



REVIEW

Energy costs of the sponge pump

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ABSTRACT: Sponges pump large volumes of water to obtain nutrition from a dilute suspension of food particles and dissolved organic matter. Our review of the literature shows pumping power ranging from 0.85% up to 28% of the total metabolic respiration rate R_{tot} , where the pumping power (P_p = pumping rate \times pump pressure) is the energy per unit time transferred to the water flow. Some published values of pumping costs are high while others are low due to incorrect estimates of some pressure losses in the aquiferous system of sponges. However, as improved descriptions of detailed structures and function, especially of the filter apparatus of the choanocytes, have become available, our corrected values for pressure losses show the respiration-specific pumping costs of P_p/R_{tot} = 1.3 to 22%. The stated pumping cost is based on the minimal (theoretical) pump power delivered to the water, which excludes a mechanical efficiency of pump action and a metabolic efficiency that expresses the fraction of total metabolism that is devoted to driving the pump action, considerations that should be included in future studies.

KEY WORDS: Choanocyte · Respiration · Filtration · Filter-feeding · Pump pressure · Glycocalyx

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1. INTRODUCTION

Filter-feeding occurs widely among marine invertebrates that feed on suspended food particles, mainly phytoplankton, but also free-living bacteria, dissolved organic matter (DOM), and detritus in the sea (Jørgensen 1966, 1975, de Goeij et al. 2013, Luskow et al. 2019, Ribes et al. 2023). These animals have adapted to a life in a low concentration of suspended food particles, and they show great variations in particle-capture mechanisms and pump design. However, because these animals have evolved to solve common basic problems, many similarities exist between various taxa, such as sponges, bryozoans, polychaetes, bivalves, and ascidians (Riisgård & Larsen 1995, 2000, 2001). The low concentrations of small, suspended food particles in the sea suggests that filter-feeding evolved according to a principle of 'minimal dimensioning' (or 'minimal scal-

ing'; Riisgård & Larsen 1995) of the filter and pump systems dimensioned for 'continuous feeding at low rates, rather than for discontinuous feeding at correspondingly higher rates' (Jørgensen 1975, p. 72). Hence, the energy costs of pumps (P_p) should be a small fraction of the total metabolic energy expenditure measured as the total respiration rate (R_{tot}) of the organism. This view was supported by reported values of fractions of at most a few percent for several suspension-feeders, including 0.85% for sponges (Riisgård & Larsen 1995, their Table 3). Since then, however, much higher values have been reported for sponges, e.g. 25% (Hadas et al. 2008), 28% (Leys et al. 2011), and 12–15% (Ludeman et al. 2017). Altogether, Leys & Kahn (2018) suggested that pumping in sponges is costly due to the resistance caused by the small filter size and that the mechanisms to reduce the cost of filtration have 'driven innovations' in both the physiology and morphology of sponges.

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The objective of this study was to first review the methods used to estimate the cost of pumping and total metabolic expenditure. We then examined published values considering more recent data now available on the aquiferous system morphology and choanocyte pump units, which led to the adjustment of some published values. Finally, we discuss to what degree the pumping process in sponges is costly.

2. ENERGY COSTS OF PUMPING

In sponges, the pump comprises the groups of parallel-coupled flagella-beating choanocytes in chambers that all deliver the same total pressure rise Δp_{tot} that is needed to maintain the observed volume flow F through the aquiferous system, i.e. the filtration (or pumping) rate. The water flow receives the (theoretical) pumping power $P_p = F \Delta p_{\text{tot}}$, but the mechanical power of beating flagella is larger, say P_p/η_{mec} where the mechanical efficiency η_{mec} accounts for the frictional losses in the water during the mechanical pumping process. Further, the conversion of metabolic power to mechanical motion of the beating choanocyte flagellum takes place in a certain tissue volume with a certain energy expenditure that should be added to the mechanical pump power. Effectively, it can be expressed as metabolic efficiency η_{met} ; hence, the total power responsible for the pumping is $P_{p,\text{tot}} = P_p/(\eta_{\text{mec}} \eta_{\text{met}}) = F \Delta p_{\text{tot}} / (\eta_{\text{mec}} \eta_{\text{met}})$. However, a concept such as 'energy costs of pumping' is a matter of definition, and most published results appear to be based on the theoretical pump work rate received by the water, $P_p/R_{\text{tot}} = F \Delta p_{\text{tot}}/R_{\text{tot}}$, which is most readily obtained. Yet, in future studies, it would be of interest to see estimates of mechanical and metabolic efficiencies.

The flow rate F may be determined by different methods. Here, we used $F =$ pumping rate, which equals filtration rate obtained as clearance rate provided 100% retained particles. In the 'steady-state method', with a feeding sponge placed in a chamber, the inlet and exit values of food concentration are recorded for a given throughflow (Hadas et al. 2008, Larsen & Riisgård 2012). In the 'clearance method', the exponential decrease over time in food concentration in the chamber is observed (Riisgård et al. 1993, 2016). In the 'direct method' (Figs. 1 & 2), the exhaled water is physically separated from the surrounding water, collected, and measured (Riisgård et al. 1993), and the 'velocity method' measures the velocity of the exhalant jet from the osculum of the recorded area (Reiswig 1971, 1974, Leys et al. 2011, McMurray et al. 2014,

