65.479	066.149	3.72	06 Sept 93	65.484	065.477	7.09	1
LTER93C	09 Sept 93	66.254	067.337	5.42	NO NET COLLECTION			N/A	
LTER93C	09 Sept 93	66.129	067.655	67.44	NO NET COLLECTION			N/A	
LTER93C	10 Sept 93	66.004	067.971	8.89	10 Sept 93	66.008	067.940	21.03	1
LTER93C	11 Sept 93	65.878	068.283	14.22	11 Sept 93	66.876	068.279	106.98	1
LTER93C	12 Sept 93	65.751	068.592	14.50	11 Sept 93	65.763	068.582	28.18	1
LTER93C	13 Sept 93	65.496	069.202	7.93	12 Sept 93	65.493	069.199	3.84	1
LTER93C	13 Sept 93	65.367	069.502	11.64	13 Sept 93	65.365	069.492	0.00	1
LTER93C	13 Sept 93	65.238	069.800	12.71	13 Sept 93	65.228	069.770	127.32	1

Estimates of larval abundance as determined by divers and from net catches are arranged as paired comparisons for each sampling station.

1. Oblique net tow (0–300 m), fished both up and down, 333-μm mesh, 1-m^2 rectangular net.
2. Vertical net tow (0–300 m), fished both up and down, 505-μm mesh, 1-m diameter ring net.
3. Vertical net tow (0–150 m), fished both up and down, 505-μm mesh, 1-m diameter ring net.
4. Vertical net tow (0–300 m), fished both up and down, 505-μm mesh, 0.6-m diameter bongo net.
5. Oblique net tow (0–300 m), fished both up and down, 333-μm mesh, 2-m^2 rectangular net.

September 1993 were with a 1 square meter (mouth area) net (333 μm mesh). In September 1991, a 1 × 2 m frame with paired nets (1-m diameter, 505-μm mesh) was towed obliquely at two stations, and a bongo frame with paired nets (0.6-m diameter, 505-μm mesh) was towed vertically at four of six stations. During June 1993, a 1-m diameter ring net (505-μm mesh) was fished vertically to collect larval krill. In all cases, nets were rigged with a General

Oceanics flow meter, and fished both up and down without an opening and closing mechanism.

Differences in net sampling methods among the three cruises were a consequence of sampling regimes established for other objectives or to accommodate variable ice conditions, as during September 1991. Nets with mesh sizes of 333 and 505 μm will both retain larval krill >3 mm in length, and there are no reported data to suggest that any of the above methods are more or less selective for larval krill in the Southern Ocean. Vertical tows made in heavy sea ice filter less water than oblique tows to comparable depths, but differences in escape responses of larval krill were not anticipated.

Quantitative catch information

For vertical net tows, the number of larvae captured was expressed per square meter over the depth range sampled, i.e. generally 0–300 m (Table I). For each oblique net haul, the entire catch of larval krill was enumerated and the volume of water filtered determined so as to derive an estimate of the number of larval krill per cubic meter. The number of larvae per cubic meter for each catch was then standardized so as to reflect the number of individuals per square meter over the integrated depth range of the tow (generally 0–300 m). Larval abundances were expressed as the number per square meter of sea surface, assuming that the maximum depth of occurrence or the full depth of the water column had been sampled. Larval abundance estimates for the entire water column were then compared directly with estimates made by a diver of larval krill occupying the shallow layer associated with the ice habitat in the same general location.

Sizes and stage frequency distributions

Larval krill used for analyses of size distribution and stage frequency were from the same net collection used for the abundance estimates above (see Figure 1). All of the larval krill, or a random sample (minimum number = 35) from each collection, were staged and measured for total length as described above for diver-collected samples. Measurements were of animals preserved in 10% buffered formalin.

