

Distribution and growth of larval and adult *Thysanoessa macrura* (Euphausiacea) in the Bransfield Strait Region, Antarctica

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ABSTRACT: *Thysanoessa macrura* was the most common euphausiid in the western Bransfield Strait region, with highest abundances of 5000 individuals per 1000 m³ in Gerlache Strait in December 1986 and 4500 ind. 1000 m⁻³ in January 1987, which coincided temporally and spatially with the annual spring bloom of phytoplankton. With the progression of the austral summer, high larval abundances extended into Bransfield Strait, apparently advected there by the Bransfield Current, estimated both geostrophically and with Lagrangian drifters. A discrete spawning period prior to December 1986 gave rise to a distinct cohort which persisted through March 1987. The study area was highly variable in phytoplankton biomass. Waters of northern Gerlache Strait reached 25 mg chl a m⁻³ in January 1987, whereas Drake Passage always had <2.0 mg chl a m⁻³ from December 1986 to March 1987. No differences in development or growth rate were found in regions with different levels of algal biomass. The development time from calyptopis 2 to furcilia 6 was ca 90 d. Larvae of *T. macrura* did not appear to perform diel vertical migration between the 0 to 100 and 100 to 200 m depth layers.

INTRODUCTION

The early concept of the Southern Ocean as being high in primary production has changed dramatically over the past decade. Recent evidence suggests that the productivity of Antarctic waters is similar to that of oligotrophic gyres of the oceans (Hempel 1985, Hewes et al. 1985, Smetacek et al. 1990). However, coastal regions with shallow mixed layers are characterized by high algal productivity and are thus of special importance in the life cycles of Antarctic zooplankton (Hewes et al. 1985, Holm-Hansen & Mitchell 1991, Huntley et al. 1991).

All major zooplankton taxa occur in the Antarctic, but the bulk of the biomass consists of a few large copepod species and large stocks of euphausiids (Knox 1970, Hopkins & Torres 1988, Smetacek et al. 1990, Smith & Schnack-Schiel 1990, Conover & Huntley 1991). *Thysanoessa macrura* is the most consistently distributed euphausiid in Antarctic waters and frequently exceeds *Euphausia superba* in number (Baker 1954, Makarov 1979a, Kittel & Stepnik 1983, Kittel et al. 1985, Piatkowski 1985a, Sebutal Pires 1986, Daly & Macaulay 1988). The highest abundances of *T. macrura* have been observed between 0 and 200 m depth

(Hempel 1981, Loeb & Shulenberger 1987) and diel vertical migration is reported not to occur (Kittel et al. 1985, Piatkowski 1985b, Lancraft et al. 1989). All stages are found in open water, but only postlarvae and adults have been observed to occur under pack ice (Daly & Macaulay 1988).

Much of the life cycle of *Thysanoessa macrura* is unknown (Ward et al. 1990). Adult females are thought to reach maturity after 1 or possibly 2 yr (Fevolden 1979). Repetitive spawning during one season and in consecutive years cannot be excluded. Larvae of *T. macrura* appear in the upper 200 m of the water column early in austral spring (Makarov 1979a, Hempel & Hempel 1982); a developmental ascent has been described for *T. macrura* (Makarov 1979a) which is similar to that of *E. superba* (Marr 1962). Nauplii and metanauplii prevailed in the deepest layers sampled between 1000 and 200 m, above which they were practically absent (Makarov 1979a). Calyptopis 1 is the first stage to appear in the photic zone (Makarov 1982). Highest abundances of early life stages (nauplius, metanauplius, calyptopis and furcilia) have been found from September through March (Makarov 1979a, Hempel 1981).

Information on the type of food consumed by *Thysa-*

noessa macrura is limited and contradictory. Nemoto & Harrison (1981) suggest that *T. macrura* feeds on phytoplankton. However, Hopkins (1985) found a variety of food items in its gut, including some phytoplankton and euphausiid molts, and concluded that the species is primarily a predator on small zooplankton, especially crustaceans. The copepods *Calanoides acutus* and *Metridia gerlachei* were the most common identifiable food items. The anatomy of the thoracopods, and in particular the very long second thoracopod, is distinct from the feeding basket of other Antarctic euphausiids (Brinton pers. comm.). While the mouthparts of species of the genus *Thysanoessa* are suited for filter-feeding, capture of copepods through the rapid lateral spreading of the thoracic limbs has been described for *T. longipes* and *T. inermis* (Mauchline & Fisher 1969).

The lipid composition of *Thysanoessa macrura*, which is very different from that of other euphausiids, supports this observation (Reinhardt & Van Vleet 1986). *T. macrura* stores large amounts of wax esters and phospholipids, which are presumably used as energy reserves during winter and for gonad development in spring (Hagen 1988). This may be an indication that *T. macrura* does not feed during winter, unlike *Euphausia superba* (Marschall 1988), and may explain the early spawning.

This investigation was conducted as part of the RACER (Research on Antarctic Coastal Ecosystem Rates) program, which was specifically designed to study the dynamics which lead to the development and decline of the spring bloom and its effect on zooplankton assemblages in western Bransfield Strait and adjacent Gerlache Strait (Huntley et al. 1991). This region is known for its high primary productivity and may serve as a nursery area for zooplankton (El-Sayed 1984). The 4 sequential surveys covered broad spatial and temporal scales. This paper describes the abundance and distribution of larval and adult *Thysanoessa macrura* in a heterogeneous habitat. An attempt is made to relate the distribution and growth rates of larval *T. macrura* to the observed physical oceanography and primary production in highly different water masses.

