

# The energetic cost of egg production in Antarctic krill (*Euphausia superba* Dana)

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**Abstract:** A female Antarctic krill loses 34% of its body mass when it lays a batch of eggs. This represents a considerable input of energy which was estimated using a combination of measured mass and energy differences in female krill and from the measured energetic content of ovarian tissue. Large (c. 50 mm) female krill lose 2.9–3.8 kJ each time a batch of eggs is laid. Calculations using this figure indicate that multiple spawning by Antarctic krill in a season would require above average phytoplankton concentrations ( $> 0.5 \mu\text{g chl a l}^{-1}$ ) and filtration rates which are close to the maximum reported ( $> 10 \text{ l h}^{-1}$ ).

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## Introduction

Antarctic krill (*Euphausia superba*) were initially envisaged as a short-lived species which spawned once in their second year (Bargman 1945). More recent investigations have indicated that not only do Antarctic krill have the potential to live for up to 11 years (Ikeda 1985) but that they may also produce several (up to seven) batches of eggs during an austral summer (Ross & Quetin 1983, 1986 Cuzin-Roudy 1987). Studies which have suggested multiple spawning episodes in female Antarctic krill have used either histological examinations (Cuzin-Roudy 1987) or have depended on calculations based on the proportion of spawning females in wild populations (Ross & Quetin 1983). Laboratory studies have not yet demonstrated repeated spawning by female Antarctic krill over a protracted period (Harrington & Ikeda 1986, Nicol 1987) but it is unlikely that such studies would have provided optimal conditions for ovarian maturation and subsequent spawning.

Although the energetic outlay involved in spawning has been calculated from the biochemical composition of the ovary (Clarke 1980) and a preliminary energy budget for Antarctic krill has been constructed (Clarke & Morris 1983) and modified (Quetin *et al.* 1993), there have not been any reports of direct measurements of the cost of reproduction or measurements of the energetic loss associated with spawning in female *E. superba*. In this note we report estimates of the energetic loss associated with spawning in female *E. superba*. These estimates are based on measurements of the energy content of gravid and spent females and of the mature ovary, combined with observed mass losses associated with spawning. The question of multiple spawning is re-examined from the point of view of its energetic cost.

## Materials and methods

Gravid female *E. superba* were collected from surface waters at 67°19'S, 70°02'E (water depth 150–200m) on 28 January 1990.

Eightyone females in the final stage of ovarian maturity (stage 7) and 68 spent females (stage 8) were frozen individually in liquid nitrogen (ovarian development stages classified according to Cuzin-Roudy & Amsler 1991).

During 1991, gravid krill were collected from a number of locations in the Prydz Bay region between the 22 January and 1 March. Gravid females (stage 7) were kept individually in 2 l plastic jars at 0°C on board and 72 spawned. The eggs were preserved in Steedman's solution (Steedman 1976) and were counted in the laboratory. The mature ovaries were dissected from a large number of freshly caught stage 7 females, batched and stored in liquid nitrogen for later analysis.

In the laboratory, whole female krill were measured (standard length No. 1, and carapace length No. 4, Mauchline 1980), weighed wet, freeze dried and weighed again. The energetic equivalent of the various samples was determined by microbomb calorimetry (Philipson 1964). Five samples of ovarian tissue, five spent females and 13 gravid females all randomly selected were pelletized and fired in a bomb calorimeter using benzoic acid as a standard. The spent females ranged in dry mass from 186–266 mg with a mean of 241.7 mg, the gravid females ranged in dry mass from 213–522 mg, with a mean of 356.9 mg.

## Results

Gravid females were significantly larger in total length ( $t = 3.964$ , 147 df,  $P < 0.0001$ ), and carapace length ( $t = 3.328$ , 149 df,  $P < 0.001$ ) as well as being heavier (wet mass:  $t = 9.09$ , 148 df,  $P < 0.0001$ ; dry mass  $t = 13.82$ , 147 df,  $P < 0.0001$ ) than spent females in the samples used in this study (Table I).

