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Feeding of Antarctic krill *Euphausia superba* in Weddell Sea

ABSTRACT: During austral summer phytoplankton is the main component of food of *E. superba* postlarval stages. Diatomeae: *Thalassiosira* spp., *Nitzschia* spp. and tiny Pennatae constitue 98% of all consumed food particles. 91% of algae consumed were of 8–40 µm, and their mean size is 21.4 µm. The mean amount of algae found in of *Euphausia superba* was about 1700 per individual. The differences in species composition and the size of algae eaten by juvenes, preadult and adult individuals decrease the food competition between particular age groups of *E. superba*.

Key words: Antarctic, *Euphausia superba*, food composition

Introduction

During austral summer, in the period of phytoplankton bloom in the Southern Ocean, phytoplankton is the main component of food of *Euphausia superba*. This concerns mainly Diatomeae, Silicoflagellata, Chrysophyceae. Less significant components of *E. superba* diet are Dinoflagellata, Foraminifera and Radiolaria (Barkley 1940, Hart 1942, Marr 1962, Nemoto 1968, Ligowski 1982, Maciejewska, in press).

The density of the filtering apparatus setae allows to filter food particles (phytoplankton cells) of the size of 10 µm (Barkley 1940, Nemoto 1968), or, according to C.M. Boyd, Heyraud and C.N. Boyd (1984), even 3–4 µm. Most efficiently filtered are bigger particles — with the 20–30 µm diameter (Morris 1984, Ishi, Omori and Murano 1985). During the food uptake the most important is the size of food particles, whereas their shape and chemical composition are not so important, (Clarke and Morris 1983, C.M. Boyd, Heyraud and C.N. Boyd 1984, Morris 1984, Quetin and Ross 1985).

So far, there are no data in the literature on the relation of *E. superba* food composition to the size and age of individuals. Only Tanoue (1985a, 1985b), on the basis of the faeces' chemical content, inferred that "small krill" feeds only on diatoms, and "big krill" feeds also on other phytoplankton groups.

The aim of this work was an attempt to answer the question, if *Euphausia superba* individuals of different size and age feed on the same kind of food or on different fractions of food particles available in the natural environment, in this case, phytoplankton.

To answer this question an analysis of stomach contents of *E. superba* individuals of different size and age (the degree of maturity) was carried out. Algae found in the stomachs were divided into well recognized indicator groups (e.g. tiny Pennatae, *Thalassiosira* spp., Silicoflagellatae gen. sp. etc.). This allowed for relatively easy qualitative and quantitative differentiation of the food composition of particular krill age groups. The taxa mentioned should be regarded only as indicators of the food type, and not as full list of phytoplankton species on which Antarctic krill feeds. Such list were thoroughly worked out by Barkley (1940), Kittel and Ligowski (1980) and Ligowski (1982).

The choice of indicator taxa was induced by the easiness of their identification in water slides. Low number of such indicator taxa allowed for quick noticing of significant differences in food composition of particular age groups.

Material and methods

Animals for the analysis of stomach content were caught during austral summer in the eastern part of the Weddell Sea.

Animals were caught with a Melnikov plankton trawl (Melnikov 1993) in the 0–7 m layer during night. Immediately after catching the animals were preserved in 4% formaline and next their stomachs were dissected. Algae cells from the stomach content were counted and identified in the water slides under a microscope (magnification for counting — 160 ×, for identification — 400 ×). The following indicator taxa were chosen: *Thalassiosira* spp., *Nitzschia* spp. (*Fragilariopsis* complex), Pennatae gen.sp., *Exuviella* sp., *Coscinodiscus* spp., Silicoflagellatae gen.sp., *Navicula* spp., *Thalassiothrix antarctica* Cl. et Grun., *Distephanus* sp., *Chaetoceros* spp., *Rhizosolenia* spp, *Asteromphalus* sp., and the group of unidentified species ("others").

Food particles (phytoplankton cells), belonging to particular indicator groups (taxa), were counted and their length was measured. Only these cells were counted of which more than a half of their original size was left. Other cell fragments were regarded to be the parts of the cells of better condition. During this kind of counting the cells which were totally crushed were not counted.

