Distribution, reproduction and population dynamics of the Antarctic gammaridean amphipod *Eusirus perdentatus* Chevreux, 1912 (Crustacea)

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Abstract: The geographical distribution and depth zonation of *Eusirus perdentatus* Chevreux, 1912 in the eastern Weddell Sea and adjacent Lazarev Sea (Antarctica) is described. A total of 963 individuals of this carnivorous predator caught during six successive cruises at 71 stations between 176 and 799 metres water depths were used. Individuals of *E. perdentatus* have been kept alive for nearly five months in the laboratory. During this period females released 53 juveniles in April. Oocytes and embryos of females have been counted and measured. The duration of embryonic development in *E. perdentatus* was estimated at *c.* 12 months, using an empirical relationship based on the mean diameter of 4390 fertilized eggs. There is strong evidence that this species is semelparous with hatching of juveniles at the end of austral summer. Two methods, herein termed as Year Class Model and Moult Class Model, have been applied in order to describe the growth of females by means of cumulative length-frequency data.

Introduction

The aim of the present paper is to summarize the data available concerning different aspects of the biology of the Antarctic gammaridean amphipod *Eusirus perdentatus* (Eusiridae) collected in the eastern Weddell Sea and the adjacent Lazarev Sea. Studies of benthic invertebrate biology in such regions are few, mainly due to restricted access caused by heavy pack-ice conditions limit both spatial and temporal sampling (Gutt 1991). Even when benthic invertebrates are kept alive in the laboratory in order to study their life cycle, their very longevity causes problems for researchers (Wägele 1990). Therefore, the bulk of information on the biology of Antarctic marine invertebrates has been obtained for species or populations occurring at shallow water sites such as McMurdo Sound in West Antarctica or the islands in the vicinity of the Antarctic Peninsula (White 1984). For example, comprehensive accounts on scavenging amphipods such as *Cheirimedon femoratus*, *Tryphosella kergueleni* and *Orchomene plebs*, as well as on carnivores or herbivores like *Bovallia gigantea* and *Paramoera walkeri* have been published (Bone 1972, Bregazzi 1972, 1973, Rakusa-Suszszewski 1972, 1982, Sagar 1980, Thurston 1968, 1970). This situation has changed in recent years, at least in the cases of distributional patterns, biomass and abundance estimates of macrobenthic invertebrates living at deeper sites in the Weddell Sea with sampling from ice-strengthened vessels (Arntz & Gorny 1991, Gerdes *et al.* 1992, Gutt 1991, Gutt *et al.* 1991, Klages 1991, Voß 1988). Data on the early life history traits, reproduction and population dynamics of Weddell Sea molluscs (Brey & Hain 1992, Hain & Arnaud 1992), isopods

(Wägele 1987, 1990), shrimps (Gorny *et al.* 1992), gammaridean amphipods (Klages 1991), a sea urchin (Brey 1991), and holothurians (Gutt 1991, Gutt *et al.* 1992) are now available. Reviews of invertebrate reproduction in shallow water sites have been published by Clarke (1982), Pearse *et al.* (1991) and Picken (1980). However, considerably less is known about the biology and life cycle of most benthic invertebrates of the Weddell Sea. This is particularly true for *E. perdentatus* and most of the other Antarctic members of this genus. To improve our knowledge of amphipod crustacean biology within the benthic ecosystem of the eastern Weddell Sea shelf, typical representatives, including *E. perdentatus*, have been chosen by Klages (1991) for detailed study. With the exception of a laboratory feeding study (Klages & Gutt 1990) and the work of Coleman (1991), who described some features of the relatively short stomach of *E. perdentatus*, there is little information about the biology of this common species. Morphological charcteristics and the internal structures of calceoli in *E. perdentatus* have been described by Lincoln (1985).

Materials and methods

In the Antarctic summer seasons 1985–91 and late winter/early spring 1986 a total of 963 specimens of *Eusirus perdentatus* were collected during RV *Polarstern* cruises ANT III/3, ANT VI/3, ANT VII/4, ANT VIII/5, ANT IX/3 (summer) and ANT V/3 (late winter) on the shelf of the eastern Weddell Sea. In addition during ANT IX/3 14 stations were sampled in the adjacent Lazarev Sea (Fig. 1). For detailed descriptions of the
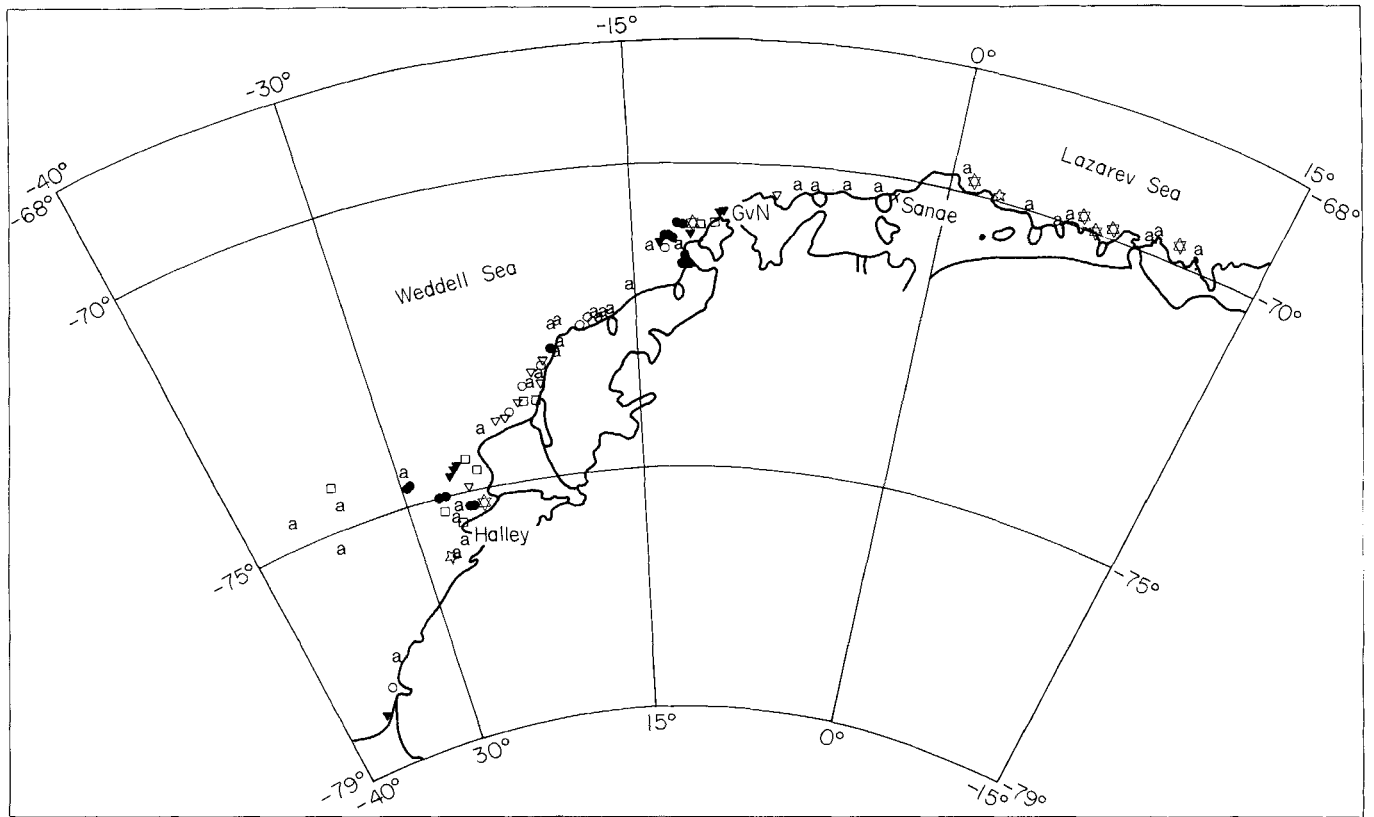
Fig. 1. Map of the Weddell and the Lazarev Sea with catch localities. Polar stereographic projection; Scale: 1 : 5 000 000; Standard parallel 73° 30'S. ○ PS ANT III/3; △ PS ANT V/3; ▲ PS ANT VI/3; ● PS ANT XII; □ PS ANT VIII/5; ☆ PS ANT IX/3; a. = *Eusirus perdentatus* absent at this station.

