

Winter abundance and distribution of *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macrura* in Gerlache Strait and Crystal Sound, Antarctica

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ABSTRACT: *Euphausia superba* and *Thysanoessa macrura* were the 2 most abundant euphausiids in the ice-covered waters west of the Antarctic Peninsula during July and August 1992. *E. crystallorophias* was limited to inshore waters. Detailed stratified sampling revealed that *E. superba* formed dense aggregations well below the ice, but was not inhabiting the ice itself. In general, *E. superba* occupied the depth stratum from 15 to 130 m; few or no other zooplankton were found within *E. superba* swarms. *T. macrura* displayed a depth preference for the strata from 90 to 250 m. Size-frequency distributions for *E. superba* and for *T. macrura* showed that larvae were absent and that both populations were dominated by small adults. A life cycle for *T. macrura* is proposed.

KEY WORDS: *Euphausia superba* · *Euphausia crystallorophias* · *Thysanoessa macrura* · Antarctic winter · Vertical and horizontal distribution · Size-frequency · Life cycle

INTRODUCTION

The Antarctic winter is a critical period in the life cycle of zooplankton. Long nights, and the prevalent ice cover which further decreases the total light available for phytoplankton, severely reduce primary production. Antarctic species are adapted physiologically and behaviorally to the extreme seasonality of the Southern Ocean. Because winter research in Antarctica has until recently been complicated by logistical difficulties and is restricted by its comparative expense, data about the distribution patterns of even the most prominent zooplankton species are scarce.

Antarctic krill *Euphausia superba* Dana is possibly the most abundant animal of its size on earth (Washburn & Wooster 1981), and has long been the euphausiid species most studied in the Southern Ocean. Its important role in the Antarctic marine food chain, commercial value, and unique biology have justified numerous studies which have included investigations focused on its distribution and abundance (Hempel & Marschoff 1980, Hempel 1981, Nast 1982,

Brinton 1985, Kittel et al. 1985, Piatkowski 1985, Daly & Macaulay 1988) and their interannual variations (Brinton et al. 1987, Loeb et al. 1993); development rates (McClatchie 1988, Huntley & Brinton 1991); age structure (Ettershank 1983, Brinton 1985); and physiological activities such as feeding (Kato et al. 1982, Segawa et al. 1982, Holm-Hansen & Huntley 1984, Morris & Priddle 1984), respiration, and excretion of ammonia and phosphate (Ikeda & Mitchell 1982, Ikeda & Bruce 1986, Ikeda & Kirkwood 1989). Comparatively few studies have included other euphausiids (Makarov 1979, Kittel & Stepnik 1983, Kittel et al. 1985, Pires 1986, Brinton & Townsend 1991), although *Thysanoessa macrura* and *E. crystallorophias* have both been reported to outnumber *E. superba* in some areas (Brinton 1991, Hosie 1991, Nordhausen 1992).

Most studies on euphausiids have been conducted during the austral spring and summer, and a few during the fall. It is not surprising then that the biology and ecology of *Euphausia superba* is better understood for the period from October through April. However, very little is known about its biology and ecology dur-

ing winter. The few existing winter studies have given rise to hypotheses that sometimes conflict. For example, the overwintering strategy of *E. superba* is obscure. This euphausiid is known not to accumulate lipids as energy reserves for winter as *Thysanoessa macrura* does (Clarke 1984, Hagen 1988), and diapause by *E. superba* has never been reported even for periods when phytoplankton, the primary summer diet of krill, become almost undetectable in the water column. Recent studies indicate that krill can feed on ice-algae on the underside of pack-ice in the Weddell Sea (Marschall 1988), Bransfield Strait (Gúzman 1983, Stretch et al. 1988), Scotia Weddell Sea (Daly 1990), and in the Indian Ocean north of Enderby Land (O'Brien 1987). Benthic feeding on detritus during the winter in shallow Lützw-Holm Bay has also been observed (Kawaguchi et al. 1986). Regressive body shrinkage during consecutive molts has been observed in long-term (Ikeda & Dixon 1982) and short term (less than 1 molt cycle) (Nicol et al. 1992) laboratory experiments with starved krill. Quetin & Ross (1991) proposed reduced metabolism in combination with starvation-induced body shrinkage as the overall wintering strategy of *E. superba*. However, remains of small crustaceans (e.g. copepods) have been found in the guts of krill during summer (Hopkins 1985) and fall (Hopkins & Torres 1989), and krill consumption of copepods has

been demonstrated in laboratory experiments conducted in the summer (Price et al. 1988) as well as in winter (Nordhausen et al. 1992, Huntley et al. 1994).

One principal goal of the RACER IV (Research on Antarctic Coastal Ecosystem Rates IV) expedition in austral winter 1992 was to investigate the distribution and activity of the common euphausiid species *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macrura* in the ice-covered waters west of the Antarctic Peninsula.

MATERIALS AND METHODS

Zooplankton sampling. The RACER program was a series of ship-based studies conducted from 1986 to 1993. This paper discusses results from RACER IV, which studied a 4000 km² grid of 29 stations including previously surveyed Gerlache Strait and 6 additional stations (hereafter referred to as 'ice stations') along a transect from Anvers Island to Crystal Sound (Fig. 1). The sampling grid was occupied by the RV 'Nathaniel B. Palmer' from July 10 through August 15, 1992. The survey in Gerlache Strait took approximately 7 d to complete. Each of the 6 'ice stations' was occupied for 30 h.

Zooplankton sampling was conducted, weather and ice conditions permitting, at all stations. A Multiple Opening Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al. 1976), equipped with 333 μ m NITEX mesh nets, was deployed at depth intervals that had been designed to be consistent during the entire RACER program. The nets used in this study fished upward in the depth intervals 290–250, 250–210, 210–170, 170–130, 130–90, 90–50, 50–15, and 15–0 m. Each of the upward-fishing nets filtered approximately 150 m³ water, a volume generally sufficient to catch a number of zooplankton that was large enough for statistical purposes and yet still allow the analysis of the whole sample. Ship speed was kept between 2 and 2.5 knots. The research vessel's large size created an ice-free area behind the ship which permitted net tows even in 100% ice cover. At some stations net tows were performed in a previously broken channel. Additionally, Acoustic Doppler Current Profiler (ADCP) data were collected during MOCNESS tows and when steaming between stations (Zhou et al. in press).