In the case of the damaged cells the remaining parts were measured and on this basis the original size of undamaged cells filtered by the animal was estimated.

According to their size food particles found in *E. superba* stomachs were arbitrarily divided into subsequent classes: smaller than 10 μm, in the range from 10 to 90 μm — every 10 μm class, in the range from 90 to 150 μm — every 30 μm class, in the range from 150 to 350 μm — every 50 μm class, then the class 350 – 900 μm and then the class over 900 μm.

Due to the applied method (water slides) only food particles (phytoplankton cells) bigger than 8 μm were taken under consideration.

The data obtained were presented as mean values for three krill age groups: juvenes (length 21 – 28 mm, mean wet weight 0.10 g), preadults (29 – 39 mm and 0.27g, respectively), adults (40 – 49 mm and 0.71g, respectively). The dependencies between number and size of food particles and the animals body length was calculated using the least squares method.

The analysis of food composition for 6 juvenes, 7 preadult and 7 adult individuals was carried out.

This work was done on board of r/v "Dmitry Mendeleev".

Results

— The qualitative food content

During austral summer (February 1989), the main mass of *Euphausia superba* food was composed of phytoplankton: diatoms and Flagellatae (Tab. 1). The majority of the tiny diatoms (tiny Pennatae, *Thalassiosira, Nitzschia*) were only slightly damaged, whereas big cells (*Navicula, Thalassiothrix*) were damaged in great part.

Table I

Indicator taxa of phytoplankton found in stomachs of *Euphausia superba* (Weddell Sea, February 1989)

Bacillariophyceae
Centricae
Thalassiosira spp.
Thalassiothrix antarctica Cl. et Grun.
Chaetoceros spp.
Rhizosolenia spp.
Coscinodiscus spp.
Asteromphalus sp.
Pennatae
Nitzschia spp. (*Fragilariopsis* complex)
Navicula spp.
Pennatae gen.sp.
Silicoflagellatae
Distephanus sp.
Silicoflagellatae gen.sp.
Dinoflagellatae
Exuviaella sp.
Gymnodinium sp.

Table II

Size of food particles (algae) in the stomachs of *Euphausia superba* (Weddell Sea, February 1989)
Number of cells per animal, mean values for all 20 individuals of various age

Takson	Size class (μm)													%
	>10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–120	120–150	150–200	200–<900*	
Thalassiosira spp.	65.2	136.8	37.0	1.1	1.9	1.3	0.5	0.2	0.1					61.0
Nitzschia spp.		3.1	24.0	35.2	14.1	7.4	0.1		0.1					20.8
Pennatae gen.sp.			4.4	53.4	2.0	3.8		0.4	0.6	0.4		0.8		16.2
Exuviaella sp.		0.1	3.0											0.8
Coscinodiscus spp.		0.3	0.4	1.1	0.4	0.1	0.1	0.1		0.1				0.7
Silicoflagellatae gen.sp.		0.4	1.5	0.1										0.5
Thalassiothrix antarctica											0.1	0.1	0.9	0.2
Navicula spp.		0.2	0.3		0.1	0.3								0.3
Distephanus sp.		0.1	0.8											0.2
Chaetoceros sp.			0.1	0.5		0.1								0.2
Rhizosolenia spp.									0.1					0.0
others		0.5	0.1											0.2
Mean	65.2	142.7	71.7	91.5	18.8	13.0	0.8	0.7	0.9	0.5	0.1	0.9	0.9	
%	16.0	34.8	17.6	22.5	4.6	3.2	0.2	0.2	0.2	0.1	0.0	0.2	0.2	

* Classes 200–250, 350–900 and <900 were not numerous and were collected to one class: 200– <900.

In addition to diatoms and Flagellatae in the stomach of *E. superba* yellow-green amorphous mass was encountered being probably the remnants of diatom cells and microplankton with not maintained structure.

Qualitative food preferences of *E. superba* are presented in Tab. II. *Thalassiosira* spp., *Nitzschia* spp. and tiny Pennatae constitute 98% of all eaten food particles (phytoplankton cells).

