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Comparison of the ultrastructure of the food-concentrating filter of two appendicularians

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ABSTRACT: Houses of *Oikopleura longicauda* were removed from preserved zooplankton samples and prepared for transmission electron microscopy. Pore size and fiber diameter of the food-concentrating filter were determined for comparison with similar measurements on larger oikopleurids from cold ocean waters. The filter was composed of 3 types of fibers arranged in a regular rectangular array. In accordance with nomenclature used previously, we identified microfibers, nodulated fibers, and smooth fibers. There were dense nodes where microfibers and nodulated fibers crossed. Mean pore size was 0.15 ± 0.02 × 0.61 ± 0.13 µm (± SD), with a mean width-to-length ratio of 0.25 ± 0.03 and mean porosity of 0.85 ± 0.01. Mean pore size is similar to that of *Oikopleura dioica*, a temperate-ocean oikopleurid of similar body size, but is smaller than that of *Oikopleura vanhoeffeni*, a large, cold-ocean oikopleurid. The microfibers of *O. longicauda* were 17.1 ± 2.6 nm in diameter, while the nodulated fibers were 38.9 ± 8.8 nm in diameter, and the smooth fibers 48.1 ± 10.2 nm in diameter. All 3 fiber types formed branches, which contributed to high variance of mean pore size.

INTRODUCTION

Appendicularians utilize a system of fine mucous nets to remove food particles from suspension. One of these nets, the food-concentrating filter (*sensu* Deibel et al. 1985), concentrates the food suspension by sieving a large portion of the incoming water through small rectangular pores. The food-concentrating filter occupies a large portion of the internal volume of the house, enabling the oikopleurid to process large volumes of water while maintaining the ability to retain very small particles. However, fluid mechanical aspects of the operation of this filter remain unknown. A prerequisite to fluid mechanical calculations is knowledge of the ultrastructure of the filter, i.e. of its pore size and fiber diameter.

The ultrastructure of the food-concentrating filter of a number of oikopleurid appendicularian species has been described (Fjerdingstad in Jørgensen 1966, Flood 1978, 1981, Deibel et al. 1985). The filter is composed of fine mucous fibers arranged in a regular rectangular array, with a pore width (i.e. minimum dimension) range of 0.10 to 0.22 µm (Deibel et al. 1985). The porosity of the filter is high, about 90 to 91 %. The major difference between the filters of these oikopleurid species seems to be that *Oikopleura dioica* lacks smooth fibers (Flood 1981).

It has been axiomatic that oikopleurid appendicularians feed mainly on nanoplankton and picoplankton, although this notion has recently been revised for the large, cold-ocean appendicularian *Oikopleura vanhoeffeni*, which consumes larger net-plankton (Deibel & Turner 1985). Thus, we took advantage of the availability of preserved houses of the small, warm ocean *Oikopleura longicauda* to examine the ultrastructure of the food-concentrating filter using the same techniques we had used earlier to describe the ultrastructure of the food-concentrating filter of *O. vanhoeffeni*. The house of *O. longicauda* is small and gelatinous (Alldredge 1977), while that of *O. vanhoeffeni* is large and mucinoid. Also, there are well-known differences in size and concentration of available food particles between warm and cold ocean waters. Warmer waters are dominated by smaller cells marked by aperiodic blooms of larger dinoflagellates and diatoms, while colder waters are dominated by larger cells and seasonally predictable blooms of diatoms during the

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spring increase. In addition, the house of *O. longicauda* is unique because of the absence of incurrent filters which pre-screen the incoming water and prohibit large and spinous cells from entering and fouling the food-concentrating filter and pharyngeal filter (Alldredge 1977). We wondered if these differences of habitat and morphology would be reflected in a fundamental difference in the ultrastructure of the food-concentrating filter. This ultrastructural information will add to our knowledge of species-specific characteristics of oikopleurid mucous nets and is needed for further fluid mechanical studies of particle capture and feeding of these important marine zooplankters.