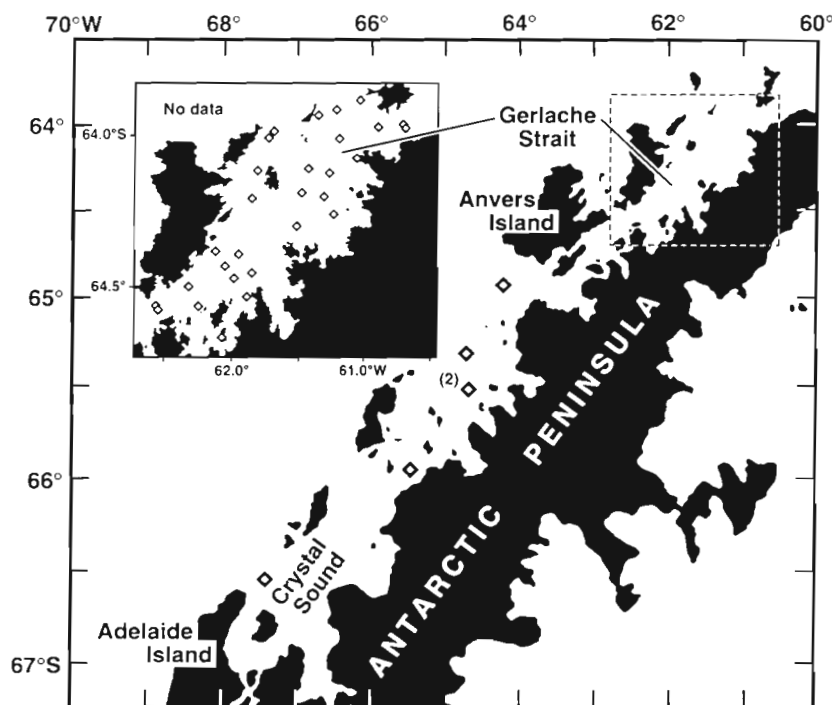


Fig. 1. Study area west of the Antarctic Peninsula, showing stations where MOCNESS tows were taken during July and August 1992. Inset shows locations of 29 sampling stations; locations of the 6 ice stations are shown in the main map portion; '(2)' indicates where 2 ice stations were co-located

All zooplankton samples were preserved in borate-buffered 5% formaldehyde solution and later analyzed at the Scripps Institution of Oceanography.

Sample analyses. All euphausiids were identified and enumerated as previously described (Nordhausen 1992). Animals were classified according to stage; the term 'juveniles' is used for post-larval organisms in which the metasoma or thelycum was not yet evident, and 'adults' are defined here as post-larval euphausiids for which sex could be determined by external morphology. If fewer than approximately 300 euphausiids were present in a sample, the entire sample was analyzed. The few larger samples were divided using a Folsom plankton-splitter and the appropriate corrections made.

Abundances were calculated based on flow-meter readings using standard equations (Wiebe et al. 1976). For most analyses the number of individuals per m² integrated over the entire depth sampled (0 to 290 m) was calculated from:

$$N_S = \sum \frac{b_i Z_i}{v_i} \quad (1)$$

where N_S is the number of euphausiids per m² at station S , b_i the number caught in depth interval i , v_i the volume filtered (m³) in depth interval i , and Z_i the thickness of depth interval i (m).

RESULTS

Hydrography

During July and August 1992, the northern and eastern parts of Gerlache Strait were covered by solid pack-ice with numerous large embedded icebergs. Pack-ice thickness was estimated to be between 0.5 and 1.0 m. Solid fast-ice covered the coastal bays in southern Gerlache Strait. Occasional leads and some smaller areas of less compressed pack-ice were found at some of the stations in northwestern Gerlache Strait. To the south of Gerlache Strait, ice cover was solid and nearly always consisted of 100% fast-ice, with some occasional compressed pack-ice. Few small leads were found in the increasingly thick fast-ice south of Anvers Island and Crystal Sound. Fast-ice was up to 1.5 m thick, usually with an additional 0.2 to 0.3 m of snow cover.

Chlorophyll *a* (chl *a*) concentrations in the surface water column were at least 2 orders of magnitude lower than in summer (Holm-Hansen & Vernet 1990), with highest values between 0.06 and 0.1 mg chl *a* m⁻³ (Vernet

unpubl. data). The sea-ice throughout the area was white, rather than green as has been observed elsewhere, and ice cores taken revealed low chl *a* concentrations (W. Cochlan pers. comm.).

Abundance and horizontal distribution

Four euphausiid species — *Euphausia superba*, *E. crystallorophias*, *E. triacantha*, and *Thysanoessa macrura* — were found in July and August of 1992. Abundance data of all stages found (i.e. juveniles and adults; no larvae were found) for *E. superba*, *E. crystallorophias*, and *T. macrura* are presented in Table 1. The abundances of *E. superba* and *T. macrura* at the ice stations are shown in Table 2. The contour graphs (Fig. 2) were generated with a commercially available program (SURFER 4.12; Golden Software, Inc.), which uses the kriging method to interpolate between stations. Neither of the 2 most common euphausiid species, *E. superba* and *T. macrura*, dominated the entire Gerlache Strait (Fig. 2); one or the other was more abundant at most stations. *T. macrura* and *E. superba*

Table 1 *Euphausia superba*, *E. crystallorophias* and *Thysanoessa macrura*. Statistics on abundance (ind. m⁻², 0 to 290 m depth) of all individuals collected (adults and juveniles; no larval stages were found) from all stations sampled during RACER IV in July and August 1992 in Gerlache Strait. n: no. of stations

	<i>E. superba</i>	<i>E. crystall.</i>	<i>T. macrura</i>	Total
n	35	35	35	35
Minimum	0	0	0	1
Maximum	810	83	92	868
Mean	89	6	38	133
SE	152	15	29	27
Variance	232 273	216	819	25 844
Skewness ^a	3.33	4.38	0.37	3.03
Kurtosis ^b	12.59	20.29	-0.96	10.78