— Ingested food size composition

In the stomach of *E. superba* food particles (algae) with size from 8 to 900 µm were found. The most frequently ingested was 8–40 µm fraction (91% of all ingested particles); 8–20 µm fraction constituted 50% of all ingested particles (Tab. II). The mean size of food particles ingested by *E. superba* was 21.4±1.9 µm. As it was mentioned above only particles bigger than 8 mm were analyzed.

— The amount and size of ingested food particles

The amount of food particles in *E. superba* stomachs varied from 500 to 11000 cells, the average was 1.8±0.7 thousand. The relation of the amount of food particles in krill stomachs on the size of animal is presented in Fig. 1 (line A). It can be seen that the amount of food decreased with the size of animals. However, there are two groups of animals for which this relation is clearly different. For 21–39 mm animals, the amount of food increased with their size (line B), and for animals 40–49 mm it remained constant (Fig. 1, line C).

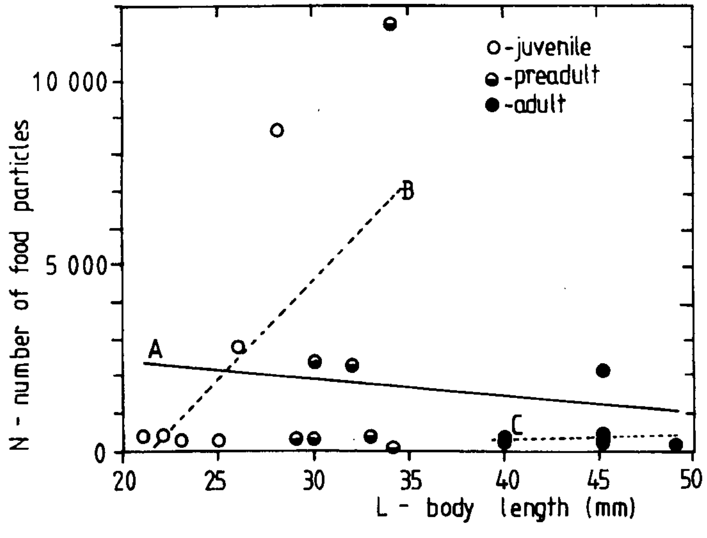

Fig. 1. The relationship between mean number of food particles (N) in the stomach and body length (L) of *Euphausia superba*. Weddell Sea, February 1989. A — regression line for all stages (N=3301–45.11 L, df=18, r=–0.1231); B — regression line for juvenile and preadult animals (N=8167+385 L, df=11, r=0.4529); C — regression line for adult animals (N=88+9.3 L, df==6, r=0.0404)

— Species composition, the amount and size of food particles ingested by particular developmental stages

The above mentioned relations of the amount and size of ingested food particles on the size of animals (Figs. 1, 2) suggest that there may also exist some relation of the age of animals to the quality of food ingested. *Thalassiosira* spp.,

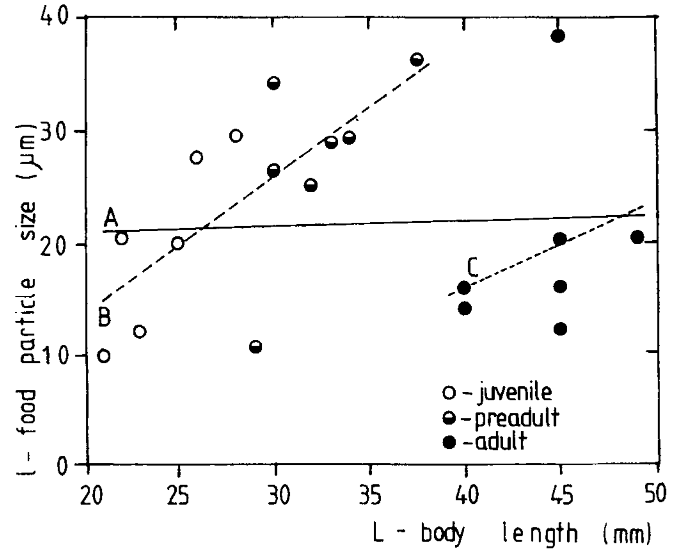

Fig. 2. The relationships between mean size of food particles (l) in the stomach and body length (L) of *Euphausia superba*. Weddell Sea, February 1989. A — regression line for all stages (l = 19.8 + 0.048 L, df = 18, r = 0.0518); B — regression line for juvenile and preadult animals (l = 11.3 + 1.22 L, df = 11, r = 0.6464); C — regression line for adult animals (l = −16.7 + 0.82 L, df = 6, r = 0.2960)