RESULTS

Krill abundance (diver census versus net catch)

A sign test (Sokal and Rohlf, 1981) was employed to determine whether either of the above methods consistently provided a greater estimate of larval numbers per square meter. Paired estimates of larval krill abundance, from direct diver observation and net sampling, were used to test a null hypothesis that positive and negative differences occurred in equal proportions, i.e. empirical data were compared with expected binomial distributions. Data were log transformed prior to analysis. A similar non-parametric procedure, Wilcoxon's signed-ranks test for two groups, arranged as paired comparisons (Sokal and Rohlf, 1981), was used to determine whether mean abundance estimates differed for the two sampling procedures. Statistical significance was accepted at the 5% level.

Estimates of larval krill abundance as determined by net sampling techniques were usually greater than those obtained by direct observation at the same location (Figure 3). However, paired comparisons made within cruises (September 1991 and 1993) were not statistically significant (sign-test, $P > 0.05$ for each year). Only three paired comparisons were available for June 1993, an early winter sampling period, and in two instances the greater estimate of larval krill abundance resulted from a net sample (see Table I). Although the mean numbers of larval krill per square meter, as estimated from net catch data, were consistently greater than estimates made by divers (Table II), statistical comparisons were not significant ($P > 0.05$ for all three cruises).

Larval size distributions (diver census versus net catch)

Mean sizes of larvae collected by divers and larvae sampled with nets were compared with a T-test assuming equal variances. Samples were pooled into groups of either diver- or net-collected larvae within each of the three sampling periods for each comparison. Statistical significance was accepted at the 5% level.

Within each of the three cruises, larval krill collected by divers were significantly larger (mean TL) than those sampled with nets (Figures 4–6). In addition, a comparison of the mean lengths of larval krill collected by divers during June 1993 and September 1993 showed that larval

Table II: Median number of larval krill for all samples collected during each of the three cruise periods

	June 1993	September 1993	September 1991
Net estimate	24.00	26.03	27.42
	(0.00–52)	(0.00–144.99)	(3.54–260.50)
Diver estimate	1.57	11.04	16.31
	(0.02–4.52)	(0.74–45.69)	(2.99–95.62)

Ranges are given in parentheses. None of the within sampling period comparisons yielded statistically significant results (Wilcoxon signed rank test, $P > 0.05$).

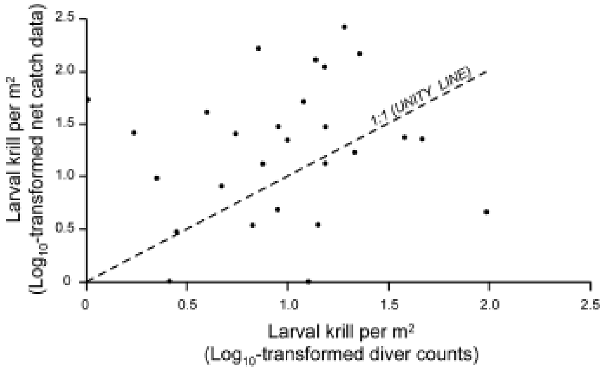

Fig. 3. A comparison of larval krill abundances as estimated by direct observation and from net catch information. Abundance data have been $\log_{10}$-transformed. Paired estimates resulting from both methods are expressed as the number of larval krill per square meter, although net data reflect the number of larval krill over an integrated depth range (generally 0–300 m, see Table I), and diver estimates are only of those animals associated with the surfaces of sea ice. Points above the unity line occur when net estimates exceed counts made by divers at a given sampling station, and points below the line occur when counts made by divers exceed the corresponding net estimate.

