Seasonal distribution and life history of *Thysanoessa macrura* (Euphausiacea, Crustacea) in high latitude waters of the Lazarev Sea, Antarctica

Matilda Haraldsson[1],*, **Volker Siegel[2]**

[1]University of Gothenburg, Department of Biological and Environmental Sciences, Kristineberg, 451 78 Fiskebäckskil, Sweden
[2]Thünen Institut für Seefischerei, Palmaille 9, 22767 Hamburg, Germany

ABSTRACT: Although *Thysanoessa macrura* is one of the most abundant and widely distributed euphausiid species in the Southern Ocean, knowledge about its seasonal distribution and over-wintering strategy remains sparse. We describe the variation in abundance, demography, and distribution of *T. macrura* during 3 seasons in the Lazarev Sea, located in the south-east Atlantic sector of Antarctica. Adult and larval *T. macrura* were widely distributed across the Lazarev Sea in all seasons, but with large seasonal variability in the adult population. Mean summer densities (4.9 and 7.0 ind. m^{-2} in 2005/06 and 2007/08, respectively) were 20-fold higher than densities recorded during autumn (0.4 ind. m^{-2}) and winter (0.2 ind. m^{-2}). Comparison of length–frequency distributions and sex ratios, particularly between shallow (0–200 m) and deep (0–2000 m) samples taken during winter, suggest a seasonal vertical migration. A large proportion of the adult population seems to migrate to greater depth during winter, possibly as an overwintering strategy. Further, the demographic data and a set of growth models suggest that females and males have deviating life history traits. Females grow to larger size but their growth rate is slower, and they may mature later than males. The presence of mature males and females with spermatophores attached during late June to August indicated that spawning had already started during mid-winter conditions. These data, which were uniquely sampled in the same region from summer to winter, provide a new perspective on the seasonal behavior and general life history of *T. macrura.*

KEY WORDS: Euphausiid · Seasonality · Demography · Seasonal vertical migration · Overwintering · Southern Ocean

INTRODUCTION

Seasonality in light and primary productivity is one of the major characteristics that drive marine life in the Southern Ocean. The shift from long, light days into long, dark nights, i.e. from summer to winter causes extreme seasonality (Smith & Nelson 1990). The forcing effect of seasonal conditions influences all trophic levels (Clarke 1988), from light-dependent primary producers (Constable et al. 2003) to top predators, such as baleen whales that undergo extensive seasonal migrations to feed in the Southern Ocean during the productive summer months (Mackintosh 1966). Winter is a critical period for the survival of many Antarctic marine organisms (Lancraft et al. 1991, Nordhausen 1994a, Siegel & Loeb 1995), and they have therefore evolved morphological, physiological, and behavioral traits to survive under these harsh conditions.

Euphausiids (krill) are among the most abundant zooplankton and micronektonic taxonomic groups in the Southern Ocean, and their ecological importance as a link in the Southern Ocean food web is well documented (Everson 2000, Fisher et al. 2004). The most

abundant euphausiid species are *Euphausia superba* and *Thysanoessa macrura* (Hosie 1991, Nordhausen 1994a, Hagen & Kattner 1998). *E. superba* has the highest biomass and is of greatest commercial interest (Croxall & Nicol 2004, Atkinson et al. 2009), while *T. macrura* is the most ubiquitous euphausiid species (Kittel & Stepnik 1983, Kittel et al. 1985, Nordhausen 1994b, Fisher et al. 2004). *T. macrura* is present in extensive areas of the Southern Ocean, is typically evenly distributed and rarely found forming large aggregations (Daly & Macaulay 1988). This species mostly inhabits the epipelagic realm (upper 200 m), and generally occurs at greater depth than other epipelagic Southern Ocean euphausiids (Hopkins & Torres 1988).

Thysanoessa macrura seems well adapted to the seasonality of the Southern Ocean. Its omnivorous diet makes the species less dependent on seasonal phytoplankton blooms (Donnelly et al. 2006) than other Southern Ocean euphausiids. The lipid composition of *T. macrura* is unique compared to other Antarctic euphausiid species, as it has large lipid storage reserves mostly consisting of wax esters (Kattner et al. 1996, Hagen & Kattner 1998, Lee et al. 2006) that are typical lipids stored by diapausing copepods. It is believed that these stored lipids are partly the reason for the early spawning of *T. macrura* during late winter/early spring (i.e. September to November). However, details of the overwintering strategy of *T. macrura* remain unknown.

Several overwintering strategies have been suggested for Antarctic pelagic crustaceans in general. One of them is the accumulation and storage of energy that allow for dormancy during the winter months (Torres et al. 1994). This is a common strategy among crustaceans with a preference for herbivorous feeding, and is often combined with deep vertical migration to survive at low temperatures. A second strategy is simply to continue as normal,
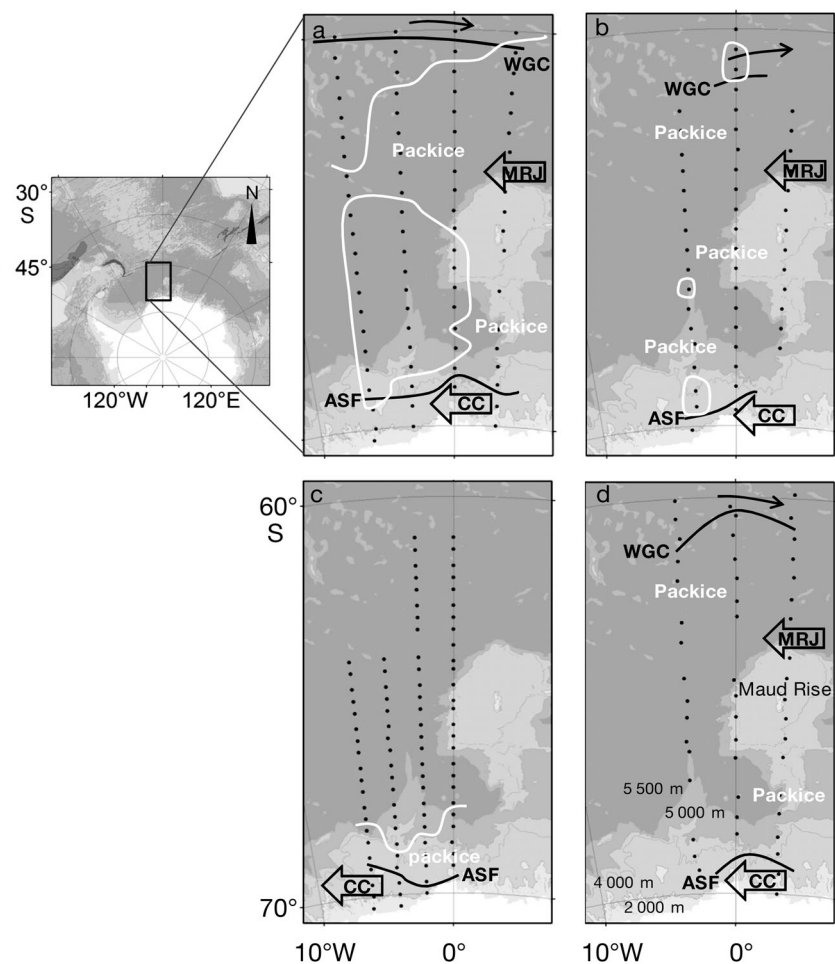

