ABSTRACT
The F/R-ratio (litres of water filtered per ml of oxygen respired) was determined for the filter-feeding demosponge Halichondria panicea to be 15.5 l H2O (ml O2)−1 which was used to evaluate the potential of the sponge to nourish solely on nano- (2–20 µm) and micro- (20–200 µm) phytoplankton cells in the sea. It was estimated that in order to balance the maintenance requirement of H. panicea the necessary content of suspended particulate organic carbon must be at least 0.03 mg C l−1, which may be compared with actually reported values of 0.04 to 0.2 mg C l−1. Finally implying that H. panicea may be able to nourish on a sole diet of phytoplankton in nature. However, the amount of carbon represented by free-living heterotrophic bacteria, cyanobacteria and other small (0.2–2 µm) picoplankton which are also accessible to the sponge lies in the range of 0.05–0.10 mg C l−1, and therefore bacteria seem to be an important, although in many cases apparently a somewhat insufficient food source relative to phytoplankton. Video-microscope observations of the osculum cross-sectional area (OSA) and simultaneous measurement of the filtration rate of H. panicea showed that the filtration rate varied considerably over time concurrently with often pronounced variations in the OSA caused by disturbance when the aquarium through-flow was stopped during filtration rate measurements in the laboratory. It is concluded that the optimal and undisturbed filtration rate may be considerably higher than measured here, i.e. 6.1 ml water (ml sponge)−1 min−1, thus increasing the F/R-ratio to > 15.5 l H2O (ml O2)−1, which is comparable to values for more advanced eumetazoan filter-feeding marine invertebrates grazing on phytoplankton.

Introduction
In sponges, the basic element for both pumping and filtering is the choanocyte with a flagellum that pumps water through a collar of microvilli acting as a sieve that captures free-living heterotrophic bacteria, cyanobacteria and other small (0.2–2 µm) picoplankton particles (Fjerdingstad 1961a; Jørgensen 1966; Brill 1973; Riisgård & Larsen 2000; Leys et al. 2011). The functional and morphological similarities between choanoflagellates and choanocytes has led to the assumption that sponges have evolved from choanoflagellates (e.g. James-Clark 1867; Afzelius 1961; Fjerdingstad 1961b) but although choanoflagellates are monophyletic, and therefore did not give rise to sponges, many researchers consider them to be in some sense homologous or convergent (e.g. King et al. 2008; Nielsen 2008; Mah et al. 2014, but see Maldonado 2004, Leadbeater 2015 and Budd & Jensen 2015). One crucial difference between sponges and choanoflagellates is the ability of the former to feed also on nano- (2–20 µm) and micro- (20–200 µm) phytoplankton cells (Reiswig 1971; Pile et al. 1997; Duckworth & Pomponi 2005; Yahel et al. 2006) which are retained, phagocytosed and digested in the extensive inhalant channel system before the water is finally filtered through the collar slits of the choanocytes (Kilian 1952; Fjerdingstad 1961a; Bergquist 1978; Simpson 1984). However, diatoms that settle on the surface of Antarctic sponges may also be directly taken up via exopinacocytes (Gaino et al. 1994; Ribes et al. 1999), but otherwise only particles smaller than the diameter of the incident pores (ostia), which vary in size from 10 to 200 µm with a mean of about 50 µm, are captured inside the sponge aquiferous system, and studies have revealed feeding efficiencies in the range of 75–99% on 0.1–70 µm plankton (Kilian 1952; Bergquist 1978; Reiswig 1981; Yahel et al. 2006; Leys & Eerkes-Medrano 2006). Thus, sponges ingest...
food particles of varying types and sizes, although apparently with highest retention efficiencies of particles <10 µm (Reiswig 1971; Pile et al. 1996; Ribes et al. 1999). In addition, filtration activity may also be temporally influenced by cyclic or spontaneous contractions of excurrent openings (e.g. Reiswig 1975a).