Nitzschia spp. and tiny Diatomeae dominated the food of all krill age groups studied (Tabs. II, III). However, juveniles and preadult individuals evidently preferred tiny Pennatae (84.0 and 84.3% of all ingested algae, respectively), and adults preferred larger *Thalassiosira* spp. (69.6% — Tab. III).

Adult individuals had more diversified food composition — algae from the group "others" constituted about 5% of their stomachs content. This value for juvenes and preadults was only 0.5% (Tab. III).

Juvenes and preadults preferred similar size of particles: 30–40 μm (84.9 and 85.8% of all ingested particles, respectively), adults preferred smaller algae, these of 10–20 μm (54.5% of all ingested particles, Tab. IV). However, the mean size of ingested food particles for juvenes and adults was the same — 19 μm, for subadults — 28 μm (Tab. V).

The amounts of food particles in juvenes and preadult stomachs were practically the same — 2200 and 2500, respectively, in adult stomachs this value is lower — 500, on average (Tab. V).

Table III

Number of food particles (algae) consumed by juvenile, preadult and adult individuals of *Euphausia superba* (Weddell Sea, February 1989)
Mean values ± standard error, *n* — number of analysed animals

Takson	Juvenile ($n=6$)		Preadult ($n=7$)		Adult ($n=7$)	
	Number	%	Number	%	Number	%
Thalassiosira spp.	264±67	12.2	277±81	11.2	365±206	69.6
Nitzschia spp.	72±38	3.3	102±51	4.1	84±33	15.9
Pennatae gen.sp.	1813±1333	84.0	2088±1520	84.3	56±35	9.6
Exuviaella sp.	2±2	0.1	1.3±1.3	<0.1	6±4	1.2
Coscinodiscus spp.	3±2	0.1	3.7±2.9	0.1	2±1	0.3
Silicoflagellatae gen.sp.	0.5±0.3	<0.1	0.7±0.3	<0.1	0	0
Thalassiothrix antarctica	0.2±0.2	<0.1	1.0±0.8	<0.1	2±1	0.4
Navicula spp.	0	0	1.7±1.6	<0.1	1.0±1.0	0.2
Distephanus sp.	0.3±0.3	<0.1	0.1±0.1	<0.1	2±2	0.3
Chaetoceros sp.	0.5±0.5	<0.1	0.1±0.1	<0.1	1.0±1.0	0.3
Rhizosolenia spp.	0.2±0.2	<0.1	0	0	0.4±0.4	0.1
Asteromphalus sp.	0	0	0.1±0.1	<0.1	0	0
others	1.2±1.0	<0.1	0.4±0.3	<0.1	0.4±0.3	0.1

Table IV

Size of food particles (algae) in the stomachs of juvenile, preadult and adult individuals of *Euphausia superba* (Weddell Sea, February 1989)
Mean values ± standard error, *n* — number of analysed animals

Particle size (μm)	Juvenile ($n=6$)		Preadult ($n=7$)		Adult ($n=7$)	
	Number	%	Number	%	Number	%
>10	36 ± 24	1.6	157 ± 65	6.3	9 ± 5	1.6
10–20	211 ± 41	9.7	93 ± 29	3.7	286 ± 157	54.5
20–30	47 ± 11	2.2	67 ± 24	2.7	116 ± 63	22.2
30–40	1836 ± 1333	84.9	2126 ± 1520	85.8	90 ± 47	17.1
40–50	21 ± 12	1.0	31 ± 18	1.2	14 ± 7	2.7
50–60	8 ± 3	0.4	4 ± 1	<0.1	4 ± 2	0.8
60–70	0.5 ± 0.2	<0.1	0	0	0.8 ± 0.8	0.2
70–80	1.0 ± 0.3	<0.1	0.3 ± 0.3	<0.1	1.1 ± 0.7	0.2
80–90	1.4 ± 1.0	<0.1	0	0	0.1 ± 0.1	<0.1
90–120	0.5 ± 0.3	<0.1	0.5 ± 0.2	<0.1	0	0
120–150	0	0	0	0	0.3 ± 0.2	<0.1
150–200	0.7 ± 0.3	<0.1	0	0	0.6 ± 0.4	<0.1
200–250	0	0	0	0	0.1 ± 0.1	<0.1
250–300	0	0	0	0	0.1 ± 0.1	<0.1
350–900	0.2 ± 0.2	<0.1	0	0	0.4 ± 0.4	<0.1
<900	0	0	0	0	0.7 ± 0.7	<0.1

