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Sexual regression, shrinkage, re-maturation and growth of spent female *Euphausia superba* in the laboratory

P. G. Thomas and T. Ikeda *

Antarctic Division, Department of Science; Channel Highway, Kingston, Tasmania 7150, Australia

Abstract

Live female *Euphausia superba*, Dana were collected from Prydz Bay, East Antarctica in January 1985, and observations of intermoult period, growth and maturation changes were made on individuals which spawned and were subsequently maintained in the laboratory for 12 mo. Over this experimental period an instrinsic cyclic reproductive pattern was observed. Following spawning, there was a regression of the female copulatory organ, the thelycum, coupled with a decrease in body length and an increase in the krill's mean intermoult period. This was followed by a period of sexual re-maturation, associated with positive growth and a decrease in the mean intermoult period. This study indicates multi-year spawning of *E. superba* and a life-span greater than 4 yr.

Introduction

Euphausia superba Dana, is considered to be an important component of the Antarctic marine ecosystem (Marr, 1962; Mauchline, 1980). Acoustic estimates of stock size, based on data collected by various countries during FIBEX (First International BIOMASS Experiment) in 1981, is in the range of 200 to 600 million tons (Hampton, 1983; Hempel, 1983). Relatively little, however, is known about this animal's physiology (Clarke and Morris, 1983). While the maintenance of live *E. superba* outside Antarctic waters (Murano *et al.*, 1979; Ikeda *et al.*, 1980) has allowed extended observations of these krill, there are still conflicting data concerning their life history, growth rate (see Ikeda *et al.*, 1985; Ikeda, 1985) and fecundity (Harrington and Ikeda, 1986).

To maintain *Euphausia superba's* large biomass, despite predation pressures, the species would be expected to have a high fecundity. Since fecundity depends on both the number and size of broods produced during the life span of a species (Denys and McWhinnie, 1982), it is necessary to determine these parameters as well as larval mortality and predation to enable accurate estimation of annual recruitment.

From field samples, Bargmann (1945) proposed that female *Euphausia superba* spawned once and died after a life span of 2 yr. Later investigations supported this hypothesis (Marr, 1962; Mackintosh, 1972). Other studies, however, indicate a longer life span of 3 to 4 yr (Ivanov, 1970; Mauchline, 1980) to greater than 7 yr (Ettershank, 1983; Ikeda, 1985). Fecundity would therefore be increased if females spawned for more than one year, in these hypothesised longer life spans.

Makarov (1975, 1976), analysing field data, proposed that female *Euphausia superba* spawn in successive years with intervening ovarian regression and rematuration the following year. McWhinnie *et al.* (1979) noted that spent females, kept in tanks over winter (at Palmer Station, Antarctica), continued to feed and moult while reverting to a less mature form, referring to this sexual regression as "rejuvenation" in a later report (McWhinnie and Denys, 1980). Further, Denys and McWhinnie (1982), investigating maturation changes in live krill maintained at Palmer Station, suggested that *E. superba* would have at least two successive breeding years, although their post-spawned experimental individuals did not survive through the austral winter. Ikeda *et al.* (1985), confirmed experimentally that regression and re-maturation of secondary sexual characteristics occurred and hypothesised, based on a correlation between maturity stage and body length, that sexual regression was related to a decrease in body length.

The present study investigates this hypothesis in post-spawned female *Euphausia superba*, examining the time scale of regression and re-maturation of sexual characteristics and related growth indices in the laboratory.

* Present address: Japan Sea Regional Fisheries Research Laboratory, 5939-22, 1 Suido-cho, Niigata 951, Japan

Materials and methods

Live female *Euphausia superba* Dana were collected using a rectangular midwater trawl net (Baker *et al.,* 1973) from Prydz Bay, East Antarctica, during the second phase of the Second International BIOMASS Experiment (SIBEX II) in January 1985. Subsamples of net hauls from 66°00.9′S, 058°00.3′*E; 67°00.4′*S, 069°03.4′E; and 64°00.0′S, 077° 58.2′E were maintained in plastic buckets filled with surface seawater for 2 to 5 h. Undamaged gravid females (Maturity Stages IIIC-IIID: Makarov and Denys, 1980) were selected for fecundity studies. On completion of these investigations by Harrington and Ikeda (1986), 15 post-spawned females were returned to Australia and maintained in culture (0 °C ± 0.5 C°) at the Australian Antarctic Division.