Fig. 1. Station map for (a) summer 2005/06, (b) summer 2007/08, (c) autumn 2004, and (d) winter 2006 in the Lazarev Sea, Antarctica. Grey scale contours indicate bathymetric layers, depth intervals are shown in panel (d). Arrows indicate current directions; thick arrows show stronger currents or jets. White lines show the extension of pack ice at the date of sampling. ASF: Antarctic Slope Front, WGC: Weddell Gyre Centre line, CC: Coastal Current, MRJ: Maud Rise Jet

adapted among carnivores or omnivores (Torres et al. 1994). The reality is often much more complex, and often a combination of the 2 strategies is observed, with decreased metabolic activity during winter in combination with opportunistic, omnivorous feeding (Torres et al. 1994, Meyer et al. 2010). Some of these overwintering strategies have been proposed for *Euphausia superba* in which sea ice seems to play a significant role for the species' survival during winter (Siegel & Loeb 1995, Flores et al. 2012). In contrast, *Thysanoessa macrura* has not shown any strong close association with the sea ice habitat (Donnelly et al. 2006, Flores et al. 2012).

Although *Thysanoessa macrura* has an extensive distribution and plays a relevant trophic role as a food source for many Antarctic predators (Nemoto &

Nasu 1958, Hopkins 1985, Croxall et al. 1999), the seasonal changes in its distribution, abundance, and life strategies are still poorly known. Here we report on the abundance, spatial distribution, and demography of *T. macrura* over 3 seasons in the high-latitude waters of the Lazarev Sea. We further discuss its general seasonal behavior and report new findings on the life history of this species.

MATERIALS AND METHODS

Sampling area

Sampling of euphausiids was conducted onboard RV 'Polarstern' during 4 cruises in the Lazarev Sea, east of the Weddell Sea in the Atlantic sector of the Southern Ocean (Fig. 1). The study was part of the Lazarev Sea Krill Study (LAKRIS), and the cruises took place during austral summer 2005/06, summer 2007/08, autumn 2004, and winter 2006 (Table 1). Sampling was conducted along 3 to 4 meridian transects, with sampling stations separated 20 (for autumn 2004) to 30 nautical miles (the other 3 cruises) from each other (Fig. 1). In total, 275 stations were sampled. Cruises will consistently be mentioned in seasonal rather than chronological order, due to the seasonal focus of this study.

The sampling area has a narrow continental shelf with an extensive deep-sea ocean basin (82% of stations sampled were at >3500 m depth). The Maud Rise, a seamount, is located in the eastern part of the sampling area and modifies the local hydrography (Leach et al. 2011). The hydrographic conditions recorded during the surveys were described by Cisewski et al. (2011) and Hunt et al. (2011). Ice conditions varied with seasons and cruises (Fig. 1, see also Pakhomov et al. 2011).

Collection of euphausiids

Adult and larval euphausiids were collected using a rectangular midwater trawl (RMT)8+1 (Baker el al. 1973). The trawl consisted of an RMT 8 net in the bottom with a mouth opening of 8 m^2 and mesh size of 4.5 mm, designed to catch micronekton and adult euphausiids. The smaller RMT 1 net with a 1 m^2 opening and 330 µm mesh size was mounted on top, and designed to catch euphausiid larvae and other mesozooplankton. Standardized double oblique hauls down to 200 m depth were conducted both during day and night. During trawling, the ship kept an average speed of 2.5 (± 0.5) knots. Volumes were recorded with a calibrated flow meter fixed to the bridle outside the net opening. Further details of the

Table 1. *Thysanoessa macrura.* Number of stations sampled (N) and counts (n, in parentheses) of *T. macrura* caught during the 4 cruises and later included in various statistical analyses. The second winter 2006 column reports the 3 non-quantitative stations sampled down to 2000 m depth, compared to the same 3 stations sampled to 200 m depth. K-W: Kruskal-Wallis rank sum test, VB: Von Bertalanffy, VB-S: VB-successive, OVB: oscillating VB. Only the number of stations (N) is indicated for the CMIX analyses, as these were based on length–frequency distributions. No sex classification was done during the autumn 2004 cruise, hence the lack of sex-specific CMIX analyses. Similarly, CMIX analyses on juvenile data in winter 2006 are lacking as too few juveniles were caught. Red.: reduced dataset; for detailed explanation of n > 20 and autumn, see 'Materials and methods: Demography' and 'Results: Adult abundance and distribution' respectively

	Summer 2005/06 6 Dec–1 Jan	Summer 2007/08 5 Dec–23 Jan	Autumn 2004 7–26 Apr 2004	Winter 2006 26 Jun–13 Aug	2000 vs. 200 m	Analyses
N stations	81	50	93	51	3	
n caught	(49 193)	(30 840)	(2 011)	(1 364)	(492 vs. 136)	
n measured	(8 321)	(11 174)	(2 010)	(1 312)	(492 vs. 136)	
Total	81 (49193)	50 (30840)	93 (2011)	51 (1364)		Trawl-CI, K-W test
Day	71 (44798)	38 (23142)	37 (355)	8 (112)		Trawl-CI, K-W test
Night	10 (4395)	12 (7698)	56 (1656)	43 (1252)		Trawl-CI, K-W test
All red. (n>20)	77 (49080)	47 (30812)	31 (1461)	19 (1078)		Cluster analyses
All red. (autumn)	81	50	56	51		CMIX (VB, VB-S, OVB)
Males	80	50		49	3[a]	CMIX (VB Males), sex ratio[a]
Females	80	50		44	3[a]	CMIX (VB Females), sex ratio[a]
Juveniles	78	50				CMIX (VB Males, Females)

[a]Samples only analyzed for sex ratio

sampling protocol can be found in Siegel (2012). During the winter cruise 2006, 3 additional stations were sampled down to 2000 m. Euphausiids were counted and measured for relative comparison with the standard 200 m samples regarding sex ratios and length–frequency distributions.

Treatment of samples

Thysanoessa macrura were sorted quantitatively on board from the RMT 8 net and stored in 4 % formalin-in-seawater solution. Samples >1 l were sub-sampled using a Folsom plankton splitter (van Guelpen et al. 1982). After 2 to 3 d of preservation, the subsequent analyses were performed on board. Adults were measured from the tip of the rostrum to the tip of the telson to the nearest lower mm ('standard length' according to Mauchline 1980). *T. macrura* was classified by sex (female, male) and maturity stage (with spermatophores [mature] or without spermatophores), and where sex could not be determined, individuals were classified as immature (juveniles).