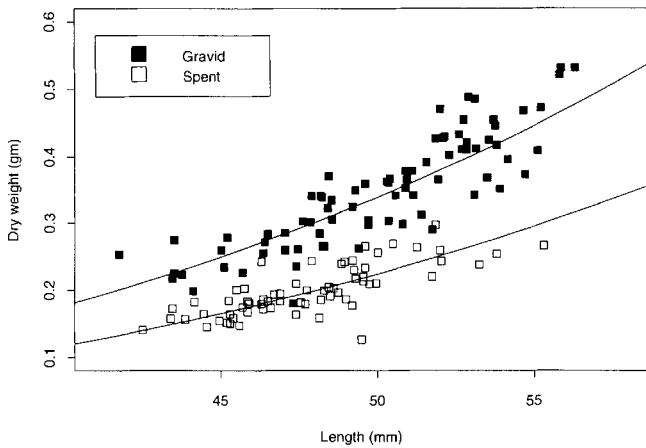
The difference in mean length between the spent and gravid females is difficult to explain since all samples were obtained on the same night from one population. It is possible that there may be some contraction in the total length following the release of tension in the exoskeleton accompanying spawning. The differences in both wet and dry mass, however, mainly reflect the

**Table I.** Wet mass, dry mass and mass differences of gravid and spent female Antarctic krill.

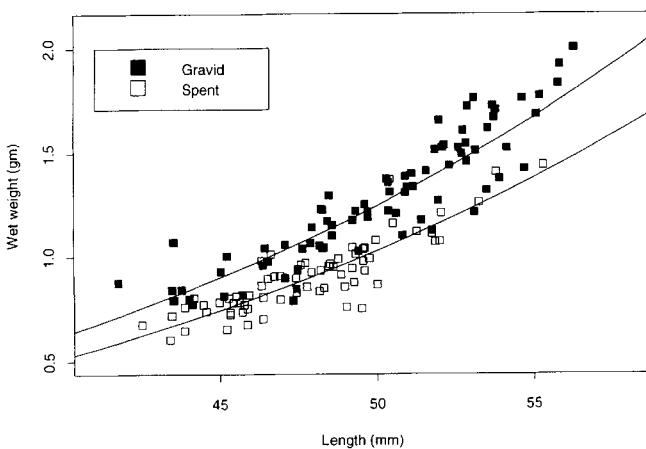
	<i>n</i>	Mean total length	Mean carapace (mm)	Mean mass (mg)	Mean mass (mg)
Gravid females	81	50.01	17.37	1279	349
Spawmed females	68	47.91	16.41	903	199
Mass difference (mg)			376	150	

loss of ovarian material during spawning. The ratio of the wet mass to dry mass was significantly higher for spent females than for gravid females ( $t = 13.32, 147 \text{ df}, P < 0.001$ ) reflecting the loss of ovarian tissue at spawning and its replacement by a visible, fluid filled cavity in the post-spawning females.

The wet and dry weights of the spent females were corrected to take into account the significantly different mean lengths of the gravid and spent females in this study. The wet weights and dry weights were regressed against total length (Figs 1 & 2). No



**Fig. 1.** Regression of dry mass against body length for gravid and spent female *E. superba*. Regression lines fitted from equations 1 and 2, Comparisons of regressions presented in Table II.



**Fig. 2.** Regression of wet mass against body length for gravid and spent female *E. superba*. Regression lines fitted from equations 3 and 4, Comparisons of regressions presented in Table II.

**Table II.** ANOVA tables for log-log regressions of mass against length for gravid and spent female *E. superba*.

	SSR	df	MS	F ratio
a) Dry mass				
Length	10.4045	1	10.4045	6.71.69**
Spawning status	5.4337	1	5.4337	350.79**
Length	0.0325	1	0.0325	2.098
Interaction				ns
				$\chi^2_{ns} (P > F = 0.15)$
Error	2.1994	142	0.01549	
Total	18.0701	145		
b) Wet mass				
Length	3.38	1	8.3870	849.31**
Spawning status	1.1982	1	1.1982	121.34**
Length	0.008	1	0.008	0.81
Interaction				ns
				$\chi^2_{ns} (P > F = 0.15)$
Error	1.422	144	0.009875	
Total	11.01	147		

significant interaction was detected (Table II) so a single exponent was estimated for both spawning categories.