Individual krill were isolated in 4-litre glass bottles and maintained in darkness. Seawater (ca. 34‰ S) filtered through 0.45 μm Millipore filters was changed weekly. Bottles were examined every 24 h for exuviae, which were collected and preserved with 0.4 ml buffered formalin (40%) in 20 ml seawater (Ikeda and Dixon, 1982). Measurements of the length of the uropod exopodites (EL, mm) and carapace lengths were made and body lengths (BL, mm, from tip of the rostrum to distal end of the telson) were estimated from the equation BL = 0.12 + 7.90 EL (modified from Ikeda *et al.,* 1985).

Sexual maturity was assessed on the thelycum morphology examined from cast exuviae using Bargmann's (1945) classification (Table 1). The recommended method of determining sexual maturity in investigations of population dynamics (Makarov and Denys, 1980) was not used in this study, as it was not precise enough to identify all observed changes in thelycum development.

Stages of thelycum development (Bargmann, 1945) were examined using a JEOL JSM-840 scanning electron microscope (SEM). For SEM observation, thelyca were detached from cast exuviae and post-fixed with 4% osmium tetroxide for 1 h. Following fixation, specimens were dehydrated in a graded series of ethanol, critical point dried with carbon-dioxide and sputter-coated with 50 nm gold.

Table 1. *Euphausia superba.* Thelycum development stages used to determine sexual maturity from cast exuviae (modified from Bargmann, 1945)

Stage	Thelycum description
A	Thelycum either not visible, or represented only by a straight band across sternum
B	Two small coxal outgrowths at each end of sternal band
C	Thelycum half-developed: coxal part larger than sternal part but not heavily chitinized
D	Thelycum similar to adult shape except smaller and not well chitinized; some pigmentation
E	Thelycum large and firm (well chitinized); usually coloured bright red
G	Thelycum swollen and red in colour; male spermatophores attached but empty

In parallel with morphological examinations of thelyca, histological observations on ovarian development were made on two specimens sacrificed on completion of the experiment. Specimens were individually fixed in Baker's formal-cobalt-calcium solution (Simpson, 1977), dehydrated, and embedded in wax. Medial sagittal sections (7 μm), of the entire ovary, stained with haematoxylin and eosin, were used to classify the ovary according to Kikuno and Kawamura (1983).

To examine the effect of food on the re-maturation process of spent female *Euphausia superba,* three feeding groups (A, B, C) were established, containing 7, 2 and 6 individuals respectively. *Phaeodactylum tricornutum,* a pennate diatom, cultured in *f*/2 medium (Guillard and Ryther, 1962) at 10 °C was used as food. Food concentrations are expressed in carbon units (C) throughout this study. A million cells of *P. tricornutum* are equivalent to 10 μg C (Ikeda *et al.,* 1985). Food concentrations were determined using a Coulter Counter (TA II).

For the period between January and mid-May 1985, Groups A and C were each fed 2.0 mg C l^{-1} each week, while Group B was given 4.0 mg C l^{-1}. From mid-May, Groups A and B were combined (Group A + B) and fed 2.0 mg C l^{-1}, and Group C was maintained in filtered seawater and given no food until December 1985, when it was again fed 2.0 mg C l^{-1}.

A previous study (Ikeda and Thomas, 1987) has shown that *Euphausia superba* fed 2.0 mg C l^{-1} of *Phaeodactylum tricornutum* each week achieved a maximum growth rate. Increasing the food concentration beyond 2.0 mg C l^{-1} did not produce any increase in growth rates.

Results

All individuals of *Euphausia superba* used in this study were mature females (40.28 to 58.75 mm in length), each having an enlarged ovary with spermatophores attached to a swollen thelycum (Maturity Stage G). Each individual was observed to spawn in January 1985 (Harrington and Ikeda, 1986).

