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Daphnia's filters are not solid walls

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With 2 tables in the text

Abstract

Two fluid dynamic models are used to estimate the amount of energy required to pass a volume of water equivalent to the filtration rate through the filtering limbs of *Daphnia*. Although Reynolds numbers are very small ($\approx 10^{-3}$), the pressure drop across the filter is low (less than 0.5 mbar). Both models predict that the energy needed to press water through the filters is about 5 % of the total metabolic requirements of the animal. Thus, consideration of fluid dynamics provides no reason to reject the hypothesis that *Daphnia* collects food by sieving water through its thoracic limbs.

Introduction

Early descriptions of the feeding of *Daphnia* and other phyllopods were based on the assumption that food particles were collected by sieving water through the filter-like thoracic limbs (Storch 1924, Cannon 1933). Recent analyses of fluid dynamics, however, have purported to show that the "filters" of *Daphnia* cannot act as sieves but work like paddles that only create water currents (Gerritsen & Porter 1982, Porter et al. 1983, Ganf & Shiel 1985 a, b). These authors believe that *Daphnia*'s feeding appendages function as "solid walls" because overlapping boundary layers surrounding the fine bristles prevent water from passing through the open spaces. This idea was probably derived from micro-cinematographic observations of low Reynolds number flow around the feeding appendages of copepods (Koehl & Strickler 1981). In copepods the sieve-like structures are surrounded by open space so that water may flow along the surface of the filter screen without penetrating it. The phyllopods, however, possess a different system. "Filtering" limbs form a closed chamber that acts like a suction-and-pressure pump (Storch 1924, Cannon 1932). When the limbs move forwards and backwards they alternatively create a slight vacuum at the outside of the filter screen or pessure in the inner space. Thus, there is a permanent pressure drop across the filter. If, in fact, the filter system of *Daphnia* works in this way, it is of interest to know how much energy would be required to overcome the fluid mechanical resistance associated with the overlapping boundary layers. In this paper we try to estimate this amount of energy with data available for *Daphnia pulicaria.*

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Calculations

All the parameters used for the calculations are listed in Table 1. Morphometric analyses of the filtering appendages were made by SEM using the technique of Brendelberger (1985) and Brendelberger & Geller (1985). Total metabolic requirements (R) were derived from literature values (Lampert 1977). Maximum clearance rates were determined with radioactively labelled algae (Lampert, unpubl. data). They are very similar to the data reported by Geller (1975).

The energy needed to pump the water through the filter (R_f) is

$$R_f = \Delta p \cdot Q \tag{1}$$

where Δp is the pressure drop across the filter and Q is the volume of water pumped per unit time. Q equals the maximum clearance rate (F_{max}) of an animal if we assume that sieving is the only mechanism of retaining the particles and that particles which impinge on the filters are efficiently ingested.

Since linear dimensions of the filter structures are in the order of 1 μm and the average flow rate (U), calculated from $U = F_{max}/A_o$ (A_o = open area of the filter) is about 0.1 cm s^{-1}, Reynolds numbers at setules are in the order of 10^{-3}. Thus inertial forces are negligible. To be sure that the flow can be assumed time independent (steady flow) the following dimensionless quantity $\hat{\tau}$ must be much greater than one:

$$\hat{\tau} = \frac{\nu \cdot T}{l^2},$$

with the kinematic viskosity ν, a characteristic time T and length l, respectively. Choosing $\nu = 0.01$ Stokes, $T = 0.1$ s and $l = 10\,\mu$m we find $\hat{\tau} = 10^3$; thus the quasi-steady flow condition is justified (Schlichting 1982, p. 94). Given these conditions we can calculate the pressure drop Δp. We estimated Δp by two different models, a cylinder model (Tamada & Fujikawa 1957) and a model with parallel slits which we call gap model.

The cylinder model considers the filter as a plane row of equal, parallel, circular cylinders (Tamada & Fujikawa 1957). This model has been used by Fenchel (1980) and Jørgensen (1983) to estimate the resistance of filter structures in ciliates and a variety of marine invertebrates. The pressure drop can be calculated from

$$\Delta p = \frac{8 \cdot \pi \cdot \mu \cdot U}{h \cdot \lambda_o(\tau)} \tag{2}$$

where

$$\tau = 2 \cdot \pi \cdot \frac{a}{h}$$

and

$$\lambda_o = 1 - 2 \ln \tau + \frac{1}{6}\tau^2 - \frac{1}{144}\tau^4 + 0(\tau^6).$$

μ is the dynamic viscosity (10^{-2} Poise), a is the radius of the cylinder, h is the distance between the centers of adjacent cylinders, and U is the velocity of the water flow.

Daphnia's filter, however, may be better described by two rows of parallel cylinders which are arranged perpendicularly so that they form a grid-like structure. One row is formed by the setae the second one by the setules. The geometrical dimensions needed for the calculations are (cf. Table 1):
for the row of setae

$$a_1 = \mathrm{Sdm}_1/2; \; h_1 = \mathrm{Sdm}_1 + \mathrm{Sps}_1$$

for the row of setules

$$a_2 = \mathrm{Sdm}_2/2; \; h_2 = \mathrm{Sdm}_2 + \mathrm{Sps}_2.$$

We have used an average velocity (U) of the water flow across the filtering structures, although the flow in a phyllopod filter is not a steady stream as assumed in the cylinder model. In fact, U will oscillate rhythmically with the motion of the limbs, so that, according to Equ. 2, the pressure drop will vary, too. However, this will not appreciably affect the energy required to filter a certain amount of water (Equ. 1).

