

Analyses of field moult data: prediction of intermoult period and assessment of seasonal growth in Antarctic krill, *Euphausia superba* Dana

FRIEDRICH BUCHHOLZ¹, DAVID J. MORRIS² and JONATHAN L. WATKINS²

¹ Institut für Meereskunde Kiel, Düsternbrooker Weg 20, D-2300 Kiel, Federal Republic of Germany

² British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Abstract: A technique for moult staging Antarctic krill (*Euphausia superba* Dana) was used in the analysis of field samples to predict intermoult periods and hence assess growth and the effects of seasonal changes in food availability. The proportion of moulting krill was used, in conjunction with laboratory data on the duration of this phase, to predict the moulting frequency (intermoult period, IMP). The moulting frequency was then combined with appropriate daily growth increments from laboratory study to assess overall growth in the krill sampled. The effects of seasonal fluctuations in food availability on moulting frequency were examined for samples taken at five different locations and times of year. Moulting rate was not linearly related to the availability of phytoplankton, although it is likely that this factor has a marked effect. Similarly, although temperature affects IMP, the data indicate that this is not a simple relationship either. These preliminary data indicate the value of utilizing this technique in the analysis of field samples of Antarctic krill.

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Introduction

The moulting of Antarctic krill (*Euphausia superba* Dana) is an integral part of its growth and energetics and, as such, can provide data that will contribute to our further understanding of these two important aspects of krill biology. The ability to determine the phase of the moult cycle occupied by an animal, by a simple visual examination means that physiological data can be obtained easily without the need for complex maintenance or experimental techniques. The adaptation of the generalized crustacean moult staging system of Drach (1939) to euphausiids (Buchholz 1982) has allowed this technique to be applied to studies of moult and growth in *E. superba* in the laboratory (Buchholz 1983, 1985, Morris & Keck 1984, Cuzin-Roudy 1987, Buchholz & Buchholz 1989) and in the field (Morris & Priddle 1984, Buchholz 1985). These studies essentially concentrated upon growth and the specifics of the moult cycle, including biochemical and histological studies. Morris & Priddle (1984) did, however, present a limited interpretation of field samples taken in winter, as did Buchholz (1985) for summer. In general, physiological studies on krill in the laboratory, including moult, remain unlinked to studies of populations of krill in the field. The technique of moult staging does, however, allow field samples of krill to be analysed for a physiological parameter of direct relevance to growth without the overheads of relatively complex and time-consuming culture experiments.

In this paper, field data and the results of a laboratory

experiment on moulting and growth are synthesized in an analysis specifically directed at the possibilities of extending the application of the moult staging technique to a wider range of field samples. Data are presented from a number of field studies in which krill moult stages were determined, demonstrating the value of this technique, by predicting moulting frequency (intermoult period, IMP) and by examining differences between samples taken in summer and winter in various locations. In addition, the implications of changing moult frequencies on the growth patterns of Antarctic krill are considered. These data indicate the potential value of applying this technique to samples from a wide seasonal and geographic range.

Materials and methods

Sample collection

Summer samples of Antarctic krill were taken during three field studies (sampling sites shown in Fig. 1) as follows:

- a. FS *Meteor*. Cruise ANT III.3, 10 February–3 March 1981. Samples obtained on a transect from the northern Weddell Sea to north of Elephant Island (Klages 1982). Gear used was an RMT8+1 (Baker *et al.* 1973), mesh size 4.5 mm. The source for the associated chlorophyll data was Schneider (1983).
- b. Admiralty Bay, King George Island, 3 January–9 March 1983. Samples were obtained by RMT with a net opening of c. 2 m² and a mesh size of 6 mm. The source for associated chlorophyll data was Tokarczyk (1986).

- c. RRS *John Biscoe*. Cruise JB05, 23 February–9 March 1985. Samples obtained from near Elephant Island (Watkins *et al.* 1986) by Large Longhurst-Hardy Plankton Recorder (Bone 1986). The source for associated chlorophyll data was J. Priddle (personal communication 1988).

