

REVIEW

On measurement of filtration rates in bivalves — the stony road to reliable data: review and interpretation

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ABSTRACT: This review deals with the measurement of filtration rates in suspension feeding bivalves. Currently used methods are described, and some reliable filtration rate data obtained under optimal laboratory conditions are presented. The different methods have often caused troubles, and a number of problems and shortcomings are brought to light. The conflicting data on filtration rates seem partly to be due to the incorrect use of methods, and partly to be caused by differences in experimental conditions.

KEY WORDS: Suspension feeding · Filtration rates · Methods · Problems and shortcomings

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INTRODUCTION

Many attempts have been made to determine the filtration rates of suspension feeding bivalves, but the results are often difficult to interpret and compare. The conflicting data on filtration rates seem partly to be due to incorrect use of methods, and partly to be caused by differences in experimental conditions.

The intention of this review, which deals with the measurement of filtration rates in suspension feeding bivalves, is (1) to discuss the advantages and disadvantages of the different methods currently being used, and (2) to point out some reliable (i.e. no methodical flaws) filtration rate data obtained under optimal laboratory conditions.

The different methods used for measurement of filtration rates have often caused troubles, and some flaws have been repeated over and over again. Especially for new readers of the staggering bivalve literature, heaps of conflicting data may pose an insurmountable barrier for a meaningful understanding of bivalve filter feeding. Therefore, a number of problems and shortcomings are brought to light here to clear the

road for progress. From the present review it appears that until now it has been a stony road to reliable data.

Different terms are used in the literature for expressing the rate of water processing of bivalves and this sometimes causes confusion. In the present review the following definitions apply: filtration rate = pumping rate = volume flow rate; clearance rate = volume of water cleared of suspended particles per unit of time. The term 'clearance rate' always refers strictly to its definition. Only under certain specified conditions is the clearance rate representative of the filtration rate. This should be remembered when reading 'Examination of methods' below.

EXAMINATION OF METHODS

The purpose of this section is to thoroughly examine the methods currently being used for measurements of filtration rates. Advantages and disadvantages of the different methods are accentuated, and examples of imperfections are mentioned to warn against pitfalls.

Direct method. Direct methods, where the exhaled water is physically separated from the surrounding water (e.g. by means of a rubber apron), collected, and

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measured, have been used in many filtration studies on bivalves over the years (Moore 1910, Galtsoff 1926, Nelson 1936, Loosanoff & Engle 1947, Collier & Ray 1948, Davis 1964, Drinnan 1964, Bernard 1974, Hildreth 1976, Davenport & Woolmington 1982, Redpath & Davenport 1988) (for a review of the older literature, see Jørgensen 1966). However, reliable filtration rates were first obtained by means of the sophisticated direct technique developed by Famme et al. (1986). Earlier attempts to use direct methods failed because of: (1) mechanical disturbance, e.g. due to attachment of a rubber apron to the valves around the exhalant siphon, and (2) pressure gradients between inflow and outflow apertures. Using the direct method of Famme et al. (1986) it has been shown that the build-up of even small unintended back-pressures can suppress the low pressure ciliary pump of *Mytilus edulis* (Jørgensen et al. 1986, 1988).

A version of the apparatus developed by Famme et al. (1986) is shown in Fig. 1. The inhalant and exhalant currents of the experimental mussel are physically separated by a silicone rubber membrane so that the water being pumped from the inhalant chamber (C_1) is collected in the exhalant chamber (C_2). The increasing water level in C_2 is monitored with a laser beam striking a mirror fixed on a floating ping-pong ball. The mirror reflects the laser beam onto a scale situated about 10 m from the mirror, and a deflection of 1 cm on the scale corresponds to about a 0.1 mm change in the water level in C_2 . When the mussel pumps water from C_1 to C_2 , a pressure difference develops which may be fixed at any selected value by adjusting a calibrated peristaltic pump that pumps water back from C_2 to C_1 .

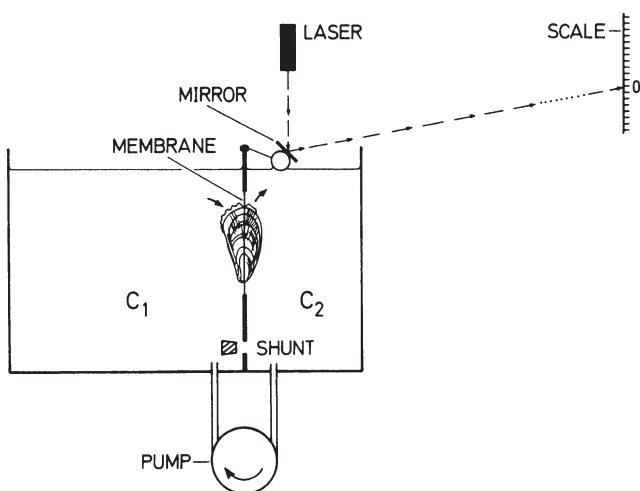


Fig. 1. Direct method. Set-up measurement of filtration rate at zero or imposed back-pressures in *Mytilus edulis* (From Jørgensen et al. 1986) C_1 : inhalant chamber; C_2 : exhalant chamber

By means of this method, both the pumping rate at zero back pressure (= normal filtration rate) and the back pressure characteristic can be determined experimentally. The use of this method in bivalves is limited to species which have a well-defined exhalant siphon. Famme et al. (1986) showed that the filtration rates of unrestrained 3 to 4 cm shell *Mytilus edulis* were highly correlated with the degree of valve opening. High pumping rates were correlated with wide open valves and extended and diverging mantle edges. It was also shown that the filtration rates measured with the direct method agree with the filtration rates measured on the same set of animals with the 'suction' method and the 'clearance' method (see below). When *M. edulis* is forced to pump against a hydrostatic pressure, the filtration rate decreases linearly with increasing hydrostatic pressure towards a maximum pressure head of about 3.5 mm H₂O (Jørgensen et al. 1988, 1990). An unintended back pressure of, e.g., 2 mm H₂O will reduce the filtration rate by about 50%. Proper use of the direct method requires a good deal of practice, and only 1 size group of 'standard' mussels fit to the apparatus. The main reason for using the direct method is its suitability in physiological investigations. Thus, measurements of filtration rates at well-defined back pressures have been performed by means of this method in order to study the properties of the bivalve pump, including pump and system characteristics, effects of temperature, serotonin, and valve opening degree (Jørgensen et al. 1986, 1988, 1990).

Flow-through chamber method. An advantage of the flow-through chamber method is that a constant algal concentration can be maintained during the experiment. Many attempts have been made to use this method (e.g. Haven & Morales-Alamo 1970, Thompson & Bayne 1972, Vahl 1972, 1973a,b, Walne 1972, 1974, Hildreth & Crisp 1976, Bayne et al. 1976, Hibbert 1977, Riisgård 1977, Villiers & Allanson 1988).

Correct use of the flow-through method and possible pitfalls were pointed out by Riisgård (1977). But erroneous use of the method continues to give incorrect values of filtration rates, hence leading to conflicting data in the literature. A brief examination of the flow-through technique is therefore appropriate.

The clearance rate (Cl) of a suspension feeding bivalve placed in a flow-through chamber may be determined by using the equation:

$$Cl = Fl(1 - C_2/C_1) \quad (1)$$

where Fl = flow rate through the chamber, and C_1 and C_2 = concentration of suspended algal cells before and after passage of the chamber. The size and shape ('geometry') of the flow-chamber, as well as the flow rate, are of great importance when using this method and the following conditions should be satisfied: (1) the

water flowing through the chamber should come within reach of the bivalve, (2) the water leaving the exhalant aperture must be prevented from mixing with the inhalant water (i.e. no recirculation of once filtered water), and (3) the algal cells must be 100% efficiently retained by the gills (e.g. algal diameter $>4\ \mu\text{m}$ for mussels and other bivalves with eu-laterofrontal cirri, and $>7\ \mu\text{m}$ for pectinids and other bivalves with pro-laterofrontal cilia; Møhlenberg & Riisgård 1978, Jørgensen et al. 1984, Riisgård 1988, Riisgård et al. 1996). One way of checking these conditions is to plot CI versus FI . For smaller flow rates, data tend to depart little from the line given by $CI = FI$, but above a certain critical flow rate the clearance values depart from the line and form a plateau (Fig. 2).

Only at flow rates above the critical level will the clearances obtained by using Eq. (1) be representative of the true filtration rate. This has generally not been sufficiently recognised (see section 'Problems and shortcomings', and Appendix 1).

Suction method. Filtration rate measurements may be determined by means of the 'suction' method described by Møhlenberg & Riisgård (1979), and used in bivalve studies conducted by Kiørboe & Møhlenberg (1981), Famme et al. (1986) and Kryger & Riisgård (1988).