Larsen & Riisgård (1994) investigated the sponge pump and concluded that the basic pump units in demosponges are the choanocyte chambers, which constitute 30–50% of the wall structure separating inhalant and exhalant canals, and furthermore, that all pump units operate in parallel and at essentially the same flow and pressure. In this way large sponges have evolved to become filter feeders capable of feeding on phytoplankton, but it is unknown if sponges are sufficiently effective to nourish solely on phytoplankton in the same way as the many more advanced invertebrates (with true tissues, organs, body symmetry) that have evolutionarily adapted to filter-feeding in the sea (Riisgård et al. 1993; Thomassen & Riisgård 1995; Riisgård & Larsen 2000).

The amount of phytoplankton in the sea can be expressed by the measured concentration of chlorophyll a (chl a), and the mean concentration in various marine areas around the globe is typically between 1 and 5 µg chl a l⁻¹ (Riisgård et al. 2013). To balance a metabolic energy requirement (R) equivalent to the consumption of 1 ml O₂ (equivalent to 0.46 mg C; Stuart & Klumpp 1984), assuming 100% particle retention efficiency and 80% assimilation efficiency of ingested food, a filter-feeding animal exposed to a phytoplankton concentration of for example 1.5 µg chl a l⁻¹ (C, equivalent to 1.5 × 40 (see ‘conversion factors’)/1 000 = 0.06 mg C l⁻¹) must filter F = R/(C × 0.8) = 0.46/(0.06 × 0.8) = 10 l of water (Riisgård & Larsen 2000).

From the above F/R-ratio reference value of 10 l H₂O (ml O₂)⁻¹ it is possible to evaluate the adaptation of an animal to feed on phytoplankton (Riisgård & Larsen 2000). Here we use the F/R-ratio determined for the demosponge Halichondria panicea (Pallas, 1766) to evaluate its filter-feeding potential to nourish solely on phytoplankton (> 2 µm) versus free-living bacteria (< 2 µm) in the sea. To evaluate otherwise unexplained variations in the measured filtration rate and thus the F/R-ratio, repeated measurements of filtration rate, combined with simultaneous video observation of an osculum, were performed.

Materials and methods

Long-term filtration rate experiment – Series #1

The aim was to measure the filtration rate of a Halichondria panicea sponge colony over an extended period of time by means of two methods, the steady-state method and the clearance method, in order to determine the mean filtration rate and to detect possible variations and changes caused by the laboratory conditions. The experiments were conducted on a H. panicea colony from the nearby inlet to Kerteminde Fjord (Denmark).

Steady-state method

The sponge colony was transferred to an aerated aquarium (8.8 l) with constant through-flow (F/I = 230 ml min⁻¹) of bio-filtered (mussels) seawater and added algal cells (Rhodomonas salina (Wislouch) D.R.A. Hill & R. Wetherbee) from a pure culture at a constant rate (P = 6 ml min⁻¹) by means of a dosing pump, and the filtration rate (F) was calculated as:

\[
F = \frac{(P \times C_o - F \times C)}{C_c},
\]

where \(C_o\) = algal concentration in added culture and \(C_c\) = steady-state algal concentration in the sponge aquarium. The algal cells had a diameter of about 6 µm and were therefore retained by the sponge with 100% efficiency and air-stone mixing of the water ensured no sedimentation during the experimental period (60–80 min). The algal concentration was measured with an electronic particle counter (Elzone 5380). A typical steady-state experiment is shown in Figure 1.

