

Larval development and spawning ecology of euphausiids in the Ross Sea and its adjacent waters in 2004/05

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Abstract: The horizontal and vertical distributions of larvae and reproductive timing of euphausiids were investigated in the Ross Sea and its adjacent waters during austral summer 2004–2005. Occurrences of larvae of *Euphausia frigida* and *E. triacantha* were confined to the northern oceanic area where the Upper Circumpolar Deep Water prevailed, although their juvenile and adult stages extended the distribution further southward to the area where cooler Lower Circumpolar Deep Water prevailed. Larvae of *Thysanoessa* spp. were widely distributed within the oceanic to slope areas but did not occur on the shelf as juvenile or adult stages. Eggs and larvae of *E. superba* occurred with gravid females along the slope, but no juveniles occurred concurrently. Thus the slope does not appear to be a nursery ground for this species. The distribution of *E. crystallorophias* larvae was mostly confined to the shelf in the juvenile and adult stages. The onset of deepening was from early and later fructification stages onward for *E. triacantha* and *E. frigida*, respectively. However, *Thysanoessa* spp. were concentrated increasingly within the surface layers from fructification I onward. The onset of recruitment to calyptopis I appeared to be earlier in the more northern species with the exception of *E. crystallorophias*, which recruited before *E. superba*. The intense spawning of *E. crystallorophias* and *E. superba* coincided with a period of development of a coastal polynya. Generally, the onset of spawning of euphausiids appeared to be related to the latitudinal distribution and timing of sea-ice melting. Relationships between surface temperatures and development and recruitment of larvae of euphausiids are discussed.

Key words: distribution, euphausiid, larval development, polynya, Ross Sea

Introduction

Five to six species of euphausiids can usually be found in a circumpolar pattern around the continent in the Southern Ocean, including *Euphausia superba* Dana, *E. crystallorophias* Holt & Tattersall, *E. frigida* Hansen, *E. triacantha* Holt & Tattersall, *Thysanoessa macrura* G. O. Sars, and *T. vicina* Hansen (Everson 2000). For the *Euphausia* species, *E. triacantha* is generally the northernmost species, occurring from the Antarctic Polar Front to north of the continental shelf, and *E. crystallorophias* the southernmost species, restricted to the continental shelf (Everson 2000). For the *Thysanoessa* spp., *Thysanoessa macrura* is broadly distributed south of the Antarctic Polar Front (Brinton 1985), and its congener *T. vicina* is dominant near the Antarctic Polar Front (Nemoto 1966).

Several studies on larval development and spawning ecology of Antarctic species of euphausiids have been reported in the Atlantic Sector (Ross & Quetin 2000). The onset of spawning usually occurs earlier in the more northern species found in warmer waters, with the exception of the southernmost species *E. crystallorophias*, which spawns earlier than *E. superba* (Makarov 1979a, Hempel & Hempel 1982, Makarov et al. 1990a, Men'shenina 1992, Nordhausen 1994). Spawning of a single species sometimes occurs earlier in northern or warmer habitats than in southern or cooler ones (Makarov 1977, Brinton 1985, Makarov et al. 1990a, Makarov & Men'shenina 1992). Several species of euphausiids exhibit a vertical distribution pattern indicating developmental ascent, with sinking eggs and calyptopis I being the youngest larvae to appear near the surface (Fraser 1936, Marr 1962, Makarov 1977, 1979b, Hempel & Hempel 1986). The geographical distribution of the larvae usually overlaps with that of the adults (Fevolden

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1980, Hempel & Marschoff 1980, Hempel & Hempel 1982).

The high latitudinal Ross Sea area in the Pacific Sector is considered a unique region of the Antarctic, as it has the most extensive shelf and ice-shelf in the Antarctic and contains numerous significant polynyas (Smith et al. 2007). The very short duration of the ice-free season (less than 3 months) may create harsh conditions with respect to both female maturation and larval development for euphausiids in this area (Spiridonov 1995). The horizontal distribution and development of the larval stages of *E. superba*, *E. crystallorophias*, and *T. macrura* have been studied in this area (Men'shenina 1988, Makarov et al. 1990b). However, the survey regions of these studies had narrow latitudinal ranges because of extensive sea-ice coverage. Thus the reproductive sites of these species are less definitely identified. Wider latitudinal survey coverage is required for an understanding of the spatial aspect of the reproductive ecology of *E. superba* in this region (Makarov et al. 1990b). In addition, the vertical distribution of euphausiid larvae in this area has not been reported until now.

The distribution and population structure of euphausiids in the Ross Sea and its adjacent waters were investigated during the summers of 2004 and 2005 (Taki et al. 2008). The Ross Sea area was almost ice-free during the survey period, therefore the survey was conducted over a wide area, from the oceanic region (at 60°S) to locations near the ice shelf (at 78°26'S). The objective of this study was to clarify the horizontal and vertical distribution of larvae and reproductive and recruitment timing of euphausiids in relation to the oceanographic conditions of this region, using stratified tows at depths of up to 1,000 m.

Materials and Methods

The surveys were conducted along three transect lines, 175°E and 60–77°33'S (15 stations), 180° and 60–66°32'S (four stations), and 170°W and 73°07'–78°26'S (seven stations; Fig. 1). The southernmost stations of the 175°E and 170°W transects were very close to the Ross Ice Shelf. The stations were identified by station number and sampling time [day (D) or night (N)]. For example, "Stn. 1N" refers to samples collected at night from Station 1. Given that the duration of darkness decreased at southward stations, sampling was mainly conducted during the day. A rectangular midwater trawl (RMT; Baker et al. 1973) with nominal mouth areas of 8 and 1 m² (1+8) and mesh sizes of 4.5 and 0.33 mm was towed obliquely at approximately 2 knots. The net was usually dropped down to 1,000 m or near the sea bottom at depths of <1,000 m, but trawls were only conducted at depths of 200 m at stations 1N–2N (60°00'–62°50'S, 180°), 3D–4D (65°40'–66°32'S, 180°), 9D (64°16'S, 175°E), 11D (67°05'S, 175°E), and 13D (69°55'S, 175°E). At stations where nets were run down to 1,000 m, sampling was conducted at three depths (1,000–500 m, 500–200 m, and 200–0 m), and nets were sequen-

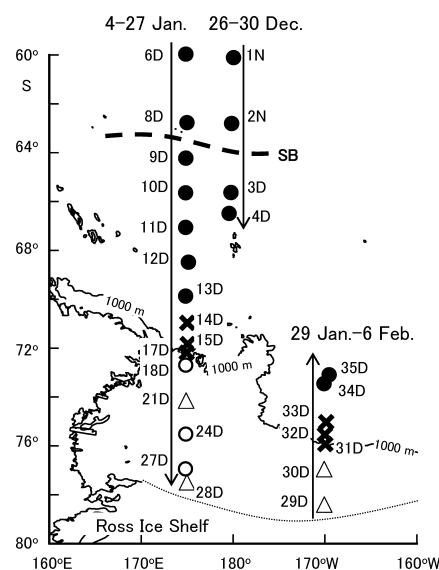


Fig. 1. Locations of sampling stations and isobaths (m). Sampling dates for each transect line are inserted. ●: offshore stations where the sea bottom depth was >3,000 m, ×: stations in the continental slope area where the sea bottom depth was 1,000–3,000 m, ○: shallower stations on the continental shelf where the sea bottom depth was <500 m, △: deeper stations on the continental shelf where the sea bottom depth was 500–1,000 m, SB: Southern Boundary of the Antarctic Circumpolar Current.

tially opened and closed to sample three stratified layers for respective tows, resulting in a total of nine stratified layers (0–50, 50–100, 100–200, 200–300, 300–400, 400–500, 500–600, 600–800, and 800–1,000 m). The stations at which the nets were run down to 1,000 m or near the sea bottom are hereafter designated as “deeply towed stations.”