Samples of inhaled and exhaled water are sucked through glass tubes placed 2 to 4 mm above the bivalve's inhalant and exhalant openings (Fig. 3). The flow rate through the glass tubes is varied by gravity, or by means of an adjustable peristaltic pump. The clearance CI (volume of exhaled water cleared of particles per unit time) may be calculated according to the equation:

$$CI = FI (1 - C_e/C_i) \quad (2)$$

where FI is the suction flow rate through the glass tubes, and C_i and C_e the concentrations of 100% retained algal cells in water collected simultaneously from inhalant and exhalant currents, respectively. For smaller suction flow rates, data tend to depart only little from the line given by $CI = FI$, but above a certain critical suction flow rate the clearance values depart from this line and form a plateau (Fig. 3). At high flow rates, when all the exhaled water is sucked through the glass tube, the clearance becomes independent of suction flow rate and thus representative of the true filtration rate of the bivalve.

The close kinship with Eq. (1) and the flow-through chamber method is obvious. But the suction method is superior to the flow-through chamber method because the 'geometry' problems of the flow-through method can be eliminated. Furthermore, the suction method allows measurements on undisturbed infaunal bivalves buried in the sediment. *In situ* measurements in the

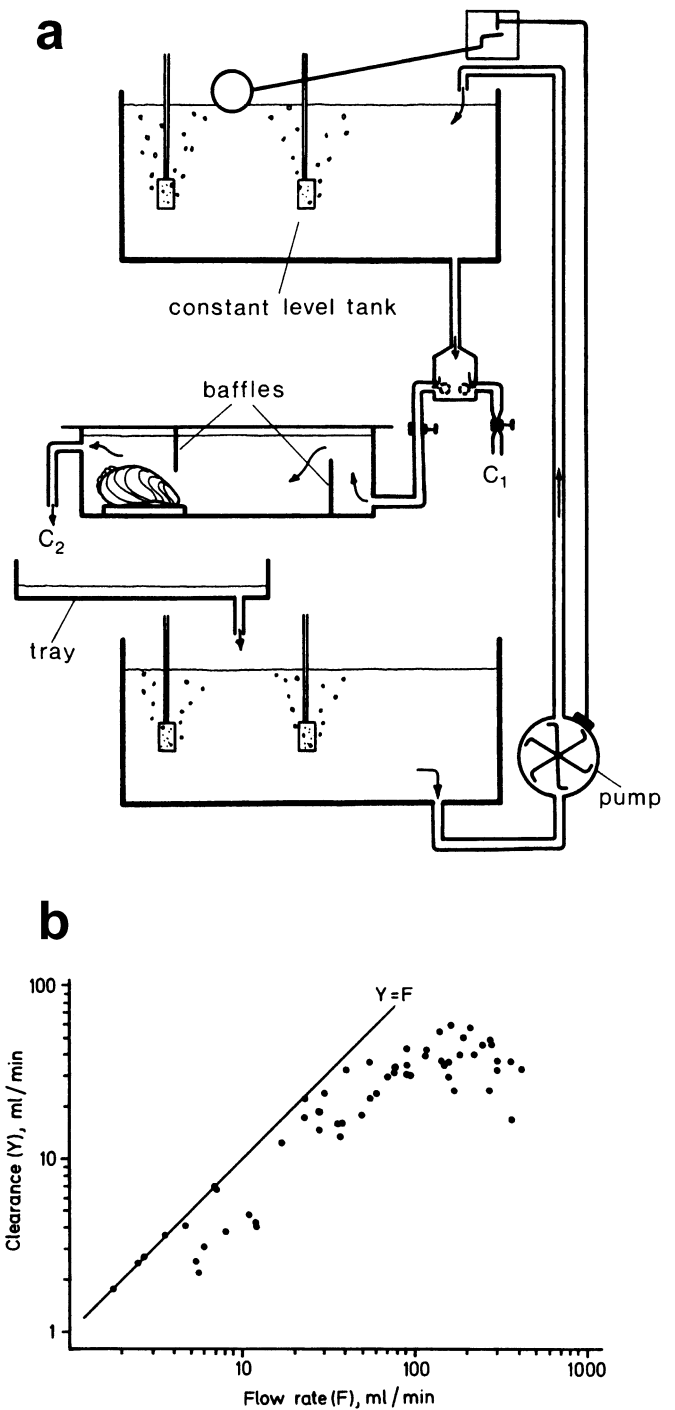


Fig. 2. (a) Flow-through apparatus used by Riisgård (1977) to measure filtration rate of *Mytilus edulis*. (b) Clearance rate, estimated according to Eq.(1), as a function of flow-through rate. At low flow rates, estimated clearance rates approach the line clearance rate = flow-through rate. Clearance rates are only representative of true filtration rate at flow rates above a critical level where clearance values form a plateau. In the present case of a 120 mg body dry wt mussel, the plateau indicates a filtration rate of 30 to $40\ \text{ml}\ \text{min}^{-1}$

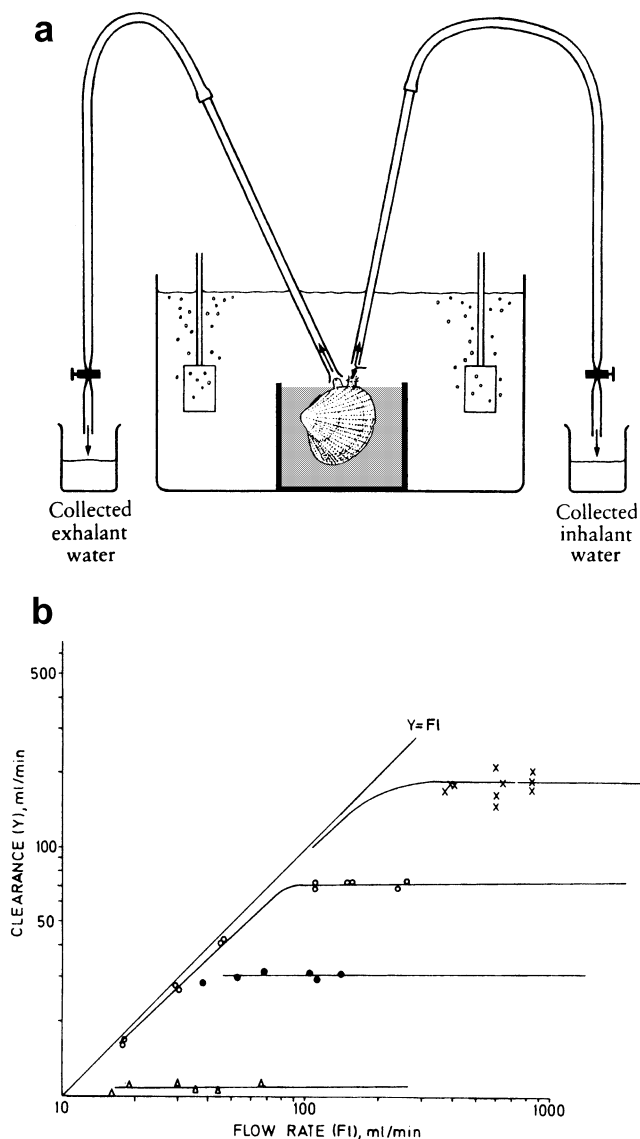


Fig. 3. Suction method. (a) Set-up used for measurement of filtration rates in suspension feeding bivalves. The glass tubes collect water from the inhalant and exhalant siphons by means of gravity. (b) Clearance rate, estimated according to Eq. (2), as a function of suction flow rate. When flow rates are low, estimated clearance rates approach the line clearance rate = suction-flow rate. Clearance rates are representative of the true filtration rate above the critical level where clearance values form a plateau. The example shows measurements on 4 mussels *Modiolus modiolus* with different size (42, 281, 627, and 1555 mg body dry wt). (a) Taken from Møhlenberg & Riisgård (1978), (b) taken from Møhlenberg & Riisgård (1979)

field would be possible, although they have not yet been attempted. For both methods, it is equally important to fulfil the prerequisites for using the equations, i.e. check of 'geometry' and identification of the clearance-plateau representing the true filtration rate.

By means of the suction method, Møhlenberg & Riisgård (1979) measured the filtration rate (F , $l\ h^{-1}$) as a function of dry body weight (W , g) in 13 species of marine bivalves. In cases where the size distribution was sufficiently large it was found that the data could be described by the allometric equation: $F = aW^b$, where the exponent b varies between 0.62 and 0.75, (Table 1). In the case of *Mytilus edulis* (from The Sound, Denmark) it was found that $F = 7.45W^{0.66}$. Here, the b exponent is the same as the exponent of the gill area (G , cm^2), expressed as a function of body size: $G = 24.58W^{0.66}$. This shows that F is determined by the size of the gills. A similar conclusion was attained by Meyhöfer (1985), who found that F and G increase at the same rate in *Clinocardium nuttallii*, *M. californianus* and *Chlamys hastata*, and by Kryger & Riisgård (1988), who measured F and G as a function of size in the freshwater mussel *Dreissena polymorpha*.