^aMeasure of asymmetry of the distribution
^bMeasure of 'peakedness' of the distribution

Table 2. *Euphausia superba* and *Thysanoessa macrura*. Individual and total abundances at the ice stations (ind. m⁻², integrated from 0 to 290 m)

Station	Latitude	Longitude	<i>E. superba</i>	<i>T. macrura</i>	Total
IC1	65.536° S	64.678° W	140.5	3.0	143.5
IC2	65.536° S	64.678° W	18.2	91.9	110.1
IC3	66.596° S	67.490° W	40.6	50.9	91.5
IC4	65.977° S	65.423° W	3.1	77.2	80.3
IC5	65.335° S	64.698° W	22.3	40.5	62.8
IC6	64.933° S	64.294° W	0.5	50.7	51.2

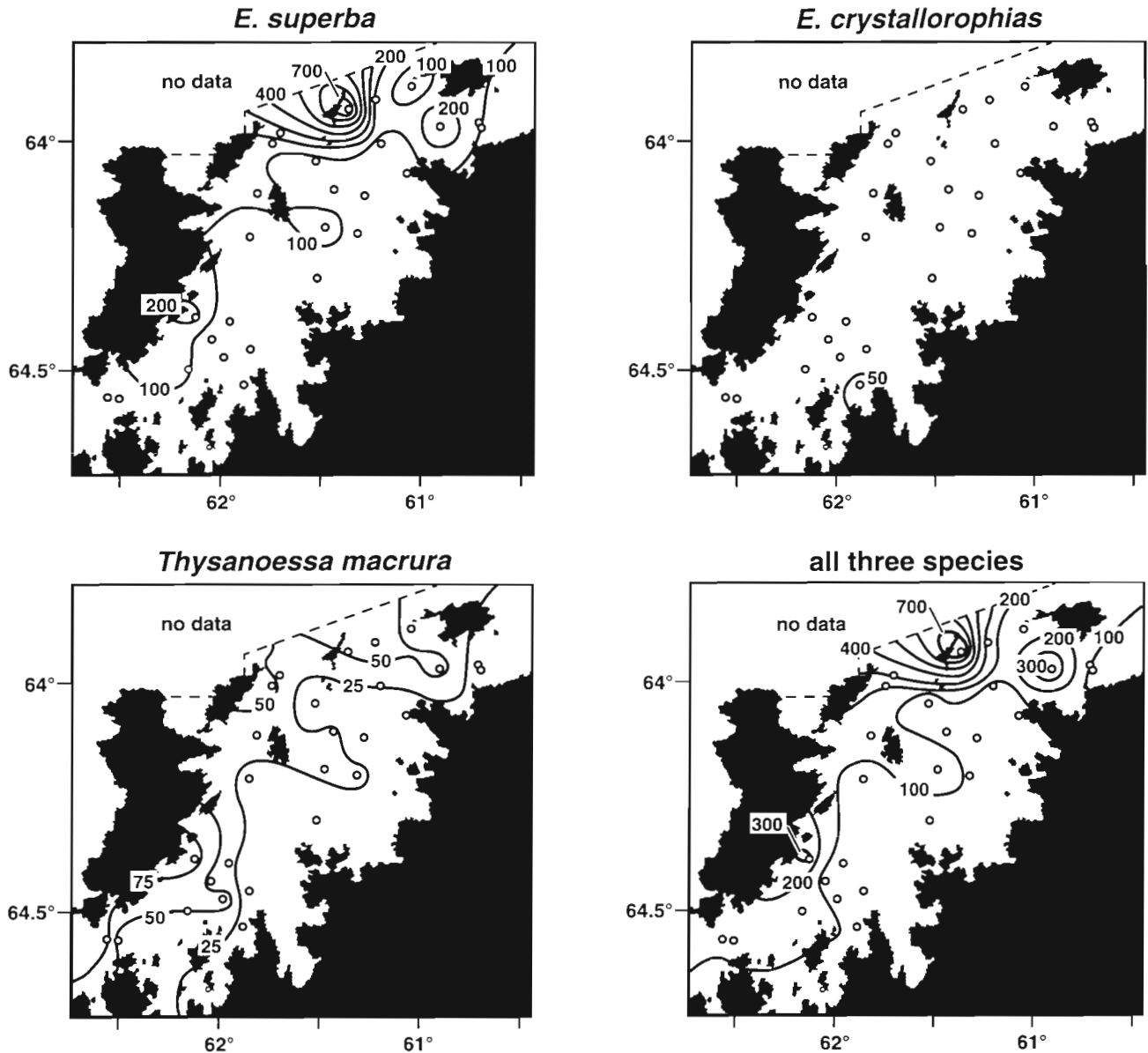


Fig. 2. *Euphausia superba*, *E. crystallorophias* and *Thysanoessa macrura*. Distribution of each species, and of all 3 species combined, for all stages in Gerlache Strait during July 1992. Abundance data are given as ind. m^{-2} , integrated from 0 to 290 m depth. Circles indicate station locations

were found at all but 1 of 35 stations. *E. superba* was most abundant overall, with the highest observed abundance of 810 ind. m^{-2} found at one station in northern Gerlache Strait. The greatest abundance of *T. macrura* was lower (91 ind. m^{-2}). The distributions of *E. superba* and *T. macrura* were very similar (Fig. 2). Both species had higher abundances in northern and western Gerlache Strait. *E. crystallorophias* was, on average, less abundant than *E. superba* and *T. macrura*, and was absent at 8 of the 35 stations sampled, but was the most numerous species at some coastal stations (Fig. 2). A total of only 4 adult *E. triacantha* were found

at 2 of the ice-stations, and for this reason this species is not discussed further.

Numerous strong echo-returns from large (hundreds of meters in extent) targets in the upper 100 m of the water column were detected by the ADCP surveys conducted throughout the study area. MOCNESS samples intentionally collected from these acoustical targets consisted almost exclusively of *Euphausia superba* (Zhou et al. in press). An attempt was made to compare the distribution patterns of the 3 common euphausiid species. The normalized mean abundance per station for each of the 3 euphausiid species (ind.