Dry mass/length relationships

Gravid: Mass ( $W_g$ ) =  $3.8838 \times 10^{-6} \text{ length}^{2.908}$  (Eq 1)

Spent: Mass ( $W_s$ ) =  $2.568 \times 10^{-6} \text{ length}^{2.908}$  (Eq 2)

$W_s/W_g = 0.661$  i.e. 34% mass loss at spawning

Average mass loss as a function of length:

$W_g - W_s = 1.3158 \times 10^{-6} \text{ length}^{2.908}$

Wet mass/length relationships

Gravid: Mass ( $W_g$ ) =  $7.3351 \times 10^{-6} \text{ length}^{3.078}$  (Eq 3)

Spent: Mass ( $W_s$ ) =  $6.056 \times 10^{-6} \text{ length}^{3.078}$  (Eq 4)

$W_s/W_g = 0.826$  i.e. 17% mass loss at spawning

Average mass loss as a function of length:

$W_g - W_s = 1.2785 \times 10^{-6} \text{ length}^{3.078}$

Female krill spawned an average of 1914 eggs during the experiments in the 1991 season (range 171–4845), and the mean length of the females which spawned was 50.22 mm (Fig. 3). There was a poor relationship between the length of the females and the number of eggs spawned, although this may merely reflect the small size range of gravid females found in these two studies when compared to other studies.

The energy content of gravid females was significantly higher than that of spent females (Fisher PLSD = 1.46) and the energy content of ovarian tissue was significantly higher than that of whole gravid females (Fisher PLSD = 1.37) (Table III).

*Energetic cost of spawning in Euphausia superba*

Two sets of measurements were used to determine the amount of energy contained in a single spawning episode. One was

**Table III.** Energetic content of gravid female krill, spent female krill and excised krill ovarian tissue.

	Gravid females	Spent females	Ovarian tissue
Sample size	13	5	5
Mean energy content (J mg <sup>-1</sup> )	23.11	21.38	25.81
sd	1.049	1.971	1.472

ANOVA: Energy content of spent and gravid females and ovarian tissue

Source	DF	Sum of squares	Mean square	F-Test
Between groups	2	57.52	28.76	16.122
Within groups	21	37.46	1.78	$P = 0.0001$
Total	23	94.98		

Model II estimate of between component variance = 3.74.

based on the mean mass of spent and gravid females and the energy content of ovarian tissue, and the other used the energy content of spent and gravid females.

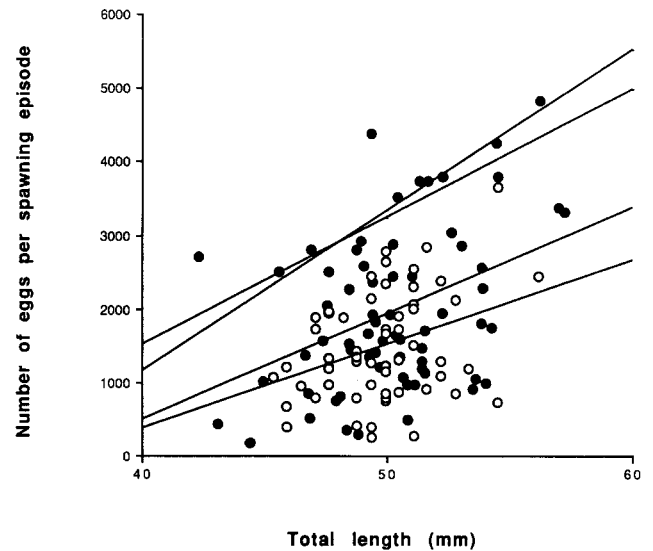
1) Energetic cost derived from mass differences:

Three interpretations of the data have been used in arriving at the energetic cost of spawning derived from mass differences.

- a. Measured mass difference assuming that the differences in size between the spent and gravid krill is a product of the spawning process, and is not indicative of two different populations being sampled. Using just the measured mean dry mass, the mass difference between gravid females and spent females is 150 mg. The mean energy content of the ovary is 25.81 J mg<sup>-1</sup> (Table III). If all the mass difference observed is assumed to be ovarian tissue then the mean energy lost as eggs during a single spawning episode is 3871 J.
- b. Predicted mass difference assuming that the differences in size between the spent and gravid krill is a product of the spawning process, and is not indicative of two different populations being sampled. The predicted dry mass difference (from equations 1 and 2) between a 50 mm gravid and a 47.91 mm spent *E. superba* is 141 mg. If all the mass difference observed is assumed to be ovarian tissue then the energy lost as eggs during a single spawning episode is 3642 J.
- c. Predicted mass difference assuming that the difference in length between the two samples indicates significant differences in the mean size of the samples of gravid and spawning females. The predicted dry mass difference (from equations 1 and 2) between a 50 mm gravid and a 50 mm spent *E. superba* is 115 mg. The mean energy content of the ovary is 25.81 J mg<sup>-1</sup> (Table III). If all the mass difference observed is assumed to be ovarian tissue then the energy lost as eggs during a single spawning episode is 2968 J.