Table 1. Filtration rates in suspension feeding bivalves measured by means of different methods under optimal laboratory conditions. Filtration rates (F , $l\ h^{-1}$) as a function of size (W , g body dry wt), and in some cases shell length (L , mm), are presented as allometric equations: $F = aW^b$ and/or $F = aL^b$. For clarity, temperature, size range, correlation coefficients, etc. have been omitted

Suction method	
Møhlenberg & Riisgård (1979)	
<i>Cardium echinatum</i>	$F = 4.22W^{0.62}$
<i>Cardium edule</i>	$F = 11.60W^{0.70}$
<i>Mytilus edulis</i>	$F = 7.45W^{0.66}$
<i>Modiolus modiolus</i>	$F = 6.00W^{0.75}$
<i>Arctica islandica</i>	$F = 5.55W^{0.62}$
Kjørboe & Møhlenberg (1981)	
<i>Mytilus edulis</i>	$F = 0.0012L^{2.14}$
Photoaquarium method	
Riisgård & Møhlenberg (1979)	
<i>Mytilus edulis</i>	$F = 7.37W^{0.72}$
Clearance method	
Griffiths (1980)	
<i>Choromytilus meridionalis</i>	$F = 5.37W^{0.60}$
	$F = 0.006L^{1.58}$
Berry & Schleyer (1983)	
<i>Perna perna</i>	$F = 8.85W^{0.66}$
	$F = 0.027L^{1.86}$
Riisgård (1988)	
<i>Crassostrea virginica</i>	$F = 6.79W^{0.73}$
<i>Geukensia demissa</i>	$F = 6.15W^{0.83}$
Replacement method	
Coughlan & Ansell (1964)	
<i>Mercenaria mercenaria</i>	$F = 2.5W^{0.78}$
	$F = 0.026L^{1.81}$
Thermistor method	
Meyhöfer (1985)	
<i>Clinocardium nuttallii</i>	$F = 3.1W^{0.80}$
<i>Mytilus californianus</i>	$F = 7.9W^{0.72}$
<i>Chlamys hastata</i>	$F = 8.7W^{0.94}$

F ($l\ h^{-1}$) of *Mytilus edulis* (from the Danish Wadden Sea) as a function of shell length (L , mm) was measured by means of the suction method by Kiørboe & Møhlenberg (1981), who found that $F = 0.0012L^{2.14}$ (shell length 10 to 70 mm, $r = 0.99$; equation corrected according to Kiørboe pers. comm.). As expected, F (and G) is nearly proportional to the square of the length of the bivalve, i.e.: $F = aL^2$. Further, it was to be expected that W is proportional to L^3 , or reversed: L is proportional to $W^{1/3}$ so that $F = a(W^{1/3})^2 = aW^{2/3} = aW^{0.67}$, which is actually in good agreement with most of the b exponents shown in Table 1. The relationship between W (g) and L (mm) of *M. edulis* was determined by Jones et al. (1992, their Table II) as $W = 3.3 \times 10^{-6}L^{3.16}$. From this it is found that a 1 g *M. edulis* has a shell length of about 54 mm, and according to the equation given by Kiørboe & Møhlenberg (1981) this mussel filters $6.1\ l\ h^{-1}$. It should however be stated that the relationship between shell length and body size is not constant, but may vary during the year and from population to population (due to, e.g., spawning in spring, rapid growth during summer, and starvation during winter months). Thus, in each month over several years, Dare (1976) recorded the changes in the relationship between L (cm) and W (mg) in *M. edulis*. A condition index for mussels may be expressed as $CI = W/L^3$, and according to Dare (1976, his Fig. 15) the CI for 5.5 cm standard shell length mussels varied as follows: CI = 6.6 in April 1970 and decreased to 3.6 in June due to spawning in spring, followed by a rapid summer recovery phase to become 7.8 in October. Then, during the following winter-starvation period (and possible spring spawning) the CI decreased to become 4.2 in May 1971, again followed by a rapid summer-recovery period resulting in CI = 8.4 in September 1971. Such pronounced annual cycle variations, especially observed in large adult mussels, will of course influence the weight-specific filtration rate of mussels of same shell length because the relationship between G and L remains constant, unaffected by the large annual cycle variations in total flesh weight.

Clearance method. A large number of filtration measurements have been performed by means of the so-called 'indirect' clearance method, first used in bivalve studies by Fox et al. (1937) and Jørgensen (1943, 1949, 1955). Coughlan (1969) reviewed the many ways in which different authors have expressed the exponential decline in particle concentration with time.

In the clearance method, which is still frequently used, F is measured as the volume of water cleared of suspended particles per unit of time. The reduction in the number of particles as a function of time is monitored by taking water samples at fixed time intervals and measuring the particle concentration, usually with an electronic particle counter. In an aquarium with

bivalves and well-mixed seawater and algal cells, CI is determined from the exponential decrease (e.g. verified as a straight line in a semi-log plot, see Fig. 4) in algal concentration as a function of time using the formula:

$$CI = (V/nt) \ln(C_0/C_t) \quad (3)$$

where C_0 and C_t = algal concentration at time 0 and time t , V = volume of water, and n = number of animals. If the suspended particles are 100% efficiently retained by the gills of the experimental bivalves, then $CI = F$. The clearance method has proved to be a reliable method in many filtration studies on bivalves (e.g. Jørgensen 1975a,b, Griffiths 1980, Riisgård et al. 1980, 1981, Wright et al. 1982, Berry & Schleyer 1983, Famme et al. 1986, Jørgensen & Riisgård 1988, Riisgård 1988, 1991, Jørgensen et al. 1990, Wildish et al. 1992, Clausen & Riisgård 1996, Dupuy et al. 2000), but a disadvantage of the method is that the concentration

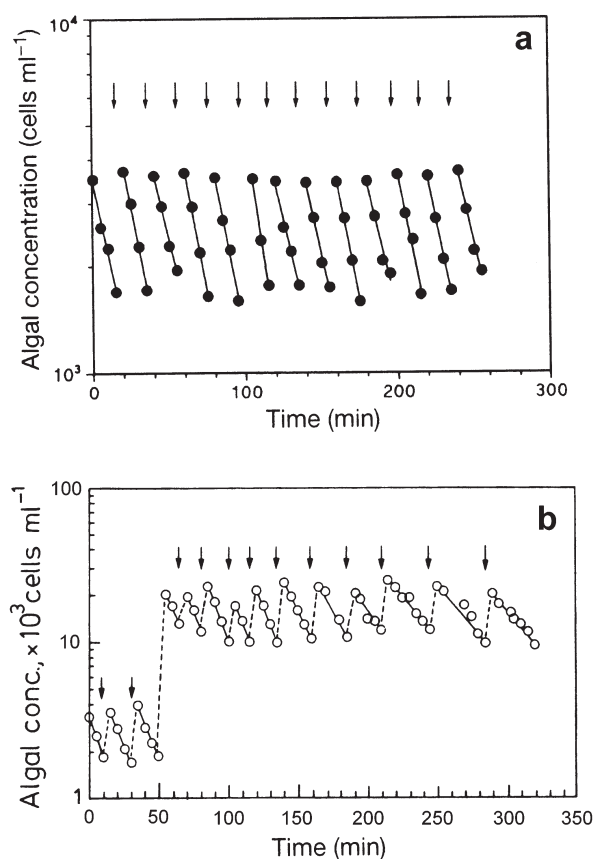


Fig. 4. (a,b) Clearance method. Reduction of algal cell concentration due to grazing by mussels. Arrows indicate additions of algal suspension. The slope of lines express the mussels' filtration rate. (b) Filtration rate is being reduced more and more with time at the high algal concentration. (a) Taken from Clausen & Riisgård (1996), (b) taken from Riisgård (1991)

of particles declines during the experiment. This drawback may, however, be partly eliminated by making new algal additions to keep the concentration within a certain range (Fig. 4).