Table V
Mean size and total number of food particles (algae) in the stomachs of juvenile, preadult and adult individuals of *Euphausia superba* (Weddell Sea, February 1989)
Mean values ± standard error, *n* — number of analysed animals

Parameter		Juvenile ($n=6$)	Preadult ($n=7$)	Adult ($n=7$)
Size of food particles (μm)	Mean	19.7 ± 3.2	27.9 ± 3.7	19.3 ± 3.3
	Median	20.1	27.5	16.0
	Range	8–700	8–100	8–900
	Prefered	30–40	30–40	10–20
Number of food particles in stomach (per individual)	Mean	2162 ± 1350	2479 ± 1554	525 ± 278
	Median	418	460	263
	Range	304–8607	15–11538	50–2179

Discussion

— Some remarks concernig the method

Due to the methods used (water slides, magnification) our interpretation of the results is limited. Indicators of *Euphausia superba* food composition chosen are far from the comprehensive list of phytoplankton species ingested by this animal. Secondly, the results presented concern only food particles bigger than 8 μm. Theoretically *E. superba* is able to filter particles of 1–2 μm size (the range of size corresponding to picoplankton (Morris 1983, Quetin and Ross 1985).

There are different calculations of the relative share of nanoplankton in Antarctic plankton. According to Hewes, Ried and Holm–Hansen (1984) and Hewes, Holm–Hansen and Sakshaug (1985), particles of 2–20 μm (nanoplankton) may constitute 20–75% of phytoplankton biomass. On the other hand, from the data given by Fisher (1980), it is possible to calculate that in the Atlantic sector of the Souther Ocean, at 50 m depth, particles smaller than 8 μm constitute only 22% of nanoplankton (in terms of numbers), i.e. the plankton of 2–20 μm size. Bröckel (1981) estimated that the contribution of forms smaller than 2 μm (picoplankton) in the Antarctic suspended matter biomass is about 16%.

From the above literature data one can infere that the analyzed here size fraction of food particles (cells bigger than 8 μm) constitutes an absolute majority in the Antarctic phytoplankton biomass (probably about 80%). Therefore, it seems reasonable to base our considerations on the differentiation of *E. superba* diet starting from this size.

— The kind of food

E. superba is the only species of Euphausiidae which can feed on phytoplankton only (Marr 1962, Mauchline and Fischer 1969, Bottino 1975), at least during the austral summer. The preferred group of phytoplankton are Diatomae (Hart 1934, 1942, Hustedt 1958, Pavlov 1969, 1971, Ligowski 1982), and especially *Fragilariopsis antarctica* = *Nitzschia kerguelensis* (O'Meara) Hasle) (Barkley 1940, Marr 1962).

The food composition found in the present work does not differ from the literature data — Diatomeae constituted 99.6% of all algae ingested by the investigated animals; in this number — 62.3% were Centricae, 37.3% are Pennatae; *Nitzschia* spp. constituted 20.8% of all ingested algae (all in terms of numbers).

— The size of ingested algae

Euphausia superba utilize different size of phytoplankton cells (Clarke and Morris 1983, Mayer and El-Sayed 1983, Ishi, Omori and Murano 1985). Barkley (1940), Nemoto (1968) and Kawamura (1981) stated that *E. superba* prefers small forms of phytoplankton, whereas Hart (1934, 1942) suggested the opposite.

