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ORIGINAL PAPER

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Comparisons of morphology and neritic distributions of *Euphausia crystallorophias* and *Euphausia superba* furcilia during autumn and winter west of the Antarctic Peninsula

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Abstract *Euphausia crystallorophias* and *E. superba* larvae often overlap in distribution in Antarctic coastal regions. Here, we describe the morphology and ecology of *E. crystallorophias* furcilia stages F3–F6, with emphasis on characteristics that distinguish them from *E. superba*, based on samples collected west of the Antarctic Peninsula during autumn and winter 2001 and 2002. During autumn most *E. crystallorophias* occurred as F4s (53%) and F5s (35%), while *E. superba* occurred in all furcilia stages (F1–F6). During winter, F6 was the dominant stage (>67%) for both species. On average, body lengths of *E. crystallorophias* larval stages were significantly greater than those of *E. superba*. During autumn, densities of the two species were similar (range: 0.003–11.8 m^{-3}) at many on-shelf stations, with lower densities during winter. Where both species occurred, >58% of *E. crystallorophias* furcilia were collected between 50 and 100 m depth, while 82% of *E. superba* were shallower (25–50 m). Younger stages of *E. crystallorophias* occurred more frequently (54% of F3s) in water >100 m than older stages (11% of F6s). Thus, many larval *E. crystallorophias* were vertically segregated from *E. superba*, thereby reducing grazing competition between the young of these morphologically similar species.

Introduction

Euphausia crystallorophias (Holt and Tattersall 1906) inhabits nearshore waters surrounding the Antarctic continent where it is an important food source for upper trophic level predators, including fishes (Hopkins 1987; Hubold 1985), Adélie and chinstrap penguins (Emison 1968; Thomas and Green 1988; Ainley et al. 1998, 2003), Crabeater and Weddell seals (Plötz et al. 1991) and whales (Marr 1962). *E. crystallorophias* also may exert a significant grazing impact on neritic systems with dense schools consuming between 13 and 96% of the daily primary production (Pakhomov and Perissinotto 1996). Despite their important role in nearshore ecosystems, the morphology of some of the larval development stages has not been completely described and, in general, the biology of *E. crystallorophias* has remained poorly known.

Pertzova (1976) and Makarov (1979, 1980) provided descriptions, drawings, and the size ranges of nauplius, metanauplius, calytopis, and furcilia (F) 1 and 2 stages of *E. crystallorophias*. Fevolden (1980) supplied additional drawings of these stages and discussed features distinguishing them from *E. superba* larvae. Brinton and Townsend (1991) added further comments, noting that development in *E. crystallorophias* was always direct through F2, unlike *E. superba*. Menshenina (1990) was the first to provide drawings of the later stage furcilia. Based on limb development in a small number of specimens (1–12 per stage), she described stages F3–F8. Euphausiacea typically have variations in ontogenetic development within and between species, especially in the furcilia phase (Fraser 1936; Einarsson 1945). All other Antarctic euphausiid species (i.e., *E. frigida*, *E. triacantha*, *Thysanoessa macrura*), however, are described as having only six dominant furcilia stages (Fraser 1936; Makarov 1980); thus, it is reasonable to expect that *E. crystallorophias* has six dominant stages. Brinton et al. (2000) summarized the development information for all Antarctic euphausiids. To our knowledge there is no information currently available to distinguish larval stages of *E. crystallorophias* from other Antarctic *Euphausia* larvae (e.g., Kirkwood 1982; Brinton et al. 2000). The lack of information on *E. crystallorophias* late furcilia stages is due, in part, to that fact that these stages are primarily present during autumn and winter (Kirkwood 1996) when few

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investigations take place and sampling is difficult in nearshore Antarctic environments.

As part of the U.S. Southern Ocean GLOBEC Program, we collected zooplankton in waters over the shelf west of the Antarctic Peninsula on four cruises in autumn and winter during 2001 and 2002. Larval, juvenile, and adult stages of *E. crystallorophias* and *E. superba* co-occurred at a number of locations across the shelf, especially within large bays and fjords. Because the endopodites of the thoracopods on larval *E. crystallorophias* often are broken off in preserved net samples, the thoracopod development method (Menshenina 1990) could not be used to classify furcilia stages. Here we describe stages of *E. crystallorophias* after F2, ascribing them to furcilia stages F3–F6 using the terminal telson spine nomenclature of Fraser (1936). Our intent is to provide sufficient information on their morphology to aid in distinguishing them from *E. superba* furcilia. Finally, we discuss the interactions of these two euphausiid species in relation to their autumn and winter abundances and distributions within the study area.

Materials and methods

Euphausia crystallorophias and *E. superba* larvae were collected in the vicinity of Marguerite Bay off the west coast of the Antarctic Peninsula during four cruises; two cruises during austral autumn (23 April–6 June 2001 and 7 April–20 May 2002) aboard the R.V. *Laurence M. Gould* and two cruises during austral winter (24 July– 31 August 2001 and 31 July–18 September 2002) aboard the RV.I.P. *Nathaniel B. Palmer* (Fig. 1). During autumn, stations were limited to one