Winter samples of *Euphausia superba* were taken from two sampling sites (Fig. 1):

- d. Admiralty Bay, King George Island, 14 September 1984. For methods and chlorophyll data see data for summer samples taken from the same location.
- e. RRS *John Biscoe*. Cruise JB04, 13 August–18 September 1983. Samples obtained by RMT8+1. Data presented here are a subset of the krill (frozen) analysed by Morris & Priddle (1984) who presented moult assessment on the basis of exoskeleton hardness only (fresh krill). The source for associated chlorophyll data was Heywood *et al.* (1985).

A laboratory sample was collected from Admiralty Bay, King George Island, in January 1983 using a ring-trawl (1 m²) of mesh size 1 mm. Maintenance was in individual aquaria (Buchholz 1983, 1985) with daily feeding of *Chlorella* spp. (9×10^6 cells l⁻¹) i.e. high levels of food availability. Moulting stages were determined at known periods post-moult on 152 specimens, giving a mean intermoult period of 16.4 (sd ± 1.8) days.

Moult staging

Moult staging was undertaken on fresh krill according to Buchholz (1982). In the frozen material (*John Biscoe*, summer, and winter samples) it was often difficult to distinguish the first premoult stage (D0) from the intermoult stage (BC), therefore these the stages were grouped in the initial analysis. However, this difference is unimportant because in order to simplify analysis, we grouped the moult stages into three broad categories to describe the moult cycle: moult, postmoult and premoult. The moult category comprises the stages immediately before and after ecdysis (D3–4, A; see Buchholz 1982), encompassing krill actively involved in the moulting process and further distinguished by a flexible or soft integument. The postmoult category comprises stages BC and D0 whilst premoult is characterized by progressing setogenesis and development of the new cuticle (D1 and D2). An overview of criteria, abbreviations and further data are in Table I.

Calculation of moult frequency

To derive a moulting frequency or intermoult period from the proportion of krill occurring in the various moult stages it is necessary to know the duration of at least one moult