After spawning, all post-spawned females underwent a regression of sexual organs at an approximate rate of one maturity stage per moult (Fig. 1). As a consequence, 12 females regressed to Maturity Stage B and 3 females to Stage C. This regression occurred over five successive moults, so that by late May-early June, all individuals appeared to be sexually immature. Following this sexual regression, the krill gradually advanced in maturity to the final maturity stage (E), in late November – early December through 4 to 5 moults (Fig. 1). Ovaries increased in size, filling the thoracic cavity only after the thelycum reached Stage E. Ovaries developed rapidly, while external characteristics remained unchanged (Stage E) through

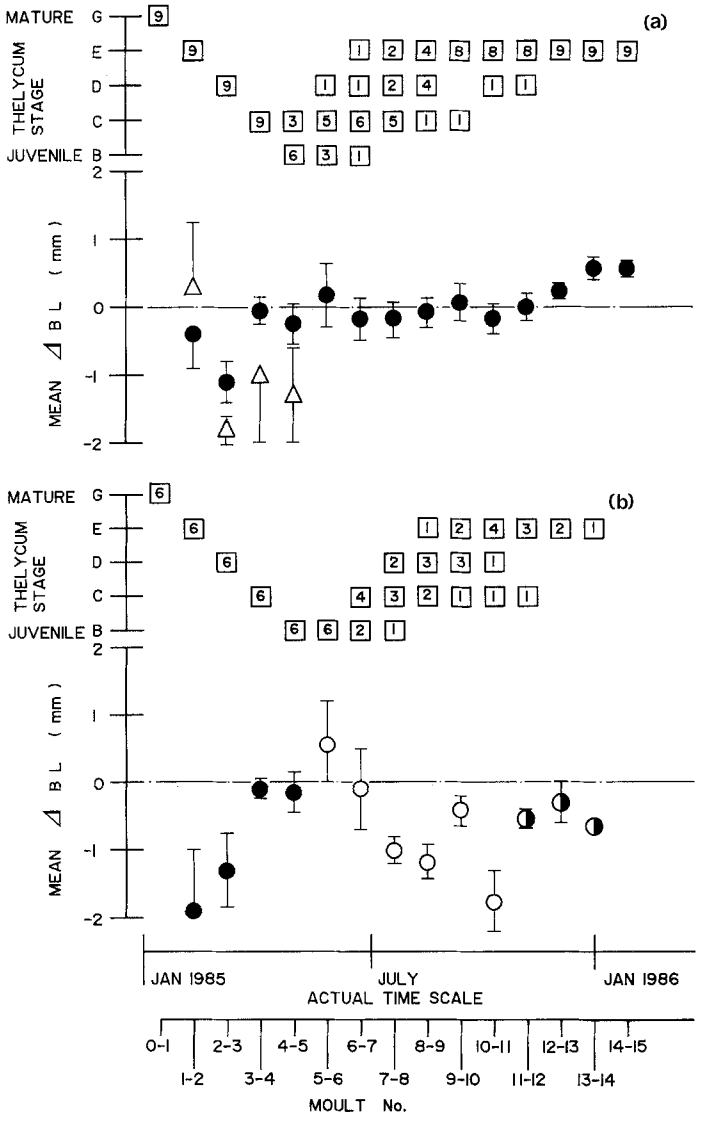


Fig. 1. *Euphausia superba.* (a) Changes in mean ΔBL (body length, mm) ±SE of spent females fed *Phaeodactylum tricornutum* equivalent to 2.0 mg C l^{-1} (Group A, ●) and 4.0 mg C l^{-1} (Group B, △) over time in the laboratory; Groups A and B were combined (A+B) after 4th moult (see "Results" for details); Maturity Stages (B, C, D, E, G (see Table 1) over time are indicated (□), with number of individuals inside each square. (b) Changes in mean ΔBL (mm)±SE of spent females (Group C) maintained in laboratory and fed *P. tricornutum* equivalent to 2.0 mg C l^{-1} until mid-May (●), then starved (○) until December, when they were again fed 2.0 mg C l^{-1} (◑); Group C maturity stages over time are indicated (□), with number of individuals inside each square

each successive moult, so that by late December-early February, the krill's thoracic cavities contained ripe ovaries beneath a swollen carapace, with the thelycum enlarged and iridescent red.

One-way analysis-of-variance (Zar, 1984) revealed no significant difference in mean ΔBL between feeding groups (A, B, C) for the first four moults. Groups A and B were therefore combined (Group A+B) and fed 2.0 mg C l^{-1}, while Group C was starved.

Progression of maturity in Group A+B (fed) usually occurred with each successive moult. Rate of thelycum development was marginally slower in starved individual's (Group C) than in Group A+B, due to a replication of the same maturity stages between successive moults which was only occasionally seen in Group A+B. However, all but one starved individual reached maturity (Stage E) by late November. Thus a pattern of maturity regression, followed by the redevelopment of external sexual characteristics was common to all groups, both starved and fed (Fig. 1).