The RMT 1 net catch was preserved in a 4 % formalin-in-seawater solution immediately after net retrieval and stored for 2 to 3 d before further sorting. Samples generally required sub-sampling before analysis, which was done using a Folsom plankton splitter. Larvae of *Thysanoessa macrura* were picked out from the subsample using a stereomicroscope and classified into developmental phases (nauplius, metanauplius, calyptopis [stages 1 to 3], and furcilia [stages 1 to 6]) according to Kirkwook (1982). Damaged calyptopis or furcilia larvae which could not be identified to stage were categorized as unidentified calyptopis or furcilia phases, respectively. In subsequent analyses, unidentified calyptopis and furcilia were distributed in proportion to the frequency of each identified calyptopis or furcilia stage in the same sample. Because the furcilia stage 6 and juvenile phase were difficult to distinguish in winter samples, all furcilia 6 and juveniles were pooled into 1 arbitrary group (F6–J). During summer 2007/08 and winter 2006, total larval length was measured to the nearest mm using a measurement ocular in the dissecting microscope.

Data analysis

Abundance and distribution

Adult and larval count data were standardized into density (ind. m^{-2}) using the calibrated flowmeter readings. Due to a skewed density distribution, mean densities for each cruise were calculated using the 'trawl data confidence interval' (TRAWLCI) method of de la Mare (1994a). Differences in mean density among seasons and between day and night samples were tested using a Kruskal-Wallis rank sum test (K-W). All data analyses were performed using R and SPSS software. Spatial density distributions were also plotted using the arcGIS software package with the bathymetry data from the Australian Antarctic Data Centre (http://trove.nla.gov.au/result, accessed November 2008).

Demography

Sex ratios were compared to a 1:1 sex ratio using a Pearson χ^2-square goodness of fit test, except for autumn 2004 when no sex or stage was identified.

Geographical patterns in population length structure were examined using agglomerative hierarchical cluster analysis. Bray-Curtis dissimilarity measures were derived from adult length–frequency distributions using 2 mm length intervals. The Weighted Pair Group Method using Averaging (WPGMA) linkage methods were used to combine the hierarchical clusters. Only stations with more than 20 measured specimens were included, so as to avoid random fluctuations caused by samples containing too few size classes. The resulting dendrograms were visually assessed and clusters identified to minimize the level of similarity. The composite length–frequency distributions were standardized station by station before being aggregated for each of the derived clusters. All multivariate analyses were carried out using the MVSP software package (Kovach Computing Services).

Age and growth

Species that lack hard structures for estimating age or growth such as crustaceans can be assessed by models that follow modal progression in length frequency/density distributions to identify cohorts, and provide estimates of important demographic components (e.g. ELEFAN: Pauly & David 1981, FISAT: Gayanilo et al. 2005, CMIX: de la Mare 1994b). These methods are successful only for fast-growing, short-lived species, since the overlap in size of older cohorts can limit the ability to discern proportions of older age classes. The largest age class is often a 'plus class' in which larger specimens accumulate,

although most likely in relatively low absolute numbers caused by mortality. These methods have several assumptions, including that the same population is sampled over time, and develops isocratically and symmetrically. These are simplifications, as at least some euphausiids show variability in growth both individually and through time (e.g. Atkinson et al. 2006). Therefore, the estimated lengths-at-age depict the average progression in length of the population sampled, and should be interpreted accordingly. Alternative experimental methods such as the instantaneous growth rate described by Tarling et al. (2006) also make certain assumptions (e.g. survival and molting under experimental conditions are believed to reflect natural behavior). This method is difficult to use with *Thysanoessa macrura* since the species is extremely fragile and rarely survives net sampling.

We used CMIX (de la Mare 1994b, a well-established method for Antarctic krill in assessment work by the Commission for the Conservation of Antarctic Marine Living Resources) to identify age classes in the adult length–density distributions using all stations. No prior knowledge about the von Bertalanffy growth parameters (L_t, K, and t_0) was used in the settings for *Thysanoessa macrura*. In addition to estimating length at age from the full dataset, juveniles, females, and males were analyzed separately in order to get sex-specific length-at-age estimates.

The resulting unweighted length-at-age data were used to fit the von Bertalanffy growth model (VB) (von Bertalanffy 1938):

$$L_t = L_\infty\left(1 - e^{-(K(t-t_0))}\right) \qquad (1)$$

The model describes the length (L_t) at a given time t, where L_∞ is the asymptotic length when growth is theoretically 0, and K is the growth constant. In order to find the best fit of the model to the data, the negative log likelihood estimate was minimized by varying the parameter values (L_∞, K, and t_0), using the solver function in MS EXCEL. Time 0, corresponding to the hatching date of *Thysanoessa macrura*, was estimated by back-calculating from the oldest larval stage for each season to the possible hatching date, using developmental times from Makarov (1979) and Menshenina & Spiridonov (1991). The resulting hatching day estimate was 1 November. We included the average lengths of larval *T. macrura* taken during winter 2006 and summer 2007/08 and estimates of age based on the developmental times in the VB models to better constrain the 0 and 1+ section of the growth curves. Four models were produced with the classical VB model: first, sex-specific models fitted to

(1) all male *T. macrura* plus larval as well as juvenile length at age (VB Male), and (2) all females plus larval and juvenile length at age (VB Female). The models were further fitted to (3) the full dataset (VB) and (4) the full dataset, but only for the year classes that could be followed over successive years (i.e. cruises) (VB-S). The latter model was consequently fitted to 7 length-at-age estimates excluding the larval data, compared to 11 length-at-age estimates in the full VB model.

Seasonality in growth rates was further investigated by fitting an oscillating VB growth model (OVB; Pauly & Gaschütz 1979) to the full dataset only. The OVB model allows for seasonal variation in growth, and has the general form:

$$L_t = L_\infty\left(1 - e^{-(K(t-t_0)+CK/2\pi)\cdot\sin 2\pi(t-t_0-t_s)}\right) \qquad (2)$$

where C is a constant describing the degree of seasonality commonly ranging between 0 and 1 (0 results in no oscillation trend and values near 1 result in 0 growth, values greater than 1 would indicate overall population shrinkage during winter), and t_s is the winterpoint and describes the time between hatching and the onset of the first growth oscillation modulated by a sine wave curve of a 1 yr period. Using the OVB model, a fifth model was produced: (5) fitted to all data combined. To compare and test the different seasonal and sex-specific models, the Akaike Information Criterion (AIC) was calculated:

$$\text{AIC}_i = -2L(Y\,|\,M_i) + 2p_i \qquad (3)$$

where $L(Y|M_i)$ is the likelihood (L) that the model (M) is correct given the data (Y), and p_i is the number of parameters in the ith model.

RESULTS

Adult abundance and distribution

During the 4 seasons, *Thysanoessa macrura* was found at most locations (251 out of 275 stations). Catches containing 0 *T. macrura* occurred only during autumn 2004 (22 stations) and winter 2006 (2 stations). Twenty-fold higher densities were found during the summer seasons (mean ± SE, 2005/06: 4.9 ± 0.98 ind. m^{-2} and 2007/08: 7.0 ± 2.06 ind. m^{-2}) compared to autumn 2004 (0.3 ± 0.06 ind. m^{-2}) and winter 2006 (0.2 ± 0.05 ind. m^{-2}), which were significantly lower (Fig. 2).

