

THE OVERWINTERING STRATEGY OF ANTARCTIC KRILL  
(*EUPHAUSIA SUPERBA* DANA) UNDER THE COASTAL  
FAST ICE OFF THE ONGUL ISLANDS IN  
LÜTZOW-HOLM BAY, ANTARCTICA\*

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**Abstract:** During the BIOMASS study of the SIBEX (1984/85), some aspects of overwintering strategies of Antarctic krill (*Euphausia superba* DANA) were studied in the Kita-no-ura Cove (69°00'N, 39°35'E) off the East Ongul Island in Lützow-Holm Bay. Krill were collected monthly with a light trap from May through early November 1984. Krill under the coastal fast ice survive the food deficient Antarctic winter principally by the following strategies: (1) changing their habitat from the pelagic to the benthopelagic during the dark period to subsist on detritus on the sea bed, (2) lowering their oxygen consumption rate down to the level of 0.27 ml/g dry wt/h. They show positive phototaxis, swim actively in the darkness, and probably extend their food retention time in the gut in late fall and early winter. Their C and N composition, C : N ratio and fatness are supposed to be mainly effected by the change in metabolic rate and reflect their nutritional condition. The difference in metabolic dynamics of krill between fall and winter to early spring period was recognized through the seasonal change in C and N composition.

## 1. Introduction

The information on the life of Antarctic krill (*Euphausia superba* DANA) during austral winter has been extremely restricted, especially for the population under fast ice. It has been supposed that a considerable amount of krill exist under the coastal fast ice in Lützow-Holm Bay because the local Adélie penguins actively feed on krill, diving under ice near their rookery in spring and summer. But nothing has been studied on the life of krill under fast ice because of the difficulties of sampling them and the severe field conditions in winter. During the BIOMASS study of SIBEX (1984/85) in Japanese Antarctic base, Syowa Station, Antarctic krill were successfully collected under fast ice with a light trap and some studies were made on their winter phototaxis, behavior, seasonal changes in habitat, feeding habits, respiration rate and nutritional condition.

## 2. Methods and Materials

Sampling of *E. superba* was made with a light trap monthly from May to November

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1984 in the Kita-no-ura Cove off the East Ongul Island where the Japanese Antarctic Station Syowa is located (Fig. 1). The design, field handling procedure of the light trap and preliminary sampling results are described elsewhere (KAWAGUCHI *et al.*, 1986). Respiration rate was measured by a closed bottle method with the single krill in bottles of 290 to 310 ml volume. The measurements were made at  $-1.5^{\circ}\text{C}$  in a dark room. Incubation time was 6 to 24 hours depending on the size of krill. The seawater was membrane-filtered, cooled to  $-1.5^{\circ}\text{C}$  and fully aerated before the experiment. The modified Winkler procedure of STRICKLAND and PARSONS (1972) was adopted for the determination of dissolved oxygen. Stomach fullness of krill was examined in the transparent live krill under a stereoscopic microscope. Size of krill was expressed in carapace length (CL) which was measured as the dorsal distance between the anterior tip of rostrum and the mid-dorsal posterior edge of carapace (standard 4, MAUCLINE, 1980a, b). Each specimen was dried at  $60^{\circ}\text{C}$  for 24 hours to measure dry weight of the body. Carbon and nitrogen contents of krill were determined for dried material by Yanagimoto CHN recorder MODEL-MT-2.

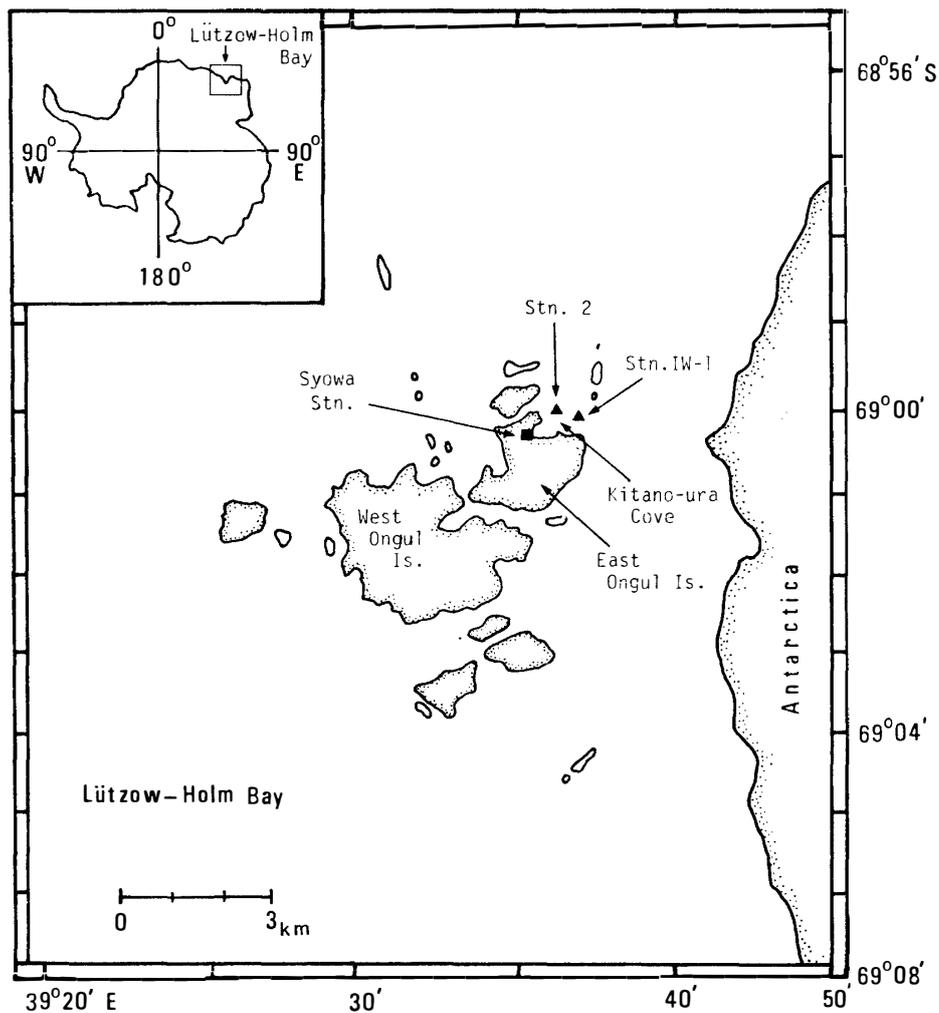


Fig. 1. Locality of sampling station (Stns. 2 and IW-1) of *Euphausia superba* in the Kita-no-ura Cove off the East Ongul Island in Lützow-Holm Bay, Antarctica.

### 3. Results

#### 3.1. Phototaxis

Positive phototaxis of *E. superba* and other organisms is briefly noted in the preliminary sampling results of the light trap (KAWAGUCHI *et al.*, 1986). Table 1 shows the comparison between catches with lighted trap and control trap without light, both of which were placed in the same conditions within a 1-m circle on the sea bottom in the Kita-no-ura Cove on May 2, 4 and 23, 1984. In the sampling of May 4 the two lighted traps collected 34 and 31 krill respectively, whereas only one individual was collected with the control trap. In the other two cases the control traps caught no krill, while the traps with lights caught 377 and 47 krill respectively. These results proved that krill showed positive phototaxis during the dark period and were effectively taken with a light trap. The light trap became ineffective for krill from November onward as the back ground light intensity increased under fast ice.

Table 1. Comparison of catches between trap with light and control trap without light. All the trap set on the sea floor.

Stn.	Date	Time	Lighting duration (h)	Depth (m)	Catch
2	May 2	1615-2000	3.8	38	E(377)
2	"	"	no light	"	no catch
2	May 4	1600-2000	4.0	38	E(34), A(3)
2	"	"	4.0	"	E(31), F(1)
2	"	"	no light	"	E(1)
IW	May 23	1330-1820	4.8	40	E(47), A(1)
IW	"	"	no light	"	no catch

E: *Euphausia superba*, A: Amphipoda, F: notothenid fish juvenile.