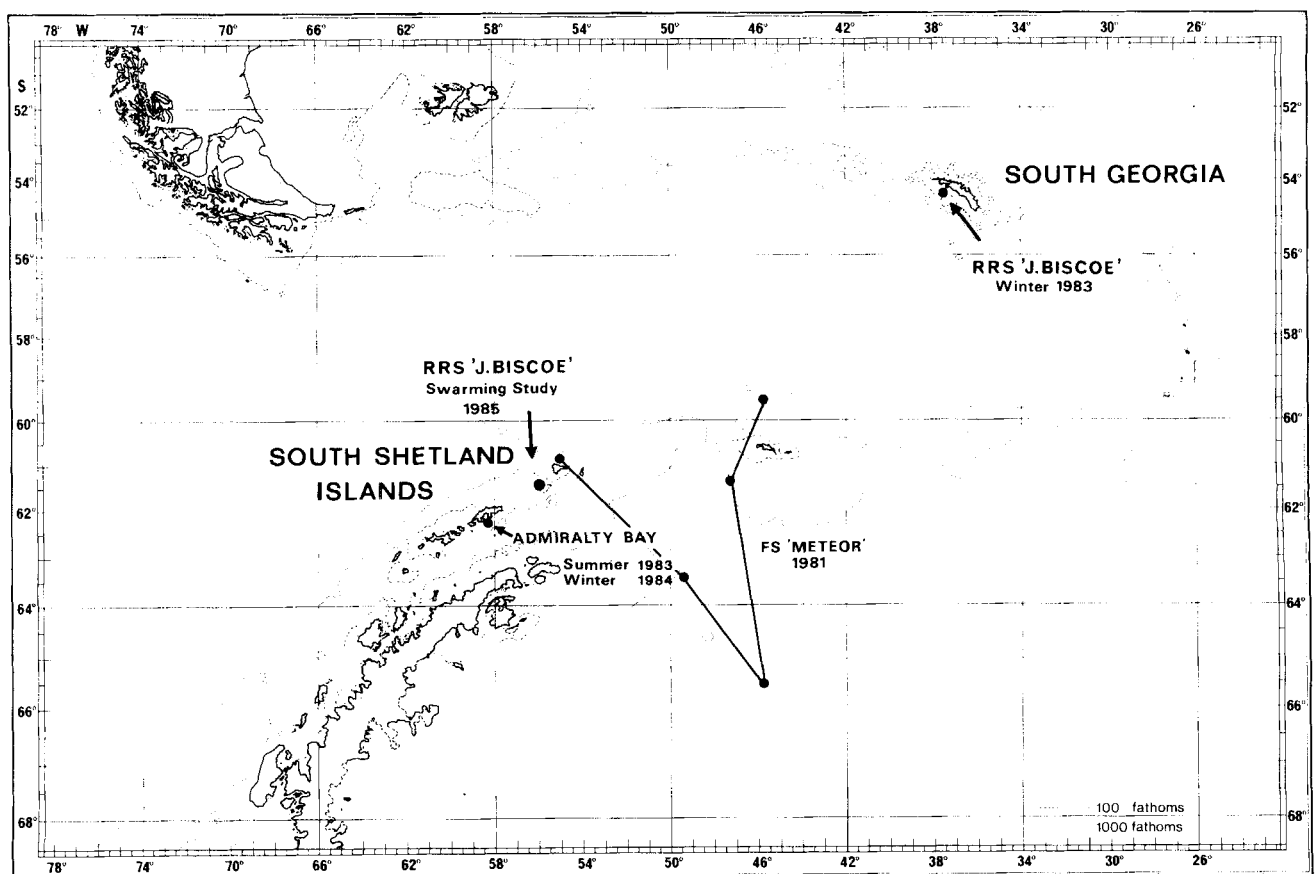


Fig. 1. Map of location of sampling stations (transect of FS *Meteor*: stations connected by line).

Table I. Nomenclature, criteria, duration and percentage of the moult cycle (aquarium) of the three main moult phases — moult, postmoult and premoult; moult stages, ref. Buchholz 1982.

Phase	Stages	Criteria	Duration days	% of moult cycle
Moult	A, D3–4	Cuticle: soft/flexible	3.2	19.6
Postmoult	BC, D0	Cuticle: hard	5.4	33.0
Premoult	D1, D2	Setogenesis Cuticle doubled	7.8	47.5

stage. For most stages this time will probably vary with season, temperature, sex, maturity, maintenance conditions and other factors to an unknown extent. However, it is less likely that those stages closely associated with ecdysis will be as variable in duration because of the disadvantages of prolonged loss of motility and increase in vulnerability this would entail. Furthermore, the complex series of events necessary to undergo ecdysis are likely to be tightly linked as the consequences of a failure or delay in the chain will result in complete failure of moult and probably death. We have assumed, therefore, that the moult stages immediately before and after ecdysis (D3–4, A) have a relatively fixed duration irrespective of the duration of all other stages. Obviously, this assumption is most accurate for the actual period of ecdysis itself, but this period lasts for the order of a minute (F. Buchholz, personal observation 1985). Because we have grouped moult stages we have extended the assumption to include stages D3–4 and A in the moult category. Thus we are assuming that the processes from final setogenesis, to the complete separation of the cuticle, reabsorption of cuticular material, ecdysis itself and the tanning of the new exoskeleton take 3.2 days, this being the mean duration observed in the laboratory. Obviously this assumption requires further testing but the data used are the best available (Buchholz 1985, unpublished data, Morris & Keck 1984). We have, furthermore, assumed that the duration of the category moult under laboratory conditions is the same as in the field and that the mean proportion of any given moult stage analysed in a large field sample reflects the average duration of this stage under those conditions present in the field.