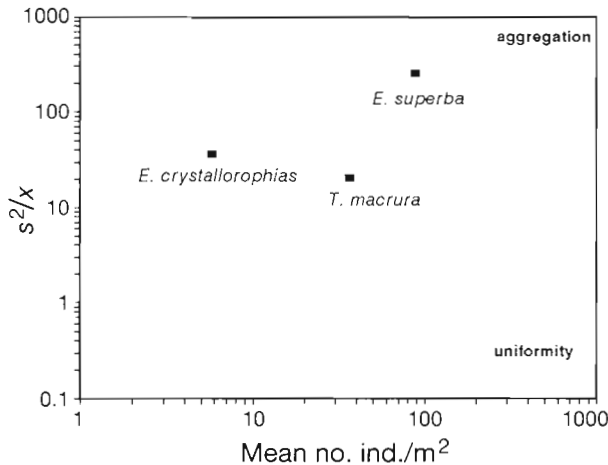


Fig. 3. *Euphausia superba*, *E. crystallophias* and *Thysanoessa macrura*. Valiela's index of aggregation (see text). s^2 : variance; x : mean

m^{-2}) is plotted in Fig. 3 against Valiela's (1984) index of aggregation (variance/mean). Use of this index is not intended to imply probabilities since by necessity normalized data are used here. The volume filtered per net was intended to be $150 m^3$ but varied from 100 to $200 m^3$. However, this index is useful for showing the relative species-specific distribution patterns: the distribution of *E. superba* is most aggregated, that of *Thysanoessa macrura* most uniform, and that of *E. crystallophias* intermediate.

Because of the short daylight period (7 h) during the survey, most net tows were conducted at night. *Euphausia crystallophias* and *Thysanoessa macrura* showed no statistically significant difference in abundance for samples collected during the daylight versus dark period (Mann-Whitney U -test). However, abundances of *E. superba* were significantly lower in daylight samples than in those taken at night (Mann-Whitney U -test, $p < 0.001$), suggesting net avoidance since diel vertical migration was not observed (see following section). For this reason only samples collected during the night were used in the analyses of size-frequency and vertical distribution of *E. superba*, in order to minimize possible effects of net avoidance, particularly by larger specimens.

Vertical distribution

Under-ice video camera observations throughout the area using a remotely operated vehicle (ROV) revealed the absence both of ice discoloration due to microalgae and of euphausiids directly under the ice. Additionally, discolored ice was not observed in the ship's wake. The absence of ice algae did not completely preclude the

presence of krill under the ice, however. Our ship-mounted (downward looking) ADCP did not sample the stratum 0–15 m, and thus could not provide any data for krill abundance directly under the ice, nor was it possible to sample directly under the ice with the MOCNESS.

The ROV was therefore used for direct under-ice observations, but no krill were found under the ice. MOCNESS data are thus not biased by our not having sampled krill associated with ice. *Euphausia superba* was most often collected by the MOCNESS in the stratum 15–50 m. *Thysanoessa macrura* and *E. crystallophias* were found at greater depths.

Fig. 4 shows the vertical distribution pattern of each species plotted for individual stations. Each of the 3 euphausiid species displayed a consistent pattern in its vertical distribution and no vertical migration was observed when the depth of the center of mass (Vinogradov 1970) was plotted against time of day (data not shown). The distribution maximum of *Euphausia superba* was generally at about 30 m depth, although this species also frequently occurred between 50 and 150 m. *Thysanoessa macrura* occurred primarily between 120 and 220 m with a mean distribution maximum at 190 m. Interestingly, *T. macrura* was strikingly scarce at depths above 50 m, the stratum occupied by the majority of *E. superba* caught. *E. crystallophias* did not show a clear preference for any depth. The vertical distribution profile of all 3 species combined was dominated by *E. superba* because of the high abundances of this species throughout most of the study area, with the maximum found at 30 m and a smaller secondary peak, attributable to *T. macrura*, at around 200 m depth.

The size-frequency distribution of *Euphausia superba* by depth stratum is presented in Fig. 5, and mean body length per stratum given in Table 3. At stations where swarms of *E. superba* were found, all other zooplankton were scarce or absent in the depth strata that it occupied. At these stations, a distinct stratification of individuals according to body size was evident, with smaller animals (18 to 35 mm) found mostly above 130 m and larger individuals (36 to 55 mm) below 130 m (Fig. 5). Few *E. superba* were found below 210 m depth.

Size-frequency distribution

The size-frequency distributions for the 3 species are shown in Fig. 6. The data for *Thysanoessa macrura* and for *Euphausia crystallophias* are from all samples collected in Gerlache Strait and along the transect through the Grandidier Channel to Crystal Sound. The corresponding data for *E. superba* are taken only from samples collected at night, in order to minimize possible effects of net avoidance (particularly by larger specimens).

For *Euphausia superba*, body lengths of 25 to 26 mm predominated, but all sizes between 20 and 30 mm were commonly found. No larvae or small juveniles were caught, and larger adults up to 50 mm occurred. Most male *E. superba* were larger than 35 mm. No significant difference in mean length was detected in a comparison of samples collected during day and night (Mann-Whitney *U*-test).

The size-frequency distribution of *Thysanoessa macrura* was clearly unimodal and peaked at 14 mm. Larvae were absent and very few juveniles smaller than 13 mm were found.

The size-frequency distribution of *Euphausia crystallorophias* differed strikingly from that of *E. superba* and *Thysanoessa macrura*. Late larval stages of 8 and 9 mm length predominated, although adults of 20 to 31 mm body length were found.

Comparison of summer and winter distribution of *Euphausia superba*

High abundances of *Euphausia superba* were found in the northern part of Gerlache Strait in summer (Brinton in press) as well as in winter (this study). Comparison of the size-frequency distributions from Brinton's (unpubl.) December/January 1991 data to those from July/August 1992 revealed striking similarities in the shape of the 2 distributions (Fig. 7). Both display at least 2 relative distribution maxima of adult *E. superba* of <30 mm body length: these were at 21 and 24 mm body length in December/January, and at 24 and 27 mm in July/August.