To survey temperature and salinity profiles, conductivity–temperature–depth profilers (CTD, model SBE-9 plus; Sea Bird Electronics Corp.) were used at each station. The salinity data obtained by the CTD sensors were calibrated based on Guildline AUTOSAL (8400B) salinity measurements.

The conditions of the sea-ice concentration at 10-km mesh meso-scale in the Ross Sea and its adjacent waters before and during the survey (from 10 November 2004 to 1 February 2005) were obtained from information provided by Weather and Marine Corp. (Yokohama, Japan).

In the laboratory, euphausiid individuals were sorted under the microscope from the 1-m² net samples. Species, developmental stage, sex, and the existence of spermatophores for females were determined for each individual. Euphausiids of all developmental stages were typically identified to species and enumerated under a dissecting microscope. However, in instances where a given stage was abundant, the sample was divided using a Motoda splitter (Motoda 1959) into aliquots to reduce their numbers. Euphausiid eggs were further classified into three stages as Stage I (2 to approximately 16 cells), Stage II (many cells or differentiation of embryo occurring), and Stage III (limb

buds visible or completion of appendages). Calyptopis and furcilia stages were classified into three and six sub-stages (or seven sub-stages for *Euphausia triacantha* and *Thysanoessa* spp.), respectively, by referring to Brinton et al. (1999). For *E. superba* and *E. crystallorophias*, reproductive maturity stages were further evaluated by referring to Makarov & Denys (1980). Body length for calyptopis I and successive stages was measured from the tip of the rostrum to the distal end of the telson (to the nearest 0.1 mm) for each individual. Measurements of eggs and early larvae (nauplii and metanauplii) were made to the nearest 0.01 mm according to the methods reported by Suh et al. (1993).

The filtered water volumes for each net were calculated from the calibrated flowmeter values using the formulas of the Southampton Oceanography Centre (2004), assuming that the mouth angle during hauling remained constant at approximately 2 knots. For analyses of horizontal distributions, the number of individuals per m² integrated over the entire depth was calculated as follows: $N_s = \sum (b_i \times Z_i / v_i)$, where N_s is the number of euphausiids per square meter at station S , b_i is the number caught at depth interval i , v_i is the volume filtered (m³) for depth interval i , and Z_i is the thickness of the depth interval i (m).

The average contribution (%) of the j th layer to the total abundance of euphausiids in all layers at deeply towed stations (X_j) was calculated as follows: $X_j = \sum x_{ij} / \sum \sum x_{ij} \times 100$, where x_{ij} is the abundance (standardized as individuals per square meter) in the j th layer at the i th station. The data for juvenile and adult stages was compared to that collected in 8-m² nets towed simultaneously (Taki et al. 2008).

Using the developmental time of sub-stages reported in the literature, the duration and intense period of recruitment to calyptopis I were estimated for euphausiids that were considered to have completed spawning (i.e. no evidence of eggs, early larvae, or mating females) on the sampling date. The duration of recruitment to calyptopis I was estimated by back-calculation using the youngest and oldest stages of the 0+ year class at each station. The intense period was defined as the period during which the stages that existed within the 80% range of the total abundance of the 0+ year class from the median stage had recruited to calyptopis I, and was estimated by back-calculation using the oldest and youngest stages within this range. The mean duration of development for each sub-stage from calyptopis I onward was defined as 16, 14, 13, 20, and 10 days for *E. crystallorophias*, *E. superba*, *E. frigida*, *E. triacantha* and *Thysanoessa* spp. respectively, referring to Men'shenina & Spiridonov (1991). For example, the oldest stage corresponded to furcilia I (fourth stage from calyptopis I onward), at Stn. 28D on 27 January for *E. crystallorophias*; therefore, the start of the period was estimated as follows: 27 January $-(4-1) \times 16$ days = 10 December. Only the beginning of recruitment was estimated for euphausiids that showed continuous spawning on the sampling date.

The duration and intensity of spawning were also estimated for *E. superba* and *E. crystallorophias* by subtracting

the development time of the eggs through calyptopis I from the respective date of recruitment to calyptopis I estimated as above. The development times from eggs to calyptopis I for *E. superba* and *E. crystallorophias* were defined as 30 and 34 days by referring to Ikeda (1984) and Ikeda (1986), respectively.

Results

Environment

Along the 175°E transect, the Upper Circumpolar Deep Water (UCDW), which is >2°C at the surface and comprises the upper portion of the Circumpolar Deep Water (Callahan 1972), occurred in the northern oceanic area north of Stn. 8 (62°50'S; Fig. 2). Given that the potential temperature on the 27.6 σ_θ isopycnal changed from 2 to -1°C, the Southern Boundary of the Antarctic Circumpolar Current (SB) existed between Stns. 8 and 9 (64°16'S; Orsi et al. 1995, Yabuki 2006; Figs. 1, 2). Cold water with temperatures <-1.5°C at the surface and the Lower Circumpolar Deep Water (LCDW), which exhibits temperatures around 0.5–2°C and salinities of 34.7 below the surface water (Russo 2000), was found in the oceanic and slope areas south of SB [at Stns. 9–17 (72°13'S)]. Shelf Water (SW), with temperatures <-1.5°C and salinities >34.4 below the surface, mainly occurred on the continental shelf (Stns. 18–28; 72°45'–77°33'S). Warmer water with temperatures >0°C at the surface was found in the same area. This may be due to warming by solar radiation after ice-melting (Yabuki pers. comm.).

At the 180° transect, the UCDW existed north of Stn. 2 (62°50'S) and SB existed between Stns. 2 and 3 (65°40'S). In contrast, the LCDW occurred below the surface at Stns. 3 and 4 (66°32'S).

The 170°W transect showed the lowest temperatures of the three transect lines, with water columns at temperatures of <0°C dominant over the surface layer. The LCDW occurred below the surface in the slope and offshore areas (at Stns. 31–35; 73°03'–75°57'S), but the SW was dominant below the surface on the continental shelf (at Stns. 29 and 30; 77°00'–78°26'S).