METHODS

Preserved houses of *Oikopleura longicauda* were obtained from P. McGillivary (Skidaway Institute of Oceanography). The houses were taken from zooplankton samples that had been collected along the western wall of the Gulf Stream (28 May 1983) off Jacksonville, Florida, by oblique tows of a 1000 µm

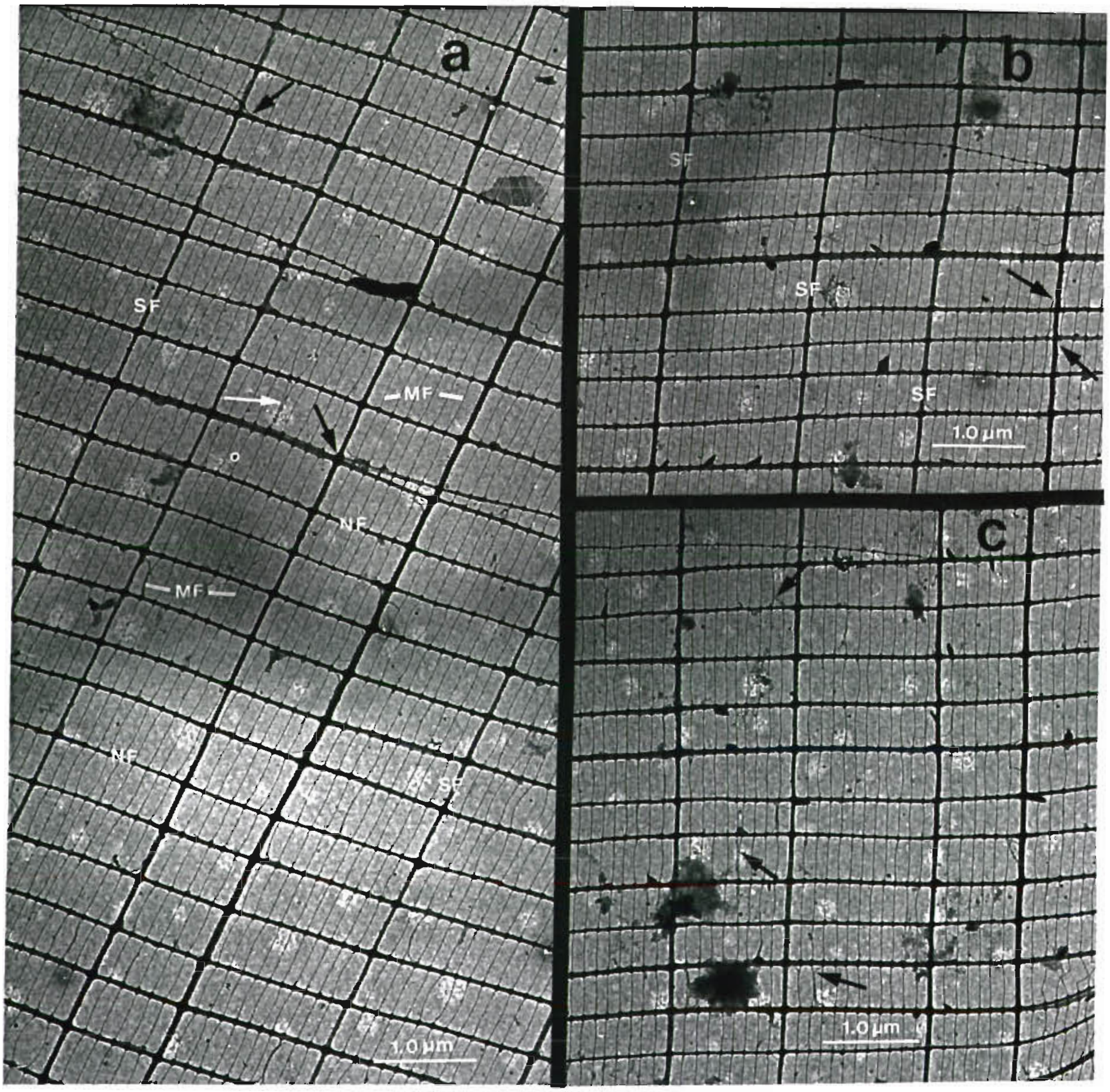

Fig. 1 *Oikopleura longicauda*. Transmission electron micrographs of the mucous mesh of the food-concentrating filter. (a) A large area of filter showing the 3 types of fibers and branches of nodulated fibers (NF: black arrows) and of a microfiber (MF: white arrow). (b) A smaller area of filter showing the spatial variability between adjacent smooth fibers (SF), and a smooth fiber branching into microfibers (arrows). (c) Notice the complex branching of microfibers (arrows)

Table 1. *Oikopleura longicauda.* Mean (± SD) pore width, pore length, and fiber diameter of the food-concentrating filter. Also given: [coefficient of variation, %]; (n), the number of pores or fibers measured