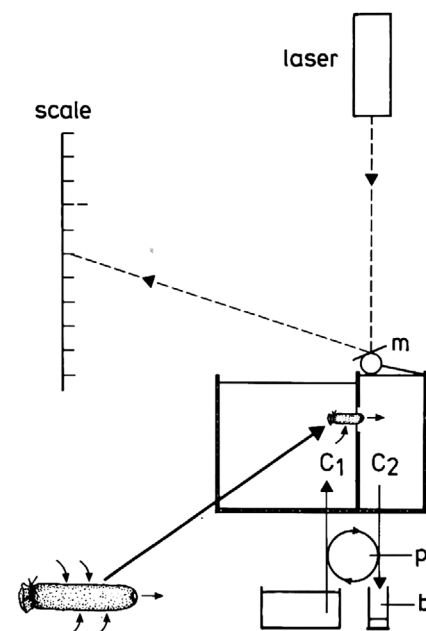


Fig. 1. Set-up for direct measurement of pumping rate (filtration rate) in a branch cut from a sponge (*Haliclona urceolus*). An aquarium is divided into 2 chambers (C_1 and C_2) by a latex membrane with a circular hole into which the sponge branch with the osculum at the tip is inserted so that the sponge pumps water from C_1 into C_2 . The water level in the exhalant chamber (C_2) is monitored with a laser beam striking a mirror (m) that is fixed on a tethered floating ping-pong ball. The mirror reflects the laser onto a scale 8 m from the mirror. Pumping rate of the sponge is equal to volume of water collected over a known time in a beaker (b) when the laser deflection point is maintained in a constant position on the scale by activating the pump (p). The measured back-pressure pumping-rate characteristic is shown in Fig. 2. From Riisgård et al. (1993)

Strehlow et al. 2016, Ludeman et al. 2017, Goldstein et al. 2019, Morganti et al. 2019, 2021). The different methods are equally relevant and accurate when properly used, and they give approximately the same results as shown by Ludeman et al. (2017). However, Hadas et al. (2008) did not check the prerequisite for using the steady-state method (see Section 7).

The total pressure loss Δp_{tot} is determined by either of 2 methods. In one, it is the sum of pressure drops for each of the resistances encountered in the flow path through the sponge from inlet to exit (Riisgård et al. 1993) (Fig. 2). In the other, all resistances are treated by the Hagen–Poiseuille equation with appropriate account of area, length, and flow of each resistance (Leys et al. 2011). See Ludeman et al. (2017) for a comparison of these methods.

Available data do not indicate how the cost of pumping by sponges may depend on the amount of microbial symbionts, as found in high and low micro-

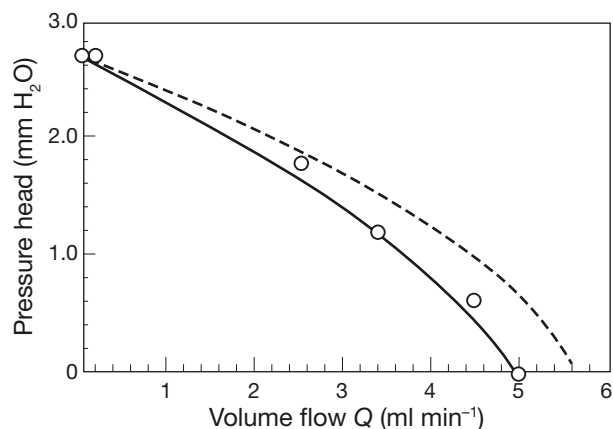


Fig. 2. Back-pressure characteristic (continuous line, based on experimentally determined values \circ ; see Fig. 1) and modeled pump characteristic (dashed line) for the demosponge *Haliclona urceolus*. At zero back-pressure, the pumping rate (= filtration rate) of the sponge is 5 ml min^{-1} , which decreases with increasing back-pressure to become zero at $2.7 \text{ mm H}_2\text{O}$ (shut-off head). The normal operating pump pressure O_p at zero back-pressure can be estimated by means of different equations that estimate the frictional resistance as water flows through the sponge's aquiferous system, and in the present case estimated at $O_p = 0.673 \text{ mm H}_2\text{O}$, or 4 times lower than the shut-off head. From Larsen & Riisgård (1994), with permission from Elsevier

bial abundance (HMA and LMA) sponges (Morganti et al. 2021, Lesser 2023), where the total respiration R_{tot} may be expected to be greater for HMA than for LMA sponges. Thus, Reiswig (1981) found that in terms of high respiration rate, the HMA demosponge *Verongia fistularis* (= *Aplysina fistularis*) had a high oxygen retention efficiency of $EE = 5.33\%$, which is about 5 times higher than estimated here (see Section 7) for the LMA demosponge *Halichondria panicea*. Further, Lesser (2023) also stated that total respira-

tion R_{tot} may be greater for HMA than for LMA sponges, which always maintain higher specific pumping rates. Definitions, units, and constants used here are shown in Box 1.