Clearance method

Filtration rates were measured as the volume of water cleared of suspended algal cells (R. salina) per unit of time (= clearance rate). The reduction in the number of cells as a function of time was followed by taking water samples (10 ml) at fixed time intervals from an aquarium containing a sponge colony in well-mixed seawater with initially added R. salina cells. The filtration rate (F) was determined from the exponential

![Figure 1. Halichondria panicea (Series #1, steady-state experiment, Day 1). Mean estimated filtration rate, cf. Equation (1) = 338 ± 25 ml min⁻¹.](image)
decrease in algal concentration as a function of time using the formula:

\[ F = V \times b \]  

(2)

where \( V \) = water volume in the aquarium in ml, and \( b \) = slope of the regression line in a semi-ln plot for the reduction in algal concentration with time. A control experiment without a sponge showed that there was no sedimentation of algal cells. The mean algal concentration during a clearance experiment was estimated as \( C_m = (C_0 \times C_t)^{0.5} \) where \( C_0 \) and \( C_t \) are the initial and final algal concentration, respectively. A typical clearance experiment is shown in Figure 2.

The filtration rate was measured over a period of 49 days and the sponge colony was kept in through-flowing bio-filtered (mussels) seawater between the measurements (mean temperature about 12°C). After the last measurement the volume of the sponge colony was measured to be 25 ml (= 3.3 g DW).

Osculum contractions and variations in filtration rates – Series #2

*Halichondria panicea* colonies were collected from the nearby inlet to Kerteminde Fjord, placed on 5 x 5 cm PVC plates and tied with nylon strings (Marlow Ropes No. 4) to ensure an upward direction of the exhalant jets and firm attachment in the flow-through system. The sponge colonies, which attached themselves to the plates within about 10 days, were kept in the laboratory in an air-mixed tank (60 l) with through-flowing seawater (1.8 l min\(^{-1}\)) and were fed daily with algal cells (*Rhodomonas salina*). To evaluate the otherwise unexplained variations in the filtration rate of the sponge colony in Series #1, repeated measurements of the filtration rate combined with simultaneous video-microscope observation of an osculum were performed during a 6 day experiment with one colony transferred to an observation chamber (0.5 l) with through-flowing seawater. During the observation period, the flow-through was temporarily stopped and series of clearance experiments were subsequently made by repeated algal (*R. salina*) additions. To investigate the sponge osculum dynamics, digital images of the osculum were taken at certain time intervals (one picture every 2 min during the clearance experiments, otherwise every 5 min) using a stereo-microscope (Leica MZ8) connected to a USB 3.0 industrial camera (Imaging-source, DFK23UM021) controlled by an image acquisition software (IC Capture, 2.3). Image sequences were analysed using software (ImageJ, 1.50f) to estimate the osculum cross-sectional area (OSA). After the experiment the size of the sponge colony was measured to be: volume = 9 ml, dry weight (DW) = 0.66 g (24 h, 100°C), and ash-free dry weight (AFDW) = 0.46 g (6 h, 500°C). Further details of the experimental setup and other examples of repeated measurements of filtration rate combined with simultaneous video-microscope observation of an osculum in various sponge colonies are shown in the supplementary material for this article.

Conversion factors

The following equation and conversion factors were used: dry weight (DW, g) of *Halichondria panicea* correlates to sponge colony volume (\( V_c \), ml) according to: 

\[
DW = -0.162 + 0.139V_c 
\]  

(Riisgård et al. 1993, Figure 7 therein); 1 µg chl \( a \) \( 1^{-1} \) corresponding to 799 *Rhodomonas salina* cells ml\(^{-1}\) (Clausen & Riisgård 1996); 1 ml O\(_2\) corresponding to 0.46 mg C (Stuart & Klumpp 1984); 1 µg chl \( a \) corresponding to 40 µg C (Li et al. 2010); \( 10^6 \) free-living bacteria ml\(^{-1}\) corresponding to 0.1 mg C \( 1^{-1} \) (Fenchel 1982b). The respiration rate \( (R) \) of *H. panicea* was estimated according to Mills et al. (2014) who found that the maximum weight-specific respiration rate measured between 40 and 100% air saturation was \( R = 7.93 \mu M O_2 h^{-1} (g \text{ DW})^{-1} = (7.93 \times 32/1000 \times 0.7) = 0.178 \text{ ml O}_2 \text{ h}^{-1} (g \text{ DW})^{-1} \).