The two northernmost stations (1N and 6D) were ice-free, whereas the southern two stations north of SB (2N and 8D) were located near the ice-edge, and the other southern stations were completely ice-covered until early November 2004 (Fig. 3a). In early November, the polynya started to widen along the western part of the Ross Sea Shelf. By the end of November, the polynya spread northward to north of 75°S at 175°E and had just extended to the shelf at 170°W (Fig. 3b). Meanwhile, the northern circumpolar ice-edge progressed southward. In mid-December, the polynya widened up to the slope area of both the 175°E and 170°W lines, while the two northernmost stations in the LCDW (3D and 9D) became ice-free (Fig. 3c). In early January, the polynya spread further and reached the northern slope area

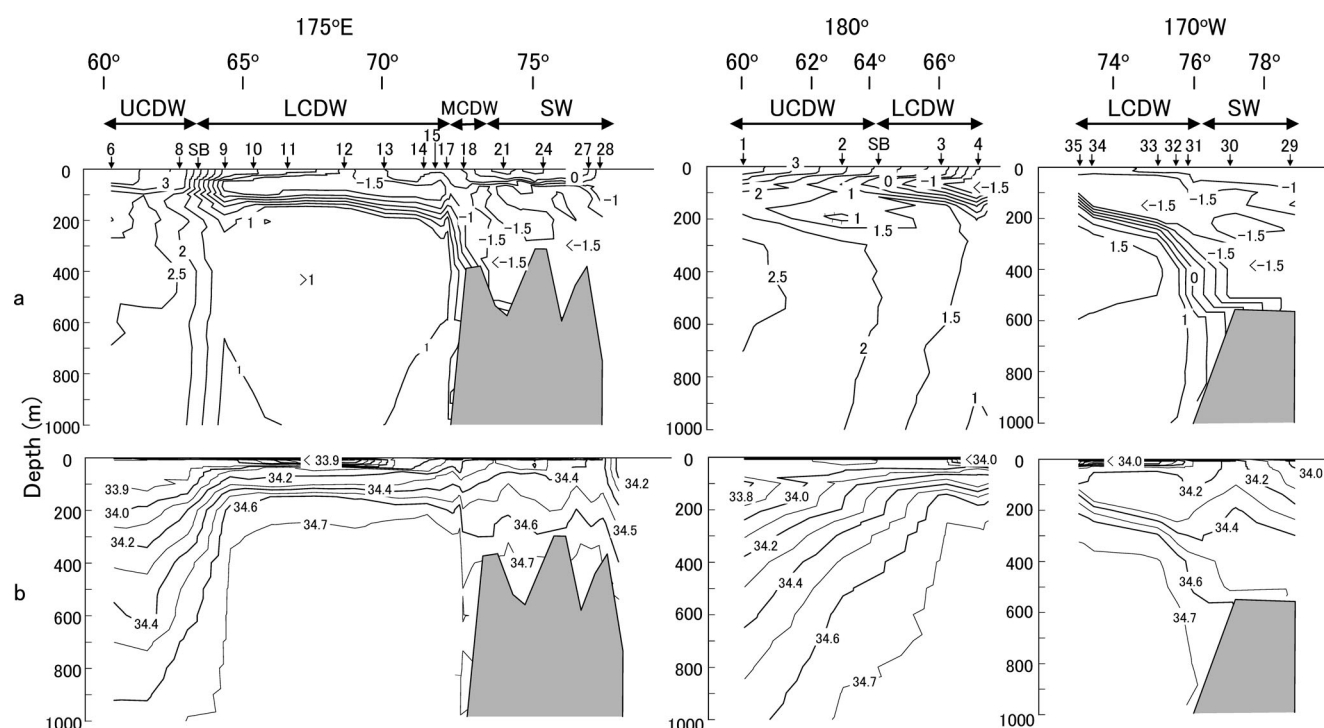


Fig. 2. Temperature (°C; a) and salinity (b) profiles along three transect lines. UCDW: area where the Upper Circumpolar Deep Water existed at the surface, LCDW: area where the Lower Circumpolar Deep Water occurred below the surface, MCDW: area where the Modified Circumpolar Deep Water was found below the surface, SW: area where the Shelf Water occurred below the surface, SB: Southern Boundary of the Antarctic Circumpolar Current.

at 175°E (Fig. 3d). By mid-January 2005, the polynya encountered the circumpolar ice-edge and joined with the Southern Ocean proper in the western part (Fig. 3e). In addition, the slope area along 170°W became almost ice-free. By early February, most of the Ross Sea area became ice-free (Fig. 3f).

Horizontal distribution

In total, six species of euphausiids were identified from the 1-m² net samples in the survey area, including *Euphausia crystallorophias*, *E. superba*, *E. frigida*, *E. triacantha*, *Thysanoessa macrura*, and *T. vicina*. On the shelf of the Ross Sea where shelf waters dominated, calyptopis stages of *E. crystallorophias* tended to be dominant among the developmental stages of euphausiids (Fig. 4), whereas calyptopis stages of *E. superba* tended to be dominant along the slope area along 170°W (Stns. 31D–33D). In the oceanic area, calyptopis and furcilia stages of *Thysanoessa* spp. were generally dominant but were much lower in numerical abundance than the larval stages of *E. crystallorophias* and *E. superba* in their respective areas of dominance.

The distributions of larval stages of *E. frigida* and *E. triacantha* were confined to the UCDW, but the distributions of their juvenile and adult stages extended to the stations in the LCDW (Figs. 5, 6).

For *Thysanoessa* spp., the upper flagella of the anten-

nules, the structure that is used as an indicator to classify the two species *T. macrura* and *T. vicina*, were torn off in all specimens. Thus, only males of this species could be identified due to the structure of the petasma. Juvenile and adult stages of *Thysanoessa* spp. were widely distributed, except on the shelf area (Fig. 7). However, males of *T. vicina* were only encountered in the UCDW. A high abundance of larval stages occurred in the oceanic area (UCDW and northern LCDW). Furcilia stages were dominant in the UCDW, whereas calyptopis stages were dominant in the LCDW.

Juveniles of *E. superba* occurred at the northern stations in the LCDW (3D and 10D), while gravid females occurred in the slope area along 175°E (Fig. 8). The larvae occurred in high abundance in the slope area along 170°W. Euphausiid eggs with an average diameter of 613 μ m (range 580–700 μ m), which were thought to belong to *E. superba* as discussed later, mainly occurred at Stn. 17 D in the slope area along with early larval stages of *E. superba*. Nauplii and metanauplii also occurred on the shelf area near the shelf break (at Stns. 18D and 21D). Eggs and early larvae occurred in small numbers, compared to calyptopis stages.

Larval, juvenile and adult stages of *E. crystallorophias* were mainly distributed on the shelf but also occurred in very low abundances in the slope area (Fig. 9). Calyptopis I and II were dominant in terms of abundance on the shelf.