3. CHOANOCYTE PUMP

To interpret the published data on pump performance in sponges, it is useful to understand the structure and functioning of the choanocyte pump, as well as the models developed (Reiswig 1975, Langenbruch & Scalera-Liaci 1986, Weissenfels 1992, Larsen & Riisgård 1994, Leys et al. 2011, Mah et al. 2014, Ludeman et al. 2017). Larsen & Riisgård (1994) made an initial model of the sponge pump based on data from the demosponge *Halichondria urceolus* (Riisgård et al. 1993). Knowing the flagellum length, beat frequency, wavelength, and amplitude, the authors estimated the operating pump pressure of a free-living choanoflagellate, which was considered as representative of a sponge-choanocyte because the 2 cell types were assumed to be structurally and functionally identical, with a flagellum that pumps water through a collar of microvilli acting as a filter. The estimated pump pressure was insufficient to handle the pressure drop in a sponge. Therefore, it was instead suggested that the closely spaced flagella in the choanocyte chambers of sponges, possibly confined as a bundle by the apopyle, might all together act as a peristaltic pump being able to create the necessary pump pressure to overcome the resistance in the extensive canal system (Larsen & Riisgård 1994). Although numerical results gave the right order of magnitude, the model was not based on a pumping principle that agreed with the

Box 1. Definitions, SI units, and constants

ΔH_0 = pump pressure (m H_2O)

Δp_{tot} = pump pressure = $\rho g \Delta H_0$ (Pa)

P_p = [pump pressure] \times [volume flow] = $\rho g \Delta H_0 F$ (W)

ρ = density of seawater (35 psu) = $1.024 \times 10^3 \text{ (kg m}^{-3}\text{)}$

g = acceleration of gravity = $9.81 \text{ (m s}^{-2}\text{)}$

R_{tot} = total respiration rate (W)

P_p/R_{tot} = cost of pumping (-)

F = volume flow = pumping rate ($\text{m}^3 \text{ s}^{-1}$)

Conversions:

F/R ratio = liters of water filtered per ml of oxygen consumed = $1 \text{ H}_2\text{O (ml O}_2\text{)}^{-1}$

$1 \text{ ml O}_2 \text{ h}^{-1} = 5333 \text{ } \mu\text{W}$ (rate of consumed oxygen converted to metabolic power)

EE = oxygen extraction efficiency, estimated from reciprocal F/R ratio as total amount of oxygen passing through a sponge per ml of oxygen taken up (Riisgård 2024): $EE = 1/(F \times [\text{O}_2]_{\text{conc}})$ where the maximum oxygen concentration $[\text{O}_2]_{\text{max}} = 6.3 \text{ ml O}_2 \text{ l}^{-1}$ (30 psu, 15°C)

actual structure and function of the choanocytes (Weissenfels 1992, Asadzadeh et al. 2019, Lavrov et al. 2022, Nielsen 2023).

According to the present view, the choanocyte pump consists of a vaned flagellum beating in the microvilli collar that is sealed by a fine glycocalyx mesh over the distal 2/3 part but open for inflow at the proximal 1/3 part (see Nielsen 2023, their Fig. 1B; Lavrov et al. 2022, their Fig. 5; Asadzadeh et al. 2019, their Fig. 2; Weissenfels 1992, their Figs. 4 & 5). The discovery of the fine glycocalyx mesh on the collar was first interpreted to imply that all water entering the collar should overcome the increased pressure drop through the mesh, but flow only enters through the proximal 1/3 part of the collar. The tips of collars are connected by a fine glycocalyx mesh to form a seal (gasket) above which exists the high pressure produced by the flagella to overcome the pressure losses in the aquiferous flow system. Due to this complexity, it would require a numerical computational fluid dynamics (CFD) approach to model the pump, as done by Asadzadeh et al. (2019) for the leuconoid-type marine demosponge *Haliclona urceolus*. The beating vaned flagellum in the sealed part of the collar resembles a peristaltic pump, which is effectively a leaky positive displacement pump where the leak gap between flagellum and collar is a key parameter for pumping rate and pump pressure along with frequency, wavelength, and amplitude of the beating flagellum.

Lavrov et al. (2022) studied the ultrastructure of the choanocyte filter apparatus in the asconoid calcareous sponge *Leucosolenia variabilis* using fixation with 0.1% ruthenium red, which revealed microvilli in a collar sealed by a fine glycocalyx mesh and a glycocalyx strainer or gasket, very similar to the ultra-structures described for some demospoges and noted many years earlier by Weissenfels (1992). Fjerdingstad (1961) studied the ultrastructure of choanocyte collars in the freshwater sponge *Spongilla lacustris* and observed 'microfibrils that connect the individual collar fibrils' (Fjerdingstad 1961, p. 653), and suggested that the microfibrils were of great importance for the 'stability and rigidity' of the collar. Later, Brill (1973) made similar observations of microfibrils forming a network between the collar fibrils in the freshwater sponge *Ephydatia fluviatilis*. Lavrov et al. (2022) suggested that the pumping function in all sponges may rely on the common principles described above, even if not all sponges may have the physical 'gasket' preventing backflow. In the syconoid calcareous sponge *Sycon coactum*, for example, which has a more open-type aquiferous system, the

flow creates a 'hydrodynamic gasket', having much the same function of preventing recirculation, as shown in a numerical CFD model by Asadzadeh et al. (2020). As noted by Nielsen (2023), especially the extracellular material constituting the glycocalyx mesh and strainer is difficult to preserve intact and therefore may also be present in species in which it has not yet been observed.