Results

Figure 3 shows the filtration rates of *Halichondria panicea* (Series #1) measured during the 49 day experimental period by means of the two methods used. The mean algal concentration used in the experiments was always < 5000 algal cells ml\(^{-1}\) (corresponding to < 6.3 µg chl \( a \) \( 1^{-1} \)). There was good agreement between the two methods and little variation in filtration rate over time (linear regression, \( t = -1.44, P = 0.17 \)). The mean filtration

![Figure 2. *Halichondria panicea* (Series #1, clearance experiment, Day 1). Filtration rate = slope of regression line (b) × volume of sponge aquarium \((V) = 0.0191 \times 8800 = 168 \text{ ml min}^{-1}\), cf. Equation (2).](image-url)
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Variations in the filtration rate were systematically studied over an extended period of time in the follow-up study (Series #2; Figure S6, supplementary material). From Figures 4 and 5 and Table I it appears that the filtration rate varies considerably over time (i.e. 48%, or CV = 0.48), in this case over an experimental period of 6 d (but see Table SI and Figure S1, supplementary material), concurrently with often pronounced variations in the osculum cross-sectional area which is apparently being reduced after stoppage of the through-flow (Figure 5, Figures S2, S3 and S6). This response to water flow seems to indicate a high degree of sensitivity of the sponge colony to environmental changes and disturbances causing temporal variations in OSA of two adjacent exhalant apertures in single sponge colonies (Figures S4 and S5). Thus, it seems likely that the pronounced variations in filtration rates observed in Series #1 (Figure 3) may partly have been caused by stoppage of through-flow during the clearance experiments.

Using the mean filtration rate of 152 ml min⁻¹ (Figure 3), the F/R-ratio for the 25 ml H. panicea colony (Series #1) is estimated to be (0.152 x 60/ (0.178 x 3.3)) = 15.5 l H₂O (ml O₂⁻¹). Thus, to balance the maintenance energy requirement of H. panicea the food content of suspended particles in 15.5 l seawater must at least be able to cover a respiration rate of 1 ml O₂ corresponding to 0.46 mg C, implying that the particulate organic carbon content should be above 0.46/15.5 = 0.03 mg C l⁻¹.

Discussion

F/R-ratio and diet of sponge

For Halichondria panicea it was estimated that F/R = 15.5 l H₂O (ml O₂⁻¹) and to balance the sponge’s energy requirement the particulate organic carbon content should be > 0.03 mg C l⁻¹. Apart from brief spring blooms, the mean chl a concentration in marine areas around the globe is typically between 1 and 5 µg l⁻¹ (Riisgård et al. 2013), or (using a chlorophyll a/carbon ratio = 0.025, e.g. Li et al. 2010) between 0.04 and 0.2 mg C l⁻¹. This implies that H. panicea may in general be able to cover all or most of its carbon requirement on a sole diet of phytoplankton, assuming that all sizes of phytoplankton can be ingested.

The amount of carbon represented by free-living bacteria in near-shore waters, which lies in the range of 1 to 3 x 10⁹ cells l⁻¹ equivalent to about 0.05 to 0.10 mg C l⁻¹ (Fenchel 1984), may additionally contribute to the accessible particulate carbon sponges can feed on. According to Fenchel (2008) the bacteria density in the water column usually remains relatively constant at around 10⁶ cells ml⁻¹ (within the range of 0.5 to 2 x 10⁶ cells ml⁻¹; Fenchel 1982b), and because each cell contains about 10⁻¹⁰ mg C (Fenchel 1982b) this abundance of bacteria is equivalent to about 0.1 mg C l⁻¹. From these considerations it seems likely that phytoplankton is a slightly more important food source for H. panicea than free-living bacteria. However, symbionts and possible uptake of dissolved organic matter may also play a role, but will not be considered further here.