physical characteristics in the area of investigation see Hellmer & Bersch (1985). The overall period in which specimens were obtained was 12 October to 13 March.

Eusirus perdentatus was caught with bottom trawls at 178–799 m. Gears used included: 1) a commercial bottom trawl (BT) [net opening *c.* 22 m; mesh size in the cod end 10 mm], 2) a modified Agassiz trawl (AGT) [1 x 3m mouth opening; mesh size in the cod end 10 mm], 3) a commercial-scale sized 1088 meshes semipelagic (benthopelagic) trawl (BPN) with a 12 mm liner in the cod end (approximate mouth opening was 18 x 18 m), 4) an epibenthic sledge (ES) (1x1 m mouth opening, 4 mm mesh size]. The majority of individuals were collected with BT and AGT which means that small specimens were under-represented. Trawling time depended on water depth but was generally between 15–30 min at a speed of 1–1.8 km h^{-1} for the AGT and ES, and 30 min at 5.5–7.5 km h^{-1} for the BPN and BT. During most hauls the gear was on the bottom for about 15 min, except for the BPN which touched the sea floor only by accident. For culture purposes 112 living and seemingly healthy specimens of *E. perdentatus* were selected during three cruises (ANT VI/3, VII/4 and IX/3) and maintained at -1°C ± 0.5°C in 30 and 140 l aquaria inside a laboratory container and later at the Institute. These individuals were not considered for length-frequency distribution, depth zonation and other length related studies, but were used to describe geographical distribution. The

laboratories were illuminated by low intensity red light (1 μE m^{-2} s^{-1}, measured with LI 185B Quantum Radiometer/ Photometer using a 2 π sensor). Further technical details are given by Hain (1992). Feeding behaviour, hatching of juveniles and moulting of some specimens were observed in aquaria. Other specimens were preserved in a 4% buffered formalin-seawater solution during all cruises. These were measured (resolution 0.1 mm) using a binocular microscope along the dorsal line from the tip of rostrum to the base of the telson (bt). The length to the apex of the telson (at) can be calculated easily using a simple linear regression equation:

$$at = 1.12\ bt + 0.04 \qquad r^2 = 1 \qquad (1)$$

Sex was determined according to external sexual differences (oostegites, genital papillae). Eggs (roughly classified as recently fertilized, visible differentiation and embryos well developed) and juveniles were removed from the marsupium, counted and measured. Non-ovigerous and ovigerous females were dissected in order to measure the oocytes found in the ovary and the oostegite of the fourth pereiopod. A semi-automatic image analysing system (VIDS III Mobrey Bestobell, Tektronics) was used either to count or to measure the diameter or length of oocytes, fertilized eggs, embryos and oostegites. After measurement, representative oostegites were drawn using a Wild M5 binocular with camera lucida. Length-frequency

distribution data was compiled using all preserved specimens. Distinct cohorts were choosen by eye and tested with regard to normal distribution. Median sizes of cohorts were taken to represent either mean year class or moult class values. The von Bertalanffy growth function (VBGF)

$$L_t = L_\infty * (1 - e^{-K(t-t_0)}) \quad (2)$$

with

$L_t =$ length at age t;

$K=$ von Bertalanffy growth coefficient;

$t=$ age;

$L_\infty =$ the asymptotic length an individual would reach if it were to grow indefinitely;

$t_0 =$ the age of an individual at zero length;

was fitted to moult class – size pairs using a SIMPLEX algorithm.

Results

The contents of trawl catches showed that *Eusirus perdentatus* is a common species which occurs on the shelf (≤ 600 m in the Weddell Sea, Carmack & Foster 1977), and upper slope of the Weddell Sea south to 78° latitude. Altogether 963 specimens were collected at 71 stations out of 113 investigated. The specimens obtained included 492 females, 251 males and 28 juveniles together with 80 damaged specimens (used only for geographical distribution and bathymetrical zonation analysis). Additionally 112 specimens were kept alive in aquaria. Some of them released a total of 53 juveniles some weeks after capture. Mortality in aquaria was rather high.

Distribution and depth zonation

Most samples in the eastern Weddell Sea were taken off Kapp Norvegia and the area off Halley Bay (Fig. 1). However, the distributional range of *Eusirus perdentatus* encompassed the entire study area, being found on the shelf and upper slope of the eastern Weddell Sea and western Lazarev Sea from 69–78° southern latitude at water depths between 176 and 799 m.

