COMPARATIVE MORPHOLOGY OF FILTERING STRUCTURE OF FIVE SPECIES OF *EUPHAUSIA* (EUPHAUSIACEA, CRUSTACEA) FROM THE ANTARCTIC OCEAN

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Abstract: Morphology of the filtering apparatus, in particular mesh size and filtering area, of five *Euphausia* species was investigated. Mesh sizes and filtering areas were measured utilizing an SEM. Among adult krill the filtering areas vary from 17.7 mm² in *E. frigida* to 276.8 mm² in *E. superba.* By applying sieve hypothesis, it is proposed that the presumptive lower limits of filterable particle sizes based on the morphology of fine filter meshes range 2–3 μm in *E. superba*, 8–11 μm in *E. vallentini*, 15–19 μm in *E. frigida*, 16–23 μm in *E. crystallorophias* and 27–39 μm in *E. triacantha*. In *E. superba*, the filter mesh sizes do not increase considerably with growth. In *E. triacantha*, the mean secondary setal distances increase from 28–37 μm to 41–56 μm. Species can be grouped according to the mesh sizes and filtering area; i) fine mesh filter feeder represented by *E. superba*; ii) medium mesh filter feeders such as *E. vallentini*, *E. crystallorophias* and *E. frigida*; and iii) coarse mesh filter feeder, *E. triacantha*. Potential food size spectra of these *Euphausia* species are discussed.

1. Introduction

Two major feeding modes in euphausiids are the capture of large food materials and the filtration of small particles. Although *Euphausia superba* uses various methods of feeding at different times depending on conditions (CLARKE and MORRIS, 1983; KILS, 1983), it has generally been accepted that in *Euphausia* species the main feeding mode is filtration by the food basket (KILS, 1983; HAMNER *et al.*, 1983; BOYD *et al.*, 1984). Therefore, the food basket fine structure, especially filter mesh sizes, considerably affect the filterable particle size (KILS, 1979, 1983; MCCLATCHIE and BOYD, 1983; BOYD *et al.*, 1984).

From morphological evidence, it has been reported that *E. superba* has the capability of retaining particles as small as 5–7 μm (BARKLEY, 1940) and 4–5 μm (DZIK and JAZDZEWSKI, 1978). Furthermore, observations using a scanning electron microscope (SEM) revealed more detailed features of the food basket, *e.g.* the tertiary setal distance is 1–2 μm for adult *E. superba* (MCCLATCHIE and BOYD, 1983) and approximately 1 μm for larvae (MARSCHALL, 1985).

In contrast with the extensive studies on the morphology and fine structure of the food basket of *E. superba* (BARKLEY, 1940; NEMOTO, 1967; KILS, 1983; MCCLATCHIE and BOYD, 1983), little is yet known concerning those of other Antarctic species in the

genus *Euphausia*.

This study aims to elucidate fine structure of food baskets by comparing five Antarctic species of *Euphausia* in order to contrast their adaptations to different size spectra of food particles.

2. Materials and Methods

All specimens examined in this study were collected from different regions in the Southern Ocean (Table 1). For SEM observation, the first to sixth thoracopods

Table 1. Source of five Euphausia *samples examined in this study. KH, KY and BS indicate cruises by* HAKUHO MARU, KAIYO MARU *and No. 2* BANSHU MARU, *respectively.*

Species	Cruise	Date	Location
E. superba DANA	KH83-4	Jan. 19, 1984	65°02′S, 118°12′E
E. crystallorophias HOLT and TATTERSALL	BS	Feb. 11, 1978	66°10′S, 139°54′E
E. vallentini STEBBING	KH83-4	Dec. 16, 1983	52°07′S, 149°53′E
E. frigida HANSEN	KY	Jan. 7, 1985	52°01′S, 30°00′W
E. triacantha HOLT and TATTERSALL	KH83-4	Dec. 16, 1983	52°07′S, 149°53′E

(endopods of thoracic limbs) were removed from 5–10% neutral formalin-fixed specimens, hardened through 4% glutaraldehyde for 24 h, and dehydrated through a graded series of ethanol. Thoracopods were then transferred into isoamylacetate as a transitional fluid and critical-point dried with liquid carbon dioxide, coated with gold and examined with an Akashi Alpha-25A Scanning Electron Microscope.