The intermoult period (IMP) was therefore derived from:

$$\text{IMP} = 3.2 / \text{proportion of specimens in moult} \quad (1)$$

In the laboratory specimens analysed for the duration of

moult stages after a known moult, the category moult lasted for 3.2 days i.e. 19.6% of the moult cycle. The remaining categories, postmoult and premoult, occupied some 30% and 50% of the cycle respectively (Table I).

Results and discussion

Calculation of IMP

The data on the proportion of krill in each of the three moult categories and the calculated intermoult periods (IMP) were grouped by season (Table II). The calculated IMP for krill in summer varied between 7.8 and 14.7 d, whilst that for the krill in the laboratory was 16.4 d. The longer IMP agree well with previous observations (Clarke & Morris 1983) whilst the shorter estimates (approximately 8 and 10 d) indicate a very rapid progression through the moult cycle. This may have been the result of differences in temperature or food availability between the samples or result from a sampling artefact. The sensitivity of the IMP of krill to different temperatures appears, on the basis of current evidence (Clarke & Morris 1983) to be high; however, these authors point out that the available data are inadequate. Similarly, there are insufficient data on the effects of food availability on the moulting frequency of krill. Nevertheless, the calculation of a short IMP in the summer field samples from the *John Biscoe* may indicate an effect of favourable feeding conditions on krill growth. The phytoplankton biomass in the sampling area was variable but high (between 100 mg m⁻², Fig. 2, and a maximum of 400 mg m⁻², J. Priddle, personal communication 1989, see also Heywood & Priddle 1987). A sampling artefact resulting in the calculation of a short IMP is a possibility in the summer *John Biscoe* samples. Here, individual swarms were sampled and the proportion of moulting krill found to be highly variable between swarms (Morris & Watkins 1986, Watkins *et al.* 1986). These authors, Buchholz (1985) and Morris (1985) all found evidence for the occurrence of synchronous moulting in swarms of krill. It is not clear to what extent such synchronous moulting occurs in general, nor is it known whether such swarms are more susceptible to capture. What is clear is that the summer *John Biscoe* samples did contain a few swarms in which moulting or recently moulted krill predominated, possibly biasing the overall estimate of the proportion of krill in moult. Since a large number of swarms (38) with an overall

Table II. Duration of intermoult period (IMP) for the five field samples, IMP based on calculation in equation (1). Growth rate in mm d⁻¹ calculated from IMP and the size increase following moult (3.8%; 1.2 mm: laboratory data) of a standard specimen of 32 mm length.

Season	'Summer'			'Winter'	
Sample	<i>Meteor</i>	Admiralty Bay	<i>John Biscoe</i>	Admiralty Bay	<i>John Biscoe</i>
Number	465	834	2941	93	76
% in moult	21.7	30.6	41.0	6.5	5.3
IMP (d)	14.7	10.5	7.8	49.2	60.4
mm d ⁻¹	0.083	0.116	0.156	0.025	0.020

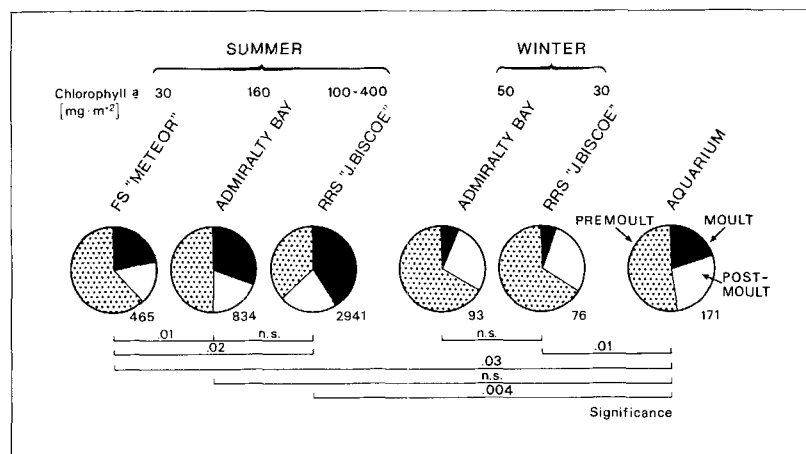


Fig. 2. Proportion of moult stages in *Euphausia superba* from different regions (see Fig. 1) and seasons. Mean phytoplankton biomass as indicated. In the aquarium study krill was fed on *Chlorella* spp. at approximately 9×10^6 cells l⁻¹. Levels of significance refer to contingency tests (χ^2 ; n.s. = not significant, $p > 0.05$). Sample size (n) as indicated below diagrams.