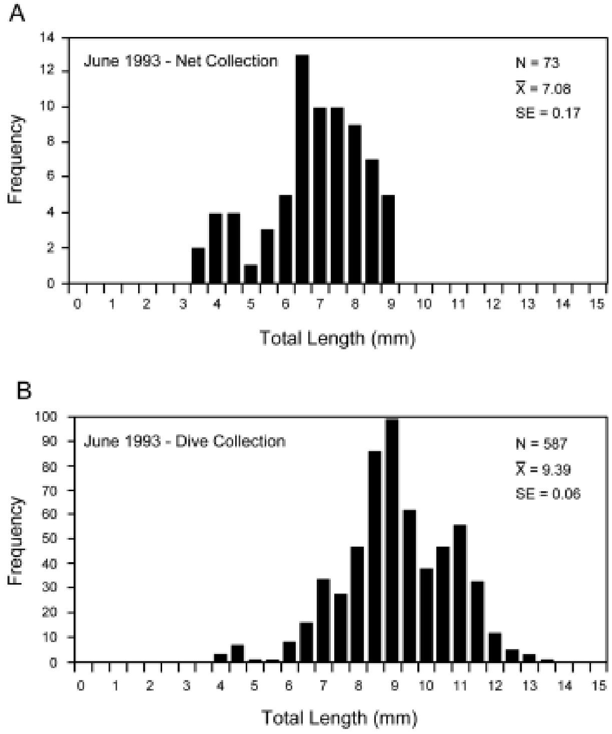

Fig. 4. Size–frequency distributions for larval krill collected with nets (**A**) and by divers (**B**) during June 1993. Descriptive statistics are as follows: *N*, total number of krill measured; $\bar{X}$, mean size (TL) of larvae; SE, the standard error of the mean estimate. Note the scale differences between (A) and (B).

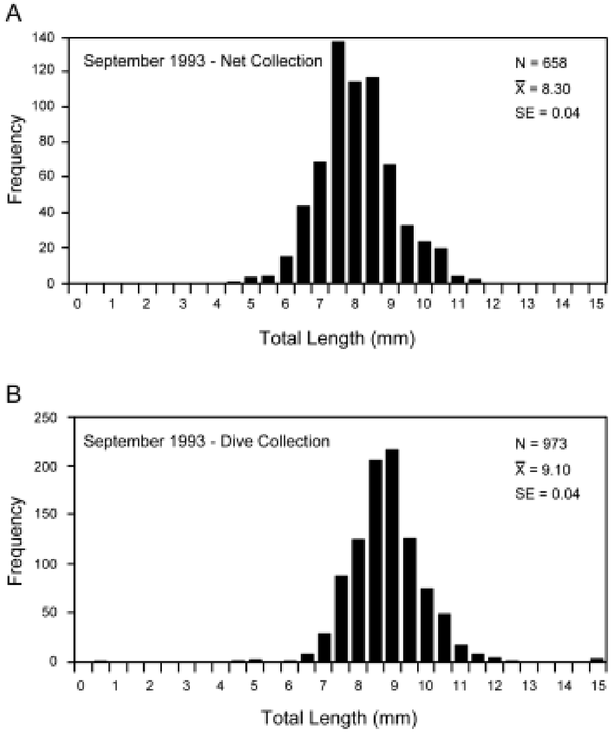

Fig. 5. Size–frequency distributions for larval krill collected with nets (**A**) and by divers (**B**) during September 1993. Descriptive statistics are as in Figure 4.

krill captured during early winter (June 1993) were significantly larger than those collected during late winter of the same year (September 1993) (*T*-test, $P < 0.001$).

Larval stage frequency distributions (diver census versus net catch)

The larval stage frequency distributions for pooled diver- and net-collected samples were compared with a χ^2 test (Sokal and Rohlf, 1981) for each cruise. Statistical significance was accepted at the 5% level.

Within sampling periods, the stage composition of larval krill was dependent on the collection procedure. Net-collected samples contained a disproportionate number of early furcilia larvae during early winter, i.e. June 1993 (Figure 7), but during both late winter sampling periods, September 1991 and September 1993, nets sampled more juveniles than were expected (Figures 8 and 9); expected values for each cruise were generated from pooled dive- and net-collected data.

