GROWTH, MOULT AND FILTERING RATE OF KRILL IN LABORATORY CONDITIONS

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Abstract: Experiments on moult frequency, growth, filtering and ingestion rates, and size selection of food particles were conducted in the Antarctic krill, *Euphausia superba*. The intermoult period ranged from 14 to 28 days, with a slight tendency that it was longer for larger specimens than for smaller ones. The dry weight proportion of the exuvium to the body varied between 4.7 and 14.1%. Carbon and nitrogen contents in the exuviae were 10.50 ± 3.22 and 1.84 ± 0.69% of the dry weight, respectively. During the rearing experiments, some krill clearly showed an increase in body length, but some showed a decrease. The most rapid growth is expressed by the regression equation $y=0.0116x+5.88$ (y: carapace length in mm, x: time in days). Growth rate expressed as an increase in body length per month was 4.5% for krill of 25 mm in length. The filtering rate increased with the increase in body dry weight, while the filtering rate per unit dry weight decreased. The filtering rates at high phytoplankton concentrations were much higher than at low concentrations. Krill ingested phytoplankton by active filter feeding when it was plentiful. If phytoplankton was scarce, the filter feeding became inactive. In this case, krill cannot compensate for their metabolic loss and thus depend on predatory feeding. Krill ingested food particles larger than 8 μm through their filter feeding when the particles were composed of various sizes, but they can also take minute particles less than 8 μm when the majority of particles in medium were smaller than 8 μm.

1. Introduction

In the Antarctic marine ecosystem, the Antarctic krill, *Euphausia superba* DANA, is one of the most important organisms because it makes up a large portion of the biomass. During the past sixty years, many studies have been made concerning the biology of krill (RUUD, 1932; FRASER, 1936; MARR, 1962) mainly in connection with food for the baleen whales. However, there is still a lack of knowledge on the growth, moulting, feeding and related physiological processes of the krill.

Because of recent improvements in biotechniques, many experimental works on live krill have been made. MACKINTOSH (1967) and CLARKE (1976) determined the moulting interval of the krill at an Antarctic experimental station. Later MURANO *et al.* (1979) and IKEDA and DIXON (1982) also made observations of the moulting in low temperature laboratories in Japan and Australia, respectively. KATO *et al.* (1979, 1982) estimated the filtering and ingestion rates of the krill.

In this paper, we report the results of the experiments on the moulting, growth, filtering and ingestion rates and size selection of food particles of the Antarctic krill. Although partial results of the experiments on moulting and growth have been reported

elsewhere (MURANO *et al.*, 1979), the present report includes more additional data. Since details of the experiments on filtering and ingestion rates were already reported (KATO *et al.*, 1982), there is no new data to add.

2. Material and Methods

2.1. Material

Live krill used in the present experiments consisted of three groups. The specimens of the first group were collected with a fish pump (Kyoei Zoki Co. Ltd., Kyoei Model 3 1/2 Type Volute Pump) in the Antarctic Ocean at about 65°49′S, 150°33′E on January 28, 1978, during the cruise of the "Fisheries Investigation of the Antarctic Krill Population" on board the T.S. UMITAKA MARU, Tokyo University of Fisheries (MURANO *et al.*, 1979). These animals were carried to Tokyo, having been maintained in an incubator at about 0°C on board the ship, and were reared under dark conditions at 0.7°C in the low temperature laboratory of the Museum of Fisheries Science, Tokyo University of Fisheries. They were used for experiments on the moulting and growth.

The specimens of the second group were captured with a KOC-A net in the Antarctic Ocean (64°28′–64°56′S, 101°51′–115°34′E) in January 1980 during the cruise of the R.V. KAIYO MARU, Fisheries Agency. They were reared in the low temperature laboratory under the same conditions as the first group, and were used for experiments on the moulting and food size selection.

The specimens of the third group were obtained either with a fish pump (Kyoei Zoki Co. Ltd., Kyoei Model 3 1/2 Type Volute Pump) at about 64°50′S, 120°00′E on January 5–6, 1981, or with a KMT–1000 net and a hand net at about 65°30′S, 150°05′E on January 27–28, during the BIOMASS/FIBEX Cruise of the T.S. UMITAKA MARU. They were used for experiments on the filtering and ingestion rates on board the ship.