Mean change in body length (ΔBL) for each feeding group through successive moults is also given in Fig. 1. Comparison of mean ΔBLs between Group A+B and Group C over Moults 5 and 11 showed significant differences ($p < 0.01$) in each group's growth pattern (Fig. 1).

Negative mean ΔBL occurred in all feeding groups in parallel with the regression of external sexual characteristics, indicating that body shrinkage after spawning is not related to food availability. This trend of negative mean ΔBL continued in Group C following starvation, yet external and internal sexual characteristics began and continued to mature (Fig. 1 b). Mortality only occurred in Group C, where three individuals died at the end of the starvation period and a further two individuals died during the re-feeding period; no deaths were recorded in Groups A or B.

Group A+B (fed) on the other hand, after undergoing sexual regression and a corresponding negative ΔBL, showed little change in their mean ΔBLs until Moult 11 to 12 (late December), when a positive mean ΔBL was observed with each subsequent moult (Fig. 1 a). This positive growth occurred once females had become externally mature (Stage E, Fig. 1 a), and their ovaries matured at the same time, filling the thoracic cavity (Fig. 2 a).

Following thelycum re-maturation at the end of this experiment (January, 1986), oocytes were in the final maturity stage (Fig. 2 b), according to Kikuno and Kawamura's (1983) classification. A few cells were also observed which were immature and of the peripheral nucleolus stage.

In conjunction with the decrease in body length and regression of sexual characteristics, the mean intermoult period (IP) of all feeding groups had increased through successive moults from 23 to 28 d by mid-year. Thereafter, Group C's mean intermoult period gradually increased to 33 d, and then decreased to 26 d after re-feeding (Fig. 3). Group A+B's mean IP steadily increased throughout the year, peaking at 29.5 d, and then decreasing to 25 d in late January 1986 (Fig. 3). No significant difference ($p < 0.01$) was observed in mean IP between each feeding group, probably due to the large individual variation of IP in Group C. The general trend observed in Fig. 3 could be described as cyclic, with IP gradually increasing to a plateau around July, and decreasing from November to January. The increase in IP occurs in conjunction with a decrease in BL and regression of external sexual characteristics after spawning. The decrease in IP is associated with an increase in BL and the development and maturation of internal ovaries prior to spawning.