METHODS

Study site. The RACER program (Research on Antarctic Coastal Ecosystem Rates) is a multi-disciplinary field study, designed to investigate the physical and biological processes which give rise to the observed high productivity west of the Antarctic Peninsula. The RACER pilot program (1986–87) studied mesoscale physical and biological dynamics of the spring bloom. Detailed measurements on the hydro-

graphy, ocean optics, vertical flux, microbiology, and phyto- and zooplankton were made during four 2 wk cruises between 15 December 1986 and 30 March 1987 in a 25 000 km² study area in the western Bransfield Strait region (Huntley et al. 1987, 1991).

Zooplankton sampling. A grid of 69 stations west of the Antarctic Peninsula in the waters of Drake Passage, Bransfield Strait, and Gerlache Strait (Fig. 1) was sampled from aboard RV 'Polar Duke' from December 1986 to March 1987. Basic physical, chemical, and biological observations were made at all 69 stations during 4 'fast grid surveys'. Zooplankton samples were taken by oblique bongo net tows to between 40 and 45 m depth. This was followed by a 'slow grid' of 25 stations evenly distributed over the same area. These stations were occupied for up to 24 h during which stratified net tows

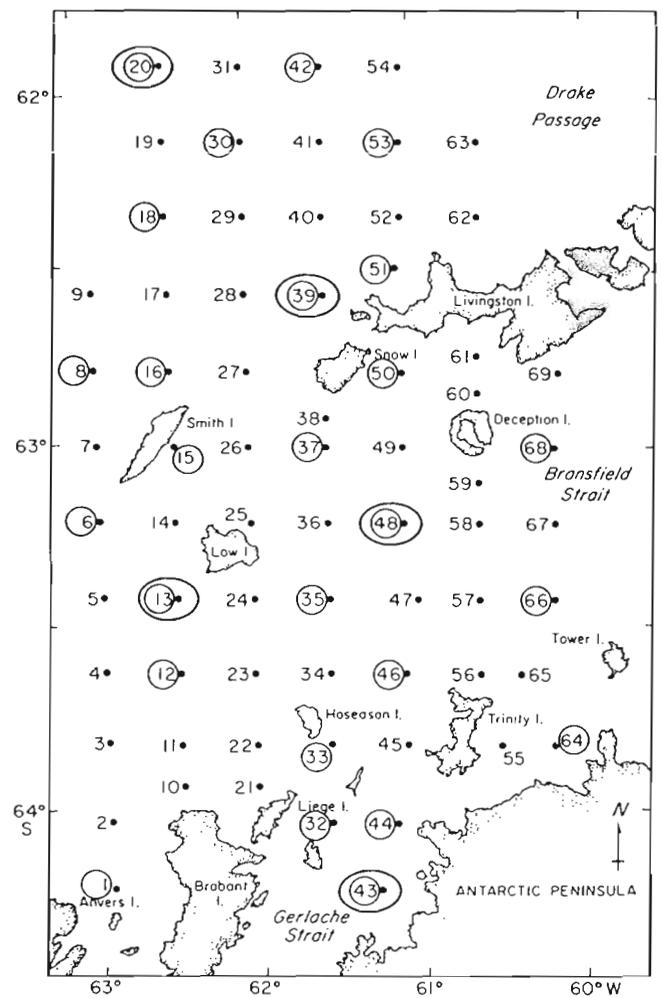


Fig. 1. Study area of RACER 1986–87. The 'fast grids' included 69 stations. The 25 stations of the 'slow grid' (circled) were visited after the completion of the 'fast grid'. Double-circled stations were 24 h stations; all others were sampled for 1 to 3 h. The slow and fast grids were completed 4 times between December 15, 1986 and March 30, 1987.

(0 to 100 m, 100 to 200 m) were taken using a double-messenger, opening-closing net of 1 m² diameter. Mesh size was 333 µm. Sampling was done at all times of day and night. The duration of darkness varied from about 3 h in December to about 10 h in March. The volume of water filtered was calculated from measurements made with TSK flowmeters. Samples were preserved in 5% buffered formalin for laboratory analysis. Depths permitting, deep tows were performed in some cases down to 2700 m (Stn 20).

All *Thysanoessa macrura* were identified and counted in samples collected. Abundances (individuals per 1000 m³) were calculated based on volume filtered calculated from flow meter readings. Specimens were measured to the nearest millimeter, from the tip of the rostrum to the tip of the telson, and classified by developmental stage (nauplius, metanauplius, calyptopis 1 to 3, furcilia 1 to 6, juveniles and adults (Rustad 1934, Makarov 1979b). For postlarvae of 10 to 13 mm the term 'juveniles' is used. Individuals larger than 14 mm, roughly the onset of maturity, were sexed according to external characteristics.

Distinction between larvae of *Thysanoessa macrura* and *T. vicina* is difficult (Rustadt 1930, 1934, Ruud 1932, Nemoto 1966). However, adult *T. vicina* occur farther north and have not been reported south of 57° S (Lomakina 1964, Nemoto 1966, Makarov 1979a, Brinton 1985). This study was conducted between 62° and 64° 30' S and no *T. vicina* adults were found. Without a spawning population present and considering the northeast flow it is unlikely that larvae of *T. vicina* occurred in the study site.

RESULTS

Abundance and distribution of larvae and adults

Thysanoessa macrura was found throughout western Bransfield Strait and at all depths to 2700 m. Only 6% of 202 analyzed samples of the slow grid did not contain *T. macrura*. Larvae were consistently most abundant in the upper 100 m (Mann-Whitney *U*-test, $p < 0.05$); there was no significant diel variation in larval abundance in either depth stratum (0 to 100 m and 100 to 200 m) (Mann-Whitney *U*-test, $p < 0.05$).

The day and night net catches of *Thysanoessa macrura* during December 1986 through March 1987, normalized for duration of darkness, revealed no significant differences (Mann-Whitney *U*-test). In contrast, *Euphausia superba* showed diel catch differences, believed to be due to net avoidance by these larger organisms, which optically detect approaching nets during daytime (Brinton et al. 1987). Net avoidance appears to be less of a problem in abundance

estimates of *T. macrura* than for the larger *E. superba*.