2.2. Moulting and growth

Each krill isolated from the first and second groups was reared in 1-litre glass containers (12 cm in depth and 12 cm in diameter) containing about 600 m*l* of seawater which had been taken from Sagami Bay and filtered through a glassfibre filter (Whatman GF/C). Krill were principally fed on the cultured green alga, *Dunaliella tertiolecta*, and sometimes on natural plankton (predominantly consisting of diatoms) collected from Tokyo Bay. Two-thirds of the medium in the container was removed every day along with faecal pellets and excess food and was replaced with fresh medium. The experiments consisted of two series, which run from April 1978 to December 1979 for 11 specimens from the first group and from April to September 1980 for 10 individuals from the second group.

Each animal was observed daily, and the exuvium was removed when present. The relationship between the body length (from the tip of the rostrum to the distal end of the telson) and the carapace length (from the tip of the rostrum to the posterior dorsal median margin) was approximately linear and was given by the equation, $y=2.857x+2.626$, where y is the body length in mm and x is the carapace length in mm.

After moulting in September 1980 some of the krill in the second group were killed and the dry weights of their bodies and exuviae were separately measured with an elec-

tro-microbalance (Sartorius, Type 2462) after drying at about 60°C for 24 hours. Their carbon and nitrogen contents were analysed with a CHN-Corder (Yanagimoto, MT-500).

2.3. Filtering and ingestion rates

Animals used in this experiment were 15–54 mm in body length and 7–400 mg in dry weight. For measuring the filtering and ingestion rates of an individual animal, vinyl chloride bottles from 300 to 2000 m*l* in volume were used as feeding chambers according to the size of animals. The incubation was run at 0°C in an incubator for 24 hours. For mass experiments, 30 large-sized krill or 300 small-sized ones were transferred into 40-litre polyethylene buckets which were placed in the shade on the open deck of the ship for 6–9 hours. These animals were kept in media with different concentrations of phytoplankton made by adding concentrated natural phytoplankton (with 1 mm mesh net) to the natural seawater. The experiments were conducted twice by using the same krill.

Their filtering and ingestion rates were determined by measuring the decrease in chlorophyll *a* concentration in the media during incubation. GAULD's (1951) formula and PAFFENHÖFER's (1971) equation were used to calculate the filtering rate and the ingestion rate, respectively. After the experiments, the animals were dried at about 60°C for 24 hours and kept frozen on board, and their dry weight was determined after transportation to a land laboratory.

2.4. Size selection in feeding

Some specimens from the second group were used for experiments on the particle size selection in feeding. Two kinds of food were used: one was a granulated food for young fish made by Nippon Formula Feed MFG. Co. Ltd. (commercial name: artificial plankton), and the other was cultured *Dunaliella tertiolecta*. The first type of food was used for a krill of 31.2 mm in body length and the latter for two krill of 22.9 and 30.0 mm. These animals were individually maintained for 12 hours in 1-litre glass containers to which food was added. The particle size composition of the medium was measured over the range of 4.8 to 83 μm in diameter with a Coulter Counter ZB-1 (with a 200 μm aperture tube) before and after the incubation.

3. Results and Discussion

3.1. Moulting

In the first group, a total of 229 moultings occurred between April 1978 and November 1979. In the second group, 71 moultings occurred from April to September 1980. The intermoult period was obtained in 204 and 48 occasions for the first and second groups, respectively. The relationships between the intermoult period and the size of krill for the first and second groups are shown in Figs. 1 and 2, respectively. Except for five cases in the first group, the intermoult periods ranged from 14 to 28 days with mean value and standard deviation (S.D.) of 22.3 ± 2.7 and 21.3 ± 3.4 days for the first and second groups, respectively. The present values coincide with those in our previous paper (16–26 days with the mean value and S.D. of 20.9 ± 3.8 days, MURANO

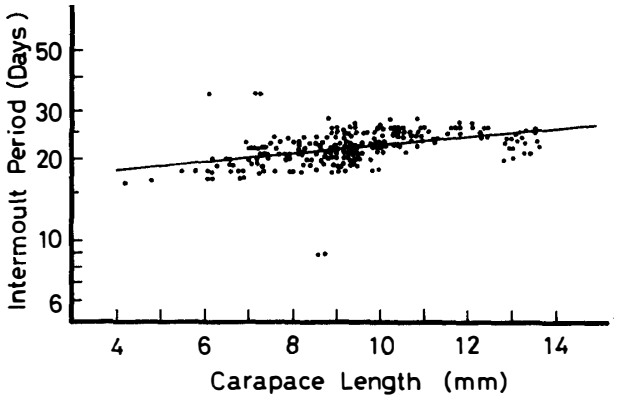

Fig. 1. Relationship between the carapace length and the intermoult period of Euphausia superba *for the first group.*

