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Filtration rate capacities in 6 species of European freshwater bivalves

Jakob Kryger and Hans Ulrik Riisgård
Institute of Biology, Odense University, Campusvej 55, DK-5230 Odense M, Denmark

Summary. Filtration rate capacities in undisturbed freshwater bivalves were determined by means of two different methods (indirect "clearance" and "suction" methods) in *Anodonta anatina* (L.), *Unio tumidus* Philipsson, *Unio pictorum* (L.), *Unio crassus* Philipsson, *Dreissena polymorpha* (Pallas) and *Sphaerium corneum* (L.). In *A. anatina*, *D. polymorpha*, and *S. corneum* the filtration rate (FR, $l\ h^{-1}$) at 19–20° C as a function of dry tissue weight (DW, g) or ash-free dry weight (AFDW, g) could be expressed by the equations: $1.10\ DW^{0.78}$, $6.82\ DW^{0.88}$, and $2.14\ AFDW^{0.92}$, respectively. In *U. tumidus*, *U. pictorum*, and *U. crassus* filtration rates were comparable with those of *A. anatina*. In *D. polymorpha* the *b* value of the corresponding regression of gill area on dry weight was 0.87. The rates of water transport in freshwater bivalves are 2–8 times lower than in marine bivalves of comparable size. A corresponding difference in the filtration rate per gill area unit is found. The measured filtration rates in undisturbed bivalves are substantially higher (at least 4 times) than previously reported. This indicates that the impact of bivalve water processing on freshwater ecosystems is greater than hitherto suggested.

Key words: Freshwater bivalves – Filtration rate capacity – Indirect methods

Suspension feeding bivalves (especially *Dreissena polymorpha)* are often a major component of the lake benthos (Stańczykowska 1977), and they may be of great importance in transformation and circulation of material and energy in lake ecosystems (Klee 1971; Izvekova and Lvova-Katchanova 1972; Stańczykowska et al. 1975; Stańczykowska 1984). Reliable data on filtration rate in freshwater bivalves are thus needed in order to assess their ecological role.

Considerable amounts of data on filtration rates in suspension feeding marine bivalves have been published (e.g. Winter 1977; Møhlenberg and Riisgård 1979). Much less attention has been paid to freshwater bivalves, and the existing data show wide discrepancies between filtration rates measured by different authors in the same species (Walz 1978; Benedens and Hinz 1980; Stánczykowska et al. 1975) and, generally, the values are remarkably low compared to filtration rates in marine bivalves.

Møhlenberg and Riisgård (1979) showed by means of a new indirect technique that filtration rates in marine bivalves had often been seriously underestimated due to adverse experimental conditions (e.g. measurements on infaunal bivalves outside their natural substrate, mechanical or chemical disturbance, abnormally high algal concentrations). Further, it has been shown by Famme et al. (1986) that previously published data on pumping rates (= filtration rates) of marine bivalves determined by direct "constant-level-tank" methods are invalidated due to unintentional pressure bias in the experimental set-up and adverse conditions reducing the opening of the valves. Similar artifacts and adverse conditions might explain the low filtration rates of freshwater bivalves recorded in the literature.

This paper deals with filtration rate measurements in freshwater bivalves by means of the same techniques that have allowed precise determinations in undisturbed marine bivalves.

Materials and methods

The experiments were conducted at the Institute of Biology, Odense University, from July to October, 1984, and at the Biological Station at Bøgebjerg, Funen, Denmark, from June to September, 1985.

Specimens of *Sphaerium corneum* (L.) were collected in a small stream, the Ladegårds Å, near Vissenbjerg, Funen. *Anodonta anatina* (L.) (= *Anodonta piscinalis* Nilss.), *Unio tumidus* Phillipsson, and *U. pictorum* (L.) came from Lake Søholm, Funen. *U. crassus* Phillipsson was collected in the stream Hågerup Å, Funen, and *Dreissena polymorpha* (Pallas) came from the lake Jels Nedersø, South Jutland. The bivalves were kept in the laboratory in aquaria with natural stream or lake water and acclimated to 18–20° C for 2–4 days prior to the experiments. All experiments were conducted at 19–20° C.