The depth zonation of 743 adult and 28 juvenile specimens in 50 m depth strata showed that there was a preference in both sexes for depths between 400 and 500 m (Fig. 2). Males have been collected in relatively higher numbers at shallower sites between 200 and 350 m. The numbers of stations sampled within 50 m depth intervals are also shown in Fig. 2. Twentythree stations were sampled in the depth strata between 400 and 500 m. However, the total of females collected at 13 stations between 400 and 450 m is considerably lower than the number of individuals collected at 10 stations between 450 and 500 m. At five stations sampled in the western Lazarev Sea 72 specimens of *E. perdentatus* (42 females, 30 males) were collected from depths between 185 and 465 m.
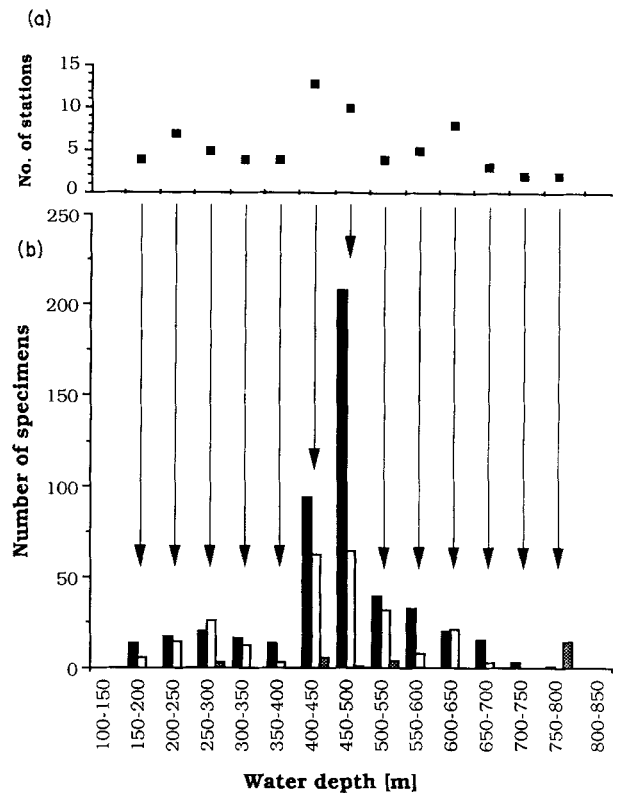

Fig. 2a. Number of stations sampled in different depth strata. b. Depth zonation of *Eusirus perdentatus* in 50 m intervals on the shelf and upper slope of the eastern Weddell Sea and adjacent Lazarev Sea ($n = 754$; ■ = 491 females; □ = 249 males; ▨ = 14 juveniles). No specimens collected at stations sampled below 800 m.

The largest female of 86.9 mm was collected during ANT III/3 at station no. 300 (77°S, 41°W, 627 m). To find out whether the bathymetrical zonation of females and males differ or not a contingency table has been calculated using seven depth strata (100 m width each). The calculated $\chi^2_{6;0.05}$ of 12.59 indicates significant differences in the bathymetrical zonation between males and females. However, this result has to be considered preliminary because different sampling dates and different gears used may have influenced the data.

Size & sex ratio

The size range was considerable (7.5–86.9 mm). The cumulative length-frequency distribution (Fig. 3) was obtained from data for 720 individuals. No specimen smaller than 19 mm was collected with trawls, and all specimens within the group of 7–18 mm are juveniles that hatched in aquaria. The largest individuals of *Eusirus perdentatus* were females up to 86.9 mm, whereas males did not exceed 65 mm. The difference in size distribution between the sexes is significant ($P \leq 0.001$; Mann-Whitney test; two-sided).
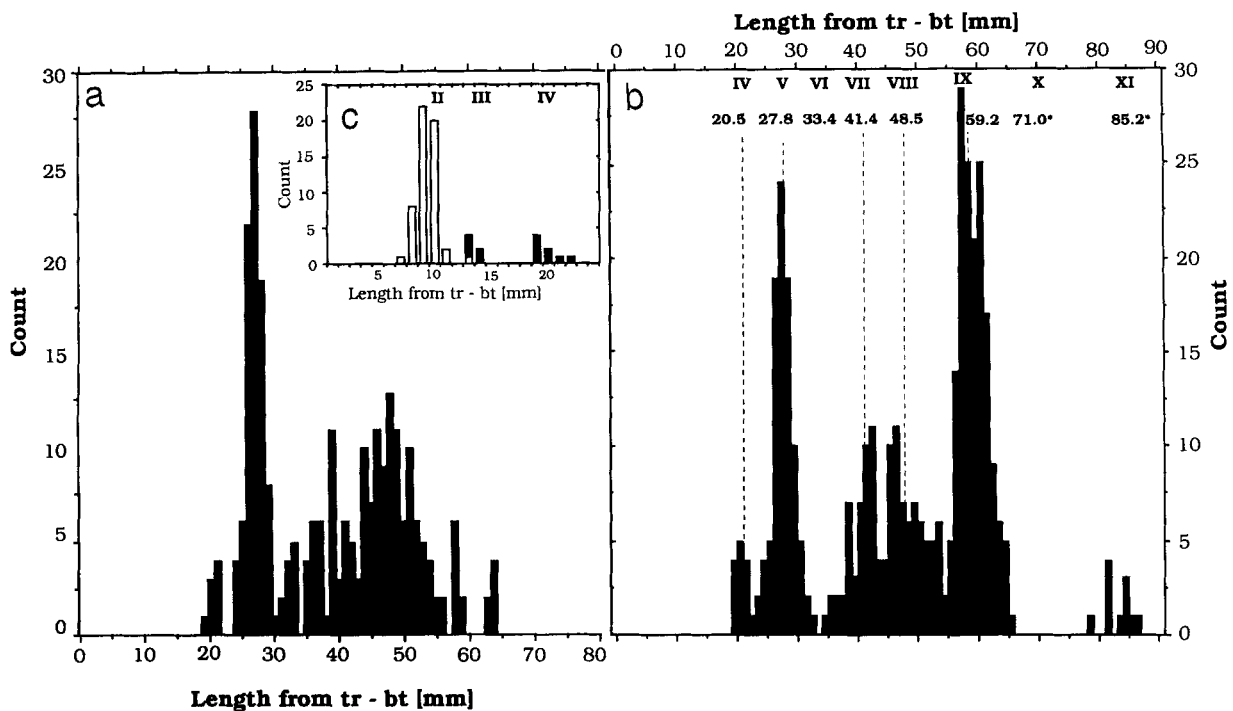
Fig. 3. Cumulative length-frequency distribution of *Eusirus perdentatus* (■ collected with trawls; □ = hatched in laboratory); **a.** = 262 males; **b.** = 392 females; **c.** = 66 juveniles.

