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PRESSURES GENERATED BY THE PUMPING MECHANISM OF SOME CILIARY FILTER-FEEDERS

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Abstract: An apparatus is described that enables measurements to be made of the low pressures generated by ciliary filter-feeders. Such pressures range from 0.1 to 5.2 mm of water (10 to 520 dyn cm^{-2}) with the higher pressures in bivalves with long siphons. In these bivalves the frictional resistance of the siphons accounts for a major part of the total resistance to water flow. Pressures observed in bivalves with short siphons, in tunicates, and in sponges are all similar. Hydrodynamical equations have been used to see whether the pressures can be predicted from the dimensions and pumping rate of the bivalve *Mya arenaria* L.

INTRODUCTION

Small pressures are generated by the pumping mechanisms of ciliary filter-feeders. Parker (1914) measured pressures of between 0.5 and 4.0 mm water when he inserted a glass tube in an osculum of the sponge *Stylotella.* Bidder (1926) calculated pressures of between 0.6 and 1.2 mm water to be generated in the flagellated chambers of the sponge *Leucandra* and recently Foster-Smith (1976a) has calculated that the pressures generated by bivalves with short siphons might be expected to be 1 mm of water or less. The rate of water transport created by such pressures depends upon the resistance of the system through which water is flowing. Pressure losses are caused by frictional resistance as water flows through tubes and also by loss of kinetic energy as water enters and leaves tubes (Fox, 1974). Foster-Smith (1976a) has calculated that in a siphonate bivalve such as *Venerupis* frictional resistance in the siphons may account for a large proportion of the total resistance to flow, so that if the rate of water transport for bivalves with long siphons are to be similar to those for bivalves with short siphons the former must generate higher pressures.

Measurement of low pressures requires an apparatus more sensitive than the transducers which have been developed to measure blood pressure in mammals. This paper describes a simple device for recording low pressures and gives the results of an investigation into the pressures generated by some ciliary filter-feeders.

MATERIALS AND METHODS

CONSTRUCTION OF THE PRESSURE MEASURING DEVICE

The pressure measuring device was made from a plastic cylinder 3 cm high and 6 cm in diameter, open at one end. A rubber diaphragm, cut from an inspection glove, was stretched over the open end. The vessel was connected to a pressure probe by plastic tubing and the tubes and vessel filled with de-aerated sea water from a reservoir (Fig. 1). Any increase in pressure at the open end of the probe causes a force to be exterted on the rubber diaphragm which was converted into an electrical signal by a UF1 (50 g) force transducer (Pye Ether Ltd., Stevenage) and which was amplified and displayed on a pen recorder. The device is similar to that used to measure pressure and volume changes in the proboscis of *Arenicola* (Foster-Smith, 1976b) where pressures of up to 60 cm of water were developed. It was found, however, that pressures of 0.05 mm of water could be measured satisfactorily with the present force transducer giving an output of 2.5 mV/mm of water at 10 V excitation.

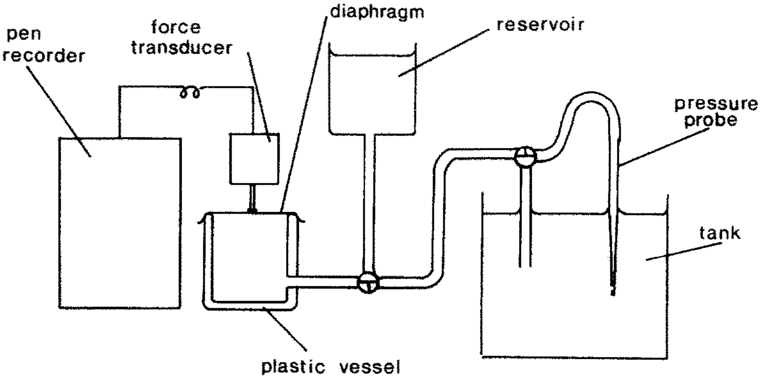

Fig. 1. The arrangement of the apparatus used for measuring low pressures in ciliary filter-feeders.

Pressure displaces the rubber diaphragm by a small amount (0.005 ml/mm of water) and because of this the response of the device to changes in pressure was not so fast as with conventional microdisplacement blood pressure transducers but has the advantage that high frequency vibrations are damped.

USE OF THE PRESSURE MEASURING DEVICE

Two types of probes were used. The first type consisted of a hypodermic needle with a bore of 0.8 mm and a needle length of 2.5 cm and was used to measure the pressure in the mantle cavity and suprabranchial cavity of two species of bivalves with long siphons (*Mya arenaria* L. and *Scrobicularia plana* (da Costa)). A small hole was drilled into the shell through which the needle could be inserted, and the needle fixed into place with wax and its position checked by flushing with dye and, after the experiment, by dissection. The second type of probe could be inserted through the inhalant or exhalant apertures and manipulated from the outside; this was made from drawn-out glass tubing. The tip of the glass tubing was sealed in a flame and the pressures were measured through a small hole drilled into the side of the probe just behind the sealed tip.