DISCUSSION

Horizontal distribution

These results are from one of the few Antarctic sampling programs ever conducted in the solid pack- and fast-ice of the austral winter. Krill in pack-ice have been observed from ships since the turn of the century (Marr 1962), but vertical net tows and echo sounders have

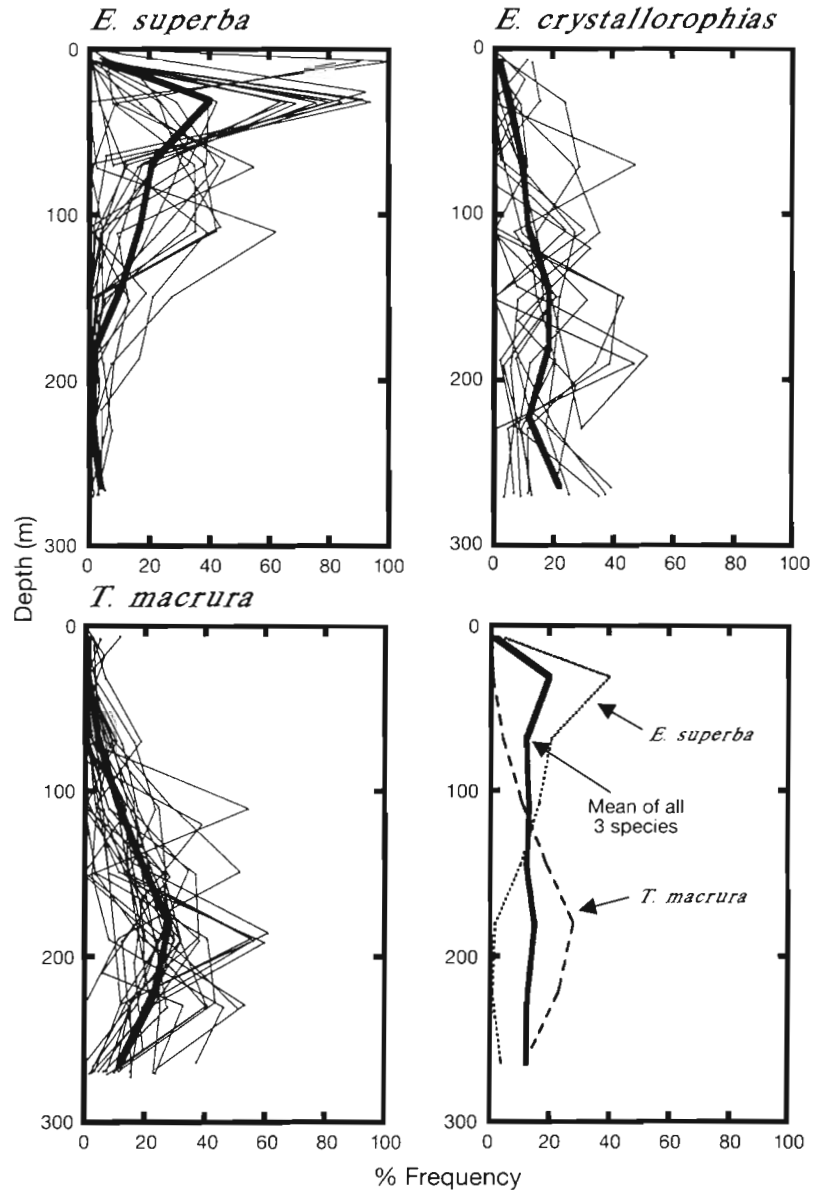


Fig. 4. *Euphausia superba*, *E. crystallorophias* and *Thysanoessa macrura*. Vertical distribution of abundances expressed as percent of the total. In the graphs for each species, the thin lines represent actual measurements and the thick line the mean of each individual species. The bottom right graph shows the mean distribution of the dominant species *E. superba* and *T. macrura* and of all 3 species combined

failed in the past to locate large krill stocks during winter in ice-free (Heygood et al. 1985) or ice-covered areas (Marr 1962, Gúzman 1983, Stepien 1983). More recent observations by SCUBA divers and video-equipped ROVs have provided direct evidence for the presence of Antarctic krill under sea ice (O'Brien 1987, Marschall 1988, Stretch et al. 1988, Daly 1990).

During the present investigation, all 3 common species of Antarctic euphausiids — *Euphausia superba*, *E.*