Comparing the mean density between day and night, only autumn 2004 had significantly higher densities during night than during day (K-W rank
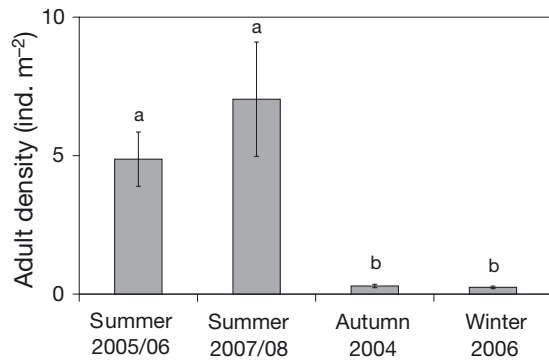
Fig. 2. *Thysanoessa macrura.* Mean ± SE density (ind. m^{-2}) of adults, calculated using the TRAWLCI program based on all stations. Different letters indicate that values differ significantly (p < 0.05) from each other

sum test: summer 2005/06 χ^2 = 0.030, p = 0.86, df = 1; summer 2007/08 χ^2 = 0.004, p = 0.95, df = 1; autumn 2004: χ^2 = 26.546, p < 0.01, df = 1; winter 2006 χ^2 = 1.074, p = 0.30, df = 1). As a consequence of the day and night difference during autumn 2004, only night-time samples were used in subsequent analysis in order to avoid bias caused by this difference.

While densities differed remarkably among seasons, within-season spatial variability was considerably lower (Fig. 3). Common for all seasons were the lower densities along the coastline. Slightly higher densities appeared around or north of Maud Rise during the summer seasons and at the northernmost stations during winter 2006 (around 62 to 60° S). However, no prominent high-density areas could be distinguished for any of the cruises (Fig. 3).

Demography

Cluster analysis revealed 2 groups with different length structure for all seasons (clusters A and B separated at 0.70, 0.65, 0.90, and 0.70 Bray-Curtis distance in the 4 seasons, respectively, Figs. 3 & 4), but the stations represented in each cluster were fairly spatially scattered (Fig. 3), indicating a relatively homogeneously spread population. Generally, during summer seasons, smaller individuals (10 to 15 mm) tended to inhabit regions with a shallower seafloor close to the coastline, and the northern section of Maude Rise during summer seasons (cluster B, Figs. 3a,b & 4a,b), while surrounding areas were dominated by relatively large individuals (18 to 28 mm; cluster A, Fig. 3a,b). During winter 2006, the opposite pattern occurred, with slightly smaller indi-
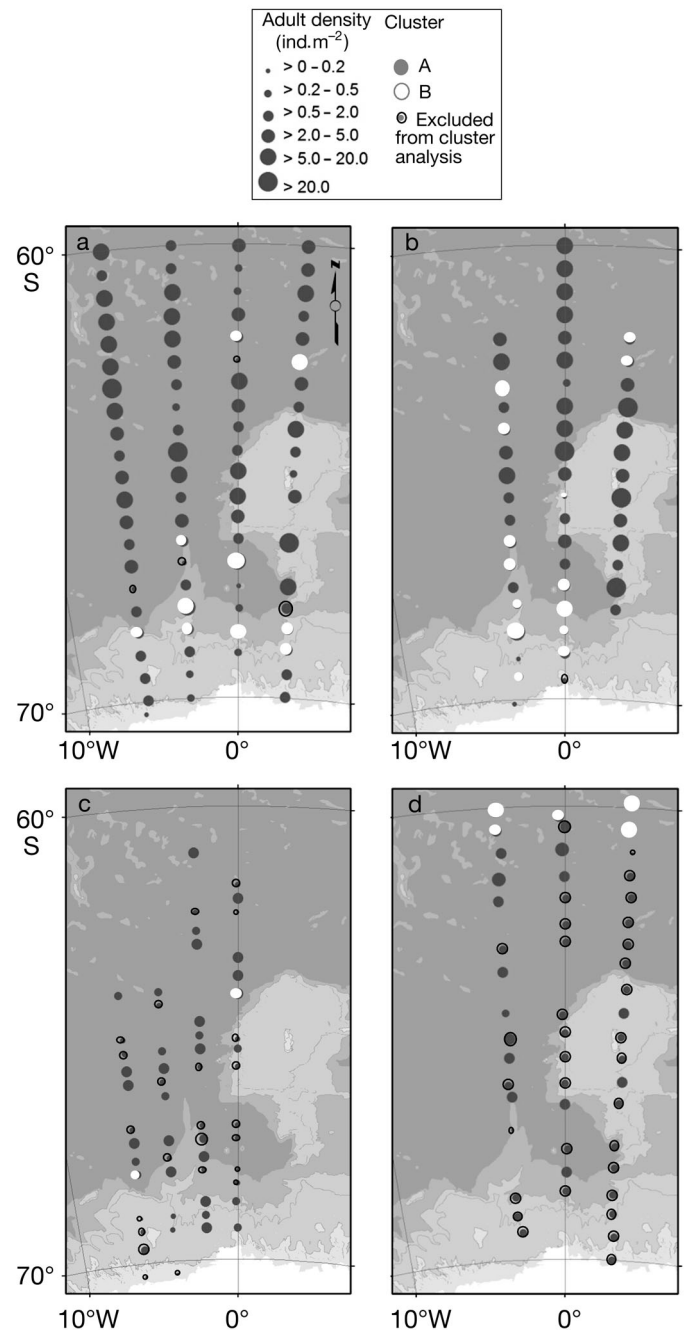

Fig. 3. *Thysanoessa macrura.* Spatial density distribution (ind. m^{-2}) of adults in the Lazarev Sea (indicated by dot size), and spatial distribution of stations showing similarity in length–frequency distribution derived from hierarchical agglomerative cluster analysis (indicated by grey or white circles) during (a) summer 2005/06, (b) summer 2007/08, (c) autumn 2004, and (d) winter 2006. A and B are the respective clusters, and density dots encircled with a black ring indicate stations not included in the cluster analysis. The associated length–frequency distribution for each respective cluster is shown in Fig. 4. Grey scale shows the bathymetric contours (see Fig. 1)

viduals inhabiting the northernmost part of the sampling area (Figs. 3d & 4d). Autumn 2004 showed very weak spatial separation (Figs. 3c & 4c).