House	Pore width (µm)	Pore length (µm)	Width/length	Porosity	Fiber diameter (nm)	
					Microfiber	Nodulated
1	0.15 ± 0.02 [11.7] (84)	0.51 ± 0.10 [18.7] (200)	0.29	0.84	17.1 ± 2.6 [15.2] (35)	37.7 ± 9.7 [25.7] (73)
2	NA	0.70 ± 0.11 [15.8] (116)	NA	NA	NA	NA
3	0.15 ± 0.01 [8.7] (144)	0.64 ± 0.12 [18.4] (132)	0.23	0.85	NA	39.5 ± 7.5 [19] (52)
4	0.17 ± 0.02 [10.8] (24)	0.71 ± 0.12 [17.5] (39)	0.24	0.86	NA	43.8 ± 7.4 [16.9] (13)
Houses 1–4	0.15 ± 0.02 [11] (252)	0.61 ± 0.13 [22.3] (487)	0.25 ± 0.03 [12.9] (3)	0.85 ± 0.01 [1.2] (3)	17.1 ± 2.6 [15.2] (35)	38.9 ± 8.8 [22.6] (138)

mesh net from 40 m to the surface. The samples were preserved onboard ship in 2 % seawater-formaldehyde and 50 % propylene-phenoxetol/propylene-glycol.

In preparation for transmission electron microscopy intact houses were transferred to 2 % glutaraldehyde. Further processing was identical to that used by Deibel et al. (1985) for examining the food-concentrating filter of *Oikopleura vanhoeffeni*. Mounted specimens of filter were viewed with either a Zeiss EM9A or a Zeiss EM109 transmission electron microscope.

Transmission electron micrographs containing specimens of mucous net that could be measured were obtained from 4 houses. The protocol for measuring pore size and fiber diameter was identical to that used previously (Deibel et al. 1985). Sources of variability in mean pore size and fiber diameter were assessed using Model II, unbalanced, nested ANOVA (Ray 1982, Sokal & Rohlf 1982).

RESULTS

The food-concentrating filter of *Oikopleura longicauda* was composed of 3 types of mucous fiber arranged in a regular rectangular array (Fig. 1a to c). In accordance with our earlier nomenclature, we identified microfibers, nodulated fibers, and smooth fibers (Fig. 1a). While there were no nodes where smooth and nodulated fibers crossed, there was a node at every intersection of a microfiber with a nodulated fiber (Fig. 1). Branches of nodulated fibers were most common (Fig. 1a), while branching microfibers and smooth fibers were much less frequent (Fig. 1a to c). Smooth fibers had an extremely variable spatial pattern. Nodulated fibers and microfibers were more evenly spaced.

The minimum pore dimension (i.e. pore width, or the distance between microfibers) ranged from 0.15 to 0.17 µm, and pore length (i.e. the distance between nodulated fibers) ranged from 0.51 to 0.71 µm (Table 1). There was a significant component of the total variance of mean pore width and length between micrographs within houses ($p < 0.001$), and a further component of the total variance of mean pore length between houses ($p < 0.001$). Based on the mean pore size of each house, the width-to-length ratio of the food-concentrating filter ranged from 0.23 to 0.29, and the porosity from 0.84 to 0.86 (Table 1). Smooth fibers occurred on a variable spatial scale, with a mean distance between fibers ranging from 1.95 to 2.34 µm (Table 2). Because of this variability the variance within each micrograph dominated the total variance of mean distance between smooth fibers, with no additional contribution to the total variance between micrographs within each house or between houses ($p > 0.05$).

Microfiber diameter could be measured on 1 house only, and was 17.1 ± 2.6 nm (Table 1). Nodulated fiber diameter ranged from 37.7 to 43.8 nm, with a significant component of the total variance between micrographs within each house but not between houses ($p < 0.001$). Smooth fibers were slightly thicker than were nodulated fibers, with a mean fiber diameter ranging from 45.2 to 55.8 nm (Table 2).