Patch characteristics of larval krill in the ice habitat

The mean number of larval aggregations, i.e. patches, per transect (2-m wide × 30-m long) for each sampling station

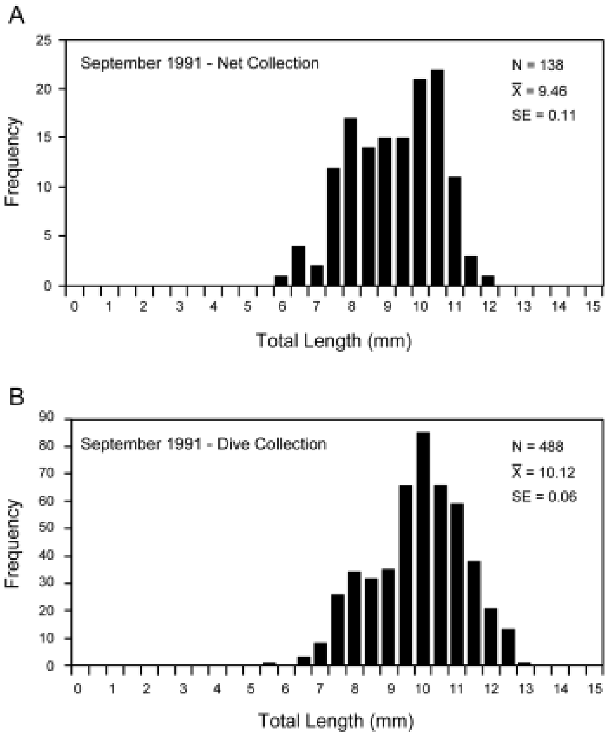

Fig. 6. Size–frequency distributions for larval krill collected with nets (**A**) and by divers (**B**) during September 1991. Descriptive statistics are as in Figure 4.

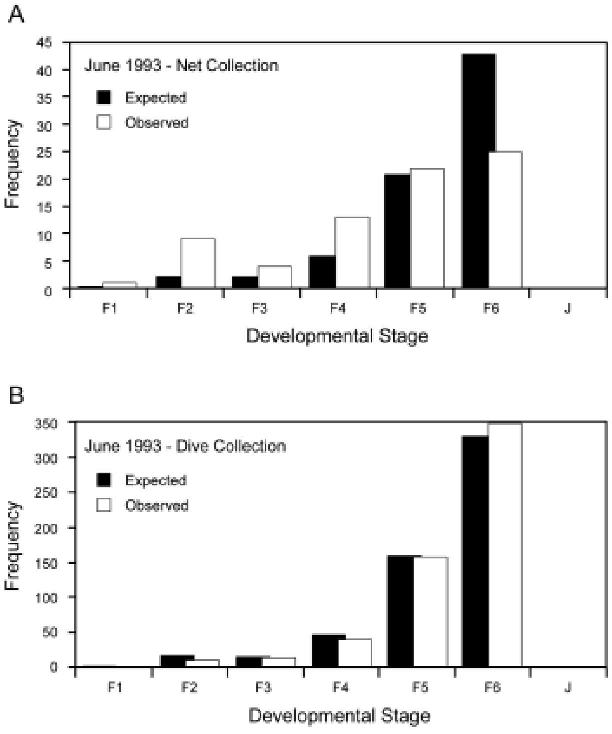

Fig. 7. Expected and observed frequencies of different larval stages collected with nets (**A**) and by divers (**B**) during June 1993. Furcilia stages 1–6 are abbreviated as F1–F6. The two observed frequency distributions are significantly different at the $P < 0.001$ level ($\chi^2 = 44.19$, d.f. = 5).

was used to calculate the mean number of aggregations per square meter (note, however, that the scale of sampling at each station is on the order of 100 m^2) for each of the three cruises. A Kruskal–Wallis non-parametric procedure with χ^2 approximation (Sokal and Rolf, 1981) was used to compare the numbers of larval aggregations.

The association of larval aggregations with ice surfaces of different spatial orientation (relative to the plane of the air/water interface) was recorded secondary to the count data above. In some instances, no surface orientation data were recorded. In other instances, larvae were noted simply as occupying an eroded area or complex habitat; the implication being that larvae occupied an area where two or more surfaces of different spatial orientation were present. If krill were reported to occupy an upward-facing surface (see Figure 2), then, by implication, an adjacent downward-facing ice surface must have been present. If, however, larvae were reported to occupy a downward-facing surface, it could not be determined subsequently whether an upward-facing ice surface had been present below.