sample size of 3000 specimens were analysed, the extent of such a bias is considered minor. Equally, this large data set should have resulted in a good estimate of growth, despite the high variability in the proportion of moulting krill found. Nevertheless, the existence of synchronous moulting and its potential effects on sampling bias must be recognized, especially when the number of swarms sampled is low (Watkins *et al.* 1986).

The IMP data for krill in winter show, in marked contrast to those in summer, a much longer IMP, some 5 to 10 times greater than observed in summer (Table II). The results are based on a comparatively small sample size and the assumption that under low temperature conditions the moult period does not deviate substantially from 3.2 days. These winter IMP estimates are considerably in excess of those predicted by extrapolating the IMP/temperature relationship provided by Clarke & Morris (1983) to winter temperatures (30–35 °C). Note, however, that both winter data sets indicate that *E. superba* continued to moult in winter, this observation substantiating the conclusions of Morris & Priddle (1984) and Buchholz (1989). Continuation of moulting in winter does not necessarily have to imply positive growth as moulting is also a prerequisite to the possible shrinking of overwintering krill described by Ikeda & Dixon (1982). However, such shrinkage in Antarctic and other krill species (Hosie & Ritz 1989) was found only in laboratory growth studies, and may thus be a maintenance artifact. In a pelagic population of *Meganyciphanes norvegica*, body shrinkage during winter

did not occur (Buchholz 1985). The proposed method of moult staging could help to further investigate this interesting phenomenon in the field, particularly in under-ice populations.

Seasonal and geographic effects

The possible seasonal effects of changes in food availability on IMP are highlighted in Fig. 2 which compares the various proportions of krill in the three moult categories for both seasonal and geographic variation. For the three moult category distributions taken in the summer, contingency table analysis on the basis of χ^2 distributions (Sachs 1984) showed that the Admiralty Bay and *John Biscoe* samples were not significantly different whereas the *Meteor* sample was different from the others (Fig. 2). In three samples there were considerable changes in the proportion of krill in moult and premoult, whereas the proportion in postmoult showed the least variation. The longest IMP for the samples in summer was found in krill caught in an area where the ambient chlorophyll level was low (30 mg m⁻², Fig. 2) indicating that food availability may affect moult frequency. The two winter samples, with lower moulting frequencies than in summer were also obtained from areas with low ambient chlorophyll levels (Fig. 2) reinforcing the potential effects of food availability but also suggesting that temperature may alter IMP. However, for the *John Biscoe* samples in the summer the water temperature ranged from 2°C at the

Table III. Percentages of krill found in the main moult phases moult, postmoult and premoult in the aquarium sample and the five field samples

Season	'Summer'				'Winter'	
	Aquarium	<i>Meteor</i>	Admiralty Bay	<i>John Biscoe</i>	Admiralty Bay	<i>John Biscoe</i>
Number	171	465	834	2941	93	76
% in moult	20	22	31	41	7	5
% in postmoult	33	17	20	22	27	29
% in premoult	48	62	50	37	67	66

surface to 0.5°C at 200 m (Heywood & Priddle 1987) while winter water temperatures around South Georgia varied between 0.5 and 1°C (Heywood *et al.* 1985). It therefore seems unlikely that temperature alone would account for such marked changes in IMP. The two winter samples were not significantly different from each other but were significantly different from the summer and laboratory samples (Fig. 2). In the case of the winter samples, all three moult categories were similar in proportion in both samples.

