Mem. Natl Inst. Polar Res., Spec. Issue, **44**, 96-106, 1986

FEEDING BEHAVIOR OF THE ANTARCTIC KRILL, *EUPHAUSIA SUPERBA* DANA
II. EFFECTS OF FOOD CONDITION ON PARTICLE SELECTIVITY

Haruto Ishii*

Tokyo University of Fisheries, 5-7, Konan 4-chome, Minato-ku, Tokyo 108

Abstract: Effects of particle size distribution, total particle concentration, and animal size on selective feeding of the Antarctic krill, *Euphausia superba* Dana, were studied using natural particles as food. Percent particle retention efficiency calculated from the filtering rate for each particle size spectrum increased abruptly for large size particles. This selective feeding for large particles was apparent regardless of abundance of smaller particles. However, the minimum particle size with 50% retention efficiency (half-retention size) increased with increasing total particle concentration. These results suggest that the feeding of the krill shows intensive selection for large particles when food is abundant, but its feeding is rather passive when food is scarce. This flexible feeding seems to be an adaptive behavior to obtain the energy more effectively in the food scarce ocean.

1. Introduction

Heterogeneous distribution of phytoplankton and zooplankton is commonly observed in the ocean (*e.g.* Mullin and Brooks, 1976). For herbivorous plankton in the food scarce oceanic water, it is very important to encounter and utilize phytoplankton-rich waters. In this connection, variable nature of particle size selectivities of zooplankton with food condition is thought as a strategy to obtain required energy effectively under the condition of heterogeneous food distribution.

Although the Antarctic krill, *Euphausia superba* Dana, are believed to perform selective feeding (Meyer and El-Sayed, 1983; Boyd *et al.*, 1984; Morris, 1984; Ishii *et al.*, 1985), there arise questions as to whether the mechanism of selective feeding is due to passive filtering (Boyd *et al.*, 1984) or active searching for suitable food particles due to chemical stimulus (Hamner *et al.*, 1983). Furthermore, the question of whether or not intensity of selectivity changes with total particle concentration (Richman *et al.*, 1977; Cowles, 1979) or developmental stage (Allan *et al.*, 1977; Uye and Kasahara, 1983), has not been reported on the krill.

The present experiments were made in order to clarify the effects of particle size distribution, total particle concentration, and animal size on the intensity of particle selectivity of the krill.

---

* Present address: Laboratory of Oceanography, Faculty of Agriculture, Tohoku University, 1-1, Tsutsumidori-Amamiyamachi, Sendai 980.

2. Materials and Methods

Experiments were carried out on board the T.V. Umitaka Maru during the cruise to the Antarctic Ocean (SIBEX) in the austral summer of 1983/84 (Fig. 1). Live krill were collected from five swarms encountered in the waters south of 64°S. They were immediately transferred to a 500-liter plastic container with natural seawater and maintained for at least 24 hours under ambient conditions until experiments were commenced. The krill used for the experiments varied in size and were divided arbitrarily into five size groups according to their origin; small (juvenile; 11.2 to 19.6mg dry weight), medium (juvenile; 28.4 to 49.7mg), large I (81.6 to 112.1mg), large II (105.6 to 269.8mg), and large III (173.4 to 360.0mg) (Table 1). The last three groups consisted of both males and females.

Incubation seawater was pumped up from the sea surface by means of a plankton pumping system with Ebara DVS submerged semi-vortex pump (Omori, 1985). The natural seawater was either diluted with GF/C filtered seawater or gently concentrated