Thysanoessa macrura calyptopis and furcilia 1 (C1 to C3 and F1) stages were already abundant at the beginning of the study in late December. Even though larvae were found at all stations, the abundance varied over 3 orders of magnitude with highest numbers of up to 5000 ind. 1000 m⁻³ in Gerlache Strait. Lowest abundances were found in the waters of Drake Passage (80 ind. 1000 m⁻³). Abundances of 300 to 1200 ind. 1000 m⁻³ in Bransfield Strait were greater than in the northwestern part of the study area (Fig. 2a).

A similar distribution was found during January, but the highest abundances (3700 to 4600 ind. 1000 m⁻³) were found over a larger area extending from Gerlache Strait into southern Bransfield Strait. Abundances of 100 to 1200 ind. 1000 m⁻³ were found in central Bransfield Strait, again with a gradient from northwest to southeast. Lowest abundances were still found at the northern stations in Drake Passage (Fig. 2b).

Distribution and abundance in the latter half of February 1987 were quite different. The abundance of larvae decreased to less than 1100 ind. 1000 m⁻³ with highest abundances in central Bransfield Strait. Abundances in Gerlache Strait (110 to 140 ind. 1000 m⁻³) were similar to those in western and southern Bransfield Strait. Lowest abundances were found again in northern Bransfield Strait and in Drake Passage (10 to 50 ind. 1000 m⁻³; Fig. 2c).

Abundances in March were lower than at any other time in the study period, with highest values in Gerlache Strait (360 ind. 1000 m⁻³). Larval abundances in other areas were < 70 ind. 1000 m⁻³ (Fig. 2d).

Thysanoessa macrura adults were found in most samples from December through March. Their abundances did not exhibit the large variations observed for larvae. Highest abundances of adults were generally found in the northwestern part of the study area; the phytoplankton-rich Gerlache Strait never showed highest numbers (Fig. 3).

Cohort analyses

The composition and distribution of larval *Thysanoessa macrura* stage and length were analyzed to identify specific cohorts. The mean stage was calculated from:

$$S = [(C1 \times 1) + (C2 \times 2) + \dots + (F6 \times 9)] / N \quad (1)$$

where S = mean stage; C1 to F6 = abundances of larval stages calyptopis 1 through calyptopis 3 and furcilia 1 through furcilia 6; and N = sum of abundances of all stages.