It was useful, especially with implanted probes, to register the pressure in the tank relative to the device at various times throughout the experiments to establish a 'zero' level. For this reason the pressure measuring device was connected to the tank, by-passing the probe, by a tube and 3-way tap (Fig. 1). The diaphragm of the device was place very approximately at the same level as the water in the tank.

The device was calibrated at the end of each recording by adding a known volume of sea water to the tank; the change in depth was calculated from the dimensions of the tank. A thermistor flow meter was used to check that animals were pumping when measurements of pressure were taken (Foster-Smith, 1976a).

The animals used were: bivalves; *Mytilus edulis* L., *Modiolus modiolus* (L.), *Cerastoderma edule* (L.), *Scrobicularia plana* (da Costa), *Mya arenaria* L.: tunicate; *Ciona intestinalis* L.: sponges; *Sycon coronatum* Ellis & Solander, *Halichondria panicea* Pall.

RESULTS

Table I summarizes the pressures found in the exhalant and inhalant chambers of the animals investigated. From these values it appears that the highest pressures are generated in those species which have the most restricted flow because of the possession of long siphons (*Mya arenaria* and *Scrobicularia plana*). The pressures generated by the other species are all similar in value.

TABLE I

Recorded pressures for a number of species: all pressures in the mantle and atrial cavities are negative with respect to the ambient pressure and positive for the suprabranchial and exhalant cavities and the spongocoels.

Species	No. of animals	Average soft body wet wt (g)	Pressure (mm of H_2O)	
Bivalves			Mantle	Suprabranchial
Mya arenaria	12	4.0	1.0–1.5	1.6–3.7
Scrobicularia plana	5	2.25	0.3–0.9	2.0
Modiolus modiolus	6	5.6	0.1–0.3	0.1–0.5
Mytilus edulis	10	3.0	<0.05–0.1	0.1–0.25
Cerastoderma edule	6	1.7	<0.05–0.1	0.2–0.3
Tunicate			Atrial	Exhalant
Ciona intestinalis	10	2.6	0.05–0.08	0.1–0.33
Sponges				Spongocoel
Sycon coronatum	5	1.25	—	0.2–0.28
Halichondria panicea	5	3.0	—	0.24–3.5

BODY SIZE AND PRESSURES

The gills of bivalves and the pharynx of tunicates may be considered to have numerous, small pumps in parallel. The pressure generated by a number of pumps in parallel is equal to that generated by one of the pumps (Fox, 1974), so that an increase in the area available for pumping with the ciliary filter feeders investigated should not lead to increased pressures but only to an increase in the flow of water.

Measurements were made of the pressures on the exhalant side of the pharynx of *Ciona intestinalis* of different sizes. The tunicate was selected because of the ease with which the probe could be inserted through the exhalant aperture of small animals. Only values of pressure when the exhalant aperture was open widely are included in Table II. The results indicate that for *C. intestinalis* the pressures are independent of body size. When, however, the exhalant aperture became restricted in diameter pressure increased and in the case of animals 5–6 cm long, pressures up to 0.4 mm H_2O were developed.

TABLE II

Pressures on the exhalant side of the pharynx of *Ciona intestinalis* of different sizes.

Length (cm)	No. of animals	No. of measurements	Pressures (mm of H_2O) (mean ±S.D.)
2 –2.5	3	16	0.11±0.06
3.5–4	5	22	0.15±0.05
5 –6	10	38	0.14±0.06

PRESSURE GRADIENTS THROUGH WATER FLOW SYSTEMS IN CILIARY FILTER-FEEDERS

The pressures in the inhalant and exhalant siphons of *Mya arenaria* were investigated in more detail by inserting a glass probe through the siphonal apertures and recording pressures at increasing depths within the siphons. The animals were buried in the sand so that the siphons were extended until the distal tips were just above the surface. It was not possible for the probe to reach the mantle or suprabranchial cavities without touching the siphon at some point and because of this, the recordings are incomplete. Fig. 2 shows an example of pressures at different depths within the inhalant and exhalant siphons of one individual. It is important to note that, relative to the ambient pressure in the tank, the pressures are negative in the case of the inhalant siphon and positive in the case of the exhalant siphon.

The apertures at the distal end of the siphons of *M. arenaria* cause a sharp pressure change whilst there is a constant pressure gradient along the siphons. The gradient is steeper in the exhalant siphon than in the inhalant siphon and this is to be expected since the exhalant siphon has a smaller internal diameter. Table III summarizes the entrance and exit losses, and the pressure gradients in eight *M. arenaria* all with a soft body wet weight of about 4 g.

