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Article

Actual and Model-Predicted Growth of Sponges—With a Bioenergetic Comparison to Other Filter-Feeders

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Abstract: Sponges are one of the earliest-evolved and simplest groups of animals, but they share basic characteristics with more advanced and later-evolved filter-feeding invertebrates, such as mussels. Sponges are abundant in many coastal regions where they filter large amounts of water for food particles and thus play an important ecological role. Therefore, a better understanding of the bioenergetics and growth of sponges compared to other filter-feeders is important. While the filtration (pumping) rates of many sponge species have been measured as a function of their size, little is known about their rate of growth. Here, we use a bioenergetic growth model for demosponges, based on the energy budget and observations of filtration (F) and respiration rates (R). Because F versus dry weight (W) can be expressed as $F = a_1 W^{b_1}$ and the maintenance respiratory rate can be expressed as $R_m = a_2 W^{b_2}$, we show that if $b_1 \sim b_2$ the growth rate can be expressed as: $G = aW^{b_1}$, and, consequently, the weight-specific growth rate is $\mu = G/W = aW^{b_1-1} = aW^b$ where the constant a depends on ambient sponge-available food particles (free-living bacteria and phytoplankton with diameter < ostia diameter). Because the exponent b_1 is close to 1, then $b \sim 0$, which implies $\mu = a$ and thus exponential growth as confirmed in field growth studies. Exponential growth in sponges and in at least some bryozoans is probably unique among filter-feeding invertebrates. Finally, we show that the F/R -ratio and the derived oxygen extraction efficiency in these sponges are similar to other filter-feeding invertebrates, thus reflecting a comparable adaptation to feeding on a thin suspension of bacteria and phytoplankton.

Keywords: bioenergetic growth model; energy budget; filtration rate; respiration; F/R -ratio; filter-feeding



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1. Introduction

Sponges are simple multicellular filter-feeders that actively pump volumes of water equivalent to five times or more their body volume per minute through their canal system by using flagellated choanocytes, which constitute the pumping and filtering elements of the smallest particles [1–4]. Sponges feed on suspended microscopic particles, including free-living bacteria and phytoplankton [5,6]. Water enters the sponge body through numerous small inhalant openings (ostia) and passes through incurrent canals, where phytoplankton cells with diameters smaller than the ostia diameter but larger than 5 μm are trapped, leading to the choanocyte chambers, where bacteria and other smaller particles are captured by the collar-filter of the choanocytes. Then, the filtered water flows through excurrent canals to be expelled as a jet through an exhalant opening (osculum) [7–9]. The water pumping also ensures ventilation and a supply of oxygen for respiration via diffusive oxygen uptake [10]. Although sponges lack nerves and muscle tissues, coordinated contraction-expansion responses, including partial or complete closure of the osculum to mechanical and chemical stimuli, are common among sponges due to the presence of contractile cells (myocytes) [10–13], which results in temporary reduced or arrested water flow.

Sponges are one of the earliest evolved and simplest groups of animals [14], but they share basic characteristics with more advanced and later-evolved filter-feeding invertebrates such as mussels, in which filter-feeding is a secondary adaptation [15]. Sponges are also abundant today, especially in polar-shelf and tropical-reef communities as well as in many coastal regions, where they filter large amounts of water for food particles and thus play an important ecological role [5,16–21]. Therefore, a better understanding of the bioenergetics and growth of sponges in comparison with other filter-feeders is important.

Here, we first use an earlier approach for setting up a bioenergetic growth model, based on the energy budget and observations of filtration and respiration rates, which suggest that the growth of sponges is exponential; next, we use data in the literature to verify this hypothesis. Finally, we compare sponges to other filter-feeding invertebrates in order to compare the evolutionary adaptation of these animals to feed on the same thin soup of bacteria and phytoplankton.

2. Materials and Methods

Based on sponge data in the literature, we first set up a growth model based on the energy budget for growth (G) by making use of near identical exponents in the power functions for filtration rate (F) and respiration rate (R) versus body dry weight W . This development follows the earlier approach for the growth of the blue mussel *Mytilus edulis* [22], for which F or $R = aW^{0.66}$ leads to a decrease in the weight-specific growth rate of mussels with increasing size, given by: $\mu = G/W = aW^{0.66} - 1 = aW^{-0.34}$, which showed good agreement with field data. For many sponges, it is suggested that exponents b_1 and b_2 of power functions for F and R are close to $b_1 \sim b_2 \sim 1$, and, therefore, the model predicts that the weight-specific growth rate must be constant with increasing sponge size, which implies that the growth must be exponential. This hypothesis is subsequently verified by sponge-growth data from the literature obtained in field experiments conducted in periods with positive growth, typically in the spring. The development of sponge size in time intervals was used to estimate the specific growth rates in each interval and was subsequently used for the evaluation of growth patterns. Exponential growth is characterized by a constant specific growth rate, which is reflected as a trendless scatter of the interval-specific growth rates, in contrast to a power function growth pattern, where the interval-specific growth rate will decrease with increasing size; for such data, an exponential curve fit will systematically underestimate the actual data in the first half period and then overestimate the data in the remaining period. Data were replotted from other publications using an in-house graphical program, 'Gtpoints', which generates a table of data point coordinates according to the scales of axes in a *.bmp image of a given graph.

