

OBSERVATIONS ON THE FEEDING AND MOULTING OF THE ANTARCTIC KRILL, *EUPHAUSIA SUPERBA* DANA, IN WINTER

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ABSTRACT. Antarctic krill (*Euphausia superba* Dana) were sampled during the latter part of the austral winter (August–September) of 1983. Levels of plant pigment in the alimentary tract and the moult stage of krill were assessed at different times and locations around South Georgia and off Elephant Island. Krill were found both to moult and to feed during the winter, with higher proportions of krill both in the intermoult phase and with empty alimentary tracts than in summer. There were fewer krill in winter in the pre-moult phase compared to summer. These data suggest a decrease in moulting activity, although the proportion of krill assessed as moulting in the later part of the sampling period approximated to that observed in summer. A smaller proportion of the krill was feeding on phytoplankton in winter than in summer. This is partly explained by a reduction in feeding activity and partly by an increase in the depth range occupied by krill. During the study period, there was an increase in the proportion of krill feeding, associated with an increase in both the depth range and biomass of the phytoplankton. The winter phytoplankton was characterized by a uniform species composition and a homogeneous vertical distribution.

INTRODUCTION

The overwintering strategy of the Antarctic krill, *Euphausia superba* Dana, has been the subject of much speculation but little study. Although Clarke (1980, in press), working with limited samples, detected only equivocal evidence for a build-up of lipid reserves in krill prior to winter, it is possible that a limited reserve of some sort could be made. Ross and Quetin (1983) report that krill are able to convert food rapidly into lipid (in the form of eggs) and this may occur after the final spawning of the summer. It is unlikely that krill will rely completely on filter feeding throughout the year, as phytoplankton standing crop and production fall drastically in the winter over most of the Southern Ocean (Hart, 1934, 1942; El-Sayed, 1967). The utilization by krill of zooplankton as a primary food source in winter has been questioned by Ikeda and Dixon (1982) on the grounds of their insufficient abundance both in summer (see Halland, 1970) and in winter (see Foxton, 1956; Hopkins, 1971). Further possibilities are detritus feeding, reported by Pavlov (1969) to occur in summer, and utilization of body tissues (Ikeda and Dixon, 1982).

Closely connected with the overwintering feeding strategy are the changes in the patterns of growth (and hence moulting). It has been suggested that growth ceases during the winter (Mauchline, 1980) and, on the basis of laboratory observations, Ikeda and Dixon (1982) have suggested that body shrinkage is a potential overwintering strategy for krill. Ikeda and Dixon maintained starved krill through a series of moults for periods of up to 211 days, during which time their size decreased by up to 56% of the initial wet weight. Such body shrinkage would explain the broadly similar size ranges of the older age classes of *E. superba* (Ettershank, 1983). Ettershank proposed that krill grow, mature, reproduce and regress in size during a single year and repeat this process for a number of years. Makarov (1975) and Mauchline (1980) indicated that krill spawn in successive years, and the occurrence of a regression in sexual

maturity after the final spawning of the season has been reported (Denys and McWhinnie, 1982; Ross and Quetin, 1983).

During the 1983 cruise of RRS *John Biscoe* in the Scotia Sea, direct observations were made on the feeding and moulting of *E. superba* in winter. These observations were limited in number and scope by the marked absence of krill in the areas surveyed but they do serve to indicate the potential for filter feeding by *E. superba* as a mechanism for surviving the winter.

MATERIALS AND METHODS

E. superba were caught from RRS *John Biscoe* using either an RMT 1+8 trawl (Roe and Shale, 1979) or a surface net deployed from the foredeck. Krill were assessed visually for the fullness of the alimentary tract and the hardness of the exoskeleton (see Morris and Ricketts, 1984). Plant pigment (chlorophyll *a* + phaeopigment) in the water and in the stomach and hepatopancreas were measured fluorometrically (UNESCO, 1980). In addition, moult stage was determined by histological examination of the uropods (Buchholz, 1982). Because of the very limited number of krill caught, samples have been pooled into four geographic localities which were sampled for periods of between one and eight days during August and September. Four nominal depth ranges were fished, given a sufficient depth of water: surface, 10–250 m, 250–500 m and 500–1000 m. The deepest range in which krill were caught is given in parentheses for each of the four geographic areas. These were:

- (1) N and NW of South Georgia (around Bird Island, 250–500 m);
- (2) N of Elephant Island (500–1000 m);
- (3) S and SW of South Georgia (~ 130 km SW to ~ 280 km S, 250–500 m);
- (4) SE of South Georgia (near Clerke Rocks, 0–110 m, bottom at 150 m).