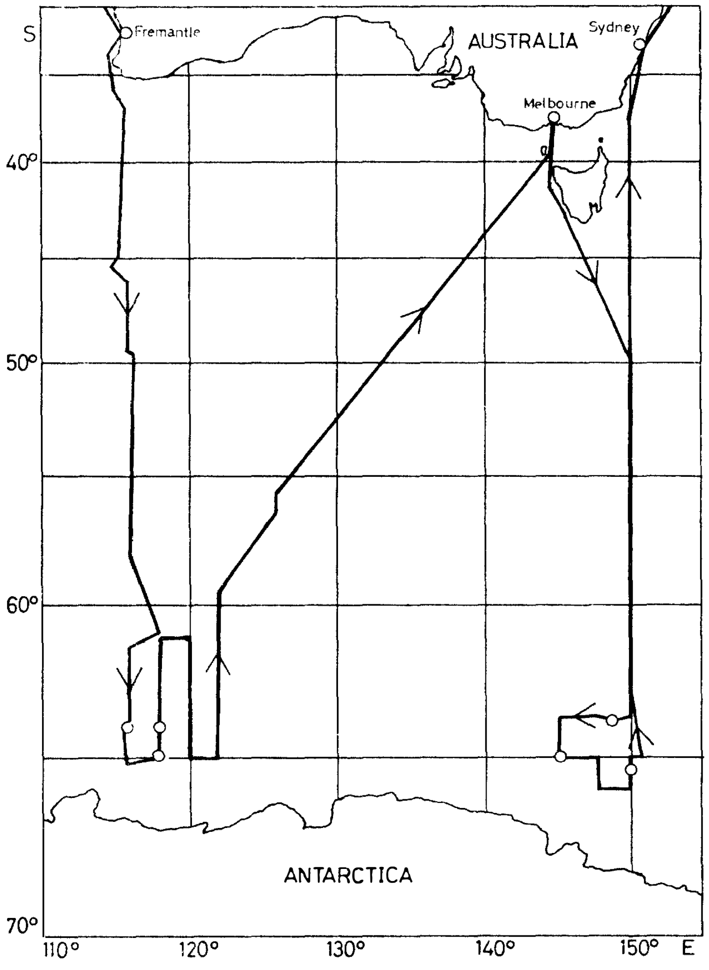

Fig. 1. Cruise track of the T. V. Umitaka Maru to the Antarctic Ocean (SIBEX) in the austral summer of 1983/84. Sampling locations are indicated by open circles.

Table 1. Euphausia superba. *Total particle concentration, equivalent spherical diameter (ESD) of upper limit and volumetric peak in initial incubation water, and the ESD of maximum ingestion.*

Exp. No.	Size group	Runs (Number of individuals)	Total particle concentration ($\times 10^3$ μgC/l)	ESD (μm)		
				Upper limit	Volumetric peak	Maximum ingestion
1	Small	4	0.22	38.15	14.88	27.64
2		4	0.33*	72.69	62.64	62.64
3		4	1.10	72.69	48.89	56.73
4		4	1.21	69.17	15.63	55.34
5	Medium	3	0.17	25.66	23.24	23.24
6		4	0.18*	50.11	50.11	50.11
7		5	0.62	50.11	50.11	50.11
8		6	1.06	44.27	14.88	23.24
9	Large I	2	0.15	32.08	26.97	32.08
10		3	0.24*	69.17	69.17	69.17
11		2	0.66	72.69	64.21	64.21
12		3	1.63	67.48	15.25	15.25
13	Large II	1	0.18	50.11	50.11	50.11
14		2	0.29*	58.15	17.69	58.15
15		3	0.68	72.69	72.69	72.69
16		2	1.46	72.69	64.21	64.21
17	Large III	3	0.16	27.64	27.64	27.64
18		2	0.17	42.13	42.13	42.13
19		3	0.21*	41.10	41.10	39.10
20		4	0.61	56.73	16.43	56.73
21		2	1.02	67.48	14.88	67.48
22		4	3.39	69.17	16.84	16.84

* Particle concentrations without dilution or concentration processes.

by 30μm mesh net. Thus, I prepared incubation waters with particle concentrations ranging from 0.13×10^9 to $29.53 \times 10^9 \mu\mathrm{m}^3/l$.

Feeding rates of the krill were measured by the balance method (Omori and Ikeda, 1984). One to four individuals were immersed in each dark plastic bottle (2-liter) filled with incubation water, and placed on a grazing wheel rotating horizontally at 1 rpm. The temperature was controlled between -1.0 and 3.8°C by circulation of the surface seawater around the bottles. After 12 hour incubation, about 50 ml of water was siphoned out of each bottle and the concentration and size distribution of particles between 4.00 and 72.69μm ESD (equivalent spherical diameter) were determined with an ELZONE Particle Counter model 80XY (120μm orifice and a 128-channel analyzer interfaced with a teletype; model TP-140). Subsequently, 250 ml of water was fixed with Rudhe's iodine for later microscopic analysis. Microscopic analysis was made under an inverted microscope by the sedimentation method.

Ingestion rate and filtering rate were calculated using the equation from Frost (1972). I calculated percent particle retention efficiency (R_i) from the filtering rate on a given particle size ($i\,\mu$m) spectrum using the following equation,

$$R_i\,(\%)=\frac{F_i}{F_{\max}}\times 100,$$

where $F_{\max}$ refers to the maximum filtering rate at a given particle size spectrum over the particle distribution and F_i is the filtering rate of a certain particle size i. If all particle sizes were equally filtered, R_i values are all 100%. Therefore, the retention efficiency is considered to be an index of the selectivity for each particle size.

After the experiments, the krill were rinsed with isotonic ammonium formate and kept frozen. An aliquot of incubation water was filtered through a pre-combusted GF/C filter and also kept frozen. In the land laboratory, the krill were lyophilized and weighed. Carbon contents of the krill and of particles in the incubation water were analyzed using a Yanaco CHN Corder model MT-3.