#### 3.2. Depth distribution and swimming behavior

On five occasions traps were set at different depths at the same sampling site to discover the effect of trap depth on catches. In three of the five cases *E. superba* were collected only with traps set on the sea floor (Table 2). In the other two cases krill were not collected from any layer, although on May 21 all of the catches were lost because of a break in the collection bucket. The average catch of krill for a total of 23 samplings made on the sea floor from May to October was 34.9 individuals per sampling, whereas no catch was present in the other 11 samplings in the mid layers of 15m depth and subsurface. *E. superba*, therefore, overwinter in the layer close to the sea floor during the dark period in the coastal region such as Kita-no-ura Cove. Because of the sampling restriction of the light trap, we could not determine the habitat of krill during daytime in late fall and late winter to spring when the sunlight is enough to penetrate into the sea water. It is likely that krill undertake a diel vertical migration in late fall and also in late winter or early spring when both dark and light periods of the day are clearly distinguishable.

Of the 23 samples taken close to the sea floor, eight samples were recovered after the light was extinguished and only three krill were found in two of the eight samples.

Table 2. The effect of trap depths on the catches of *Euphausia superba* and other animals, showing the Antarctic krill were collected only from the bottom layer.

Stn.	Date	Time	Lighting duration (h)	Depth (m)	Catch
2	May 2	1615-2000	3.8	0	A (5)
2	"	"	"	38 (btm.)	E (377)
2	May 21	1315-1650	3.6	0	no catch
2	"	"	"	24	no catch
2	"	"	"	38 (btm.)	collect. bucket broken
IW	June 14	1400-2100	7.0	0	no catch
IW	"	"	"	40 (btm.)	M (3), F (1)
2	August 9	1700-2200	5.0	0	C (9)
2	"	"	"	15	A (4), C (7), F (1)
2	"	"	"	38 (btm.)	E (1), M (2), A (7)
2	November 1-2	2000-0300	7.0	0	C (1720)
2	"	"	"	15	C (18)
2	"	"	"	38 (btm.)	E (1), C (1), T (3)
2	November 23-24	2230-2530	6.0	0	C (11910)
2	"	"	"	15	C (31)
2	"	"	"	38 (btm.)	C (33)

E: *Euphausia superba*, A: Amphipoda, M: *Antarctomysis maxima*, F: notothenid fish juvenile, C: Copepoda, T: Tanadacea.

In the remaining 15 samples retrieved before the light was extinguished, a total of 800 individuals were caught in 11 samples. The average catch per sample and the frequency of occurrence in the samples were much higher in the 15 samples recovered prior to the extinguishment of light than in the eight samples recovered after the extinguishment of light, *i.e.* 53.3 vs. 0.3 individuals per sampling and 73 vs. 25% of occurrence respectively. Therefore, it may be concluded that *E. superba* can escape from the trapping chamber through the narrow entrance after the extinguishment of light probably owing to their randomly spiral swimming behavior even in the darkness.

These sampling results prove that *E. superba* overwinters under the coastal fast ice and shifts its habitat from the pelagic to the benthopelagic layer swimming continuously during the dark period. HAMNER *et al.* (1983) pointed out, based SCUBA diving observations, that schools of krill seem to be maintained primarily by rheotactic cues and such schooling behavior would be effective in the dark period. The present results seem to be relevant to their note.

### 3.3. Size frequency distribution

The size frequency histogram of krill taken from May through October is shown in Fig. 2, although only 10 specimens were available in October. Three vague modes are discernible from May to August, which showed de-growth rather than growth of krill during this period. A slight recovery of the modal size was seen on September 25, since then no change was seen until October 26. It has been suggested that a mode in a size frequency histogram of krill does not always represent single year class, but usually several successive year classes (MAUCHLINE and FISHER, 1969; ETTERS HANK, 1984). It is

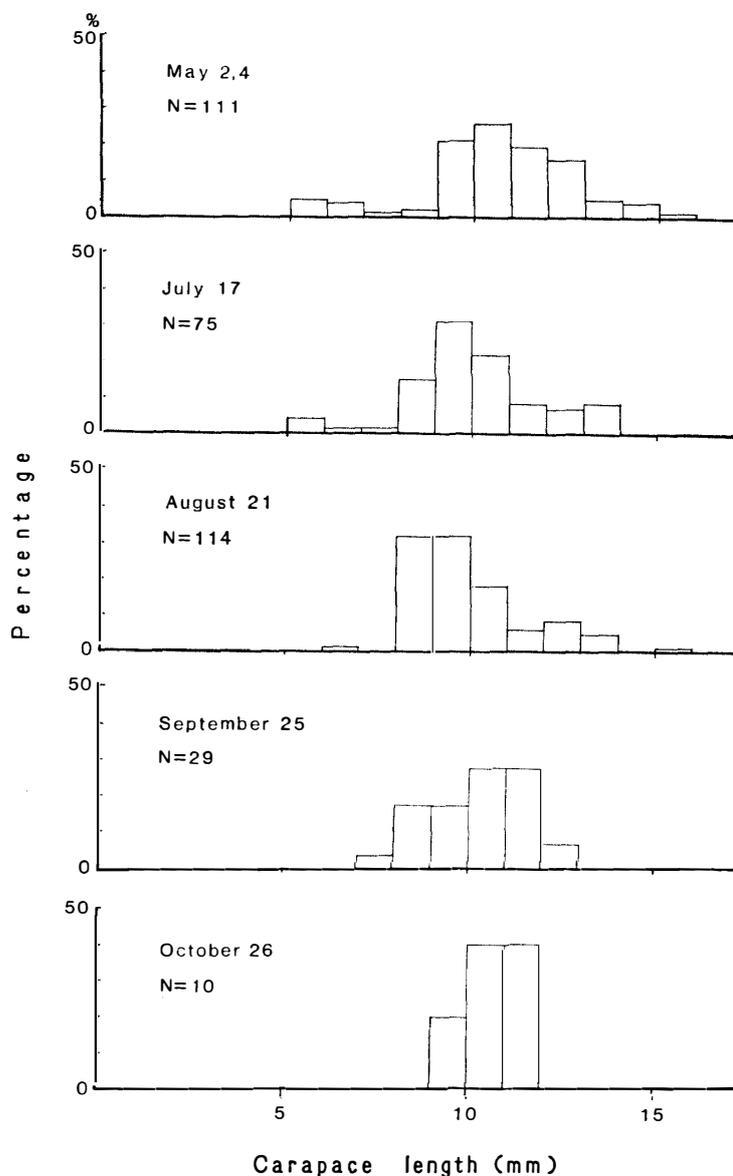


Fig. 2. Size frequency histograms of *Euphausia superba* taken under fast ice in different months in the Kita-no-ura Cove.

not known whether the krill collected from the Kita-no-ura Cove belong to the same discrete population or not. However, it can be said at least that no significant growth of krill was seen during austral winter. All of the specimens taken are sexually immature, mainly juveniles, with a size range of 5 to 15 mm CL which is referable to 18 to 45 mm in total length and 10 to 220 mg in body dry weight.

#### 3.4. Feeding activity

**Stomach fullness:** *E. superba* shows considerable feeding activity even in winter under fast ice. Stomach fullness was examined from May through October, 1984 (Table 3a). Krill were kept for in the laboratory about 15 hours to collect fecal material prior to the examination of stomach fullness. In May and July, 10–35% of the krill had full

stomachs and 5–27% had empty stomachs, while these values in August, September and October were 0–10 and 40–65% respectively. If the stomachs were examined just after the collection, these values could have been higher for full stomach and lower for empty stomach than the present results. In spite of this delay in the examination of stomach contents, seasonal difference was apparent in stomach fullness, indicating that clearance rate of food from the stomach is slower in May to July than in August to October. This seems to be closely related to seasonal changes in food availability, quality and also metabolic rate.

Table 3a. Seasonal change in stomach fullness of krill collected from May to October 1984 in the Kita-no-ura Cove.