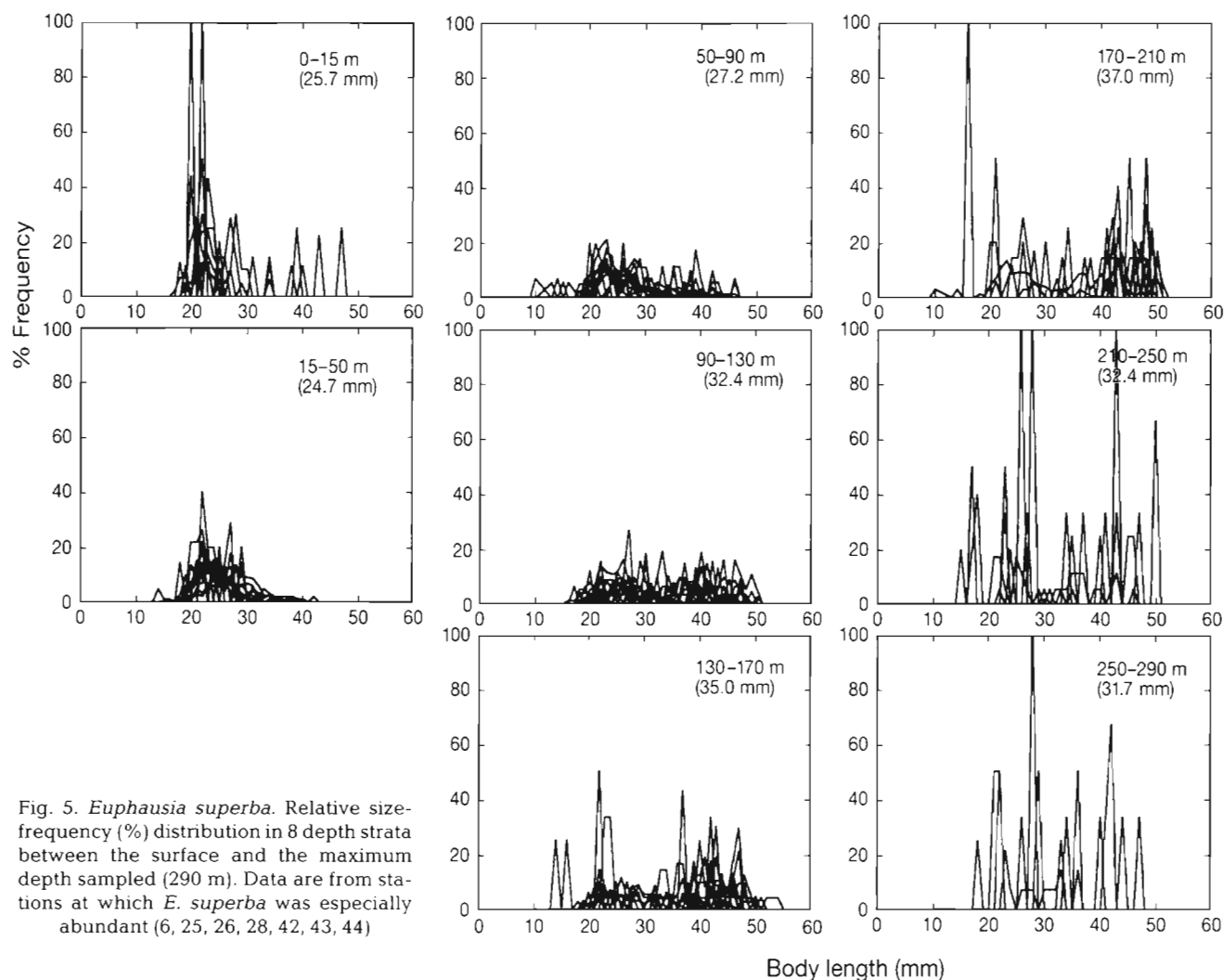


Fig. 5. *Euphausia superba*. Relative size-frequency (%) distribution in 8 depth strata between the surface and the maximum depth sampled (290 m). Data are from stations at which *E. superba* was especially abundant (6, 25, 26, 28, 42, 43, 44)

crystallorophias, and *Thysanoessa macrura* — were present throughout the study area west of the Antarctic Peninsula in July and August 1992. The distribution of *E. superba* was similar to that observed in December 1991 and January 1992 (Brinton pers. comm.). It was the most abundant euphausiid overall during this winter study, with a mean abundance higher by a factor of 2 than that of the next most common euphausiid, *T. macrura*. The catch of *E. superba* was characterized by the complete absence of larval stages, and was composed primarily of small sub-adults. The swarming behavior observed during the present investigation by continuous ADCP measurements (Zhou et al. in press) was supported by the MOCNESS catches directed at strong acoustic returns: concentrations as high as 810 ind. m⁻² were found in one large swarm.

Although reported as early as 1908 to be the euphausiid species second in dominance to *Euphausia superba* (Tattersall 1908, Rustad 1930), *Thysanoessa macrura* has received little attention. The present sur-

vey gives the first detailed description of *T. macrura*'s winter abundance, spatial distribution, and size-frequency distribution under solid ice in the region of the Antarctic Peninsula. *T. macrura* was the most uniformly distributed euphausiid throughout Gerlache Strait, the Grandidier Channel, and Crystal Sound. The mean abundance found during this winter study was 39 ind. m⁻², roughly half the number observed in the same study area in summer (84.1 ind. m⁻² in November 1989; Nordhausen in press). However, the spring/summer population in the same region had been dominated by larval stages (82.5% of the total) (Nordhausen in press), in strong contrast to the winter catch, which was composed entirely of post-larval individuals, most of which were adults larger than 12 mm. A greater overall number of post-larval stages was therefore present during the winter than in summer. The relatively high winter abundances of *T. macrura* reported here for Gerlache Strait differ markedly from the low numbers (0.55 ind. m⁻² integrated over 0 to 200 m) observed for oceanic

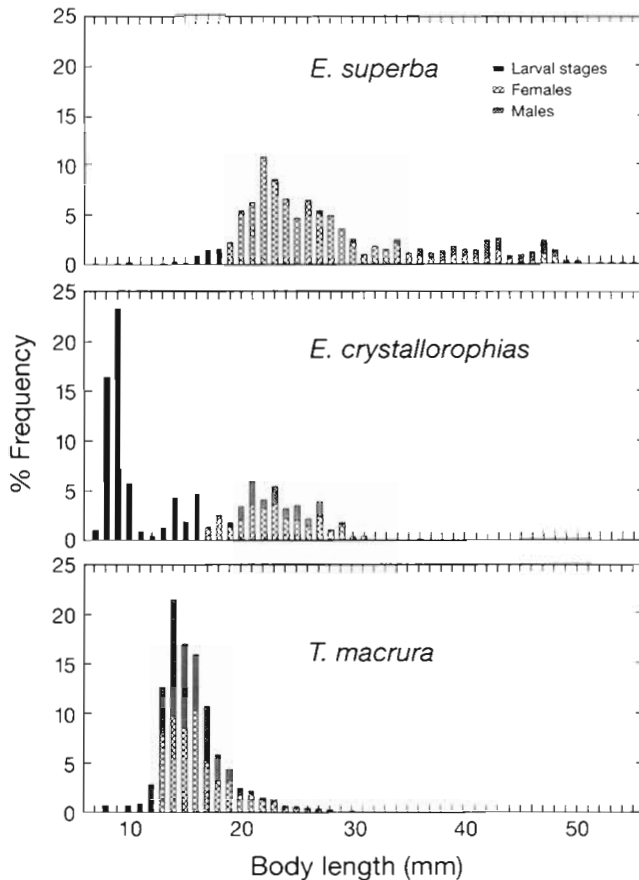


Fig. 6. *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macrura*. Relative size-frequency (%) distribution

communities at the Weddell-Scotia Confluence during winter 1988 (Lancraft et al. 1991).

Euphausia crystallorophias was almost always collected in small numbers, at inshore stations near the Antarctic Peninsula, with a maximum catch of 81 ind. m^{-2} . This generally neritic distribution and occasional high abundance accords with other published reports (Rakuza-Suszczewski & Stepnik 1980, Siegel 1987, Brinton 1991).