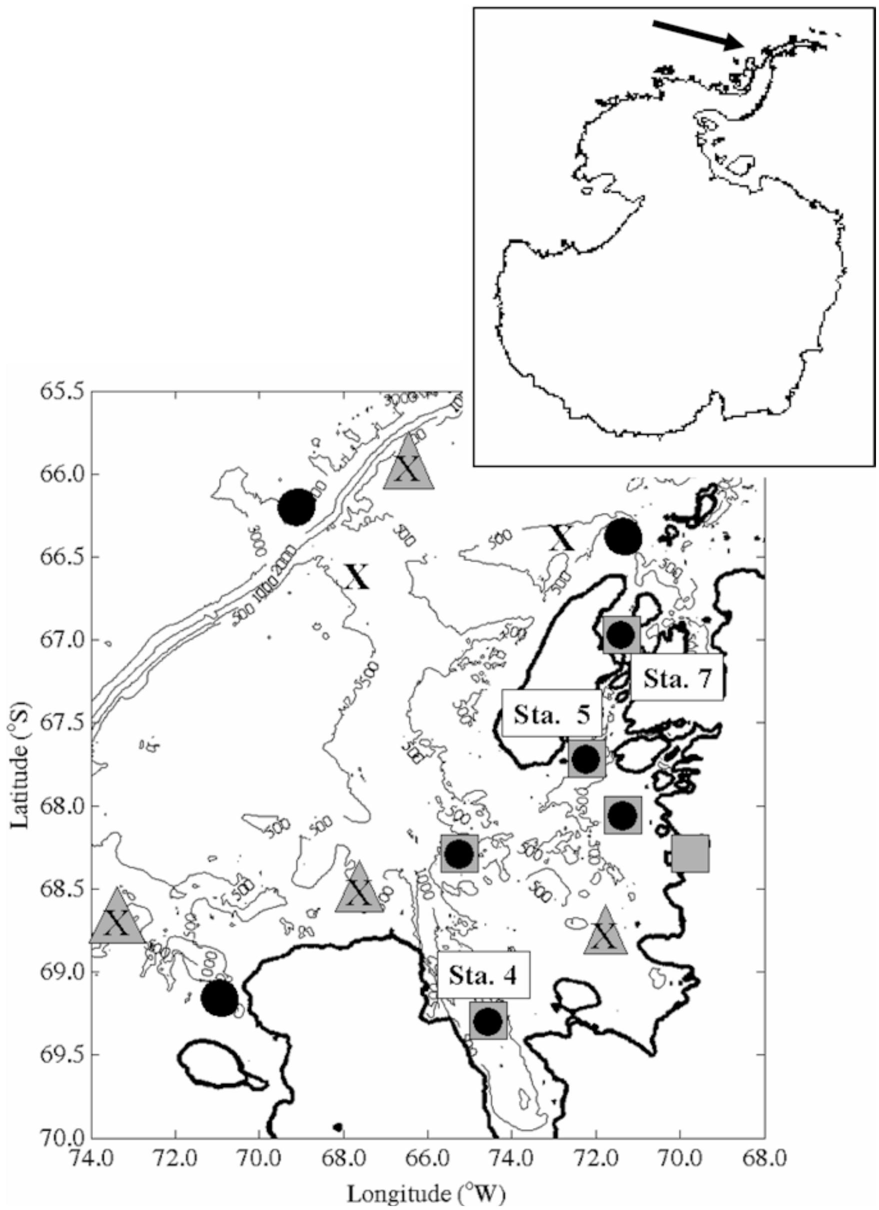


Fig. 1 The seasonal distribution of *E. crystallorophias* and *E. superba* furcilia in the vicinity of Marguerite Bay west of the Antarctic Peninsula. *E. crystallorophias* distributions are denoted by *squares* (autumn) and *triangles* (winter). *E. superba* distributions are denoted by *circles* (autumn) and *Xs* (winter). Station numbers shown for locations of vertical distributions in Fig. 9. Station 4 was in George VI Sound, Station 5 was in Laubeuf Fjord, Station 7 was in Hanusse Bay

location offshelf and a few locations on-shelf for extensive net sampling and experimental rate measurements. During winter, most stations were located on the outer shelf owing to heavy ice conditions inside Marguerite Bay. Day length ranged from 6 to 8 h during all cruises, with light levels being lowest in May and July. Larvae were collected with a 1-m^2 MOCNESS net (333 μm mesh) during autumn and several nets [1-m ring net, a 1-m Reeve Net, a 1-m^2 plummet net (Daly and Macaulay 1988), all with 333 μm mesh] during winter depending on ice conditions. The MOCNESS was towed obliquely over discrete depth intervals (from 0 up to 500 m, depending on the bottom depth) during autumn ($n = 18$ in 2001; $n = 16$ in 2002). The downward-fishing, closing plummet was used to collect samples at four stations in sea ice during winter at depths ranging from 0 to 300 m. Both MOCNESS and plummet net samples were preserved in buffered 10% formalin. Ring and Reeve nets also were used in sea-ice during winter and were hung in tandem at 10 and 15 m depth, respectively, at ten stations. Larvae from these nets were flash frozen in liquid nitrogen and kept at −80°C until analyzed.

Body lengths were measured from the tip of the rostrum to the tip of the telson minus the terminal telson spines following the protocols of Fraser (1936) and Fevolden (1980), using an Olympus B061 Stereomicroscope. Terminology and staging of furcilia follows the methods described in Makarov (1980). More than 99% of the 4,310 *E. crystallorophias* specimens and all *E. superba* larvae ($n = 5{,}774$) measured for length were from preserved samples; the remaining *E. crystallorophias* were frozen prior to measurement. In addition, 25 specimens of each stage and for each species were assessed for rostrum shape, eye diameter, presence of a dorsal keel on the carapace, and length of the mandibular palp. Eye diameter was measured in lateral view across the widest dorsal–ventral section. Both frozen and preserved samples were used, with typically < 10% difference in mandibular palp length per larval size from these two sources. Digital images of the mandibular palps under microscope slides were obtained using a Magnafire SP-S99819 microscope camera and measurements were made using Image Pro Express software. All drawings were traced from digital images using Canvas 8.0.