4. QUANTIFYING METABOLIC ENERGY EXPENDITURE

During normal pumping operations, the total aerobic metabolic energy expenditure can be measured in the laboratory as the steady-state rate of oxygen consumption (respiration) by the sponge, $R_{\text{tot}} = F_c (C_{\text{in}} - C_{\text{out}})$, i.e. the product of measured chamber flow rate (F_c) and the reduction of measured oxygen concentration from the inflow (C_{in}) to the outflow (C_{out}) of a sealed flow-through respiration chamber with a magnetic stirrer to mix the water (Hadas et al. 2008). The respiration rate can also be measured *in situ* by comparing the dissolved oxygen concentration in the incurrent and excurrent water of an individual sponge, as in the InEx method of Yahel et al. (2005), and at the same time measure the excurrent flow rate using a thermistor sensor (Reiswig 1971) or an acoustic velocimeter (Leys et al. 2011). Further, oxygen consumption may be measured by incubating a sponge in a sealed gas-tight chamber and measuring the decrease in oxygen over time with an oxygen microelectrode (Hoffmann et al. 2008, Mills et al. 2014). For each ml of oxygen that an animal consumes, approximately 20 J of energy are released, dependent on the composition of metabolized substance (lipid, protein, carbohydrate). For sponges, we use the conversion $1 \text{ ml O}_2 \text{ h}^{-1} = 5333 \mu\text{W}$ (Ludeman et al. 2017).

5. FILTRATION AND RESPIRATION: F/R RATIO

The amount of water a marine filter-feeding invertebrate needs to filter to balance a metabolic requirement equivalent to 1 ml O_2 when exposed to a (low) phytoplankton concentration of $1.5 \mu\text{g chl a l}^{-1}$ was estimated by Riisgård & Larsen (2000) to be 10 l of water filtered per ml of oxygen consumed = $F/R = 10 \text{ l H}_2\text{O (ml O}_2)^{-1}$, which assumes 100% retention of food particles.

For traditional reasons, we use the F/R ratio, where filtration (F) is a proxy for pumping rate, since 100%

retention is assumed. The F/R ratio was determined for the demosponge *Halichondria panicea* to be $15.5 \text{ l H}_2\text{O (ml O}_2\text{)}^{-1}$ by Riisgård et al. (2016), who evaluated the potential of the sponge to feed on phytoplankton. It was found that the sponge may be able to feed on a sole diet of phytoplankton, assuming that all sizes of phytoplankton are ingested, but free-living heterotrophic bacteria, cyanobacteria, and other small picoplankton also seem to be an important, albeit insufficient, food source relative to phytoplankton (see also Lüskow et al. 2019). Jørgensen (1966, his Table 1.6) reported F/R ratios of $20 \text{ l H}_2\text{O (ml O}_2\text{)}^{-1}$ for *H. panicea* and $13 \text{ l H}_2\text{O (ml O}_2\text{)}^{-1}$ for the calcareous sponge *Grantia compressa*. In field investigations of 2 tropical marine sponges, *Tectitehya crypta* and *Mycale* sp., the F/R ratios were found by Reiswig (1974) to be 22.8 and $19.6 \text{ l H}_2\text{O (ml O}_2\text{)}^{-1}$, respectively. However, in a third tropical sponge, *Verongia gigantea*, the F/R ratio was only $4.1 \text{ l H}_2\text{O (ml O}_2\text{)}^{-1}$, because this sponge consists of a tripartite community: sponge–bacteria–polychaete (Reiswig 1974). In the present review, as a rule of thumb, we use $F/R \approx 15 \text{ l H}_2\text{O (ml O}_2\text{)}^{-1}$ as the reference for an optimally (undisturbed) pumping sponge. However, the F/R ratio may be expected to be higher in sponges inhabiting waters poorer in particulate organic matter (Jørgensen 1975). Further, some coral reef and deep-sea sponges may primarily rely on uptake of DOM as their food source (de Goeij et al. 2013, 2017, Bart et al. 2021), and therefore, the above rule of thumb may not apply to these sponges, which not only filter the ambient water but may absorb DOM across the inner surfaces of the aquiferous system. Thus, the uptake of DOM is probably related to the pumping rate by a certain extraction efficiency, which (to our knowledge) has not yet been determined for any sponge.

6. REPORTED VALUES OF ENERGY COST OF THE SPONGE PUMP

Riisgård et al. (1993) determined the theoretical pumping power by measurements and theoretical calculations for the demosponge *Haliclona urceolus* (Fig. 2). The experimentally measured back-pressure characteristic showed that the maximum pressure (shut-off head) the sponge pump could deliver at zero pumping rate was $2.7 \text{ mm H}_2\text{O}$ and the maximal pumping rate (filtration rate) at zero back-pressure was 6 ml min^{-1} . From these data and calculated pressure drop through the flow system, the pump characteristic was modeled for a 'standard sponge' to show a normal operating pressure of $\Delta H_0 = 0.673 \text{ mm H}_2\text{O}$ or

$\Delta p_{\text{tot}} = [1.024 \times 10^3 \times 9.81 \times 0.673 \times 10^{-3}] = 6.76 \text{ Pa}$ and $F = 6 \text{ ml min}^{-1} = [6/60 \times 10^{-6}] = 0.1 \times 10^{-6} \text{ m}^3 \text{ s}^{-1}$, hence $P_p = F \Delta p_{\text{tot}} = 0.68 \text{ } \mu\text{W}$. With a measured respiration rate of $R = 15 \text{ } \mu\text{l O}_2 \text{ h}^{-1} [= 15 \times 5.333] = 80 \text{ } \mu\text{W}$, the pumping costs become $P_p/R_{\text{tot}} = 0.68/80 = 0.85\%$ (all data from Riisgård et al. 1993 and recalculated here as an example).