The demographic structure of the population changed among the seasons. Females dominated the population significantly during both summers, contributing 63 and 74% for each summer cruise (Fig. 5a, χ^2 goodness of fit test summer 2005: $\chi^2 =$
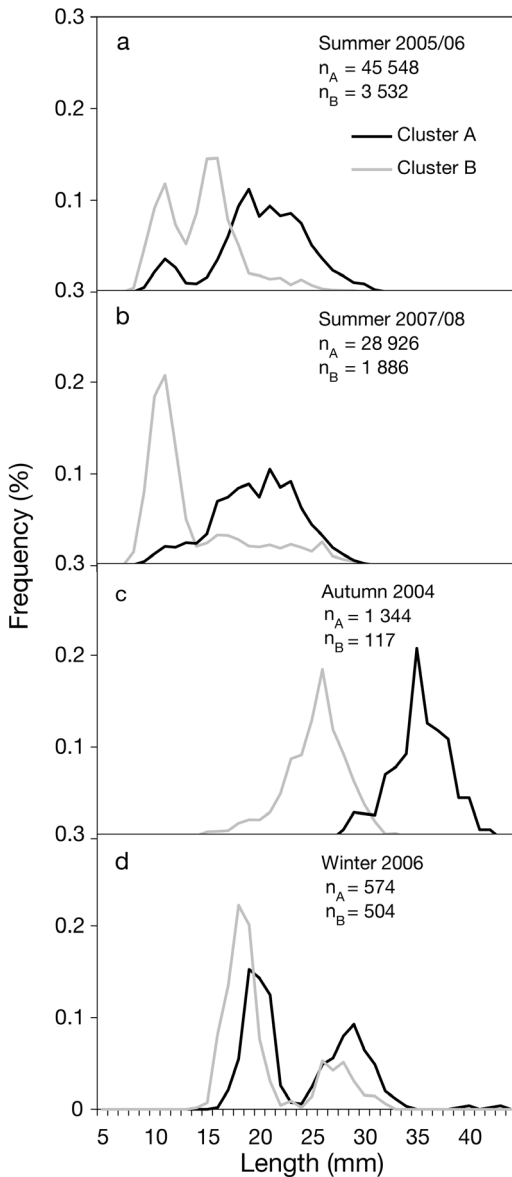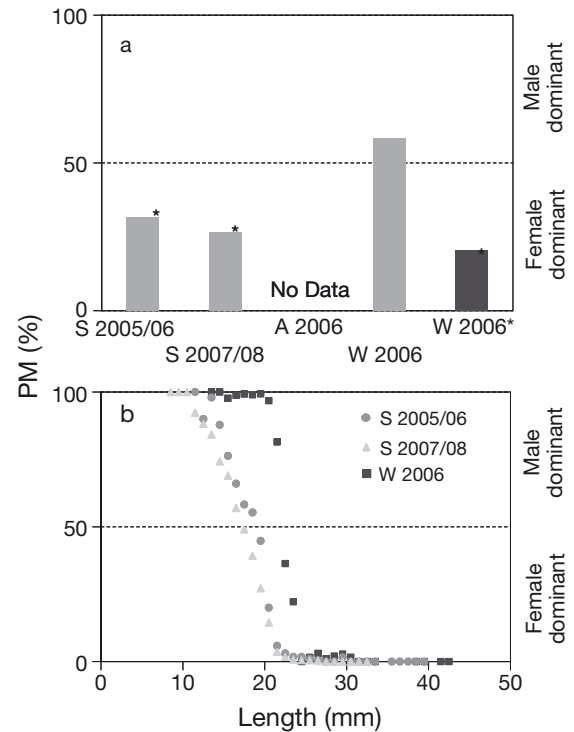

Fig. 5. *Thysanoessa macrura*. Sex ratio given as proportion of males (PM) (a) during summer (S) 2005/06, summer 2007/08, autumn (A) 2004, and winter (W) 2006, respectively. The dark grey bar (deep, winter 2006) is the sex ratio calculated from non-quantitative samples taken down to 2000 m depth. (b) Sex ratio with increasing length for summers 2005/06 and 2007/08, and winter 2006. Asterisks (*) indicate significantly uneven sex ratio, and the dotted line at 50% denotes an equal number of females and males

6.515, p = 0.01, df = 1; summer 2007: χ^2 = 23.292, p << 0.0001, df = 1). In contrast, during winter 2006, males contributed 59% of the adult population (winter 2006: χ^2 = 3.048, p = 0.08, df = 1; Fig. 5a). Sex ratios calculated from 3 samples taken down to 2000 m depth during winter 2006 (compared to 200 m for all other seasons) revealed a high (79%), and significant, female dominance similar to that observed during summer cruises (Fig. 5a; deep RMT winter 2006: χ^2 = 34.697, p << 0.001, df = 1). This was in contrast to the same 3 stations sampled in the regular 0 to 200 m interval, where only 36% of all caught individuals were females. This suggests that females in these locations might have a deeper distribution than males, causing the male dominance in the upper 200 m layers.

The proportion of maturity stages was almost identical during summer seasons, with females and males without spermatophores dominating the population structure (Table 2). In contrast, during winter 2006,

Fig. 4. *Thysanoessa macrura*. Composite length–frequency distributions for clusters A and B from stations separated using hierarchical agglomerative cluster analysis based on adult data for (a) summer 2005/06, (b) summer 2007/08, (c) autumn 2004, and (d) winter 2006. n_A and n_B represent the number of animals caught at the stations within cluster A and B, respectively. See Fig. 3 for geographical representation for each respective cluster

Table 2. *Thysanoessa macrura*. Proportion of sex, including juveniles, and maturity stages during all seasons except autumn 2004. 'w/sperm.' indicates adult females (F) or males (M) with spermatophores

	Juvenile	M	F	M (w/sperm.)	F (w/sperm.)
Summer 2005/06	0.19	0.30	0.40	0	0.11
Summer 2007/08	0.19	0.21	0.57	<0.03	0.03
Winter 2006	0.01	0.16	0.14	0.42	0.26

Table 3. *Thysanoessa macrura.* Estimated mean ± SD length at age for each season derived from adult length–density distributions using the CMIX software described by de la Mare (1994b). ♀: females, ♂: males Gaps indicate age groups/sexes for which no data or too few data existed to identify a robust age class. No sex classification was undertaken for the autumn 2004 cruise; age class 4+ was only identified during autumn 2004, therefore no sex-specific age classes are shown. For an explanation of the missing age class 2 in autumn 2004 and winter 2006, see 'Results: Age and growth'. All length-at-age estimates except those indicated with a superscript [a] were included in the ordinary (all), successive (all), oscillating (all), or sex-specific (female and male) von Bertalanffy growth model. n/a: not applicable

Age class	Summer 2005/06	Summer 2007/08	Autumn 2004	Winter 2006
1				
All	11.1 ± 1.4	11.3 ± 1.4	18.0 ± 2.2	19.1 ± 1.5
Juvenile	11.2 ± 1.3	11.5 ± 1.7		
♀				19.5 ± 2.1
♂				19.0 ± 1.5
2				
All	18.3 ± 2.2	17.6 ± 2.1	n/a	n/a
Juvenile	16.5[a] ± 1.5	16.5[a] ± 2.0	n/a	n/a
♀	19.5 ± 2.4	19.4 ± 2.1	n/a	n/a
♂	18.0 ± 1.8	17.3 ± 2.1	n/a	n/a
3				
All	24.2 ± 2.8	23.1 ± 2.7	25.8 ± 2.5	28.5 ± 2.1
♀	24.0 ± 2.9	23.6 ± 2.6		28.5 ± 2.1
♂	24.5 ± 1.8	23.5 ± 2.4		
4+				
All			34.5 ± 2.9	

adults with spermatophores dominated and were present during the entire cruise, indicating that *Thysanoessa macrura* were already spawning at the end of June.