On the basis of the length of several parts as shown in Fig. 1, we define the filtering area (FA) as:
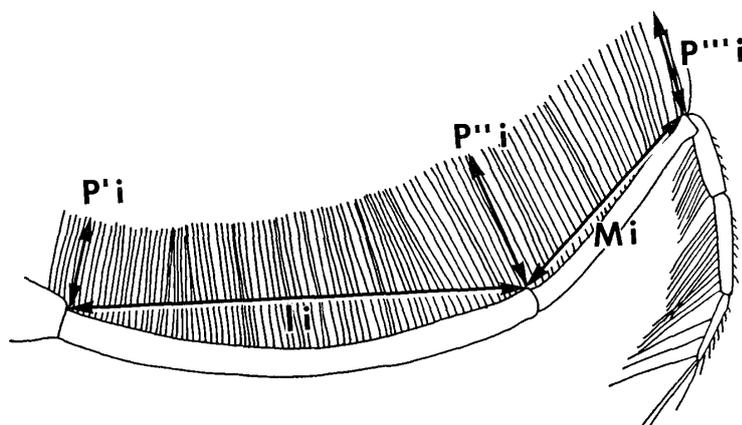
Fig. 1. *The positions measured for the calculation of the filtering area; Ii is the length of ischium of thoracopod i, Mi is the length of merus of thoracopod i, P'i is the length of primary setae at the proximal part of ischium of thoracopod i, P"i is the length of primary setae at the distal part of ischium of thoracopod i, P'''i is the length of primary setae at the distal part of merus of thoracopod i, and i is integrated over the six thoracopods (n=6) in* Euphausia *species.*

$$FA = 2 \sum_{i=1}^{n} \left\{ \frac{(P'i + P''i)Ii}{2} + \frac{(P''i + P'''i)Mi}{2} \right\} , \tag{1}$$

where FA is the filtering area in mm^2.

The relationship between the FA and body length was calculated from the power function as described by McClatchie (1985).

$$FA = aBL^b , \tag{2}$$

where BL is the body length in mm, a is the intercept of the y axis and b is a proportionality constant. Body length was measured from the tip of rostrum to the posterior margin of telson.

Setal distances were measured using SEM. The primary setal distances were measured (at 500 to 1000 × magnifications) between the bases of every second seta along the ischium and merus of thoracopod V, except for *E. superba* in which every fifth seta was measured. The secondary setal distances were measured (at 1000 to 5000 ×) between the bases of every seta along the two or three primary setae located at the middle part of the ischium and merus of thoracopod V. Tertiary setal distances were measured (at 10000 to 15000×) between the apical parts of all setae along the two or three secondary setae at the middle part of the same primary setae as measured previously.
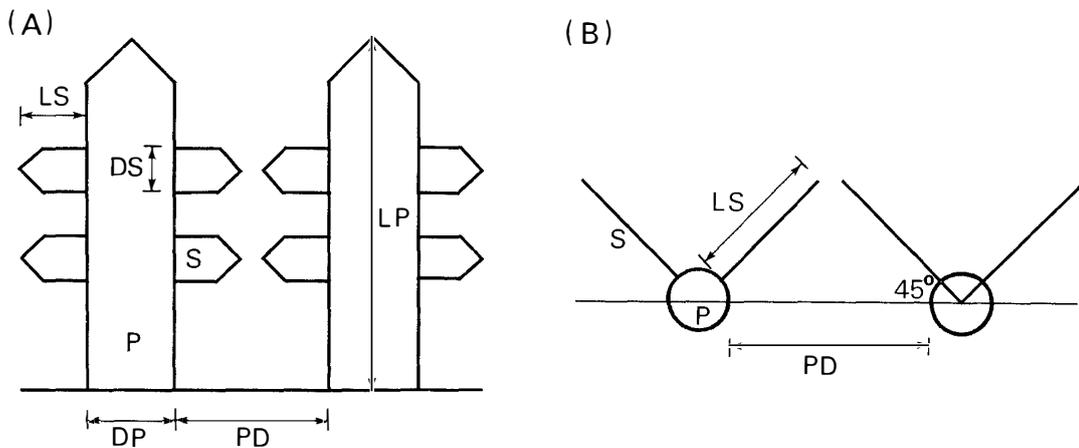
Fig. 2. Schematic presentation of the measured and calculated structural characteristics of Euphausia *filters*: (A) lateral view of the filtering area, (B) dissected view of the primary setae. All drawings are simplified (for explanation see text).

The proportion of the open space between setae (OS), or the percentage of FA through which water can flow, was calculated (Fig. 2).