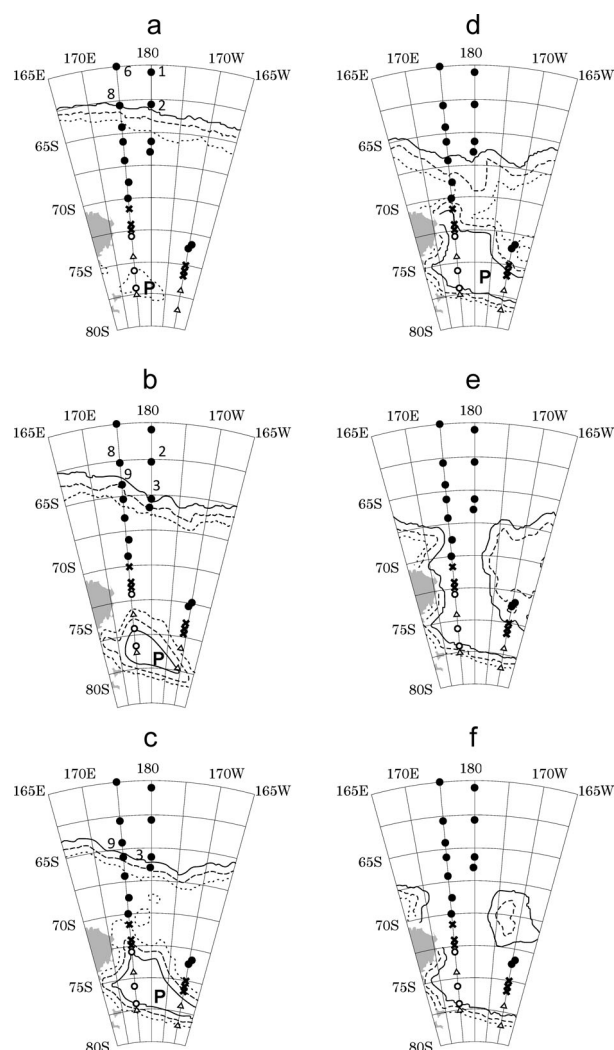


Fig. 3. Antarctic ice concentration in the survey area from 10 November 2004 to 1 February 2005 (modified from Corp. Weather and Marine). Solid line: 0%, broken line: 40%, dotted line: 80%. P: polynya. Some station numbers are inserted. a: 10 November 2004, b: 30 November 2004, c: 15 December 2004, d: 1 January 2005, e: 15 January 2005, f: 1 February. Symbols are the same as in Fig. 1.

Vertical distribution at deeply towed stations

Average contribution (%) of abundance in each depth interval compared to the total water column for each euphausiid stage at deeply towed stations is shown in Fig 10.

Furcilia I of *Euphausia triacantha* occurred in the 50–100 m layer, but furcilia II occurred in the 50–300 m layer, and older furcilia stages up to VI occurred at 200–300 m (Fig. 10a). Juvenile and adult stages occurred mainly between 200 and 600 m.

Metanauplii of *E. frigida* occurred mainly in the 400–600 m layer (Fig. 10a). Most furcilia stages (II through V) were collected in the 50–100 m layer, but furcilia VI, juveniles and adults occurred in deeper layers, with a large proportion of individuals found in the 200–300 m layer.

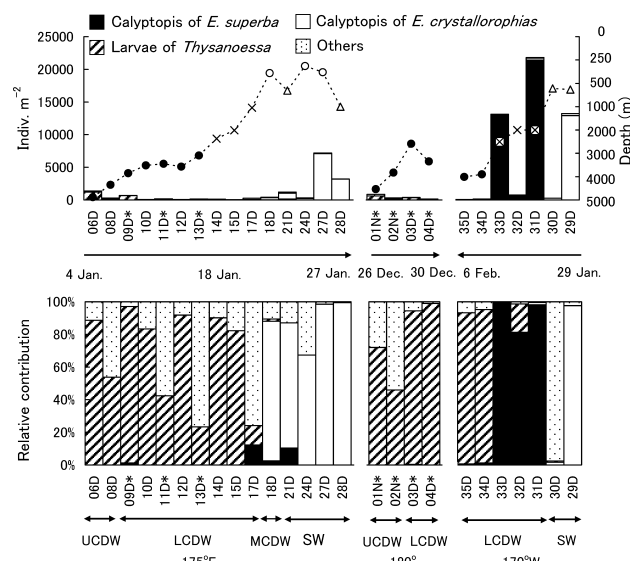


Fig. 4. Abundance composition for the dominant stages of euphausiids (top) and their relative contribution (%) to the total abundance (bottom) at each station. Sampling dates for each transect are inserted below the stations. Sea bottom depths (broken line) were inserted in the top figure. *: shallow-towed stations (0–200 m). Other details are the same as in Figs. 1 and 2.

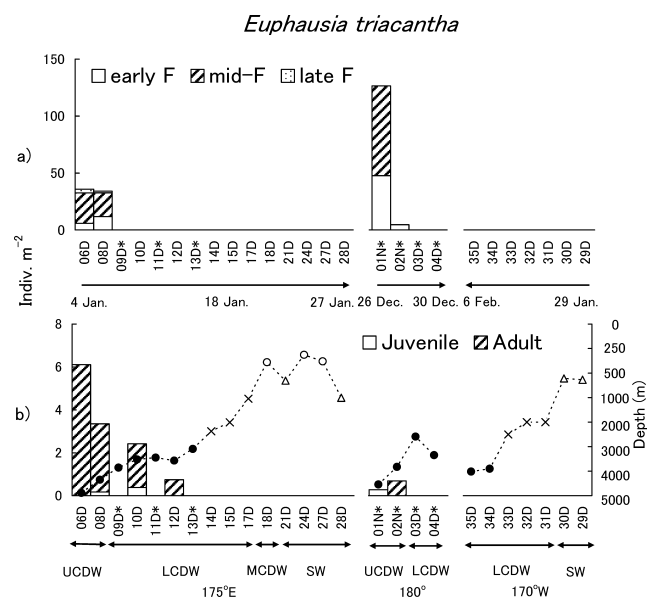


Fig. 5. Abundance of developmental stages of *Euphausia triacantha*. a) furcilia stages (early F: furcilia I–II, mid-F: furcilia III–IV, late F: furcilia V–VI), b) juveniles and adults. Other details are the same as in Fig. 4.

Calyptopis II and III and furcilia I of *Thysanoessa* spp. occurred mainly above 100 m, whereas older furcilia and juvenile stages were primarily found above 50 m (Fig. 10a). Conversely, adults occurred throughout the entire vertical range.

Eggs and early larvae of *E. superba* had two occurrence peaks (Fig. 10a). The youngest egg stage (Stage I) occurred

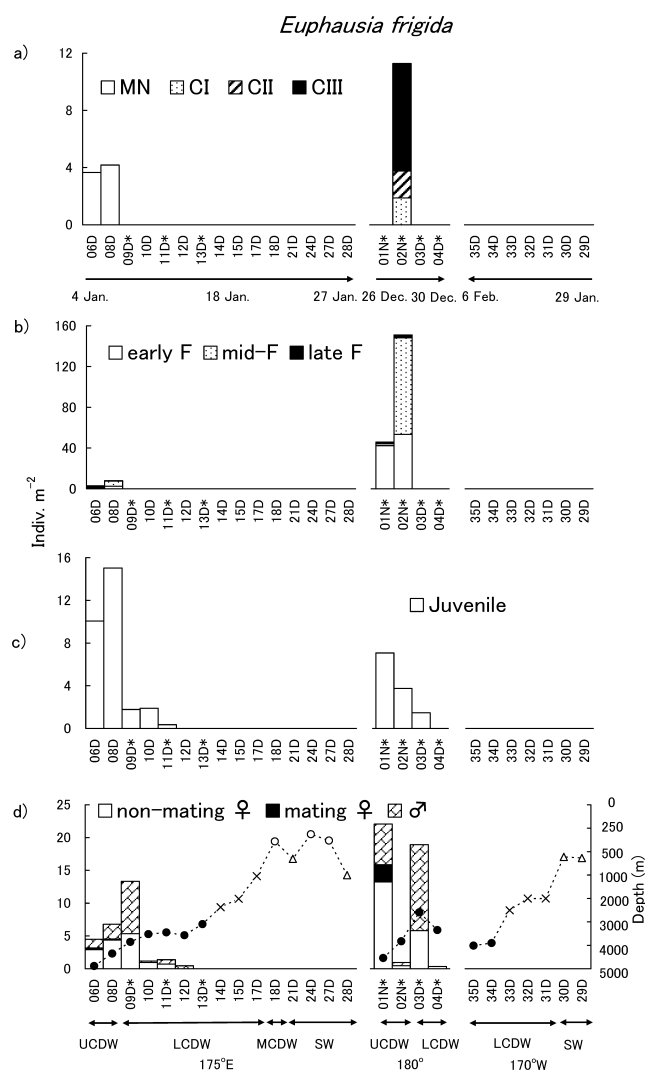


Fig. 6. Abundance of developmental stages of *Euphausia frigida*. a) metanauplii and calyptopis stages, b) furcilia stages (early F: furcilia I–II, mid-F: furcilia III–IV, late F: furcilia V–VI), c) juveniles, d) adults. Other details are the same as in Figs. 4 and 5.