By using the clearance method, Berry & Schleyer (1983) found that F ($l\ h^{-1}$) as a function of W (g dry flesh wt) and L (mm) of the brown mussel *Perna perna* could be expressed as $F = 8.85W^{0.66}$ and $F = 0.0027L^{1.86}$, respectively. Likewise, the equation for *Choromytilus meridionalis* was found by Griffiths (1980) to be $F = 5.37W^{0.60}$. For *Crassostrea virginica* and *Geukensia demissa*, Riisgård (1988) found $F = 6.79W^{0.73}$ and $F = 6.15W^{0.83}$, respectively. Further, for small post-metamorphic *Mytilus edulis* (0.7 to 10 mg), Riisgård et al. (1980) found that the filtration rate as a function of total organic dry weight could be expressed as $F = 37.8W^{1.03}$. Here, the b exponent = 1.03 is significantly different from the exponent of about 0.66 for larger *M. edulis*. It is striking that a similar allometric scaling seems to apply for respiration as a function of size throughout the ontogeny of *M. edulis*. Here, the b exponent tend to be ≈ 1 in small individuals falling to $b = 0.6$ to 0.7 in larger stages (Riisgård 1998). Therefore, *M. edulis* and other suspension feeding bivalves seem to consume oxygen and pump water at weight-specific rates that are nearly identical over the greater part of the body growth, as stated by Jørgensen (1976).

Photoaquarium method. Winter (1973) developed an automatic recording apparatus that could maintain a constant algal concentration, thus allowing continuous measurements of the filtration rate in suspension feeding bivalves. The apparatus was later improved by Riisgård & Møhlenberg (1979) to avoid recirculation, and to make it possible to carry out experiments at (natural) low algal concentrations. In the apparatus, water from a photoaquarium is pumped at high speed (to prevent recirculation) through a mussel chamber, and algal concentration is kept nearly constant by means of a photocell-circuit that starts and stops a pump dosing algal suspension from a chemostat when the concentration exceeds a pre-set range. F is estimated by means of the equation:

$$F = (z/tn)(vC_s/C_e - v) - o/n \quad (4)$$

where z = number of algal additions, t = time, n = number of mussels, v = volume of 1 algal addition, C_s = algal concentration in chemostat, C_e = algal concentration in photoaquarium, and o = through-flow rate of fresh, particle-free seawater.

Riisgård & Møhlenberg (1979) found that F ($l\ h^{-1}$) as a function of W (g) of *Mytilus edulis* could be expressed as $F = 7.37W^{0.72}$. As appears, a 1 g dry wt *M. edulis* filters $7.37\ l\ h^{-1}$, which is in good agreement with the a value = $7.45\ l\ h^{-1}$ obtained by means of the suction method (see Table 1).

Steady-state method. Since *Mytilus edulis* is continuously filtering within a certain range of algal concentrations, the rate at which mussels filter the well-mixed water in an aquarium, added algal suspension from a chemostat at a constant rate (P) by means of a dosing pump and with a constant through-flow of particle-free seawater (Fl) (Fig. 5), F can be calculated according to Riisgård & Randløv (1981), or Poulsen et al. (1982):

$$F = (PC_c - FlC_a)/(nC_a) \quad (5)$$

where n = number of mussels, C_a = algal concentration in chemostat, and C_c = steady-state algal concentration in the mussel aquarium. During longer experimental periods where the mussels may grow and increase their filtration rate, C_c can be kept nearly constant by adjusting the dosing rate (P).

Using the steady-state method, constant algal concentrations were maintained for up to 47 d in growth and energy-budget experiments performed on *Mytilus edulis* by Riisgård & Randløv (1981) (Fig. 5).

The filtration rates obtained by means of Eq. (5) were in good agreement to clearance rates obtained by means of Eq. (3) in cases where the algal dosing pump and the seawater through-flow were stopped in order to follow the exponential decrease in the aquarium.

Another way of expressing F in Eq. (5) is as follows: (number of algal cells into the aquarium) – (number of algal cells consumed) = (number of algal cells flowing out), or $FlC_1 - FC_2 = FlC_2$, or

$$F = Fl(C_1 - C_2)/C_2 \quad (6)$$

where Fl = flow rate through the bivalve chamber, and C_1 and C_2 = concentration of algal cells in inflow and outflow water, respectively. This expression was presented by Hildreth & Crisp (1976) as a 'corrected formula' (to overcome the problems of recirculation) for calculation of filtration rate of bivalves when using the flow-through chamber method, i.e. Eq. (1). But this statement is not correct. Although there is a superficial similarity between Eqs. (1) & (6), the fundamental differences between the 2 methods should be realised: Eq. (1) is based on principles of optimal flow and no recirculation of once filtered water whereas Eq. (6) is based on principles of steady-state and momentary mixing of all exhalant water in the whole water volume of the flow-through chamber. Hildreth & Crisp (1976) stated that their approximation 'would be helped by some artificial stirring' although this was not done in their own experiments, or in clearance experiments on *Cardium edule* performed by Newell & Bayne (1980), or in clearance experiments by Yukihiro et al. (1998a,b) on pearl oysters *Pinctada margaritifera* and *P. maxima*. However, Vismann (1990) recognised mixing as a basic prerequisite for using Eq. (6) and he therefore used a stirrer in his mussel chamber.

Video observation method. Water motion and filtration rates may also be deduced from particle tracking by means of microscope-video recording with subsequent image analysis (Nielsen et al. 1993, Riisgård et al. 1996, Riisgård & Larsen 2000). Water motion by *Mytilus edulis* gill filaments were studied by Nielsen et al. (1993). Video observations and numerical modeling showed that the mean water velocity (v) through the interfilament canals was about $v = 1.7 \text{ mm s}^{-1}$. This value corresponds to velocity calculations based on laboratory measurements of F and G using the ratio $v = 2F/G$, because the interfilament gap occupies about 50% of the gill area (Jørgensen 1990, Riisgård & Larsen 2000). Estimated velocity values were $v = 1.68 \text{ mm s}^{-1}$ (Møhlenberg & Riisgård 1979), 1.73 mm s^{-1} (Jørgensen et al. 1990), 1.41 mm s^{-1} (Riisgård 1991), and 1.68 mm s^{-1} (Meyhöfer 1985). From this it appears that the approach velocity of water to the gill surface must be about $v_0 = F/G = 0.85 \text{ mm s}^{-1}$. Video observations were subsequently made on intact actively feeding *M. edulis* by Riisgård & Larsen (2000). When a small mussel was fixed on its side, and by using a dissecting microscope, the gills could be seen behind the gaping valves. Video recordings through the microscope revealed that the approach speed was about 1 mm s^{-1} , in agreement with the above predicted speed for v_0 .

Replacement method. This method, developed by Coughlan & Ansell (1964), is based upon complete replacement of the inhalant current by a metered stream of water colored by a soluble, non-toxic dye. The bivalve remains in a natural position, and an adequate flow of new water is maintained around the animal.

Coughlan & Ansell (1964) measured the filtration rate (l h^{-1}) of *Venus (Mercenaria) mercenaria* as a function of size (W , g flesh dry wt; L , mm shell length) in clams that had been allowed to bury and establish themselves in sand. From their Table 1, the following regression equations have been calculated: $F = 2.51 W^{0.78}$ ($r = 0.97$, $n = 12$) and $F = 0.026 L^{1.81}$ ($r = 0.97$, $n = 14$). The filtration rates are generally higher than those measured by Riisgård (1988) for the same species, but without being allowed to bury themselves in sediment. This may have disturbed the clams and caused reduced feeding activity.

Thermistor method. Methods based on the measurement of velocity of exhalant streams by a small thermistor probe (LaBarbera & Vogel 1976, Vogel 1994, Meyhöfer 1985) require accurate positioning, temperature control and probe calibration. The sensing element in a thermistor is a small resistor that is