$$OS = \frac{\Sigma LP(PD + DP) - \{(\Sigma LP\ DP)/2 + (\Sigma LS\ DS/2)/2\}}{\Sigma LP(PD + DP)} 100 , \tag{3}$$

where Σ LP is the summed length of all primary setae, PD is the primary setal distance, DP is the diameter of primary setae, Σ LS is the summed length of all secondary setae and DS is the diameter of secondary setae. As shown in Fig. 3, the primary and
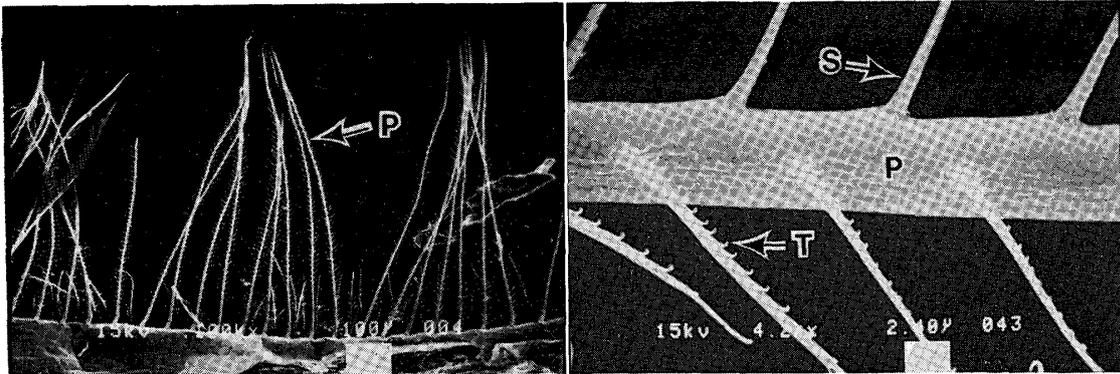
Fig. 3. Fine structure of setae of E. vallentini; *P is the primary setae, S is the secondary setae and T is the tertiary setae.*

secondary setae have a tapered shape. Thus they were divided by a factor of 2 when areas of primary and secondary setae were calculated.

Filter mesh sizes vary with setal distance, length of setae and the angle of setal projection. The proportions of projection of secondary setae (PPS) and tertiary setae (PPT) show whether the secondary and tertiary setae are longer or shorter than the primary and secondary setal distances, respectively. The PPS and PPT are calculated from the following equations:

$$PPS = \frac{LS \cos 45°}{(PD/2)} 100 , \tag{4}$$

and
$$PPT = \frac{LT}{SD} 100 , \tag{5}$$

where LS is the length of secondary setae, PD is the primary setal distance, LT is the length of tertiary setae and SD is the secondary setal distance. As shown in Fig. 3, although a single row of tertiary setae is present on the secondary setae, the two rows of secondary setae protrude from the basal plane of the primary setae at an angle of 45°, therefore, PD in eq. (4) were multiplied by a factor of cos 45°.

3. Results

3.1. Filtering area

A comparison of the body length and FA revealed that a power curve describing an allometric relationship ($Y = aX^b$) gave the best fit in all the species investigated ($P < 0.01$). In Fig. 4, the line relating area to length is expressed in terms of eq. (2) as determined by regression analysis of the logarithms of the original data. In general the FA tends to increase with the square of body length, *E. triacantha* exhibiting the largest slope ($b = 2.20$), *E. vallentini* the smallest slope ($b = 1.41$). The intercept of the allometric equation ranged from -0.08 in *E. superba* to -1.75 in *E. triacantha*. The FA ranged from 10.0 mm^2 in adult *E. frigida* to 276.8 mm^2 in adult *E. superba*. When FA was compared with body length within the range where the five species coincide in body length (19.5–37.5 mm), the FA of *E. superba* exceeded that of the other species at any given length.
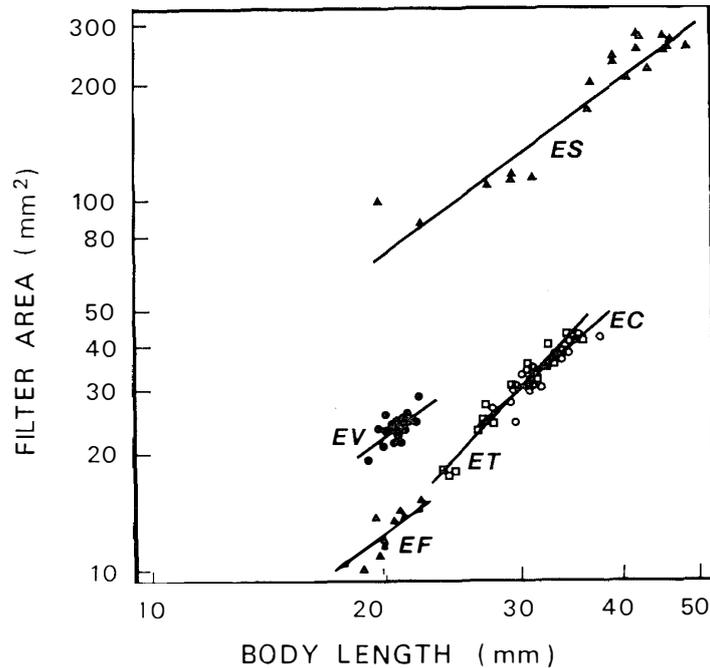
Fig. 4. Relationship between the filtering area (FA) and the body length (BL) in five Euphausia species. Filtering areas increase differently with body length by species: E. superba (ES) log FA=1.51 log BL−0.08, r=0.94, n=21; E. crystallorophias (EC) log FA= 1.72 log BL−1.05, r=0.91, n=21; E. triacantha (ET) log FA=2.20 log BL−1.75, r=0.98, n=20; E. vallentini (EV) log FA=1.41 log BL−0.47, r=0.61, n=19; E. frigida (EF) log FA=1.90 log BL−1.38, r=0.86, n=11; log is base 10.