Fullness	May 4 n=22	May 23 n=20	July 17 n=75	August 21 n=51	September 25 n=9	October 26 n=10
Empty	27.3%	20.0%	5.3%	64.7%	55.5%	40.0%
+	45.5	35.0	13.3	19.6	22.2	10.0
++	13.6	35.0	46.7	15.7	22.2	40.0
Full	13.6	10.0	34.7	0	0	10.0

+ : trace ~  $\leq 25\%$ ; ++ :  $> 25\%$ .

Table 3b. Seasonal change in color of stomach contents of krill collected in different months.

Date 1984	YB	B	GB	G	Fragments	Total No. of stomachs examined
May 23	14	1	0	0	0	15
July 17	34	1	3	0	0	38
August 21	12	1	2	0	5	18
September 25	2	2	0	0	0	4
October 26–27	0	0	3	3	0	6

YB: yellowish brown to light brown; B: brown; GB: greenish brown; G: green to dark green; fragments including sand.

Monthly change in color of stomach content: The seasonal change in color of stomach contents was recognized from winter to spring (Table 3b). The color showed various tones, but broadly classified into the four categories in this study, *i.e.* yellowish brown or ochre (YB), brown (B), greenish brown (GB), green (G). In October the stomach contents were all green or greenish brown, indicating that krill begin to change the feeding habit from detritus to others, most probably ice algae. No green (G) stomach contents were recognized before October. Stomach color of krill collected before October was mostly yellow brown. Occurrence of brown and greenish brown colored stomachs were few and infrequent. Occurrence of fragmentary substances, including sand, in August seems to indicate that the feeding activity of krill increases when food is still restricted but may be related to the increased respiration rate.

Seasonal variation of chlorophyll *a* abundance: As an indicator of food abundance of krill, seasonal abundance of chlorophyll *a* and phaeopigment in the seawater was measured monthly at Stn. 2, the sampling site of the krill study (Fig. 3). In most months, the peak abundance was observed in the upper 2.5 m layer. The maximum concentration

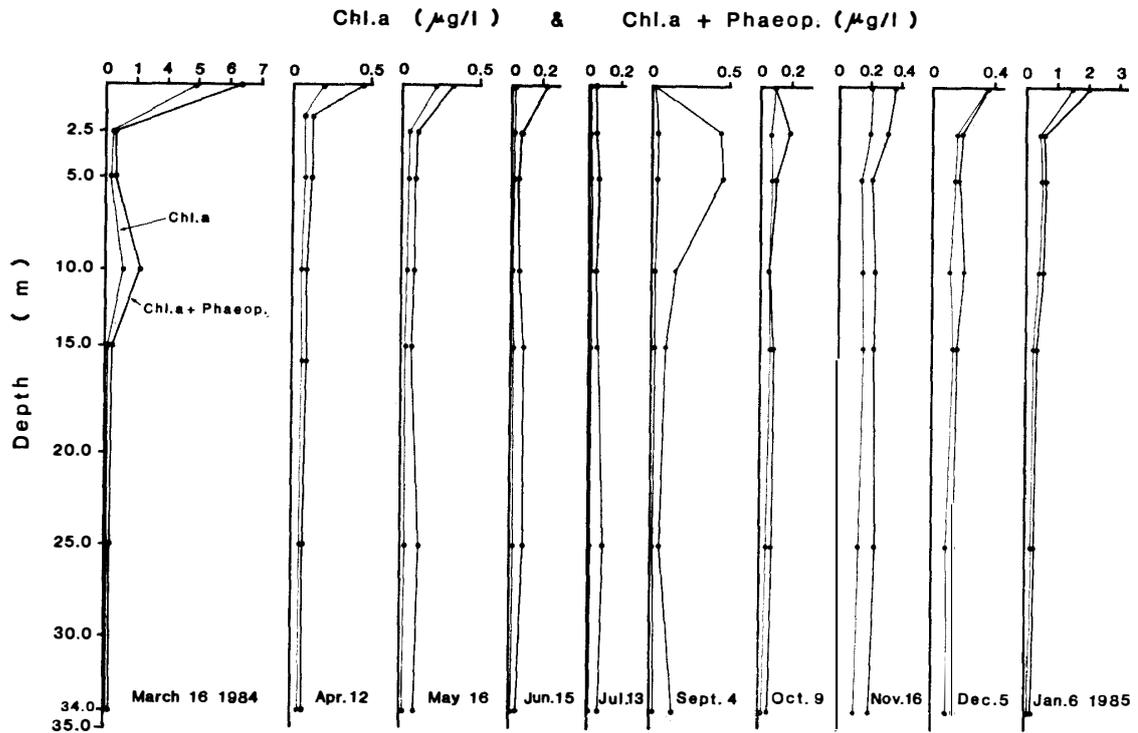


Fig. 3. Monthly changes in chlorophyll *a*, phaeopigment abundance and their vertical distribution pattern from May 1984 to January 1985 at Stn. 2, the sampling station of krill in the Kita-no-ura Cove.

of Chl. *a* decreased abruptly in April, *i.e.* from  $5 \mu\text{g Chl. } a/l$  in March to  $0.25 \mu\text{g Chl. } a/l$  in April 1984. The level of Chl. *a* concentration was below  $0.25 \mu\text{g/l}$  from April through November, especially below  $0.1 \mu\text{g/l}$  from June to October 1984. A similar result is also reported at the same sampling site in 1982 by FUKUCHI *et al.* (1984), *i.e.* Chl. *a* concentration was less  $0.1 \mu\text{g/l}$  from April to November 1982.

### 3.5. Oxygen consumption

Seasonal changes in the oxygen consumption rates of krill were measured during the period May through October 1984 using the specimens from the Kita-no-ura Cove. In January 1985 an additional measurement was made aboard the icebreaker SHIRASE on samples collected by a plankton net of 160 cm in mouth diameter in the seasonal pack-ice zone off Lützow-Holm Bay.

The relationship between oxygen consumption rate of whole animal ( $QO_2$  ml/h) and body weight (BW: g wet wt) is usually expressed by a power function:  $QO_2 = a \cdot BW^b$ . The constants, *a* and *b*, were calculated by the least square method for krill taken from May through September 1984 (Table 4) together with the predicted oxygen consumption rates (ml/h) for krill of different body weights (g wet wt) from each regression equation. As the values of *b* are close to 1, the relationship between whole animal oxygen consumption rates and body weights is almost linear, although the value was slightly lower in July. The values of *a*, together with *b*, are lowest in July and increase from August to September, showing that whole animal oxygen consumption rate was lowest in July.

The rate in May was referable to the level in August. As wet : dry wt ratio show no significant monthly variation (Table 7),  $QO_2$  (ml/h)-BW (g dry wt) relationship also show the similar pattern as above.

Dry weight-specific oxygen consumption rate showed some variation especially in

Table 4. Relationship between oxygen consumption rate ( $QO_2$ , ml/h) and wet body weight ( $W$ , g) in *Euphausia superba* DANA.

Date 1984	Range of BW (W, g)	$QO_2 = aW^b$				Predicted oxygen consumption rates (ml/h) for krill of different wet weight (g)			
		$a$	$b$	$n$	$r^*$	0.1	0.5	1	2
May 4	0.06-0.53	0.0882	1.0619	8	0.92484	0.0076	0.042	0.088	0.184
July 17	0.08-1.01	0.0504	0.8659	11	0.84626	0.0068	0.028	0.050	0.092
August 21	0.07-0.61	0.0782	0.9956	12	0.83272	0.0079	0.039	0.078	0.156
September 25	0.16-0.59	0.2447	1.0044	8	0.96922	0.0242	0.122	0.245	0.491

\* A correlation coefficient of a linear regression  $\ln QO_2 = \ln a + b \ln W$ .