Results

Comparisons of larval F3–F6 morphology

Overall appearances of *E. crystallorophias* and *E. superba* larvae are similar (Fig. 2). Telson spine configurations following the methods of Fraser (1936) and Makarov (1980) are used to determine larval stage for furcilia 3–6. Examples of larval antennae and mandibular palps, which are the primary morphological characteristics used to distinguish the two euphausiid species, are shown in the Figs. 4 and 5, respectively. Each rostrum shown (Fig. 6) is of the most frequently occuring shape for each stage. Specific diagnostic characteristics also are summarized in Table 1. The length measurements in Table 1 are for specimens from both seasons combined for comparison with measurements of other Antarctic larval euphausiid species listed in Makarov (1980). Lengths of stages F3–F6 in each season are given in the following text.

Furcilia 3

All pleopods are setose, the telson has seven terminal spines with the innermost postero-lateral spine widened at the base.

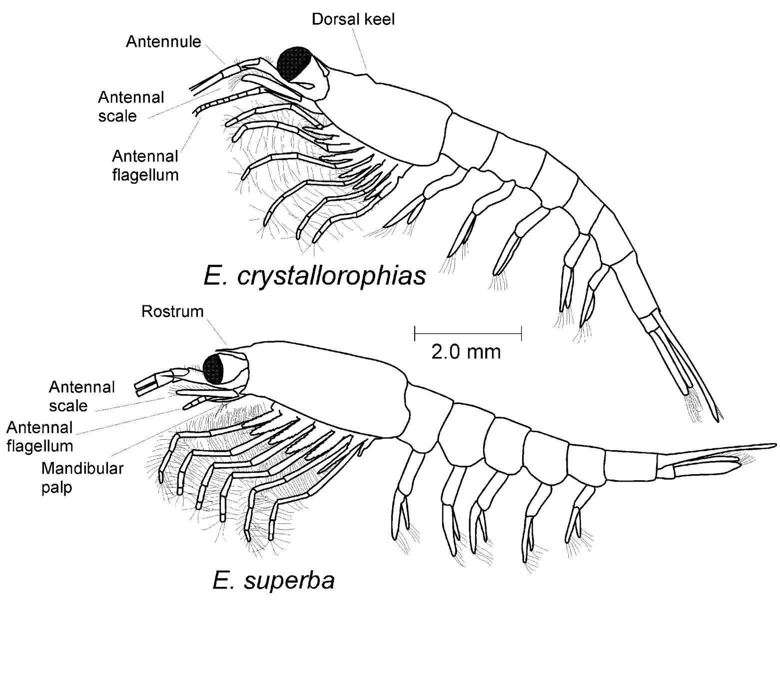


Fig. 2 Morphological characteristics of *E. crystallorophias* and *E. superba* furcilia stage 5 shown in lateral view

Euphausia crystallorophias F3 The antennal scale and flagellum are developed, with a segmented flagellum that is much longer than the scale. The flagellum often was broken off so that a ratio of the length of the flagellum to the scale could not be determined. However, it was always clear that the flagellum was longer than the scale. The antennal scale has a large spine projecting from its base. A dorsal keel is present on the carapace behind the rostrum. The mandibular palp is short relative to that in *E. superba* and hardly visible macroscopically. It is composed of three segments with the distal segment having one to two large bristles protruding distally. The average length of the distal segment is 0.107 ± 0.016 mm (± 1 SD) and the average width is 0.057 ± 0.005 mm.

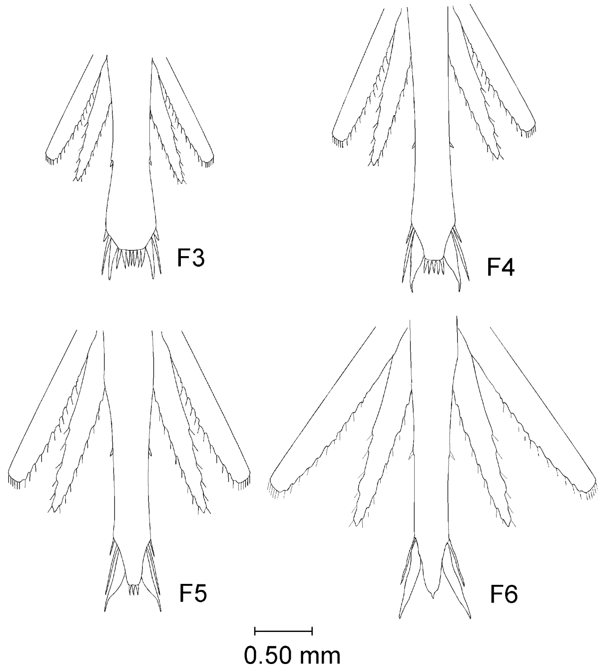


Fig. 3 *Euphausia crystallorophias* telsons for furcilia stages F3–F6 showing the arrangement of terminal spines

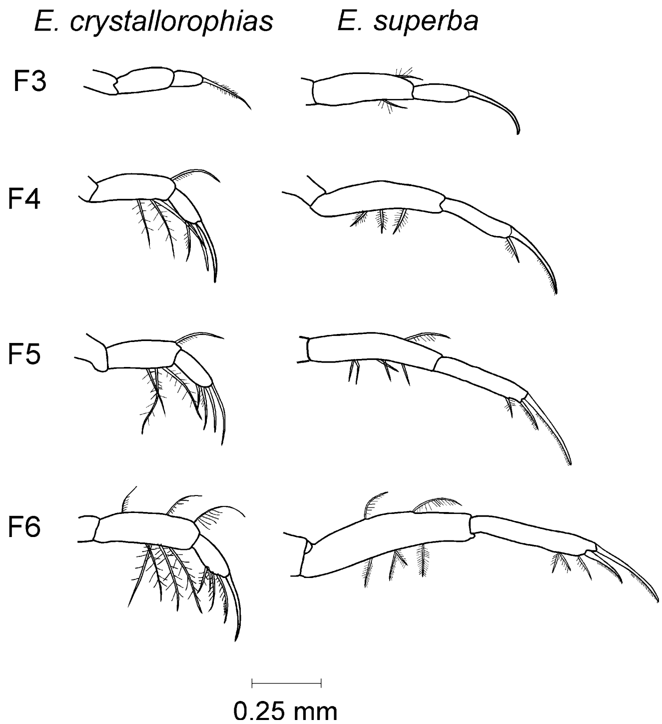


Fig. 5 Mandibular palps for *E. crystallorophias* and *E. superba* furcilia stages F3–F6