An examination of the postmoult category for summer field samples (Fig. 2 and Table III) reveals a similar proportion for each sample. Although postmoult may occupy such a fixed proportion of the moult cycle (and our data are insufficient to determine this), it does not imply that postmoult is of fixed duration (Fig. 3). Here moult is shown as the fixed interval of 3.2 d. It is obvious that when the IMP increases, the duration of the postmoult and the premoult phase increase accordingly, irrespective of season. This may be seen in contrast to data on other crustaceans (e.g. Passano 1960) which indicate that a specific 'resting phase' is inserted at the end of postmoult (stage BC), when conditions for feeding become unfavourable. Such a resting phase does not exist in krill caught in summer, i.e., when phytoplankton levels are high (Buchholz & Buchholz 1989). Our data indicate that no specific moult stage is extended under winter conditions, but lengthening of both phases of post- and premoult account for the prolongation of the moult cycle.

In addition to the obvious seasonal difference between the sets of samples, some of the variation in moulting frequency may be due to geographical position. Differences between the samples may be the result of temporal (i.e. inter-annual) and spatial differences. The most obvious spatial difference would be between the krill from the Weddell Sea (*Meteor*) and the Bransfield Strait (*John Biscoe*). Particularly, hydrographic conditions differ substantially in these two areas (Siegel 1986). However, with the limited number of observations on the moult cycle of *E. superba* in the field it

is not possible to distinguish between annual and spatial variation.

Assessment of growth

The disparate nature of the samples compared precludes anything but a preliminary outline of the potential uses of the moult staging technique in analysing field samples of Antarctic krill and the discussion of a few fundamental aspects of the biology of *E. superba*. One potential use for this technique is in the refinement of assessments of growth in krill from field samples. The calculation of moulting frequency means that samples of krill can be used to predict growth in specific areas for periods from weeks through to months or even to a season. Obviously there are intimate relationships between the environmental effects on the growth of the krill, the degree of food availability and duration of the intermoult period which complicate our methodology. However, in the absence of an adequate understanding of the mechanism and rates of growth in *E. superba* (Clarke & Morris 1983), we propose a simple application of growth rate data (expressed as a % increase in body length at moult) multiplied by the calculated IMP.

An example of such a procedure is given using data from our laboratory study of the duration of moult stages. Here, the mean increase in length at moult was 1.2 mm (mean length = 32 mm, $n = 152$) or some 3.8%. Rather than divide this increment by the observed IMP to get a daily growth rate we have simply applied the increase at each moult, the number of moults in any period of interest being determined by the IMP. Thus, using the IMP for the *Meteor* sample (14.7 d) we could expect a 3.8% increase in length every fortnight. A 35 mm animal would thus be expected to grow to nearly 38 mm after a month and 41 mm after two months. In contrast, the winter *John Biscoe* sample of krill (IMP = 60.4 d) would increase, assuming positive growth in winter from 35 mm to only 36 mm in a corresponding time period. The simple example quoted takes no account of any of the complicating factors affecting moulting, such as food supply, temperature, overwinter shrinkage (Ikeda & Dixon 1982), under ice feeding on ice algae (Marschall 1988), and is considered preliminary, awaiting considerable refinement. However, the utilization of moult data can provide growth estimates now which will highlight differences in this important parameter in samples obtained from different temporal spans, geographical areas or environmental conditions.

In terms of aspects of the biology of *E. superba*, this study highlights the extreme variability of the moult cycle and growth process. The calculated IMP values vary by nearly an order of magnitude. The growth increments observed in the laboratory (3.8% per moult) are considerably less than those observed by Mauchline (1980) and Morris & Keck (1984), 7% per moult (32 mm krill) and 6% per moult (26 mm krill) respectively. However, the calculated growth