Hadas et al. (2008) measured filtration and respiration rates in the Red Sea coral reef demosponge *Negombata magnifica* and found that the amount of oxygen required for water pumping activity was about 25% of the total oxygen consumption of the sponge. The filtration rate was measured by means of the steady-state method: $F = F_c (C_1 - C_2)/C_2$, where F_c is the flow rate through the experimental chamber with the sponge and C_1 and C_2 are the concentration of cells in inflow and outflow water, respectively. The respiration rate was measured at 3 different flow rates ($F_c = 600, 300, \text{ and } 100 \text{ ml min}^{-1}$) through the respiration chamber, assumed to represent 3 activity levels of sponges, i.e. 'active', 'no filtration', and 'basal'. When the flow rate through the respiration chamber was reduced to $F_c = 300 \text{ ml min}^{-1}$, the respiration rate decreased, resulting in 'a reduction of $25.1 \pm 3.6\%$ relative to the rate at full activity level' for the assumed 'no filtration' state (Hadas et al. 2008, p. 2188). Thus, the amount of oxygen required for water pumping was 'about 25% of the sponge's total oxygen consumption' (Hadas et al. 2008, p. 2188). Nevertheless, the experimental procedures and results reported by Hadas et al. (2008) are not fully clear regarding how respiration could be measured when the filtration rate ceased and what was the difference between cases 2 and 3 of the 3 through-flow cases.

Leys et al. (2011) quantified the pumping activity and respiration of the glass sponge *Aphrocallistes vastus* and modeled the filtration system. Here, the head loss across the sponge collar filter was $1.2 \text{ mm H}_2\text{O}$, or 10 times higher than previously estimated for *Haliclona permollis* by Riisgård et al. (1993) due to the presence of a fine glycocalyx mesh on the collar that had previously been overlooked. Based on *in situ* measurements of respiration and pumping rates for their model, it was found that the operating pump pressure was $6.2 \text{ mm H}_2\text{O}$ and that energy directed towards pumping pressures would therefore represent at least 28% of the total respiration. Therefore, the authors suggested that current-induced flow might be highly beneficial due to this high cost, and called for reevaluation of the cost of pumping in sponges.

Ludeman et al. (2017) measured pumping rate and oxygen removal in 5 species of demosponge. The energy costs of pumping P_p/R_{tot} ranged from about 1

to 5% for 4 of the sponges but amounted to 12–15% for one tropical sponge. Furthermore, by changing filter size and volume flow rate using data from the literature, Ludeman et al. (2017) estimated that the cost of filtration increased by up to 5 times the previous estimates by Riisgård & Larsen (1995) and Leys et al. (2011). Regardless of whether a single equation was used for all structures of the aquiferous system (Leys et al. 2011) or different equations were used to estimate the energy lost due to frictional resistance as water flows through the sponge (Riisgård & Larsen 1995), the estimate of energetic cost was very similar. The small differences were caused by differences in dimensions and water flow velocities. The greatest head loss 'occurred at the glycocalyx mesh filter, which had the smallest dimensions and therefore offered the greatest resistance' (Ludeman et al. 2017, p. 1003).

7. DISCUSSION

For the demosponge *Haliclona permollis*, Riisgård et al. (1993) found low energy costs of $P_p/R_{tot} = 0.85\%$, assuming that the full collar was open for inflow. However, since only the proximal 1/3 length of the collar is open, the velocity of flow upstream of the collar must be 3× higher than assumed, and the estimated pressure drop across the microvilli filter must therefore be 3× higher, i.e. $[3 \times 0.122 =] 0.366 \text{ mm H}_2\text{O}$. Adding this extra head loss to that of the 'standard sponge' of Riisgård et al. (1993), the total head loss is $0.671 + 0.366 = 1.037 \text{ mm H}_2\text{O}$, and therefore, the $P_p/R = [0.677/0.673 \times 1.037/80 =] 1.3\%$.

Hadas et al. (2008) measured the filtration rate (F) of the sponge by means of the steady-state method, but here the design must ensure that inflow water becomes fully mixed with the sponge's excurrent flow to establish a uniform steady-state chamber concentration (Riisgård 2001). A prerequisite for this is to check a plot of F versus varying F_c , which should give the same F at all through-flows (Larsen & Riisgård 2012) (Fig. 3), but this was not done, and the study was instead (wrongly) designed to measure F at 3 values of chamber through-flow rate, F_c . The respiration rate (R) was measured at 3 different flow rates. At the first level ($F_c = 600 \text{ ml min}^{-1}$), results showed $F/R = [70 \times 60 \times 10^{-3}]/0.33 =] 12.7 \text{ l}$ of water filtered per ml of oxygen consumed, which is close to our reference value of $F/R \approx 15 \text{ l H}_2\text{O (ml O}_2\text{)}^{-1}$ as a minimum to sustain the performance of a filter-feeding marine invertebrate.

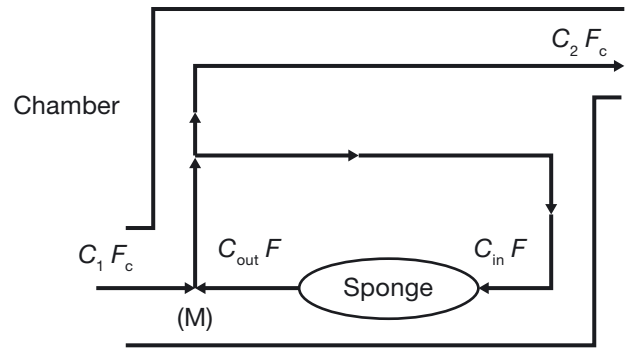


Fig. 3. Steady-state method. (M) denotes the point of perfect mixing. C_1 and C_2 denote food particle concentration of chamber inflow and outflow, respectively, C_{in} ($= C_2$) and C_{out} ($= 0$ for 100% retention) are the concentration of inhalant and exhalant flows of the sponge, respectively, F_c = chamber through-flow, and F = pumping rate given by $F = F_c (C_1 - C_2)/C_2$. To obtain reliable F measurements, inflow water must become fully mixed with the excurrent flow of the sponge to establish a uniform chamber concentration, which can be checked by a plot of F versus increasing F_c , which should give the same true F at all through-flows. Adapted from Larsen & Riisgård (2012), with permission from Biology Open