3. Results

Particle size distribution in natural seawater varied with sampling location and concentration or dilution processes. Microscopic analysis revealed that small particles (<*ca.* 5 μm ESD) were almost entirely detritus, but most of the particles larger than *ca.* 12 μm were live diatoms. In most samples, pennate diatoms were more dominant in both number and volume than centric diatoms. *Fragilariopsis antarctica* (5–16 μm ESD with mode size of *ca.* 10 μm) was especially numerous throughout the samples. In some other samples, *Rhizosolenia* spp. (17–52 μm ESD with mode size of *ca.* 32 μm) were volumetrically abundant. Coupled analyses by microscope and electronic particle counter revealed that the peak of the size class, *ca.* 10 μm, in the particle size spectrum consisted of *F. antarctica*, and particulary those larger than 30 μm consisted of *Rhizosolenia* spp.

I expressed the particle size distribution in initial incubation water by the ESD of upper limit and volumetric peak (Table 1). The ESD of the maximum ingestion peak is also shown. Except for one experiment (Exp. 19), it was the same or larger than the ESD of the volumetric peak of initial incubation water. For example, in initial incubation waters having volumetric peaks in smaller sizes (Exp. 1, 4, 8, 12, 14, 20, 21, and 22; 14.88–17.69 μm), the krill more intensively ingested the particles larger than these volumetric peaks.

The relationship between carbon content (C: μgC/l) and particle volume (P: $\times 10^9$ μm^3/l) was expressed by the equation,

$$C=(110\times P)+140. \quad (r=0.98)$$

Then, I calculated the particle concentrations in terms of carbon. Percent particle retention efficiency for each particle size spectrum with different animal sizes under different total particle concentrations (Figs. 2–6) clearly showed the intensive selection for large particles. There was a remarkable difference between the retention efficiency in larger particles (>80% retention efficiency) and that in smaller particles (<10%) through all sizes of the krill examined.

In the small krill (Fig. 2), the retention efficiency of small particles (<15 μm ESD) was always lower than 10%. It increased at particle size of 15 to 25 μm in experiments with two low particle concentrations, and at about 50 μm with two high particle con-

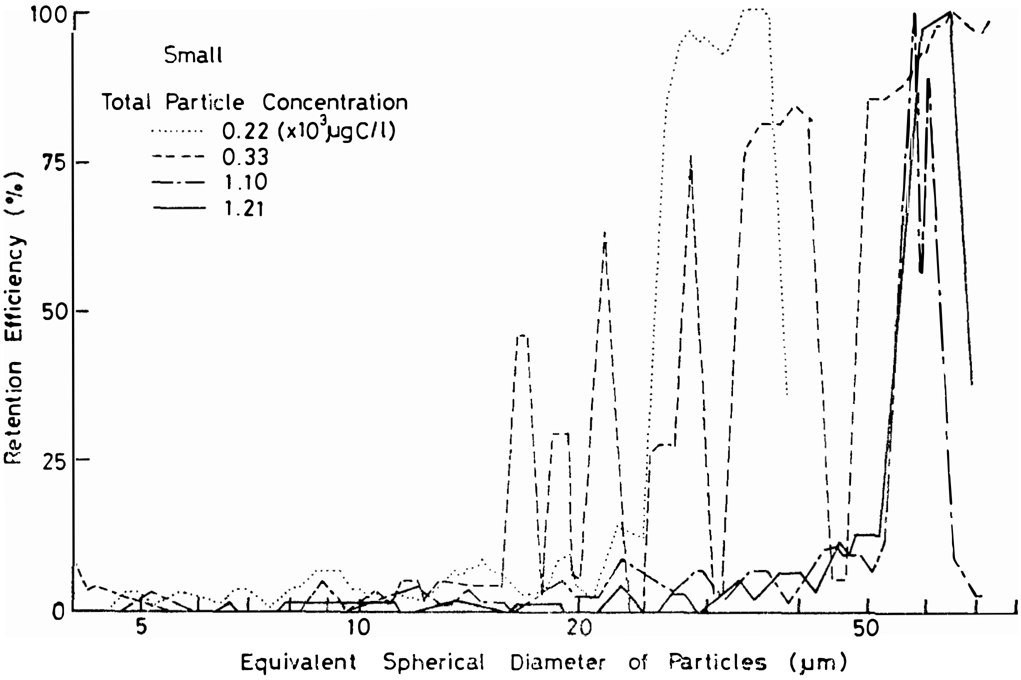

Fig. 2. Euphausia superba. *Percent particle retention efficiency for every particle size in small krill (11.2 to 19.6 mg dry wt).*