2) Energetic cost derived from energy values:

The mean energy difference between gravid and spent *E. superba* is 1.773 J mg<sup>-1</sup>. A gravid krill of mean dry mass



**Fig. 3.** The relationship between the body length of spawning females and the number of eggs produced. Data from this present study (1991 data) are compared to those from an earlier study (1988 data, Nicol 1989) and to regressions obtained from two previous studies (Ross & Quetin 1983 and Harrington & Ikeda 1983). ●  $y = -5293.1 + 144.84 x$ ,  $r^2 = 0.163$  (1991 data); ○  $y = -4198.7 + 114.26 x$ ,  $r^2 = 0.114$  (1988 data);  $y = -7597.0 + 219.00 x$  (Ross & Quetin 1983);  $y = -5492.0 + 175.00 x$  (Harrington & Ikeda 1986).

349 mg would contain 8065.4 J of energy and a spent krill of mean dry mass 199 mg would contain 4246.06 J. The energy difference between average sized gravid and spent krill would thus be 3819.34 J.

## Discussion

Female *E. superba* in this study lost a significant amount of mass and energy at spawning. The proportional amount of mass lost, expressed either as wet or dry mass, remained constant with length and there is some suggestion that the length of female krill may change as a result of the spawning process.

The krill that spawned were large females with a restricted size range and showed a poor relationship between size and the number of eggs spawned in one episode. Such a poor relationship has been shown in an earlier study from this region (Nicol 1989). Spawning females used in some other studies have shown a much clearer relationship between size of the female and the number of eggs spawned but these have used much wider ranges of female sizes (e.g. 36–57 mm Ross & Quetin 1983). The mean number of eggs spawned (1914) in this study is higher than the mean number of eggs (1495) found in a previous study from this region (Nicol 1987). Earlier studies (Ross & Quetin 1983 and Harrington & Ikeda 1988) appear to show a relationship indicating an increase in spawning capacity with length. This finding could result from a number of factors, but the relationship

between spawning capacity and environmental features, such as season and area, has not yet been examined.

Our measured values for the energetic content of whole krill are similar to those obtained by others using a variety of techniques, different developmental stages, both sexes, dissected tissue and different species. Chekunova & Rynkova (1975) reported measured energetic values of adult krill of 20.96–23.05 J mg<sup>-1</sup> dry mass (converted from calories g<sup>-1</sup>). Clarke (1980) reported energy values for *E. superba* of 3.8 J mg<sup>-1</sup> fresh mass (males), 5.45 J mg<sup>-1</sup> fresh mass (gravid females) based on analysis of the biochemical composition, which are equivalent to 19.64 J mg<sup>-1</sup> dry mass (males) and 24.73 J mg<sup>-1</sup> dry mass (gravid females). Clarke & Morris (1983) used similar calculations to arrive at a calorific value for ovarian tissue of 6.11 kJ g<sup>-1</sup> fresh mass which is equivalent to 21.94 kJ g<sup>-1</sup> dry mass, slightly lower than our measured values of 25.8 kJ g<sup>-1</sup> dry mass. Kulka & Corey (1982) report a figure for whole *Meganyctiphanes norvegica* of 4.7 kcal g<sup>-1</sup> which is equivalent to 19.7 J mg<sup>-1</sup>.

The two methods used to calculate the energetic cost of a single spawning episode arrive at figures of between 3.0 and 3.8 kJ. Clarke & Morris (1983, table 7) in their energy budget for *E. superba*, provide figures for calculated mass and energy losses associated with spawning based on composition data in Clarke (1980). Using their calculations, a 1.28 g wet mass gravid female *E. superba*, the mean value for our study, would lose 577.3 mg of ovarian tissue — nearly twice our predicted value of 252 mg. Their calculations suggest that a 1.28 g female krill experiences an energy loss of 3.47 kJ at spawning. This is similar to our figures of 3.0–3.8 kJ. However, Clarke & Morris

used the mass of a whole ovary in their calculations. At spawning, the entire ovary is not spawned at one time; a spent female still has a number of small and some mature oocytes left in the ovary which will either mature to form the next batch of eggs or will be resorbed (Cuzin-Roudy 1987). So their calculated loss based on the mass of the whole ovary may have been overestimated. This is compensated for somewhat by the higher energetic values that we measured for ovarian tissue, so the total energy loss at spawning is similar for the two types of estimation.