Exponential regression curves (LM) were fitted in [23] for growth rate estimates based on wet weight, ash-free dry weight, or length of sponge over time.

3. Results and Discussion

3.1. Sponge Growth Model and Test of Exponents

The growth of a sponge can be expressed by the energy (or carbon) budget as:

$$G = I - R - E = A - R \quad (1)$$

where G = growth (production), I = ingestion, R = respiration (total) = R_m (maintenance respiration) + R_g (growth respiration, i.e., metabolic cost of synthesizing new biomass), E = excretion, and A = assimilated food. The budget can also be written as $G = (F \times C \times AE) - (R_m + R_g)$, where F = filtration rate, C = food concentration, and $AE = A/I$ = assimilation efficiency. Thus, equating the rate of the net intake of nutritional energy to the sum of various rates of consumption, the energy balance for a growing sponge may now be written as:

$$G = [(F \times C \times AE) - R_m] / a_0 \quad (2)$$

where the constant a_0 is the metabolic cost of growth, which constitutes a certain amount of energy equivalent to a constant percentage of the growth (biomass production). Because the filtration rate (F) of a sponge can be estimated from the sponge dry weight (W) according to $F = a_1 W^{b_1}$, and the maintenance respiratory rate (R_m) can be estimated according to $R_m = a_2 W^{b_2}$, then if $b_1 \approx b_2$, the growth rate may now be expressed as:

$$G = (C \times AE \times a_1 - a_2) W^{b_1} / a_0 = aW^{b_1} \tag{3}$$

which seems to be an equation that would apply to sponges in general (and other marine filter-feeding invertebrates, see later). Thus, [24] found that $b_1 = 0.914$ and $b_2 = 0.927$ for *Halichondria panicea*, while [17] found that $b_1 \approx b_2 \approx 1$ for three tropical marine sponges (up to a size of 2.5 l sponge). Because the percentage of oxygen removed from the water pumped through the sponge is rather constant [17], this implies that b_2 tends to be similar to b_1 , as in a recent review of the volume-specific pumping rate of demosponges versus sponge volume (V) approximated by the power-law $F/V = a_3 V^{b_3}$ [25], where $b_3 = b_1 - 1$, assuming that dry weight was proportional to volume. By comparing the exponents reported by various authors, it appears that $b_1 \approx 1$ or $b_1 \geq 0.9$ [17,24,26–32], but in other cases, $b_1 < 0.9$ has been reported [21].

Therefore, if $b_1 \approx 1$ in Equation (3), the resulting model for weight-specific growth rate ($\mu = G/W = aW^{b_1}/W$) becomes:

$$\mu = a \tag{4}$$

which is a constant and thus the growth is exponential.

On the other hand, if $b_1 \approx b_2 \approx 0.9$, then $b = 0.9 - 1 = -0.1$, and the resulting model may be expressed as:

$$\mu = aW^{-0.1} \tag{5}$$

Here, using published growth data, we first test the prediction of Equation (4), which, with Equation (3), may be expressed as:

$$\mu = G/W = (C \times AE \times F - R) / a_0 \tag{6}$$

In the case of *Halichondria panicea*, the following numbers apply: F = volume specific filtration rate = 6.1 mL water (ml sponge)⁻¹ min⁻¹ [4], R = weight specific respiration rate = 7.93 μM O₂ h⁻¹ (g W)⁻¹ ([33] = (7.93 × 32/1000 × 0.7) = 0.178 mL O₂ h⁻¹ (g W)⁻¹, and $a_0 = 2.39$ since the cost of growth (SDA) is equivalent to 139% of the biomass production [24], where W henceforth denotes sponge dry weight. Furthermore, 1 mL sponge = 90.019 mg W [6], 1 mL O₂ = 0.46 mg C [34], and 1 mg W = 0.142 g C [24]. Assuming $AE = 0.8$ and inserting numbers in Equation (6), we find: $\mu(\text{d}^{-1}) = G/W = [(C \times (\mu\text{g C L}^{-1}) \times 0.8 \times 6.1 \times 60 \times 24/1000 \text{ (per mL sponge = 12.78 mg C)} - 0.178 \times 0.46 \times 24 \text{ (per g W = 0.142 g C)})] / 2.39 / 1000$, or:

$$\mu = a = [(C \times 0.55 - 13.8) / 2.39] / 1000 \tag{7}$$

From this, for $\mu = 0$, the maintenance food concentration is estimated at $C_m = (13.8/0.55 =) 25.1 \mu\text{g C L}^{-1}$. If the total sponge-available carbon biomass (TCB, i.e., free-living bacteria and phytoplankton with diameters smaller than the ostia diameter) is 5 times as large (i.e., $C = 125.5 \mu\text{g C L}^{-1}$), the predicted specific growth rate is estimated as $\mu = [(125.5 \times 0.55 - 13.8) / 2.39 = 23.11 \mu\text{g C d}^{-1} / 1000 \mu\text{g C}] = 0.023 \text{ d}^{-1} = 2.3\% \text{ d}^{-1}$, which may be compared with actually measured growth rates in the field as appears from the following examples. It should be mentioned that the influence of temperature, salinity, and spawning have not been addressed in Equation (7) and that $AE = 0.8$ will decrease if the ingestion exceeds the amount of food needed for maximum (biologically possible) growth.

3.2. Verification of Hypothesis: Growth Rates of Sponges in the Field

Example 1. The growth of *Halichondria panicea* was measured in the inlet to Kerteminde Fjord, Denmark, in a 104-d experiment conducted by [6]; see Figure 1. The exponential curve fit indicates a weight-specific growth rate of $\mu = 0.6\% d^{-1}$ (Figure 1), which may be compared to the algebraic mean $\mu = 0.62\% d^{-1}$ (Table A1), but the big scatter in calculated μ -values during the time of growth indicates no meaningful correlation between μ and sponge dry weight. The growth experiment was conducted in the period April–August, when the temperature was 20 °C at both the beginning and end of the experiment, with a peak of about 25 °C between June and July. The growth rate of 0.6% d^{-1} indicates, according to Equation (7), that the mean food availability (TCB) had been about 50 $\mu g C L^{-1}$, which may be compared to the mean TCB of about 90 $\mu g C L^{-1}$ measured in the ambient water during the sponge-growth period March–August [6].

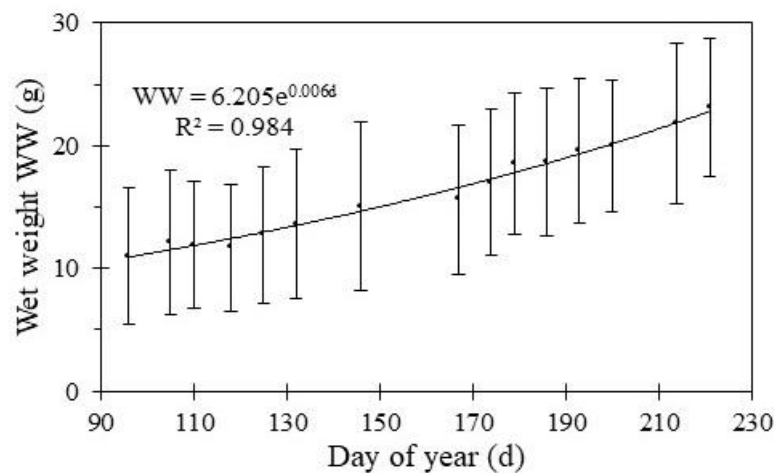


Figure 1. *Halichondria panicea*. Development of mean \pm SD wet weight as a function day of year. Exponential regression curve (LM, $t_{0.015, 13} = 9.3 \times 10^{-5}$, $p = 6.8 \times 10^{-13}$) shows a weight-specific growth rate of 0.6% d^{-1} . Data from [6].

Example 2. Growth of *Halichondria panicea* in the field at Kiel Bight was measured by [35,36]. Replotting the data of [35] for the period March–June of intense growth shows an approximately exponential growth $AFDW = 83.6 e^{0.007d}$ (Figure 2), which suggests an average specific growth rate of $\mu_{avg} \sim 0.7\% d^{-1}$. Calculated values of specific growth rate μ show a large scatter but the same value of an algebraic average growth rate. Temperature seemed to be the controlling factor for growth during this period, where it was recorded to increase from 1.8 to 13.8 °C (Table A2), but the concurrent increase in phytoplankton and bacteria biomass was not monitored. Therefore, both biological and physical effects might have contributed to the accelerated growth during the latter part of the period. Later, [36] presents data on biomass changes in a field study on populations of *H. panicea* at 3 different water depths of 6, 8, and 10 m. Replotting the data for the growth period up to the peak values in August shows growth in terms of sponge biomass (ashfree dry mass) $AFDM g m^{-2}$, with exponential growth constants being $\mu_{avg} = 1.0, 2.2$ and $0.6\% d^{-1}$, respectively (Figure 3). The temperature at 10 m depth was observed to increase from 1.4 to 16.1 °C during the period of growth from February to August of 1984.