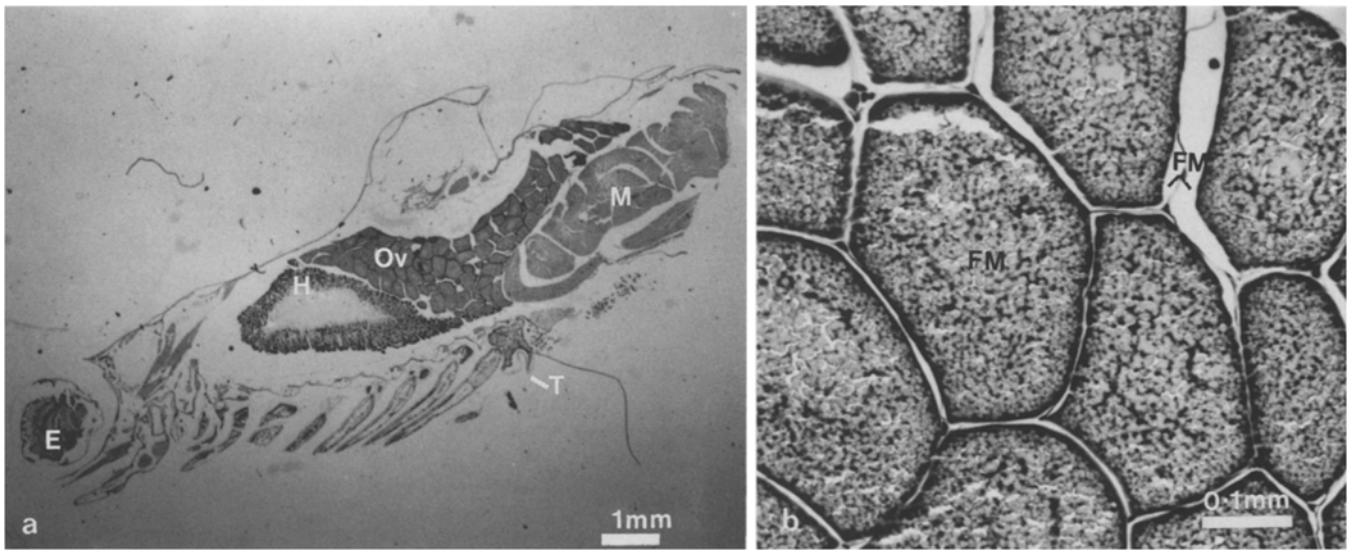


Fig. 2. *Euphausia superba.* (a) Medial sagittal section (7 μm) of re-matured female which had spawned 12 mo previously; mature ovary (Ov) lies between hepatopancreas (H) and muscle tissue (M); position of eye (E) and thelycum (T) are indicated. (b) Enlarged portion of ovary, showing oocytes in final maturity stage (FM)

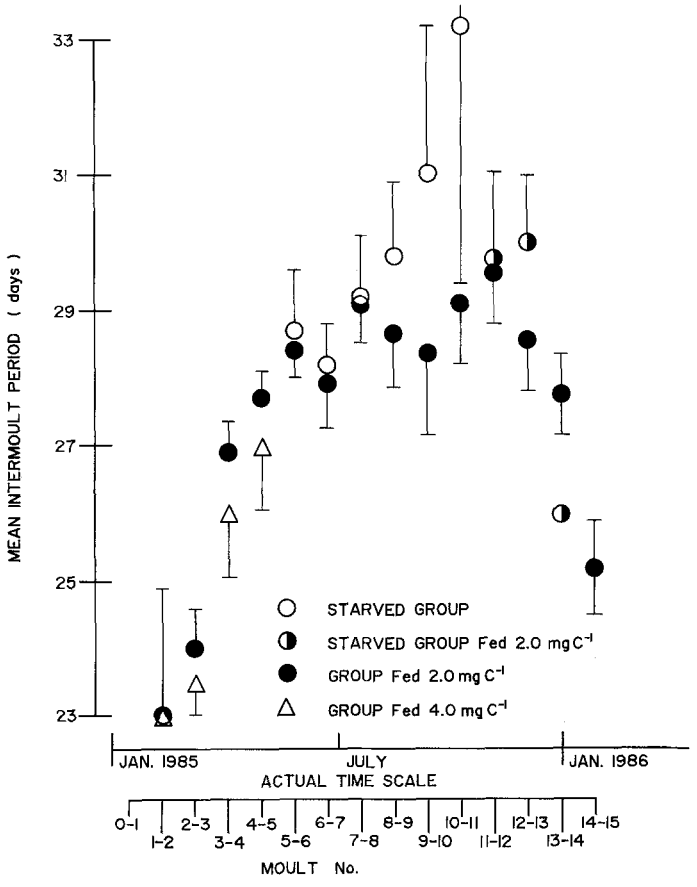
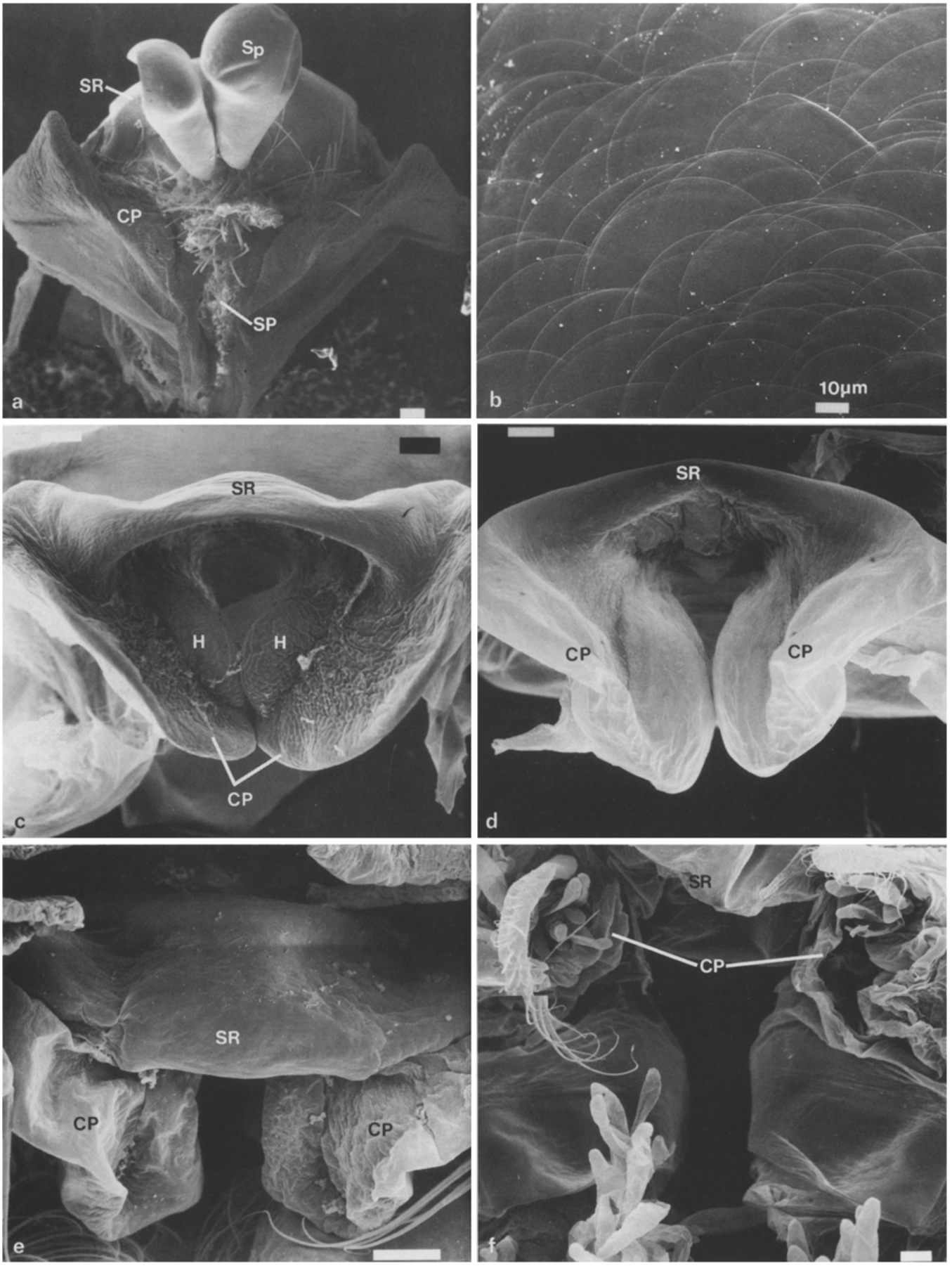