The definitions by Hadas et al. (2008) of 'active', 'reduced', and 'basal' stages of respiration rates in sponges assume that oxygen uptake reflects the energetic costs of water pumping and that these expenses can be physiologically regulated, as also suggested by Leys & Kahn (2018). However, this assumption is unwarranted. Oxygen is taken up through the surfaces of the canals where the flow is laminar, and the rate of oxygen uptake is physically determined by diffusion through the boundary layer between the feeding current and the tissues of the sponge. Defined as the ratio of oxygen actually respired to oxygen available in the water pumped through the sponge, the extraction efficiency of our reference sponge is (Riisgård 2024, Eq. 1 therein) $EE = [1 / (15 \times 6.3) =] 1.1\%$, when fully oxygenated seawater ($6.3 \text{ ml O}_2 \text{ l}^{-1}$) is available, and EE passively increases when the oxygen concentration is reduced. Measurement of respiration and filtration rates in *Halichondria panicea* have shown that the pumping rate remains constant down to low oxygen concentrations, and likewise, the respiration rate remains constant and independent of decreasing oxygen concentration because EE increases, i.e. the respiration rate is not physiologically regulated but independent of the filtration rate down to very low filtration rates (Hoffmann et al. 2008, Mills et al. 2014, Riisgård 2024). Reduced respiration rate at very low filtration rate, caused, for example, by disturbance and reduced

opening degree of the osculum, does not reflect physiological regulation but is a consequence of increased diffusional resistance due to a thicker boundary layer at very low flow rate. The concept of 'active', 'reduced', and 'basal' stages as presented by Hadas et al. (2008) is unwarranted, as also pointed out for mussels by Jørgensen (1990). A temporary exchange of helium for oxygen in water flowing through a chamber with the demosponge *Geodia barretti* stopped the filtration and the tissues became anoxic, but later, when, over 6 h, the sponge slowly returned to filter at a normal rate, the oxygen in the excurrent quickly (within 1 h) returned to normal (Leys & Kahn 2018, their Fig. 4). This shows that respiration (i.e. the rate of diffusional oxygen uptake) is independent of the filtration rate except at very low filtration rates. However, Leys & Kahn (2018, p. 666) suggested that 'the volumetric flow rate is reduced at lower oxygen levels' and that sponges tolerate hypoxia by reducing the filtration rate at the 'cost of filtration, indicating that normal feeding is energetically expensive'. However, at very low pumping rates, respiration may be affected, and if the water flow rate stops (no pumping by flagella or closure of the osculum), the oxygen uptake will cease, resulting in anoxia within the sponge (Hoffmann et al. 2008, Kumala et al. 2021).

Leys et al. (2011) assumed that all flow went through the fine glycocalyx mesh on the collar, which gave an additional head loss ($2 \times 0.455 \text{ mm H}_2\text{O}$) that represented 44% of the total head loss $\Delta p_{\text{tot}} = 2.075 \text{ mm H}_2\text{O}$, as seen from their Table 2. However, as mentioned, flow enters the open collar slits over the proximal 1/3 length of the collar (Fig. 3), and the estimated head loss and pumping power given by Leys et al. (2011) should therefore be reduced by $([-2 \times 0.455 + 3 \times 0.168] / 2.075 =)$ about 20% to become $\Delta p_{\text{tot}} = 1.66 \text{ mm H}_2\text{O}$. Furthermore, it is also the low oxygen consumption, hence respiration, that leads to the high energy costs of filtration. Thus, Riisgård et al. (1993) found that the demosponge *Haliclondria panicea* typically filters 11 l of water per ml of oxygen consumed, or $1/11 = 0.09 \text{ ml O}_2 \text{ l}^{-1}$ which may be compared to $0.53 \mu\text{mol O}_2 \text{ l}^{-1} [= 0.53 \times 22.4 \times 10^{-3}] = 0.01 \text{ ml O}_2 \text{ l}^{-1}$ reported by Leys et al. (2011). More recently, Riisgård et al. (2016) determined the F/R ratio to be $15.5 \text{ l H}_2\text{O} (\text{ml O}_2)^{-1}$, and the approximately 9 to 6.5 times lower oxygen demand may explain the high P_p/R_{tot} ratio of $[63 \text{ mJ l}^{-1}/228 \text{ mJ l}^{-1} =]$ 28% reported for the glass sponge *Aphrocallistes vastus* by Leys et al. (2011), or, with a 20% reduction of pressure loss, a P_p/R_{tot} ratio of about 22%. Another potential factor affecting the oxygen demand would be the augmented flow through the