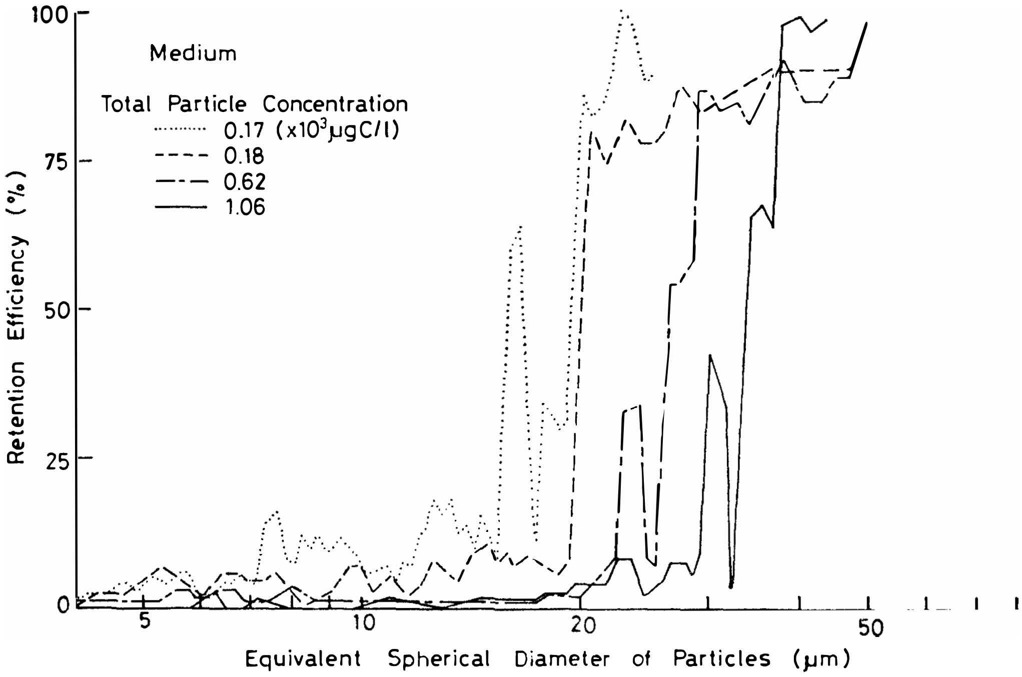

Fig. 3. Same as Fig. 2 except for medium krill (28.4 to 49.7 mg dry wt).

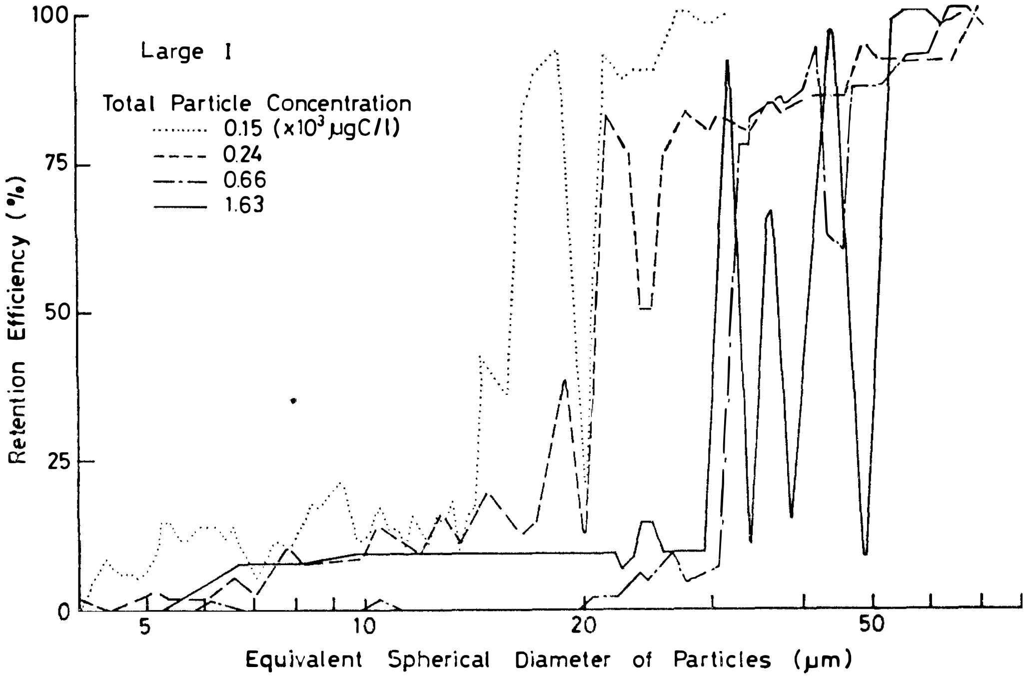

Fig. 4. Same as Fig. 2 except for large krill (large I; 81.6 to 112.1 mg dry wt).