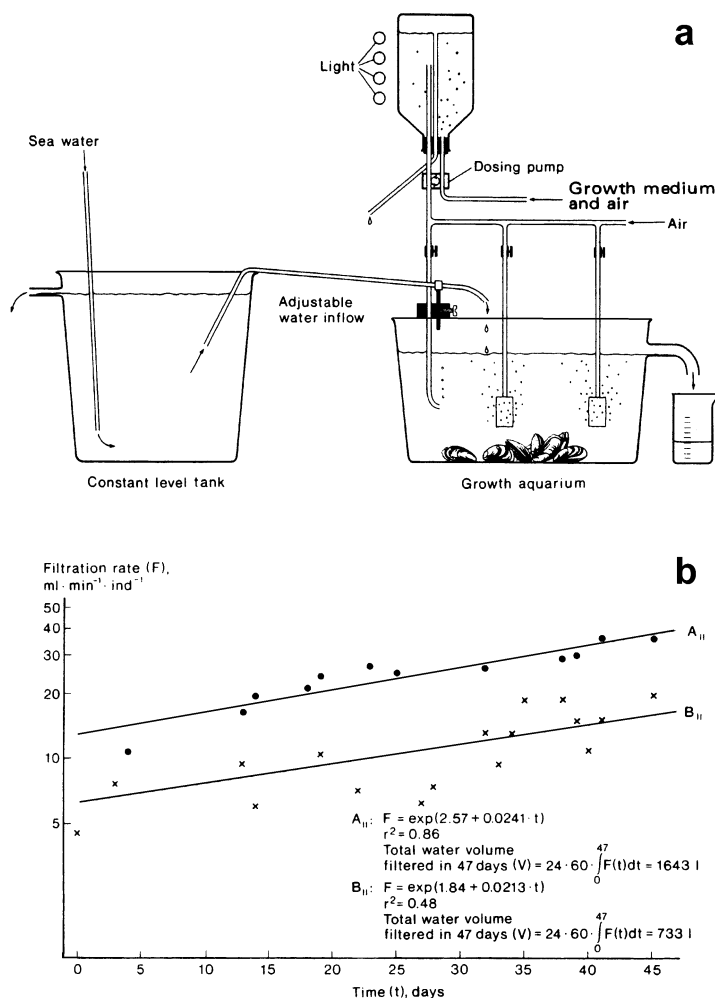


Fig. 5. (a,b) Steady-state method. Set-up used for performing growth and energy budget experiments at defined algal concentration levels. Constant through-flow of water, constant addition of algal suspension from a chemostat, and constant mussel filtration rate ensure steady-state. The filtration rate is calculated from Eq. (5). (b) Filtration rate as a function of time in a 47 d growth experiment with *Mytilus edulis*. Calculations of total water volume filtered during the experimental period are indicated (From Riisgård & Randløv 1981)

heated to a temperature above that of the surrounding fluid by passing an electrical current through it. The cooling of the element depends on the flow velocity past it, hence the electric power, or the resistance, which depends on its temperature, becomes a measure of velocity. In principle, the complete velocity distribution over the full flow area of the exhalant aperture should be recorded to give the filtration rate. In practice, however, a single velocity measurement may give the desired result provided the probe has been calibrated in a flow from an aperture of identical geometry and an identical velocity distribution (Foster-Smith 1976).

Filtration rates in undisturbed suspension-feeding bivalves was measured with a thermistor microflowmeter by Meyhöfer (1985). The filtration rates as a function of size measured on *Clinocardium nuttallii*, *Mytilus californianus* and *Chlamys hastata* are shown in Table 1. The values for filtration rates for these 3 species are in the same range as measured on other species by means of other methods. The filtration rate (F , ml min⁻¹) as a function of body size (W , g dry wt) in e.g. *M. californianus* can be described as $F = 7.98W^{0.72}$ which is very similar to values given for *M. edulis* (e.g. Møhlenberg & Riisgård 1979).

Bio-deposit method. Hawkins et al. (1996) calculated the clearance Cl in *Mytilus edulis* from direct collection of bio-deposits according to the ratio:

$$Cl = (\text{inorg. matter egested as faeces and pseudofaeces}) / (\text{conc. of inorg. matter in seawater}) \quad (7)$$

The calculated clearance rates (filtration rates) were standardised to a 1 g dry body wt mussel using a b exponent of 0.67 (and not 0.38 as reported by Thompson & Bayne 1974 and Widdows 1978a, or 0.34 as found by Bayne & Widdows 1978, but in agreement with b values in Table 1 here). From this, the average clearance rate was found to be 2.6 l h⁻¹ g⁻¹, which the authors compared to 1.4 l h⁻¹ g⁻¹ measured by Prou et al. (1994) on 250 mussels in a common chamber with a through-flow of only 40 ml min⁻¹ mussel⁻¹, which was not sufficient to prevent re-circulation (see section 'Flow-through chamber method').

A somewhat similar bio-deposit method was used by Cranford et al. (1998) and Cranford & Hill (1999). Because ash is not absorbed during digestion, the rates of ash ingestion (I_{ash}) and egestion (E_{ash}) are equal. Measurements of the proportion of ash in the food (F_{ash}) can then be used to calculate total ingestion rates (I_T) according to $I_T = E_{\text{ash}}/F_{\text{ash}}$ (Cranford & Hargrave 1994). Cl may then be calculated as:

$$Cl = I_T / \text{TPM} \quad (8)$$

where TPM = total suspended particulate matter. Cranford et al. (1998) calculated that Cl averaged 17.1 l h⁻¹ (or 1.8 l g⁻¹ h⁻¹) for 10 cm shell height sea scallops *Placopecten magellanicus* during a post-storm period in a coastal embayment in Nova Scotia, Canada. In a recent study, however, Cranford & Hill (1999) measured the *in situ* clearance rates of *P. magellanicus* and *Mytilus edulis* in Bedford Basin and Mahone Bay, Nova Scotia. In this case, the mean clearance rate of *P. magellanicus* was about 4 times lower (0.451 l g⁻¹ h⁻¹) than previously measured by Cranford et al. (1998), and the mean filtration rate of *M. edulis* was about 10 times lower than measurements shown in Table 1 here. From this observation Cranford & Hill (1999) con-

cluded that bivalves seldom utilize their full clearance potential in nature.

A plausible explanation for the low filtration rates reported by Cranford & Hill (1999) is lacking, but low or sometimes even negative somatic growth indicates that sub-optimal conditions may have been prevailing and caused valve closure during parts of the exposure period (no observations were made on opening degree of valves). Kiørboe et al. (1980, 1981) and Møhlenberg & Kiørboe (1981) studied the effect of silt on filtration rate and production of pseudofaeces. They showed that bivalves feeding on a mixture of algae and silt sort algae from silt for preferential ingestion of the algal cells. The threshold concentration for production of pseudofaeces is about 1 mg total dry matter l⁻¹ in *Mytilus edulis* (Kiørboe et al. 1980). The concentration of TPM is frequently (considerably) higher in nature, and Eq. (8) does not take possible pseudofaeces production into account. This may invalidate the bio-deposit method in many situations. Both Eqs. (7) & (8) are based on the assumption that the bivalves filter the suspended matter with 100% efficiency (or to be equal to that of a 1.2 µm pore-size filter as used by Cranford & Hill 1999); however, this is not true, for retention efficiency in mussels decreases rapidly for particles <4 µm, and in pectinids for particles <7 µm (Møhlenberg & Riisgård 1979, Riisgård 1988).

Impeller method. A new impeller method for measurement of filtration rate was used by Jones et al. (1992) for studies on *Mytilus edulis*. The flow velocity of the exhalant current was determined by means of a flow meter consisting of a 5-bladed impeller 'friction-fitted' onto a glass capillary tubing which in turn rotated on a stainless steel pin. One of the blades was white and the rotation rate of the impeller was optically recorded and calibrated to measure water flow velocity.

Jones et al. (1992) measured the filtration rate (F , l⁻¹) of *Mytilus edulis* as a function of size (W , g body dry wt; L , mm shell length) as $F = 1.78W^{0.70}$ and $F = 1.55 \times 10^{-4}L^{2.19}$, respectively. Whereas the b exponents are comparable with those shown in Table 1, and expected values as also discussed by Jones et al. (1992), a filtration rate of 1.78 l h⁻¹ for a 1 g mussel is low, about 4 times lower than values shown in Table 1. On the basis of gill area measurements, Jones et al. (1992) calculated the approach velocity of water to the gill surface as 0.23 mm s⁻¹, which is about 4 times lower than actually measured in an intact actively feeding *M. edulis* by Riisgård & Larsen (2000) using video observation (see section 'Video observation method'). This indicates that the impeller method may not have been able to precisely measure the filtration rate.

PROBLEMS AND SHORTCOMINGS

The precondition for studying possible physiological regulation of filtration rate is the ability to make precise measurements. The below examples show that this has not always been the case. A critical examination of the older literature seems to be justified, because some flaws are being repeated and some erroneous interpretations are still being cited in the literature. The filtration rates as a function of size in a number of bivalve species, measured by means of different methods under optimal laboratory conditions, have been placed together in Table 1. The methods agree well and the filtration rates are considered to be uninfluenced by methodical flaws and may therefore be used as references for performance under near optimal laboratory conditions.

The flow-through chamber method has caused particular trouble, and some of its problems and shortcomings are discussed below. The prerequisites for using the method have often been disregarded. Walne (1972) intended to study the influence of current speed on the filtration rates in bivalves by using the flow-through chamber depicted in Fig. 6. The particle concentration was measured at different flow rates before and after passage of the chamber holding a bivalve, and the filtration rate was subsequently estimated by means of Eq. (1). Walne assumed that the 'experiments showed that the filtration rate was positively correlated with the flow rate' (Fig. 6). However, this interpretation is wrong, because the critical flow rate at which clearance values form a plateau was never attained. Further, an inspection of Walne's data (Fig. 6) shows that all the clearance values fall below the line clearance rate = flow rate, indicating a rather poor design ('geometry') of the chamber. The assumption that filtration rate in bivalves in this way can vary with the external current has often been repeated (e.g. Vahl 1973b, Jones et al. 1992, Judge et al. 1992, Vogel 1994).