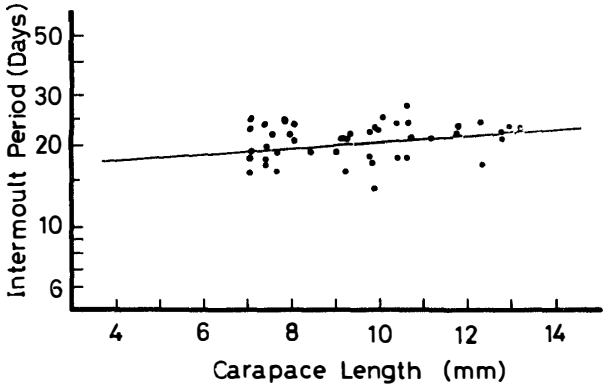

Fig. 2. Relationship between the carapace length and the intermoult period of Euphausia superba *for the second group.*

et al., 1979).

MACKINTOSH (1967) examined the intermoult period of the Antarctic krill at a temperature range of 1.4–3.5°C and obtained shorter duration by about 4 to 7 days (13.5±1.0 days) than those of the present investigation. IKEDA and DIXON (1982) also investigated the intermoult period at a temperature of $-1 \sim 0$°C using specimens from the same swarm as the second group of the present study and obtained an intermoult period of 36.8±2.3 days. They suggested that their value which was considerably greater than those obtained by MACKINTOSH (1967) and MURANO *et al.* (1979) was due to the lower maintenance temperature.

For the measurement of the first group, there was a slight tendency for the intermoult period to be longer in large-sized individuals than in small-sized ones. The regression equation is $\log y = 0.0175x + 1.1826$, where y is the intermoult period in days and x is the carapace length in mm. The coefficient of correlation of this equation is 0.5126 and the slope is significantly different from 0 at the confidence limits of 95% ($n-2=202$, $t=10.28$). However, the equation for the second group, $\log y = 0.0108x + 1.2085$, has the coefficient of correlation of 0.2758 and the slope is not different from 0 ($n-2=46$, $t=0.62$). It might be mentioned as a reason that the body range of krill in the second group (7.07–13.23 mm in carapace length) was narrow compared

with that in the first group (4.2–13.55 mm in carapace length), especially in smaller size. Since an indication that in juvenile and immature krill less than 11 mm in carapace length, the intermoult period became longer with the increase in body length is seen in Fig. 1, calculations were made again on younger krill less than 11 mm in carapace length. The new equation is $\log y = 0.0245x + 1.1226$ which resulted in a higher correlation ($r = 0.5426$).

FOWLER *et al.* (1971) observed a similar increase of the intermoult period with the increase of the body length for three species of euphausiids, *Meganyctiphanes norvegica*, *Euphausia krohnii* and *Nematoscelis megalops*. IKEDA and DIXON (1982), however, found no significant effects of the body length on the intermoult period of *Euphausia superba*. Since their specimens were composed of relatively large-sized krill, the absence of the clear relationship between the intermoult period and the body length is convincing.

The proportion of the exuvium dry weight to the body dry weight was examined in 34 exuviae cast off by 10 animals (7.07–13.25 mm in carapace length). These values ranged from 4.7 to 14.1% with a mean value and S.D. of 8.3 ± 2.3% and did not correlate with the body dry weight of krill. The present results are fairly high in comparison with the values of 2.5–3.1% reported by CLARKE (1976) and 2.6–4.4% reported by IKEDA and DIXON (1982) using the same species, but agree approximately with the values determined in other euphausiid species such as *Euphausia pacifica* (10.6%), *E. eximia* (6.4%), *E. recurva* (10.1%) and *E. gibboides* (7.7%) (JERDE and LASKER, 1966). IKEDA and DIXON (1982) reported that the mean value of specimens fed on micro-algae, *Dunaliella tertiolecta* and *Phaeodactylum tricornutum*, was significantly greater than that of specimens starved or fed on artificial pet fish food. This suggests that one of the reason for such a high percentage obtained in the present study may be due to the fact that *Dunaliella* was abundantly given as food.