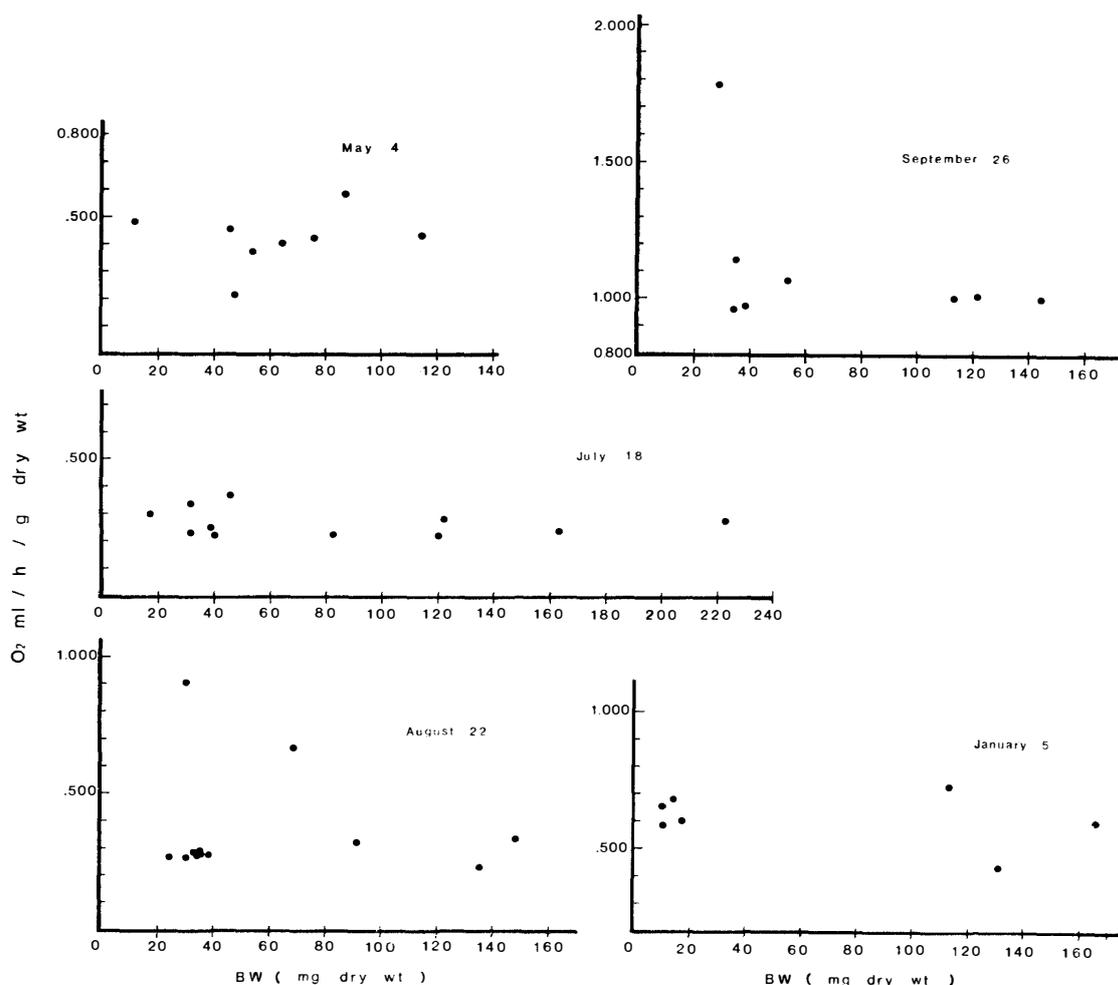


Fig. 4. Relationship between weight specific oxygen consumption rate (ml/h/g dry BW) and body weight (mg dry wt) for krill taken from May to October 1984 in the Kita-no-ura Cove, showing the independency of the two variables.

August and September, but no significant correlation with body weight and is probably independent of body weight (Fig. 4). This reflects the almost linear relationship between whole animal oxygen consumption rate and body weight (value of  $b$  close to 1, Table 4). Therefore, the rates measured for krill of wide size range were averaged by each month to examine the monthly change. Seasonal change in respiration rate is obvious in the overwintering krill. Average values ( $\text{ml O}_2/\text{h}/\text{BW g dry wt}$ ) for each month are  $0.420 \pm 0.104$  ( $\bar{x} \pm 1$  s.d.) in May,  $0.272 \pm 0.061$  in July,  $0.359 \pm 0.206$  in August,  $1.058 \pm 0.340$  in September,  $0.956$  in November and  $0.597 \pm 0.104$  in January (Fig. 5). Differences among average values for different months are significant between May–July ( $p < 0.003$ , t-test), July–August ( $p < 0.09$ ). August–September ( $p < 0.0001$ ) and September–January ( $p < 0.001$ ). Statistical test for the difference between September and November is not amenable, since the measurement was made for only one krill in November.

Summer respiration rate of krill was measured on those from outer pack ice edge, instead of the Kita-no-ura Cove. The mean summer rate was  $0.597 \text{ ml O}_2/\text{h}/\text{BW}$  (range:  $0.434\text{--}0.728$ ), which is close to the previous summer rates of krill determined by various workers (*cf.* CLARKE and MORRIS, 1983). Combined all seasonal data obtained in this study, a seasonal variation in the respiration rate of krill was established (Fig. 5).

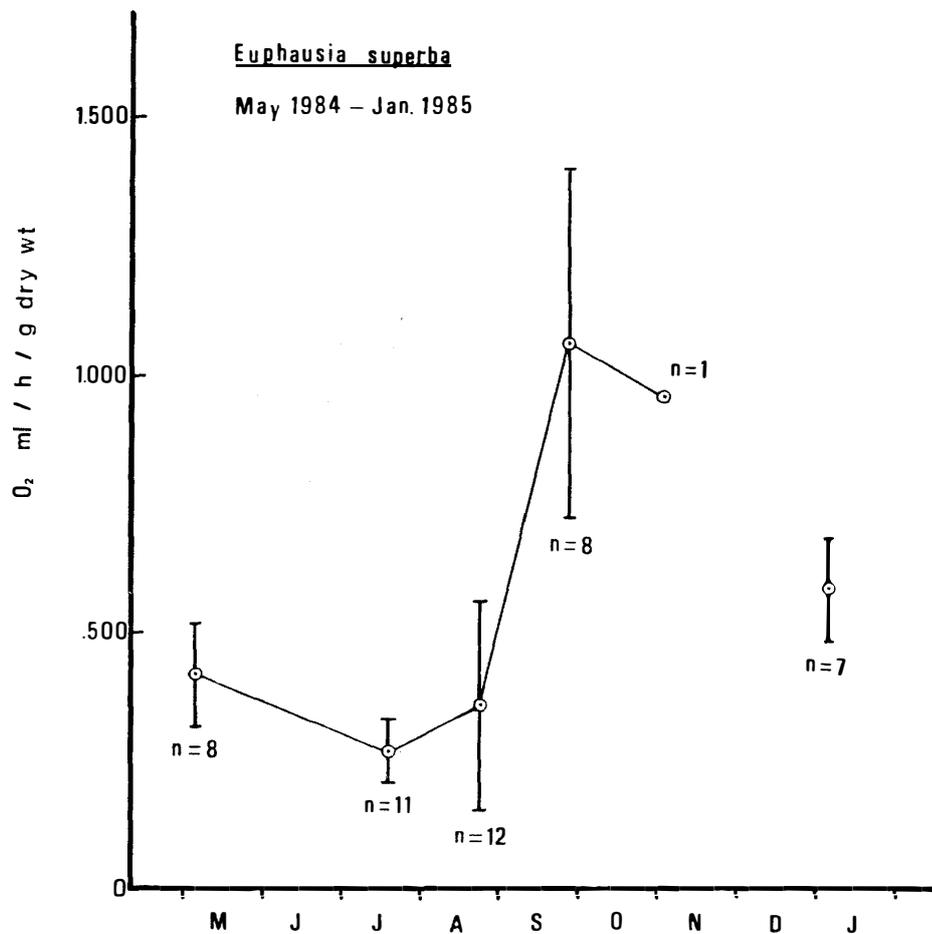


Fig. 5. Monthly change in the weight specific oxygen consumption rate ( $\text{ml/h/g dry BW}$ ) of krill taken from May to October 1984 in the Kita-no-ura Cove.