The null hypothesis that larval aggregations occupy areas of complex structure, i.e. areas with two or more ice surfaces, in equal proportion to smooth, downward-facing ice surfaces was tested with a χ^2 goodness of fit procedure with data pooled from all three cruises. With regard to the analysis of these data, an assumption was made that krill occupied downward-facing surfaces only in those areas where ice was not over-rafted and/or eroded. This assumption allowed for a conservative test of the hypothesis since smooth, unilayer floes with only downward-facing surfaces were generally most common during the three cruises (T. Frazer, personal observation).

The mean number of aggregations per square meter for each sampling period depended, of course, on the size classification scheme that was employed (Figure 10). There were more total aggregations, and larger aggregations during late winter sampling periods (September 1991 and 1993) than in early winter (June 1993). In fact, no large aggregations were observed in early winter, and on only two occasions were medium-sized aggregations censused by divers during the same period. The mean numbers of aggregations and the relative proportions of aggregations of varying sizes were remarkably similar among the two late winter sampling periods.

Aggregations of larval krill occupied upward-facing ice surfaces and structurally complex microhabitats, i.e. areas with two or more adjacent ice surfaces, more often than

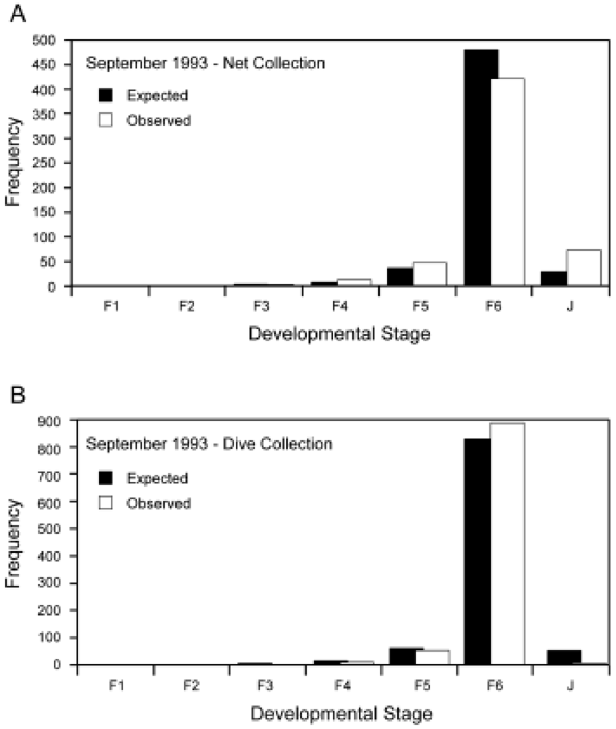

Fig. 8. Expected and observed frequencies of different larval and post-larval stages collected with nets (**A**) and by divers (**B**) during September 1993. Furcilia stages 1–6 are abbreviated as F1–F6, and young-of-the-year juvenile krill abbreviated with the letter J. The two observed frequency distributions are significantly different at the $P < 0.001$ level ($\chi^2 = 119.37$, d.f. = 4).