Reproduction

In the 340 females investigated with respect of reproductive biology, the smallest female in which oostegite buds were found was 20 mm long. Oostegites on the 4th pereiopod of 89 females of different size and sexual maturity were dissected off, measured and drawn. Oostegite length (OL) and width (OW) were found to range from 0.5–21.6 mm and 0.18–6.1 mm, respectively, and were correlated with female size. These correlations can be described by the linear regressions:

$$\text{OL [mm]} = 0.29 * \text{length [tr-bt]} - 7.72 \qquad r^2 = 0.86; \quad n = 89 \quad (3)$$

and

$$\text{OW [mm]} = 0.07 * \text{length [tr-bt]} - 1.83 \qquad r^2 = 0.83; \quad n = 89 \quad (4)$$

Fully functional setose oostegites are developed at a body length of 57–58 mm (Fig. 4a). Thirtyfour females were dissected and the 5413 oocytes found in their ovaries measured 0.128–1.06 mm. The number of oocytes in the ovaries varied widely from 34–358. Fertilized eggs or embryos from 55 ovigerous females were counted and measured. The mean diameter of 4390 eggs was 2.75 ± 0.25 mm within a size range of 2.31–3.39 mm (Fig. 4a). There was no significant correlation between the mean diameter of eggs and latitude. Females larger than 55 mm were generally found to carry eggs (the single specimen of 53 mm carrying eggs seems to be exceptional). The number of eggs found in marsupia varied between 9–149. Ovigerous females captured at the same station showed differences in the developmental stage of eggs (classified as mentioned in materials and methods). No females with eggs in the brood pouch were found with maturing oocytes in the ovaries (Fig. 4b).

Oocyte development and size frequency are summarized in Fig. 4. All groups of oocytes had an approximately normal size distribution. In a female of 20.8 mm length, 150 oocytes with a mean size of 173 ± 34 μm were found. In individuals between 47 and 50 mm, mean oocytes size increased to about 800 μm. There is no sign of a second cohort appearing during development of the first. Whether the small oocytes in the female of 67 mm consisted of a residue from the first generation which had not been spawned previously, or a second generation is not clear.

Based on literature data (Bregazzi 1973, Rakusa-Suszczewski 1972, 1982, Richardson 1977, Thurston 1970) an empirical relationship between egg diameter (ED) and the duration of the embryonic development (DED) of six gammaridean amphipod species has been developed to estimate the DED in relation to the ED as;

$$\text{DED [days]} = 119.4 * \text{ED [mm]} + 24.4 \qquad r^2 = 0.83 \quad (5)$$

Using the mean egg diameter of 4390 measured eggs, the lowest and the highest mean values found in single specimens, the following estimates were calculated:

Overall mean egg diameter (2.75 mm):
  DED: 352 days (12 months)

Lowest mean egg diameter (2.31 mm):
  DED: 300 days (10 months)

Highest mean egg diameter (3.39 mm):
 DED: 429 days (14 months)

a
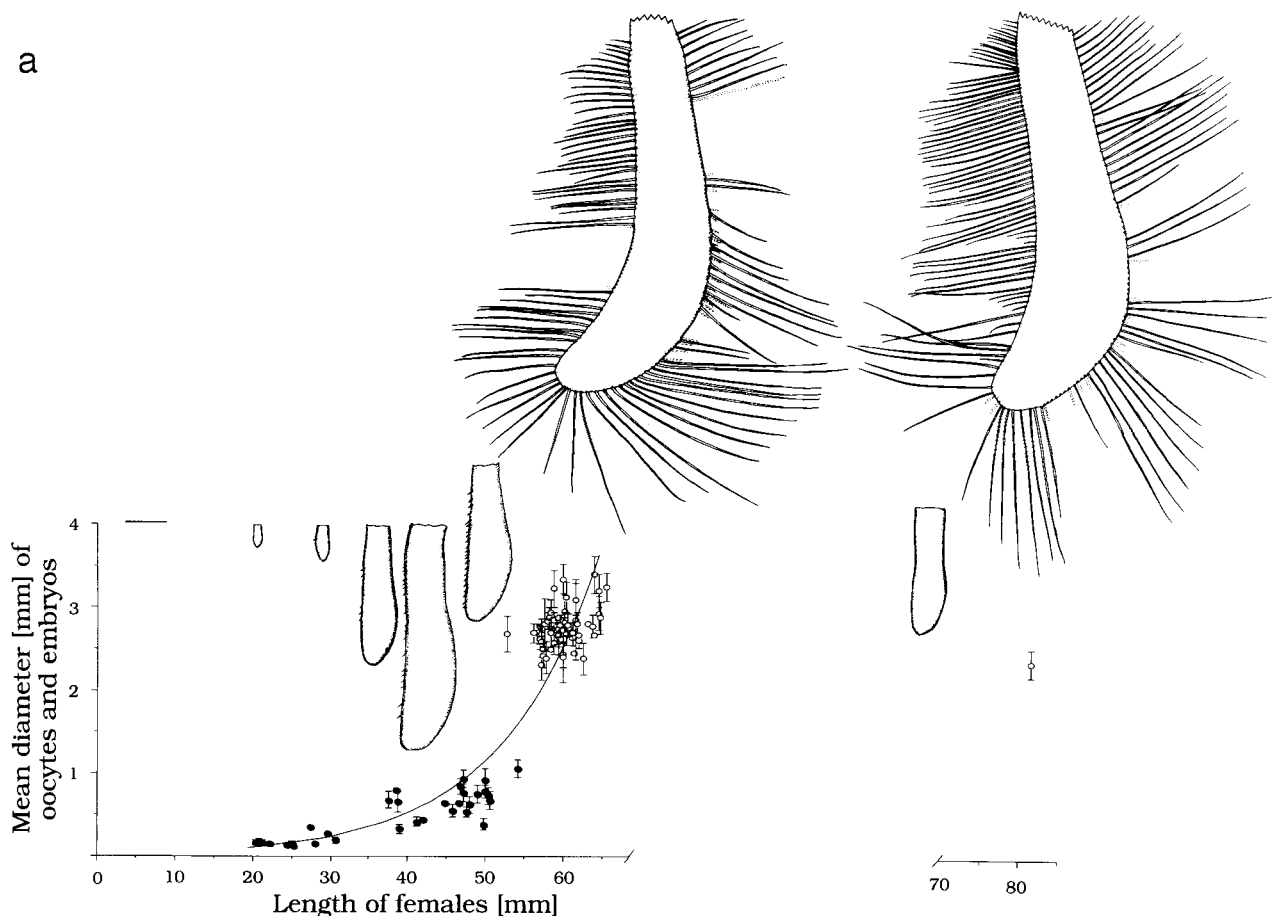
In three females hatching of juveniles in aquaria was observed, and 53 juveniles, 7.5–13.1 mm long were released between the end of March and mid-April. This event took place at a time which could be considered as Antarctic autumn. Additionally the dates of observed hatching in aquaria of 13 other amphipod species are summarized in Table I.
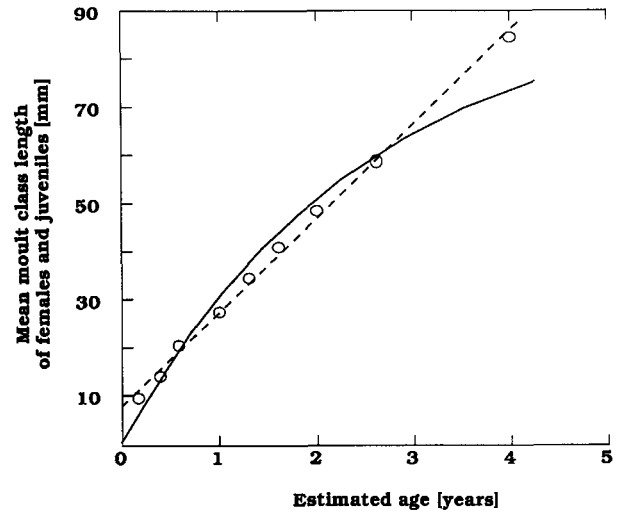
Growth