Fig. 4 Antennal scales and flagella for *E. crystallorophias* and *E. superba* furcilia stages F3–F6

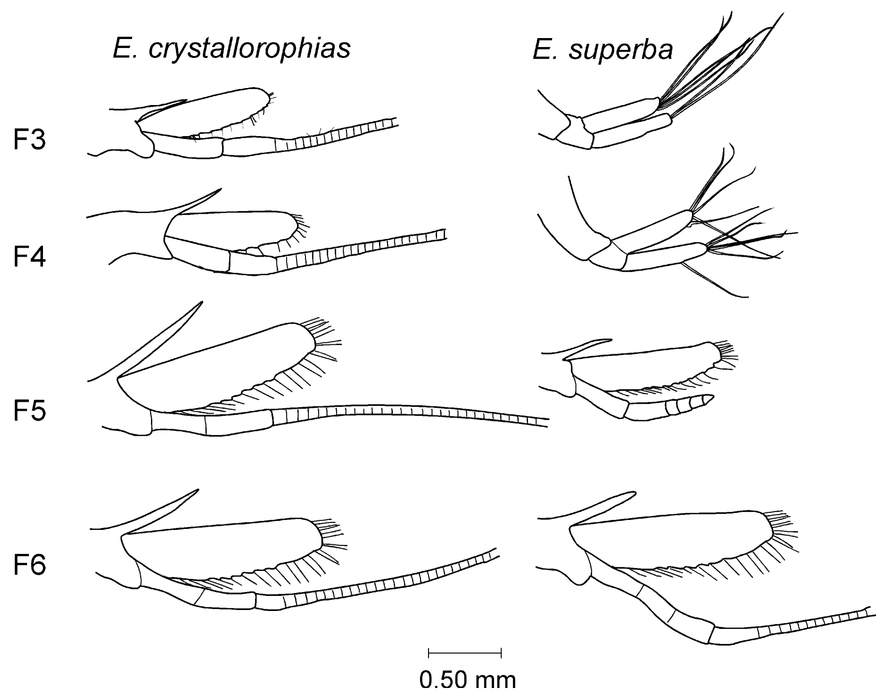
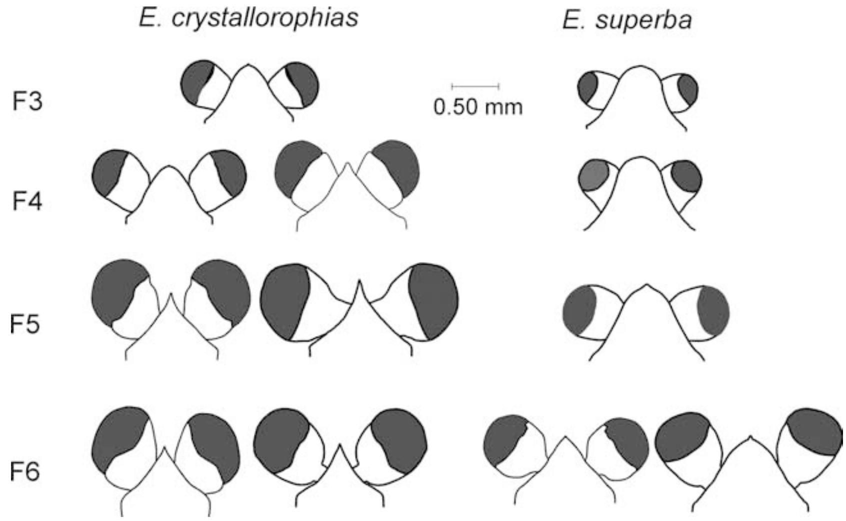


Fig. 6 Variation in rostrum shape and eye size in dorsal view for *E. crystallorophias* and *E. superba* furcilia stages F3–F6



The compound eye is large relative to that in *E. superba*, with an average diameter of 0.51 mm (range: 0.39–0.62 mm). The rostrum is triangularly rounded, has a denticle at the apex in the majority of specimens, and extends about three-fourths to full length of the eye. The shape of the rostrum is not highly variable in this stage; but some individuals are more rounded or more pointed than those shown in Fig. 6. The thoracic limbs (varying from one to five segments) are not all fully developed and are relatively short with more widely spaced setae compared with setae on the thoracic limbs of *E. superba*. The fifth and sixth limbs may be shorter than the other limbs. The telson occasionally has six terminal spines instead of seven, possibly a result of indirect development (Fraser 1936). Average total body length (range, number of specimens) in autumn: 8.80 mm (6.75–10.25 mm, $n=379$); no F3s were collected in winter.

Euphausia superba F3 The antenna is less developed than that in *E. crystallorophias*. The antennal scale is equal in length with the antennal flagellum and does not have a basal spine. The antennal flagellum is not segmented. No dorsal, carapace keel is present. The mandibular palp is composed of three segments, with the distal segment having one to two large distal bristles. The average length of the distal segment is 0.160 ± 0.030 mm and the average width is 0.061 ± 0.015 mm. The eye diameter ranges from 0.38 to 0.48 mm with an average of 0.43 mm. The rostrum is anteriorly rounded with some specimens having a denticle at the apex. The rostrum extends to the forward edge of the eyes. The thoracic limbs are not fully developed. The first limb is shorter than the others, which are relatively elongate and densely setose. The telson occasionally has six terminal spines instead of the more common seven. Average total body length in autumn: 7.52 mm (5.25–9.25 mm, $n=654$); no F3s were collected in winter.