sponge induced by ambient currents. Leys et al. (2011) found that flow out of the sponge was enhanced by ambient flow rates above 15 cm s^{-1} to reach 3–8 times the pumping rate measured at low ambient flow. Thus, increase in the ambient flow correlated with increased excurrent velocities, and the largest increase 'occurred in dead sponges whose tissue had been removed' (Leys et al. 2011, p. 12; see also their Fig. 5E). Likewise, flow out of the osculum of a model of just the skeleton of the glass sponge *Euplectella aspergillum* was observed in simulations of streamlines by Falcucci et al. (2022, their Fig. 2). Therefore, it remains to be verified if any of the passive induced flow is being filtered by the living sponge. A potential factor affecting the pumping rate would be an augmented flow through the sponge walls induced by ambient currents. Here, the 2 mm open holes through the wall of *A. vastus* (Schulze 1880) could contribute to give a higher rate of pumping (as measured by the velocity method) and a lower rate of respiration, and hence the estimated high energy costs. Likewise, ducts that are suggested to bypass the choanocyte chambers in the glass sponge *Scolymastra joubini* (Bavestrello et al. 2003) and the demosponges *Spongia officinalis* and *Cliona viridis* (Burlando et al. 1990) could result in increased current-induced exhalant velocities in sponges in strong flowing water, but the extra current-induced water is neither filtered nor used for respiration by the sponge.

Ludeman et al. (2017) found a considerable variation in energy costs of pumping, correlated with pumping rates, among 5 sponges studied. Values were highest for the tropical sponge *Cliona delitrix*. In calculating pressure losses, it was also assumed here that all flow went through the fine glycocalyx mesh on the collar. For the tropical sponge *C. delitrix*, the pressure loss here ($2.3 \text{ mm H}_2\text{O}$) represents 16% of the total head loss ($\Delta H_0 = 14.3 \text{ mm H}_2\text{O}$), as seen from their Table 3. Reducing the total pressure loss by 16% leads to an energy cost of pumping of $P_p/R_{\text{tot}} = (6.377 \times 0.84/42.102 =)$ 12.7%, which still appears to be a high value. Among other results, there was less variation in the F/R_{tot} values. For *C. delitrix*, for example, $F/R_{\text{tot}} = 2668 \times 5.333/42102 = 20.3 \text{ l}$ of water per ml of oxygen consumed (Ludeman et al. 2017, their Table 1), with the mean value for the 5 sponges being 21.5 l of water per ml of oxygen consumed, in agreement with our reference value of $F/R \approx 15 \text{ l H}_2\text{O} (\text{ml O}_2)^{-1}$.

Leys & Kahn (2018) suggested that filtration in sponges is costly and that sponges are able to tolerate hypoxia by reducing their feeding activity. However, Riisgård (2024) has recently shown why sponges are

Table 1. Published and corrected results for sponge respiration-specific pumping costs P_p/R_{tot} determined by various authors on various species using different methods; nd: not determined

Reference and species	Pumping rate, F	Pumping power, P_p	Respiration, R_{tot}	Published P_p/R_{tot} (%)	Corrected P_p/R_{tot} (%)
Riisgård & Larsen (1995) <i>Haliclona urceolus</i>	Direct method (Fig. 1)	$P_p = F \Delta p_{tot}$ Δp_{tot} calculated	Steady-state method $R_{tot} = F_c (C_{in} - C_{out})$	0.85	1.3
Hadas et al. (2008) <i>Negombata magnifica</i>	Steady-state method (Fig. 3) $F = F_c (C_1 - C_2)/C_2$	Not given	Reduced chamber through-flow, F_c	25	nd ^a
Leys et al. (2011) <i>Aphrocallistes vastus</i>	Osculum velocity and area	$P_p = F \Delta p_{tot}$ Δp_{tot} calculated	Measured F , C_{in} and C_{out}	28	22
Ludeman et al. (2017) 5 demosponges	Osculum velocity and area	$P_p = F \Delta p_{tot}$ Δp_{tot} calculated	Measured F , C_{in} and C_{out}	1–4 ^b 12–15	– 12.7

^aNot possible to correct
^b1–4% for 4 sponges, but 12–15% for 1 tropical sponge

tolerant to hypoxia, but not more tolerant than other filter-feeding invertebrates. Measurement of respiration rates at decreasing oxygen concentrations along with estimation of the oxygen extraction efficiency in *Halichondria panicea* showed that the respiration rate was constant down to about 1.5 ml O₂ l⁻¹ because the extraction efficiency increased with decreasing oxygen concentration, only controlled by the resistance to diffusion of oxygen across the boundary layer between the feeding current and the canals in the sponge.

Among the different methods used to determine filtration rate and system pressure losses, the one by Riisgård et al. (1993) should be particularly reliable because it directly measured the pumping rate at known back-pressures (Figs. 1 & 2). At zero back-pressure, the filtration rate F was 'directly' measured, and by imposing an increasing back-pressure, the so-called back-pressure characteristic was revealed. It appeared that the maximum pressure (shut-off head) that the sponge pump could deliver at zero pumping rate was about 2.7 mm H₂O. Subsequently, the normal operating pump pressure at zero back-pressure was estimated at $\Delta H_0 = 0.673$ mm H₂O, or 4 times lower than the shut-off head, which falls within the range found for 2 ciliary filter-feeders, the bivalve *Mytilus edulis* and the ascidian *Styela clava* for which the back-pressure characteristics were also 'directly' measured by Jørgensen et al. (1986, 1988) and Riisgård (1988), respectively. Thus, it seems likely that the maximum pressure that a choanocyte pump of a sponge can generate is about 3 mm H₂O and the normal pump pressure about 4 times lower. Here, the numerical CFD study of the shut-off pressure delivered by the choanocyte pump as a function of size of

gaps between flagella and collar should be noted (Asadzadeh et al. 2019, their Fig. 3). A value of about 3 mm H₂O, as measured for the demosponge *Haliclona urceolus*, would correspond to realistic leak gaps of $s \sim 0.2$ μm. It seems to be unlikely that the pump can produce operating pressures of 6.2 mm H₂O found for the glass sponge *Aphrocallistes vastus* by Leys et al. (2011) or 11–14 mm H₂O found by Ludeman et al. (2017, their Table 3) for the demosponge *Cliona delitrix*, which would require leak gaps half the size, i.e. $s \sim 0.1$ μm.