On considering the size frequency data of *Eusirus perdentatus* (Fig. 3), definite peaks in abundance for females can be separated. The first group of individuals (Fig. 3c) between 7.5–11.6 mm length consist of specimens which hatched in aquaria. Generally, the length-frequency distribution of females is rather untypical due to large number of specimens within the 55–66 mm group. This group consists mainly of ovigerous females whereas only some males reach this size (Fig. 3a). The females are unable to grow due to the embryos in their marsupium, and therefore females of this class are of different ages since the breeding period is about one year. It is evident from the length-frequency distribution that the majority of females die soon after release of juveniles. How the growth proceeds following release of juveniles is difficult to assess since only a few females of a larger size were found. Whether the females reaching 85 mm

b
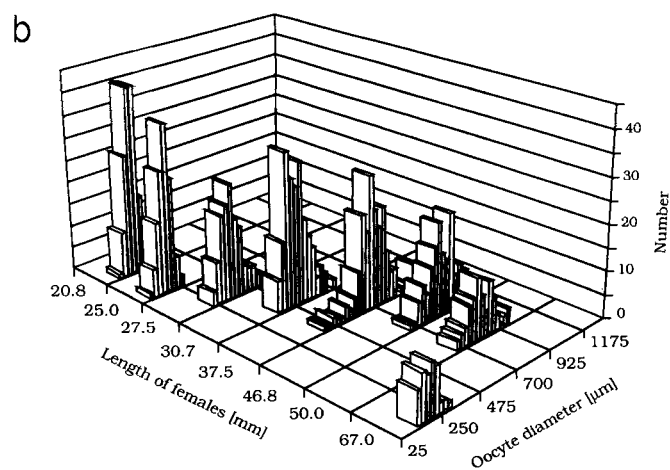
Fig. 4a. Development of oocytes (●) and embryos (○) in *Eusirus perdentatus* is adequately described by the power function: Mean diameter [mm] = 0.2334 * $10^{(0.0339 * \text{length of female [mm]})}$. Oostegites drawn here were dissected from females of the following length (left to right in mm): 21.7, 29.8, 36.4, 41.2, 47.2, 59.2, 65.9, 80.2 (scale bar = 1 mm) which coincides roughly with the mean moult class length indicated in Fig. 3b. **b.** Size frequency distribution of oocytes found in the gonadal tissue of single females related to their respective length.
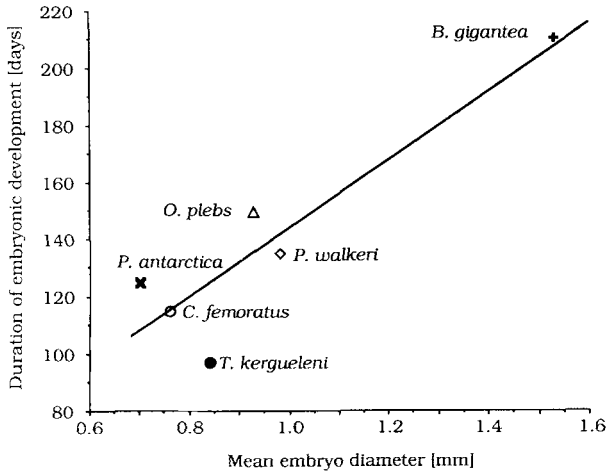
Fig. 5. Relation between egg diameter (ED [mm]) and duration of embryonic development (DED [days]) in Antarctic gammaridean amphipods according to literature data. The development is described by the equation DED = 119.4 * ED + 24.4; r^2=0.83; n=6).