Furcilia 4

The telson has five terminal spines.

Euphausia crystallorophias F4 The antennal scale and flagellum are similar in appearance to F3s. A dorsal, carapace keel is present. The mandibular palp has two to five bristles coming from the distal segment. The average length of the distal segment is 0.159 ± 0.022 mm and the average width is 0.064 ± 0.006 mm. The eye diameter ranges from 0.44 to 0.78 mm, with an average of 0.59 mm. The shape of the rostrum is more variable, ranging from similar to that in the previous stage to being more triangular in shape. In general, it is less rounded and more triangular with a narrower apex than *E. superba*. All of the anteriorly rounded rostrums have a denticle at the apex. From dorsal view, the rostrum extends about one-half to three-fourths the outermost part of the eyes. The thoracic limbs are not fully developed: the sixth leg is usually shorter with three segments. The telson occasionally has four terminal spines instead of five. Average total body length in autumn: 9.84 mm (7.25–13.25 mm, $n=2{,}237$), in winter: 9.50 mm (9.50 mm, $n=1$).

Euphausia superba F4 The antennal scale and flagellum are similar to F3, with no segmentation on the flagellum. A dorsal, carapace keel is absent. The mandibular palp has one to four bristles coming from distal segments. The average length of the distal segment is 0.230 ± 0.037 mm and the average width is 0.063 ± 0.009 mm. The eye diameter ranges from 0.40 to 0.51 mm with an average of 0.46 mm. The rostrum is slightly more narrow and triangular than in the F3. The first thoracic limb is not fully developed. The telson occasionally has four terminal spines instead of five. Average total body length in autumn: 8.33 mm (6.25–11.25 mm, $n=690$), in winter: 7.16 mm (5.50–8.00 mm, $n=37$).

Table 1 Morphological characteristics of *E. crystallorophias* (EC) and *E. superba* (ES) furcilia stages (F3–F6)

	F3		F4		F5		F6	
	EC	ES	EC	ES	EC	ES	EC	ES
No. of spines on telson	7	7	5	5	3	3	1	1
Mean length and range (mm)	8.80 (6.75–10.25)	7.52 (5.25–9.25)	9.84 (7.25–13.25)	8.27 (5.50–11.25)	11.10 (8.50–13.50)	9.46 (6.25–12.30)	11.66 (9.25–14.75)	11.34 (7.25–16.00)
Antennal flagellum vs. antennal scale length	Flagellum longer	Same length	Flagellum longer	Same length	Flagellum longer	Same length	Flagellum longer	Flagellum longer
Carapace keel	Present	Absent	Present	Absent	Present	Absent	Present	Absent
Rostrum shape in dorsal view	Conical with small point on end	Rounded, some with small point on end	Mostly triangular, some conical	Rounded, some with small point on end	Triangular	Rounded, some with small point or conical shape	Triangular	Rounded, some with small point or triangular shape
Mean MP distal segment length/width ratio and range (mm)	1.88 (0.9–2.2)	2.54 (1.6–3.5)	2.47 (1.9–3.0)	3.76 (2.6–6.2)	2.76 (2.4–3.2)	5.02 (4.0–6.4)	2.82 (2.3–4.0)	6.11 (4.8–7.9)

Examples of appendages are shown in Figs. 3, 4 and 5
Lengths are autumn and winter samples combined, sample sizes are given in the methods section
MP mandibular palp

Furcilia 5

The telson has three terminal spines.

Euphausia crystallorophias F5 The antennal scale and flagellum are similar to the previous stage. A dorsal, carapace keel is present. The mandibular palp has three to seven bristles coming from the distal segment. The average length of the distal palp segment is 0.176 ± 0.017 mm and the average width is 0.064 ± 0.009 mm. The eye diameter ranges from 0.51 to 0.79 mm with an average of 0.67 mm. Dorsally, the rostrum is more acutely triangular than that of *E. superba*. The shape varies from a broad triangle to triangular with the tip coming to a narrow, sharp point. In dorsal view, the rostrum reaches to about one-half to three-fourths the outermost part of the eye. The thoracic limbs are all fully developed. Occasionally the telson has two terminal spines instead of three. Average total body length in autumn: 11.12 mm (8.75–13.5 mm, $n=1{,}378$), in winter: 10.22 mm (8.5–12.00 mm, $n=36$).

Euphausia superba F5 The antennal scale and flagellum are still approximately equal in length, but the antennal scale is much broader and developed and the antennal flagellum shows the first evidence of segmentation. A spine now protrudes from the base of the antennal scale. A dorsal, carapace keel is absent. The mandibular palp has two to four bristles coming from the distal segment. The average length of the distal segment is 0.324 ± 0.024 mm and the width is 0.065 ± 0.009. The eye diameter ranges from 0.47 to 0.60 mm with an average of 0.52 mm. In general the rostrum is similar to that in F4, but is somewhat less rounded making it slightly narrower; all specimens have a denticle at the apex. The first thoracic limb is still shorter than the second limb. The telson may have two terminal spines instead of three. Average total body length in autumn: 9.59 mm (7.25–12.30 mm, $n=775$); in winter: 7.88 mm (6.25–9.50 mm, $n=62$).

Furcilia 6

The telson has one terminal spine.