3.2. Selection of thoracopod V

The food basket which is the principal filtering apparatus of Euphausia species is formed by six pairs of morphologically similar thoracopods (BARKLEY, 1940; MAUCHLINE and FISHER, 1969; KILS, 1983; McCLATCHIE and BOYD, 1983; BOYD et al., 1984). The results of the ANOVA indicate significant differences between the primary setal distances of the six thoracopods in four species, i.e. E. crystallorophias and E. frigida (P<0.05) and E. triacantha and E. vallentini (P<0.01). However, there is no significant difference between the primary setal distances of the six thoracopods in E. superba (P>0.01) which agrees well with the results of McCLATCHIE and BOYD (1983). In the four species having different setal distribution between the six thoracopods, the primary setal distances of thoracopods I, II and III are different from those of thoracopods IV, V and VI. In Euphausia species, dactyli of thoracopods I and II are specialized as combs (MAUCHLINE and FISHER, 1969; McCLATCHIE and BOYD, 1983) and cleaning mechanisms (ZIMMER, 1913; MAUCHLINE and FISHER, 1969), respectively. These specialized dactyli partly affect the setal distribution on the ischium and merus of thoracopods I and II. The dactylus of thoracopod III is not specialized, but the results of the ANOVA show that the setal distribution of thoracopod III is more adapted for specialized functions than filtration. Therefore, it is highly likely that the setal distributions of thoracopods IV, V and VI show more constant features for filtration than that of thoracopods I, II and III. Thus thoracopod V was selected from among the six as the representative thoracopod.

Table 2. *Mean and standard deviation of filtering structure on the thoracopod V of five* Euphausia *species. The number of measurements is shown in parentheses. BL is the body length in mm. PD is the primary setal distances in μm. SD is the secondary setal distances in μm. TD is the tertiary setal distances in μm. LS and LT are the length of the secondary and tertiary setae, respectively, in μm.*