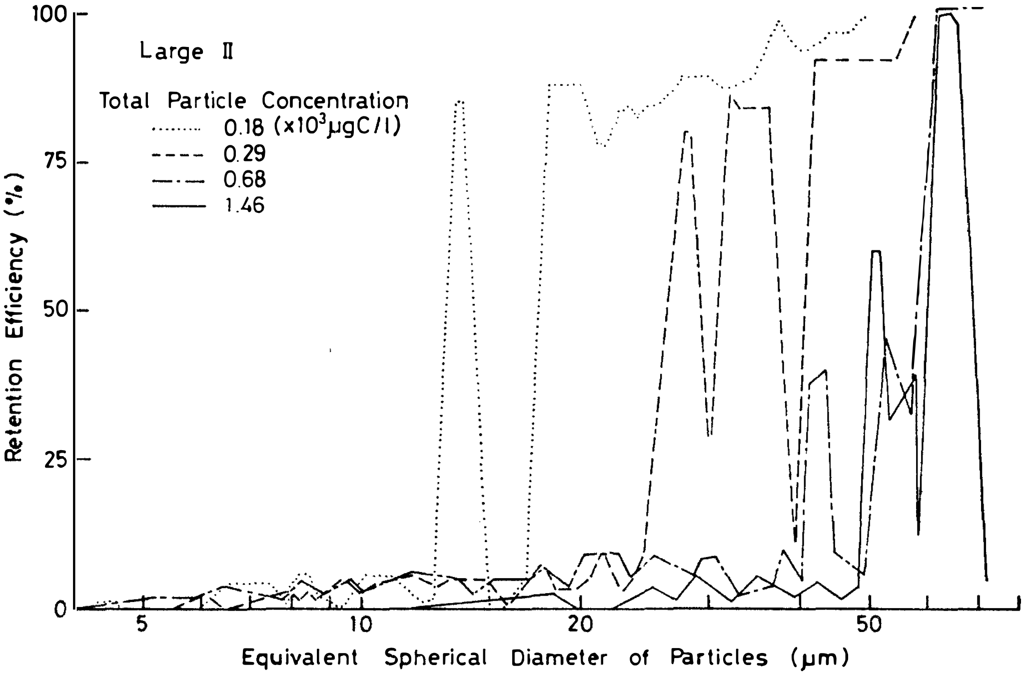

Fig. 5. Same as Fig. 2 except for large krill (large II; 105.6 to 269.8 mg dry wt).

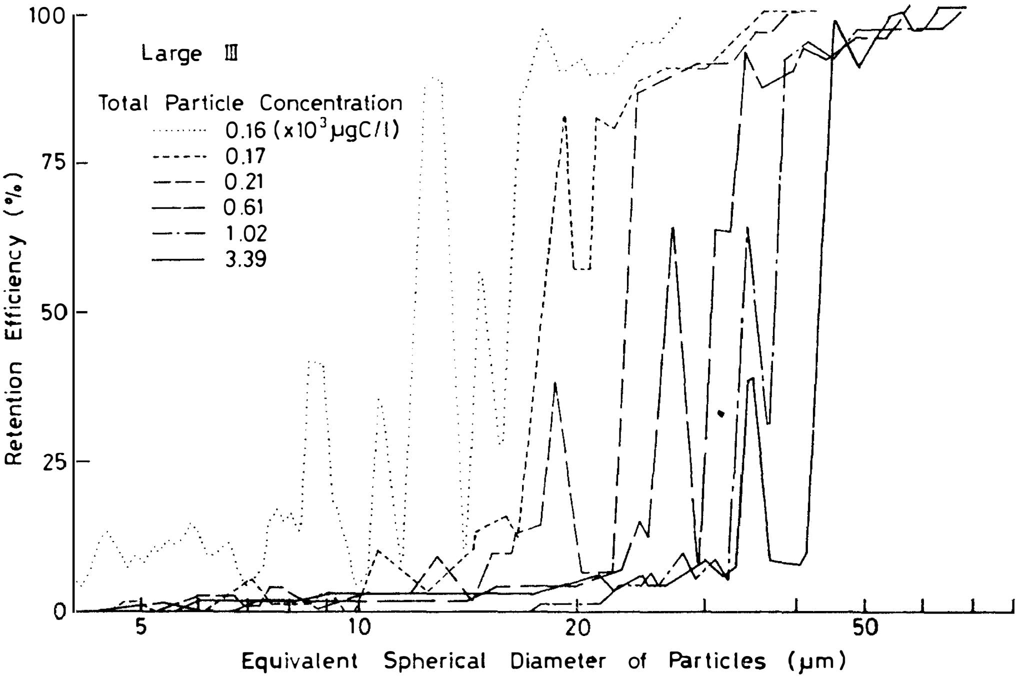

Fig. 6. Same as Fig. 2 except for large krill (large III; 173.4 to 360.0 mg dry wt).

centrations. With the particle concentration of $0.33\times10^3\mu$gC/*l*, the retention efficiency moderately increased.