Fig. 6. Growth of *Eusirus perdentatus* females as described by the VBGF (solid line) applied on moult class data with von Bertalanffy equation constants: L_∞ = 91.5 mm, K= 0.408 y^{-1} and t_0 = 0.008. The linear regression (dashed line) of mean moult class length (MMCL) against age is described by MMCL [mm] = 19.631 * age [yr] + 8.021; r^2 = 0.997.

body length represent individuals with delayed sexual maturity or those which were able to reproduce a second time is difficult to decide. Considering separated cohorts above 20 mm as age classes would lead to a linear growth pattern with a maximum life span of 7–8 years if females are semelparous, e.g. the largest females exhibit delayed sexual maturity.

However, the size distribution could be interpreted as moult classes will lead to the following. There is considerable evidence

among crustaceans and insects that growth at moulting approaches a doubling of body volume, and hence a length increase by a factor of 1.26 (Thurston 1979, personal communication). If so, the first moult class detectable has a mean length of 9.8 mm which is too large to have been derived directly from eggs of the size shown in Fig. 4a. Most likely a hatching length of 7 mm followed by a marsupial moult giving rise to the 9.8 mm class shown in Fig. 3c. If release occurs at

Table I. Hatching of juvenile Antarctic gammaridean amphipods as observed in laboratory. Note that all juveniles developed out of eggs which have already been fertilized before capture. ■ = females collected during cruise ANT VI/3 (1988); ● = females collected during cruise ANT VII/4 (1989); ▲ = females collected during cruise PS ANT IX/3 (1991); ○ = Observed by Coleman (1989); X = females collected during cruise ANT IX/3 (1991). Assumed feeding mode (AFM): D = detritus feeder; S = sediment feeder; P = predator; N = necrophagous scavenger. Arrows should indicate roughly estimated interannual and regional variations in melting and onset of sea-ice cover.

AFM	Species	January	February	March	April	May	June	July	August	September	October	November	December
D/S	*Ampelisca richardsoni*				●					■			
P	*Epimeria georgiana*								■				
P	*Epimeria macrodonta*									■■			
P	*Epimeria robusta*								●	■●			
P	*Epimeria rubrieques*	■X											
P	*Epimeria pulchra*				●								
P	*Eusirus perdentatus*				●●●								
P/S	*Paraceradocus gibber*	■				○			●				
P	*Echiniphimedia echinata*					●							
P	*Echiniphimedia hodgsoni*						●						
P	*Iphimediella sp.*						●●						
N	*Orchomene plebs*	●●				X							
N	*Waldeckia obesa*					▲	X ●						
P	*Leucothoe spinicarpa*		X										

A n t a r c t i c   W i n t e r

this size the five specimens *c.* 13 mm long form moult class III, and are poorly represented, presumably as a result of mortality in the aquarium. Class IV is represented by small numbers of juveniles, males and females of *c.* 20 mm length. If the intermoult periods of these classes were a month or two this would explain the absence of classes II and III from the trawl catches as individuals would have passed through these moults before sampling commenced in October. This interpretation would explain the apparent disparity in numbers between the 20.3 mm and 27.5 mm groups. Most individuals would have moulted to the larger size during the winter months. This assumption is supported by the finding that most of the class IV individuals were collected in the spring and early summer catches. Most of the 0-year population would be in class V (mean 27.8 mm) during the summer sampling season. Class VI (mean calculated as 33.4 mm) is missing because individuals could pass through this size during their second winter which was not sampled. The following classes (41.4 and 48.5 mm) would appear during the second summer and females would mature and enter the breeding population at some time after this, possibly at the end of their third spring at an age of *c.* 2.5 or 2.7 years. The calculated duration of 12 months for the embryonic development would fit into this scenario because hatching has been observed in March/April. Additionally this would help to explain the high numbers in the 59.2 mm class. This situation is comparable to the findings in some deep sea organisms, where growth to maturity occupies a relatively short part of the life span, and the population is dominated by large mature individuals (Gage & Tyler 1991). Relating adjacent pairs among the possible nine instars shows that the incremental factor at latter moults is close to 1.2, but higher at earlier moults. The high value of 1.41 for the factor between classes II and III (9.8 and 13.8 mm) may reflect utilization of yolk remnants in the gut of hatchlings. If the factor 1.2 is applied to class IX, then class X would average about 71 mm and class XI about 85 mm. The latter figure is remarkably close to the largest size found in the samples. If hatching, and therefore laying, are seasonal, the larger individuals would be 3.5 or 4 years old rather than 2.5 or 2.7 when entering the breeding population but still breeding for the first time. Using age-size data pairs of moult classes II–IX and XI the von Bertalanffy growth curve (Fig. 6) was found to fit the age-size data:

$$L_t = 91.5 * (1 - e^{-0.408*(t - 0.008)}) \tag{6}$$

n = 8, Residual Sum of Squares = 165.9

Separation of age classes in males failed since chosen cohorts did not reveal a normal distribution and could not be used for age estimation (Fig. 3a). If size data (mean moult class length [MMCL]) are plotted against estimated age (Fig. 6) a simple linear regression would fit this data as.

$$\text{MMCL [mm]} = 19.688 * \text{age [yr]} + 7.867 \tag{7}$$
$$r^2 = 0.997 \qquad n = 8$$

Discussion

The shelf of the Weddell Sea forms a significant part of the continental shelf around Antarctica. The area is one of permanent pack-ice (Hempel 1985) with occasional open water found for short periods during the austral summer or in coastal polynyas some of which exist throughout the year. The gammaridean amphipod fauna of this peculiar high Antarctic region was poorly documented (Knox & Lowry 1977), although more than 170 species occuring in the eastern Weddell Sea have been identified recently (Klages 1991). Together with published data (Andres 1982, Coleman 1991, Lowry & Bullock 1976, Opalinski & Jazdzewski 1978, Schellenberg 1926, Voß 1988) the present study has shown that *E. perdentatus* has a circumpolar distribution. The bathymetric zonation of *E. perdentatus* in the Weddell Sea is considerable, but not extraordinary when compared to that of many other Antarctic invertebrates (Dell 1972, Klages 1991, White 1984). The reasons for this high degree of eurybathy in Antarctic benthic invertebrates and demersal fishes are still unknown, but it is most likely that this special character of high Antarctic invertebrates enables them to colonize even deeper sites during glacial periods then those normally preferred. It has been demonstrated for the Weddell Sea shelf by Grobe (1986) that the continental ice-cap increased in mass and extension during the last glacial period so that the whole continental shelf was covered by shelf ice only 16 000 years ago. Eurybathy could explain why the continental shelf areas of high Antarctic regions are so rich (in terms of biomass and abundance) in benthic organisms soon (in geological and evolutionary time scales) after the quick retreat of the ice.