in the 100–200 m and 600–800 m layers. Older egg stages and early larvae occurred mainly in the 300–400 m and 600–800 m layers. It should be noted that egg abundance could not be assessed below 800 m at Stn. 17D, where large number of eggs occurred (Fig. 8), because net towing occurred only down to 800 m at Stn. 17D, where the sea bottom depth was approximately 1,000 m. Calyptopis stages were mainly found above 200 m. Furcilia I were found in the 50–100 m and 300–400 m layers. Juvenile and adult stages had two peaks in occurrence near the surface and middle layers (Fig. 10a). Juveniles, most of which occurred at Stn. 10D (Fig. 8), mainly occurred near the surface but also occurred in smaller abundances in the 400–600 m layer. For adults, gravid females mainly occurred in the 500–600 m layer. Another smaller peak near the surface was ascribed to the distribution of males at Stn. 14D.

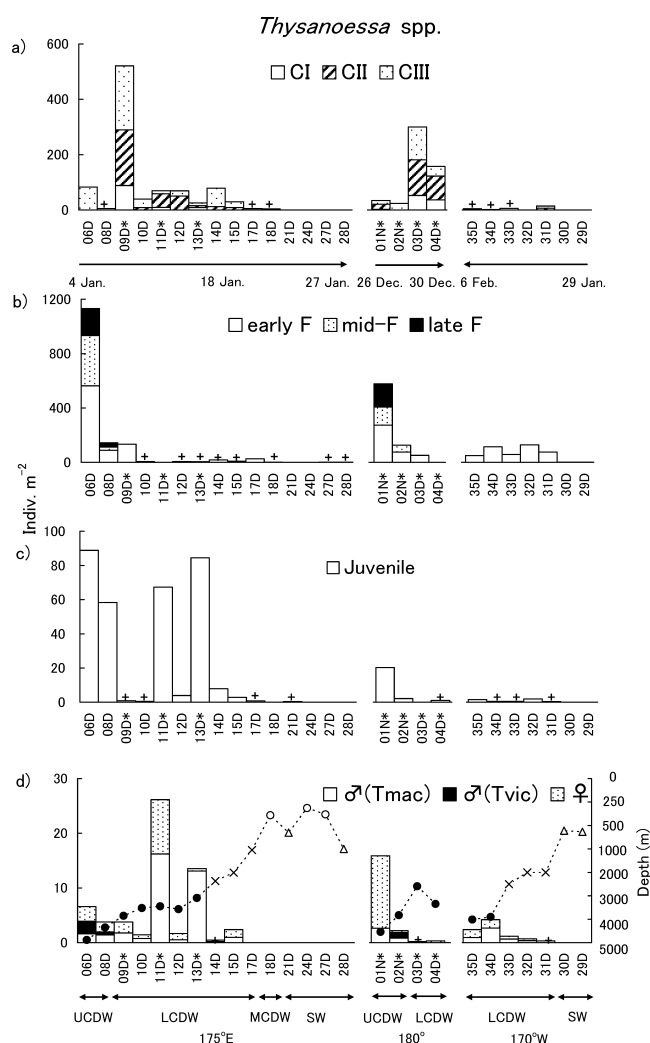


Fig. 7. Abundance of developmental stages of *Thysanoessa* spp. a) calyptopis stages, b) furcilia stages (early F: furcilia I–III, mid-F: furcilia IV–V, late F: furcilia VI–VII), c) juveniles, d) adults. Tmac: *Thysanoessa macrura*, Tvic: *Thysanoessa vicina*. +: occurrence of stages which were too low to be identified in the bars. Other details are the same as in Figs. 4 and 5.

Calyptopis and early furcilia stages of *E. crystallorophias* mainly existed above 100 m (Fig. 10a). Furcilia VI occurred in the 100–200 m layer. Juvenile and adult stages mainly occurred in the 100–300 m layer.

Juveniles collected in 8-m² nets that were towed simultaneously (Taki et al. 2008) extended their distribution to deeper layers compared to individuals collected in 1-m² nets for *E. triacantha*, *E. frigida*, *Thysanoessa* spp. and *E. crystallorophias* (Fig. 10b). On the other hand, juvenile *E. superba*, which occurred in the deep layers for the 1-m² net samples, were not observed in the 8-m² net samples. In contrast, the vertical distribution pattern of adults collected with 8-m² nets was generally consistent with that for samples collected using 1-m² nets for each euphausiid species.

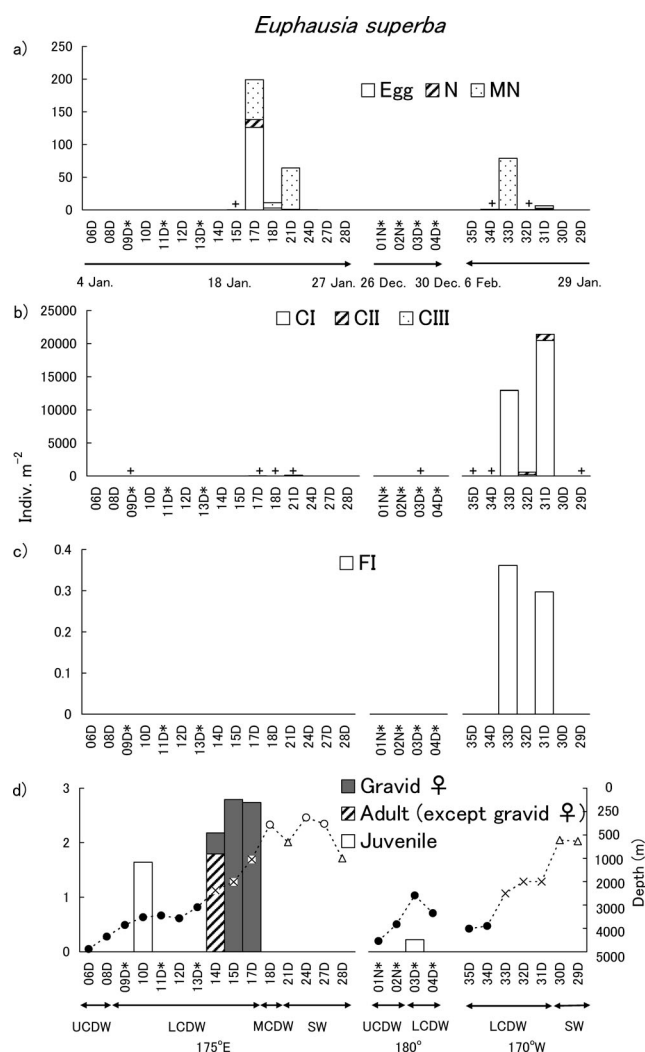


Fig. 8. Abundance of developmental stages of *Euphausia superba*. a) eggs, nauplii, and metanauplii, b) calyptopis stages, c) furcilia I, d) juveniles and adults. Other details are the same as in Figs. 4, 5 and 7.