The unicellular alga *Chlorella vulgaris* (diameter = 4–8 µm) grown in a batch culture was selected for the filtration rate measurements, because particles above ca. 4 µm are 100% efficiently retained by the gills of *Dreissena polymorpha* and unionid bivalves (Jørgensen et al. 1984).

In *Anodonta* and *Unio* filtration rates were measured by means of the "suction method" of Møhlenberg and Riisgård (1979). The bivalves were allowed to bury themselves in a sediment-containing aquarium (12 l) with lake

Offprint requests to: H.U. Riisgård

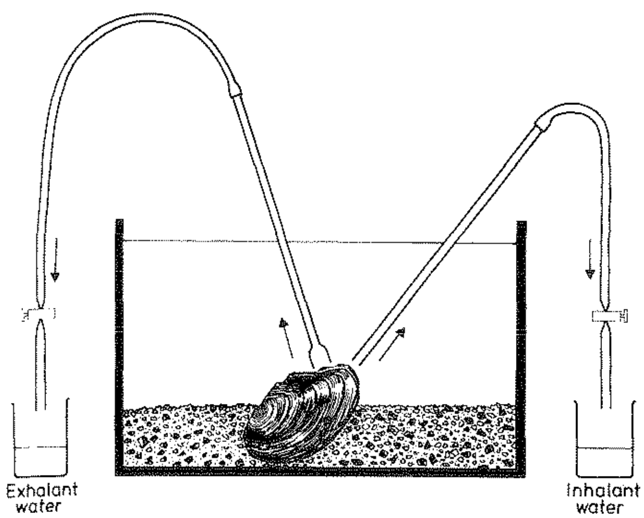

Fig. 1. Experimental set-up. The glass tubes collect water from the inhalant and exhalant current by gravity

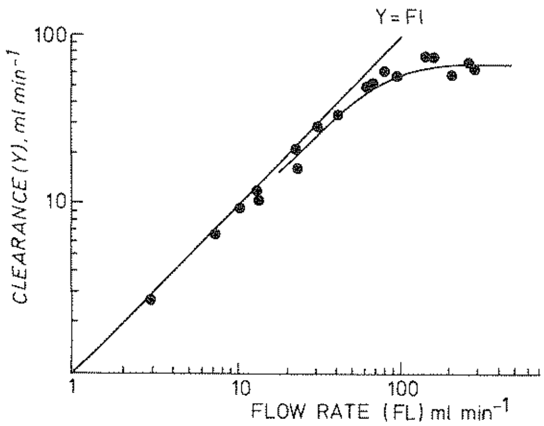

Fig. 2. Clearance (Y) as a function of flow rate (Fl) in an experiment with *Anodonta anatina* (2.856 g dry weight of soft parts). Line for clearance = flow rate (Y = Fl) is shown. The plateau represents true filtration rate

water. *Chlorella* cells were added to a concentration of 10–12 × 10^6 cells l^{-1}. When the bivalves had reached their natural position with about 2/3 of the body buried, they usually opened their valves and apertures. To estimate filtration rate samples of inhaled and exhaled water were sucked through glass tubes placed 2–4 mm above the bivalve's inhalant and exhalant apertures, see Fig. 1. The flow rate through the glass tubes was varied from 3 to 400 ml min^{-1}. The volume of exhaled water cleared of particles per unit of time (Y) was calculated as:

$$Y = Fl\,(1 - C_e/C_i),$$

where Fl is the flow rate through the glass tube, and C_i and C_e the concentrations of algal cells in the water collected simultaneously from the inhalant and exhalant currents, respectively. At high flow rates, when all the exhaled water were sucked through the glass tube, the clearance of 100% efficiently retained particles becomes independent of flow rate and representative of the filtration rate, see Fig. 2.