Carbon and nitrogen contents of the exuviae from four measurements were 10.50 ± 3.22% and 1.84 ± 0.69% of the body dry weight, respectively. These values are considerably smaller than those measured by IKEDA and DIXON (1982) (23.76 ± 1.45% in carbon and 4.35 ± 0.54% in nitrogen). The results of four measurements of carbon and nitrogen contents in the body of krill were 47.32 ± 2.09% and 10.17 ± 0.81% of the dry weight, respectively. These values correspond very well to those determined by IKEDA and DIXON (1982) (41.1–47.5% in carbon and 9.9–11.0% in nitrogen).

From the above results loss of carbon and nitrogen by moulting was 1.40–2.43% and 1.14–1.59% of body contents, respectively, which agree well with the results of IKEDA and DIXON (1982) who reported the values of 1.4–2.3% for carbon and 1.1–1.8% for nitrogen.

3.2. Growth

The results of experiments on growth conducted during April and October 1978 have been reported previously (MURANO *et al.*, 1979). The rearing experiments continued for more than one year since then. In this paper, the results for 11 animals are shown in Fig. 3. An increase in carapace length was generally evident for small-sized krill, especially for animals of Nos. 6 and 21. Inversely, there was a decrease in carapace length for large-sized animals, especially for the two largest animals, Nos. 19 and

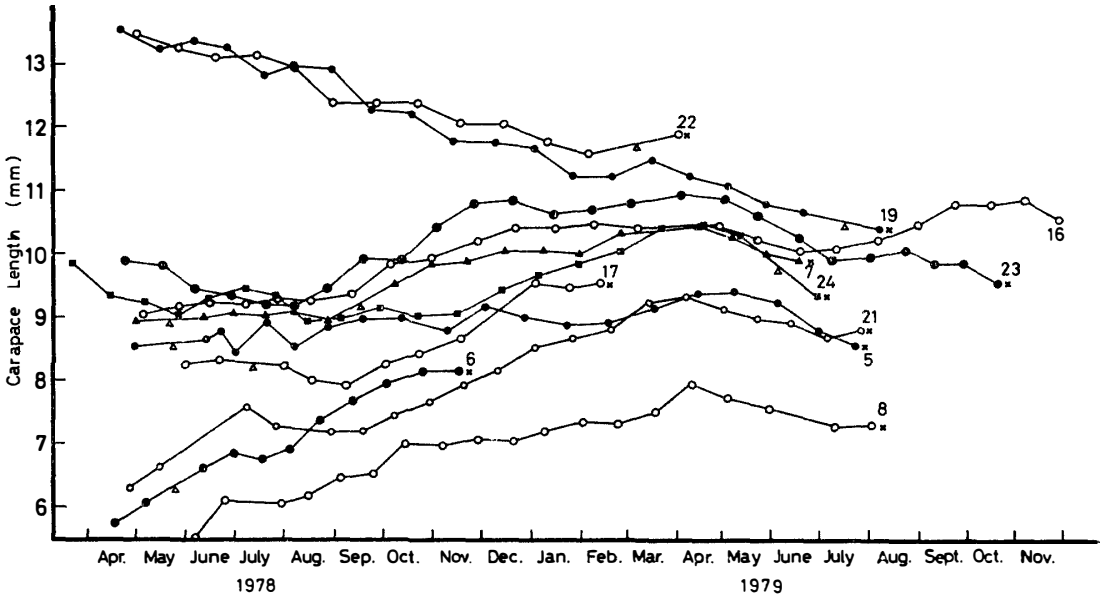

Fig. 3. Change in carapace length of 11 Euphausia superba *reared in the laboratory in the dark at 0.7°C. Open triangles: moult was performed but carapace length was not measured. ×: the time of death.*

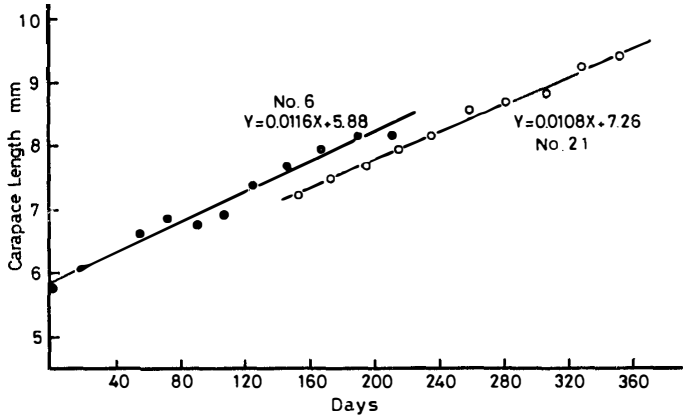

Fig. 4. Increase in carapace length of animals of No. 6 (solid circle) and No. 21 (open circle).