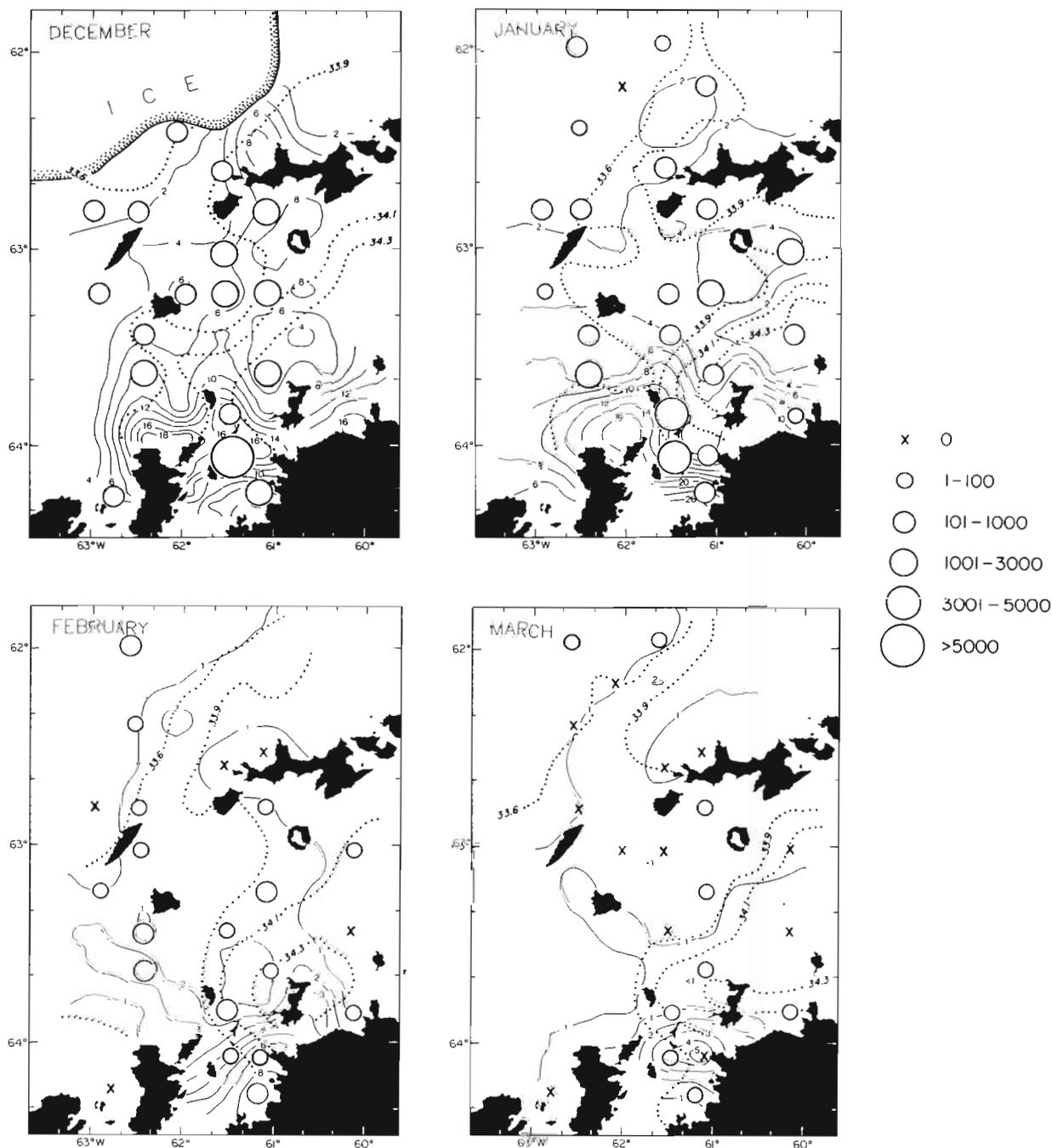


Fig. 2. *Thysanoessa macrura*. Abundance of larvae (ind. 1000 m^{-3}) based on 'slow grid' samples from 0 to 200 m. (a) December 1986, (b) January, (c) February and (d) March 1987 cruises. Contour lines give surface chlorophyll a concentrations in mg chl a m^{-3} (from Holm-Hansen & Mitchell 1991). Dotted lines show surface salinity distribution (average of top 20 m; after Niiler et al. 1991)

The mean length was calculated for larval, juvenile and adult *Thysanoessa macrura* from.

$$L = [(L_1 \times 1) + (L_2 \times 2) + \dots + (L_{31} \times 31)] / N \quad (2)$$

where L = mean length; L_1 to L_{31} = abundances of *T. macrura* size classes 1 through 31 mm; and N = sum of abundance of all size classes. No multiple modality

was observed for larvae, which demonstrates the occurrence of a single spawning period. For the purpose of distinguishing successions in larval stages, percent frequencies rather than numbers were plotted (Fig. 4).

Late calytopis and early furcilia stages (C2 to F3) dominated in December. Stage C1 were also common, especially in the upper 100 m. No eggs, nauplii, or

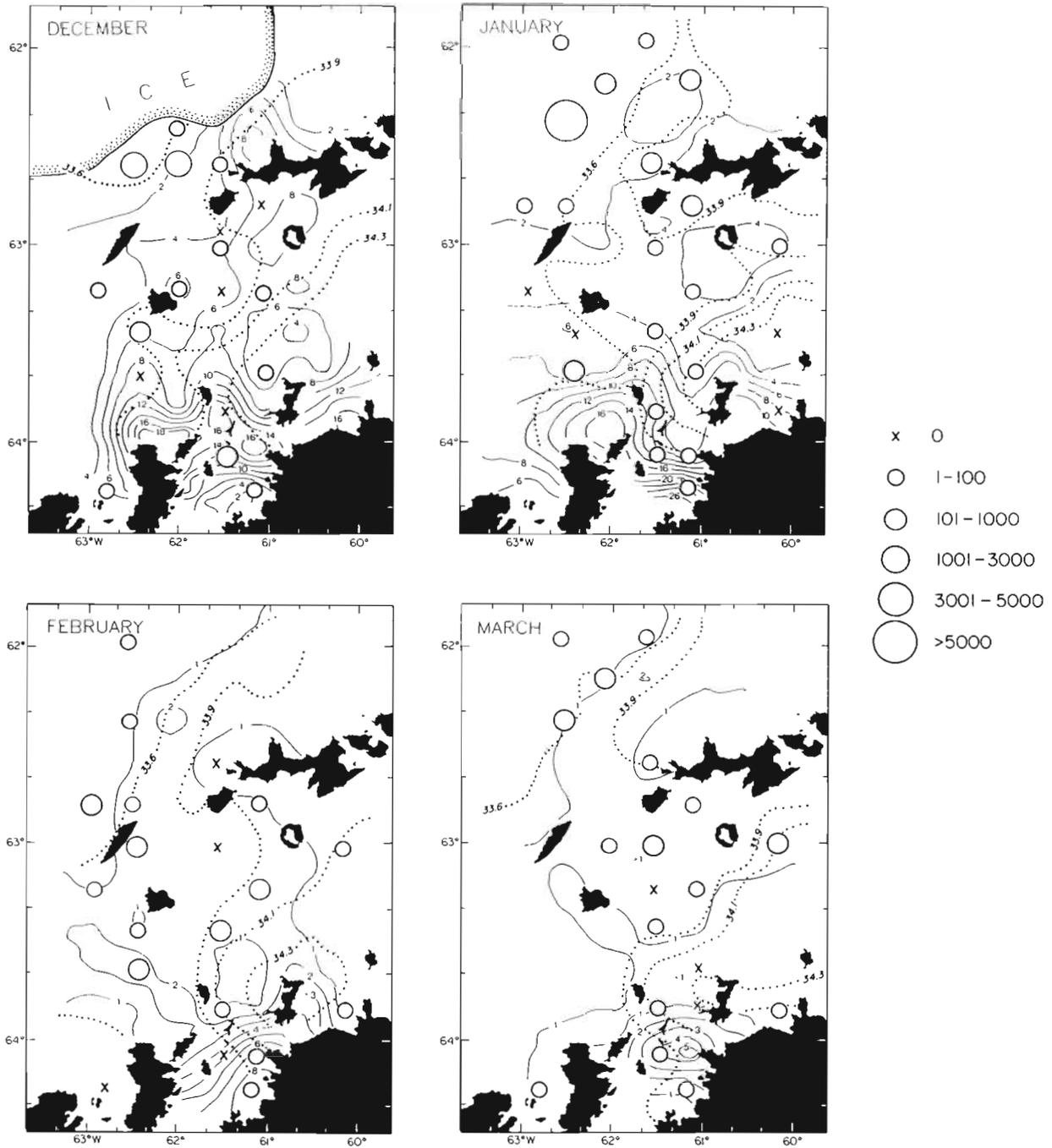


Fig. 3. *Thysanoessa macrura*. Abundance of adults. For legend see Fig. 2

metanauplii were found. The latest developmental stage found during December was F3, of which only a few were found in western Bransfield Strait.

Furcilia stages, in particular F2 and F3, were most abundant in January. Most remarkable is the fact that all developmental stages from C1 to F6 were present in January. C1 were again more abundant in the upper 100 m. The mean stage was most advanced at stations

in northern Bransfield Strait and north of Livingston Island.

