Antarctic Science 7 (4): 387–392 (1995)

# The compound eye as an indicator of age and shrinkage in Antarctic krill

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**Abstract:** Laboratory studies have shown that Antarctic krill (*Euphausia superba*) shrink if maintained in conditions of low food availability. Recent studies have also demonstrated that *E. superba* individuals may be shrinking in the field during winter. If krill shrink during the winter, conclusions reached by length-frequency analysis may be unreliable because smaller animals may not necessarily be younger animals. In this study, the correlation between the body-length and the crystalline cone number of the compound eye was examined. Samples collected in the late summer show an apparent linear relationship between crystalline cone number and body-length. From a laboratory population, it appears that when krill shrink the crystalline cone number remains relatively unchanged. If crystalline cone number is little affected by shrinking, then the crystalline cone number may be a more reliable indicator of age than body-length alone. The ratio of crystalline cone number to body-length offers a method for detecting the effect of shrinking in natural populations of krill. On the basis of the crystalline cone number count, it appears from a field collection in early spring that *E. superba* do shrink during winter.

Received 15 March 1995, accepted 11 August 1995

**Key words:** krill, age structure, shrinkage

## Introduction

Antarctic krill, *Euphausia superba* Dana, is both a keystone species in the Antarctic ecosystem and the focus of a major fishery. In the last 20 years *E. superba* has been the subject of considerable observation and experimentation. Despite this intense effort, it has not been possible to assess accurately the age structure of populations of Antarctic krill or to estimate their natural longevity (Nicol 1990).

The traditional method of estimating the age of Antarctic krill is to measure the size of the krill, and to recognize peaks in the resultant length-frequency distributions as year classes (Marr 1962, Ivanov 1970, Mackintosh 1972, Siegel 1987, Hosie *et al.* 1988, Pakhomov 1995). These studies have relied upon there being a predictable relationship between the length of krill and their age. Laboratory studies, however, have shown that when starved, individual Antarctic krill continue to moult regularly and thus shrink in length to a smaller overall body size (Ikeda & Dixon 1982). Additionally, a population of krill maintained in an aquarium in sub-optimal food conditions showed a decrease in mean size over a period of a year (Nicol *et al.* 1991). Animals taken directly from the wild during summer and subjected to food deprivation exhibit shrinking within a single moult cycle (Quetin & Ross 1991, Nicol *et al.* 1992). Krill can even lose their sexual characteristics at the end of summer, and after a number of moults again resemble year-two juveniles with no indication that they were once adults (McWhinnie & Denys 1980, Thomas & Ikeda 1987). If krill indeed shrink during the winter in nature, conclusions reached by length-frequency analysis alone may be suspect. Because krill can increase or decrease in size, depending on food conditions, there need not be a simple relationship between size and age.

Ettershank (1984) suggested that the solution of the age problem may lie in the measurement of fluorescent pigments which accumulate with age. Some success has been achieved in using measurements of age pigments to indicate age differences in a population of krill (Nicol *et al.* 1991) but a number of methodological and technical problems have delayed the widespread application of this technique (Nicol 1987). More sophisticated quantification techniques for the age pigment lipofuscin have yielded promising results for other species of crustaceans (Sheehy *et al.* 1994) but have not yet been applied to *E. superba.*

The studies in this paper examine the possibility that the compound eyes of krill may be used to determine their age. The eyes of euphausiids are prominent features. The nauplius eye of euphausiids consists of nine cells. From the furcilia stage, the compound eyes have fully developed and projected beyond the sides of the carapace. The adult *E. superba* has two well-developed compound eyes which are covered by a network of hexagonal facets, giving them the appearance of a honeycomb with a curved surface, composed of many individual ommatidia (Mauchline & Fisher 1969, Denys *et al.* 1983). The dioptric element consists of the cornea and a bipartite bullet-shaped crystalline cone. The crystalline cones of the eye are intracellularly secreted by the crystalline cone cells and connected to neural cells and the visual processing network (Denys *et al.* 1983, Meyer-Rochow &

Walsh 1978). Consequently, it seems likely that even if an animal were to shrink the crystalline cones and their neural connections would not be lost. If the crystalline cone number remains constant when a krill shrinks, this may be a more reliable indicator of the age of the krill than its length. This paper reports the first part of an investigation into the possible relationship between the crystalline cone number and the age of the krill.