The proportion of males (PM) to females decreased with increasing length during all seasons, and above 33.5 mm, all animals were females (Fig. 5b).

Age and growth

Four age classes (1 to 4+) were identified from the cohort analysis; together with the larval age group
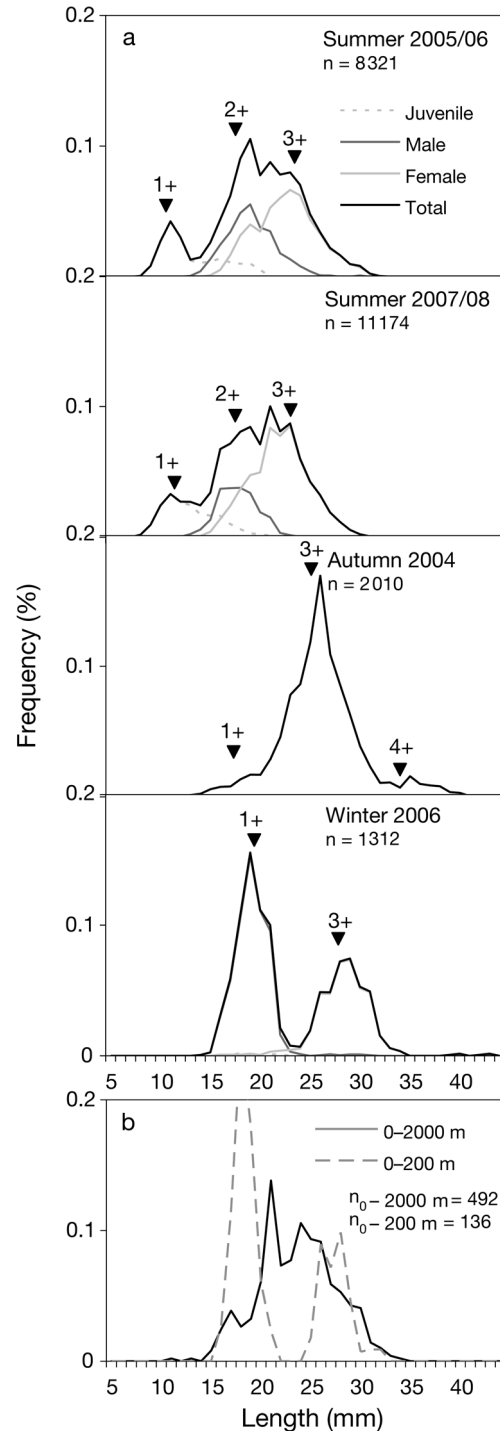

Fig. 6. *Thysanoessa macrura.* Observed length–frequency distributions for adults together with the estimated length-at-age from the CMIX analysis (black triangles, age classes 1+ to 4+) for (a) summer 2005/06, summer 2007/08, autumn 2004, and winter 2006. (b) Length–frequency distribution from 3 stations sampled during winter 2006 from 0–2000 m, and the respective stations from 0–200 m samples. The figure is cut to facilitate comparison where the maximum value for the 0–200 m dataset is 0.25 at 17.5 mm length. n is the number of measured individuals on which the size frequency is based

Table 4. *Thysanoessa macrura*. Estimated growth parameters from the von Bertalanffy (VB) growth model. K: growth constant, L_∞: theoretical asymptotic length, t_0: theoretical length at age 0, t_s: winterpoint, C: constant describing the degree of seasonality, Neg LL: resulting negative log likelihood estimate from fitting the model, AIC: calculated Akaike Information Criterion for comparing models, VB-S: Successive VB, OVB: oscillating VB; n/a: not applicable

	K	L_∞	t_0	t_s	C	Neg LL	AIC
VB Male	0.294	40.3	−0.004	n/a	n/a	−9.6	27.3
VB Female	0.269	44.4	−0.006	n/a	n/a	−11.2	30.5
VB	0.266	45.2	0.006	n/a	n/a	−10.8	29.5
VB-S	0.314	40.6	0.017	n/a	n/a	−6.9	21.7
OVB	0.312	40.8	0.042	0.151	0.181	−13.1	38.2

(0), this represented 5 age classes (Table 3, Fig. 6). For the 2 summer seasons, 3 age classes were identified. In autumn 2004, we also identified 3 age classes; however, the large size span between the first and second cohort suggests a failed identification of an in-between size class, and age classes were instead interpreted as age classes 1, 3, and 4+. Similarly, during winter 2006, only 2 cohorts were identified, showing the same issues with too large a size span between the 2 cohorts identified (e.g. 9.4 mm) and were therefore identified as age classes 1 and 3. These representations of size classes coincided with our length estimates from the summer seasons. They were further supported by the observed length–frequency distribution from the 2000 m samples in winter 2006, containing presumably 3 distinct age classes, including the missing age class 2 (Fig. 6b). Note that no CMIX analyses were performed with the 2000 m samples. The same age classes as from the full dataset were identified for females and males, except the largest age class during winter 2006 when no males were detected (Table 3). Females and males were first identified during the winter of age class 1.

The sex-specific models showed a slightly faster growth rate for males (K: 0.294) than for females (0.269), and L_∞ indicated a smaller asymptotic length for males (L_∞: 40.3) than for females (44.4 mm; Table 4, Fig. 7a).

The results from the ordinary (VB), the successive (VB-S), and the seasonal (OVB) models overall agreed well (Table 4, Fig. 7b), with a slightly better fit for VB-S, which also agreed better with the OVB. The OVB suggests a stronger effect of seasonality during the earlier years of life, with more consistent and less seasonal growth with increasing age. Although seasonal growth explained the size at age well, the additional parameters used in the seasonal

model did not improve the overall fit of the model, as indicated by the higher AIC values (Table 4). Of all growth models, the VB-S had the lowest AIC criteria, suggesting a better fit to the size-at-age estimates.