Taking the siphons as 15 cm long and presuming the gradients to be maintained along the whole length of the siphons then the pressure losses due to frictional resistance in the inhalant siphons would be 1.6 mm of water (compared with an entrance loss of 0.7 mm of water) and 3.4 mm of water for the exhalant siphon

TABLE III

Pressures recorded in the siphons of *Mya arenaria*: all pressures in mm of H_2O and gradients in terms of change in pressure/cm probe distance in the siphon: inhalant siphon pressures decreased from the distal to the proximal end; exhalant pressures increased from the distal to proximal end: means and ±S.D. for 34 recordings from 8 individuals.

Across entrance	Across exit	Pressure gradient along siphon	
		Inhalant	Exhalant
0.70±0.15	0.66±0.13	0.11±0.01	0.23±0.07

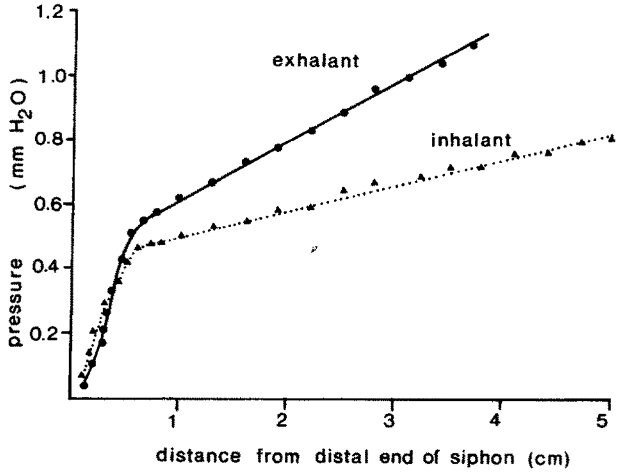

Fig. 2. The relation between internal pressure and distance from the distal tip of the siphon in a specimen of *Mya arenaria*.

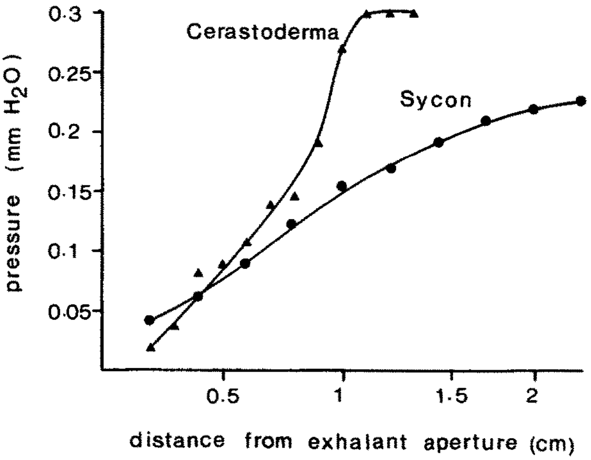

Fig. 3. The relation between internal pressure and distance from the exhalant aperture in individual *Sycon coronatum* and *Cerastoderma edule*.

(compared with an exit loss of 0.66 mm of water). In contrast, almost all of the pressure losses in *Mytilus edulis* and *Modiolus modiolus* are found as the probe is inserted through the exhalant aperture and the exit losses must account for a large proportion of the total pressure losses. In the case of *Cerastoderma edule*, which has short siphons, there is no sharp loss in pressure as the probe is inserted through the exhalant aperture and the pressure rises uniformly as the probe is lowered further into the siphon. There is, however, a sharp increase in pressure on passing from the distal end of the siphon to the suprabranchial cavity (Fig. 3). In the case of *Sycon coronatum* and *Halichondria panicea* pressure increases as the probe is inserted further into the spongocoel (Fig. 3).

DISCUSSION

Filter-feeders which pump water must generate pressures to overcome resistance to water flow. The apparatus used in this work allows pressure losses due to frictional resistance and those as the water passes through an opening to be measured and compared. The frictional resistance of the long siphons of *Mya arenaria* and *Scrobicularia plana* may be large in comparison with the total resistance of the system and yet pumping rates are similar to those shown by bivalves with short siphons. In order to overcome this frictional resistance, these species must, therefore, generate higher pressures than bivalves with short siphons. Measurements have also shown that the shape of the exhalant aperture affects pressure losses; the exhalant siphon of *Cerastoderma edule* and the spongocoel of *Scrobicularia coronatum* are tapered towards the distal end and this reduces the amount of kinetic energy lost as water passes through the exhalant aperture.