In the period from February 26 to March 6, very few calyptopis stages were found; F1 and F2 were also rare. Most abundant were F6 and F5 stages, but F4 and F3 were also common. The mean stage did not vary much over the sampling grid, but earliest stages were found in Gerlache Strait. In late March the population was

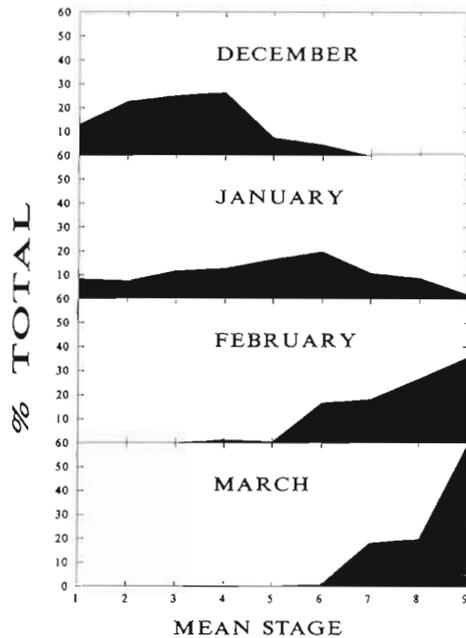


Fig. 4. *Thysanoessa macrura*. Mean stage frequency distribution of larvae during December 1986 through March 1987. Stages 1 to 3: Calyptopis 1–3, Stages 4 to 9: Furcilia 1–6

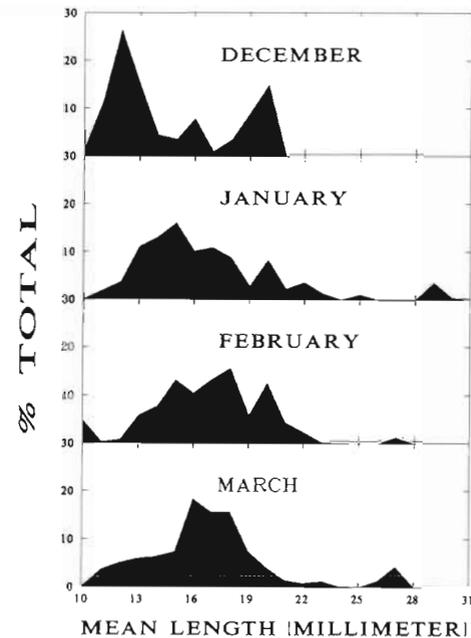


Fig. 6. *Thysanoessa macrura*. Mean body length frequency distribution of juveniles and adults during December 1986 through March 1987

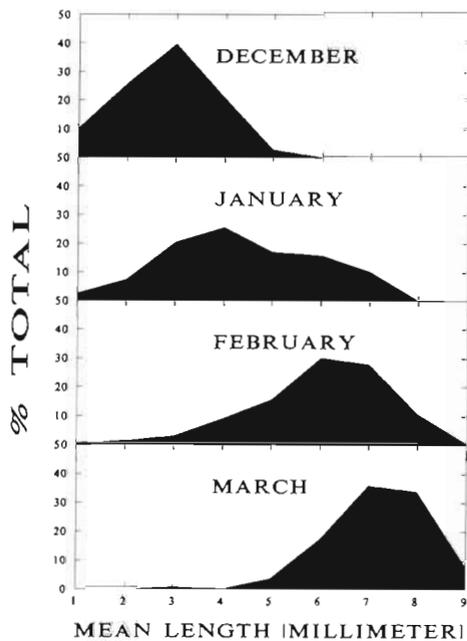


Fig. 5. *Thysanoessa macrura*. Mean length frequency distribution of larvae during December 1986 through March 1987

dominated by F6, while F4 and F5 were still abundant, as were juveniles.

The mean length frequency distribution of larvae (Fig. 5) was similar to the mean stage frequency distribution (Fig. 4). The single cohort grew from a mean length of 2.8 mm (SD = 0.6 mm) in late December to 7.1 mm (SD = 0.8 mm) at the end of March.

The adult length frequency distribution of December showed bimodality, probably due to year classes (Fig. 6). While 12.0 mm long *Thysanoessa macrura*, presumably 1 yr old, dominated, individuals of 20.0 mm were also abundant. The size frequency plots of January and February show an increase in size. The bimodal length frequency distribution could still be seen in January and February, but to a lesser extent. Mean body length increased from 14.6 mm (SD = 3.1 mm) in December to 16.9 mm (SD = 3.0 mm) in March.

Rates of growth and development

The rate of increase in maturity stage over time, or development rate, was determined for *Thysanoessa macrura* from field samples by calculating the slope of the relation between mean stage versus period of sampling (Fig. 7). The development rate is given for the 3 regions, which were distinct in their water mass characteristics (Niiler et al. 1991) and in their phytoplankton biomass (Holm-Hansen & Mitchell 1991): (1) Drake Passage in the northwest corner of the study site, (2) Bransfield Strait in the center and extending to the northeast, and (3) Gerlache Strait in the southern center of the survey area. Data from 3 depth strata (0 to 100 m, 100 to 200 m and 0 to 200 m; Fig. 7) suggest that development rate was faster during the early stages and decreased steadily with age. The stage duration of younger larvae was shorter than that of older stages. There were no obvious regional differences.