In the present study, the F/R-ratio for H. panicea was found to be 15.5 l H₂O (ml O₂⁻¹) which may be compared with 11 l H₂O (ml O₂⁻¹) reported by Riisgård et al. (1993), and to 2.7 l H₂O (ml O₂⁻¹) found by Thomassen & Riisgård (1995). This indicates that the F/R-ratio of H. panicea may generally be above the minimum reference value of 10 l H₂O (ml O₂⁻¹), but also that the ratio may be influenced by the experimental conditions (e.g. water quality, starvation, food particle concentration) and/or physiological state (i.e. feeding, growth, reproduction) causing variations in both filtration activity (e.g. Osinga et al. 2001) and respiration rate. Figure 5 shows how distinct variations in the osculum cross-sectional area are correlated with disturbance caused by stoppage of the water through-flow and also reflected in the simultaneously measured filtration rate. Therefore, it seems likely that
the pronounced variations in filtration rates observed in Figure 3 may at least partly have been caused by stoppage of the through-flow during the clearance experiments, although variations appear to be quite random, irrespective of the duration of the experimental period (Figures 3 and 5, Figures S2 and S3). The optimal, undisturbed filtration rate may thus be considerably higher (up to two times) than the mean filtration rate of 152 ml min⁻¹ found in Series #1, perhaps increasing the F/R-ratio to be > 15.5 l H₂O (ml O₂)⁻¹. In two tropical marine sponges, Tectitehya crypta (de Laubenfels, 1949) and Mycale sp., the F/R-ratios were found by Reiswig (1974) to be 22.8 and 19.6 l H₂O (ml O₂)⁻¹, respectively. Hadas et al. (2008) found that the Red Sea coral sponge Negombata magnifica (Keller, 1889) consumed 0.33 ml O₂ h⁻¹ g⁻¹ (dry mass) and this implies that the F/R-ratio = (70 × 60 × 10⁻³/0.33 =) 12.7 l H₂O (ml O₂)⁻¹. In situ respiration rates of the glass sponge Aphrocallistes vastus Schulze, 1886 measured by Leys et al. (2011) by comparing the dissolved oxygen concentration in the inhalant and exhalant canals of individual sponges showed an average oxygen demand of 0.53 µmol O₂ l⁻¹ ( = 0.53 × 22.4 = 0.0119 ml O₂ l⁻¹), indicating a F/R-ratio of (1/0.0119 =) 84 l H₂O (ml O₂)⁻¹ which is five times higher than the present value for H. panicea. This may reflect adaptation to different habitats with different concentrations of suspended food particles. Thus, the F/R-ratios for other filter-feeding marine invertebrates that are less efficient in capturing free-living bacteria are generally higher than hitherto found for H. panicea (see later). This suggests that free-living bacteria make up an important fraction (possibly in the order of 50%, or more, cf. Reiswig 1975b) of the total amount of food taken up by sponges. However, this important question can only be settled by detailed studies on the actual diet of sponges in nature (Pile et al. 1996; Ribes et al. 1999).

The present observations of the filtration activity of H. panicea (Figure 5) indicate that the sponge is sensitive to changes in water motion and possible other disturbances, but the filtration activity may also be influenced by spontaneous or cyclic contractions of...
oscula, pinacoderm and tissue as observed in other studies on other sponge species (Reiswig 1971; Lawn et al. 1981; Simpson 1984; Savarese et al. 1997; Leys & Meech 2006; Nickel et al. 2006, 2011; Elliott & Leys 2007). Temporal variations in oscular area and pumping activity seem to be a common feature among sponges (Reiswig 1971; Savarese et al. 1997; McMurray et al. 2014), indicating a behavioural response to external stimuli (Elliott & Leys 2007). In situ studies on the tropical sponge species *T. crypta* and *Verongula gigantea* (Hyatt, 1875), however, indicate periodic constrictions of oscula and apertures of exhalant canals of the same sponge specimen as part of an intrinsically generated species-specific rhythm (Reiswig 1971). In this study changes in water flow caused closure of oscula of adjacent exhalant apertures in single *H. panicea* sponge colonies (Figures S4 and S5), which may be an adaption of this intertidal species to regular disturbances (Parker 1910; Hartman & Reiswig 1973). Rhythmic constrictions of two individual oscula, albeit not always synchronized, imply a behavioural response of the entire sponge colony possessing several exhalant openings exposed to a single stimulus. From these considerations it seems likely that similar variations in osculum cross-sectional area and filtration rate may be expected in the field as a result of changes in wave and current conditions, for example, but osculum dynamics and related physiological performance of undisturbed versus disturbed *H. panicea* colonies and other sponge species need to be investigated in more detail to better evaluate variable activity patterns.