### 3.6. Condition factor

The relationship between BW (mg dry wt) and carapace length (CL, mm) is usually expressed by a power function of  $BW = a \times (CL)^b$ . Constants  $a$  and  $b$  were computed for samples taken from May through October (Table 5) and regression equations obtained for each month are plotted in Fig. 6. Apparent difference in this relationship between months leads us to examine the condition factor (CF) of krill which is defined as  $CF = BW \times CL^{-3} \times 10^3$ . CF thus calculated (Table 6) showed clear seasonal change; lowest in early May and then increasing from May through August (Fig. 6, a to d). Then fatness begins to decrease slightly from August through October (Fig. 6, e to g). Differences of averages between May 4 and May 23, between May 23 and August 21, between August 21 and September 25 were significant at the level of 0.1, 5, and 5% (t-test). That is, monthly change in CF value shows the same pattern as observed in CL-BW relationship in Fig. 6. This monthly change in condition factor seems to, more or less, reflect the nutrition condition of overwintering krill. The nutritional condition of krill is lowest in May 4, slightly recovered from May 23 through August and then is lowered again until October. The interpretation of the monthly change in fatness will be discussed later in relation to moulting.

Table 5. Relationship between body weight (mg dry wt) and carapace length (mm) in the krill collected from May to October 1984 in the Kita-no-ura Cove.

Collection date	n	BW = a × (CL) <sup>b</sup>		r*	Size range (CL in mm)
		a	b		
May 4, 1984	21	.03987	3.05398	.90840	8.9-14.4
May 23	19	.00736	3.85208	.91689	8.8-13.2
July 17	30	.00909	3.80379	.96773	8.6-13.1
August 21	30	.01297	3.67965	.94009	8.2-13.5
September 25	19	.01617	3.53559	.94742	7.7-12.6
October 26-27	10	.05514	2.98710	.70466	9.0-11.5

\* Regression coefficient of  $\ln BW = \ln a + b \ln CL$ .

Table 6. Monthly change in the condition factor (CF) of krill taken from May to November 1984 in the Kita-no-ura Cove.  $CF = BW \text{ (mg dry wt)} \times CL \text{ (mm)}^{-3} \times 10^3$  (CL: carapace length).

Date	n	Size range CL (mm)	$\bar{CF}$ (ave.)	s.d.	CF range	Level of significance*
May 4	21	8.9-14.4	45.97	± 7.84	32.90-69.12	0.1%
May 23	19	8.8-13.2	56.74	± 11.42	41.93-83.25	n.s.
July 17	30	8.6-13.1	59.50	± 9.39	35.96-78.38	n.s.
August 21	30	8.3-13.5	62.63	± 11.27	48.20-87.88	5%
September 25	19	8.5-12.6	55.56	± 10.77	37.86-85.57	n.s.
October 26-27	10	9.0-11.5	55.09	± 15.11	39.71-88.58	n.s.
November 2	1	14.1	83.08	—	83.08	n.s.

\* May 23-August 21 significant at 5% level.

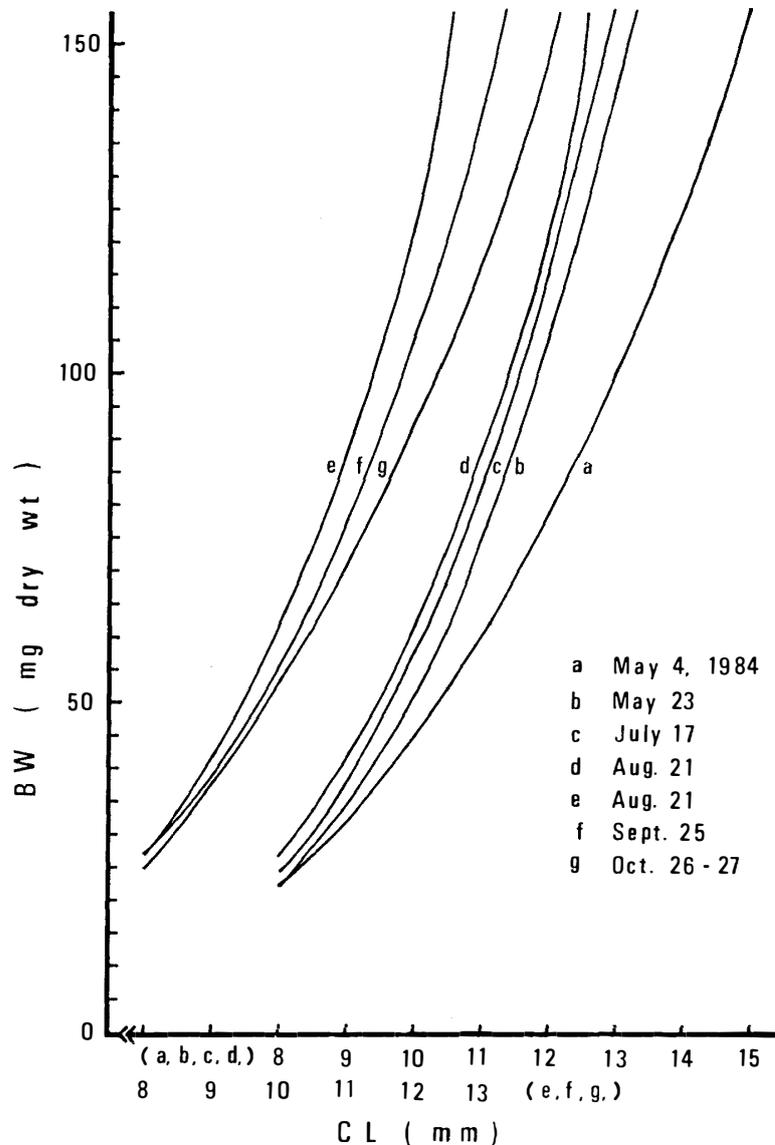


Fig. 6. Seasonal change in the body weight (mg)-carapace length (mm) relationship,  $BW = a \cdot (CL)^b$ , in krill taken from May to October 1984 in the Kita-no-ura Cove. Regression lines from May to August and from August to October are presented separately with two different scales of abscissa to show the monthly increase and decrease of fatness.

### 3.7. Chemical composition

Dry and wet body weights of krill were highly correlated with each other ( $r > 0.95$ ) and showed no significant monthly variation from May to October (Table 7). In other words, water content in the body of krill does not vary seasonally.

Carbon and nitrogen (% dry BW) and its ratio (C:N) were a linear function of BW, but some apparent monthly changes were recognized in each function (Figs. 7 and 8). Both C and N contents were lowest in May 4. During the short period from May 4 to May 23, C values abruptly increased to the highest level of the period studied, while

Table 7. Dry-wet body weight relationship in krill taken from May to November 1984 in the Kita-no-ura Cove:  $BW(g \text{ dry wt}) = a + b \times BW(g \text{ wet wt})$ .

Sampling date	<i>n</i>	Size range CL (mm)	<i>a</i>	<i>b</i>	<i>r</i>
May 4	20	8.9-14.4	-0.0087	0.2579	0.98126
May 23	19	8.8-13.2	-0.0137	0.2518	0.96947
July 17	72	5.2-13.6	-0.0033	0.2382	0.99121
August 21	52	8.0-13.5	-0.0217	0.2234	0.98199
September 25	19	8.5-12.6	-0.0087	0.2487	0.99281
October 26-27	10	9.0-11.5	0.0058	0.2255	0.94772
November 2	1	14.2	—	(0.2329)*	—

\* dry wt/wet wt.