Krill from these areas are compared with samples taken above 150 m from a patch of krill NE of South Georgia in the summer of 1982, from a maximum water depth of 220 m (Morris and Ricketts, 1984).

RESULTS

The presence or absence of food in the alimentary tract, the hardness of the exoskeleton and histological examination of the uropods can be used to deduce the proportions of krill feeding and moulting in the samples from the four geographic areas. These data are presented in Tables I and II. Table I shows the numbers of krill classified as feeding and/or moulting based upon a visual assessment of the fullness of the alimentary tract and an examination of the hardness of the exoskeleton. A more detailed analysis of the moult stages of subsamples of the krill is given in Table II. Table III shows the amounts of plant pigment in the stomachs and hepatopancreata of the krill and the concentrations of plant pigments in the seawater for each geographic location.

Moulting

North and north-west of South Georgia in August very few krill had a soft exoskeleton, a feature indicative of recent moulting (Table I). No subsample was taken for histological examination of the moult stage. Further south, off Elephant Island approximately one month later, the proportion of krill in the sample assessed as moulting was higher and comparable with the 1982 summer data (Table I). Histological examination of a subsample confirmed this increase (Table II). There was a very high proportion of krill in the intermoult phase but no krill were found in the pre-moult

Table I. Number of animals analysed for the presence or absence of food in the alimentary tract and the hardness of the exoskeleton. The proportions of krill feeding and in the moulting phase (soft exoskeleton) and the total number of krill analysed (*n*) are given; data are pooled from all depths.

Date	Location	Food Absent		Food Present		% Feeding	% Moulting	<i>n</i>
		Hard*	Soft*	Hard*	Soft*			
Winter samples (1983)								
2-10	N, NW	54	3	23	0	28.8	3.8	80
August	South Georgia							
3	N	43	8	7	0	12.1	13.8	58
September	Elephant Island							
9-11	S, SW	0	0	24	13	100.0	35.1	37
September	South Georgia							
14-18	SE	266	66	274	5	45.7	11.6	611
September	South Georgia							
Summer sample (1982)								
2-7	NE	246	573	8335	267	91.3	10.0	9421
January	South Georgia							

* Exoskeleton condition.

phase. The majority of krill in the intermoult phase was caught below 250 m whilst both the krill assessed as moulting were caught above 50 m. South and south-west of South Georgia a week later, the proportion of krill moulting was very high (Tables I and II). South-east of South Georgia the proportion of krill in the moult phase again approximated that of summer (Table I). A contrast to the samples from Elephant Island, and the small sample from south and south-west of South Georgia, the proportion of krill in the intermoult phase is lower. Furthermore, approximately half the krill in the subsample were in intermoult and half in the pre-moult phase (Table II). In summer, the ratio of krill in the intermoult phase to krill in the pre-moult phase is approximately 1:2.

Feeding

In early August, north and north-west of South Georgia, less than a third of the krill had food in the alimentary tract (Table I). All the krill caught below 250 m had an empty alimentary tract whilst over half those caught above 250 m contained food. The maximum value of plant pigment in the stomach and hepatopancreas was less than a quarter of the maximum value found in krill in summer (Table III). North of Elephant Island the proportion of krill with food in the alimentary tract was approximately half that found off South Georgia a month before. Again, all the krill caught below 250 m were empty whilst the majority of krill caught above 250 m contained food. Samples from both areas, however, consisted mainly of krill which were neither feeding nor moulting.

In the sea south and south-west of South Georgia all of the 37 krill caught and analysed were feeding (primarily at the surface at night). Plant pigment levels in the stomachs and hepatopancreata of all the krill exceeded the maximum encountered in krill in the summer (Table III). South-east of South Georgia a few days later slightly less than half of the krill were feeding (Table I). Although the proportion of krill with food in the alimentary tract is higher than in krill from north and north-west of South Georgia in August, the range of plant pigment in the animals is similar (Table III). In summer, over 90% of krill were feeding (Table I) and the maximum plant pigment content was higher (Table III).