**Figure 5.** *Halichondria panicea* (Series #2). Video observation (upper panels, A and B) of osculum cross-sectional area (OSA), and simultaneous measurement (lower panels) of filtration rate (*F*) of sponge colony in observation tank, with efficient air-mixing during 140 h experiment. To measure the filtration rate using the clearance method (Table I), the through flow of water was stopped (arrow) so that the exponential reduction of algal cells could be followed (Figure 4), and afterwards the water flow to the observation tank was re-established (punctured arrow).
Comparison of sponge with choanoflagellate

*Monosiga* sp. is a small, 3–3.5 µm in diameter choanoflagellate with a 5–6 µm long flagellum and a collar consisting of 18 pseudopodia. The flagellum pumps water through the collar-filter from the outside, and the free space between adjacent pseudopodia is 0.25 µm at the base, increasing to 0.35 µm distally (Fenchel 1982a), and this indicates that 0.5–2 µm free-living bacteria are efficiently captured. Thus, *Monosiga* is a regular filter-feeder, and the filtration rate for particles retained 100% (estimated as collar-filter area × water velocity) has been found to be \( F = 2.0 \times 10^{-9} \text{ ml h}^{-1} = 2.0 \times 10^{-9} \text{ l h}^{-1} \) (Fenchel 1982b, Table 1 therein). The respiration rate of *Monosiga*, with a cell volume of \( V = 18 \mu m^3 \), may be approximated from the relationship between \( \log_{10} R \) and \( \log_{10} V \) given for ‘growing flagellates’ by Fenchel & Finlay (1983, Figure 2 therein) to be \( 10^{-3} \text{ ml O}_2 \text{ h}^{-1} = 10^{-9} \text{ ml O}_2 \text{ h}^{-1} \). From this it is found that \( F/R = 2 \text{ l H}_2\text{O} \) (\( \text{ml O}_2 \))\(^{-1} \), which implies that the carbon content of the free-living bacteria should be above 0.46/2 = 0.23 mg C l\(^{-1} \) to cover the respiratory need. However, the mean abundance of bacteria is only about 0.1 mg C l\(^{-1} \) and it seems obvious that the estimated \( R \) for the ‘growing flagellate’ does not represent the ‘maintenance’ respiration of *Monosiga*. Thus, according to Fenchel & Finlay (1983), the energy requirements for maintenance ‘constitute an extremely small fraction of that involved in growth’, and in general when protozoans are exposed to starvation conditions the respiration rate falls soon after to a few per cent, typically about 2% (Tom Fenchel, personal communication in 2015). In the sample case of *Monosiga*, starvation may therefore result in \( F/R = 100 \text{ l H}_2\text{O} \) (\( \text{ml O}_2 \))\(^{-1} \) which is likely to indicate an ability of this choanoflagellate to survive during periods with diminished concentrations of free-living bacteria.

Respiration and growth are integrated through the energetic costs of growth and in *Halichondria panicea* the energy cost of growth was found by Thomassen & Riisgård (1995) to be equivalent to 139% of the biomass production, which is very high compared with other filter-feeding invertebrates (Riisgård 1998) – but this does not necessarily reflect that a sponge can be more or less considered as a colony of choanoflagellates, with which it undeniably shares many basic filter-feeding properties – but probably not the impressive respiratory scope that characterizes feeding and growing versus starving choanoflagellates. However, this question awaits closer examination in future comparative studies.