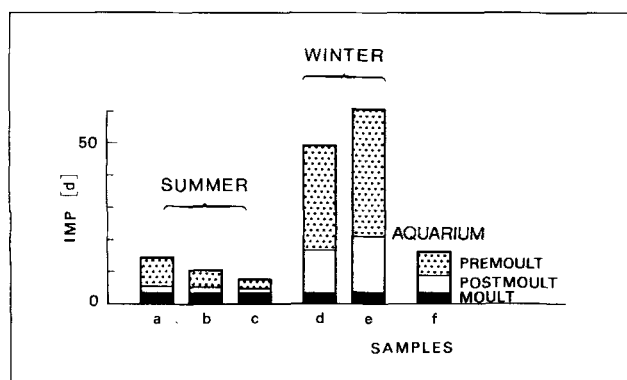


Fig. 3. Duration of intermoult period (IMP) for the five field samples, and one aquarium sample. IMP based on calculation in equation (1), i.e. Moults = 3.2 d, proportions of postmoult and premoult are converted into d accordingly.

rates of 0.083 to 0.156 mm d⁻¹ (Table II: *Meteor*, *John Biscoe*) are well within the ranges quoted by Siegel (1986) and Rosenberg *et al.* (1986), 0.07 and 0.141 mm d⁻¹ respectively.

The nature of both the biology and the study environment of Antarctic krill pose considerable problems for the experimental biologist, particularly when the process studied, in this case growth, is essentially an integration of a large number of factors. However, to be able to manage a Southern Ocean krill fishery, good estimates of growth rates are needed (Rosenberg *et al.* 1986). Growth in euphausiids of temperate regions has been estimated by following pelagic cohorts continuously (Boysen & Buchholz 1984, Stuart & Pillar 1988). However, for *E. superba* there are still considerable problems measuring growth due to the controversy over longevity of krill and the lack of agreement between rates estimated by differing techniques such as culture and cohort analysis (Siegel 1986). For Antarctic krill, the proposed approach and data presented are important because they supplement the more classical techniques and allow the investigation of the fundamentals of the krill moult cycle and growth, with particular regard to seasonality.