In the medium krill (Fig. 3), the retention efficiency increased abruptly at particle size larger than 20μm in all four experiments. The marginal size between high and low efficiencies increased with the increase in total particle concentration. In particle size classes smaller than 20μm, the retention efficiency at the lowest concentration was higher than that at the higher concentration.

In the large krill (Figs. 4–6), the retention efficiency abruptly increased from small particles to large ones in most of the experiments. For large III group at the lowest particle concentration ($0.16\times10^3\mu$gC/*l*), the marginal size was not clearly defined: relatively high retention efficiency occurred even below 10μm. With increasing total particle concentration, the marginal size also increased as observed in the medium krill. This trend was most obvious for large III group.

I used *the minimum particle size with 50% retention efficiency* (half-retention size) as an index of the marginal size between larger particles with a high retention efficiency and smaller particles with a low efficiency. If 100% of large particles with the maximum filtering rate are ingested, 50% of particles at half-retention size will be ingested by the krill in a given particle range. Larger half-retention size means that particle selection is more intensive at larger particles, and smaller half-retention size means that particle selection is more extensive. This index can show us the change of the retention efficiency spectrum and particle selectivity.

The relationship between the total particle concentration and the half-retention size for all size groups of the krill is shown in Fig. 7. The half-retention size for the krill increased with increasing total particle concentration. It was lowest (12 to 18μm) at

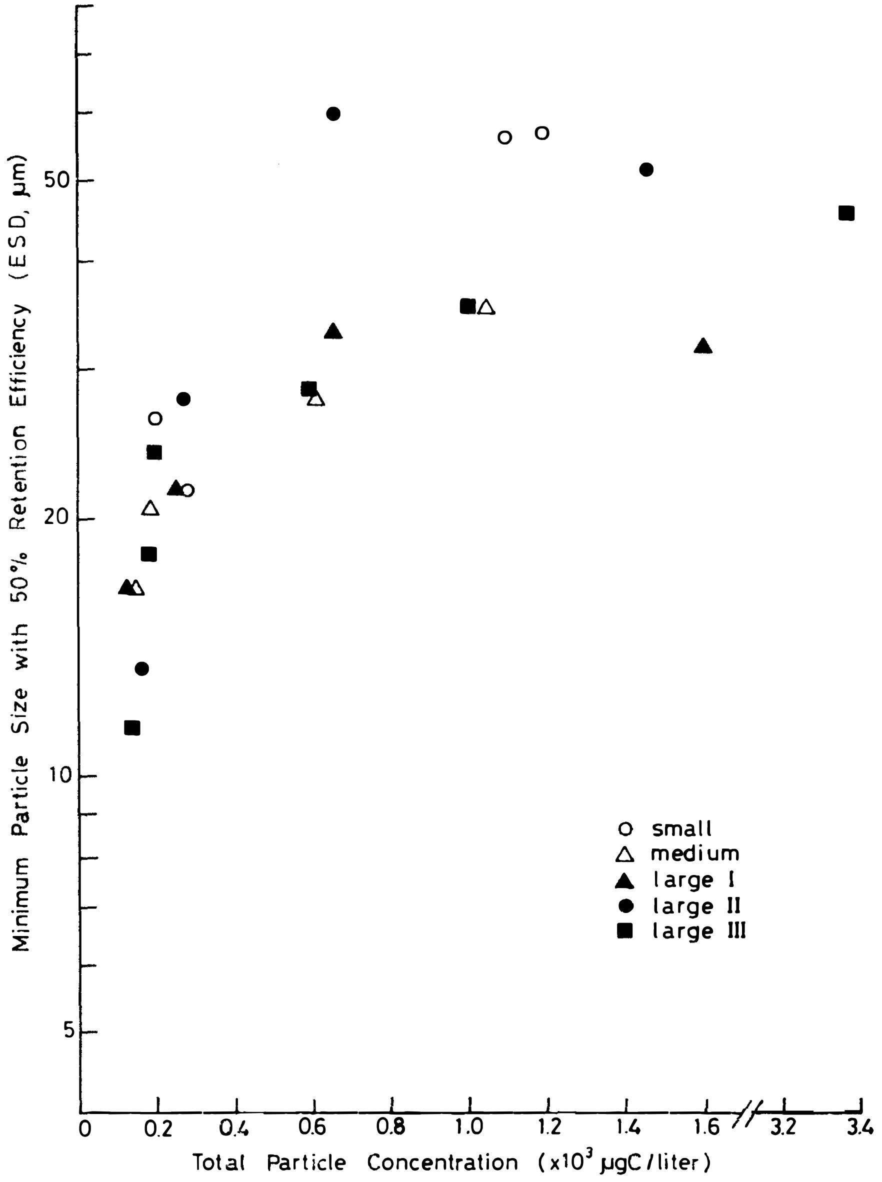

Fig. 7. Euphausia superba. *The relationship between the total particle concentration and the minimum particle size (ESD) with 50% retention efficiency (half-retention size).*