DISCUSSION

The appearance of the mucous mesh of the food-concentrating filter of *Oikopleura longicauda* was similar to that of *Oikopleura vanhoeffeni* (compare Fig. 1

Table 2. *Oikopleura longicauda*. Mean distance (± SD) between neighboring smooth fibers and smooth fiber diameter. Values as in Table 1

House	Distance between smooth fibers (µm)	Smooth fiber diameter (nm)
1	2.34 ± 1.35 [57.9] (29)	45.2 ± 10.2 [22.6] (38)
2	1.95 ± 0.64 [32.7] (28)	NA
3	2.09 ± 1.34 [64.4] (22)	51.3 ± 8.4 [16.4] (14)
4	2.05 ± 0.44 [21.5] (9)	55.8 ± 8.5 [15.2] (6)
Houses 1–4	2.12 ± 1.09 [51.5] (88)	48.1 ± 10.2 [21.2] (53)

with Deibel et al. 1985). The same 3 types of fibers were present, and there was a similar pattern of branching fibers. However, the pore size was much different, and was in accordance with the difference in body size between the smaller, warm-ocean *O. longicauda*, and larger, cold-ocean *O. vanhoeffeni* (Table 3). Also, because of the relatively small pore length, the width-to-length ratio of the mesh of *O. longicauda* was larger than that reported for any other oikopleurid (Table 3).

Although the pore size of the food-concentrating filter of *Oikopleura longicauda* was smaller than that of *O. vanhoeffeni*, the fibers making up the filter were of nearly the same diameter. Thus, the porosity (% open area) of the filter of *O. longicauda* was smaller (Table 3), suggesting that it must overcome relatively higher resistance to pump water while feeding.

Although precise information is available for only 4 oikopleurid species, it seems that pore dimensions increase with increasing body size (i.e. trunk length: Table 3). Larger oikopleurids have food-concentrating filters with coarser mesh. We may eventually be able to predict the size selectivity of oikopleurids by determining their trunk length. This would increase the realism of models of energy flow through planktonic food webs.

It seems that prior preservation of the houses in formaldehyde and propylene-phenoxetol/propylene-glycol did not fundamentally alter the ultrastructure of the food-concentrating filter. We base this conclusion on the structural and dimensional similarity of the mesh of *Oikopleura longicauda* to that published for other oikopleurid species (Table 3).

It has been suggested that oikopleurids have species-specific characteristics of their mucous filters that should allow investigators to identify the source of appendicularian-derived detritus by using the enclosed mesh as a 'fingerprint'. We have found that the only species-specific characteristic of the food-concentrating filter is pore size. An exception is the food-concentrating filter of *Oikopleura dioica*, which appears to lack smooth fibers (Flood 1981). Thus, although abandoned houses originating from *O. dioica* could be identified, houses from other oikopleurids will be more difficult to distinguish because of overlapping pore sizes.

Although information on the ultrastructure of the food-concentrating filter of oikopleurids is growing, we

Table 3. *Oikopleura* spp. Comparative transmission electron micrograph data on the mucous mesh of the food-concentrating filter (mean ± SD). Value in parentheses are the number of observations pooled for each mean

Species	Mature trunk length (mm)	Pore length (µm)	Pore width (µm)	Width/ length	Diameter (nm)			% open area	Source
					Smooth (longitudinal)	Nodulated (transverse)	Microfiber (longitudinal)		
Oikopleura vanhoeffeni	2.0–9.0•	1.04 ± 0.26 (233)	0.22 ± 0.04 (502)	0.22 ± 0.04 (5)	40 ± 12 (25)	45 ± 14 (43)	12 ± 2.7 (9)	91 ± 1 (5)	Deibel at al. 1985
Oikopleura albicans	3.0–5.0••	0.92 ± 0.06	0.19 ± 0.01	0.22	10–40	10–40	NA	90	Flood 1981
Oikopleura longicauda	0.8–1.3••	0.61 ± 0.13 (487)	0.15 ± 0.02 (252)	0.25 ± 0.03 (3)	48.1 ± 10.2 (53)	38.9 ± 8.8 (138)	17.1 ± 2.6 (35)	85 ± 1 (3)	Present study
Oikopleura dioica	0.5–1.0•	0.98 ± 0.22	0.15 ± 0.02	0.17	10–40	10–40	NA	90	Flood 1981
Oikopleura sp.	NA	0.80	0.10	0.13	NA	NA	NA	NA	Fjerdingstad in Jørgensen (1966)

• Berrill (1950); •• Thompson (1948); NA: data not available know little of the fluid mechanics that characterize the operation of the filter. We do not know the velocity of water at the filter surface, the pressure drop across the filter, or the thickness of the boundary layer around individual fibers. Because of these gaps we cannot estimate the energy required for oikopleurids to pump water while feeding. Future studies should concentrate on quantifying these processes. Only then will we be able to understand the ecology and evolution of these abundant and important zooplankters.

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