Results of the calculations for three size classes of daphnids are presented in Table 2. The pressure drop across the filter is small (less than 0.5 mbar). Assuming a conversion efficiency into mechanical work of 0.2 (LEHNINGER 1965) the power consumption for the filtration amounts to 2.3—4.4% of the total metabolic requirements.

The gap model assumes that the water current flows through a grid structure of parallel slits with a width (a) equal to the distance between two adjacent setules (Sps_2) and the length (h) equalling twice the length of a setule (Sle_2) (cf.

Table 1. Physiological and morphometric parameters of three size classes of *Daphnia pulicaria* used in the calculations. Morphometric measurements are consistent with the figures and symbols given in BRENDELBERGER & GELLER (1985).

Parameter	Symbol	Body size (mm)		
		0.68	2.13	2.95
Maximum clearance rate (ml h^{-1})	F_{max}	0.13	2.00	4.37
Metabolic rate (10^{-3} J h^{-1})	R	0.52	8.00	17.50
Diameter of a seta (μm)	Sdm_1	1.0	2.0	2.5
Open distance between setae (μm)	Sps_1	1.5	6.4	6.0
Length of a setule (μm)	Sle_2	2.5	5.8	7.0
Diameter of a setule (μm)	Sdm_2	0.09	0.18	0.22
Open distance between setules (μm)	Sps_2	0.32	0.64	1.05
Total open area of the filter[1] (mm^2)	A_o	0.049	0.418	0.748

[1] at the 3rd and 4th pair of legs.

Table 2. Energy requirements for sieving by *Daphnia pulicaria* calculated from two models of fluid dynamics.

Model	Depth (t) of slit (μm)	Body size (mm)	Flow velocity (cm s^{-1})	Pressure drop (mbar)	Mechanical energy consumption for sieving (10^{-5} J h^{-1})	Fraction of total metabolic requirements[1] (%)
Cylinder		0.68	0.074	0.34	0.45	4.4
		2.13	0.133	0.25	5.00	3.15
		2.95	0.162	0.18	7.81	2.25
Gap	0.09	0.68		0.078	0.10	0.98
	t_1 0.18	2.13		0.070	1.40	0.88
	0.22	2.95		0.039	1.70	0.49
	0.55	0.68		0.47	0.61	5.89
	t_2 1.09	2.13		0.43	8.60	5.38
	1.36	2.95		0.24	10.50	3.00

[1] conversion efficiency into mechanical work of 0.2.

Brendelberger & Geller 1985). According to Wieghardt (1965, p. 148) the pressure drop is

$$\Delta p = \frac{Q}{N} \cdot \frac{12 \cdot \mu \cdot t}{a^3 \cdot h}. \tag{3}$$

N is the number of slits ($N = A_o / a \cdot h$) and t is the depth of the slit. Since the short axes of the slits are formed by the thick setae and the long axes by the thin setules and since, moreover, the surface of the filter is not plane but folded (cf. Brendelberger & Geller 1985), t is difficult to estimate. The minimum value would be the diameter of the setule (Sdm_2). Therefore, we calculated Δp for two values of t:

$$t_1 = Sdm_2; \; t_2 = (Sdm_2 + Sdm_1)/2.$$

The latter may be more realistic. Estimates of pressure drops using t_1 are lower than those calculated for the cylinder model (Table 2). However, when t_2 is used, the two models give very similar results. R_f is again on the order of 5 % of the total energy demands.

Discussion

Our calculations yield pressure drops across the filter of *Daphnia* very similar to the values summarized by Jørgensen (1983) for ciliates, sponges and ascidians. Fenchel (1980) and Jørgensen (1983) consider these pressure drops to be consistent with the hypothesis that the filter structures function as sieves. There seems to be no reason to reject the "leaky sieve hypothesis" (Boyd 1976) in daphnids for fluid mechanical or energetic reasons. Recent experimental work, in fact, has yielded more evidence for the idea that mechanical sieving is the basis of *Daphnia*'s filtering activity. A strong correlation has been found between filter-mesh size and retention efficiency for small particles (GOPHEN & GELLER 1984, HESSEN 1985, DEMOTT 1985, BRENDELBERGER 1985). This does not, however, exclude the possibility that other mechanisms, such as direct interception (cf. RUBENSTEIN & KOEHL 1977), are involved in the retention of ultrafine particles.

The validity of our calculations depends on the applicability of the models. One important point to consider is that the cylinder model was designed for a row of infinite numbers of cylinders. TAMADA & FUJIKAWA (1957) state: "In this respect, there is an essential difference between the case when the number of cylinders is infinite and that in which it is large but finite. In the latter case, the flow may pass round the system of cylinders, leaving the fluid inside the system almost at rest." The phyllopod filtering apparatus encloses a portion of water so that it cannot pass around the system of cylinders. In this way an infinite number of cylinders is mimiced. Thus the phyllopod filtering system is basically different from the copepod system. A tennis-racket like model of a filter screen moved through a viscous fluid (GERRITSEN & PORTER 1982) is probably not an adequate description of *Daphnia*'s filter.

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