Example 3. The growth in terms of body length of two Indo-Pacific sponges, *Neopetrosia sp.* and *Stylissa massa*, were measured by [37] from late November to March of 2003 for various farming conditions. While *S. massa* showed low or no growth, it was significant for *Neopetrosia sp.* for most treatments, reaching an exponential growth constant in terms of length L of specimens that we have derived from a replot of [37] to be $\mu_{L,avg} = 0.7\% d^{-1}$ (Figure 4). To estimate an equivalent exponent for this growth in terms of volume we use the data from [37] for initial (i) and end (e) values of length and volume of *Neopetrosia sp.* and assume the relation $V \sim L^n$. This leads to the value $n = \ln(V_e/V_i)/\ln(L_e/L_i) = \ln(48.3/10.8)/\ln(10.8/5.9) = 2.48$, and $\mu_{V,avg} = 2.48 \times 0.71 = 1.76\% d^{-1}$.

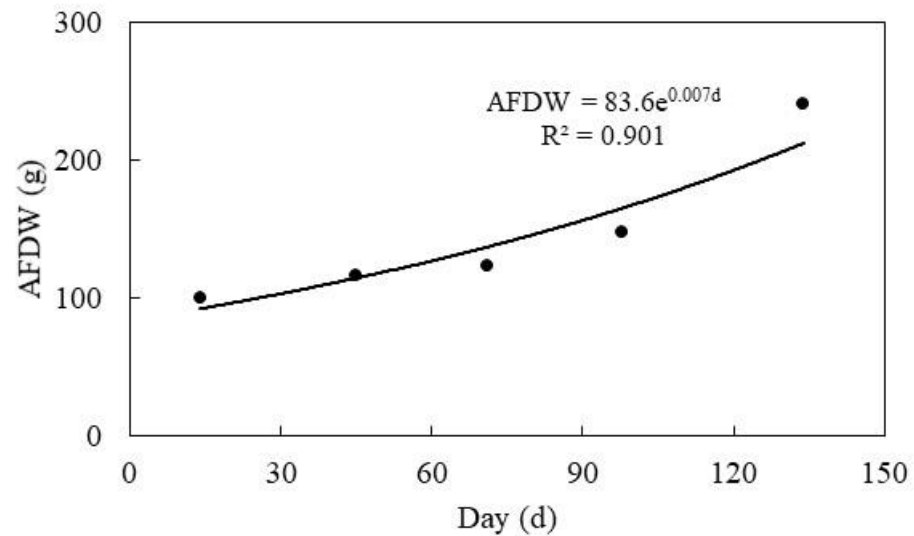


Figure 2. *Halichondria panicea*. Exponential regression curve (LM, $t_{0.045, 3} = 5.8 \times 10^{-4}$, $p = 0.014$) showing an approximately average growth rate of $0.7\% \text{ d}^{-1}$. Based on data from [35] shown in Table A2.

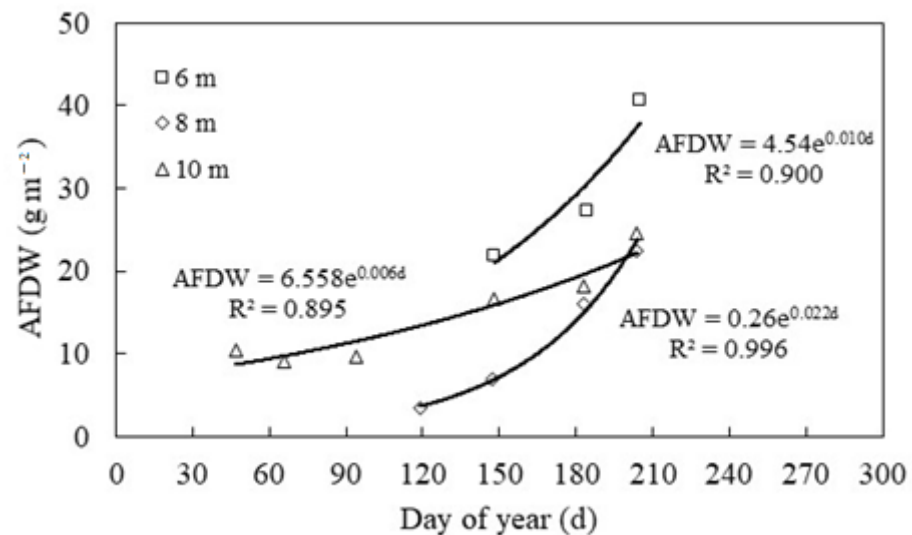


Figure 3. *Halichondria panicea*. Exponential regression curves at 3 water depths (6 m: LM, $t_{0.006, 1} = 1.5 \times 10^{-3}$, $p = 0.205$; 8 m: LM, $t_{0.030, 2} = 4.6 \times 10^{-4}$, $p = 0.002$; 10 m: LM, $t_{0.064, 4} = 4.5 \times 10^{-4}$, $p = 0.004$) showing approximate average growth rates of $\mu_{\text{avg}} = 1.0, 2.2$ and $0.6\% \text{ d}^{-1}$. Based on data from [36] shown in Table A3.