22. This fact seems to indicate that the krill may have been affected by such conditions as the size and quality of food organisms and the size of container.

The animal of No. 6 showed the quickest growth among the 11 experimental animals. No. 21 showed the second fastest growth. The regression equations are $y=0.0116x+5.88$ for the No. 6 from April to November 1978, and $y=0.0108x+7.26$ for the No. 21 from September 1978 to April 1979, where y is the carapace length in mm and x is the duration of rearing in days (Fig. 4). These rates correspond to an increase in body length of 0.031 to 0.033 mm per day. If krill grow at this rate, the post-larvae of about 15 mm in body length need 3 years to grow to mature stage of about 50 mm in body length. Moreover, if the growth rate is reduced in the winter season, the post-larvae need more than 3 years to mature.

LASKER (1966) determined the growth rate of *Euphausia pacifica* to be 0.034 to 0.048 mm per day in body length. These values are approximately equal to those of the present study but *E. pacifica* which lives in warmer waters is much smaller than *E. superba*.

RUUD (1932) and NEMOTO (1959) reported that krill takes 2 years to grow from hatching to mature stage. According to their results, the increase of the body length is 15 mm or more from January to March, while the rate attained in the present study is 12 mm per year. It is hard to accept their high growth rate since the increase of the body length at 5 mm per month is too great. MCWHINNIE and DENYS (1978) also reported the growth rates for krill maintained at high food levels in a laboratory. The rates were 1–6.5% per month for krill between 18.5 and 38 mm in body length, which are equivalent to the present study, 4.5% for krill of 25 mm in body length.

There are some reports that the Antarctic krill grow slowly. IVANOV (1970) reported that according to the examination of size composition curves, krill reach maturity at the age of 3 years and the majority breed in the fourth year of life. MAKAROV (1971) and MACKINTOSH (1972) also considered that the life span would be more than 3 years.

In the present study, the conditions for the maintenance of krill in the laboratory are not optimal since some of the experimental animals showed negative growth. However, some krill could live more than 2 years. At the beginning of the experiment, the two largest animals, Nos. 19 and 22, clearly belonged to the second year class considering that krill take 2 years to become mature. Therefore, they were surely three years old when they died in the laboratory.

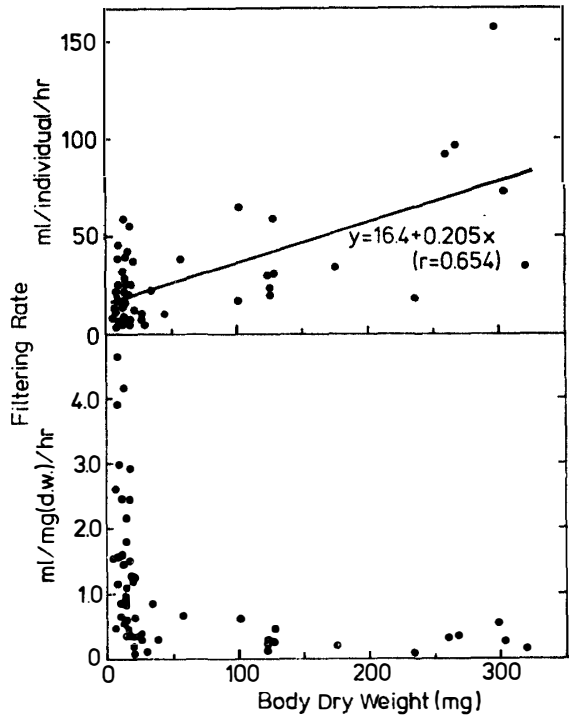

Fig. 5. Filtering rate of Euphausia superba *in relation to the body dry weight (after KATO et al., 1982).*

3.3. *Filtering and ingestion rates*

More detailed information on this subject was reported in the previous paper (KATO *et al.*, 1982). The results and discussions are summarized as follows.