Euphausia crystallorophias F6 The antennal scale and flagellum are similar to F5. A dorsal, carapace keel is present. The mandibular palp has four to seven bristles coming from the distal segment. The average length of the distal segment is 0.183 ± 0.020 mm and the width is 0.066 ± 0.009 mm. The eye diameter ranges from 0.59 to 0.79 mm, with an average of 0.70 mm. The rostrum is similar to the previous stage. In general, it is triangular, becoming narrow and sharp towards the apex, and extending to one-half to three-fourths the outermost part of the eyes. The thoracic limbs are similar to those in F5. There are no variant forms of the telson. Average total body length in autumn: 11.94 mm (9.75–14.75 mm, $n=156$), in winter: 11.27 mm (9.25–13.00 mm; $n=113$).

Euphausia superba F6 The antenna is developed with the segmented flagellum much longer than the antennal scale. A spine projects from the basal segment. A dorsal, carapace keel is absent. The mandibular palp has three to seven bristles coming from the distal segment. The average length of the distal segment is 0.451 ± 0.048 mm and the width is 0.074 ± 0.006. The eye diameter ranges from 0.54 to 0.74 mm, with an average of 0.65 mm. The rostrum ranges in shape from triangular to triangularly round with a denticle at the apex. The thoracic limbs are fully developed and becoming increasingly setose. There are no variant forms of the telson. Average total body length in autumn: 11.67 mm (7.75–16.00 mm, $n = 891$); in winter: 9.97 mm (7.25–15.00 mm, $n = 211$).

Length-frequency and spatial distributions

During autumn, length-frequencies of *E. crystallorophias* furcilia ranged from 5.25 to 14.75 mm, while *E. superba* ranged from 2.75 to 16.00 mm (Fig. 7). During winter, larval *E. crystallorophias* were 8.50–13.00 mm and *E superba* 5.50–15.00 mm. On average, *E. cystallorophias* F3–F6 larvae were significantly larger ($p \leq 0.05$) than comparable *E. superba* larvae.

Furcilia stages 1–6 were present in the study area for both of the euphausiid species during autumn. F4 (53%) and F5 (35%) were the dominant stages for *E. crystallorophias*, with $< 0.2\%$ of the larvae in stages F1 and F2 and $< 10\%$ in stages F3 and F6 (Fig. 8). *E. superba* furcilia were primarily F1 s onshelf (26%) and offshelf (68% of furcilia, 45% of calyptopis + furcilia), with all other stages occurring with a frequency between 12.0 and 18.6%. *Euphausia superba* calyptopis stages were

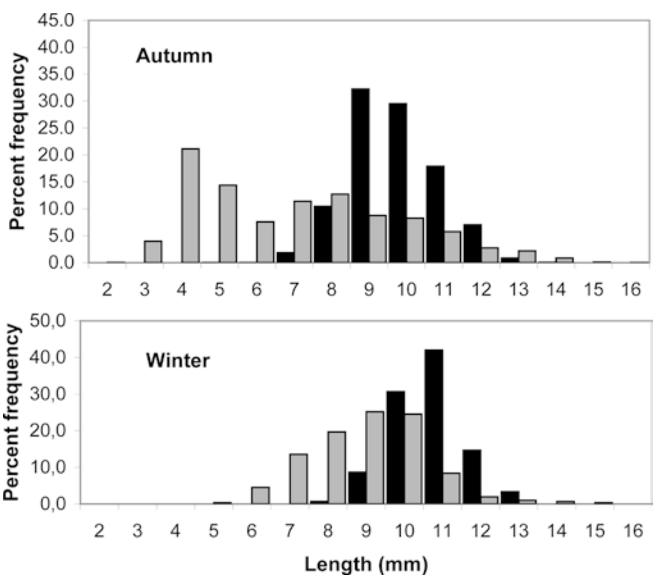


Fig. 7 Length frequencies of *E. crystallorophias* (*black*) and *E. superba* (*gray*) furcilia during autumn and winter

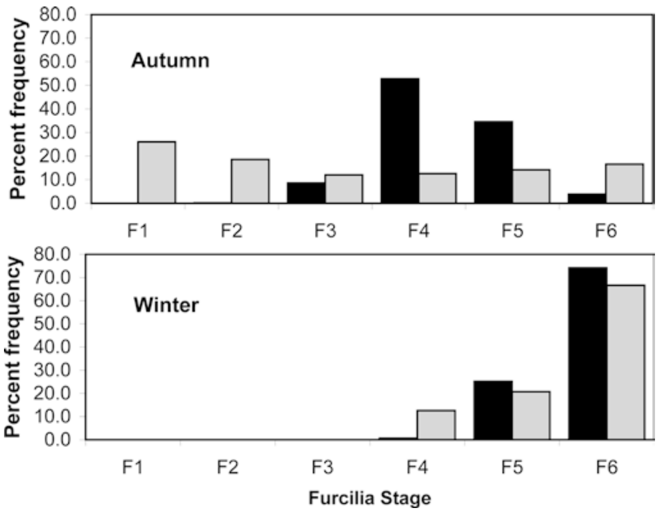


Fig. 8 Frequency of furcilia stages for *E. crystallorophias* (*black*) and *E. superba* (*gray*) during autumn and winter

present offshelf in both years, but were rare onshelf (Daly, in press). No *E. crystallorophias* calyptopis larvae were observed at any location. During winter, F4–F6 stages were present, although F6 was the dominant stage ($> 67\%$) in both species.