In *Sphaerium corneum* and *Dreissena polymorpha* filtration rates were determined from the rate (F) by which *Chlorella* cells were cleared from suspensions by means of the equation: $F = M/t \ln C_o/C_t$ (Coughlan 1969), where M = volume of suspension, t = time, C_o and C_t = particle concentrations at time 0 and time t. 1 to 30 bivalves (depending on size) were placed in a 200 ml glass beaker with 190 ml of filtered (Whatman GF/C) natural fresh water with *Chlorella* cells added to make up a concentration of 10–12 × 10^6 cells l^{-1}. Adequate mixing of the suspension was ensured by aeration. When all the bivalves had opened their valves and extended their siphons, samples (10 ml) were taken at different time from the suspension without disturbing the bivalves.

The algal cell concentrations were determined with a Coulter Counter, Model Z_B, fitted with a 50 µm tube. NaCl was added to the freshwater samples (6‰ S) to provide the required conductivity. No morphological changes in the algal cells were observed at this salinity.

Gill area of specimens of *Anodonta* and *Unio* were measured by placing the animals with one valve removed under a glass plate and drawing the contours of the outer demibranch on transparent foil. In *Dreissena* the gill contours were drawn by means of a stereo microscope with a drawing

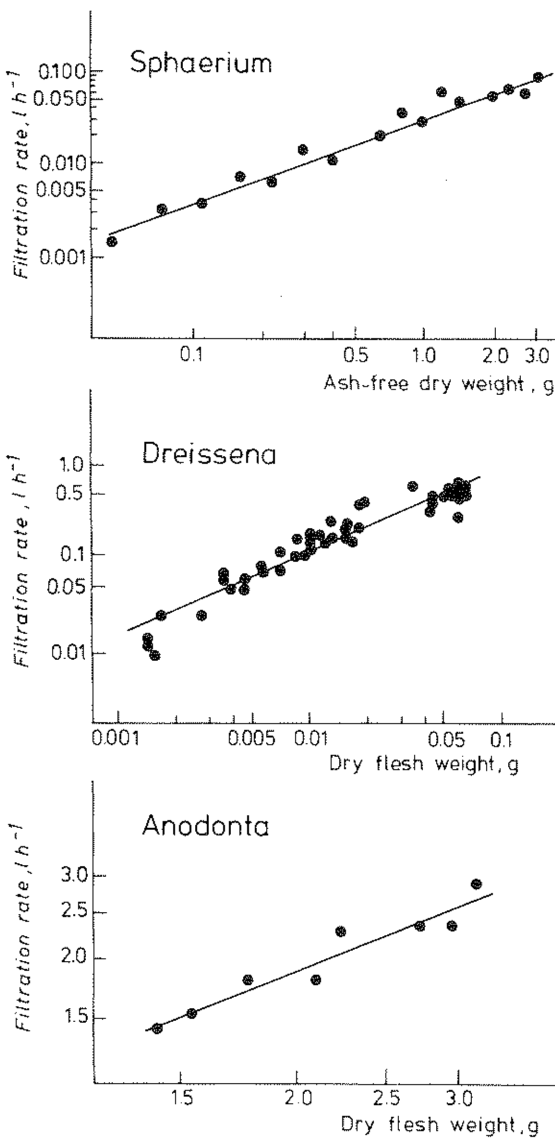

Fig. 3. Filtration rate as a function of dry flesh weight or ashfree dry weight in *Sphaerium corneum*, *Dreissena polymorpha*, and *Anodonta anatina*. Regression equations are shown in Table 1

Table 1. Terms of regression equations: in Y = ln a + b ln X, describing the relationship between Y = filtration rate (FR, l h^{-1}) or gill area (GA, cm^2) and X = dry flesh weight (DW, g) or ash-free dry weight (AFDW, g), N = number of experiments. r^2 = coefficient of determination. SE = standard error