For experiments on individuals, the relationship between the filtering rate in natural seawater and the body dry weight is shown in Fig. 5. The filtering rate per individual tended to increase with the increase in body dry weight. The regression equation is given as: $y=0.205x+16.4$ ($r=0.654$), where y is the filtering rate in ml/individ./hr and x is the body dry weight in mg. The filtering rate per unit dry weight decreased abruptly with the increase in body dry weight and became flat for individuals over 100 mg.

In order to clarify the relationship between the filtering rate and the body size, krill were classified into three groups according to their dry weight, and their filtering rates were compared (Table 1). The rates were 21.2, 34.7 and 78.5 ml/individ./hr for

Table 1. Filtering rates of 3 groups of Euphausia superba *in natural seawater (after KATO et al., 1982).*

Dry weight (mean±SD) in mg	Filtering rate (mean±SD)	
	ml/individ./hr	ml/mg (d.w.)/hr
<100 (17.8± 9.7)	3.6– 59.3 (21.2±14.8)	0.111–4.65 (1.39 ±1.10)
100–200 (125.8±22.6)	16.8– 63.8 (34.7±17.6)	0.165–0.620 (0.284±0.167)
>200 (280.8±31.4)	18.8–157.0 (78.5±49.5)	0.080–0.528 (0.287±0.161)

small, medium and large sized krill, respectively. On the other hand, the mean filtering rate per unit dry weight was 1.39, 0.28 and 0.29 ml/mg dry weight/hr for small, medium and large sized krill, respectively, and seems to change smaller abruptly at about 100 mg in body dry weight. MAUCHLINE (1980) pointed out that the Antarctic krill achieve sexual maturity at 40 mm in body length and that the growth factor would be expected to decay in krill more than 40 mm in body length which correspond to the medium and large sized krill over 100 mg in dry weight. In the Antarctic krill, the filtering rate is possibly affected not only by the body size but also by their sexual maturity.

Table 2. Filtering rates of Euphausia superba *measured in mass. Incubated in natural seawater (a) and later in seawater added with a definite amount of phytoplankton (b) (after KATO et al., 1982).*

Exp.	Number of individuals	Mean dry weight (mg)	Initial chl. *a* concentration ($\mu g/l$)	Filtering rate	
				ml/individ./hr	ml/mg (d.w.)/hr
A	30	240.4	(a) 0.924	68.9	0.129
			(b) 13.7	217	0.923
B	30	244.9	(a) 0.924	57.4	0.105
			(b) 13.7	164	0.675
C	30	247.9	(a) 0.924	54.4	0.098
			(b) 15.1	201	0.811
D	300	13.4	(a) 0.415	14.5	1.08
			(b) 11.8	29.3	2.19
E	300	10.1	(a) 0.415	15.5	0.59
			(b) 9.84	42.5	4.18
F	300	12.2	(a) 0.415	8.26	0.26
			(b) 12.9	36.0	2.95

The filtering rates obtained in the mass experiments are shown in Table 2. The filtering rates of both larger and smaller krill were much higher in seawater with high concentrations of phytoplankton than in natural seawater. FROST (1975) examined the feeding behaviour of a marine copepod *Calanus pacificus* and demonstrated that the feeding of the copepod was significantly reduced when incubated in low food levels, to save energy expenditure in looking for food particles when the food is scarce.

The ingestion rates are expressed as the amount of the particulate carbon lost from the experimental medium. If the krill ingest all sizes of particles without selection, the amount of carbon ingested can be determined from the decrease of chlorophyll *a* by using a ratio of chlorophyll *a* to particulate organic carbon in each experimental medium. The results are shown in Table 3, in which the metabolic loss calculated from the respiratory rate after SEGAWA *et al.* (1982) is also shown. The amount of carbon ingested was smaller than that of metabolic loss, indicating that the negative growth is likely to occur in natural conditions. Table 4 shows the ingestion rates determined in

Table 3. Comparison of the ingestion rates and the calculated metabolic loss of Euphausia superba *incubated in natural seawater (after KATO et al., 1982).*

Body dry weight (mg)	Ingestion rate (μg C/individ./day)	Metabolic loss (μg C/individ./day)
127.3	38.6	774
124.2	24.5	681
102.1	35.2	550
26.8	8.8	104
21.5	24.3	144
20.7	6.2	—
20.5	8.2	—
19.3	27.7	122
17.0	25.5	132
15.7	24.0	97.1
15.6	7.5	92.2
15.4	19.6	94.8
15.2	19.7	99.2
10.6	17.0	60.8
10.5	14.5	52.6
9.8	30.1	75.0
8.3	13.1	62.9