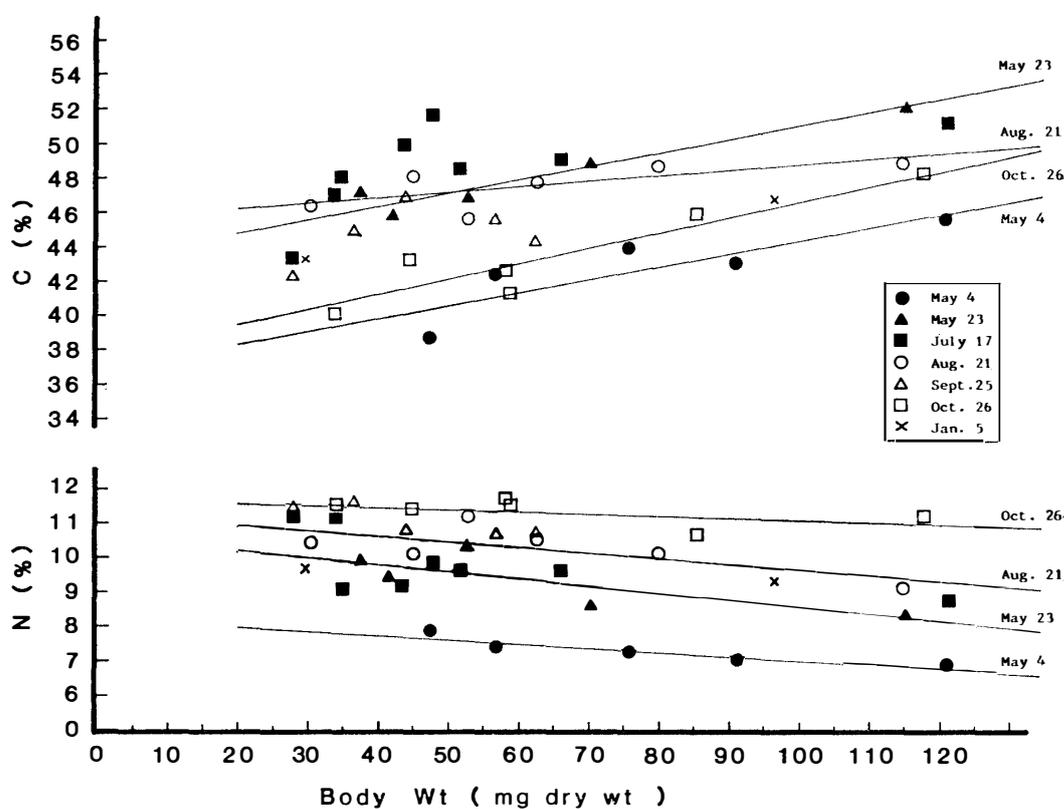


Fig. 7. Seasonal changes in the relationships between C and N composition in percent of body dry weight from May to October 1984 in the Kita-no-ura Cove.

N values increased more moderately (Fig. 7). The differences between the two regression lines of May 4 and 23 were significant at 0.1% level for C and 0.5% level for N content. The increase in C and N contents would have resulted from a lowered metabolic rate and an established diet of detritus in the layer close to the sea floor from May. Thereafter C content seems to be invariable from late May through July when the lowest metabolic rate was measured, but C content tended to decrease from August through October probably owing to the increase in metabolic rate (Fig. 7). The difference

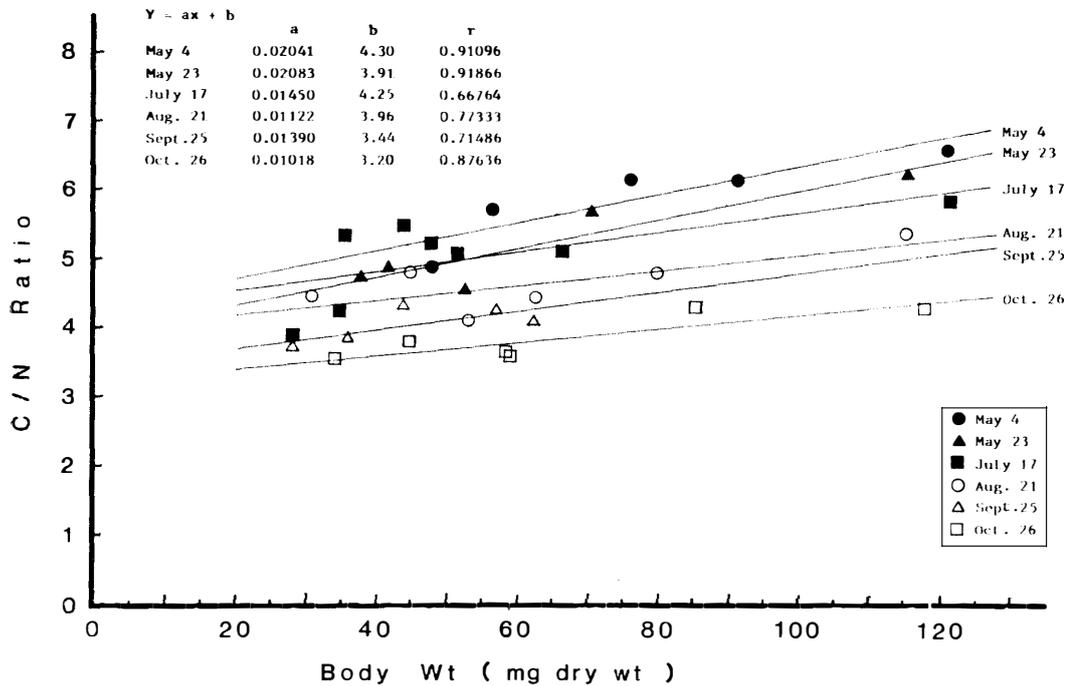


Fig. 8. Seasonal change in the relationship between C:N ratio and body weight (mg dry wt) in krill taken from May to October 1984 in the Kita-no-ura Cove.

between August and October is significant at 0.1% level, but the difference among August–September and September–October is rather vague because of the large scatter of data. N content continued to increase from May 23 through October. The significance levels are 8% between May 23 and August, 2% between May 23 and September, 1% between August and October. The C:N ratio for each month showed considerable scatter, but a regression line for each month showed a remarkable trend, *i.e.* ratios continuously decreased from May 4 through October in spite of different patterns of monthly changes in C and N content (Fig. 8). Significance levels of difference between regression lines are 5% level for late May–August, 0.2% for August–October, but the difference between two values measured at one monthly intervals were not so significant because of the scatter of values.

#### 4. Discussion

**Phototaxis:** Positive phototaxis of krill would be a good adaptation for searching food of high density under fast ice, since richer light conditions may be closely related to the higher productivity by phytoplankton or ice algae especially in fall and spring when the penetrating light intensity is extremely restricted. In this study sampling was not conducted in March through April 1984 because of the sea ice conditions. But krill were collected at the sea bottom with a light trap in the Kita-no-ura Cove in March 6, 1986 (Prof. Y. NAITO, pers. commun.), indicating that a part of the population, at least, started to inhabit the benthopelagic layer at night in early March. Therefore, the light trap was effective at least from March to October in the Kita-no-ura Cove. Krill prob-

ably performed diel vertical migration with positive phototaxis in the period when phytoplankton or ice algae are plentiful, since Chl. *a* concentration in the upper 2 m layer is still as high as 1–5  $\mu\text{g/l}$  in March (Fig. 3), and also when the ice algae is available.

*Food abundance and habitat:* ANTEZANA *et al.* (1982) reported that the apparent filtration rate of krill is dependent on Chl. *a* concentration and asymptotic at around 210 ml/krill/h, but abruptly decrease below 3  $\mu\text{g Chl. a/l}$  toward zero at about 1  $\mu\text{g Chl. a/l}$ . Therefore, Chl. *a* concentration less than 0.25  $\mu\text{g/l}$  measured in the Kita-no-ura Cove from April through November is far below the threshold concentration needed for the initiation of filtration. That is, plankton standing stock in the Kita-no-ura Cove is not enough to sustain the krill population from April to November (Fig. 3). But as reviewed by MAUCLINE (1980b), no euphausiid species probably feeds by one method alone. *E. superba* filterfeeds almost exclusively when phytoplankton is plentiful, but when poor they feed on ice algae, zooplankton and detritus and cannibalism is also pointed out (PAVLOV, 1971; KATO *et al.*, 1982; IKEDA and DIXON, 1982b). Seasonal variation of zooplankton abundance was studied with a 0.11 mm mesh Norpac net by TANIMURA (pers. commun.) at Stn. 2 in the Kita-no-ura Cove. Zooplankton density was calculated as an average from surface to the bottom. Two peaks of abundance were observed, *i.e.* 3.8 individ./l mainly composed of copepods in May and 2.9 individ./l, in the late December. The densities from August through early December were below 2 individ./l. Although the average density in the whole water column seemed not enough to sustain the overwintering krill throughout the year, copepodite stages of *Paralabidocera antarctica* make dense swarms (40–60 individ./l) just under or interstices of bottom ice from the late October to November (TANIMURA *et al.*, 1984). These copepodites, together with ice algae, seem to be one of the possible food sources of krill during the daytime in early spring, since both the copepod and krill show positive phototaxis (KAWAGUCHI *et al.*, 1986) and would have frequent chances to encounter each other just under the bottom ice when underwater light is restricted. In shallow regions euphausiids often feed on sea bed material and consequently mud or sediment particles then occur in stomachs (MAUCLINE and FISHER, 1969; BERKES, 1975). This phenomenon was observed in August in this study (Table 3b). In the Kita-no-ura Cove sediment trap observations showed that considerable amounts of fecal materials fall down on the sea bottom in summer. Furthermore, under water SCUBA observation showed that the flakes of ice algae hang down from the undersurface of the fast ice and fall in flakes to the sea bottom in summer (K. WATANABE, pers. commun.). This detritus sustains the rich benthic fauna of the cove and is the most probable food source for krill to overwinter under the fast ice.