Estimation of timing of recruitment to calyptopis I and spawning

In the Ross Sea area and its adjacent waters, the onset of recruitment to calyptopis I was estimated to be earliest for *Euphausia triacantha*, followed by *E. frigida*, *Thysanoessa* spp., and *E. crystallorophias* (Fig. 11), whereas the latest onset was seen in *E. superba*.

In *E. triacantha*, the recruitment to calyptopis I was estimated to take place between mid-August and early November in the UCDW (Fig. 11). The most intense period appeared to be between mid-September and late October.

Given the occurrence of metanauplii and females with spermatophores, spawning was assumed to continue in the UCDW in late December–early January for *E. frigida* (Fig. 6). Recruitment to calyptopis I for this species was estimated to start in early September (Fig. 11).

In *Thysanoessa* spp., the timing of recruitment to calyp-

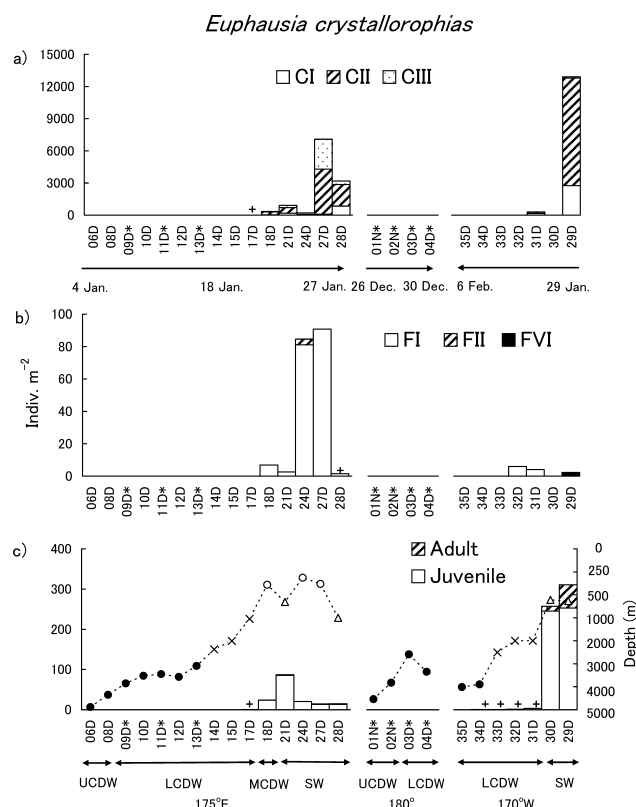


Fig. 9. Abundance of developmental stages of *Euphausia crystallorophias*. a) calyptopis stages, b) furcilia stages, c) juveniles and adults. Other details are the same as in Figs. 4, 5 and 7.

topis I appeared to differ in the UCDW and LCDW (Fig. 11). The intense period of recruitment in UCDW (early October–early December) was approximately 2 months earlier than that in the LCDW (early December–early January). However, the onset of recruitment at the northernmost stations (3D and 9D), where ice-melting occurred earlier (Fig. 3b, c), was earlier in the LCDW. The intense period in the LCDW (average of 19 days) was much shorter than that in the UCDW (average of 55 days).

Given the occurrence of eggs, early larvae, and gravid females, spawning of *E. superba* was assumed to continue in the slope area in late January–early February (Fig. 8). Recruitment to calyptopis I was estimated to commence in late December (Fig. 11).

In *E. crystallorophias*, recruitment on the shelf was estimated to take place between late November and the beginning of February (Fig. 11). The most intense period was estimated to occur between late December and late January.

The duration of spawning for *E. crystallorophias* was estimated to be between mid-October and late December on the shelf. The most intense period was estimated to be between late November and mid-December. Conversely, spawning of *E. superba* appeared to begin in late November in the slope area. Given the occurrence of an extraordinarily high abundance of calyptopis I individuals in the slope area at 170°W (Stns. 31D and 33D), it is possible that intense

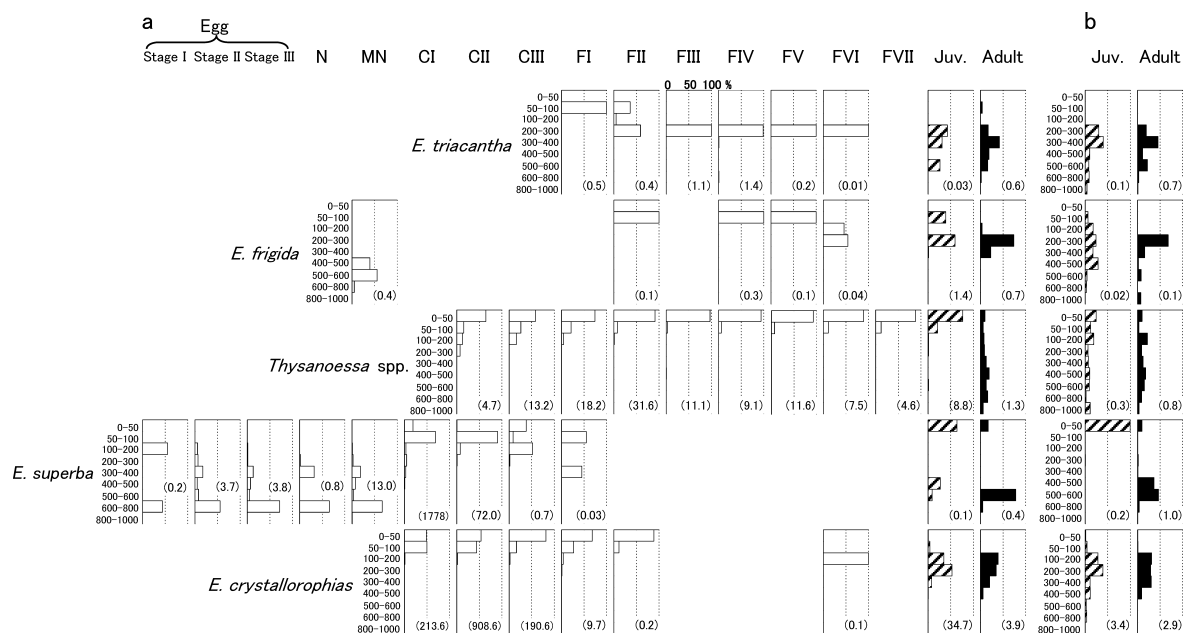


Fig. 10. Relative contribution (%) of abundance in each depth interval compared to the total water column for each euphausiid stage at deeply towed stations. Numbers in parentheses indicate abundances (indiv. m^{-2}) for each stage in the total water column. a: data from 1- m^2 net samples, b: data from 8- m^2 net samples (Taki et al. 2008).