**F/R-ratio and comparison of sponges with other filter-feeders**

The degree of adaptation of a filter-feeder to different environments with different typical phytoplankton levels can be evaluated on the basis of the F/R-ratio. Thus, as a rule of thumb without taking food-particle retention efficiency into consideration, if \( F/R > 10 \text{ l H}_2\text{O} \) (\( \text{ml O}_2 \))\(^{-1} \) this suggests that the animal is a true filter-feeder (Riisgård & Larsen 2000). F/R-ratios for filter-feeding crustaceans have recently been reviewed by Riisgård (2015, Table 15.1 therein). For the copepod
A* Acartia tonsa *Dana, 1849* it has been found to be 37 l H2O (ml O2)−1, and for the cladoceran *Daphnia magna* *Straus, 1820*, the amphipod *Corophium volutator* (Pallas, 1766), and the euphausian *Euphausia superba* *Dana, 1850* the F/R-ratios were found to be 13–18, 39–74 and 42 l H2O (ml O2)−1, respectively. Similar values have been reported by Riisgård & Larsen (2000, Table 3 therein) for other taxonomic groups and species, i.e. bryozoans *Celleporella hyalina* *Linnaeus, 1767*: 68 l H2O (ml O2)−1, polychaetes *Sabella spallanzani* (Gmelin, 1791), *Chaetopterus variopedatus* (Renier, 1804), *Hediste diversicolor* (O.F. Müller, 1776): 40–354, mussels *Mytilus edulis* *Linnaeus, 1758*: 15–50, ascidians *Ciona intestinalis* (Linnaeus, 1767): 13–82, lancelets *Branchiostoma lanceolatum* (Pallas, 1774): 79. The present F/R-ratio > 15.5 l H2O (ml O2)−1 for the demosponge *Halichondria panicea* shows that it apparently fulfills the minimum requirement of adaptation for a true marine filter-feeding animal typically grazing mainly on phytoplankton. To what degree this is actually the case for *H. panicea* is still unknown, but in Danish and other temperate waters all filter-feeders are subject to low phytoplankton concentrations and starvation during winter periods. Thus, it is well known that the blue mussel *M. edulis* in Danish waters loses body mass (stored fuel reserves, mainly glycogen) during winter (Riisgård et al. 2014). However, by strongly reducing the valve gape *M. edulis* saves energy during the starvation periods, and recently Riisgård & Larsen (2015) found that the actual weight loss was about 10–12 times lower than the estimated respiratory weight loss. However, *H. panicea* does not store large amounts of glycogen or fat during the spring bloom (Barthel 1986, 1988) and therefore it becomes of interest to know how the sponge copes with the winter-starvation period. Variations in biomass of *H. panicea* in the temperate Kiel Bight (Germany) have been studied by Barthel (1988), who found that the biomass development of the sponge through the year closely resembled that of other zoobenthos, and therefore she suggested that the sponge has to rely mostly on phytoplankton during the summer. Further, growth of *H. panicea* measured in cage experiments conducted by Barthel (1989) in a North Sea habitat showed positive growth from June until October, whereupon the sponge started to shrink in size, i.e. individual body mass decreased. On this background it seems reasonable to conclude that *H. panicea* like other filter-feeding marine invertebrates in temperate waters loses body mass during winter, but it remains unknown how the sponge copes more precisely with starvation, as compared with, for example, mussels.

Sponges represent one of the simplest groups of animals and share characteristics with other more advanced filter-feeding invertebrates, but they also share characteristics with colonies of single-celled choanoflagellates. To understand the sponge feeding strategy and the adaptation of various species of sponges to different habitats with various levels of phytoplankton and free-living bacteria that vary between summer and winter, we need reliable data on the physiological performance of undisturbed and optimally filtering sponge colonies, and here the F/R-ratio seems to be a useful guiding tool.

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