Euphausia crystallorophias and *E. superba* larvae co-occurred at a number of different locations across the study area during autumn and winter (Fig. 1). In 2001, *E. superba* furcilia were very abundant both offshelf (0.068–244 individuals m^{-3}) and onshelf (0.003–329 m^{-3}) and were ubiquitous with the exception of one station in a small coastal bay (Neny Fjord) where none were observed. The highest densities on-shelf were near the shelf break. Further inshore densities ranged from 0.003 to 11.8 individuals m^{-3}. In 2002, *E. superba* larvae were again very abundant (0.1–110 m^{-3}) offshelf during autumn, but only occurred at relatively low densities (0.009–2.34 m^{-3}) at some stations within Marguerite Bay. *E. crystallorophias* larvae were not collected offshelf in either year. They were, however, common (0.005–7.66 individuals m^{-3}) within Marguerite Bay during autumn 2001, especially in the fjords and bays nearshore, where they had densities similar to that of larval *E. superba*. Larval *E. crystallorophias* densities were lower (0.002–1.49 m^{-3}) in autumn 2002, as was found for *E. superba*. During winter, both *E. superba* (0.02–1.10 m^{-3}) and *E. crystallorophias* (0.003–1.66 m^{-3}) furcilia were collected at outer-shelf and inner-shelf stations at low densities compared to that observed in autumn.

On a vertical scale, both *E. crystallorophias* and *E. superba* larvae occurred over the upper 500 m of the water column, however their depths of maximum abundance were spatially separated during autumn. *E. superba* were collected primarily in the upper 75 m, with maximum densities of all furcilia stages between 25 and 50 m (82% of the population) (Fig. 9). In contrast, *E. crystallorophias* were more broadly distributed

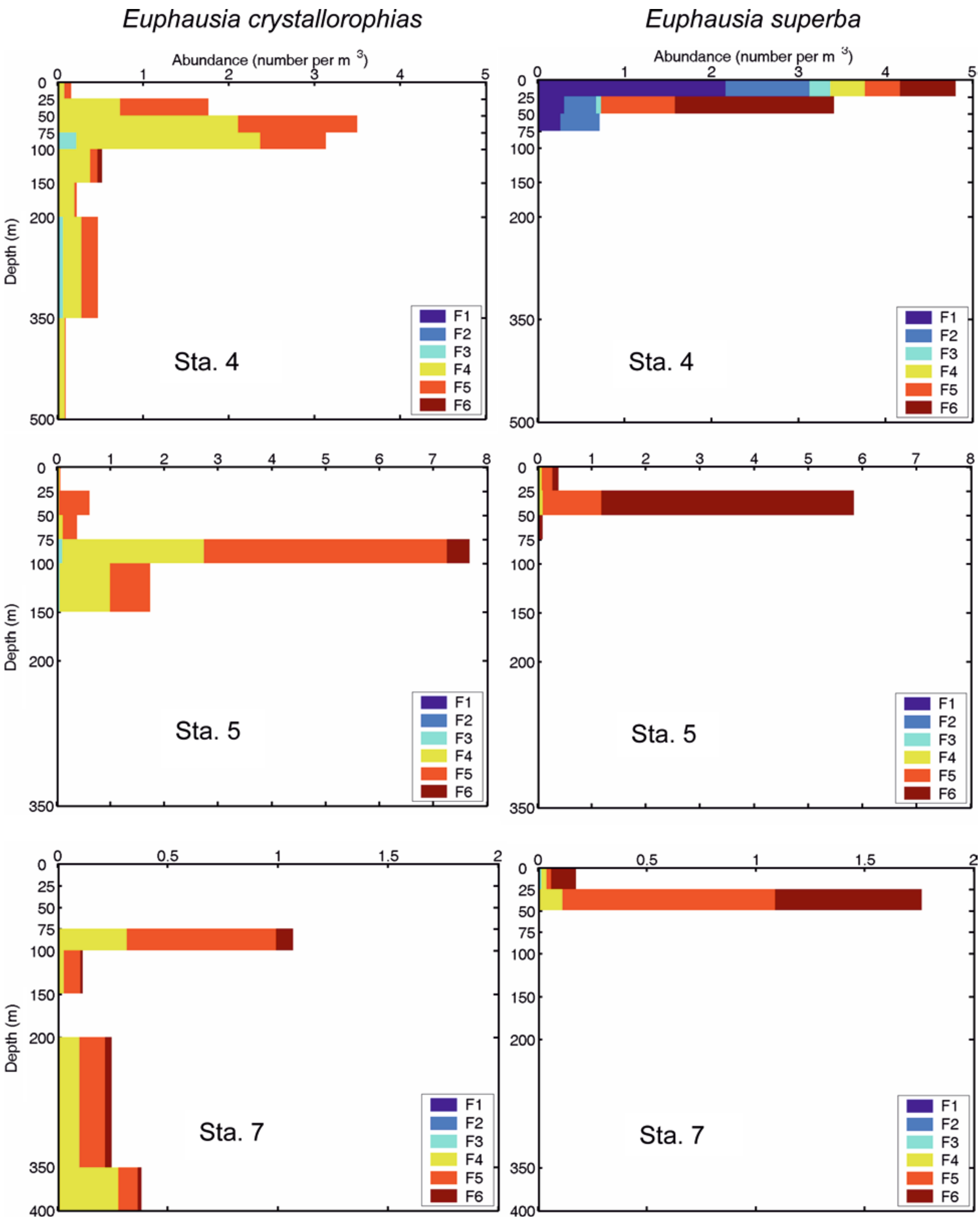


Fig. 9 Vertical distributions of *E. crystallorophias* (*left panel*) and *E. superba* (*right panel*) furcilia stages F1–F6 during autumn at three stations within the study area

throughout the upper 500 m, with a depth of maximum abundance usually between 50 and 100 m (58% of the population). Younger *E. crystallorophias* stages also tended to occur deeper (>100 m) in the water column than the older stages. A 54% of the F3s were below 100 m, but only 35% of the F4s, 27% of the F5s, and 11% of the F6s, respectively, were that deep. The vertical distributions shown for Stations 4, 5, and 7 (Fig. 9) are representative of other stations in the study area. Winter vertical distributions are not available.