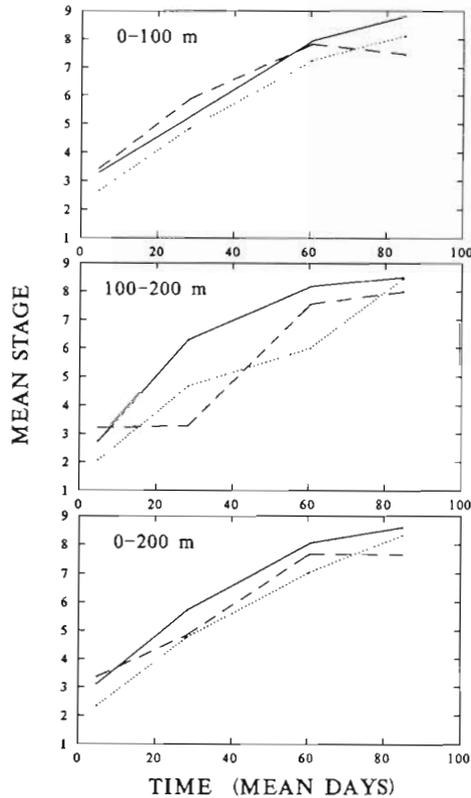


Fig. 7. *Thysanoessa macrura* development rates. Average mean stages for the Gerlache and Bransfield Straits and the Drake Passage are shown for 3 depth ranges. Days are mean values during December 1986 through March 1987 with the first day being the first day on station. (---) Drake Passage; (—) Bransfield Strait; (····) Gerlache Strait. Mean stage: 1 to 3: Calyptopis 1–3; 4 to 9: Furcilia 1–6

Proxy estimates of growth rates (increase in length over time) were calculated for *Thysanoessa macrura* from the 3 regions. The length at time t , $L(t)$, can be described from a model fitted to the observed sizes:

$$L(t) = L_{\max} [1 - e^{-(a-bt)}] \quad (3)$$

where L_{\max} = asymptotic length of an average *T. macrura* in the population; and b = the coefficient at which the growth rate began to decrease. The constant a was included to allow for a positive length at time = 0, which was the beginning of the sampling program.

Larval growth rates in Gerlache and Bransfield Straits were similar, but appear to have been slower in chlorophyll *a*-poor Drake Passage (Fig. 8). However, no statistically significant difference in growth rates was detected (ANOVA: $F_3 = 1.08 \ll F_{0.05[2,81]}$ since $F_{0.05[2,120]} = 3.07$). Daily growth rates (increase in length) were highest in Gerlache Strait, intermediate in Bransfield Strait, and lowest in Drake Passage, and decreased in all 3 regions from December through March (Table 1). *T. macrura* developed from C2 to F6 in ca 90 d. From the data one would predict a single spawning period in the region during November 1986.

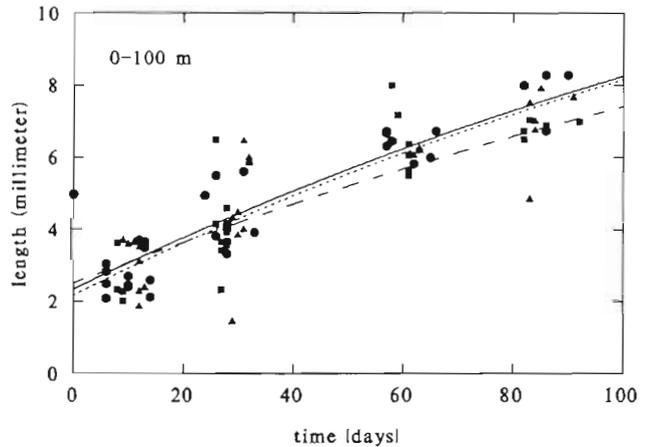


Fig. 8. *Thysanoessa macrura* growth rates. Mean body length at all stations for Gerlache and Bransfield Straits and Drake Passage are given. Time is given in days, starting with the first day of the cruise. An exponential model (Eq. 3) was fitted to the data. (▲ --- ▲) Drake Passage; (● — ●) Bransfield Strait; (■ ···· ■) Gerlache Strait

Table 1 *Thysanoessa macrura*. Growth rates (mm d^{-1}) of larvae in the western Bransfield Strait region during the period December 1986 through March 1987 calculated from: $L(t) = L_{\max} [1 - e^{-(a-bt)}]$ (see text for explanation)

Slow survey	Gerlache Strait	Bransfield Strait	Drake Passage
December	0.073	0.072	0.057
January	0.068	0.067	0.054
February	0.056	0.056	0.046
March	0.050	0.049	0.042

DISCUSSION

Thysanoessa macrura distribution and abundance

Water masses in the western Bransfield Strait region are quite complex. However, 5 regional water masses can be distinguished. The water in the northwestern part clearly belonged to the waters typical of the Southern Drake Passage. The water column in the southwestern corner was weakly stratified with a spatial transition to the most stratified upper layer water in Gerlache Strait. The fourth and fifth water masses were found around Low Island and Livingston Island (Amos et al. 1990, Niiler et al. 1991). Two 'streams' flowed through the survey grid along the salinity contour lines (Figs. 2 & 3). One flowed from the southwest to the northeast (Bransfield Current), and was joined in the southwest by flow from Gerlache Strait. The other 'stream' flowed northward along the boundary of southern Drake Passage. Lagrangian drifters recently deployed (austral summer 1989) in southern Gerlache

Table 2. *Thysanoessa macrura*. Abundance of larvae (C1 to F6) in 3 regions from December through March (1986–87). Abundances are given as individuals per 1000 m³. Mean: average number per 1000 m³; SD: standard deviation; n: number of samples

	Gerlache Strait			Bransfield Strait			Drake Passage		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
December									
0–100 m	1626	1862	4	769	499	13	284	191	8
100–200 m	610	681	5	701	978	8	211	322	5
January									
0–100 m	1262	1654	8	482	511	11	251	421	11
100–200 m	182	198	7	97	118	9	28	41	8
200–2700 m	61	0	1	42	42	2	2	1	5
February									
0–100 m	55	134	6	199	243	11	13	26	7
100–200 m	76	133	3	22	26	9	30	39	6
200–800 m				4	3	2			
March									
0–100 m	30	29	6	4	11	7	8	17	8
100–200 m	21	19	5	3	6	5	0	0	5
200–1000 m							0	0	2

Strait support the estimates from relative geostrophic current (Niiler et al. 1990, 1991).