Species	BL	PD		SD		LS	TD	LT
		Ischium	Merus	Ischium	Merus			
E. superba	19.5	23.2±8.5 (19)	45.2±8.1 (9)	4.3±0.6 (21)	10.1±1.0 (10)	45.5±6.5 (10)	3.0±1.0 (21)	1.4±0.2 (13)
	22.2	23.4±8.2 (19)	64.8±12.0 (9)	3.9±0.3 (23)	13.1±1.9 (11)	35.4±6.5 (10)	2.2±0.4 (27)	1.2±0.2 (15)
	27.0	22.1±8.5 (21)	50.8±7.6 (5)	4.2±0.8 (37)	12.2±1.9 (17)	37.2±3.9 (12)	2.5±0.8 (30)	1.1±0.2 (17)
	30.8	31.6±10.0 (17)	72.0±9.6 (10)	4.8±0.6 (11)	13.6±2.4 (18)	46.6±3.4 (10)	2.3±0.4 (18)	1.5±0.3 (15)
	40.9	33.8±13.0 (20)	86.2±3.8 (12)	4.6±0.6 (24)	15.7±3.3 (18)	46.4±8.0 (17)	3.0±1.0 (23)	1.4±0.2 (15)
	46.0	30.3±14.8 (28)	81.3±11.8 (13)	5.3±0.7 (25)	12.8±2.7 (23)	59.4±3.7 (10)	2.2±0.7 (20)	1.3±0.3 (13)
E. crystallorophias	27.3	52.2±4.5 (13)	78.9±5.7 (9)	17.1±2.1 (12)	24.0±3.0 (21)	36.0±3.2 (20)	2.1±0.4 (10)	0.8±0.1 (6)
	29.2	55.5±5.5 (12)	80.4±9.3 (10)	20.7±3.8 (11)	26.6±3.0 (14)	33.2±3.0 (11)	1.9±0.5 (10)	1.3±0.3 (6)
	31.1	61.3±6.4 (12)	84.5±11.0 (10)	22.9±2.7 (9)	27.7±3 8 (8)	34.9±4.5 (13)	2.0±0.6 (10)	1.0±0.2 (8)
	32.8	60.6±4.9 (13)	86.9±6.5 (10)	23.9±2.3 (12)	29.1±7.1 (11)	36.6±1.9 (15)	1.7±0.4 (17)	1.0±0.1 (8)
	35.2	65.7±9.2 (13)	91.1±7.3 (11)	22.1±3.0 (20)	32.7±6.6 (21)	38.8±1.2 (14)	2.1±0.7 (15)	1.0±0.1 (14)
E. vallentini	19.6	40.8±4.3 (17)	58.7±3.5 (10)	10.8±1.3 (15)	13.1±1.4 (13)	29.3±2.0 (9)	1.4±0.5 (16)	0.7±0.2 (8)
	20.5	43.2±3.0 (14)	58.0±3.1 (10)	9.4±1.0 (21)	12.0±1.3 (20)	35.2±3.6 (15)	1.3±0.3 (20)	0.7±0.2 (12)
	21.0	40.8±4.3 (15)	56.5±3.1 (11)	12.1±0.8 (13)	14.8±1.4 (15)	30.9±3.2 (11)	1.5±0.6 (13)	0.9±0.3 (16)
	21.5	37.7±5.1 (18)	55.5±5.3 (10)	11.1±0.8 (16)	14.0±1.0 (13)	29.7±7.3 (13)	1.4±0.1 (11)	0.8±0.1 (10)
	22.1	44.7±4.7 (17)	62.6±2.9 (11)	12.3±1.2 (17)	15.2±1.4 (11)	31.9±1.9 (11)	1.3±0.4 (16)	0.8±0.2 (11)
E. frigida	17.1	48.6±3.9 (9)	67.4±9.3 (7)	16.3±5.3 (8)	24.3±3.5 (7)	20.6±2.2 (9)	1.6±0.2 (16)	0.8±0.1 (11)
	18.8	63.0±7.1 (9)	76.5±13.4 (8)	19.6±3.1 (6)	20.9±1.6 (5)	20.9±1.3 (9)	0.9±0.3 (8)	0.8±0.2 (9)
	19.5	58.4±10.3 (10)	88.0±10.3 (8)	19.3±3.4 (17)	26.0±3.9 (15)	23.5±2.6 (18)	1.1±0.3 (17)	0.6±0.1 (10)
	21.0	54.5±4.5 (10)	72.9±5.5 (9)	18.0±1.8 (12)	26.4±3.7 (8)	25.9±1.7 (13)	1.2±0.4 (16)	0.8±0.1 (9)
	22.3	58.9±3.8 (10)	76.6±6.5 (9)	20.0±2.7 (12)	25.9±2.2 (7)	27.7±1.4 (10)	1.3±0.4 (18)	0.7±0.1 (9)
E. triacantha	23.5	81.9±5.9 (7)	96.9±12.1 (7)	28.0±4.6 (10)	36.5±4.7 (9)	30.4±3.9 (11)	1.3±0.5 (20)	0.8±0.1 (11)
	26.0	83.0±9.0 (8)	103.2±9.7 (8)	32.2±6.1 (12)	37.6±7.8 (12)	30.9±0.8 (10)	1.7±0.6 (13)	0.8±0.1 (9)
	32.3	108.8±10.2 (9)	133.6±12.8 (9)	42.2±9.2 (9)	49.2±13.3 (11)	34.8±1.8 (9)	1.2±0.4 (14)	0.9±0.1 (11)
	35.1	105.7±21.0 (9)	135.6±7.1 (8)	40.8±6.7 (16)	56.1±10.8 (19)	34.2±5.3 (21)	1.6±0.4 (16)	0.9±0.1 (13)

3.3. Filter mesh sizes

The setal distances and length of primary and secondary setae increased with growth, although those of tertiary setae did not vary considerably with increasing krill size (Table 2). There are significant differences in the variation of primary setal distance between the ischium and merus in *E. superba*, *E. crystallorophias*, *E. vallentini* and *E. frigida* (P<0.05, Wilcoxon paired comparison test), but no significant difference in *E. triacantha* (P>0.05, Wilcoxon paired comparison test). Among the five species investigated, the mean distances of primary setae of *E. superba* were smallest with ranges of 22.1–33.8 μm on ischium and 45.2–86.2 μm on merus. In contrast,

Table 3. Mean and standard deviation of the proportions in percentage of open space (*OS*) and projection of the secondary setae (*PPS*) and tertiary setae (*PPT*). *N* is the number of animals investigated.