Larval abundance and distribution

Larvae of *Thysanoessa macrura* were present at all stations and in all seasons, with the exception of 4 stations in total during summer 2005/06 and autumn 2004. Densities were fairly evenly distributed over the sampling area during each cruise (Fig. 8). However, the
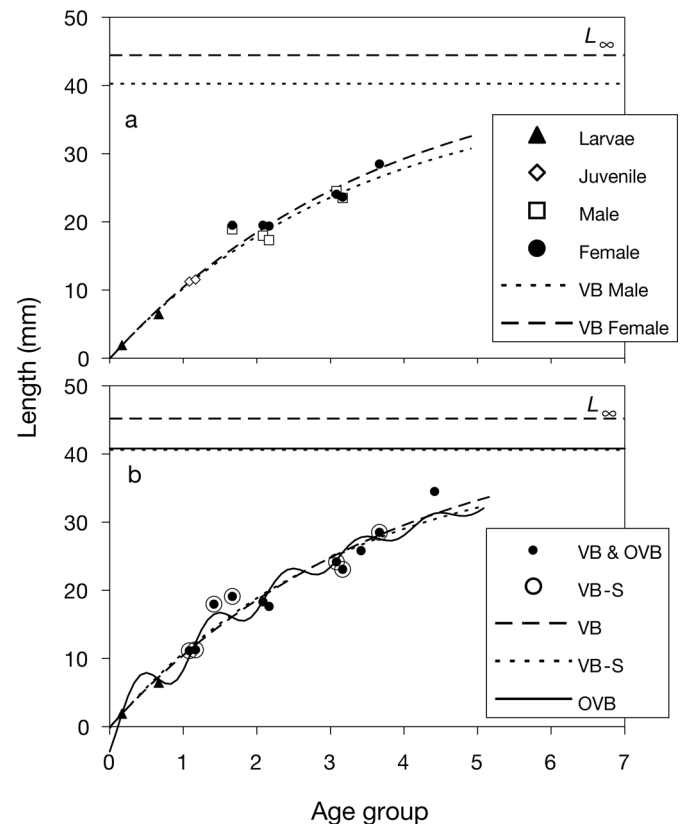

Fig. 7. *Thysanoessa macrura*. Theoretical von Bertalanffy (VB) growth curves fitted to estimated length-at-age data. (a) Sex-specific growth curves fitted to male and female data separately (VB Male and VB Female, respectively). (b) VB growth curve (VB), and the oscillating VB growth curve (OVB) fitted to the full length-at-age dataset, and the successive VB growth curve (VB-S) fitted to year classes that were followed over successive years (see 'Materials and methods: Age and growth'). Larvae (▲ in panels a and b) and juvenile (◇ in panel a) length-at-age estimates were included in all models to allow for a smoother fit. The upper lines in both figures indicate the maximum asymptotic length (L_∞) estimated by the models. For parameter estimates, see Table 4

average larval density during summer 2005/06 (mean ± SE, 47.4 ± 5.9 ind. m^{-2}) was very low compared to summer 2007/08 (218.0 ± 42.8 ind. m^{-2}; Fig. 9). Both summer seasons were numerically dominated by larval stage C1, while F1 was generally the oldest stage found (a few F2 stages were found during 2007/08; Table 5). Larval abundance during autumn 2004 (106.7 ± 11.6 ind. m^{-2}) was comparatively high (Fig. 9), dominated by F6 stage (Table 5), while winter 2006 (7.1 ± 1.0 ind. m^{-2}) had the lowest

Fig. 9. *Thysanoessa macrura.* Mean ± SE density (ind. m^{-2}) of larvae for all stations calculated using the TRAWLCI program (Kruskal-Wallis rank sum test: summer 05/06 and autumn 04: χ^2 = 98.219, p ≪ 0.00, df = 1; summer 07/08 and autumn 04: χ^2 = 72.162, p ≪ 0.00, df = 1; summer 05/06 and winter 06: χ^2 = 53.217, p ≪ 0.00, df = 1; summer 07/08 and winter 06: χ^2 = 66.850, p ≪ 0.00, df = 1)

Fig. 8. *Thysanoessa macrura.* Spatial density distribution (ind. m^{-2}) of larvae in the Lazarev Sea during (a) summer 2005/06, (b) summer 2007/08, (c) autumn 2004, and (d) winter 2006. Grey scale shows bathymetric contours (see Fig. 1)
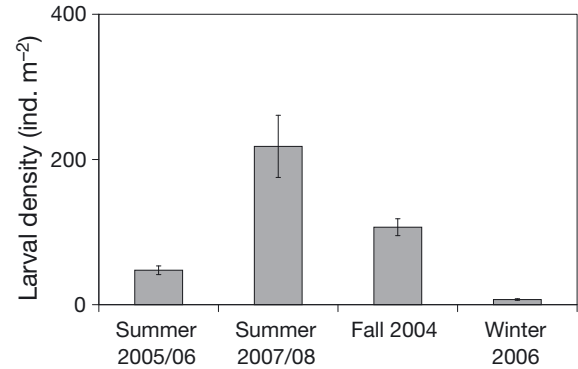
abundance (Fig. 9) and contained almost exclusively stage F6 and juveniles (Table 5). No significant differences in abundance were found between day and night samples (K-W rank sum test, summer 2005/06: χ^2 = 0.143, p = 0.71, df = 1, summer 2007/08: χ^2 = 2.15, p = 0.14, df = 1, autumn 2004: χ^2 = 1.573, p = 0.21, df = 1, winter 2006: χ^2 = 0.032, p = 0.86, df = 1).

DISCUSSION

Distribution and seasonality

As an Antarctic circumpolar species, *Thysanoessa macrura* is found throughout most parts of the Southern Ocean and is a common component of the Antarctic zooplankton assemblage (Hosie et al. 2000, Donnelly et al. 2006, Hunt et al. 2011). Similarly, we have shown that both larval and adult *T. macrura* are widely distributed across the Lazarev Sea during all seasons. However, pronounced seasonal differences in abundance were evident, showing up to 20-fold higher densities during summer compared to autumn and winter seasons, and with concomitant demographical changes as well. These 2 features indicate that large fractions of the population are transported or migrate out of the sampled region during autumn and winter months. We suggest that the large changes among seasons are due to a seasonal vertical migration.

Seasonal vertical migration is common among many zooplankton groups in the Southern Ocean (Foxton 1956, Hopkins 1971). Several Antarctic cope-

Table 5. *Thysanoessa macrura.* Proportion of larval stages during each season. C and F correspond to calyptopis and furcilia stages, respectively

Larval stage	C1	C2	C3	F1	F2	F3	F4	F5	F6
Summer 2005/06	0.58	0.31	0.10	0.01	–	–	–	–	–
Summer 2007/08	0.39	0.33	0.17	0.11	<0.01	–	–	–	–
Autumn 2004	<0.01	<0.01	<0.01	0.03	0.05	0.03	0.01	0.02	0.89
Winter 2006	–	–	–	–	–	–	<0.01	<0.01	1.00[a]