The present study has shown that *E. perdentatus* exhibits a number of characteristics generally thought to be adaptations of invertebrates to the Antarctic environment. Its reproductive biology is consistent with the general eusiroid reproductive pattern, i.e. one or few broods per lifespan, large embryos, and moderate number of embryos per brood (Sainte-Marie 1991). The observed mean embryo diameter is much greater than that predicted for eusiroids (1.49 mm for a 60 mm female) by a regression equation of embryo diameter on body length (Sainte-Marie 1991). The opposite was found for the brood size, i.e. it was calculated by another regression equation (Sainte-Marie 1991) that a female of 60 mm body length should carry 205 embryos. The 86.9 mm long female found in the samples is the largest benthic amphipod recorded so far on the Antarctic shelf. Only deep sea amphipods belonging to the Lysianassidae such as *Eurythenes gryllus* or *Alicella gigantea* become larger (De Broyer & Thurston 1987, Ingram & Hessler 1987). Factors responsible for large body size in Antarctic gammaridean amphipods have been summarized by De Broyer (1977) to be low temperature, food availability, food preference, competition and low predation pressure. Studies on size-selective predation pressure on larval fish demonstrate that large body size might serve to minimize this factor since encounter rates may increase with age (size) as a consequence of the greater swimming speeds and encounter radii (Litvak & Leggett 1992). However, the

length-frequency distribution suggests that low predation pressure does not apply to *E. perdentatus*.

The maximum mean diameter of oocytes has been found to be considerably smaller than the mean diameter of 2.75 mm of fertilized eggs. Similar results have been obtained for the amphipod *Marinogammarus obtusatus* by Sheader & Chia (1970), decapods by Wear (1974) and for the mysid *Leptomysis lingvura* by Wittmann (1981) who demonstrated that this increase is a result of water uptake. No ovigerous females were found maturing a new clutch of oocytes in the ovary. These facts are indicative of a semelparous mode of reproduction. Similar findings have been published for other Antarctic crustaceans such as the isopods *Serolis cornuta* and *Glyptonotus antarcticus* (Luxmoore 1982, White 1970). Also, the length-frequency distribution indicates that most female *E. perdentatus* die without moulting after the release of juveniles. The high variance in number of eggs found in the brood pouch makes it difficult to estimate fecundity and is likely to be a result of loss of eggs during the catch procedure and the subsequent transport, as has been described for isopods, shrimps and gammaridean amphipods by Wägele (1987), Gorny *et al.* (1992), (Fish 1975), and Sainte-Marie *et al.* (1990). Natural mortality may also result in a loss of young during the incubation period (Mauchline 1973, Wittmann 1981). The maximum number of 149 fertilized eggs found in one female demonstrates that a considerable brood can be produced. Large brood size probably reflects evolutionary adaptations ensuring the survival of a species which exhibits longevity combined with late maturity and semelparous reproduction. The maximum mean diameter of fertilized eggs found in *E. perdentatus* is one of the largest ever reported for gammaridean amphipods. In different peracaridean crustaceans larger species generally produce larger eggs (Corey 1981, Luxmoore 1982, Nelson 1980). The ecological advantages in producing large eggs have been summarized by Marshall (1953) for polar and deep sea fishes and these are to a certain extent applicable to invertebrates; (i) the greater the size of the hatched individual the smaller its relative food requirements, (ii) larger larvae (juveniles) relative to other species have an advantage in securing food, (iii) few eggs produces less intraspecific competition for food among juveniles of a single female, (iv) large larvae (juveniles) may be able to swim faster and have increased escape distance. There is apparently significant advantage in having larger eggs (see Ekau 1991 for discussion on Antarctic fishes), and it is also possible that a large yolk provision may be utilized by juveniles after hatching enabling them to survive the critical early free-living period. This hypothesis may explain the high value of 1.41 for the factor between moult classes II and III (9.8 and 13.8 mm) which probably reflects utilization of yolk remnants in the gut of hatchlings.

There is a wide spectrum of possible explanations for longevity and especially slow embryonic development of Antarctic invertebrates: (i) if secondary production rate is low then predators and parasites must have comparable slow growth rates and a reduced rate of reproduction to sustain the stability of Antarctic animal communities (Wägele 1990), (ii) DNA content of dividing cells can prolong embryonic development (Horner & MacGregor 1983), (iii) cytoplasmic clocks (as demonstrated by Hara *et al.* (1980) for *Xenopus*) with the same period as the division cycle of the eggs. Beside these explanations the most common one is that the rate of carbon dioxide or oxygen diffusion in large eggs is slower when compared to that for smaller eggs, e.g. diffusion rates will lead to lower metabolic rates (Lonsdale & Levinton 1985).

There have been a number of papers that have proposed that reproduction is coupled with the very high primary production in Antarctic mid-summer (Clarke 1988, Pearse *et al.* 1991). This is certainly true for filter and suspension feeders which often represent the majority of species and biomass in the Antarctic epibenthos. In the Weddell Sea benthic food web it is most likely that at least the adult stages of predators and scavenging species are sufficiently uncoupled from the direct impact of the primary production. They feed on motile invertebrates or carcasses which are available throughout the year, although there are still possible temporal and spatial limitations. For hatching of juveniles in the isopod *Ceratoserolis trilobitoides* it has been suggested by Wägele (1987) that mancas probably prefer to feed on juveniles of primary consumers which profit from the short summer rain of algae. Contrary to this hypothesis, the majority of observed hatching events in laboratory during this study occurred during the beginning of the Antarctic winter (in the case of *E. perdentatus*) and mid-winter in other species. Even if in some cases the embryological development was delayed or accelerated due to laboratory conditions, the results have been generally supported by similar observations of Coleman (1989) for *Paraceradocus gibber* and for *Waldeckia obesa* (G. Chapelle personal communication). The length-frequency distribution of juveniles (Fig. 3c) consists of two separate collections which implies difficulties for data interpretation. Small individuals up to 13 mm were collected in the laboratory in April whereas larger specimens from 13 mm up to 20 mm were collected with an epibenthic sledge during January and February at 75° southern latitude. This discrepancy is most likely to be explained by geographical differences in release of juveniles (see also Gutt *et al.* 1992 and Wägele 1987). Juvenile release even during austral autumn and early winter might be explained by the nepheloid layer close to the bottom consisting of drifting particles which are visible on underwater videos taken in the area of investigation (Gutt & Vogel 1988). Resuspended material might serve as a food source for suspension feeders and could sink to the bottom in areas with lower current velocities where it serves as food for juveniles of either primary consumers or others which depend on this material only for a certain phase of their life (Wägele 1987). The availability of this resuspended organic matter in the Weddell Sea is probably only loosely related to seasonal primary production (Hubold 1992). This is supported partly by the observed hatching events in aquaria in several species. The calculated linear regression (equation 5) of the DED against mean egg diameter is based on the few known values for Antarctic gammaridean amphipods

Table II. Literature data on the relationship between egg diameter and the duration of embryonic development in Antarctic benthic crustaceans.