Example 4. The growth rate of the demosponge *Haliclona oculata* was studied in its natural environment, Oosterschelde, in the Netherlands, by [38] who assumed “exponential growth” and found that the maximum average ($\pm SD$) volume-specific growth rate for 11 monitored specimens was $1.18 \pm 0.35\% \text{ d}^{-1}$ in the beginning of May 2006.

From the above examples, it appears that sponge growth in the field is approximately exponential and that the weight-specific growth rate is constant, typically a few $\% \text{ d}^{-1}$ or less. In laboratory and field experiments conducted by [24] with *Halichondria panicea* the maximum measured growth rate was about $4\% \text{ d}^{-1}$, and [38,39] give data on wet weight-based exponential growth of the freshwater sponge *Spongilla lacustris*, indicating an exponent of $\mu_{\text{WW}} \sim 4.5\% \text{ d}^{-1}$ for dark aposymbiotic conditions. Thus, the maximum possible growth rate of sponges seems to be about $4\% \text{ d}^{-1}$ and in case of *H. panicea*

maximum growth may take place at about 8 times the TCB maintenance concentration of $C_m = 25.1 \mu\text{g C L}^{-1}$. At higher TCB concentrations, the $AE = 0.8$ in Equation (7) will decrease, and no further increase in growth can be expected. The specific growth rate linearly increases from C_m to C_{max} (see also Figure A1).

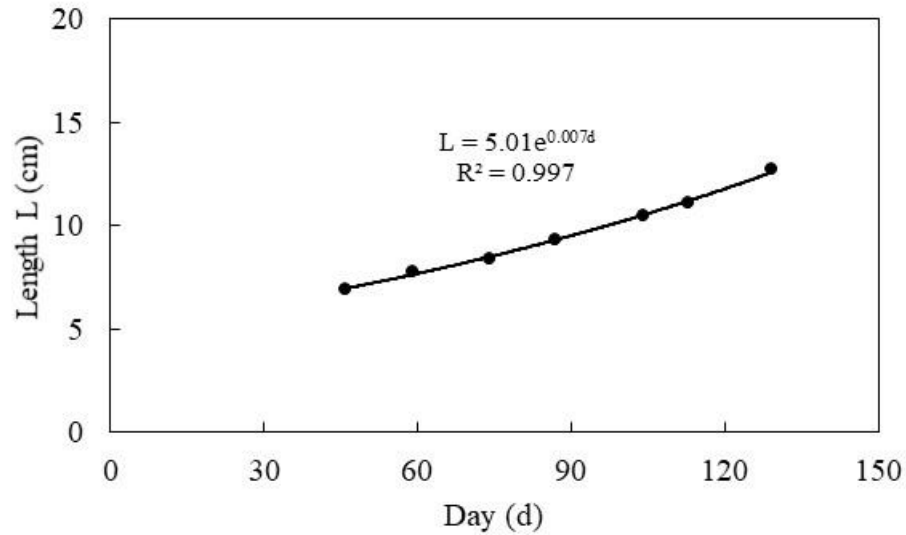


Figure 4. *Neopetrosia* sp. Exponential regression curve (LM, $t_{0.006, 5} = 7.9 \times 10^{-5}$, $p = 2.0 \times 10^{-7}$) confirming an essentially constant average growth rate of $0.7\% \text{ d}^{-1}$ in terms of specimen length L . Based on data from [37] shown in Table A4.

3.3. Evolutionary Adaptation

In the following 3 sections, we compare sponges to other filter-feeding invertebrates in order to compare the evolutionary adaptation of these animals to feeding on the same thin soup of bacteria and phytoplankton. In order to understand how sponges comply with the performance requirements for being a true filter-feeder, we first compare the F/R -ratio (amount of water filtered per ml of oxygen consumed). Next, based on data from the literature on the F/R -ratio in various sponge species, we estimate the oxygen-extraction efficiency to evaluate to what extent the respiration rate may be dependent on the filtration rate. Finally, we discuss how sponges, like other filter-feeders in temperate waters, cope with low phytoplankton concentrations during winter.