The krill in the pelagic zone would starve and be exhausted in April because of the abrupt decrease in phytoplankton abundance (Fig. 3) and the continuous food searching activities with high metabolic rate (Figs. 3, 6). The experimentally starved krill are reported to be sluggish, but continue swimming (IKEDA and DIXON, 1982a). Therefore, krill under the condition of food depletion would gradually sink down to the benthopelagic zone owing to its specific gravity. Krill is also known to “use area-intensive searching and various rapid feeding behaviors to exploit local high food concentrations” (HAMNER *et al.*, 1983). These flexible behaviors of krill and the restricted distribution

of food in their habitat explain the benthopelagic life of this animal overwintering under the ice.

*Feeding and egestion rate:* HAMNER *et al.* (1983) studied the feeding reaction of krill to particles and various chemicals, reporting that chemicals alone trigger the feeding behavior with threshold concentration of  $10^{-5}$  M for histidine, lactic acid, citric acid and acetic acid, but not diatom skeleton alone. This chemically induced feeding reaction would be advantageous mechanism for krill to gain food to exploit local high food concentrations on the sea floor during the dark period.

ANTEZANA (1982) *et al.* reported no significant diel change in egestion and ingestion rates in summer in the laboratory-reared krill. Also in this study, krill were found to feed at night during winter under the ice. Stomach clearance rate of krill was found to be slow in May and July compared with that from August to October. More than 50% of krill still had stomach contents after about 15 hours from collection in May to July (Table 3a). According to ANTEZANA *et al.* (1982), food clearance from the stomach in summer ranges from 2 to 19 hours, usually 6 to 8 hours in more than 50% of krill, although exceptional individuals retained stomach contents more than 7 days. The average rate measured in summer by ANTEZANA *et al.* (1982) would be about twice as high as that estimated in winter in this study. Factors controlling egestion rate are unknown in krill, but in the gammarid amphipod *Orchemene plebs*, starvation is known to cause an increase in retention time of food in the gut from several hours to several days and also to decrease oxygen consumption rate (RAKUSA-SUSZCZEWSKI, 1982). This suggests that low density and quality of food and resulting starvation may be one of the important factors controlling egestion and respiration rate of krill. From August, however, egestion rate, together with oxygen consumption rate, starts to increase in spite of the poor food condition. Of the various environmental factors measured here, the increase in solar radiation only corresponded to the increase in both egestion and oxygen consumption rates. The global solar radiation (MJ/m<sup>2</sup>/day) measured in 1984 at Syowa Station was: February (16.5), March (6.1), April (1.8), May (0.3), June (0.0), July (0.2), August (1.5), September (6.6), October (15.2), November (26.0) December (32.9), indicated almost no light penetration into the water through the sea ice, sometimes covered with snow, from May to July. HOSHIAI (1983) reported the development of ice algae started in late August or at the beginning of September in the snow free area near the Syowa Station when the level of solar radiation was still below 5 MJ/m<sup>2</sup>/day. This suggests that some biologically important change seems to take place in light conditions under the fast ice as early as late August, including the initiation of photosynthetic activity of ice algae which could cause the increases in food searching activity of krill related to its positive phototaxis and metabolic rate. This view was supported by the occurrence of greenish stomach content of krill in August (Table 3b).

*Oxygen consumption rate:* IKEDA and DIXON (1982a) reported the decrease in oxygen consumption rate down to  $0.250 \pm 0.050$  ml/h/g DW in the krill starved for 211 days in the laboratory which is comparable to the minimum rate of  $0.270 \pm 0.061$  measured in July in this study. Although krill in the Kita-no-ura Cove actively feed during the winter, low density and quality of food, together with low temperature below  $-1.75^{\circ}\text{C}$

and almost no light conditions under the fast ice would trigger this decrease in oxygen consumption.

*Condition factor and chemical composition (C, N):* For the interpretation of the monthly changes in fatness, chemical composition and C : N ratio measured in this study, we must consider the duration of the intermoult period in the dark period. The starved krill have been well known to reduce their body size and to continue moulting in laboratory experiments (IKEDA and DIXON, 1982b; IKEDA and THOMAS, pers. commun.). IKEDA and DIXON (1982a) reported that krill can survive without food for 211 days at  $-1^{\circ}\text{C}$  and reduce its size without showing significant changes in wet : dry wt ratio and chemical composition (C, N, P). On the other hand, CLARKE (1976) has considered that no moulting may occur in krill during winter. BUCHHOLZ (1983) doubted the shrinkage of krill in the natural field on the basis of rearing experiment. MAUCLINE (1980b) reviewed moulting of krill and noted that moulting may be more closely controlled by environmental temperature than food abundance. IKEDA and DIXON (1982b) recognized a linear relationship between intermoult period and water temperature within the temperature range of  $-1.0^{\circ}$  to  $3.5^{\circ}\text{C}$ , and supposed a duration of 33.3 days at  $-2^{\circ}\text{C}$  by extrapolation. POLECK and DENYS (1982) also reported that intermolt period was inversely proportional to temperature within a range of  $0.12^{\circ}$  to  $0.48^{\circ}\text{C}$  and further directly proportional to size of krill. Intermolt period was recently found to be food density dependent and sometimes exceeds 50 days, under the starved condition at  $-1.0^{\circ}\text{C}$  (IKEDA, pers. commun.). At present, we have no directly measured data on the duration of the intermolt period of krill kept constantly below  $-1.7^{\circ}$  to  $-1.8^{\circ}\text{C}$ , near freezing point of the sea water. But it is reported based on the laboratory reared krill that the developmental time of embryo and larvae (metamorphosis to calyptops I larvae) can be described with Belehradek's temperature function and the biological zero, that is, the theoretical temperature at which development is infinitely long is slightly less than  $-1.0^{\circ}\text{C}$  (ROSS and QUETIN, 1986). As each developmental step of krill is associated with molting, these results seem to suggest that a rearing experiment involving moulting near the freezing point of seawater is still necessary. This circumstantial evidence, however, suggests that intermolt period of krill in the Kita-no-ura Cove, where environmental temperature is below  $-1.75^{\circ}\text{C}$  from March through November with the maximum of the year  $-1.64^{\circ}\text{C}$  in January, would be longer than that previously measured (14–30 days, IKEDA *et al.*, 1985) owing to very low water temperature, darkness, and low abundance of food.

The moulting and shrinkage of the body would cause the recovery of condition factor or chemical composition of krill under the food limited condition, but within an intermolt period both fatness and chemical composition are considered to be governed by their nutritional condition. Therefore, the monthly changes in fatness and chemical composition observed in this study can be regarded as the average changes in the krill population having a long intermolt period. The considerable amount of scatter was found around each average values and this would be partly due to moulting, though infrequent, in the dark season.