It may be useful to further pursue the performance of a single choanocyte pump. Thus, in a CFD study of the beating flagellum in a model of the pump for a delivered pressure of 1.95 mm H₂O, Asadzadeh et al. (2019) determined a pumping rate of 454 μm³ s⁻¹, hence the theoretical pump power of 8.68 fW. The calculated work rate of surface forces (the mechanical power) on the beating flagellum was 12.6 fW. The ratio of these powers equals the mechanical efficiency $\eta_{mec} \approx 70\%$, which appears to be a reasonable value for a leaky positive displacement pump. Efficiency and pumping rate depend on the size of the leak gaps between flagellum and collar. For the demosponge *Haliclona urceolus*, each choanocyte pumps about 60–70 μm³ s⁻¹, producing a pressure rise of 6.7 Pa (Larsen & Riisgård 1994), giving the theoretical pump power of $P_{p,rev} = F \Delta p = 0.43$ fW. For an estimate of the metabolic power provided by the choanocyte of diameter 4–5 μm, hence volume $(33.5–65.4) \times 10^{-18}$ m³, or a mass of about $(33.5–65.4) \times 10^{-15}$ kg, we may use the resting metabolic energy conversion rate of about 0.2 W kg⁻¹ for poikilothermic animals (Garby & Larsen 1995). This gives a metabolic rate of $R = 6.7–13$ fW, and the ratio

$P_p/R_{tot} = 0.064-0.033$ or 6.4–3.3%. The ratio is probably higher because not all the metabolic power of the cell is used to drive the flagellum.

The theoretical pump work P_p/R_{tot} was estimated earlier for various ciliary filter feeders and shows values from 0.3 to 4% (Riisgård & Larsen 1995, their Table 3). Referring to powers estimated for *Mytilus edulis*, the authors argued that measures other than P_p/R_{tot} may be appropriate when characterizing the energy cost of filter feeding. Thus, if R_g denotes the respiration rate of the large, specialized water-pumping gills, this gives a much higher pumping cost of $R_g/R_{tot} = 19\%$. The gill structures are expensive to maintain irrespective of whether the mussel is pumping water, and this supports the hypothesis of 'minimal scaling'. According to this, 'energy for functions other than pump work can be supported only when the part of the organism responsible for the pumping action is scaled appropriately for continuous feeding' (Riisgård & Larsen 1995, p. 99). In the case of sponges, where the walls between inhalant and exhalant canals consist essentially of closely packed water-pumping choanocyte chambers taking up 28–46% of the wall volume (Riisgård et al. 1993), it seems likely that they may be responsible for a significant part of the total respiration.

8. CONCLUSIONS

The cost of pumping has been used for characterizing to what degree filter-feeding marine invertebrates are adapted to feeding on low concentrations of suspended food particles in the sea. So far, few values of pumping costs have been reported, and they do not include scaling effects such as the influence of sponge size on costs. It is known that pumping rate may increase or decrease with increasing volume of sponges (Larsen & Riisgård 2021, Morganti et al. 2021) but the corresponding variation in metabolic costs is unknown. The filtration process in sponges has been claimed to be costly due to flow resistance of the small dimensions of their aquiferous systems. Our examination of reported results gives an updated view. The pumping power (P_p) is the product of filtration or pumping rate and the pressure losses, which represents the energy transferred to the water flow (the theoretical pumping power). Here, the flow rate can be experimentally measured, while the total pressure losses associated with flow through the aquiferous system cannot be measured directly. Pressure losses are therefore calculated using engineering equations from hydraulics applied to the various geo-

metric descriptions of flow restrictions in the sponge. Such calculations have become increasingly more reliable, especially after studies have disclosed details of the choanocyte collar–glycocalyx mesh and the basic filter and pump mechanism. Based on measured total respiration rates (R_{tot}), the published values of respiration-specific pumping costs P_p/R_{tot} range from a few percent to 15 and 28%, but with our corrected values for pressure losses they range from 1.3 to 22% (Table 1). However, both theoretical costs and total costs including mechanical and metabolic efficiencies, which represent what the organism really spends on pumping, should be reported if possible. A way to evaluate the total metabolic costs of a demosponge is to note that up to 50% of the wall volume between in- and out-current canals is occupied by close packed water-pumping choanocyte chambers (Larsen & Riisgård 1994). Therefore, water pumps may be responsible for a significant part of the total respiration, perhaps up to 50% (Riisgård & Larsen 2022), hence costly, while the theoretical respiration-specific pumping cost P_p/R_{tot} is low, down to 1.3%.

Acknowledgements. We thank the 3 anonymous reviewers for their helpful comments.

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*Editorial responsibility: Joseph Pawlik,
Wilmington, North Carolina, USA
Reviewed by: 3 anonymous referees*

*Submitted: February 23, 2024
Accepted: August 12, 2024
Proofs received from author(s): September 26, 2024*