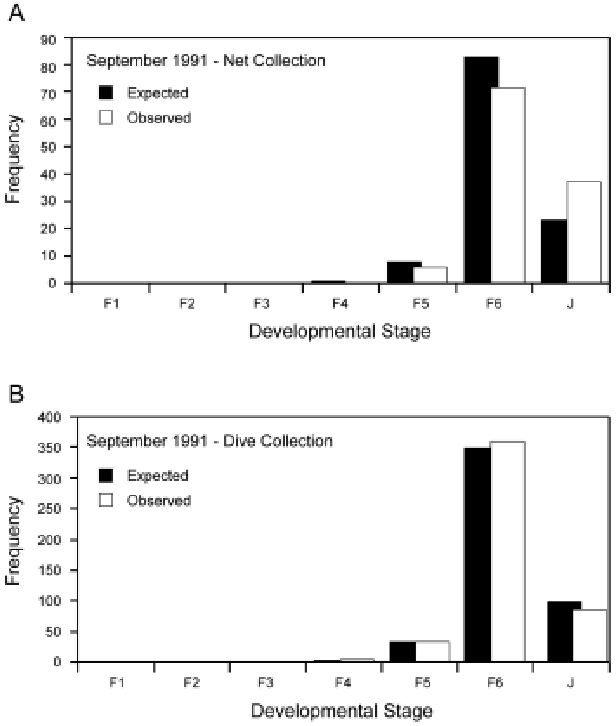

Fig. 9. Expected and observed frequencies of different larval stages collected with nets (**A**) and by divers (**B**) during September 1991. Abbreviations are as in Figure 8. The two observed frequency distributions are significantly different at the $P < 0.01$ level ($\chi^2 = 44.19$, d.f. = 3).

they occupied smooth, downward-facing ice surfaces ($\chi^2_{pooled} = 64.10$, d.f. = 1, $P < 0.001$) (Figure 11).

DISCUSSION

Larval krill abundance (diver census versus net catch)

As a research vessel is maneuvered through areas of heavy and/or consolidated ice, it is probable that animals, larval krill in particular, are decoupled from the ice and often washed into the turbulent wake of the moving ship. These displaced larvae are probably captured in nets without opening and closing mechanisms, and net catches in this study may have consisted of larval krill from both the water column and ice habitat. Comparisons of larval krill abundance, as estimated from net catches and by divers, should be viewed in this light, and quantitative interpretations of the data reported here warrant caution. The fact that nets in this study, often yielded more larval krill than divers estimated to be associated with sea ice suggests, however, that some portion of the larval population occupies the water column below sea ice during winter. Future investigators are advised to use nets with opening and closing mechanisms to more effectively sample larval krill from the water column in ice-covered seas.

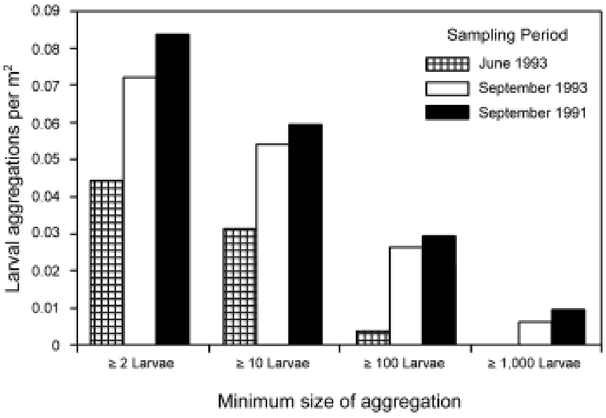

Fig. 10. Mean number of larval aggregations per square meter for all sampling stations during each of the three sampling periods: June 1993, September 1993 and September 1991. Four situations are presented: (1) total aggregations (all observations of ≥2 larval krill); (2) aggregations of ≥10 or more larvae, (3) aggregations of ≥100 larvae; and (4) aggregations of ≥1000 larvae.

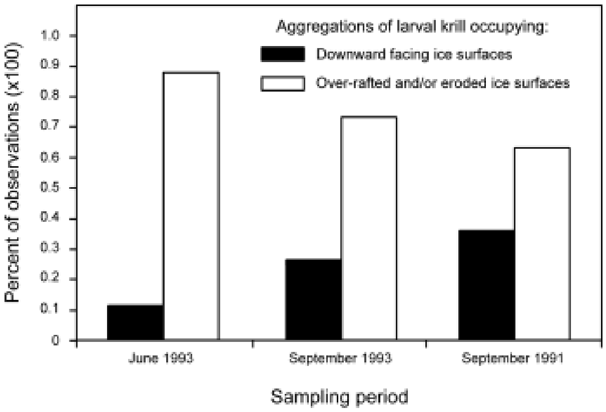

Fig. 11. The relative proportion of larval aggregations observed to occupy smooth, downward-facing ice surfaces or more structurally complex areas. Ice-surface orientation was recorded for 17 larval aggregations in June 1993, 245 larval aggregations in September 1993 and 66 larval aggregations in September 1991.