## Materials and methods

Materials examined in this experiment include both fresh krill and preserved specimens. The preserved krill were collected between 24 January and 7 February 1993 during summer in Prydz Bay. Sampling stations were located at: 64°59.84'S, 68°59.4'E; 65°00.64'S, 65°57,03'E; 65°02.11'S 67°29.9'E; 65°58.62'S, 59°59.01'E; 65°54.91'S, 61°32.49'E; 66°16.56'S, 68°58.3'E; 66°27.56'S, 77°39.48'E; 66°29.93'S, 73°29.41'E; 66°59.56'S, 73°29.2'E. 28. Specimens were also collected in spring on 22 November 1982 in Prydz Bay at 62°56.9'S, 84°41.1'E.

Two large samples were collected on 22 February 1992 and 19 March 1992 at 64°59.99'S, 77°39.85'E and 63°45.6'S, 105°10.9'E respectively. They were maintained in an aquarium under constant conditions at 0°C. A sample of the population was removed in July 1993 and the animals were preserved in commercial formalin for later analysis.

Two-hundred and seventy-eight preserved specimens and 60 aquarium-kept krill were examined. The aquarium-kept krill had been kept in low-food conditions, and were known to be shrinking. Unfortunately, length measurements were not available for individual krill, but the mean length of the samples at the time of collection for the aquarium was calculated. All the krill examined were mature females or juveniles.

The body length was measured from the tip of the rostrum to the tip of the uropod (standard 1 measurement; Mauchline 1980). The left compound eye was severed from the krill and the exoskeleton and the soft tissue were removed under a dissecting microscope. The remains of the eye, containing the crystalline cones, were placed in a 1.5 ml centrifuge tube with 0.8 ml fresh water and split by ultrasonic vibration at 400 W for 2 min. 0.5 ml of 100% alcohol was added, and the contents thoroughly mixed. The solution was poured into a 37 mm diameter glass dish with 3 ml fresh water. The crystalline cones settled to the bottom of the dish, where they could be counted under a microscope. Crystalline cones in 20 3.5 × 5 mm rectangles were counted using an image analysis system, and the total count estimated by extrapolation. The area of the 20 rectangles was 31.9% of the total area of the bottom of the glass dish. Tests using a known number of crystalline cones showed that cones were neither destroyed by ensonification nor lost in the transfer to the glass dish.

## Results

The 250 krill from the high summer field samples were selected to give approximately equal numbers within each length interval. Thus, these were not a random sample from the population. The aim was to determine the relationship between crystalline cone number and body length. At this time of season, all the krill should have experienced substantial

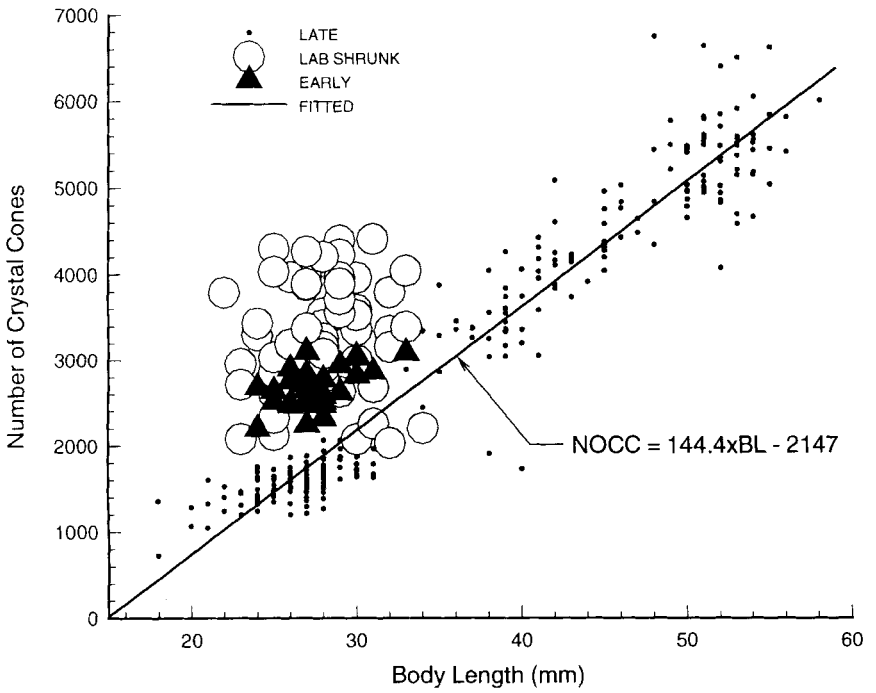


**Fig. 1.** Relationship between body-length and the number of crystalline cones in the compound eye of the Antarctic krill for samples collected in high summer (late), which is a period of rapid growth, and for a sample which has been kept in an aquarium (lab shrunk), which leads to shrinking, and a sample collected in spring (early), when the effects of shrinking over winter may still be present.