Vertical distribution

Reports on net avoidance by euphausiids are not always consistent (Bone 1986), but it appears that larger species and older stages are more likely to escape approaching nets due to their greater mobility (Mathew 1988). *Euphausia superba* has previously been reported to avoid moving objects, including nets, by visual cues (Marr 1962). In the present study, net avoidance was observed for *E. superba* but not for *E. crystallorophias* and *Thysanoessa macrura* when abundance data from day and night were compared.

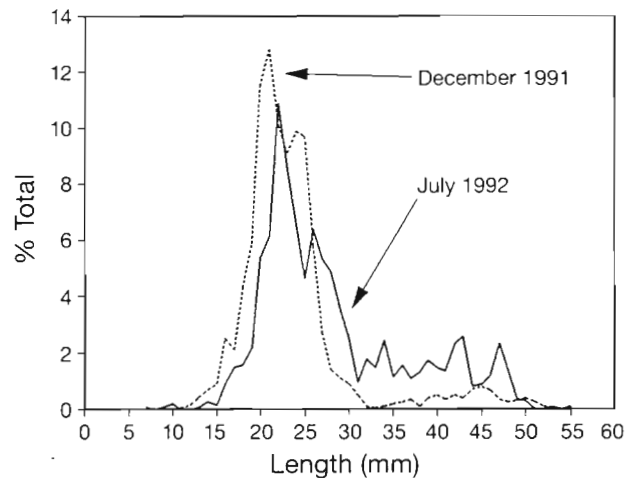


Fig. 7. *Euphausia superba*. Size-frequency (%) distribution during summer (December–January 1991–92) and winter (July–August 1992) in Gerlache Strait. Data are means of samples collected from 18 stations in summer (Brinton in press) and 35 stations in winter

Therefore, for *E. superba*, only night samples were used in the analysis of vertical distribution and size-frequency, in order to alleviate statistical bias due to visual avoidance (Witek et al. 1985, Ohman 1986).

Underwater video observations conducted during this study revealed the absence of krill directly under ice-floes or in ice-channels, in complete contrast to observations by Marschall (1988) during winter 1986 in the Weddell Sea. However, this absence of krill directly under the ice was not surprising since 'green' or 'brown' ice containing microalgae (on which the krill have been observed to feed; Marschall 1988, Stretch et al. 1988) was not found in this study area. Similar findings were reported by Daly (1990) from observations by divers in the Scotia Sea, where 'in areas [under the ice] without noticeable concentrations of ice algae, krill densities were ~ 1 individuals m^{-2} , while densities up to 28,600 individuals m^{-3} were concentrated in small crevasses containing ice algae'. Krill was rarely associated with ice that did not appear to support sea ice biota (Daly 1990).

In contrast, *Euphausia superba* was common in the water column, occurring in dense aggregations detected by both MOCNESS tows and ADCP measurements (Zhou et al. in press). Highest abundances of *E. superba* were found in the upper 100 m, in agreement with summer observations in the Weddell Sea by Siegel et al. (1990), who found that 98% of krill caught by rectangular midwater trawl were in the upper 200 m with 60 to 99% in the 0–60 m stratum. Similar results were found by Daly & Macaulay (1988) during austral spring 1983 near the ice edge in northwestern Weddell Sea, where 96% of *E. superba* swarms occurred in the upper 100 m and 81% in the upper

50 m. Miller et al. (1993) analyzed the distributional features of 4830 *E. superba* aggregations detected acoustically in the Atlantic sector of the Southern Ocean and found the mean depth of these aggregations to be 36.2 m (range = 0 to 89.0 m).

Life cycle considering winter observations

The 3 euphausiid species discussed here have geographically overlapping distributions. Although all are

euphausiids, great differences in their ecology are apparent. *Euphausia superba* is the largest species (<70 mm) (Dzik & Jazdzewski 1978). It has generally been considered herbivorous (Mauchline & Fisher 1969), which is unusual for euphausiids. Dense aggregations of krill, presumably exploiting the annual phytoplankton bloom, have been observed during the summer. Winter observations, though still limited, have led to proposals that krill undergo reduced metabolic rate or body shrinkage as overwintering strategies, with feeding on ice algae supplying limited addi-

Table 3. *Euphausia superba*, *E. crystallophias*, and *Thysanoessa macrura*. Abundances (ind. m⁻³) from all stations sampled are considered. n: no. of stations

	Depth stratum (m)							
	0–15	15–50	50–90	90–130	130–170	170–210	210–250	250–290
<i>Euphausia superba</i>								
n	35	35	35	35	35	35	35	35
Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum	8.70	20.1	2.43	3.59	1.83	1.69	0.55	1.99
Mean	0.37	1.32	0.31	0.34	0.12	0.08	0.06	0.08
SE	0.26	0.62	0.09	0.13	0.06	0.05	0.02	0.06
Variance	2.76	13.4	0.29	0.60	0.11	0.90	0.02	0.11
Skewness ^a	5.10	4.20	2.62	2.97	4.18	4.82	2.71	5.37
Kurtosis ^b	25.3	18.3	6.7	8.3	17.9	23.0	6.3	27.8
<i>Euphausia crystallophias</i>								
n	35	35	35	35	35	35	35	35
Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum	0.04	0.09	0.19	0.60	0.46	0.41	0.20	0.27
Mean	0.003	0.007	0.015	0.026	0.028	0.023	0.018	0.025
SE	0.001	0.003	0.07	0.017	0.014	0.012	0.007	0.009
Variance	0.000	0.000	0.001	0.010	0.007	0.005	0.002	0.003
Skewness	3.22	3.13	3.31	5.24	4.61	4.78	3.01	2.91
Kurtosis	9.27	9.58	11.50	26.74	22.02	23.03	9.47	8.94
<i>Thysanoessa macrura</i>								
n	35	35	35	35	35	35	35	35
Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum	0.66	0.40	1.71	0.52	0.44	1.18	0.92	0.71
Mean	0.03	0.02	0.09	0.11	0.16	0.24	0.21	0.71
SE	0.02	0.01	0.05	0.02	0.02	0.25	0.21	0.08
Variance	0.01	0.05	0.08	0.02	0.02	0.07	0.05	0.02
Skewness	5.35	4.83	5.24	1.37	0.36	1.89	1.46	3.28
Kurtosis	25.3	18.3	6.7	8.3	17.9	23.0	6.3	27.8
Total for all 3 species								
n	35	35	35	35	35	35	35	35
Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum	9.36	20.1	2.57	3.96	2.16	2.08	1.04	2.12
Mean	0.41	1.35	0.42	0.47	0.30	0.35	0.28	0.19
SE	0.28	0.62	0.10	0.14	0.07	0.07	0.04	0.08
Variance	2.68	13.4	0.36	0.64	0.15	0.17	0.07	0.14
Skewness	5.07	4.20	2.13	3.02	3.32	2.54	1.33	4.38
Kurtosis	24.9	18.3	4.03	9.37	13.59	12.2	9.82	6.47