3.3.1. F/R -Ratio

The F/R -ratio (liters of water filtered per ml of oxygen respired) can be determined using the above given volume specific rates for *Halichondria panicea*, $F = [6.1 \times 60/1000 = 0.366 \text{ L h}^{-1} (\text{mL sponge})^{-1}$, or $= 0.366/90.019 = 4.07 \times 10^{-3} \text{ L h}^{-1}] (\text{mg dry weight sponge})^{-1}$ and $R = 0.178 \times 10^{-3} \text{ mL O}_2 \text{ h}^{-1} (\text{mg dry weight sponge})^{-1}$ as: $F/R = (4.07/0.178 = 22.9 \text{ L})$ water filtered per mL O_2 consumed. This F/R -ratio is well above the minimum reference value of $10 \text{ L water (mL O}_2)^{-1}$ for a true marine filter-feeding invertebrate [40], and to balance the sponge’s energy requirements, the particulate organic carbon (sponge-available phytoplankton and free-living bacteria) should be $>C_m = 25.1 \mu\text{g C L}^{-1}$. [30] shows the measured F/R -ratio in the demosponge *Callyspongia vaginalis* to be approximately $0.42 \pm 0.03 \text{ L water } (\mu\text{mol O}_2)^{-1}$, which converts to $F/R = (420 \text{ L}/22.4 \text{ mL O}_2) = 18.8 \text{ L water (mL O}_2)^{-1}$, thus comparing well with the above example of *H. panicea*. As mentioned earlier, [17] found that $b_1 \approx b_2 \approx 1$ for three tropical marine sponges, but an actual growth rate was not reported. However, the F/R -ratios were reported to be: *Mycale* sp. = $22.8 \text{ L water (mL O}_2)^{-1}$; *Tethya crypta* = $19.6 \text{ L water (mL O}_2)^{-1}$; and *Verongia gigantea* = $4.1 \text{ L water (mL O}_2)^{-1}$. The first two species comply with the performance requirement for being a true filter-feeder, whereas *V. gigantea* does not, because it “consists of a tripartite community: sponge-bacteria-polychaete” [17]. We think that the F/R -ratio is a reliable

check in support of $b \approx 0$ in *Mycale* sp. and *T. crypta*. [30] shows for 5 demosponges that the weight-specific oxygen consumption (R) versus weight-specific filtration rate (F) could be described as $R = a_4 F^{b_4}$ where $b_4 \approx 1$ (or 0.9416), which supports the idea that $b_1 \approx b_2 \approx 1$ in these sponges.

3.3.2. Oxygen Uptake and Extraction Efficiency

When the F/R -ratio is known, the oxygen extraction efficiency may be estimated as the reciprocal of the total amount of oxygen passing through the sponge per ml of oxygen taken up by the sponge. The following conversion factors may be used: 1 mg $O_2 = 0.7$ mL O_2 ; in fully oxygenated seawater there is 9 mg O_2 $L^{-1} = 6.3$ mL O_2 L^{-1} available, so for 22.9 L there would be $22.9 \times 6.3 = 144.3$ mL O_2 available. But the uptake was only 1 mL O_2 for 22.9 L water pumped according to the estimated F/R -ratio for *Halichondria panicea*. Therefore, the extraction efficiency in this case was $EE = 1/144.3 = 0.007$, or 0.7%. This is in agreement with [15], who found that the oxygen extraction efficiency is 1% or less in coastal filter feeders. Like in other filter-feeding animals such as mussels, the ventilatory currents are laminar in sponges, and oxygen in the water is only taken up by diffusion, which implies that only a small fraction of the oxygen in the water pumped through the sponge is available for respiration. In *Verongia gigantea*, where $F/R = 4.1$ L water (mL O_2) $^{-1}$ (see previous section), the extraction efficiency is calculated at $EE = (1 \text{ mL } O_2 / (4.1 \times 6.3) \text{ mL } O_2 = 3.9\%)$, which is 5 times higher than for *Mycale* sp., *Tethya crypta*, and the above example with *H. panicea*.