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References

- BAKER, A., CLARKE, M., HARRIS, M. 1973. The N.I.O. Combination Net (RMT1+8) and further developments of Rectangular Midwater Trawls. *Journal of the Marine Biological Association of the United Kingdom*, **53**, 167–184.
- BONE, D.G. 1986. An LLHPR system for adult Antarctic krill (*Euphausia superba*). *British Antarctic Survey Bulletin*, No. 73, 31–47.
- BOYSEN, E. & BUCHHOLZ, F. 1984. *Meganyctiphanes norvegica* in the Kattegat. Studies on the annual development of a pelagic population. *Marine Biology*, **79**, 195–207.
- BUCHHOLZ, F. 1982. Drach's moult staging system adapted for euphausiids. *Marine Biology*, **66**, 301–305.
- BUCHHOLZ, F. 1983. Moulting and moult physiology in krill. In SCHNACK, S.B., ed. On the biology of *Euphausia superba*. Proceedings of the Seminar Reports of the Krill Ecology Group. Bremerhaven (FRG). *Berichte zur Polarforschung Sonderheft*, **4**, 81–88.
- BUCHHOLZ, F. 1985. Moulting and growth in euphausiids. In SIEGFRIED, W.R., CONDY, P., LAWS, R.M., eds. *Antarctic nutrient cycles and food webs. Proceedings of the 4th Symposium on Antarctic Biology*. Berlin: Springer Verlag, 339–345.
- BUCHHOLZ, F. 1989. Moulting cycle and seasonal activities of chitolytic enzymes in the integument and digestive tract of the Antarctic krill, *Euphausia superba*. *Polar Biology*, **9**, 311–317.
- BUCHHOLZ, C. & BUCHHOLZ, F. 1989. Ultrastructure of the integument of a pelagic Crustacean: moult cycle related studies on the Antarctic krill, *Euphausia superba*. *Marine Biology*, **101**, 355–365.
- CLARKE, A. & MORRIS, D.J. 1983. Towards an energy budget for krill: the physiology and biochemistry of *Euphausia superba* Dana. *Polar Biology*, **2**, 69–86.
- CUZIN-ROUDY, J. 1987. Gonad history of the Antarctic krill *Euphausia superba* Dana during its breeding season. *Polar Biology*, **7**, 237–244.
- DRACH, P. 1939. Mue et cycle d'intermue chez les crustacés décapodes. *Annales d'Institut Océanographie de Monaco*, **19**, 103–391.
- HEYWOOD, R.B. & PRIDDLE, J. 1987. Retention of phytoplankton by an eddy. *Continental Shelf Research*, **7**, 937–955.
- HEYWOOD, R.B., EVERSON, I. & PRIDDLE, J. 1985. The absence of krill from the South Georgia zone, winter 1983. *Deep Sea Research*, **32**, 369–378.
- HOSIE, G.W. & RITZ, D.A. 1989. Body shrinkage in the sub-tropical euphausiid *Nyctiphanes australis* G.O. Sars. *Journal of Plankton Research*, **11**, 595–598.
- IKEDA, T. & DIXON, P. 1982. Body shrinkage as a possible over-wintering mechanism of the Antarctic krill, *Euphausia superba* Dana. *Journal of Experimental Marine Biology and Ecology*, **62**, 143–151.
- KLAGES, N. 1982. Deutsche Antarktis Expedition 1980/81 mit FS *Meteor*. *Berichte zur Polarforschung*, **2**, 29 pp.
- MARSCHALL, H.P. 1988. The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. *Polar Biology*, **9**, 129–135.
- MAUCHLINE, J. 1980. The biology of mysids and euphausiids. *Advances in Marine Biology*, **18**, 677 pp.
- MORRIS, D.J. 1985. Integrated model of moulting and feeding of Antarctic krill *Euphausia superba* off South Georgia. *Marine Ecology Progress Series*, **22**, 207–217.
- MORRIS, D. & KECK, A. 1984. The time course of the moult cycle and growth of *Euphausia superba* in the laboratory. A preliminary study. *Meeresforschung*, **30**, 94–100.
- MORRIS, D.J. & PRIDDLE, J. 1984. Observations on the feeding and moulting of the Antarctic krill, *Euphausia superba* Dana, in winter. *British Antarctic Survey Bulletin*, No. 65, 57–63.
- MORRIS, D.J. & WATKINS, J.L. 1986. Krill swarms: does proximity imply similarity? *BIOMASS Newsletter*, **8**, 6–7.
- PASSANO, L.M. 1960. Moulting and its control. In WATERMAN, T.H., ed. *The physiology of Crustacea*. London: Academic Press, **1**, 473–536.
- ROSENBERG, A.A., BEDDINGTON, J.R. & BASSON, M. 1986. Growth and longevity of krill during the first decade of pelagic whaling. *Nature*, **324**, 152–153.
- SACHS, L. 1984. *Angewandte Statistik*. Berlin: Springer Verlag, 545 pp.
- SCHNEIDER, A. 1983. *Verbreitung und Ökologie des Phytoplanktons im atlantischen Sektor der Antarktis*. Dissertation, Christian-Albrechts-Universität Kiel, 125 pp. [Unpublished.]
- SIEGEL, V. 1986. Untersuchungen zur Biologie des antarktischen Krill, *Euphausia superba*, im Bereich der Bransfield Straße und angrenzender Gebiete. *Mitteilungen des Instituts für Seefischerei*, Hamburg, **38**, 1–244.
- STUART, V. & PILLAR, S.C. 1988. Growth and production of *Euphausia lucens* in the southern Benguela Current. *Journal of Plankton Research*, **10**, 1099–1112.
- TOKARCZYK, R. 1986. Annual cycle of chlorophyll *a* in Admiralty Bay 1981–1982 (King George, South Shetlands). *Polskie Archiwum Hydrobiologii*, **33**, 177–188.
- WATKINS, J.L., MORRIS, D.J., RICKETTS, C. & PRIDDLE, J. 1986. Differences between swarms of Antarctic krill and some implications for sampling krill populations. *Marine Biology*, **93**, 137–146.