Species	Regression	N	Weight (g)	ln $a \pm$SE	$b \pm$SE	r^2
Anodonta anatina	FR on DW	8	1.423 –3.141	0.096 ± 0.075	0.78 ± 0.20	0.92
Sphaerium corneum	FR on AFDW	16	0.0005–0.031	0.762 ± 0.237	0.92 ± 0.05	0.97
Dreissena polymorpha	FR on DW	47	0.002 –0.066	1.919 ± 0.321	0.88 ± 0.04	0.90
D. polymorpha	GA on DW	22	0.004 –0.070	4.165 ± 0.110	0.87 ± 0.03	0.98

prism. The gill area was then estimated from the weight of the drawings. The total area was found by multiplication by 8, since the 4 V-formed demibranchs are equally sized.

The shell lengths of the bivalves were measured to the nearest 0.1 mm with a dial caliper. After the experiments the dry weight of the soft parts of *Anodonta, Unio*, and *Dreissena* was determined. Ash-free dry weight of *Sphaerium* was determined as the weight difference of soft parts dried to constant weight at 95° C and the weight of the soft parts ashed at 450° C for 3 hours.

The following relations between shell length (SL, mm) and dry weight of the soft parts (DW, g) or ash-free dry weight (AFDW, g) were found:

Sphaerium corneum: $AFDW = 1.41 \times 10^{-5}\ SL^{3.15}$

Anodonta anatina: $DW = 9.4 \times 10^{-7}\ SL^{3.36}$

Dreissena polymorpha: $DW = 1.54 \times 10^{-5}\ SL^{2.42}$

The equations were used for calculating dry weight of soft parts as well as a and b values of the allometric equation for filtration rate (FR) as a function of size (W): $FR = aW^b$ from literature data.

Results

The filtration rate (FR) in *Sphaerium corneum, Dreissena polymorpha*, and *Anodonta anatina* increased with increasing body weight according to the equation $FR = aW^b$, where W is the dry weight of the soft parts (in *Dreissena* and *Anodonta*) or the ash-free dry weight (in *Sphaerium*), see Fig. 3 and Table 1. In *Dreissena* the b value of the regression of filtration rate on dry weight (0.88) is almost identical to the b value of the corresponding regression of the gill area on dry weight (0.87), see Table 1. The filtration rate per gill area unit is similar in *Dreissena* and unionid bivalves, i.e. 1.2–1.9 ml min^{-1} cm^{-2} (Table 2).

The filtration rates measured in unionid bivalves with the "suction method" may be regarded as filtration rate capacities because these measurements were made on bivalves judged to be fully open. In *Sphaerium* and *Dreissena* where the "clearance method" was employed, filtration rates are average values of several individuals. Filtration rates measured in *Dreissena* by means of the two methods did, however, closely agree, see Table 3.

When the "clearance method" was employed on unionid species lying on one valve outside the sediment, the filtration rate was always reduced due to partial closure of the valves and apertures.

Table 2. Representative minimum and maximum values of filtration rate per gill area unit in unionid bivalves and *Dreissena polymorpha*, which were judged to be fully open

Species	Dry weight of soft parts (g)	Filtration rate (l h^{-1})	Filtration rate per gill area unit (ml min^{-1} cm^{-2})
Anodonta anatina	3.141	2.6–2.9	1.2–1.3
Unio pictorum	3.017	3.2–4.6	1.2–1.7
U. tumidus	2.424	2.1–2.4	1.3–1.5
U. crassus	2.676	3.3–4.1	1.2–1.4
Dreissena polymorpha	0.065	0.5–0.7	1.4–1.9

Table 3. *Dreissena polymorpha*. Comparison of filtration rates measured by means of two different methods

Shell length (mm)	Dry flesh weight (g)	Filtration rate (l h^{-1})	
		"Clearance method"	"Suction method"
32.5	0.074	0.690	0.744
32.0	0.079	0.660	0.726
31.0	0.062	0.624	0.570

Discussion

In most previous reports on filtration rates in freshwater bivalves the size of the experimental animals is given in terms of shell length or wet weight (inclusive valves). Consequently, it is difficult to compare the filtration rates, but from relationships between shell length, wet weight, and dry tissue weight as found in this study it has been possible to estimate dry tissue weights from the original literature data.