A single batch of eggs spawned by an average sized female *E. superba* in this study contains up to 3.8 kJ of accumulated energy. How long might it take a spent krill to assimilate this amount of energy and thus how many times in a season might a female krill spawn? Making a number of simplistic assumptions, it is possible to examine the length of time that it would take for an individual krill to filter enough phytoplankton from the water to invest 3.8 kJ in the ovary at the same time as meeting all other metabolic demands.

By assuming that the energy expended in spawning a batch of eggs (3.8 kJ) is only a fraction of the energy required over the period and that other energy demands consume 86 J day<sup>-1</sup> (Clarke & Morris 1983), using a calorific value for phytoplankton of 47.73 J mg C<sup>-1</sup> (Platt & Irwin 1973) and a representative carbon: chlorophyll ratio of 50:1, it is possible to examine what filtration rates and phytoplankton concentrations might be necessary to produce a batch of eggs in selected time periods: 7 days, 30 days or 90 days (Fig. 4).

Phytoplankton concentrations reported from Southern Ocean waters range between 0.1–1.0 µg chlorophyll *a* l<sup>-1</sup> with a mean value of 0.5 (El-Sayed 1988) and the filtration rates required to take in sufficient energy for egg production at even the minimal rate (one batch every 90 days) at these concentrations are greater than 2 l h<sup>-1</sup>. To produce one batch of eggs a week at average phytoplankton concentrations would require filtration rates of greater than 20 l h<sup>-1</sup>. These estimates, based on krill filtering continuously with a 100% assimilation efficiency, must be considered as under-estimates.

Ross & Quetin (1986) examined the phytoplankton intake necessary to support egg production over a spawning season using a number of assumptions. They used slightly different parameters compared to our approach viz. a 40 mm total length female which produces 1340 eggs per spawning episode, with seven spawning episodes over 84 days. In comparison, our female krill averaged 50.2 mm and laid an average of 1914 eggs per spawning episode. They estimated a chlorophyll intake of 326 µg of chlorophyll *a* per day to maintain their estimated egg production rate for the spawning season. Converting their values to J, the energetic cost per batch of eggs is 914.5 J assuming 1340 eggs are laid. Their energetic calculations assume that each egg represents 163 × 10<sup>-6</sup> kcal (0.6824 J). Using this figure and our measured batch size (1914 eggs per spawning episode) gives an energetic cost of 1.3 kJ per spawning episode — approximately one third of our measured value. Ross & Quetin (1986) concluded that the filtration rate of krill must be higher than has been generally estimated and suggested that

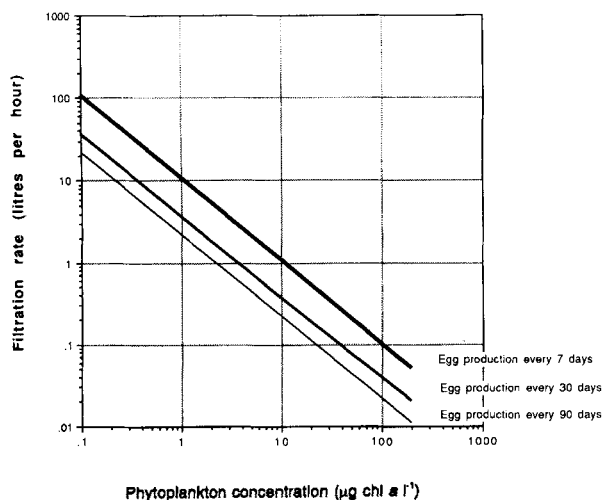


Fig. 4. The relationship between the phytoplankton concentration in the water and the filtration rate of krill required for three egg production rates. These are based on the production of a batch of eggs every 7 days, every 30 days and in 90 days, and assume the energy cost is equivalent to the cost of spawning (3.8 kJ) plus the routine metabolic costs (86 J day<sup>-1</sup>). For details of calculations, see text.



a figure of 3.6 l h<sup>-1</sup> was not unrealistic. Furthermore, they suggested that krill require high average phytoplankton concentrations (c. 1–5 µg chlorophyll *a* l<sup>-1</sup>) and may only be able to reproduce in areas where food is abundant. Our higher results tend to reinforce these conclusions.