^aMeasure of asymmetry of the distribution
^bMeasure of 'peakedness' of the distribution

tional energy. However, recent studies have suggested carnivory during periods of low phytoplankton concentrations as a mechanism to avoid starvation and allow growth during winter (Huntley et al. 1994).

Thysanoessa macrura, a much smaller (<31 mm) species, has received less attention. Its life history is still being debated in spite of its wide distribution and frequently high abundance. It is considered to be omnivorous, and its lipid composition is typical for boreal euphausiids, viz. high concentrations of wax esters, which could not only serve as energy reserves for the winter, but also explain the early spawning before the development of a phytoplankton bloom.

Euphausia crystallophias (<37 mm) is generally considered neritic, and can dominate the euphausiid population in coastal areas. Feeding on ice algae has been observed. Reproduction begins early in spring before the development of the spring bloom.

However, the part of the euphausiid life cycle that occurs during winter has been left subject to much speculation due to the paucity of data. The discussion that follows incorporates winter data from the present study into what is known about the life cycles of *Euphausia superba* and *Thysanoessa macrura* in Gerlache Strait. Because of the lack of better characters for estimating the age of euphausiids, body length data are used here to separate age groups and to estimate growth rates, as is commonly done (McClatchie 1988, Brinton 1991, Brinton & Townsend 1991, Huntley & Brinton 1991). However, the following caveats should be considered. Analysis of data from non-successive years can be misleading because of interannual variation and regional differences. For example, mesoscale variation of growth and early development rates — possibly due to varying food availability — has been reported for *E. superba* (Huntley & Brinton 1991), and body shrinkage of *E. superba* during periods of food limitation has been observed both in laboratory experiments (Ikeda & Dixon 1982) and in the field (Quetin & Ross 1991, Nicol et al. 1992).

Even though interannual variability cannot be ruled out, the observations made over the 6 yr duration of the entire RACER program were remarkably consistent, and a life cycle for *Thysanoessa macrura* can be proposed. Fig. 8 shows a schematic life cycle of *T. macrura* based on observed size-frequency distributions from field samples collected in 1986/87, 1989 and 1992. Early calyptopis stages were found in Gerlache Strait in November (1989) (Nordhausen in press). During this month, the proportion of females carrying spermatophores decreased (Nordhausen in press); as spermatophores are firmly attached to the thelycum of females and are probably not shed until the next molt (Mauchline 1980), spawning had probably begun prior to November. In December (1986), late calyptopis and

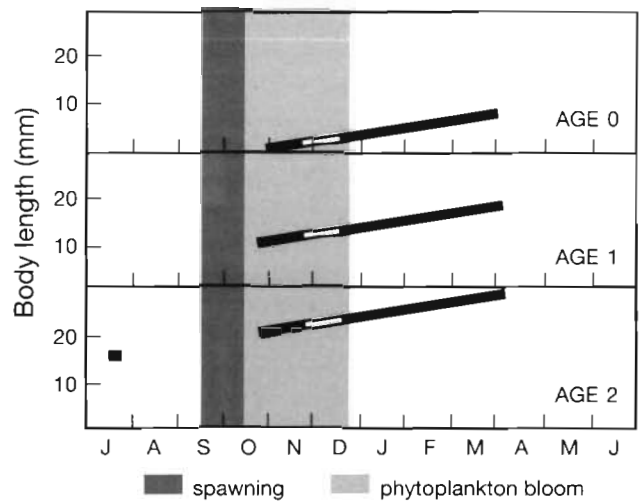


Fig. 8. *Thysanoessa macrura*. Schematic life cycle showing 3 age groups, based on size-frequency distributions from field-collected samples in 1986–87, 1989, and winter 1992 (black square in bottom graph). Shading indicates months in which *T. macrura* spawning and the annual phytoplankton bloom typically occur. The open (white) portion of the line in each graph indicates missing data

early furcilia stages were found, which developed to late furcilia and early juveniles with mean body lengths of 8.5 mm by the following March (Nordhausen 1992). In July/August (1992), the population consisted entirely of post-larval animals, mostly individuals, with unimodal maximum at 14 mm in the size-frequency distribution. In November (1989), aside from the early calyptopes already mentioned, a mode consisting of adults 14 to 18 mm long was apparent. One interpretation of these observations made over several years is the following: (1) calyptopes grow to early juveniles in the period from November to the following March, (2) by winter of that year, individuals of this cohort have matured into adults, and (3) spawning begins at some point early in austral spring (September–October), and is participated in by females as small as 14 mm long, though most are larger.

The striking similarities in shape of the size-frequency distributions of *E. superba* sampled in January (Brinton in press) and in July/August 1992 (the present study) suggest that same population may have been sampled on both occasions. Assuming that this is the case, then the observed shift of the size-frequency distribution to greater body lengths indicates an overall increase of body length of about 2 mm between January and July 1992. *Euphausia superba* females were just beginning to spawn at the end of the RACER III survey in Gerlache Strait in January 1992 (Brinton pers. comm.). Calyptopis stages of *E. superba* were found in Gerlache Strait during January and February 1987 (Brinton 1991, Huntley

& Brinton 1991). The absence of larval *E. superba* in austral winter 1992 is possibly due to a recruitment failure in that year or to advection of larval stages out of Gerlache Strait (hydrographic observations of surface water movements support the latter possibility; Niiler et al. 1990). The question of whether the early adults that were observed in winter mature by the following spring and participate in the December/January spawning remains open.

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