https://doi.org/10.1017/S0954102095000538 Published online by Cambridge University Press

growth, and even if animals do shrink during winter, they should have substantially re-grown by late summer. Fig. 1 shows that the relationship is approximately linear, and so the following function was fitted to the data:

$$N = \alpha + \beta L$$

where $N$ is the crystalline cones number, L is the body length, $\alpha$ and $\beta$ are constants estimated by simple linear regression. The following estimates were obtained:

| | | |
|---|---|---|
| $\alpha$ | = -2147 | SE = 86.2 |
| $\beta$ | = 144.4 | SE = 2.3 |
| $r^2$ | = 0.936 | |

If length is considered to be a proximate measure for age, then high correlation between body length and the crystalline cone number means that the latter can also be considered a proximate measure for age. The apparent linear relationship between crystalline cone number and body length implies that the size of the eye, or the size of the crystalline cones, or both, are related to body length.

If the eye is modelled as a truncated sphere with diameter $D$, composed of crystalline cones which are roughly cylindrical with average diameter $d$, then:

$$N \propto \left(\frac{D}{d}\right)^2$$

Forty-eight krill from the same late summer collection were measured for body length and diameter of eye. The mean diameter of the crystalline cones was determined from a sample of 50 cones from each animal. Inspection of these data indicated a linear relationship between $D$ and $L$, *i.e.*

$$D = \gamma + \eta L$$

A linear regression gave the following parameter estimates:

| | | |
|---|---|---|
| g | = -0.1450 | SE = 0.07756 |
| h | = 0.04963 | SE = 0.001897 |
| $r^2$ | = 0.936 | |

It follows from the truncated sphere model, that if both $N$ and D are proportional to $L$ then:

$$d \propto \sqrt{L}$$

This means that a regression of log $d$ against log $L$ should have a slope of 0.5. Fitting the function:

$$\log(d) = \kappa + \lambda \log(l)$$

gives:

| | | |
|---|---|---|
| k | = -5.086 | SE = 0.1105 |
| l | = 0.495 | SE = 0.03 |
| $r^2$ | = 0.851 | |

which is in good agreement with the prediction of the model. Thus, the crystalline cone number increases with body size because in growing krill, the eye diameter remains in proportion with length, but the diameter of the crystalline cones increases only as a fractional power of the body length.

To examine whether crystalline cone numbers decrease during shrinkage, counts were made from a sample of 60 krill which had been kept in the Antarctic Division's aquarium for 15 months under conditions which lead to shrinkage (Nicol *et al.* 1991). The krill were fed during this period, but not sufficiently to maintain body size. They do not seem to shrink to less than a minimum of *c.* 20 mm in length under the conditions in the aquarium.

Unfortunately, the length distribution of this particular sample at capture was unknown. However, a recent sample (March 1993) of krill, taken at a similar time of year and place to the first sample, were kept in the aquarium for a period of nine months under the same basic regimen as the sample whose crystalline cones were counted. The length distributions at capture and after nine months in the aquarium are shown in Fig. 2 for the 1993 sample. There is clear evidence of shrinking in this sample, with the mean length declining from 45–29 mm ($P$<0.001). The near absence of overlap in the two length distributions shown in Fig. 2 precludes size related mortality as a substantial contributor to the shift in the length distribution. Moreover, there is little mortality of krill in the aquarium (typically 0.6% per month). These observations confirm that the conditions under which krill are kept in the aquarium leads to shrinking, at least for larger krill.