Order Species	Mean average embryo length [mm]	Mean incubation period	Source
AMPHIPODA			
Bovallia gigantea	1.53	7 months *	Thurston (1970)
Eusirus perdentatus	2.27	~12 months **	this study
Paramoera walkeri	0.98	4.5 months *	Rakusa-Suszczewski (1972)
Pontogeneia antarctica	~0.70	4.5 months *	Richardson (1977)
Cheirimedon femoratus	0.76	6 months *	Bregazzi (1973)
Tryphosella kergueleni	0.84	~5 months *	Bregazzi (1973)
Orchomene plebs	0.93	~8 months *	Rakusa-Suszczewski (1982)
IOSPODA			
Glyptonotus antarcticus	2.30-2.40	~20 months *	Dearbom (1967), White (personal communication)
Ceratoserolis trilobitoides	3.00	23 months **	Wägele (1987)
Serolis cornuta	1.50	20 months *	Luxmoore (1982)
Aega antarctica	2.57	≥ 32 months ***	Wägele (1990)
DECAPODA			
Chorismus antarcticus	1.74	10 months **	Clarke (1985), Gorny *et al.* (1992)
Notocrangon antarcticus	1.58	10 months **	Clarke (1985), Gorny *et al.* (1992)

*) field observation; **) estimated period; ***) laboratory experiments.

(Fig. 5). This leads to the problem that the slope of the regression line is almost entirely determined by the single value for *Bovallia gigantea*. However, the estimated mean incubation period of 352 days in *E. perdentatus* coincides with similar determinations for other Antarctic crustaceans which spawn eggs, some of them of comparable size, at similar temperatures (Clarke 1982), and, perhaps more convincing, fit into the proposed reproduction scenario. It is obvious from Fig. 5 that *Bovallia gigantea*, belonging to the same family as *E. perdentatus*, also has a very long incubation period. Compared with boreal or tropical species the estimated incubation period of *E. perdentatus* is very long, but not exceptional in Antarctica (Table II). For the Antarctic isopod fish parasite *Aega antarctica* it has been estimated that the embryonic development of eggs with a mean size of 2.57 mm lasts more than 32 months (Wägele 1990). For decapod crustaceans occuring in the Antarctic, such as *Notocrangon antarcticus* and *Chorismus antarcticus*, a brooding period of 9–10 months was observed (Clarke 1985, Gorny *et al.* 1992). Compared with the embryonic development in isopod species with either similar or larger egg diameter the estimated embryonic duration seems relatively short but indicates a strong seasonal reproduction. However, relative to other Antarctic gammaridean amphipod species, *E. perdentatus* has the longest embryological development yet recorded.

A major problem in the the present study is that samples have been collected mainly during the austral summer leading to limitations in temporal resolution. Furthermore, not only crustaceans of polar regions and the deep sea but also sponges and echinoderms have been found to become very old, and they often have slow growth rates (Brey 1991, Clarke 1985, Dayton 1979, Ingram & Hessler 1987, Wägele 1990, White 1970) which may cause confusion if choosen size classes overlap. The

use of pooled samples has been considered to be appropriate under the following assumptions; (i) the food availability is constant for predators throughout the year (with the above mentioned restrictions). (ii) The temperature as one major factor determining physiological processes and growth rates is constant within a small range and similar at different sites in the area of investigation, (iii) the investigated species is motile and therefore able to choose suitable habitats. Despite this approach describing the growth patterns in females of *E. perdentatus* is difficult when using pooled length-frequency data. The order of magnitude of the calculated growth constant K is considerably higher than for other invertebrates living at high latitudes (Brey 1991, Hopkins & Nilssen 1990, Ralph & Maxwell 1977, Wägele 1990). Considering the von Bertalanffy growth curve in Fig. 6 and the calculated residual sum of squares scepticism on the applicability of the VBGF is reasonable. The estimation of VBGF parameters in *E. perdentatus* was difficult because of the uncertainties over which age the cohorts represented and how the largest females grew. If the age estimates for mean moult class length of females and juveniles used in this work are correct, linear growth would describe the situation betten that the VBGF. Males reach a maximum size around 64 mm but due to the lower number of specimens caught, length-frequency histograms did not reveal comparable definite age classes as for females and hence no age and growth estimates were possible. One may reasonably argue that the modes indicated in Fig. 3a represent six or possibly seven moult instars for males. Those few females reaching a body length close to 90 mm were either breeding for the second time or represent females with delayed sexual maturity. Similar results on delayed sexual maturity have been published for the Antarctic amphipod *Paramoera walkeri* (Sagar 1980). The analysis of female growth implies a normal

life span of *c.* 4–4.5 years if the moult class hypothesis is applied. This leads to a faster growth rate than that obtained if peaks in the length-frequency distribution were considered as age classes. In that case the maximum age of *E. perdentatus* would become *c.* 8 years old which is closer to the estimated life span of other large gammarids such as *Eurythenes gryllus* (Ingram & Hessler 1987) or isopods as *Glyptonotus antarcticus* (White personal communication). However, this is no insurmountable problem, because Clarke (1990) pointed out that growth rates of polar organisms may be more limited by food availability than by temperature. Feeding behaviour observations indicate that this large gammarid plays an important role in the Weddell Sea benthic food web (Klages & Gutt 1990). However, for a species such as *Eusirus perdentatus*, whose dependence on the primary productivity cycle is at several stages removed, food limitations may be less important than for many other polar organisms.

Acknowledgements

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