Table II. Number of animals categorized by histological moult staging as either moulting, intermoult or pre-moult as a function of the presence or absence of food in the alimentary tract. The proportions of krill feeding and in the moulting phase in each sample and the total number of krill analysed (*n*) are given; data are pooled from all depths.

Date	Location	Food	Moult phase			% Feeding	% Moulting	<i>n</i>
			Moulting	Intermoult	Pre-moult			
Winter samples (1983)								
3 September	N Elephant Island	Absent	2	19	0	8.7	8.7	23
		Present	0	2	0			
9-11 September	S, SW South Georgia	Absent	0	0	0	100.0	55.6	9
		Present	5	4	0			
14-18 September	SE South Georgia	Absent	5	14	16	38.6	14.0	57
		Present	3	9	10			
Summer sample (1982)								
2-7 January	NE South Georgia	Absent	36	9	3	73.8	*	183
		Present	27	33	75			

* Sampling in summer was biased towards moulting krill.

Table III. Ranges of total plant pigment found in krill and in seawater; seawater samples taken from water bottle casts or the surface (*). (-) Not determined. (+) Nearest water bottle casts.

Date	Location	Range of plant pigment in animal (μg)	Range of plant pigment in water ($\mu\text{g dm}^{-3}$)	Range of % phaeopigment in water samples	Depth distribution of plant pigment	Depth range where majority of plant pigment occurs (m)	Presence of predominant phytoplankton taxa
Winter samples (1983)							
2-10 August	N, NW South Georgia	0.005-0.113 <i>n</i> = 4	0.240-0.556	26-55	Homogeneous	0-100	No
3 September	N Elephant Island	(-)	0.140-0.220	31-51	Homogeneous	0-100	No
9-11 September	S, SW South Georgia	0.688-1.940 <i>n</i> = 4	0.270-0.400(*)	19-30	(-)	(-)	(-)
14-18 September	SE South Georgia	0.026-0.177 <i>n</i> = 15	0.364-0.435(*)	20-30	(-)	(-)	(-)
	E South Georgia (+)	(-)	0.397-0.531	19-31	Homogeneous	0-160	No
Summer sample (1982)							
2-7 January	NE South Georgia	0.004-0.487 <i>n</i> = 119	0.031-2.196	14-24	Stratified	0-70	Yes

Phytoplankton

Off Bird Island in August the maximum concentration of plant pigment in the seawater was approximately a quarter of that found around South Georgia in summer. The proportion of phaeopigment in the samples from winter was often high (Table III). There was no vertical stratification of the plant pigment distribution, which was uniform down to 100 m. Phytoplankton taxa at the twenty-one stations in this area were very similar and no species predominated. A wide variety of diatoms was found in net samples from all the areas studied, including several phaeococoid *Chaetoceros* spp., *Corethron criophilum* Castracane, *Nitzschia kerguelensis* (O'Meara) Hasle, *Rhizosolenia hebetata* fo. *semispina* (Hensen) Gran, *Thalassiosira tumida* (Janisch) Hasle and *Thalassiothrix antarctica* (Schimper) Karsten. Around Elephant Island plant pigment concentrations were low (Table III) and again the vertical distribution was homogeneous down to 100 m. South and south-west of South Georgia, the range of plant pigment concentrations in the water was similar to that found off Bird Island in August. South-east of South Georgia the concentration of plant pigments remained the same. The main difference was that significant plant pigment concentrations extended much deeper, to 160 m (cf. 100 m in early August), resulting in a higher algal biomass per unit area of sea surface. Subsequent samples north-east of South Georgia some two weeks later indicated that the early stages of the phytoplankton spring increase were in progress. In the summer of 1981–82, the range of plant pigment in both krill and the seawater was much greater and the vertical distribution of plant pigment was strongly affected by the presence of a thermocline. In addition, the species composition of the phytoplankton in summer is often dominated by a few taxa, unlike the winter community where no species predominated.