concentrations below $0.2\times10^3\mu gC/l$. On the other hand, it ranged 28 to 60 µm at concentrations above $0.6\times10^3\mu gC/l$. However, the relationship between the krill size and the half-retention size was not clear.

4. Discussion

Feeding behavior of marine planktonic copepods with various types of natural particle distribution has been studied. POULET (1974) reported that *Pseudocalanus minutus* ingested more intensively on particles corresponding to the volumetric peak. And RICHMAN *et al.* (1977) showed that copepods (*Eurytemora affinis*, *Acartia tonsa*, and *A.*

clausi) firstly fed on larger particles for a given size range. In this study, unlike the observation by POULET (1974), particles of the volumetric peak, especially in the medium particle size class, were not intensively ingested by the krill. The preference of larger particles by the krill was more like the observation with copepods by RICHMAN *et al.* (1977). ISHII *et al.* (1985) also reported the krill's preference of large particles by a statistical comparison of size distributions in ingested particles with that in natural incubation seawater. The krill's selectivity for large particles was also reported by a microscopic analysis of incubation water that the krill fed on net plankton ($>20\,\mu$m) more effectively than nanoplankton ($<20\,\mu$m) (MEYER and EL-SAYED, 1983).

A mechanical model of feeding behavior has been derived to explain the selection for large particles by copepods (BOYD, 1976; NIVAL and NIVAL, 1976). For the krill MCCLATCHIE and BOYD (1983) filmed the setae of the thoracic legs used as a filtering basket and calculated the predicted particle retention efficiency from cumulative frequency of mesh size which reached 50% at *ca.* 8 μm and an upper asymptote at *ca.* 12 μm. BOYD *et al.* (1984) estimated the retention efficiency derived from the filtering rate in each particle size and it almost coincided with the above prediction from the mesh interval. However, BOYD *et al.* (1984) used a particle size distribution with the upper limit of 30 μm and the total particle concentration was obscure. As shown in this study, various retention efficiencies were observed above the predicted upper asymptote, *ca.* 12 μm, suggesting that the feeding behavior of the krill is not solely passive.

Another model of particle selection behavior, *i.e.* chemical feeding (POULET and MARSOT, 1980), may explain the results of the present study, that the half-retention size by the krill was larger than the mesh size of feeding appendages, 4 to 12 μm (MCCLATCHIE and BOYD, 1983). Active selection of large particles seems to be advantageous in order to obtain the energy with little effort. In addition, since living particles including diatoms were almost entirely categorized in the large size class in this study, the active selection for large nourished particles is more effective. This is supported by IKEDA and DIXON (1984), who demonstrated a decline of ingestion and filtering rates of the krill for beads in contrast with phytoplankton or *Artemia* nauplii. HAMNER *et al.* (1983) also observed food gathering behavior of the krill in response to chemical cues, and ANTEZANA *et al.* (1982) also found active collection of food by the iterative extension-retraction of the food basket. This active selective feeding may imply the existence of chemo or mechano receptors by the krill.

The half-retention size seems to be a suitable index for the intensity of selectivity of large particles. This index changed with the change of total particle concentration. When the particle concentration was high, the krill actively fed on large particles, showing a large half-retention size. When the particle concentration was low, the krill had a small half-retention size. The lowest half-retention size was 10 μm which is close to the half-retention size predicted from mesh size, *ca.* 8 μm (MCCLATCHIE and BOYD, 1983). Increase of half-retention size with increasing total particle concentration indicates that the krill can change the feeding behavior from intensive selection for large particles at high concentrations to almost passive at low concentrations. Similar feeding behavior has been reported by COWLES (1979) for three calanoid copepods which showed selective feeding at high particle concentrations but showed decreased selectivity at low particle concentrations. RICHMAN *et al.* (1977) also observed copepods firstly feeding on large particles, then they successively switched to biomass peaks of smaller particles, and finally depended on the original particle distribution without selection. It was found that the particle concentration of averaged ambient seawater ranged between 184 and 331 μgC/*l* during this experiment and the krill would not maintain their body and population in this concentration (ISHII *et al.*, 1985). In food scarce condition, probably in the greater part of oceanic water, the krill would feed in a passive mode to obtain as much food as possible. Since the effect of animal size on particle selectivity was not clear, it was thought that there was no difference of particle size preference between juvenile and adult krill.