A gradient of decreasing phytoplankton biomass from Gerlache Strait into Bransfield Strait was observed persistently from December 1986 through March 1987 (Holm-Hansen & Mitchell 1991). Phytoplankton biomass was highest in December and was still relatively high in January. A sharp decline was observed in February and March 1987. The waters of northern Gerlache Strait as well as those near Brabant Island, Hoseason Island, and Trinity Island consistently had the highest chlorophyll *a* concentrations (> 700 mg m⁻² in December; Holm-Hansen & Mitchell 1991) (Figs. 2 & 3).

High abundances of larval and adult *Thysanoessa macrura* have been frequently reported (Hempel & Marschoff 1980, Weigmann-Haas & Haas 1980, Hempel 1981, Piatkowski 1985a). Most of these investigations covered broad regions in the Atlantic sector of the Southern Ocean (Hempel & Marschoff 1980), Scotia Sea (Makarov 1979a, Weigmann-Haas & Haas 1980), or Drake Passage and Bransfield Strait (Kittel & Stepnik 1983, Piatkowski 1985a).

The results of this study with its unique 4 sequential surveys show highest larval abundances of *Thysanoessa macrura* in Gerlache Strait during December and January. This coincided temporally and spatially with the area in which the highest phytoplankton biomass was found (Holm-Hansen & Mitchell 1991). The Bransfield Current is likely to have advected the planktonic larval stages of *T. macrura* from Gerlache Strait to the northeast into Bransfield Strait, where intermediate abundances were found in December and January

(Table 2). Low abundances of larval *T. macrura* were consistently found in the offshore part of the study area in Drake Passage (Table 2). Kittel & Stepnik (1983) reported highest abundances of *T. macrura* larvae north of the South Shetland Islands and in the water of the West Wind Drift, and lower abundances of larvae for the region near Smith Island and west of Livingston Island, in particular.

A sharp decline in the abundance of *Thysanoessa macrura* larvae occurred in February and March 1987 which coincided with greatly reduced phytoplankton biomass (Fig. 2, Table 2). While in December larval stages were found at all stations, in March larvae were found at 42% of the stations sampled. Most stations in the northwestern part of the survey area did not reveal any *T. macrura* larvae or only very low abundances (Table 2). Juvenile abundances were also low in March; the decline must be due to mortality or to advection out of the area investigated.

The distribution of adult *Thysanoessa macrura* was more even than that of the larvae. Adult abundances did not vary as much as abundances of early life stages during the period from December 1986 to the end of March 1987. The greatest abundances were never found in Gerlache Strait (Table 3), but rather in Drake Passage waters (Table 3). The ratio of females per male was greatest in Drake Passage, with a mean of 2.5 during December 1986 through March 1987. The sex ratio was lowest in Gerlache Strait (1.2) and intermediate in Bransfield Strait (1.5). However, these differences were not significant at 95% in a median test (Zar 1974) (Table 4); they show a trend similar to that described by Kittel & Stepnik (1983), who found the

Table 3. *Thysanoessa macrura*. Abundances of juveniles and adults (≥ 10 mm length) in 3 regions from December through March (1986–87). Abundances are given as individuals per 1000 m³. Mean: average number per 1000 m³; SD: standard deviation; n: number of samples

	Gerlache Strait			Bransfield Strait			Drake Passage		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
December									
0–100 m	19	27	4	27	64	13	99	36	8
100–200 m	4	4	5	25	36	8	750	716	4
January									
0–100 m	3	4	8	42	60	10	647	1813	11
100–200 m	23	28	7	79	60	10	85	201	8
200–2700 m							1	1	5
February									
0–100 m	8	6	7	111	152	10	41	80	7
100–200 m	19	12	3	43	100	9	75	107	7
200–800 m				1	1	2			
March									
0–100 m	3	5	5	67	102	6	29	40	7
100–200 m	2	2	5	182	286	5	142	273	5
200–1000 m							3	3	2

greatest sex ratio in Drake Passage (6.1) and a lower ratio in Bransfield Strait (1.8) in February and March 1981.

The ratio of larvae to adults (≥ 14 mm) was not homogeneous throughout the survey area. A median test (Zar 1974) showed that the number of larvae per adult was significantly greater in Gerlache Strait than in Bransfield Strait or Drake Passage. However, there were no significant differences between Drake Passage and Bransfield Strait (Table 5). A similar phenomenon was observed for *Euphausia superba* during the same study (Brinton 1991).

A developmental ascent has been proposed for *Thysanoessa macrura* (Makarov 1979a). Spawning occurs in the water column; eggs sink, and hatch at depth. Highest abundances of *T. macrura* nauplii and metanauplii were found between 500 and 1000 m in the Scotia Sea in December 1974 through January 1975 and a development time of 15 to 20 d from egg to C2 was reported (Makarov 1979a). However, this development period was based on cultivation experiments and plankton catches of various euphausiids in temperate waters (Heegaard 1948, Mauchline 1959) and might be longer in Antarctica.