Fig. 3. *Euphausia superba.* Mean intermoult period ± SE of spent females fed different concentrations of diatom *Phaeodactylum tricornutum*

SEM observations of regressing and developing thelyca are shown in Fig. 4. Spermatophores, their surface covered by overlapping circular chitinous plates (Fig. 4 a, b), were generally found implanted on medial projections, called "holdfasts" (Denys and McWhinnie, 1982), on the coxal plates in the first cast exuviae following spawning (Fig. 4 b, c). Once spermatophores are attached, the sperm-mass migrates into the thelycum through slits in the base of each spermatophore to form a sperm-plug in the Stage G thelycum (Fig. 4 a). Further descriptions of fertilization processes in *Euphausia superba* have been given by Bargmann (1937). The different stages of thelycum regression are shown in Fig. 4 c, d, e, f. As regression proceeded (from Stage G to B), there was a decrease in chitinization which resulted in a gradual loss of the thelycum's form and structure as well as colour. Pigmentation gradually changed from red (Stage G) to orange to pale red to colourless as the thelycum became immature through successive moults. The re-maturing thelycum became progressively more pigmented with each successive moult, until by Stage E it was red; however, once ovaries were fully developed, the thelycum became iridescent red. Morphological differences between maturity stages of developing and regressing thelyca were visible only in Stage E, due to the exoskeleton forming around the distended sperm-filled chamber in Stage G, when regressing (as shown by Denys and McWhinnie, 1982).

Fig. 4. *Euphausia superba.* Scanning electron micrographs of thelycum stage and spermatophore morphology. (a) Stage G thelycum; spermatophores (Sp) attached above sperm plug (SP); sternal plate ridge (SR) and coxal plates (CP) indicated. (b) Surface structure of a spermatophore, showing how it is composed of small circular chitin plates. (c) Stage E thelycum, showing spermatophore holdfasts (H) on inside edge of coxal plates. (d) Stage D thelycum. (e) Stage C thelycum. (f) Stage B thelycum. Scale bars = 100 μm, except where indicated otherwise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Discussion

The close relationship between maturity stage, ΔBL and IP established in this study for *Euphausia superba* supports the hypothesis of Ikeda *et al.,* (1985) that regression of sexual maturity in females of this species is related to a decrease of BL during the Antarctic winter.