Reduced flow due to increased pressure losses in canal systems [25] or to closure of the osculum will result in low and high values of F/R and EE , respectively, as observed for example for *Verongia gigantea*. As shown for the filter-feeding blue mussel *Mytilus edulis* [15], the respiration rate in a sponge is probably independent of filtration rate above about 20% or less of the filtration rate capacity of a sponge because the extraction efficiency increases with a decreasing filtration rate. Like other filter-feeders, sponges also experience low phytoplankton concentrations in temperate waters in the northern hemisphere during winter [6]. The lower threshold of total available carbon concentrations (phytoplankton plus bacterial carbon) covering the maintenance cost of *H. panicea* is found here (Example 1) to be around 50 $\mu\text{g C L}^{-1}$. *M. edulis* copes with low phytoplankton content during winter by reducing its valve gape during starvation periods [41]. A study by [42] demonstrated that alternating closing-opening of valves causes a simultaneous strong decrease in oxygen concentration in the mantle cavity and thus a reduction of the respiration rate, and in this way *M. edulis* saves energy during starvation periods, a statement supported by a starvation experiment where the metabolic weight loss was reduced 12.3 times during 159 days of starvation [41]. It is well-known that the modular colonial *H. panicea*, with an osculum on each module, is able to close its oscula and thus reduce or stop the water-through flow [4,43,44], which may result in reduced respiration and eventually in internal anoxia [45], and, therefore, closing-opening of the oscula during starvation periods might theoretically be an energy-saving mechanism comparable to that found in *M. edulis*. However, our preliminary observations on *H. panicea* do not support the existence of such a mechanism.

3.3.3. Growth and Respiration

The specific respiration rate in response to growth (specific dynamic action, SDA) constitutes 139% of the biomass production in *Halichondria panicea* [24]. This percentage, used in the present growth model (see Equation (7)), makes up a very substantial proportion of the total energy released by respiration compared to other filter-feeding invertebrates, where the cost of growth is typically between 12 and 20% of the biomass production [46]. Due to their simple structure, sponges may be regarded as colonies composed of water-pumping choanocytes that are structurally and functionally near identical to free-living choanoflagellates in the sea [47]. In these organisms, with which choanocytes share properties, energy used for maintenance only constitutes a small fraction of the energy required for growth. Thus, a doubling of the specific growth rate of e.g., a flagellate protozoan may

result in a doubling of the specific respiration rate, indicating that the energy cost of growth (mainly macromolecular synthesis) is equivalent to that of the actual growth [46].

As for the maintenance respiration, the total respiration (R) as a function of body dry weight (W) is usually described by the power function $R = a_5 W^{b_5}$ where the b_5 -exponent is frequently close to 0.75. However, the “3/4 power scaling” is not a ‘natural constant’ because many exponents differ from $b_5 = 0.75$ [46]. Thus, $b_5 = 0.66$ in the blue mussel *Mytilus edulis* [48], $b_5 = 0.68$ in the ascidian *Ciona intestinalis* [49], $b_5 = 0.86$ in the jellyfish *Aurelia aurita* [50], $b_5 = 1.2$ in the facultative filter-feeding polychaete *Nereis diversicolor* [51], $b_5 = 0.93$ in the demosponge *Halichondria panicea* [24], and $b_5 = 1$ in three tropical sponges [17]. A bioenergetic growth model based on the energy budget and making use of near identical exponents in the power functions for filtration rate (F) and respiration rate (R) versus W (i.e. F or $R = a_2 W^{b_2}$) has earlier been developed for the blue mussel *Mytilus edulis*, where $b_1 \approx b_2 = 0.66$ and where it was found that actual growth rates in the field in general were in good agreement with the model and—as predicted—that the weight-specific growth rate decreased with body dry weight as $\mu = aW^{0.66-1} = aW^{-0.34}$ [22]. As a consequence, the weight specific growth rate of 7.8% d^{-1} for a 0.01 g dry weight *M. edulis* exposed to 3 μg chl $a L^{-1}$ gradually decreases to 1.6% d^{-1} for a 1 g mussel, thus showing that the growth is not exponential. The constant specific growth rate with increasing size and thus exponential growth in sponges (and some bryozoans, see later) is unique and does not exist in other filter-feeding invertebrates where $b_1 \approx b_2 < 1$.

Referring to the “general” model for metabolic scaling $R = aW^{0.75}$, the mass-specific metabolic scaling becomes $R/W = aW^{-0.25}$, which exponent $b = -0.25$ [20] is found (apparently suggesting that F/V follows R/W) to be “consistent with the measured exponent for three of five species” of sponges in which they had measured exponents for volume-specific filtration rate (F/V) versus sponge volume (V): $F/V = a_3 V^{b_3}$ and found $b_3 = -0.19, -0.20, -0.22, -0.49,$ and -0.70 for the five sponge species, respectively [20]. However, such comparison with a suggested “general” metabolic scaling is unwarranted, and the negative b_3 -exponents may need another explanation (see later).