Diel vertical distribution and migration

The vertical distribution of *Thysanoessa macrura* observed in this study was similar to that reported elsewhere (e.g. Makarov 1979a, Kittel & Stepnik 1983, Loeb & Shulenberger 1987). Adults and larvae were most abundant in the upper 200 m; very few individu-

Table 4. *Thysanoessa macrura*. Median test of sex ratios (females per male) in 3 regions near the Antarctic Peninsula. ns: not significant

Region	n	Chi square	Probability (95 %)
Gerlache Strait/ Bransfield Strait	10	1.338	ns
Bransfield Strait/ Drake Passage	30	0.634	ns
Drake Passage/ Gerlache Strait	25	0.093	ns

Table 5. *Thysanoessa macrura*. Median test of larvae to adults (≤ 14 mm) ratios (females per male) in 3 regions near the Antarctic Peninsula. ns: not significant

Region	n	Chi square	Probability (95 %)
Gerlache Strait/ Bransfield Strait	43	3.988	<0.05
Bransfield Strait/ Drake Passage	65	0.308	ns
Drake Passage/ Gerlache Strait	70	6.636	<0.01

als of any stage were found at greater depths in the few deeper samples. Larval stages C1 to F6 were significantly more abundant in the upper 100 m than in the 100 to 200 m depth interval (Mann-Whitney *U*-test, $p < 0.05$). Abundances of nauplii and metanauplii have been reported to be greatest at depths of 200 to 1000 m (Makarov 1979a) but none were found in this study. *T.*

macrura begins spawning early in the austral summer (Makarov 1979a, Kittel 1988). By late December, the beginning of this study, the larvae had already outgrown the naupliar and metanaupliar stages.

Diel vertical migration between the 0 to 100 and the 100 to 200 m layers by larvae and adults of *Thysanoessa macrura* was not detected in this study. Near South Georgia in August, *T. macrura* were significantly more abundant in the upper 250 m (Ward et al. 1990). Kittel & Stepnik (1983) found a higher ratio of adults to larvae between 100 and 300 m in samples taken at night while daytime catches showed few adults in either stratum. Greater night than day catches of adult *T. macrura* in the top 80 m were found near Elephant Island by Loeb & Shulenberger (1987), who proposed diel vertical migration or reduced net avoidance at night as an explanation. No significant differences in day vs night catches in abundance were found in the present study. However, further investigations with greater vertical and temporal resolution are necessary to better understand the diel behavior of *T. macrura*.

Development and growth rates in Drake Passage, Bransfield and Gerlache Straits

Whether the development of euphausiid larvae is isochronal or age dependent has been debated. Pillar (1984, 1985) reported no dependence on age of moult frequency of C3 through F6 stages of *Euphausia lucens* and *Nyctiphanes capensis*. However, data of other workers indicate that the development of euphausiids is not isochronal, but changes from shorter stage durations of early larval stages to longer intermoult periods of older and larger larvae (Heegaard 1948, Mauchline 1959, 1977, Ikeda 1985, McClatchie 1988, Huntley & Brinton 1991). Euphausiids grow to a maximum body length, but continue moulting throughout their lives (Mauchline 1977). The equation (Eq. 2) used here to model the growth of larval *Thysanoessa macrura* was chosen because it best describes the underlying biology. The mean body length in each sample was plotted and the model fitted to these mean lengths. The asymptotic length attained by an average *T. macrura* was calculated from the field samples.

A distinction should be made between individual growth rates and the growth rate of cohorts. Individual growth rates are affected by food limitation as shown in laboratory experiments (Ikeda 1984, 1986), but increased mortality of slower-developing larvae causes the growth rate of the cohort to appear greater.

The growth rates of *Thysanoessa macrura* cohorts in the 3 regions of distinctly different phytoplankton concentration were compared using the log-transformed model. A statistically significant difference of growth

rates between cohorts from the phytoplankton-rich Gerlache and Bransfield Straits and those from chlorophyll *a*-poor Drake Passage (Holm-Hansen & Mitchell 1991) was not detected. This suggests that the growth rate of *T. macrura* cohorts was not limited by phytoplankton food in these regions. However, this is valid only for the survivors. The decrease in abundance of larval *T. macrura* might be linked to the observed decline in phytoplankton abundance.

Laboratory starvation experiments with *Euphausia superba* demonstrated that early calyptopis stages were more susceptible to starvation and death than older larvae (Ikeda 1984). Prolonged stage duration as a result of inadequate food could cause increased mortality for slower-developing larvae due to longer exposure of early stages to predation. Stage-specific mortality of copepodite instars tends to drive the mean development rate of cohorts towards development rates greater than those expected based on food availability (Lopez 1991). This could explain reduced abundances under unfavorable conditions but might not affect overall development rates of cohorts. Resource limitation of development rates may thus be undetectable at the level of populations.

CONCLUSION

Thysanoessa macrura was the most abundant euphausiid in the western Bransfield Strait region during December 1986 through March 1987. Females in their second and third year spawned during a discrete period prior to 15 December 1986, the beginning of this study. Adult *T. macrura* were more abundant at the offshore stations in Drake Passage, where larval abundances were low. Greatest abundances of *T. macrura* larvae coincided spatially and temporally with a phytoplankton bloom in Gerlache Strait in December and extended into southwestern Bransfield Strait by January 1987. The growth rate of *T. macrura* cohorts was not correlated with chlorophyll *a* concentration. *T. macrura* larvae developed from calyptopis 2 in late December to furcilia 6 by the end of March. Diel vertical migration of adult and larval *T. macrura* was not detected in this study, but the coarse vertical sampling might have made the detection of diel variations impossible.

The life history of *Thysanoessa macrura* is still only partly known. Preferred spawning regions have not been located and winter observations of the distribution as well as the physiological state and behavior of *T. macrura* appear not to exist. However, the high biomass and widespread distribution of this euphausiid species in Antarctic waters make it likely to have been of underestimated importance in the marine ecosystem and thus deserving of more attention.

Acknowledgements. I thank the RACER personnel, the officers and crew members on board the RV 'Polar Duke' and the Antarctic Services personnel for their expert support. I also thank the scientists who reviewed the manuscript and offered valuable suggestions, including M. Huntley, E. Brinton, and M. Unson. This work was accomplished with support from National Science Foundation grant DPP 88-17779 to Mark Huntley and Edward Brinton.

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This article was submitted to the editor

Manuscript first received: September 11, 1991

Revised version accepted: April 22, 1992