DISCUSSION

Although relatively few krill were caught during the cruise, sufficient samples are available to confirm the occurrence of both feeding and moulting in *E. superba* during the winter. The range of plant pigment amounts found in those krill that were feeding was comparable with that found in summer off South Georgia (Morris and Ricketts, 1984). The total biomass of phytoplankton, as indicated by the amount of particulate chlorophyll *a* integrated over depth, was similar in winter to the lowest values obtained during the summer (December 1981–January 1982; Whitaker, personal communication) and we suggest that it is practicable for krill to feed on phytoplankton at the concentrations found in winter. Despite the presence of plant pigment in some krill, the majority of the animals sampled in water around South Georgia and Elephant Island had empty alimentary tracts, particularly early on in the study (August and early September).

The occurrence of krill with soft exoskeletons indicates that they had moulted during the winter. Some of these krill also had a moult stage normally associated in summer with intermoult, suggesting the possibility of an increase in the duration of the post-moult hardening period in winter. An empty alimentary tract in summer was a certain indication that the animal was moulting (Morris, unpublished data). In winter this was not the case, because an empty alimentary tract reflected a decrease in feeding activity *per se* rather than the emptying of the gut prior to moulting. The overall decrease in feeding was accompanied by a decrease in the proportion of krill in the pre-moult phase and an increase in the proportion of krill in the intermoult phase, compared to summer.

The data from this study of *E. superba* in winter show that at least some animals

feed on phytoplankton at winter abundances, although more than 46% of the krill analysed were 'empty' compared with less than 3% in summer. Three main features distinguished the winter phytoplankton community from that in summer: a low biomass, a homogeneous depth distribution and probably a low turnover rate. The overall biomass of phytoplankton was low, although the mean concentration of particulate plant pigment was comparable with the low end of the range of summer values. The second feature, depth distribution of phytoplankton, was radically different in comparison with the strong stratification of summer as a result of the vertically mixed, unstable water column found in winter. In most of the areas sampled during the winter, krill were caught at depths well below the zone containing the majority of the particulate plant pigment. This alone may account for the low proportion of animals containing plant pigment in the alimentary tract. The third feature differentiating the winter phytoplankton from that in summer is the likelihood of a substantially lower turnover rate. The uniform appearance of the community during most of the sampling period supports this hypothesis when contrasted with the wide variation in species composition in the same area in summer. However, even if turnover were low, we would expect krill to utilize any available resource by feeding. Microzooplankton (tintinnids and globigerinid Foraminifera) were also abundant in most phytoplankton net samples from the upper 100 m, indicating the presence of a microheterotrophic food web which may be available to krill. In addition, the increase in the depth range occupied by krill does at least give them the opportunity of utilizing zooplankton resources, such as copepods, which overwinter in deeper waters (Hopkins, 1971; Voronina, 1972, 1975). No evidence of krill feeding on zooplankton, or detritus, was seen.

The occurrence of moulting krill in winter seems to negate Mauchline's (1980) assumption of the complete cessation of growth and moulting. Unfortunately, the proportions of krill in the moult state cannot be used to predict moulting frequency because there was no random sampling of moulting individuals. This is shown by an analysis of the summer data (Morris, unpublished data) and the existence of occasional catches of krill comprising moulting animals only. The relative predominance of the intermoult phase and the absence of the pre-moult phase in early August, however, does indicate that the duration of the histologically defined intermoult phase is extended. This implies a decrease in the frequency of moulting in the winter. Clarke and Morris (1983) have emphasized the marked effect of temperature on the intermoult period, which doubles for every 2.2 deg drop, between 4 and -1°C . Such a decrease in moulting frequency could be due to a temperature-dependent increase in the relative duration of the intermoult phase or the expression of some form of equilibrium between food input and metabolic costs (maintenance metabolism).

It seems likely, therefore, that particularly towards the end of winter, *E. superba* can feed opportunistically on plant material and possibly detritus, micro- or macrozooplankton, when available. In the absence of such resources krill probably resort to the utilization of body tissue in order to fuel maintenance metabolism, e.g. in the samples in early August. Such a strategy would decrease the energetic costs of overwintering by reducing the number of times krill moult.

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