Retention efficiency may be affected by many factors, such as total particle concentration, particle quality, and particle size. If the krill perceived a larger prey, would the krill be able to catch and ingest the prey? I observed a large krill fed on a small one immediately after its molting in a filtered seawater. Moreover, large and non-moving particles, debris and moults of zooplankton including the krill, have been observed so regularly in the stomach of a live krill (HOPKINS, 1985). Flexibility of feeding mode, depending on food condition, seems to be an adaptive behavior in the food scarce ocean.

Acknowledgments

I am most grateful to Dr. M. OMORI for his critical and valuable suggestions throughout this study. I appreciate two anonymous referees who offered constructive comments on this manuscript. I would like to thank Dr. M. MURANO and the personnel of the T.V. UMITAKA MARU for the cooperation and assistance in experiments.

References

ALLAN, J. D., RICHMAN, S., HEINLE, D. R. and HUFF, R. (1977): Grazing in juvenile stages of some estuarine calanoid copepods. Mar. Biol., **43**, 317–331.

ANTEZANA, T., RAY, K. and MELO, C. (1982): Trophic behavior of *Euphausia superba* DANA in laboratory conditions. Polar Biol., **1**, 77–82.

BOYD, C. M. (1976): Selection of particle sizes by filter-feeding copepods; A plea for reason. Limnol. Oceanogr., **21**, 175–180.

BOYD, C. M., HEYRAUD, M. and BOYD, C. N. (1984): Feeding of the Antarctic krill *Euphausia superba*. J. Crust. Biol., **4**, 123–141.

COWLES, T. J. (1979): The feeding response of copepods from the Peru upwelling system; Food size selection. J. Mar. Res., **37**, 601–622.

FROST, B. W. (1972): Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr., **17**, 805–815.

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.

HOPKINS, T. L. (1985): Food web of an Antarctic midwater ecosystem. Mar. Biol., **89**, 197–212.

IKEDA, T. and DIXON, P. (1984): The influence of feeding on the metabolic activity of Antarctic krill (*Euphausia superba* DANA). Polar Biol., **3**, 1–9.

ISHII, H., OMORI, M. and MURANO, M. (1985): Feeding behavior of the Antarctic krill, *Euphausia superba* DANA. I. Reaction to size and concentration of food particles. Trans. Tokyo Univ. Fish., **6**, 117–124.

McCLATCHIE, S. and BOYD, C. M. (1983): Morphological study of sieve efficiencies and mandibular surfaces in the Antarctic krill, *Euphausia superba*. Can. J. Fish. Aquat. Sci., **40**, 955–967.

Meyer, M. A. and El-Sayed, S. Z. (1983): Grazing of *Euphausia superba* Dana on natural phytoplankton populations. Polar Biol., **1**, 193–197.

Morris, D. J. (1984): Filtration rates of *Euphausia superba* Dana; Under- or overestimates? J. Crust. Biol., **4**, 185–197.

Mullin, M. M. and Brooks, E. R. (1976): Some consequences of distributional heterogeneity of phytoplankton and zooplankton. Limnol. Oceanogr., **21**, 784–796.

Nival, P. and Nival, S. (1976): Particle retention efficiencies of an herbivorous copepod, *Acartia clausi* (adult and copepodite stages); Effect on grazing. Limnol. Oceanogr., **21**, 24–38.

Omori, M. (1985): Vortex/semi-vortex submerged pump for collecting good samples of zooplankton. Bull. Mar. Sci., **37**, 772–773.

Omori, M. and Ikeda, T. (1984): Methods in Marine Zooplankton Ecology. New York, J. Wiley, 332 p.

Poulet, S. A. (1974): Seasonal grazing of *Pseudocalanus minutus* on particles. Mar. Biol., **25**, 109–123.

Poulet, S. A. and Marsot, P. (1980): Chemosensory feeding and food-gathering by omnivorous marine copepods. Evolution and Ecology of Zooplankton Communities, ed. by W. C. Kerfoot. New England, University Press, 198–218.

Richman, S., Heinle, D. R. and Huff, R. (1977): Grazing by adult estuarine calanoid copepods of the Chesapeake Bay. Mar. Biol., **42**, 69–84.

Uye, S. and Kasahara, S. (1983): Grazing of various developmental stages of *Pseudodiaptomus marinus* (Copepoda) on naturally occurring particles. Bull. Plankt. Soc. Jpn., **30**, 211–222.

(*Received May 9, 1986; Revised manuscript received September 22, 1986*)