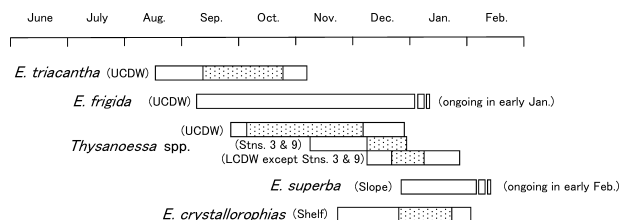


Fig. 11. Estimated periods of recruitment to calyptopis I for each euphausiid in the main area of distribution shown in parentheses. Open columns show ranges for the entire duration from the earliest to latest dates of recruitment for the corresponding area. Dotted columns show ranges from the median date of the beginning to median date of the end of the intense period of recruitment for the corresponding area.

spawning at this location commenced in early January.

Discussion

Horizontal distribution

The general confinement of *Euphausia triacantha* and *E. frigida* occurrences to the area north of SB (in UCDW) is consistent with results reported in several other regions of the Southern Ocean (Makarov et al. 1990a, Hosie 1991). However, the distribution of their juvenile and adult stages extended further southward to the oceanic LCDW, where cold water with temperatures $< -1.5^\circ\text{C}$ prevailed in the surface layer (Figs. 2, 5, 6). They were caught in substantial amounts in this cool surface layer (e.g. at Stn. 3D for *E. frigida*; Fig. 6). According to Kittel & Stepnik (1983), adult

E. triacantha and *E. frigida* were collected at temperatures ranging from -0.2 to 3.3°C and -0.9 to 2.3°C , respectively, in the southern Drake Passage and Bransfield Strait. Thus these species appear to extend their range of thermic tolerance to cooler temperatures in the vicinity of the Ross Sea.

Larval, juvenile and adult stages of *Thysanoessa* spp. exhibited the widest distribution of individuals, extending from the offshore UCDW toward $78^\circ 26'\text{S}$ except on the shelf. Because males of *T. vicina* were only encountered in the UCDW (Fig. 7), most *Thysanoessa* spp. occurring in the LCDW were likely *T. macrura*. Such a wide distribution pattern for *T. macrura* has also been observed in several other regions of the Southern Ocean (Makarov 1979b, Kittel & Stepnik 1983, Brinton 1985, Hosie 1991).

The eggs, which mainly occurred in the slope area, were considered to belong to *E. superba* due to the existence of gravid females and early larvae of the same species in the same areas, although their size range possibly overlaps that of *E. crystallorophias* eggs (e.g. average of $600\ \mu\text{m}$ near Prydz Bay; Ikeda 1986).

The relatively small numbers of eggs and early larvae that were captured, compared to calyptopis stages, could be attributed to a failure to catch specimens that stayed close to the sea-bed (Hempel et al. 1979), very patchy distributions (Hempel et al. 1979), or destruction during net hauling and sample handling (Marschall & Hirche 1984). Regarding the first case, the abundance of euphausiid eggs and early larvae of *E. superba* may be significantly underestimated because net towing occurred only down to 800 m at Stn. 17D, where the sea bottom depth was approximately

1,000 m.

No juvenile or adult *E. superba* were found on the Ross shelf; only a few eggs and individuals in larval stages were encountered, and these were mainly found on the northern outskirts (at Stns. 18D and 21D). From the combined observations of the "Discovery" and "Terra Nova" expeditions that operated at intervals over 35 years (1901–1936), Marr (1962) indicated that a very small number of early larvae of *Euphausia superba* occurred on the Ross Shelf. Thus, the present results are consistent with these historical data. Marr (1962) speculated that the larvae occurring on the shelf represented isolated stragglers from a larger population originating on the slope, and the absence of *E. superba* in large numbers on the shelf may be partly ascribed to the failure of the warm deep current, which carries ascending larvae, to penetrate more than a short distance onto the shelf.

However, from the distributional patterns of the eggs, early larvae, and gravid females, it was apparent that *E. superba* spawned along the slope area. Although no gravid females were found on the slope along 170°W, the highest concentration of calyptopis larvae occurred there. Thus, it is possible that the RMT nets missed catching gravid females given their patchy distribution, or that they had left the area after spawning. Regarding the latter hypothesis, Brinton (1985) reported that most *E. superba* larvae were associated with few or no adult *E. superba* in a small-scale survey in the vicinity of Elephant Island.

According to the present results on the distribution pattern of juveniles as well as the results obtained by surveying with a plankton net (Sala et al. 2002) and whale stomach surveys (Ichii et al. 1998), the shelf and slope areas of the Ross Sea may not be a nursery ground for *E. superba*.

Although the deeper area may not strictly restrict the distribution of larval stages of *E. crystallorophias* in the Ross Sea as observed in the Weddell Sea (Fevolden 1980, Hempel & Hempel 1982), their distribution was mostly confined to the shelf, which is consistent with previous reports from several other regions in the Southern Ocean (Fevolden 1980, Hempel & Hempel 1982, Makarov et al. 1990a, Hosie 1991, Makarov & Men'shenina 1992).

Generally, the horizontal distribution pattern of juvenile and adult stages for each euphausiid species was consistent with those previously reported for samples collected using 8-m² nets towed simultaneously (Taki et al. 2008). However, mean abundances in the integrated water column for juvenile and adult stages of *E. frigida*, juvenile *Thysanoessa* spp. and juvenile *E. crystallorophias*, most of which were <20 mm, collected in 8-m² nets were considerably lower than those collected in 1-m² nets, but vice versa for the juvenile and adult stages of *E. triacantha* and *E. superba*, most of which were >20 mm (Fig. 10a, b). This tendency was perhaps due to the difference in catchability between the two nets with different mouth areas and mesh sizes (4.5-mm vs. 0.33-mm), and is consistent with results reported in other regions (Siegel 1989, Pakhomov 1995).

Vertical distribution

According to the general description of the vertical distribution of *Euphausia triacantha* in the Southern Ocean by Baker (1959), the calyptopis stages are confined to the upper 100 m, whereas the furcilia stages extend to 250 m. In the vicinity of the Ross Sea, the distribution of this species apparently deepens from furcilia II onward, the timing of which appeared to be earlier than that of *Thysanoessa* spp. and *E. frigida*.

Metanauplii of *E. frigida* occurred mainly in the 400–600 m layer in the vicinity of the Ross Sea, which is consistent with the distribution pattern in the southern part of the Scotia Sea (Makarov 1977). The onset of deepening from the late furcilia stages onward in the present study is also consistent with the ontogenetic pattern reported in the southern part of the Scotia Sea.

In the vicinity of the Ross Sea, calyptopis II and III and furcilia I of *Thysanoessa* spp. remained mainly in the upper 100 m layer, and during the subsequent stages of development, they concentrated increasingly within the surface layers, consistent with the vertical distributional pattern reported off South Georgia Island (Makarov 1975). The range of temperatures (from –1.8 to 3.9°C) in the surface layers where high abundances of calyptopis and furcilia larvae were observed, almost covered the entire range of temperatures within the whole survey area (Figs. 2, 7). Those occurring in the LCDW were likely *T. macrura* as mentioned above. Such thermic tolerance in the larval stages of *T. macrura* could facilitate the wide geographical distribution of this species.