In *Anodonta anatina, Unio pictorum*, and *U. tumidus* the filtration rates measured by Kondratév (1962) and Alimov (1969) are about 4 times lower than the rates determined in the present study. The low rates were measured in beakers without sediment. Lewandowski and Stańczykowska (1975) attempted to estimate natural filtration rates in *Unio* and *Anodonta* using a flow system placed in a Polish lake, but the bivalves had not burrowed in the sediment which may explain the low values obtained (see Fig. 4, t). DeBruin and Davids (1970) employed a direct technique, the so-called "constant-level-tank" method, to measure the pumping rate in individuals of *Anodonta cygnea zellensis* with attached rubber tubes in order directly to collect all the exhalant water. Their results are comparable to those of Lewandowski and Stańczykowska, but this may be due to unintentional pressure bias in the experimental set-up and/or disturbance of the experimental animals. Positive hydrostatic pressures as low as 1–2 mm H_2O drastically reduce water pumping in mussels (Famme et al. 1986; Jørgensen et al. 1986).

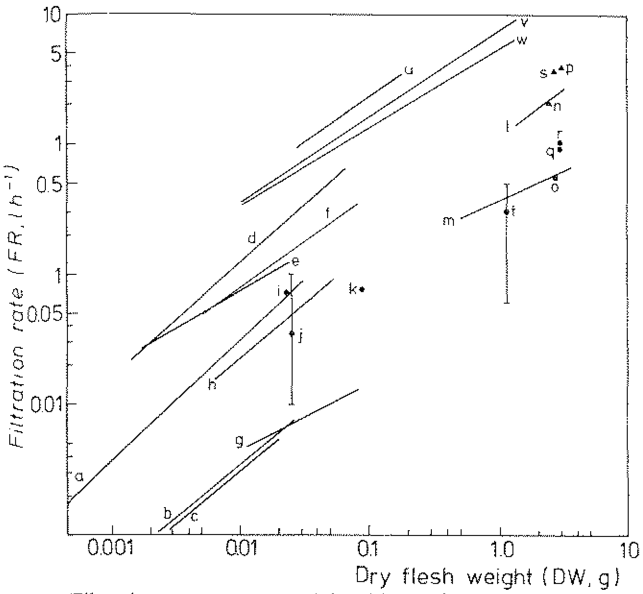

Fig. 4. Filtration rates measured in this study (a, d, l, n, p, s) compared with literature data on freshwater and marine bivalves. *Sphaerium corneum* (a–c), *Dreissena polymorpha* (d–k), *Unionidae* (l–t) and marine bivalves (u–w). Vertical lines indicate range. Small letters refer to authors in Table 4

For practical reasons the measurements on *Sphaerium corneum* (infaunal species) had to be made in beakers without sediment, and consequently the rates may underestimate natural filtration rates. Nevertheless, the present data on filtration rates are 6–8 times higher than reported by Alimov (1965) and Hinz and Scheil (1972). In *Dreissena polymorpha* (epifaunal species) the values of Kondratév (1963) and Alimov (1969), who measured rates at which suspended clay was cleared, are comparable with those determined in this study with suspended *Chlorella* cells. Most other filtration rates reported on *Dreissena* are considerably lower (see Fig. 4).