Larval size and stage frequency distributions (diver census versus net catch)

In both early and late winter, larval krill captured by divers were larger than those collected with nets. This finding further suggests that net-collected larvae are not just a random sample of animals recently decoupled from the ice. In view of the discussion above, it must be concluded that some portion of the total larval population under the ice occupies the water column, and is not closely associated with the ice.

Differences in the size distribution and stage composition of larval krill collected by divers and with nets in early winter (June 1993) were expected given the wide range of larval stages encountered, furcilia (F) 1–6. No early-stage furcilia have been collected from the sea ice habitat prior to this study. Hamner *et al.* (Hamner *et al.*, 1989) noted that larval aggregations associated with sea ice in April of 1986 did not contain larvae younger than developmental stage F4, although earlier furcilia stages, F1–3, were captured as isolates from the surface waters in adjacent areas. Daly and Macaulay (Daly and Macaulay, 1991) reported collecting F4s and earlier developmental stages from the water column, but only juveniles (age class 0) were collected from ice surfaces in late March of the same year; F3s and later developmental stages were collected from ice floes on a subsequent cruise (June/July 1988), but a wider range of developmental stages (calyptopis 3 through juvenile) was collected from the water column.

The results of this study indicate that development stages as early as F2 can be found among larval aggregations in the ice. However, the frequency of occurrence was less than expected given the total number of early furcilia in both net- and diver-collected samples. The earliest furcilia stage (F1) was not collected by divers in any of the above studies [i.e. (Hamner *et al.*, 1989; Daly and Macaulay, 1991); data herein], but F1s were present in the water column in each case. The ability of early furcilia to exploit ice-associated food resources is not clear, but the evidence suggests that the earliest stage furcilia are not closely coupled with the ice, and may not be capable of efficient ice-scraping behavior. As a consequence, krill spawned late in the summer or fall are not likely to develop quickly enough to exploit the ice and its associated resources even if ice is available. An energetic comparison of filter-feeding and ice-scraping modes of feeding for larval krill, subjected to low temperatures (below −1.5°C) and different food regimes, might prove useful in further understanding when and why krill enter and/or leave the ice habitat (see discussion below).

Larval/juvenile krill collected by divers during late winter (September 1991 and 1993) were significantly larger than those collected with nets, despite the higher proportion of juveniles (age class 0) in the latter collections. The disproportionate number of later developmental stages, i.e. juveniles, in the net samples would be expected to be reflected in a larger mean size. Thus, it appears that size (TL) is not the determining factor in krill's (age class 0) departure from the ice habitat. It is more likely that a physical process and/or developmental change accompanies the krill's habitat shift from the ice to the water column. The nuances in form and function between larval and post-larval developmental stages of *Euphausia superba* have received little attention, but are areas deserving of future research.

The comparison of mean sizes of larval krill between early and late winter of 1993 suggest that a reduction in body size may have occurred during winter for much of the larval population in the study region west of the Antarctic Peninsula. It is difficult, of course, to know with certainty that the same larval population was sampled during both cruises in 1993, and the above interpretation of the data warrants caution. However, shrinkage of adult krill has been documented [e.g. (Ikeda and Dixon, 1982; Quetin and Ross, 1991)], and Frazer *et al.* (Frazer *et al.*, 1997b) reported a reduction in the mean wet weight of late-stage furcilia in the laboratory under starved conditions. It is likely that late-stage furcilia (F4–6), under natural conditions, exhibit shrinkage when they are food limited in the Southern Ocean, although Ross *et al.* (Ross *et al.*, 1987) found that populations of larvae held in the laboratory during winter continued to advance in development even at low food concentrations. Early furcilia are less tolerant of starvation (Ross and Quetin, 1991), however, and may die rather than molting to a smaller size.