Foster-Smith (1976a) calculated entrance and exit losses and frictional losses for a hypothetical bivalve with approximately the same dimensions as *Mya arenaria* and the values suggest that frictional losses are much greater than the exit and entrance losses. These values may be compared with pressure losses measured in *M. arenaria* to see how well the equations of hydrodynamics describes flow in bivalves. First, frictional losses calculated using either the Darcy or the Poiseuille equation were 0.20 mm H_2O/cm for the inhalant siphon and 0.48 mm H_2O/cm for the exhalant siphon. The pressure gradients measured for the two siphons were 0.11 mm H_2O/cm and 0.23 mm H_2O/cm respectively. Taking into account the fact that the internal diameter of the siphons of *M. arenaria* was not known throughout their length and that the pumping rate was not measured the agreement between the calculated and measured values is quite good. Such agreement would be expected since at low Reynolds numbers (≈ 20 for water flow in the siphons of *M. arenaria* used in this work) laminar flow would be established almost immediately water enters the siphons.

Secondly, entrance and exit losses may be calculated from the $h_1 = K \cdot v^2/2\ g$ where h_1 is the head (or pressure) loss, v the mean velocity of the water, g the gravitational constant, and K a constant varying with the shape of the orifice (taken to be 0.05–0.25) (Fox, 1974). To this must be added the pressure needed to create the flow of water (velocity head $= v^2/2\,g$) giving an expected pressure difference across the inhalant aperture of 0.012 mm H_2O. The measured pressure difference for *M. arenaria* was 0.7 mm H_2O, or about 60 times greater than the expected value. At low Reynolds numbers a correction for viscous flow ignored in the above formula becomes important. A coefficient of velocity that is nearly unity for turbulent flow is much lower at low Reynolds numbers, and the velocity distribution across the siphon at low Reynolds numbers is such that the mean velocity cannot be used without correction. The pressure (or head) loss may be estimated from the formula $h_l = (1/C_v^2 - 1)\,\alpha \cdot v^2/2\,g$, where C_v is the coefficient of velocity (≈ 0.35 at *Re* 20 and 0.2 at *Re* 10) and α the correction factor for the velocity distribution (≈ 2 at *Re* 20). The new expected pressure difference across the inhalant siphon is 0.16 mm H_2O at *Re* 20 and 0.55 mm H_2O at *Re* 10.

TABLE IV

Power required to sustain pumping rates of ciliary filter-feeders.

Species	Weight specific pumping rates ($ml \cdot h^{-1} \cdot g^{-1}$)	Power ($erg \cdot sec^{-1}$)	Power g^{-1} (wet wt)	Reference
Bivalves				
Mya arenaria	350	101 –202	25.2–50.5	Foster-Smith, 1976a
Scrobicularia plana	244	35 – 44	15.6–19.6	Foster-Smith, 1976a
Modiolus modiolus	250	7.7– 31	1.4– 5.5	Winter, 1969
Mytilus edulis	400	3.3– 11.6	1.1– 3.9	Theede, 1963
Cerastoderma edule	770	7.2– 14.5	4.3– 8.5	Foster-Smith, 1975
Tunicate				
Ciona intestinalis	230	3.0– 6.8	1.1– 2.6	Jørgensen, 1949
Sponges				
Sycon coronatum	980	6.8– 9.5	5.4– 7.6	Estimated from Jørgensen, 1949, 1952
Halichondria panicea	371	7.4– 10.8	2.5– 3.6	

The pressures measured in the spongocoel of the two species of sponges were slightly lower than those calculated by Bidder (1926) for the flagellated chambers in *Leucandra*. He assumed that there would be a drop in pressure between the flagellated chambers and the spongocoel but that since the speed of water flow through the chambers is low, the drop in pressure would be small. Similarly Foster-Smith (1976a) estimated the resistance of the gill to water flow in a bivalve to be small in comparison with that of the siphons. The pressures measured in this work would be lower than the maximum pressures the cilia could produce, but it is considered that the difference will be small. From the pressures, the power needed by the animals to sustain their rates of pumping may be calculated from the relation power ($ergs\ sec^{-1}$) = pressure ($dyn\ cm^{-2}$) × volume pumped (ml) × sec^{-1}. Table IV gives filtration rates expressed in terms of soft body wet weight derived from various sources for animals of approximately the same size as those used in this work. The weight-specific filtration rates for the sponges were estimated from the data of Jørgensen (1949, 1952) and using dry weights and wet weights of the sponges collected during this investigation. (It was found that the wet weights of the sponges were between 18 and 25 times the ash-free dry weights.) Table IV also gives the total power needed to sustain pumping and that in terms of soft body wet weight. Although the values must be approximate it seems that the power requirements for all the ciliary filter feeders are similar, with the exception of *Mya arenaria* and *Scrobicularia plana* whose requirements are substantially greater. Estimation of oxygen consumption from power would give unreliable values, but the percentage of the total oxygen uptake for the animals needed by the lateral cilia must be very small. Using values given by Prosser (1973), *Mytilus edulis* would expend ≈ 1 % of its energy on water propulsion assuming a respiratory quotient of 0.85 and an efficiency of conversion of chemical energy to mechanical energy of 20 %.

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