The mussel chamber used by Thompson & Bayne (1972, 1974) for measurement of filtration rate in *Mytilus edulis* is shown in Fig. 7. A chamber with this shape does not comply with the requirements for good 'geometry' to prevent recirculation. Regardless of mussel size, and without laying down the relationship between through-flow rate and clearance rate to identify the plateau where clearance rate is representative of the filtration rate, Thompson & Bayne (1974) used a constant through-flow rate of only 50 ml min⁻¹. The obtained filtration rate as a function of dry body wt of *M. edulis* are shown in Fig. 7.

Thompson & Bayne concluded that: 'The relationship is a power function for specimens less than 1 g dry flesh wt, with a weight exponent of 0.38', and that for larger mussels 'the rate at which filtration increases with body weight gradually decreases'. This statement appears not to be quite correct.

Similar problems caused by too slow through-flow rate and/or poor chamber 'geometry' may be found in works on filter feeding bivalves by, e.g., Widdows & Bayne (1971), Vahl (1973b), Bayne (1975, 1976), Widdows (1976), Hibbert (1977), Bayne et al. (1977, 1979), Bayne & Widdows (1978), Widdows (1978a,b) MacDonald & Thompson (1986), Ward & Targett (1989),

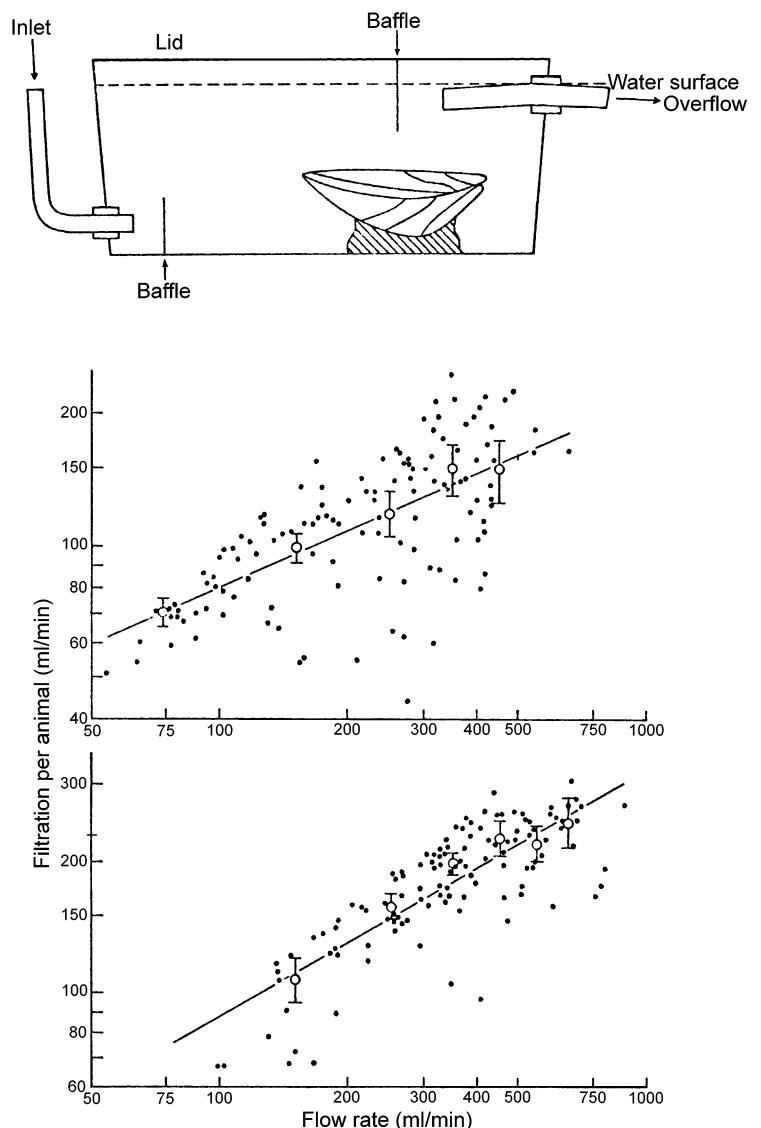


Fig. 6. Example of erroneous interpretation. Using the flow-through chamber method, Walne (1972) apparently found that the filtration rate increased with the flow rate

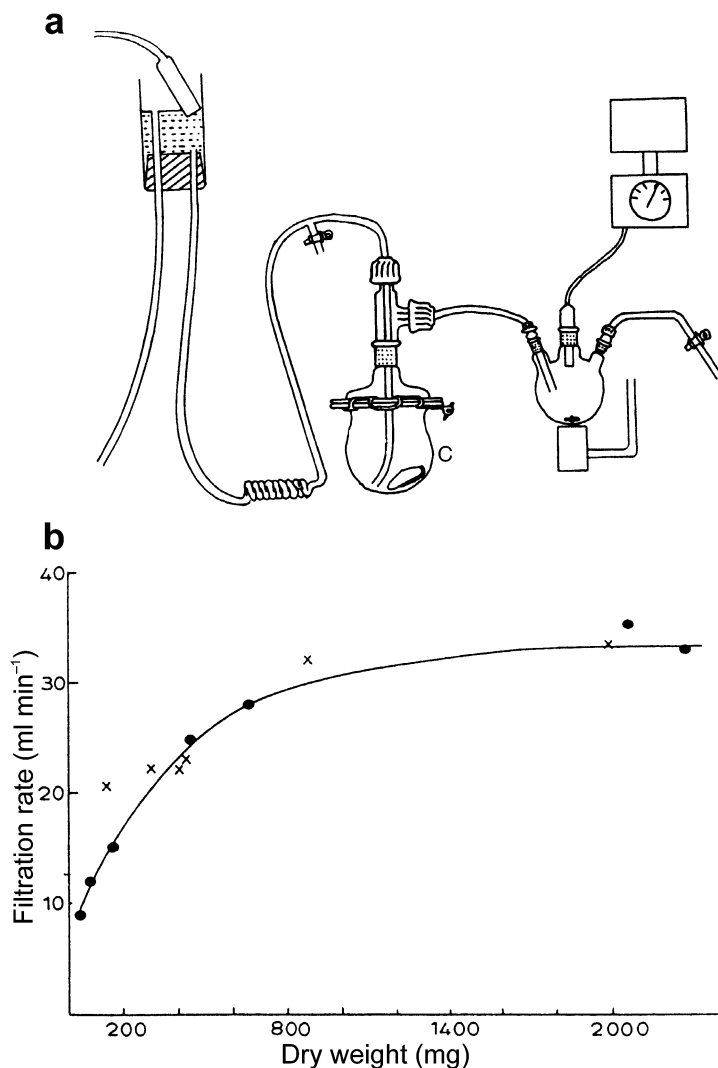


Fig. 7. Example of erroneous interpretation. (a) Set-up used by Thompson & Bayne (1972) for flow-through method measurement of filtration rate of *Mytilus edulis*. C: mussel chamber. (b) Apparent relationship between dry body wt and filtration rate of *M. edulis* measured at a flow rate of 50 ml min^{-1} (from Thompson & Bayne 1974)

Bayne et al. (1993), MacDonald & Ward (1994), Hawkins et al. (1999), Yukihiro et al. (1999), Ren et al. (2000).

Bayne (1975) used a flow rate of 94 ml min^{-1} and corrected the filtration rates 'for variations in body size by reducing all measurements to a standard size of ... $W^{0.4}$ '. Later, Bayne (1976) stated that 'we have found (Bayne, Thompson & Widdows unpubl. data) that a flow rate of 60 ml min^{-1} is sufficient to reduce the error of possible recirculation in the chamber 'to a negligible value'. Bayne et al. (1976) measured filtration rates of *Mytilus californianus* in 'glass respirometer flasks ... at a flow rate of $60\text{--}90 \text{ ml min}^{-1}$ ' and found that the following relationship between F (l h^{-1}) and W (g body