Discussion

Two primary characteristics may be used to distinguish between *E. crystallorophias* and *E. superba* furcilia stages F3–F6 as exemplified by the F5 stages shown in Fig. 2. These characteristics are the development of the antennal scale (F3–F5) and the size of the mandibular palp (F3–F6). Fevolden (1980) demonstrated that the antennal scale and antennal flagellum of *E. crystallorophias* are of equal lengths through F2. All *E. crystallorophias* F3 specimens examined had segmented antennal flagella longer than the antennal scales. *E. superba* has an antennal scale and flagellum of equal lengths through F5. The antennal flagellum does not become segmented until F5 and does not extend beyond the scale until F6. The mandibular palp is a commonly used characteristic to distinguish between juveniles and adults of *E. crystallorophias* and *E. superba* (Mauchline 1979) and can also be used to distinguish between late larval stages. The length to width ratio of the distal segment of the mandibular palp is much greater for *E. superba* than that for *E. crystallorophias* (Table 1). The mandibular palp becomes more distinguishable in F4 s. By the F6 stage the distal segment is two to three times longer in *E. superba* than in *E. crystallorophias*.

Several secondary characteristics provide additional information for separating the two species. A dorsal carapace keel is present in *E. crystallorophias* F3 through F6. *E. superba* doesn't have a dorsal carapace keel, but occasionally can appear to have one as a result of preservation or distortion from collection. The rostrum shape for both species varies considerably within stages. In general the rostrum of *E. crystallorophias* is more pointed, while the rostrum of *E. superba* is more rounded. The rostrum in both species becomes more triangular in older stages. The rostrum is distinctively different between the two species in F5 s, but not necessarily in the F6 stage. In addition, the size of the eye tends to be larger in *E. crystallorophias* than in *E. superba* larvae, a characteristic also seen in the juvenile and adult stages (Fig. 6).

Rustad (1930) described *E. crystallorophias* larvae as being morphologically similar to *E. superba*, but smaller in size. Makarov (1980) also gave lengths for furcilia stages 1–3 of both species, which indicated that *E. crystallorophias* are somewhat smaller and have a narrower size range. Our measurements, however, suggest that while there is considerable overlap in size between the two species, on average, *E. crystallorophias* are larger than *E. superba* for stages F3–F6 during autumn and winter. Fevolden (1980) also noted an overlap in size for F1 and F2 stages of these species collected in the southern Weddell Sea. Furthermore, Brinton and Townsend (1991) collected *E. crystallorophias* F2–F4 in late March near the Antarctic Peninsula, which had a body size similar to those we collected during April and May. Thus size does not appear to be a useful criterion for distinguishing between larvae of the two species.

Euphausia crystallorophias occurred primarily as late stage (F4 and F5) furcilia during autumn. *E. superba* F1–F6 were present during autumn; however, younger furcilia were more common offshore and older furcilia more common at stations over the shelf. *E. crystallorophias* are reported to spawn prior to *E. superba*, typically October to January (Fevolden 1980; Harrington and Thomas 1987; Brinton and Townsend 1991; Pakhomov and Perissinotto 1997), while *E. superba* tend to spawn between December and March (Spiridonov 1995). The differences in larval stages between the two species in this study support these observations. During a year-round sampling effort in Prydz Bay, Kirkwood (1996) found *E. crystallorophias* eggs between November and December and F6 larvae during August and estimated a mean development time of 235 days, which closely agreed with developmental times reported by Ikeda (1986) based on laboratory experiments. Other authors (e.g., Brinton and Townsend 1991) estimated similar developmental times based on field samples, although times varied per stage as would be expected for sampling in different regions and years. Kirkwood (1996) concluded that larval development time for *E. crystallorophias* may be about twice as long as that for *E. superba*. Our data indicate that by winter, however, both species are in the same larval stage (F6) and about the same size. The furcilia of both species that survive overwinter develop into juveniles during the following spring (Kirkwood 1996; Daly, in press).

The densities of *E. crystallorophias* larvae collected during autumn were within ranges reported for other neritic regions along the Antarctic Peninsula and in Prydz Bay during summer (e.g., Makarov et al. 1990; Brinton and Townsend 1991; Pakhomov and Perissinotto 1996). Although the maximum abundances of *E. superba* larvae were much higher than that of *E. crystallorophias*, those maxima occurred offshelf. Where the distributions of larval *E. crystallorophias* and *E. superba* coincided on the shelf in our study area, their densities were similar. Furthermore, even though the two species co-occurred in most inner-shelf locations during autumn, they usually were vertically segregated in the water column and thus would not compete for limited resources. The majority of *E. crystallorophias* larvae were located deeper in the water column than larval *E. superba*. The concentration of larval *E. superba* between 25 and 50 m was coincident with the chlorophyll maximum in colder ($<0°C$) surface water at most stations (Daly, in press), whereas *E. crystallorophias* were more closely associated with the pycnocline (ca. 100 m) and increasing sea-water temperatures (0–2°C) in deeper water.

There are few other reports of the depth distribution of *E. crystallorophias* larvae for comparison. In Prydz Bay, the abundances of younger larvae (e.g., nauplius, metanauplius, and calyptopis stages) in 0–200 and 0–1,000 m net tows were not significantly different (Hosie 1991). In contrast, in the southeastern Weddell Sea (Cape Norwegia) *E. superba* larvae were primarily collected below 100 m and most abundant between 225 and 325 m, while young *E. crystallorophias* larvae primarily occurred between 25 and 100 m (Hempel 1985). Makarov (reported in Fevolden 1980) also observed that young larval stages of *E. crystallorophias* were most abundant between 0 and 25 m in the southern Weddell Sea. Additional studies are needed to assess the distribution and competitive interactions between *E. crystallorophias* and *E. superba* to better understand how these similar species successfully coexist in the same environmental habitats.

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