[a]F6 stage pooled with juveniles

pods perform seasonal vertical migration; among these is the herbivorous *Calanoides acutus*, which carries out an extensive deep migration and enters diapause during winter (Hagen & Auel 2001). The carnivorous chaetognath *Eukrohnia hamata* inhabits greater depths during winter, possibly as a result of following its migrating copepod prey (Kruse et al. 2009). Observations on potential seasonal vertical migration patterns were also described for *Euphausia superba* in the Lazarev Sea, with higher densities of krill found at greater depths during autumn and winter compared to summer seasons (Siegel 2012). Our results also suggest a similar seasonal vertical migration for *Thysanoessa macrura*. Apart from the decrease in densities in the sampled upper 200 m layer during autumn and winter (Fig. 2), the demographical patterns changed considerably between fall/winter and summer seasons. Firstly, the sex ratio differed significantly between summer and winter (Fig. 5a). Also, the general structure of the length–frequency distributions shifted substantially, with different age cohorts dominating among the seasons (Fig. 6). The shift in demographic structure found during this study cannot solely be explained by mortality or translocation by ocean currents. If animals were transported out of the sampled region, this should be visible in the spatial analyses of the population length structure, particularly for the summer 2005/06 and winter 2006 seasons sampled only half a year apart. This was not the case (Figs. 3 & 4). Further, if mortality had caused the change, one would not expect such similar demographic patterns and high abundance to return during the last summer sampled (i.e. 2007/08). Finally, although only based on 3 stations, the demographic structure obtained from the deeper 2000 m samples during winter more closely resembled the summer situation than the winter (Figs. 5a & 6). Together, this suggests a seasonal vertical migration, where a large fraction of the population leaves the upper 200 m layers during autumn and inhabits greater depths during winter. This agrees with previous winter distribution pat-

terns (Lancraft et al. 1991), and the conclusions of seasonal vertical migration drawn from the general zooplankton community sampled during the same cruises in the Lazarev Sea (Hunt et al. 2011).

Physiologically, *Thysanoessa macrura* is well adapted to the low-productivity polar winter partially due to its exceptionally high lipid reserves, which are accumulated during summer (Färber-Lorda & Mayzaud 2010) and are primarily used to fuel reproduction that starts well before the spring phytoplankton blooms occur (Hagen & Kattner 1998). Because *T. macrura*, unlike *Euphausia superba*, apparently does not feed on the microalgae that live beneath the sea ice (Flores et al. 2012), a deepward migration, as we suggest, may bring alternative feeding opportunities of seasonal or ontogenetic migrating mesozooplankton prey (Hagen & Auel 2001). This is in line with the oscillating growth model (Table 4, Fig. 7b), indicating that the growth rate most likely decreases during winter months, while accelerated during summer. However, compared to *E. superba*, the degree of seasonality as predicted from the model (constant of seasonality, *C*, Table 4; Siegel 1987) is considerably smaller for *T. macrura*. This may suggest that *T. macrura*'s overwintering strategy makes it less sensitive to variable winter conditions.

Life history

Life history traits may help to understand the population patterns observed for *Thysanoessa macrura*. Earlier studies showed 3 to 4 age classes for *T. macrura*, suggesting a life span of up to 4 yr (Siegel 1987, Nordhausen 1994a). We identified 4 postlarval age cohorts (Table 3), which together with the larval age class (0) suggests longevity up to at least 5 yr. However, the fourth age class is a typical plus class consisting of few individuals over a broad length range from 32 to 42.5 mm, potentially containing multiple age classes (Fig. 6), and suggesting that some individuals might survive >5 yr. Also, the max-

imum length (42.5 mm) observed in this study is to our knowledge the largest reported individual *T. macrura* (e.g. Siegel 2000 reported a maximum size of 36.5 mm), and is in line with the number of age cohorts identified from our data.

A differentiation in length between sexes was also evident. Although 3 age classes were identified for males and females, females clearly become larger (Figs. 5b & 6). Individuals >33.5 mm were exclusively female (Fig. 5b), implying that the oldest age class is only reached by females. If females live longer than males, as our data suggest, this could explain the skewed sex ratio towards females during summer seasons when densities were high, and in the deeper RMT samples during winter 2006 when a large proportion of the population is thought to have migrated deeper. A similar skewness with female-dominated populations has been repeatedly reported for *Thysanoessa macrura* (Kittel & Stepnik 1983, Nordhausen 1992). Females of *Euphausia superba* also tend to live longer and grow more slowly than males (Kawaguchi et al. 2007). For *T. macrura*, this sexual dimorphism was also reflected in the different growth models. The sex-specific models suggest that females reach larger sizes (higher theoretical asymptotic length, $L\infty$) and grow more slowly (lower growth constant, K) than males (Table 4). The suggested difference in life span is possibly due to their physiological differences, where females contain more lipids (Mayzaud et al. 2003, Färber-Lorda & Mayzaud 2010) and may have higher probability of survival during periods of starvation (winter).

Thysanoessa macrura is the earliest spawning Antarctic euphausiid. The initiation and duration of spawning often vary with region and between years (Menshenina 1990, Everson 2000), but spawning takes place well in advance of the spring bloom that typically occurs during November/December (Hart 1934, El-Sayed 1984). This is believed to favor the first feeding larval stage (calyptopis 1) which is present in high abundance during the start of the productive season (Table 5). During our winter cruise, most adults carried spermatophores (Table 2), indicating that mating had already started in the middle of the winter (late June to July), under the ice cover. This is considerably earlier than previous recorded spawning from late August to November (Siegel 1987, Menshenina 1988, Nordhausen 1994b), and may extend until January (Menshenina 1988). We also observed some individuals with spermatophores in January. A prolonged spawning period increases the possibility for multiple spawning events, which in turn increases the population fecundity. This should

be particularly favorable for Antarctic euphausiids such as *T. macrura* which have a limited spawning season (Everson 2000). While the timing from fertilized females carrying spermatophores to the shedding of eggs is unknown (Siegel 2000), our estimated hatching date based on the oldest observed larval stages started in November. Whether the early spawning during winter 2006 was just an exception is unknown, but it is clear that *T. macrura* is capable of an extensive spawning period.

Following spawning, larval *Thysanoessa macrura* grow during the favorable summer conditions, and by the second half of their first year (year class 0) maturation from larva to juvenile likely takes place at an approximate size of 8 mm (Siegel 1987, Nordhausen 1994a). A year later, most individuals mature into adults (age class 1) and reproduction can start, at a size of 15 to 17 mm (Siegel 2000). Given the bimodal distribution of juveniles (Fig. 6, Table 3) some individuals seem to postpone their maturation for a year (age class 2). Together with the total domination of males among the first adults (100% PM, Fig. 5b), this could imply that females mature up to a year later than males. Our summer and winter data further showed that males carrying spermatophores consisted mainly of age class 2 (17.5 and 18.5 mm, respectively, for summer and winter), while females mainly belonged to age class 3 (24.5 and 28.5 mm, respectively). Maturation at a younger age among males is a common feature for some euphausiid species (Siegel 2000, Kawaguchi et al. 2007), and also appears to occur in *T. macrura*.

In summary, the distinct seasonal changes in density and demography, together with the deeper samples taken during winter, suggest that *Thysanoessa macrura* performs a seasonal vertical migration, a strategy that might improve its survival during winter. We also report on deviation between females and males regarding life history traits, where females seem to grow more slowly, mature later, and reach larger sizes (suggesting that they grow older) than males, important traits which are typically associated with increased fecundity. While knowledge of *T. macrura*'s biology starts to unfold, many of the findings here and in earlier studies would benefit from explicit field studies or experimental confirmation, such as vertically stratified sampling, seasonal diet, and bioenergetic studies. However, the increasing recognition of *T. macrura*'s role in the Southern Ocean food web is only a first step towards understanding its response to a quickly changing environment in the Southern Ocean (Flores et al. 2012).

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