dry wt) at 13°C in 'fed animals' and 'starved animals' could be described by the equations: $F = 1.64 W^{0.434}$ and $F = 1.04 W^{0.434}$, respectively. Later, Bayne et al. (1979) found that a 'single equation' could be written for each of 3 populations: Lynher: $F = 1.35 W^{0.372}$, Swale: $F = 1.79 W^{0.817}$, Kings Dock: $F = 1.15 W^{0.443}$, and that 'there were significant differences between populations as to their clearance rates'. A flow rate of 70 ml min^{-1} through the experimental chamber was used by Bayne et al. (1977), and using this through-flow Widdows (1978a) found that the relationship between F (l h^{-1}) and W (g body wt) could be described by the equation: $F = 2.65 W^{0.38}$, where the 'weight exponent was similar to that previously recorded for *M. edulis* by Thompson & Bayne (1974)'. These filtration rates, which appear quite low compared to those shown in Table 1, were used in subsequent works on 'scope for growth' performed by Widdows (1978b) and Bayne et al. (1979). Bayne & Worrall (1980) used 'water flow rates between 100 and 120 ml min^{-1} ', and in this study 'a common value for the exponent' was found to be 0.34 . More recently, following the recommendation by Widdows (1985), Smaal & Twisk (1997) used a constant flow-through rate of 50 ml min^{-1} in a filtration study with *M. edulis*. Hawkins et al. (1996) used a 'plastic tray' supplied with seawater 'at rates of 150 to 200 ml min^{-1} '. Hawkins et al. (1999) used '200 ml perspex trays' and the flow-through rate 'was adjusted so that concentrations of suspended particles were not reduced more than an average of 25% between the inflow and outflow from each shellfish tray'. The filtration rate for the green-lipped mussel *Perna canaliculus* initially increased in positive relation with chl *a* to reach $6.81 \pm 2.17 \text{ l h}^{-1} \text{ g}^{-1}$ at $1.1 \text{ mg chl a l}^{-1}$, but at chl *a* concentrations far above natural levels (up to $459 \mu\text{g chl a l}^{-1}$) the filtration decreased.

MacDonald & Thompson (1986) used 'plastic containers' ranging in volume from 0.4 to 4 l , each containing a scallop *Placopecten magellanicus* and, depending on the size of the scallop, flow-through rates of 80 to 300 ml min^{-1} . The highest measured filtration rates were about 7 to 9 l h^{-1} for a 'standard' 20 g dry body wt scallop (about 14 to 16 mm shell height). This is about half the filtration rates measured by Cranford & Gordon (1992) and Cranford et al. (1998).

Hildreth & Crisp (1976) realized the problems with recirculation when using the flow-through chamber technique, and therefore recommended that a 'corrected formula' should be used instead of Eq. (1). As previously pointed out, the 'corrected formula' may

only eliminate the problems of underestimating the true filtration rate if the mixing of water in the flow-through chamber is adequate (apparently not fully recognised by, e.g., Newell & Bayne 1980, Kreeger et al. 1988, Villiers & Allanson 1988).

The flow-through chamber design of Palmer & Williams (1980) was used by Cranford & Gordon (1992) in filtration rate studies on sea scallops *Placopecten magellanicus*, and in this case 'flow rates through the chambers were adjusted to produce less than 30% depletion of particles'. Ten cm shell height scallops cleared 15 to 19 l h⁻¹, which is comparable with the average value of 17.1 l h⁻¹ measured on similar-sized scallops by Cranford et al. (1998) using the *in situ* bio-deposit method.

Lucas et al. (1987) measured the clearance rate in *Mytilus edulis* according to Eq. (3), and the values were then 'corrected for a 1.0 g mussel using a weight exponent of 0.34 after Bayne & Widdows (1978)'. By using this exponent, which is low compared to the *b* exponents shown in Table 1, Lucas et al. found that the weight-specific filtration rate in mussels from both Lynher estuary and Whitsand Bay was 'approximately 2.6 l g⁻¹ h⁻¹ — or about 3 times lower than the filtration rates shown in Table 1.

In bioenergetic models of *Mytilus edulis*, Grant & Bacher (1998) used the following equation determined by Widdows et al. (1979): CI (l h⁻¹) = 2.416 - 0.0086 TPM. In the case of no TPM, this equation may underestimate the maximum filtration rate of a 0.7 g mussel by a factor of about 2.5 (cf. Table 1). The filtration rate of 'wild mussels from a clean reference site in the Oosterschelde (NL)' was reported by Smaal & Widdows (1994) to vary between 2.35 and 3.61 l h⁻¹ g⁻¹. These results appear quite low compared to values shown in Table 1 and this may be one more example of not using suitable through-flow rate and optimal chamber 'geometry'.

More recently, considerably higher filtration rates have been reported by Widdows et al. (1995) in their 'scope for growth' (SFG) studies on *Mytilus edulis* collected along the North Sea coastline of the UK. Filtration rates of about 6.5 l g⁻¹ h⁻¹ were measured in Shetland mussels in order 'to monitor the consistent high water quality'. A filtration rate of 6.07 ± 0.40 l g⁻¹ h⁻¹ was measured in June in mussels from Whitsand, Cornwall, UK. However, along the east coast of the UK the filtration rates varied strongly (allegedly due to different degree of pollution: 'unexplained component', 'unknown stressors', 'unidentified industrial and agro-chemical contaminants'), from 8.19 ± 0.82 (Lucky Beacon) to 2.15 ± 0.44 (at Hunstanton). The Shetland mussel reference value of 6.5 l g⁻¹ h⁻¹ is about 2.5 times higher than earlier reported in papers by Bayne, Thompson and Widdows, but an explanation for this

difference is not given. Measurements of filtration rates have been used extensively in the calculations of SFG, i.e. difference between rates of assimilation and metabolism. According to Widdows et al. (1995) SFG 'is one of the most sensitive measures of pollution induced stress'. This statement is difficult to reconcile with the unexplained variations in recorded filtration rates and thus SFG values. It is difficult to see advantages of this technique in field monitoring programmes. Precise measurement of actual growth of *M. edulis* in net bags transferred to different localities may be relatively easily and inexpensively obtained within an exposure period of about 2 wk (Riisgård & Poulsen 1981). The actual growth gives an integrated biological response over the growth period, which is not obtained by means of the SFG technique, particularly not if the filtration rates are wrongly determined.

Although filtration rates measured by means of the clearance method of Eq. (3) generally seem to be reliable, high algal concentrations may cause saturation of the alimentary canal and the bivalves close their valves and restrict the filtration rate ('saturation reduction', see Riisgård 2001). This phenomenon may explain low filtration rates reported for *Mercenaria mercenaria* and *Ostrea edulis* by Walne (1972), *Mytilus edulis* by Winter (1973) and Schulte (1975), for *Crassostrea gigas* by Gerdes (1983), and for *Tapes philippinarum* by Coutteau et al. (1994). Filtration rate as a function of algal concentration, up to 100 000 *Chaetoceros neogracile* cells ml⁻¹, was studied in *T. philippinarum* by Coutteau et al. (1994), who measured a maximum filtration rate of 2.3 l g⁻¹ h⁻¹ and an 'incipient limiting concentration' of about 25 000 cells ml⁻¹, far above most natural biomass levels of phytoplankton. The use of unnatural particles (Ward & Aiello 1973) or addition of heavy metals (Redpath & Davenport 1988) may likewise cause valve closure.

Using video endoscopy Ward et al. (1998) suggested the approach velocity of water to the *Mytilus edulis* gill surface to be 1.96 mm s⁻¹ and the mean water flow through the gill interfilament gap to be 2.65 mm s⁻¹. This would however imply the filtration rate to be about 60% higher than ever measured in intact mussels. The basis for the assumption of such high speeds, as well as a 'new explanation' of particle capture in mussels proposed by Ward (1996) and Ward et al. (1998, 2000), has been shown to be untenable by Riisgård & Larsen (2000).

Based on values from the literature, Powell et al. (1992) found that the filtration rates of different sized bivalves apparently tend to fall on 1 of 2 curves. The upper curve representing 'high gear' values predicts rates at a given size to be about 3 times those of 'low gear' values. A numerical model was used by Powell et

al. to compare the effect of high versus low gear, and the calculations 'suggest that higher filtration rates are not ... more accurate, as has sometimes been claimed', and further, 'the explanation for the bimodal form ... does not seem to reside in the methodology used'. As shown in the present review, such an interpretation is highly probable.

OVERVIEW AND CONCLUSIONS

The present review has concentrated on available methods and on comparing the methods for measuring filtration rates in bivalves. Pitfalls and examples of methodical flaws have been pointed out, but it has not been my intention to highlight how different methodologies may have led to erroneous conclusions on growth and feeding. Thus, the bioenergetic and ecological consequences derived from methodical imperfections await assessment.

The present examination of half a score of methods shows that most of them agree well when the necessary prerequisites are fulfilled. The direct method is rather difficult to use, but it may be useful in physiological investigations where, e.g., measurements of filtration rates at well-defined back pressures are needed. An advantage of the flow-through chamber method is that a constant algal concentration can be maintained during the experiment, but erroneous use of particularly this method has resulted in many incorrect values of filtration rates, hence leading to conflicting data in the literature. The prerequisites for using the flow-through chamber method have often been disregarded. According to Appendix 1 it is doubtful whether it is possible to correct erroneous filtration rates for suboptimal chamber through-flow rate and/or poor chamber design. Three factors may contribute to an underestimation of the true filtration rate: (1) use of small particles that are not 100% efficiently retained by the gills; (2) recirculation, whereby some of the exhalant water becomes part of the inhalant flow because the chambers have an inappropriate design ('geometry') and a water flow rate which is too slow; and (3) insufficient mixing of exhalant flow with the flow bypassing the bivalve at the location where the chamber exit concentration is measured. For example, 10% recirculation and 80% particle retention would give at most 70% of the true filtration rate, a value that could be even lower in the case of high bypass flows in chambers where the mixing of the exhalant flow with the bypass flow is incomplete.