In the present study an absolute dominance of small forms (8 – 40 µm) in the food of *E. superba* was found, although sporadically algae of the size over 100 µm occurred. Similar sizes (6 – 50 µm) of algae, as those most efficiently filtered, were given by C.M. Boyd, Heyraud and C.N. Boyd (1984), Morris (1984), Quetin and Ross (1985), and Maciejewska (in press).

The size of particles ingested by juvenes and subadult individuals increases with their size (Fig. 2). A similar phenomenon was observed for Copepoda — with the increase in size and with higher maturity stage *Acartia tonsa* filters bigger algae (Berggreen, Hansen and Kiorboe 1988). According to these authors this is due to anatomical changes taking place during the development of the individuals. Kills (1983) suggested the same for *E. superba*. It seems that diffferences in quality and size of food preferred by different developmental stages and size classes of *E. superba* (Tabs. III – V; Fig. 2) limits the competition for food within the species. Individuals of similar size, e.g. juveniles and preadults or preadults and adults (see Klekowski, Opaliński and Maklygin 1991), which may feed in the same place because their speed moving is similar (see Everson and Ward 1980, Miller and Hampton 1989) graze different fractions of phytoplankton, (Tab. V, Fig. 1), i.e. do not compete for food. On the other hand, groups which theoretically could compete for food, e.g. juveniles and adults (the same average size of eaten food — see Tab. V), do not occur together, in the same place and at the same time, because of their different moving speed (Everson and Ward 1980) and asynchronic vertical migration (Nast 1979, Opaliński 1992), thus they do not compete for food either.

— The amount of food

Higher food content in stomachs of juveniles and preadult individuals compared with adults (Tab. V) may be explained by different food retention in alimentary tracts of animals in different developmental stages. There are no data in the literature on the relation of food retention time to the size (age) of *E. superba*. The main stress is put on the relation of retention time to amount of food available (Clarke 1984, Quetin and Ross 1988, Drits, Semenova and Toth 1991).

Another reason for the fact that juvenile individuals ate more food particles than adult ones may be the differences in their energetic needs. Juveniles and preadult individuals are in the grow intensively (see Rakusa – Suszczewski and Godlewska 1984), the rate of growth for adults is minimal. From the data given by these authors it is possible to calculate that the daily growth rate for juveniles is 2.1%, for preadults 1.8%, for adults 0.8% of their energetic value (in calories). Also metabolic rate of juveniles is somewhat higher than that of adults (144 and 135 mm^3, O_2 $g^{-1}h^{-1}$, respectively; see Opaliński 1992).

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Streszczenie

Na podstawie analizy zawartości żołądków młodocianych, niedojrzałych płciowo oraz rozmnażających się osobników antarktycznego kryla, *Euphausia superba*, złowionych w lutym 1989 roku w Morzu Weddella stwierdzono, że 99.6% zjadanego przez te zwierzęta pokarmu stanowią okrzemki *Thalassiosira* spp., *Nitzschia* spp. i drobne Diatomea (Tab. I, II i III).

Wielkość zjadanych cząstek pokarmowych wahała się od 8 do 900 µm, ale preferowane były cząstki o wielkości od 8 do 40 µm, stanowiące 91% wszystkich zjadanych cząstek pokarmowych (glonów).

Średnia wielkość cząstek pokarmowych zjadanych przez osobniki młodociane wynosiła 19,7 µm, przez osobniki niedojrzałe płciowo — 27,9 µm, a przez osobniki rozmnażające się — 19,3 µm (Tab. V). Takie zróżnicowanie wielkości zjadanego pokarmu prawdopodobnie ogranicza konkurencję o pokarm pomiędzy poszczególnymi grupami wiekowymi *E. superba*.

Średnie ilości pokarmu znajdowanego w żołądkach osobników młodocianych i niedojrzałych płciowo były około 4-krotnie wyższe od ilości znajdowanych u osobników rozmnażających się (Tab. V). Może się to wiązać z szybszym wzrostem i wyższym tempem metabolizmu osobników młodocianych i niedojrzałych płciowo w porównaniu do osobników rozmnażających się.