Eggs and early larvae of *E. superba* had two occurrence peaks in the slope area. One of the peaks, representing the youngest egg stage (Stage I), existed in the 100–200 m layer and appeared to deepen as developmental stages progressed. This suggests that a portion of the gravid females ascended to the surface layer to spawn, although most gravid females occurred in deeper layers. Another occurrence peak was in the 600–800 m layer and included Stage I eggs, older egg stages, and early larvae; this peak might have extended the distribution below 800 m at Stn. 17D, where sampling was not conducted.

A recent modeling study showed that the hatching depth of *E. superba* corresponds to approximately 700 m in the vicinity of the Ross Sea (Hofmann & Husrevoglu 2003). The nearly immobile nauplii sink, and larvae begin to rise only when they reach the metanauplius stage (Marschall & Hirche 1984, Hempel & Hempel 1986). From this modeling study, spawning near the surface and below 600 m at Stn. 17D seems unreasonable because of increasing chances for cannibalism by gravid females in the 400–600 m layer and predation pressure from benthic organisms. Taki et al. (2008) suggested that this unusually deep distribution of gravid females is driven by extensive predation pressure.

Calyptopis I of *E. superba* occurred mainly in the upper

100 m, and this species exhibits “developmental ascent” (Fraser 1936, Marr 1962, Hempel & Hempel 1986) in the vicinity of the Ross Sea. The surface waters, in which high abundances of calyptopis I were observed, had cool temperatures ranging from -1.8 to -0.9°C (Figs. 2, 8). Ross et al. (1988) reported that three out of four batches of larvae died within three days of becoming calyptopis I if reared at -1°C . Therefore such low temperatures likely cause a substantial drop in larval recruitment. The unfavorable conditions for larval development regarding temperature could partly explain the lack of juveniles of *E. superba* in the slope area.

Euphausia crystallorophias usually spawn neutrally buoyant eggs near the surface or at shallow depths (Ikeda 1986, Harrington & Thomas 1987) and exhibit a deeper distribution with age from eggs onward (Makarov 1979b). On the Ross Sea shelf, calyptopis and early furcilia stages also mainly occurred in the upper 100 m as well as in the eastern Weddell Sea (Hempel 1985). The surface waters, in which high abundances of calyptopis stages were observed, had high temperatures ranging from -1.1 to 0.1°C compared to the temperatures below the surface (Figs. 2, 9). Warming at the surface due to solar radiation after ice-melting might accelerate the development time for the larval stages of *E. crystallorophias*, as has been shown for *E. superba* in the laboratory (Ross et al. 1988, Yoshida et al. 2004).

Recruitment and spawning periods

Given the estimation of the timing of recruitment to calyptopis I, the onset of spawning generally appears to occur earlier in the more northern species, with the exception of *Euphausia crystallorophias* which reproduced before *E. superba*. This latitudinal trend is consistent with that reported for other waters in the Southern Ocean (Makarov 1979a, Hempel & Hempel 1982, Makarov et al. 1990a, Hosie 1991, Men'shenina 1992, Nordhausen 1994).

Makarov (1979a, b) reported the existence of two physiological races of *Thysanoessa macrura* that exhibit different spawning periods between the West Wind Drift waters and the cooler waters of the Weddell Sea in the southern Scotia Sea. No information is available about the duration of time necessary for development from eggs to calyptopis I for *Thysanoessa* spp.; thus the spawning period and its timing in relation to ice-melting could not be estimated in the present study. Given the timing of recruitment to calyptopis I, however, the spawning period of *Thysanoessa* spp. appeared to differ between the UCDW and the LCDW in the vicinity of the Ross Sea.

Conversely, the onset of spawning appeared to be earlier at the northernmost stations (3D and 9D) in the LCDW, where ice melted earlier. Men'shenina (1992) suggested that the thickness of the ice might be correlated to the induction of *Thysanoessa* spawning because earlier spawning occurred where ice cover was thinner among the ice-covered

regions of the Weddell Gyre. The present results support this hypothesis. However, it should be noted that differences in spawning periods between water masses could be partially caused by temperature effects on developmental time; warmer temperatures might accelerate the developmental time for this species, as was shown for *E. superba* in the laboratory (Ross et al. 1988, Yoshida et al. 2004).

The commencement of spawning by *E. superba* (in late November) may occur under the ice, but the onset of substantial spawning (in early January) coincided with the period of coastal polynya development (Fig. 3c–e). It should be noted that development time, from embryo to hatching or to the calyptopis stage, in *E. superba* shows a curvilinear decrease as the temperature of rearing increases (Ross et al. 1988, Yoshida et al. 2004). If the exponential model of Ross et al. (1988) is applied to the mean temperature of the entire water column (ranging from 0.18 to 0.68°C) in the eastern slope area (Stns. 31D–33D), where calyptopis I were abundant, the hatching time from embryo to calyptopis I ranges from 23.9 to 27.9 days, which is only 2–6 days shorter than the initial 30 day development time suggested by Ikeda (1984). Thus, the hypothesis that the commencement of substantial spawning coincided with the period of coastal polynya development at this location seems plausible.

The commencement of spawning in *E. crystallorophias* (in mid-October) may also occur under the ice, but the most intense spawning (in late November through mid-December) also coincided with the period of coastal polynya development (Fig. 3b, c). This relationship between intense spawning and sea-ice melting is consistent with that observed in the shelf region of the Cooperation Sea (Pakhomov & Perissinotto 1997).

An increase in the level of phytoplankton productivity near the ice-edge, which is often induced by the development of coastal polynyas (e.g. Carrada et al. 2000, Saggiomo et al. 2000), appears to boost food availability and enhance spawning activity for *E. superba* and *E. crystallorophias* in the Ross Sea. However, no detailed investigations on the quantitative or qualitative food conditions near the ice-edge or the mechanism of energy accumulation leading to final gonad maturation for the two species were conducted during the present study.

The present method used for the estimation of recruitment and spawning dates had several problems, especially in relation to temperature and feeding conditions, which affect the estimation of developmental duration (Ross et al. 1988, Huntley & Brinton 1991, Yoshida et al. 2004). Therefore, repeated sampling, with short intervals, is needed to investigate the distribution of euphausiids, including in the marginal ice-zone and pack-covered waters where we failed to assess euphausiid distributions in the present study. Such results are needed to accurately estimate the timing of recruitment and spawning and the development time of each stage in euphausiids.

In conclusion, the distribution of developmental stages of

Table 1. Substantial distribution areas (○) of developmental stages of euphausiids in relation to water masses in the Ross Sea and its adjacent waters. L: larvae, J: juvenile, A: adult.

Water mass	<i>E. triacantha</i>			<i>E. frigida</i>			<i>Thysanoessa</i> spp.			<i>E. superba</i>			<i>E. crystallorophias</i>		
	L	J	A	L	J	A	L	J	A	L	J	A	L	J	A
UCDW	○	○	○	○	○	○	○	○	○						
Oceanic LCDW		○	○		○	○	○	○	○		○				
Slope LCDW							○	○	○	○		○			
SW													○	○	○

euphausiids is apparently related to the water mass (Table 1). The distribution of larval, juvenile and adult stages is similar for each of *Thysanoessa* spp. and *E. crystallorophias*. Although all stages commonly occur in the UCDW, juvenile and adult stages of *E. triacantha* and *E. frigida* extend their distribution toward the cooler oceanic LCDW. The slope LCDW is an important area for spawning but does not appear to be a nursery ground for *E. superba*. The origin of the high abundance of adults of this species along the slope area remains unknown.

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