One of the main reasons for the low filtration rates measured by several workers on *Sphaerium* and *Dreissena* may be the widespread use of high concentrations of inorganic particles such as colloidal graphite for clearance experiments. Morton (1971) measured very low rates in *Dreissena* using graphite particles with an average diameter of 0.5–1.5 µm. Addition of various species of algal cells to the graphite suspension increased the filtration activity. Possible explanations of the low filtration obtained from experiments with graphite particles are: abnormally high particle concentration, particle retention less than 100%, and "chemical disturbance". Particle concentrations have usually been determined photometrically, requiring high

Table 4. Data on bivalve species, authors, methods employed and filtration rates (FR, $l\,h^{-1}$) in various freshwater and marine bivalves (*Cardium, Mytilus, Arctica*). Where possible *a* and *b* values according to the allometric equation $FR = a DW^b$ were calculated using original data on shell length (1), wet weight incl. shells (2) or dry weight of the soft parts (3). Calculated values are shown in brackets. Small letters in front of authors refer to Fig. 4

Species		Authors	Suspended particles	Method	Temp. (°C)	*a*	*b*	Original size data
Sphaerium corneum	a	This study	*Chlorella vulgaris*	"Clearance"	19	2.14	0.92	3
	b	Alimov (1965)	Clay particles	do	17–18	(0.14)	(0.81)	1
	c	Hinz and Scheil (1972)	Graphite	do	14	(0.13)	(0.82)	1
Dreissena polymorpha	d	This study	*Chlorella vulgaris*	do	20	6.82	0.88	3
	e	Kondratév (1963)		do	16–17	(1.07)	(0.58)	1
	f	Alimov (1969)	Clay particles	do	18–20	(1.98)	(0.70)	2
	g	Morton (1971)	Graphite	do		(0.04)	(0.49)	1
	h	Micheev (1966)	Natural seston		20–22	(1.16)	(0.86)	1
	i	Hinz and Scheil (1972)	Graphite	do	20			1, 3
	j	Stańczykowska et al. (1976)	Natural seston	*In situ* flow system				2
	k	Walz (1978)	*Nitzschia*	"Clearance"	15			1, 3
Anodonta anatina (=*piscinalis*)	l	This study	*Chlorella vulgaris*	"Suction"	20	1.10	0.78	3
	m	Alimov (1969)	Clay particles	"Clearance"	18–20	(0.37)	(0.46)	2
Unio tumidus	n	This study	*Chlorella vulgaris*	"Suction"	20			3
	o	Alimov (1969)		"Clearance"	18–20			2
U. pictorum	p	This study	*Chlorella vulgaris*	"Suction"	20			3
	q	Kondratév (1962)		"Clearance"				2
	r	Alimov (1969)	Clay particles	do	18–20			2
U. crassus	s	This study	*Chlorella vulgaris*	"Suction"	20			3
Unionidae	t	Stańczykowska et al. (1976)	Natural seston	*In situ* flow system				2
Cardium edule	u	Møhlenberg and Riisgård (1979)	*Phaeodactylum, Dunaliella,* and *Tetraselmis*	"Suction"	10–13	11.60	0.70	3
Mytilus edulis	v	Møhlenberg and Riisgård (1979)	do	do	10–13	7.35	0.66	3
Arctica islandica	w	Møhlenberg and Riisgård (1979)	do	do	10–13	5.55	0.62	3

concentrations, which may reduce water transport in bivalves (Winter 1977; Walz 1978). Particles below about 1 μm in diameter are not retained 100% by the gills of *Dreissena* (Jørgensen et al. 1984). The fraction of inefficiently retained particles in the suspension will increase over time, and this may lead to underestimation of the true rate of water transport (Williams 1982). Finally, the filtration activity may be affected by "unpalatability" of the particles or by chemicals in the commercially available particle suspensions (Benedens and Hinz 1980).

The rates of water transport measured in the present work under optimal conditions are 4–8 times lower in *Sphaerium*, *Unio*, and *Anodonta* and about 2 times lower in *Dreissena* than in marine bivalves of comparable size (see Fig. 4).

The filtration rate capacities reported in this paper indicate that water processing of bivalves, especially (*Dreissena polymorpha* which is often present in very great numbers, are of greater importance in affecting freshwater ecosystems than previously suggested. It would therefore be of interest to assess to what extent the filtration rate capacities measured in undisturbed bivalves in the laboratory are exploited in nature.

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