As stated before, krill are expected to be exposed to severe food limitation from April through May (Figs. 3, 5). From May through August they maintained lower

metabolic rate and shifted to a benthopelagic life to feed on detritus on the sea floor. This change in life history strategy associated with food abundance would explain the reason why they show the minimum values for condition factor and C, N content in early May and the slight recovery of the values from late May through August. After August metabolic rate start to increase in spite of low food abundance (Figs. 3, 5), which would account for the slight decrease in CF observed after August to October (Fig. 6).

In terms of CF value and C content, krill taken in May and October were most starved. C and N composition, however, are different between the samples in May and October, *i.e.* both average C and N contents are lowest in May, but in October only C content showed the second lowest value and N content showed the highest average value of the period studied (Fig. 7). There seems to be an apparent difference in metabolic dynamics of krill between fall and spring. In fall, krill seem to use both carbon rich body component such as lipid or carbohydrate and nitrogen rich component such as protein, but with progress of the season they begin to depend much more on carbon rich components. This agrees well with the results of laboratory experiments hitherto reported that starvation causes the depression of ammonia excretion, *i.e.* catabolic break down of protein, in krill (IKEDA and DIXON, 1982a; GEORGE and FIELDS, 1984).

*Overwintering strategies:* The following strategies or behaviors would help *Euphausia superba* to overwinter under the Antarctic coastal fast ice. (1) Control of metabolic rate in relation to food availability, (2) change of habitat from pelagic zone in summer to benthopelagic zone in the dark period in relation to the seasonal change in distributional pattern of food in their habitat, (3) extension of gut clearance time which seems closely related to metabolic rate and probably helpful for effective digestion of low quality food such as detritus, and (4) positive phototaxis which would lead krill to more productive area like open water and snow free fast ice where phytoplankton and ice-algae are plentiful respectively.

The present study deals with krill population in the Antarctic coastal region and its results would be applicable to the shelf area shallower than 200 to 300m which occupy only a small part of ice-covered area. The depth of much of the ice-covered area is far greater than 500m at which depth adult krill is reported to be succumbed to pressure (GEORGE, 1984). If it is true, in the greater part of the ice covered area krill would not be able to lead a benthopelagic life to feed on detritus during the winter. On the other hand, it is also known that Antarctic krill were commonly found in the stomach contents of notothenid fishes such as *Notothenia gibberifrons*, which is a typical benthos feeder, collected by the bottom trawl at the depths of about 800m off Snow Island west of South Shetland Islands (TAKAHASHI, pers. commun.). Furthermore, he collected *E. superba* with a plankton net attached to the bottom trawl to confirm their distribution in the benthopelagic layer, about 800m deep. Problem on the overwintering krill under ice in offshore region is still open as the challenging subject of future work.

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#### References

- ANTEZANA, T., RAY, K. and MELO, C. (1982): Trophic behavior of *Euphausia superba* DANA in laboratory conditions. *Polar Biol.*, **1**, 77–82.
- BERKES, F. (1975): Some aspects of feeding mechanisms of euphausiids crustaceans. *Crustaceana*, **29**, 266–270.
- BUCHHOLZ, F. (1983): Moults and growth in Euphausiids. *Antarctic Nutrient Cycles and Food Webs*, ed. by W. R. SIEGFRIED *et al.* Berlin, Springer, 339–345.
- CLARKE, A. (1976): Some observations on krill (*Euphausia superba* DANA) maintained alive in the laboratory. *Bull. Br. Antarct. Surv.*, **43**, 434–440.
- CLARKE, A. and MORRIS, D. J. (1983): Towards an energy budget for krill; The physiology and biochemistry of *Euphausia superba* DANA. *Polar Biol.*, **2**, 69–86.
- ETTERSHANK, G. (1984): A new approach to the assessment of longevity in the Antarctic krill *Euphausia superba*. *J. Crustacean Biol.*, **4** (spec. No. 1), 295–305.
- FUKUCHI, M., TANIMURA, A. and OHTSUKA, H. (1984): Seasonal change of chlorophyll *a* under fast ice in Lützow-Holm Bay, Antarctica. *Mem. Natl. Inst. Polar Res., Spec. Issue*, **32**, 51–59.
- GEORGE, R. Y. (1984): Ontogenetic adaptations in growth and respiration of *Euphausia superba* in relation to temperature and pressure. *J. Crustacean Biol.*, **4** (spec. No. 1), 252–262.
- GEORGE, R. Y. and FIELDS, J. R. (1984): Ammonia excretion in the Antarctic krill *Euphausia superba* in relation to starvation and ontogenetic stages. *J. Crustacean Biol.*, **4** (spec. No. 1), 263–272.
- HAMNER, W. M., HAMNER, P. P., STRAND, S. W. and GILMER, R. W. (1983): Behavior of Antarctic krill *Euphausia superba*; Chemoreception, feeding, schooling, and molting. *Science*, **220**, 433–435.
- HOSHIAI, T. (1983): Autumnal proliferation of ice-algae in Antarctic sea-ice. *Antarctic Nutrient Cycles and Food Webs*, ed. by W. R. SIEGFRIED *et al.* Berlin, Springer, 89–92.
- IKEDA, T. and DIXON, P. (1982a): Body shrinkage as a possible over-wintering mechanism of the Antarctic krill, *Euphausia superba* DANA. *J. Exp. Mar. Biol. Ecol.*, **62**, 143–151.
- IKEDA, T. and DIXON, P. (1982b): Observation on moulting in Antarctic krill (*Euphausia superba* DANA). *Aust. J. Mar. Freshwater Res.*, **33**, 71–76.
- IKEDA, T., DIXON, P. and KIRKWOOD, K. (1985): Laboratory observations of moulting, growth and maturation in Antarctic krill (*Euphausia superba* DANA). *Polar Biol.*, **4**, 1–9.
- KATO, M., SEGAWA, S., TANOUE, E. and MURANO, M. (1982): Filtering and ingestion of the Antarctic krill, *Euphausia superba* DANA. *Trans. Tokyo Univ. Fish.*, **5**, 167–175.
- KAWAGUCHI, K., MATSUDA, O., ISHIKAWA, S. and NAITO, Y. (1986): A light trap to collect krill and other micronektonic and planktonic animals under the Antarctic coastal fast ice. *Polar Biol.*, **6**, 37–42.
- MAUCLINE, J. (1980a): Measurement of body length of *Euphausia superba* DANA. *BIOMASS Handb.*, 37–42.
- MAUCLINE, J. (1980b): The biology of mysids and euphausiids. *Adv. Mar. Biol.*, **18**, 1–681.
- MAUCLINE, J. and FISHER, L. R. (1969): The biology of euphausiids. *Adv. Mar. Biol.*, **7**, 1–454.
- PAVLOV, V. Y. (1971): On the feeding habits of *Euphausia superba* DANA. *Proceedings of Joint Oceanographic Assembly*, ed. by M. UDA. Tokyo, Japan Society for the Promotion of Science, 469–471.
- POLECK, T. P. and DENYS, C. J. (1982): Effect of temperature on the molting, growth and maturation

- of the Antarctic krill *Euphausia superba* (Crustacea: Euphausiacea) under laboratory conditions. *Mar. Biol.*, **70**, 255–265.
- RAKUSA-SUSZCZEWSKI, S. (1982): The biology and metabolism of *Orchemene plebs* (HURLEY 1965) (Amphipoda: Gammaridea) from McMurdo Sound, Ross Sea, Antarctic. *Polar Biol.*, **1**, 47–54.
- ROSS, R. M. and QUETIN, L. B. (1986): How productive are Antarctic krill? *BioScience*, **36**(4), 264–268.
- STRICKLAND, J. D. H. and PARSONS, T. R. (1972): A practical handbook of seawater analysis. *Bull. Fish. Res. Board Can.*, **167**, 310 p.
- TANIMURA, A., MINODA, T., FUKUCHI, M., HOSHIAI, T. and OHTSUKA, H. (1984): Swarm of *Paralabidocera antarctica* (Calanoida, Copepoda) under sea ice near Syowa Station, Antarctica. *Nankyoku Shiryô (Antarct. Rec.)*, **82**, 12–19.

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