Species	N	OS	PPS Ischium	PPS Merus	PPT Ischium	PPT Merus
E. superba	6	76±2.5	235±35.6	99±24.3	29±3.2	10±1.9
E. crystallorophias	5	88±0.9	86±6.5	60±2.5	5±0.8	4±0.7
E. vallentini	5	85±0.7	107±5.9	76±6.0	7±0.5	6±0.3
E. frigida	5	88±2.3	60±8.3	44±6.3	4±0.7	3±0.6
E. triacantha	4	88±1.5	49±4.1	40±4.2	2±0.4	2±0.3
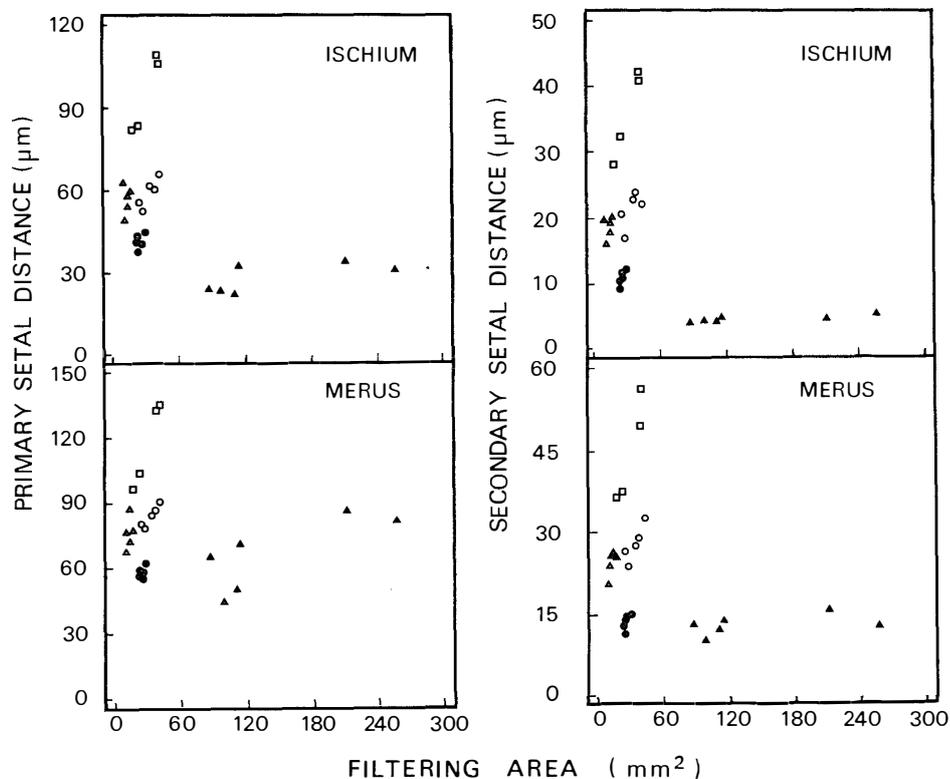
Fig. 5. Relationship between the filtering areas and mean setal distances in the five Euphausia species; open circles in E. crystallorophias, solid circles in E. vallentini, open triangles in E. frigida, solid triangles in E. superba and open squares in E. triacantha.

those of *E. triacantha* were largest with ranges of 81.9–108.8 μm on ischium and 96.9–135.6 μm on merus. The length of secondary setae ranged 35.4–59.4 μm in *E. superba* and 20.6–27.7 μm in *E. frigida.* Furthermore, tertiary setal distances were 2–3 μm in *E. superba* and 1–2 μm in the other species, and the length of the tertiary setae were 1–1.5 μm in *E. superba* and about 1 μm or less in the other species. Thus the setal distribution on ischium is more appropriate for a survey of fine mesh sizes as a presumptive lower limit of filterable particle sizes.

3.4. Proportions of open space and setal projection

The mean and standard deviation of OS, PPS and PPT are given in Table 3. In the five *Euphausia* species, three different values were calculated for OS: i) 88% for *E. crystallorophias, E. frigida* and *E. triacantha*; ii) 85% for *E. vallentini*; iii) 76% for *E. superba.* This shows that *E. superba* has the finest meshed food basket among the five species investigated. Although the PPS was more than 40% in all species investigated, the highest PPT of 29% was found in only *E. superba.*

3.5. Relationships between filtering area and mesh size

Although both variables depend on body size, four different types of relationships can be distinguished between FA and mesh size (Fig. 5): i) with increasing body length mesh size remains small, but FA increases considerably (*E. superba*); ii) FA increases considerably with body growth (*E. triacantha*); iii) FA increases but mesh size remains small (*E. vallentini*); iv) intermediate between *E. triacantha* and *E. vallentini* (*E. frigida* and *E. crystallorophias*).