The crystalline cone number versus body length for the sample of laboratory shrunk krill are shown in Fig. 1 as large circles. A multiple regression model was used to test the significance of the observed differences in the intercepts and slopes of the regression lines fitted to the two samples. The

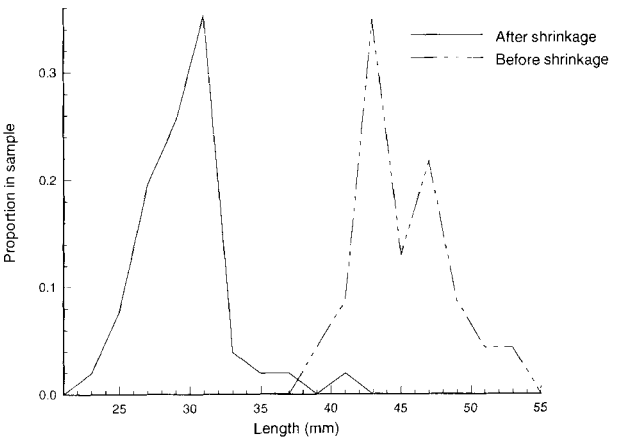


**Fig. 2.** Length distributions of samples at capture (before shrinkage) and after maintenance in the aquarium (after shrinkage).

https://doi.org/10.1017/S0954102095000538 Published online by Cambridge University Press

**Table I.** ANOVA for differences between late field and laboratory shrunk samples.

| Source of variation | Sum of squares | Degrees of freedom | Mean square | F ratio |
|---|---|---|---|---|
| Body length | 1796348 | 1 | 1796348 | 2807** |
| Lab kept \| Body length | 252695 | 1 | 252695 | 395** |
| Interaction | 21044 | 1 | 21044 | 32.9** |
| Error | 213706 | 334 | 639.8 | |
| Total | 2283793 | 337 | | |
| $r^2 = 0.906$ | | | | |

**Table II.** ANOVA for differences between early and late field samples.

| Source of variation | Sum of squares | Degrees of freedom | Mean square | F ratio |
|---|---|---|---|---|
| Body length | 2237396 | 1 | 2237396 | 4180** |
| Early vs Late \| Body length | 57983 | 1 | 57983 | 108** |
| Interaction | 2061 | 1 | 2061 | 3.85 |
| Error | 161640 | 302 | 535.2 | |
| Total | 2459080 | 305 | | |
| $r^2 = 0.934$ | | | | |

ANOVA given in Table I shows that both the slopes and the intercepts are significantly different at the $P<0.001$ level.

It is clear that the crystalline cone numbers for the laboratory shrunk sample are significantly greater than for the late summer field samples at the same body length. This result supports the hypothesis that crystalline cone numbers do not decline as animals shrink (or if they do, they do so at a lesser rate).

Given this result we analysed the only sample we had in our preserved collection of krill taken in spring (November), very soon after the retreat of the sea ice, when it would be expected that the effects of any natural shrinking would still be present. If the sample had shrunk, we would expect to see the crystalline cone number from the early field sample at a given length lying above the scatter of points from the late field sample. The results from the 28 specimens for the early field samples are shown in Fig. 1 as large solid triangles. An ANOVA comparing these data with the late field sample is shown in Table II.

The difference between the slopes of separate regressions (the interaction) is not quite statistically significant at the $\alpha = 0.05$ level ($P[F>3.85] = 0.0506$). However, the key result is that there is a significant difference between the mean crystalline cone number from the two samples, after correcting for length (the analysis of covariance derived from Table II gives $F = 107.3_{1,303;} P<0.001$).

## Discussion

The mean crystalline cone number, corrected for length, is higher in a laboratory-shrunk sample of krill than in a sample collected in late summer, which would have experienced an extended period of growth. The mean crystalline cone number, corrected for length, is also higher in a sample of krill collected in spring, which is likely to have experienced food limitation over winter, than for the sample collected in late summer. The relative similarity of the lab shrunk and early field samples leads us to conclude that over-winter shrinking of the field sample is the most likely mechanism explaining these observations. The prospect that the crystalline cone number appear to be relatively unaffected by shrinking indicates that they may be a more reliable indicator of age than that obtained from length data alone. At a minimum, the ratio of crystalline cone number to body-length offers a method for detecting the effect of shrinking in natural populations of krill. One important practical outcome of this method is that it appears possible to use the crystalline cone number to distinguish older krill from new recruits. This is sufficient information to estimate the key parameters of recruitment and mortality using methods similar to those given in de la Mare (1994a, 1994b).