Table 4. Ingestion rates and metabolic loss of Euphausia superba *incubated in seawater added with phytoplankton (after KATO et al., 1982).*

Body dry weight (mg)	Ingestion rate (μg C/individ./day)	Metabolic loss (μg C/individ./day)
247.9	1915	998
244.9	1468	989
240.4	1668	976
13.4	183	130
12.2	218	122
10.1	183	107

the mass experiment, in which the animals were incubated in seawater with high concentration of phytoplankton, together with the metabolic loss. At these high phytoplankton concentrations, the krill ingested carbon more than metabolic loss.

In conclusion, the Antarctic krill actively ingest by filter feeding when phytoplankton is plentiful, but when phytoplankton is scarce, they reduce their filtering activity and their feeding habit becomes more predatory. In fact, cannibalism was observed in the stock culture kept in tanks on deck during the cruise.

3.4. Size selection in feeding

Figure 6 shows the change of the particle size spectrum after 12 hours of grazing upon the artificial plankton by a krill. The number of particles larger than 8 μm clearly decreased but no change was observed in particles smaller than 8 μm. The feeding seems to be almost nonselective with particles more than 8 μm in size. The present result agrees well with the value of BARKLEY (1940) who found 7 μm to be the lower limit for food particle size from the structure of the feeding organs of krill.

Figure 7 also shows the results of food size selection when a micro-alga *Dunaliella tertiolecta* was given, which indicates that krill can feed on particles smaller than 8 μm when particles larger than 8 μm are insufficient.

There is a complicated mechanism in the filter feeding of krill because it involves various factors, such as shape, size and concentration of food particles available and

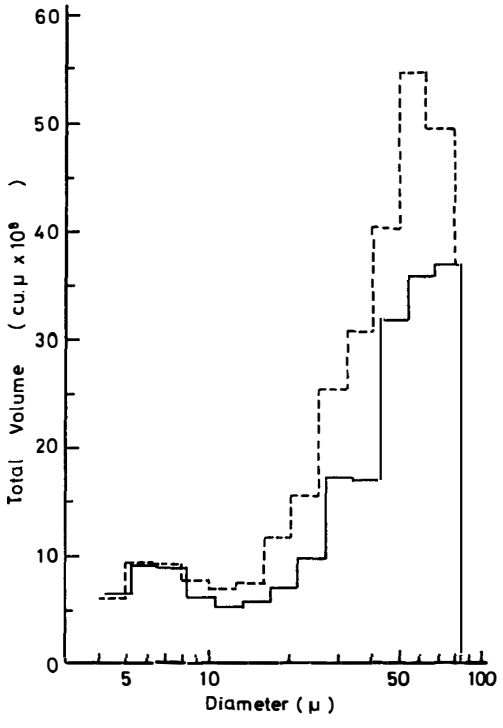

Fig. 6. Size spectrum of particulate material (artificial plankton) in control (broken line) and after grazing (solid line) by an Euphausia superba *(31.2 mm in body length).*

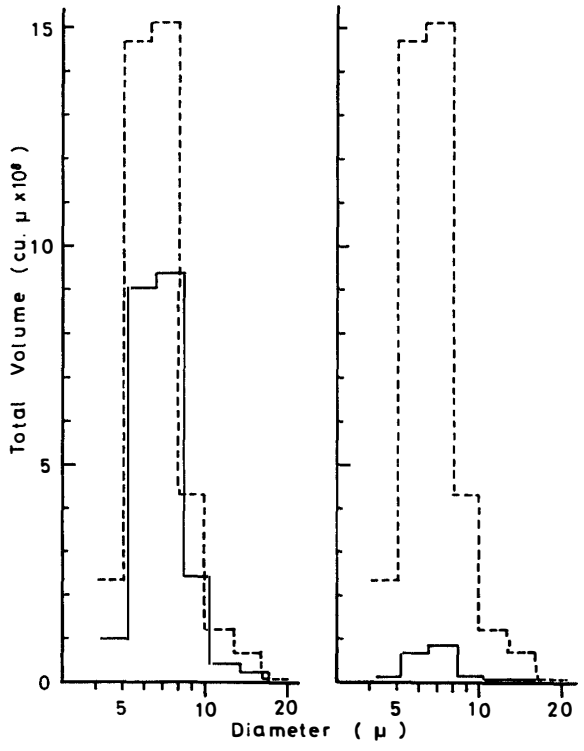

Fig. 7. Size spectrum of particulate material (Dunaliella tertiolecta) *in controls (broken line) and after grazing by an* Euphausia superba *(left: 22.9 mm in body length, right: 30.1 mm in body length).*

the structure of mouth parts of the krill. It is apparent that further studies on these problems are required to clarify the filter feeding of *E. superba*.