Clarke *et al.* (1988) suggested, from measurements of faecal production rates, that *E. superba* can have an energy intake of 20% body carbon per day. If krill are able to maintain such a high energy intake rate and incorporate the energy into ovarian tissue, then spawning events could follow each other relatively rapidly. This carbon intake rate would, however, require that krill be able to feed at a far greater rate than has generally been supposed.

Most estimates of krill filtration rates are below 1 l h<sup>-1</sup> (see Morris 1984 for review) and if these are correct, it is very difficult to see how *E. superba* can produce more than one batch of eggs in a season even at the most optimistic phytoplankton concentrations. More recent experimental studies (see Price *et al.* 1988 and Quetin *et al.* 1993 for a review) suggest that earlier investigations into feeding rates were flawed and that higher rates of filtration (up to 4 l h<sup>-1</sup>) are likely to be more realistic. Nevertheless, even higher food intake rates would be necessary to produce multiple spawning in Antarctic krill at average phytoplankton concentrations and these higher rates have only been inferred from energetic calculations, such as those presented here, or from indirect measures of food intake such as faecal egestion rates (Clarke *et al.* 1988).

If female Antarctic krill do lay more than one batch of eggs per season then they require efficient mechanisms for detecting and ingesting large quantities of food. Current methodologies for examining the rate of feeding of krill have been unable to demonstrate these mechanisms although there have been hints that euphausiid feeding behaviour is more complex than was at first supposed (Hamner 1988). It is unlikely that refinement of the energy budget of krill will occur until more realistic estimates of field feeding rates are obtained.

The peak of spawning activity by *E. superba* is during January–February whereas phytoplankton levels are maximal in late spring–early summer (Siegel 1985). This would suggest that either krill require a long build-up period before a prolonged egg laying period commences or that each bout of spawning requires an input of food energy that can only be obtained by intensive feeding over a long period. Given the results of the calculations presented here it would seem unlikely that female krill would be able to maintain sustained energy intake rates sufficient to produce a batch of eggs *de novo* on the time scale of 6.7 days as suggested by Ross & Quetin (1983). Since gravid female krill appear to lose up to 54% of their lipid on spawning (Clarke 1980) spent female krill may have some energy reserves which could be used to produce a mature ovary more rapidly than can be calculated from simple ingestion rates. Clarke's (1980) figures for male energy content (19.64 J mg<sup>-1</sup>) are some 9% lower than our figures for spent females (21.38 J mg<sup>-1</sup>). This may indicate that, even in spent females, there is a reserve of energy which may be used in the rapid development of the ovary.

The difference in energy content between spent females and males (1.74 J mg<sup>-1</sup>) is similar to the difference between gravid and spent females (1.73 J mg<sup>-1</sup>) which may indicate that there are sufficient internal energy reserves in the female to allow the post-spawning ovary to develop quickly. The rate of any such development would depend on a complex combination of phytoplankton concentrations in the water, food intake rates, the speed at which lipid reserves could be mobilized and the pace of cellular development of the ovary.

Laboratory studies tend to support the idea that there is a long period during which the ovary develops in spring (Ikeda 1987). Thomas & Ikeda (1987) showed that sexual development of female krill occurred over a period of 4–5 moults (equivalent to 4–5 months at 0°C) in animals which had undergone regression of their sexual characteristics over winter. The secondary sexual characteristics developed first followed by a rapid development of oocytes over a period of less than two months. If it takes less than two months for a sexually mature female krill to produce a ripe ovary from an essentially immature ovary in the laboratory then this puts an upper time limit on the period that might be required for a spent female to produce a further batch of eggs in the wild. Unfortunately, however, no laboratory study has yet been able to demonstrate multiple spawning episodes so there are no clues available from this source about what lower limits might be set on the brood production rate of krill.

The lack of synchrony between the spawning and moulting cycles (Nicol 1989) suggests that the timing of spawning may be tied to the availability of food rather than to more endogenous cycles. This study has been unable to indicate whether multiple spawning by *E. superba* does occur but it has provided some further evidence to suggest that, if female krill spawn more than once during a season, this would require feeding rates which have not yet been demonstrated and above average phytoplankton concentrations. Histological information seems to suggest that multiple spawning does occur (Cuzin-Roudy 1987) but further observations and experimentation are necessary to determine how the required high feeding rates occur and where appropriate phytoplankton concentrations are to be found.

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