Five species of euphausiids have been shown to shrink in the laboratory: *Euphausia pacifica* (Lasker 1966), *E. superba* (Ikeda & Dixon 1982), *Meganyctiphanes norvegica* (Buchholz 1985), *Thysanoessa inermis* (Dalpadado & Ikeda 1989), *Nyctiphanes australis* (Hosie & Ritz 1989). Field studies which have used the "instantaneous growth rate" technique have shown that *E. superba* shrink in winter (Quetin & Ross 1991) and, in some cases, in summer too (Nicol *et al.* 1992). These results cannot be considered unequivocal evidence of natural shrinkage because this technique involves some (minimal) experimental manipulation and caution should be exercised when applying laboratory results to the field situation (Buchholz 1991). However, these studies also yield growth rates in summer which are comparable to other estimates so their utility in providing reliable growth rates has been demonstrated. Field studies which have sampled krill populations throughout the year are rare but the one notable example of this type of study did result in some evidence of a decrease in mean size of the population though the authors did not consider this as evidence of shrinkage (McClatchie *et al.* 1991). Other studies have reported demographic information for Antarctic krill from various regions of the Antarctic based on length frequency information (Siegel 1987, Hosie *et al.* 1988, Pakhomov 1995). Interpretation of growth rates derived from this information is confounded by uncertainty about whether the same population has been sampled on each occasion.

Several studies of the seasonal population biology of temperate euphausiids have been conducted in enclosed seas or fjords, in which the same population can be sampled repeatedly. Such studies, using length frequency analysis, have revealed apparent winter shrinkage in particular size classes or in whole populations (Hollingshead & Corey 1974, Kulka & Corey 1978, Hopkins *et al.* 1984, Falk-Petersen 1985, Astthorsson 1990, Bollens *et al.* 1992). The

observed decrease in mean sizes of these populations has alternatively been attributed to over winter mortality amongst the older (larger) animals.

Krill occur in an environment where food is patchy and summer growth rates, estimated using the "instantaneous growth rate" technique, both of individuals and of populations, have been shown to be quite variable (Nicol *et al.* 1992). There is, therefore, no expectation that all populations of krill sampled from diverse locations in similar seasons would exhibit similar growth rates. There is still considerable debate over the ways in which Antarctic krill survive winter, with authors suggesting a range of possible mechanisms: a change to a carnivorous diet (Huntley & Nordhausen 1995), lowered metabolism (Quetin *et al.* 1994), starvation (Ikeda & Dixon 1982), a hyperbenthic existence (Kawaguchi *et al.* 1986), a summer-like pelagic existence (Nordhausen 1994, Zhou *et al.* 1994) and utilization of the under ice habitat (Marschall 1988). There is direct evidence for all of these behaviours occurring in certain instances, and it would be unlikely that all of these strategies would yield similar growth rates. Antarctic krill occur over a large area and the wintering behaviour of certain populations of krill are bound to be different from others. For example, krill around South Georgia live in an ice free environment all year and therefore could not utilize the under ice habitat in winter, whereas krill in the Weddell Sea rarely experience ice-free conditions. Evidence for winter growth from one area, therefore, cannot be taken to indicate that continuous growth occurs in all populations of Antarctic krill throughout the range and a similar statement can also be made for shrinkage. There are very few measurements of any rate processes of krill from the winter and it is thus difficult to make generalizations about the ways in which they survive the winter. There are obviously a number of ways in which the population of Antarctic krill utilises its overall habitat during winter; the relative importance of each of these ways is yet to be determined.

The results of this study suggest that *E. superba* shrink in length during winter and that such shrinkage can be detected through the relationship between the number of crystalline cones in the compound eye and the body length. The utility of measures of eye size to examine age structure and recruitment in *E. superba* requires further experimentation. These experiments should examine the effects of sexual dimorphism in eye size between males and females (Makarov & Denys 1980). Studies also should examine the critical question of whether the number of crystalline cones begins to increase immediately at the onset of growth following a period of shrinkage or whether the number only begins to increase once the original body length has been regained. This latter point will be critical if the number of crystalline cones is to be used as an indicator of age for demographic studies.

## Acknowledgements

We are grateful to the Australian Antarctic Foundation for providing additional financial support for Sun Song during his time, as a visiting scientist, at the Australian Antarctic Division. We are also grateful to Jon Watkins and an anonymous reviewer for helpful comments on the draft manuscript.

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