Suggestions of female *Euphausia superba* undergoing regression of reproductive organs over winter with subsequent redevelopment by the following summer are not new (Makarov, 1976; McWhinnie *et al.,* 1979, McWhinnie and Denys, 1980; Denys *et al.,* 1981). Our one-year study on individual post-spawned female *E. superba* confirms this phenomenon.

Post-spawned female krill in this study, despite being supplied with adequate food for growth (Ikeda and Thomas, 1987), underwent a regression of external sexual characteristics after spawning. Individuals regressed through each of Bargmann's (1945) maturation stages with each successive moult. Thus, mature females following spawning in January 1985 had reverted to the sub-adult form by mid-May. This regression of sexual characteristics with each moult was accompanied by a negative ΔBL and an increase in IP. In the second half of the year, females reversed this process; maturing, decreasing IP and showing a positive mean ΔBL with each successive moult. Ovaries were not observed to develop until secondary characteristics reached maturity (Stage E) in December, with oocytes then rapidly developing, reaching final maturity in January 1986, one year after spawning.

Our results do not support Bargmann's (1937) hypothesis of a long oogenesis period. Our finding of a more rapid oogenetic development is supported by Kikuno and Kawamura's (1983) histological observations on ovarian development, and the over-wintering study of *Euphausia superba* maintained at Palmer Station (Denys *et al.,* 1981). The Palmer Station study indicated that, following spawning, the ovary reorganizes, reverting to a juvenile appearance followed by a long reproductive diapause (Denys and McWhinnie, 1982). Although their experimental krill did not survive the winter, these authors proposed that they would have become reproductively mature the following summer, thereby suggesting that *E. superba* has two successive breeeding years. Our results support this, as experimental individuals used in this study spawned in the laboratory (Harrington and Ikeda, 1986), regressed sexually over winter, and re-matured the following summer. We suggest that, once mature, females spawn in two or more successive breeding years, each year undergoing a cyclic pattern of sexual regression and shrinkage over winter followed by positive growth and re-maturation in summer. Continuation of the present study into a second year has indicated that krill re-mature a third time in the laboratory (Thomas, unpublished data).

Ikeda (1987) has shown that female krill hatched from eggs in the laboratory reach maturity (Stage E in their third year. Assuming this developmental rate is similar to that of individuals in the field, then krill used in this study were at least 2 to 3 yr old at the time of capture and now, at the completion of this experiment, are in their second successive breeding year, i.e., they are now at least 4 to 5 yr old. Such a protracted life span for *Euphausia superba* has been suggested by Ettershank's (1983) lipofuscin analysis and Ikeda's (1985) laboratory growth models.

An integral part of any crustacean growth model is knowledge of the animal's moulting physiology (Clarke and Morris, 1983). Our laboratory observations on female *Euphausia superba* showed an increase in IP, coupled with a negative ΔBL and sexual regression over winter. Late in the year (Antarctic summer), IP was seen to decrease as the krill matured, and showed a positive ΔBL. Examining moult stages of freshly collected specimens throughout a winter cruise on the R.R.S. "John Biscoe", Morris and Priddle (1984) considered there was a decrease in the moulting frequency of *E. superba* over winter, suggesting that this was caused by lower water temperatures. The results of the present study suggest that the state of maturity in post-spawned *E. superba* is an additional cause for an IP increase over winter in adult females. Such a mechanism would reduce energetic costs over winter by reducing the number of moults.

Re-maturation of post-spawned female internal and external sexual organs was observed in both starved and fed experimental groups. While feeding is not considered to be essential for completion of the maturation cycle, lack of food will reduce the size of the individual, thereby affecting the brood size. Smaller individuals tend to have smaller brood sizes (Harrington and Ikeda, 1986). In addition, results of the present study indicate that the female reproductive cycle is apparently not governed by food availability, temperature, light or salinity, as these environmental variables remained constant throughout the experimental year. We suggest that this cyclic event is controlled by an endogenous rhythm, as our laboratory results agree closely with Makarov's (1976) and Stepnik's (1982) observations on the maturity cycle of females from field samples. The significance of this mechanism is unknown, however it could be argued that it would allow krill to reach maturity, and spawn independent of environmental cues such as food availability, light and temperature, thereby ensuring survival of the species.

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