Interannual variation in the timing of formation and extent of annual sea ice is expected to have consequences for the size and condition of larval krill during the austral winter [see (Ross and Quetin, 1991)]. Annual sea ice formed relatively late over much of the area sampled in September 1993 (Stammerjohn and Smith, 1996), and little ice-algae seemed to be present during either June or September of that year (personal observation based on ice coloration). Sea ice formed earlier along the Antarctic Peninsula in 1991 (Stammerjohn and Smith, 1996), and ice-algal abundance appeared to be greater than in 1993 (T. Frazer, personal observation based on ice coloration). The above data and observations are suggestive of more favorable ice conditions for larval krill in 1991 than in 1993, and may explain the size differences reported here for larvae collected in late winter during the two different years. Data on the winter growth rates of larval krill are lacking [see (Quetin *et al.*, 1994) for a review], but are much needed information.

Patch characteristics of larval krill in the ice habitat

The term ‘aggregation’, as it is used here to describe discrete patches of larval krill, is synonymous with the term ‘swarm’ or ‘group’, and does not imply polarization or schooling of individuals. Schools of polarized larval krill have been observed by Hamner *et al.* (Hamner *et al.*, 1989), but larvae censused in this study were generally oriented to the structure of sea ice rather than to one another. Hamner *et al.*’s observations of schooling furcilia in relation to ice may be a reflection of the predominant ice types present during April, i.e. small, isolated bits of ice and/or moving brash ice. Both of the above types of ice and the resources provided are extremely ephemeral in nature, and fundamentally different than the large floes and consolidated pans of annual sea ice surveyed in this study during austral winter. Hamner *et al.*’s (Hamner *et al.*, 1989) suggestion that the presence of ice provides cover and inhibits directed horizontal swimming of furcilia implies that schooling of larval krill may be a behavior exhibited primarily in the absence of sea ice or during winter transitional periods when ice and its associated resources are more patchy in nature. However, schooling behavior probably occurs throughout the austral winter and may facilitate encounters of larval aggregations with patchy food resources in the annual sea ice habitat (see related discussion below).

Appreciable movement (inclusive of a distributional shift of animals from the water column to the ice) and coalescing of larval aggregations within the annual sea ice habitat are necessary to explain the increase in numbers and sizes of larval aggregations observed during late winter. Clearly, if we are to understand the mechanisms associated with the formation of large patches of larvae in the ice, then the small-scale movement patterns of larval krill must be characterized. Frazer *et al.* (Frazer *et al.*, 1997a) reported that aggregations of larval krill associated with sea ice were site attached at small spatial (<1 m) and temporal (<1 h) scales during daylight hours. One conclusion to be drawn from the above observations is that larger-scale movements of larval krill in the ice, and within the study region, are restricted to periods of darkness or extreme low light. The above hypothesis is consistent with the idea that sea ice functions both as a refuge from predation and as a food source for larval krill.

Larval krill associated with sea ice are too small to be an important food source for large vertebrate predators [see e.g. (Croxall *et al.*, 1985; Lowry *et al.*, 1988)]. In this regard, larvae may have a refuge in their size (Hamner *et al.*, 1989; Quetin and Ross, 1991). Sea ice, however, may afford larval krill a refuge from smaller invertebrate predators, such as ctenophores and amphipods (Hamner *et al.*, 1989), which are common in the water column below sea ice during the austral winter (L. Quetin and T. Frazer, personal observation). This study clearly illustrates the affinity of larval krill for areas of upward-facing sea ice and more structurally complex microhabitats, and the associated refuge, although other reasons may also explain, to varying degrees, krill’s tendency to aggregate in these areas; energetic and ecological considerations have been discussed elsewhere (Frazer *et al.*, 1997a).

The structural characteristics of sea ice and the patch characteristics of ice-associated flora on a scale relevant to the biology and ecology of larval krill have not been described. Such information is needed, however, to more fully understand the behavior of krill in the sea ice habitat, and to further evaluate the role of ice-associated algae in the ecology of this important species. Diving has proven to be a requisite research tool to investigate the krill–ice interaction, and future advances in our understanding of this significant ecological linkage will rely on our ability to exploit this method further.

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