4. Discussion

4.1. Hydrodynamics

The feeding of *E. superba* has been described with the assumption that food particles are collected by sieving with the filter mesh of the food basket (BARKLEY, 1940; KILS, 1979, 1983; BOYD et al., 1984). Analysis of hydrodynamics, however, has purported to show that the tertiary setae of *E. superba* cannot act as sieves but only serve to narrow the secondary setal intervals by increasing their boundary layer (MCCLATCHIE and BOYD, 1983). This idea was derived from micro-cinematographic observation of low Reynolds number flow around the feeding appendages of copepods (KOEHL and STRICKLER, 1981). In copepods the filter-like structures are surrounded by open space, so that water may flow along the surface of the feeding appendages without penetrating it (JØRGENSEN, 1983). However, *E. superba* has a closed chamber-like food basket which acts as a pressure-pumping mechanism (ANTEZANA et al., 1982; KILS, 1983; HAMNER et al., 1983; BOYD et al., 1984). The food basket compresses metachronically at 1–5 strokes/s (ROSS and QUETIN, 1986). These mechanical and behavioral constraints thus seem to create a slight vacuum at the outside of the filter mesh or pressure in the inner space, and there is a pressure drop across the filter mesh of *E. superba.* JØRGENSEN (1983) considered these pressure drops to be consistent with "the leaky sieve hypothesis" (from BOYD, 1976) that the filter structures function as sieves. Therefore, the lower limit of filterable particle size is strongly correlated with fine structure of the secondary and tertiary setae.

4.2. Filtering area

McClatchie and Boyd (1983) and McClatchie (1985) measured the filtering areas of *E. superba* and *Meganyctiphanes norvegica* using light microscopy. However, they did not state the exact positions measured. Thus we propose eq. (1) for measurement of filtering area. If *Euphausia* species filter in the same way at similar weight specific rates, krill with the larger FA would capture more food particles per unit time. As shown in Fig. 4, the FA of *E. superba* exceeds that of the other species at any given length (19.5–37.5 mm). This shows that in the Antarctic Ocean *E. superba* has a more efficient structure for filtration than the other species.

4.3. Fine structure of filter mesh

An important question is whether the lower limit of filterable particle size can be estimated from morphological characteristics of the secondary and tertiary setae. If the leaky sieve hypothesis is appropriate for *Euphausia* feeding, filterable particle sizes can be predicted from morphological characteristics of filter meshes. SEM observations have revealed that the fine structure of the *Euphausia* filter is very complicated; two rows of secondary setae along the primary setae are inserted at an angle of 90°, so that the whole filter structure is three-dimensional, and there is a single row of tertiary setae along the secondary setae (see Fig. 3).

The filter mesh sizes vary strongly not only in setal distances and length of setae but also in angle of setal projection. For the interpretation of the filter mesh size from the morphological characteristics of the secondary and tertiary setae, PPS and PPT are compared in this study (Fig. 2B). With the exception of 29% in *E. superba*, PPTs of all the species examined were below 10% (Table 3). The results show that the tertiary setae of all *Euphausia* species investigated are not longer than the secondary setal distances. The tertiary setae are too short to filter particles based on the sieve
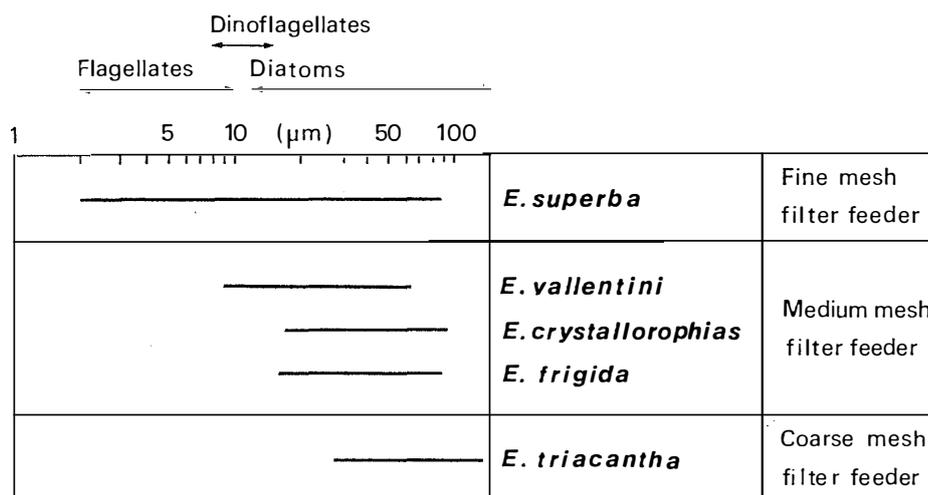
Fig. 6.   The food spectra of adult animals in five Euphausia species as related to food size. The upper limits of food size refer to the primary setal distances. The lower limits of food size refer to the data of tertiary setal distances in E. superba and secondary setal distances in the other species. The different species can be classified as three filtering types according to their apparent ability to feed on nanoplankton (2–20 μm in size) and flagellates (2–10 μm). Size fractions of nanoplankton are according to Bröckel (1981).

hypothesis and therefore will only serve to narrow the secondary setal distances with their length. That is, the secondary setal distances will proportionally decrease with increasing PPT. In *E. superba*, for example, the secondary setal distances ranging 4–5 μm will be decreased by a factor of 30% (average PPT in ischium). Thus fine mesh sizes were finally calculated at about 2–3 μm as the presumptive lower limit of filterable particle size in *E. superba*. *E. crystallorophias* has secondary setal distances ranging 17–24 μm with 5% of PPT. Thus the presumptive lower limit of particle sizes may be 16–23 μm in diameter. The presumptive lower limits of potential food of *E. vallentini*, *E. frigida* and *E. triacantha* may be 8–12 μm, 15–19 μm and 27–39 μm in diameter, respectively (Fig. 6).