References

BARKLEY, E. (1940): Nahrung und Filterapparat des Walkrebschens *Euphausia superba* Dana. Z. Fisch., **1**, 65–156.

CLARKE, A. (1976): Some observations on krill (*Euphausia superba* Dana) maintained alive in the laboratory. Br. Antarct. Surv. Bull., **43**, 111–118.

FOWLER, S. W., SMALL, L. F. and KEČKEŠ, S. (1971): Effects of temperature and size on molting of euphausiid crustaceans. Mar. Biol., **11**, 45–51.

FRASER, F. C. (1936): On the development and distribution of the young stages of krill (*Euphausia superba*). Discovery Rep., **14**, 1–192.

FROST, B. W. (1975): A threshold feeding behavior in *Calanus pacificus*. Limnol. Oceanogr., **20**, 263–266.

GAULD, D. T. (1951): The grazing rate of planktonic copepods. J. Mar. Biol. Assoc. U. K., **29**, 695–706.

IKEDA, T. and DIXON, P. (1982): Observations on moulting in Antarctic krill (*Euphausia superba* Dana). Aust. J. Mar. Freshwater Res., **33**, 71–76.

IVANOV, B. G. (1970): On the biology of the Antarctic krill *Euphausia superba*. Mar. Biol., **7**, 340–351.

JERDE, C. W. and LASKER, R. (1966): Molting of euphausiid shrimps; Shipboard observation. Limnol. Oceanogr., **11**, 120–124.

KATO, M., MURANO, M. and SEGAWA, S. (1979): Estimations of the filtering rate of the Antarctic krill under laboratory conditions. Trans. Tokyo Univ. Fish., **3**, 107–112.

KATO, M., SEGAWA, S., TANOUE, E. and MURANO, M. (1982): Filtering and ingestion rates of the Antarctic krill, *Euphausia superba* Dana. Trans. Tokyo Univ. Fish., **5**, 167–175.

LASKER, R. (1966): Feeding, growth, respiration and carbon utilization of a euphausiid crustacean. J. Fish. Res. Board Canada, **23**, 1291–1317.

MACKINTOSH, N. A. (1967): Maintenance of living *Euphausia superba* and frequency of moults. Nor. Hvalfangst-Tid., **56**, 97–102.

MACKINTOSH, N. A. (1972): Life cycle of Antarctic krill in relation to ice and water conditions. Discovery Rep., **36**, 1–94.

MAKAROV, R. R. (1971): Composition of the population and reproduction of *Euphausia superba* Dana. Oceanology, **11**, 90–98.

MARR, J. W. S. (1962): The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). Discovery Rep., **32**, 33–464.

MAUCHLINE, J. (1980): The Biology of Euphausiids. London, Academic Press, 681 p. (Advances in Marine Biology, Vol. 18).

MCWHINNIE, M. A. and DENYS, C. J. (1978): Antarctic marine living resources with special reference to krill, *Euphausia superba*; Assessment of adequacy of present knowledge. A report submitted to the National Science Foundation, 209 p.

MURANO, M., SEGAWA, S. and KATO, M. (1979): Moult and growth of the Antarctic krill in laboratory. Trans. Tokyo Univ. Fish., **3**, 99–106.

NEMOTO, T. (1959): Food of baleen whales with reference to whale movement. Sci. Rep. Whales Res. Inst., Tokyo, **14**, 149–290.

PAFFENHÖFER, G. A. (1971): Grazing and ingestion rates of nauplii, copepodids and adults of the marine planktonic copepod *Calanus helgolandicus*. Mar. Biol., **11**, 286–298.

RUUD, J. T. (1932): On the biology of southern Euphausiidae. Hvalradets. Skr., **2**, 105 p.

SEGAWA, S., KATO, M. and MURANO, M. (1982): Respiration and ammonia excretion rates of the Antarctic krill (*Euphausia superba*). Trans. Tokyo Univ. Fish., **5**, 177–187.

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