The suction method is superior to the flow-through chamber method because the 'geometry' problems of the chamber are eliminated. The suction method is

simple, easy to use, and also allows precise measurements on undisturbed infaunal bivalves buried in the sediment; furthermore, *in situ* measurements in the field would be possible. Unfortunately, the suction method has not yet achieved the wide use it obviously deserves. The clearance method is a reliable method used in many filtration studies. A disadvantage of this method is that the concentration of particles declines during the experiment, but this drawback may be eliminated by making new algal additions to maintain the concentration. The photoaquarium method is based on a complicated automatic recording apparatus that maintains a constant algal concentration. The method is sophisticated, but also rather difficult to use, compared to, e.g., the steady-state method where a constant algal concentration is maintained over longer periods by means of a dosing-pump that can be adjusted to balance the increased clearance of growing bivalves. The video observation method deduces the filtration rate from particle tracking by means of microscope-video recording with subsequent image analysis. The replacement method, which is based upon replacement of the inhalant current by a metered stream of colored water, may be used on bivalves remaining in their natural positions. This also applies to the thermistor method, based on the measurement of velocity of exhalant streams by a thermistor probe, which, however, requires very accurate positioning and temperature control. The bio-deposit method may be a useful field supplement to laboratory methods, but the preconditions for proper use should be further tested and specified. *In situ* studies may also be supplemented with video observations of valve opening degree to allow credible interpretations to be made. The impeller method has not yet been able to precisely measure the filtration rate.

The maximum filtration rates as a function of size in different bivalves using different methods under optimal laboratory conditions are shown in Table 1. It may be argued against this selection of 'reliable' data that they have been obtained under well-defined artificial conditions that may be irrelevant to populations in nature, and short-term physiological measures may not reflect longer-term rates when bivalves may reduce pumping for a variety of reasons, including gut fullness or starvation.

It is well known that very low algal concentrations (<ca 0.5 $\mu\text{g chl a l}^{-1}$) may cause reduction of water pumping due to closure of the valves, and likewise, high algal concentrations (ca >5 to 10 $\mu\text{g chl a l}^{-1}$) may lead to reduced valve gape and reduction of the filtration rate (e.g. Riisgård & Randsløv 1981, Riisgård 1991, Clausen & Riisgård 1996, Dolmer 2000, 2001). Prevailing algal concentrations in nature lie between these extremes and it seems reasonable to suggest

that the maximum filtration rates shown in Table 1 may often—or usually—be exploited in nature (for further discussion, see Riisgård 2001, Riisgård & Larsen 2001). The precondition for studying possible physiological regulation of filtration rate is the ability to make precise measurements. In future studies it is crucial that the method used should enable measurement of the maximum filtration rate under optimal laboratory conditions. This maximum rate may subsequently act as a reference value in longer-term studies of environmental factors, e.g. effects of algal concentration and silt.

The filtration rate (F) as a function of body dry weight (W) can be described by the allometric equation $F = aW^b$, where the exponent b is close to $2/3$

(varies between 0.62 and 0.75, see Table 1). The filtration rate (and gill area) is proportional to the square of the shell length (L) of the bivalve, i.e. $F = aL^2$ and W is proportional to L^3 so that $F = aW^{2/3}$. However, the relationship between shell length and body size is not constant, but may vary during the year and from population to population. This will influence the weight-specific filtration rate of mussels of same shell length because the relationship between gill area and shell length remains constant. The main reason for conflicting data on filtration rates is partly due to incorrect use of methods, partly caused by different experimental conditions and differences in shell length/body weight ratio ('condition').

Appendix 1. A note on the through-flow chamber method

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For the through-flow chamber method, Fig. A1 shows the general case in which volume flow Q_1 with algal particle concentration C_1 enters the mussel chamber, and $Q_2 = Q_1$ having concentration C_2 leaves the chamber. We specifically seek the pumping rate of the mussel Q_{in} . Flow Q_b bypasses the mussel while the remainder ($Q_1 - Q_b$), as well as a possible recirculation Q_r of once filtered water enters the animal having a particle retention efficiency R . We employ the notation of Fig. A1 for quantities of flow and concentration, and the conservation of volume flows and mass concentration. The mixing process at A in the figure satisfies the equations

$$(Q_1 - Q_b) + Q_r = Q_{in} \quad (A1)$$

$$(Q_1 - Q_b) C_1 + Q_r (1 - R) C_{in} = Q_{in} C_{in} \quad (A2)$$

where $C_{out} = (1 - R) C_{in}$ has been used. Mixing at B gives

$$Q_b C_1 + (Q_{in} - Q_r) (1 - R) C_{in} = Q_2 C_2 \quad (A3)$$

Using Eq. (A1) to eliminate Q_b from Eqs. (A2) & (A3) gives

$$C_{in}/C_1 = (Q_{in} - Q_r) / [Q_{in} - Q_r(1 - R)] \quad (A4)$$

$$Q_{in,comp} \equiv Q_1(1 - C_2/C_1) = (Q_{in} - Q_r)[1 - (1 - R) C_{in}/C_1] \quad (A5)$$

where $Q_{in,comp}$ denotes the usually computed pumping rate, cf. main text Eq. (1).

In general, in the absence of recirculation, $Q_r = 0$, Eq. (A4) shows $C_{in} = C_1$, and Eq. (A5) yields $Q_{in,comp} = RQ_{in}$, irrespective of amount of bypass flow, so the retention efficiency must be known to get the true pumping rate. Any recirculation ($Q_r > 0$) reduces C_{in} , and hence leads to underestimation, $Q_{in,comp} < Q_{in}$. For $R = 1$ this underestimation is simply given by Q_r . It is therefore important to ensure that no recirculation takes place. The bypass flow Q_b , on the other hand has no effect on the value of the pumping rate Q_{in} , provided there is perfect mixing at the outlet B as assumed in the present analysis.

A few further remarks can be made. First, if $Q_1 < Q_{in}$, Eq. (A1) shows that there must be recirculation, and assuming furthermore $R = 1$ and $Q_b = 0$, it follows that $C_2 = 0$, and

using Eq. (A5) yields the computed pumping rate $Q_{in,comp} = Q_1$, corresponding to the line $y = Fl$ of Fig. 2. Second, to attain finite values of C_2 (e.g. not less than 70% of C_1 , as suggested by some workers) there must be a sizeable bypass flow to suppress recirculation in a well-designed chamber so that a plateau, as suggested in Fig. 2, can be reached. Of course, if Q_b becomes large, C_2 approaches C_1 , hence impairing the accuracy of the result.

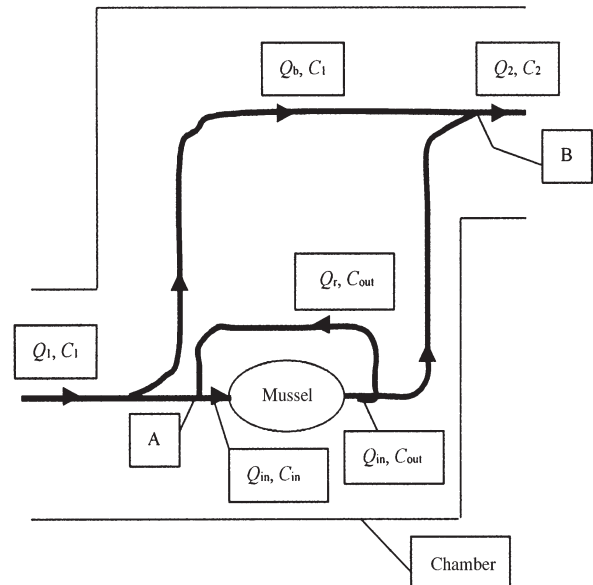


Fig. A1. Through-flow chamber method, notation. General case with bypass and recirculation

Disparity between filtration rates measured by different authors may not necessarily be an indication of some measurements not being 'reliable', but may reflect differences in the bivalves 'condition' and/or the influence of environmental factors. Hopefully, the present paper will stimulate further, and more thorough, examination of why results differ, in some cases by several orders of magnitude. Better knowledge of the mechanisms underlying the differences observed between experiments will provide a better understanding of how to integrate studies that have been conducted under a suite of environmental conditions.

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