4.4. Ecological implications

The retention capabilities of euphausiids have been assumed according to the setal distances of the food basket (BARKLEY, 1940; NEMOTO, 1967; ARTIGES *et al.*, 1978; MCCLATCHIE and BOYD, 1983). These assumptions are based on the sieve hypothesis, *i.e.* all particles smaller than the smallest mesh-size can pass through the filter and all particles larger than the largest mesh-size cannot pass through the filter. Nevertheless, it is not denied that some other mechanisms, *e.g.* surface chemical effects (GERRITSEN and PORTER, 1982), diffusional deposition, direct interception, inertial impaction or gravitational deposition (RUBENSTEIN and KOEHL, 1977), might perhaps play an additional role in filter feeding. If this is true, the size limit of potential food must be lower than the presumptive size limit predicted in the present study.

In the ice-free area of the Antarctic Zone *E. triacantha*, *E. frigida* and *E. superba* are usually found, while *E. vallentini* occurs between the Subtropical Convergence and the Polar Front. *E. crystallorophias* is a neritic species living along the Antarctic continent (JOHN, 1936; BAKER, 1965; MAUCHLINE and FISHER, 1969). In the Antarctic Ocean, the major phytoplankton biomass consists of organisms below 20 μm; these are responsible for 70% (BRÖCKEL, 1981) and 76% (EL-SAYED and WEBER, 1985) of the total phytoplankton biomass. BRÖCKEL (1981) reported that the Antarctic nanoplankton (2–20 μm) were mainly flagellates (5–10 μm), microflagellates (about 2 μm), dinoflagellates (8–15 μm) and diatoms (12–20 μm). Flagellates ranging 2–10 μm in size lack refractory structures. Furthermore, *Euphausia* species have a well-developed stomatogastric system in the foregut (SUH and NEMOTO, 1988). These factors make it difficult to quantitatively and qualitatively analyze nanoplankton in stomach contents. It has been suggested that the green amorphous material predominant in *E. superba* stomach probably consists partly of other less refractory nanoplankton, notably flagellates (MCCLATCHIE and BOYD, 1983).

This paper confirms the fact that *E. superba* can potentially use particles of 2–3 μm as food. This effect on competitive advantage over other *Euphausia* species is considerable. The ability to feed on particles of 2–3 μm becomes more and more important under conditions when the number of flagellates is high. *E. crystallorophias* is a neritic Antarctic species (JOHN, 1936), thus the food of this species may be different from oceanic species. By analysis of stomach contents of *E. crystallorophias*, KITTEL and LIGOWSKI (1980) reported that the contribution of the over 10 μm size fraction to the total size fraction is over 95%. This result agrees with our presumptive lower

limit of potential food sizes in this species. Antarctic nanoplankton ranging 16–23 μm are mainly small diatoms which are probably used by this species. *E. vallentini* has a competitive advantage in being able to feed on suspended single cells of dino-flagellates ranging from 8 to 15 μm in size. However, *E. triacantha* would be unable to feed on nanoplankton ranging 2–20 μm, whereas the other species would be able to feed on nanoplankton. It is suggested that *E. triacantha* feeds mainly on larger particles.

Species-specific differences in the relationship between mesh size and FA were found in this study (Fig. 5). The development of different types of allometric relationships may be the result of selection pressure due to different size spectra of food. However, the mesh size of *E. superba* is nearly consistent from juvenile to adult. This shows that juveniles most likely compete with adults in utilizing even tiny food particles.

Within the five *Euphausia* species compared in Fig. 6, three different types of filter meshes can be established. With respect to the potential ability to feed on flagellates, the smallest food particles in the marine environment, these three filter mesh types can be considered as indicators of ecological groups: (1) one presumptive "high efficiency flagellates feeder" which has fine filter meshes (2–3 μm): *E. superba*; (2) three presumptive "low efficiency flagellates feeders" which have medium sized filter meshes (8–16 μm): *E. vallentini*, *E. crystallorphias* and *E. frigida*; and (3) one presumptive "macrofiltrator" which has coarse filter meshes (27 μm) and would be unable to feed on nanoplankton; *E. triacantha*.

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