The volume of a sponge is not always closely related to the living sponge biomass, which is evident from the seasonal variation in the sponge condition index $CI = \text{ratio of organic to inorganic matter} = AFDW/(DW - AFDW)$ [35,52]. Thus, a decreasing value of CI reflects a decreasing relative density of water-pumping choanocytes in a sponge, hence a lower pumping rate for a given sponge volume. So, if CI decreases while volume increases, this may explain the negative exponents for volume-specific filtration rate versus sponge volume in these sponges. Thus, it can be put forward as a hypothesis that spicules with decreasing CI form an increasing and major component of the volume in some sponge species, and thus a decreasing volume-specific filtration rate is associated with increasing size; see also [53]. In addition, or alternatively, the observed dependence of filtration rate on size of sponges “might primarily be governed by the hydraulics of pump and pressure losses of the aquiferous system” and not by, e.g., “a reducing density of choanocytes with increasing size”, as suggested by [25]; see next section. From the present study, it is obvious that sponges have many features in common with other filter-feeding invertebrates. Thus, the F/R -ratios and oxygen extraction efficiencies are comparable because all filter-feeding organisms have to cope with the same challenge of living in a thin soup of suspended microscopic food particles.

Sponges are modular organisms that consist of a set of repetitive modules. Likewise, filter-feeding bryozoans are colonial animals that consist of a set of repetitive zooids, which may also give rise to exponential growth, e.g., in *Celleporella hyalina*, *Electra pilosa* [54,55], *Cryptosula pallasiana*, and other bryozoan species [56]. Because the individual filtration rate and respiration rate of a module, or of a zooid, remain the same when a sponge or bryozoan colony grows, both the total filtration rate (F) and respiration rate (R) of the organisms increase linearly with the increasing number of modules/zooids (W), i.e., F and $R = a_2 W$, which implies exponential growth according to the bioenergetics growth model. However, in many bryozoan species the rate of asexual zooid replication increases

with colony size [57], and, therefore, the rate of growth in the number of zooids occurs in a different way, following power function. Exponential growth probably does not exist in non-modular and non-colonial filter-feeding invertebrates where the exponents in the equation for F and $R = a_2W^{b_2}$ are usually <1 and tend to be equal. In such cases where $b_2 < 1$, the growth follows a power function. Thus, for $b_2 = -0.34$ in the blue mussel *Mytilus edulis* the weight-specific growth rate as a function of W can be described by a power regression line in a log-log plot in which the slope has been found to be close to the predicted $b_2 = -0.34$ [21]. In the filter-feeding jellyfish *Aurelia aurita* it has been shown that $b_2 = -0.2$, which shows that the weight-specific growth rate is not constant but decreasing with size as reflected in systematic deviation between exponential regression curve fit for W versus time that underestimates W in the first half of the growth period while it overestimates it in the second period [58]. Thus, although growth versus time may be fitted approximately by an exponential curve a systematic deviation indicates that the specific growth rate is not constant. No such systematic deviations have been observed in the present study, which supports that the growth of sponges is exponential, as does the bioenergetic model and the application of the concept of modules.

An explanation for this may—as a theory—be derived from the high F/R -ratio and the low oxygen extraction efficiency in filter-feeding invertebrates. Because the proportion of biomass with low metabolism (e.g., lipid and glycogen store, gonads) may increase with body size, the weight-specific respiration (R/W) may concurrently decrease due to a negative exponent ($b_2 - 1$) in the equation $R/W = a_2W^{b_2-1}$. When the biomass of a filter-feeder increases, the total respiration consequently increases, but the oxygen demand should easily be met by an increase in the oxygen extraction efficiency. However, the animal must also increase the filtration rate, and thus the ingestion of food needed to cover the respiratory need to ensure that the F/R -ratio remains unchanged because a reduction in the F/R -ratio will cause starvation. Thus, the exponents in the equation for F and $R = a_2W^{b_2}$ may have (during the evolution) become near equal depending on species and adaptation to living site. Due to the simple structure of sponges, which have no organs or real tissue that may store energy reserves (such as fat, lipids, or glycogen) [6,35] to overcome starvation periods, the exponents for F and R versus W tend to be close to 1, as seen in those sponge species where both F and R have been measured, supported by growth experiments and model predictions presented in this study.

4. Conclusions

The power function exponents $b_1 \sim b_2 \sim 1$ for F and R versus W may probably apply to most demosponges, and therefore Equation (3) may be a general sponge equation. The resulting model for the weight-specific growth rate is a constant, and the growth is therefore exponential. This prediction is confirmed by actual field growth data for a group of sponges for which the F/R -ratios and oxygen extraction efficiencies are comparable to the values of other filter feeders. However, the constant specific growth rate with increasing size in sponges and some bryozoans is unique, and exponential growth probably does not exist in other filter-feeding invertebrates where $b_1 \approx b_2 < 1$, giving rise to a decreasing weight-specific growth rate with increasing body size.

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Appendix A

Table A1. *Halichondria panicea*. Development of sponge wet weight (WW), dry weight (W), average dry weight (W_{avg}) in time interval and weight-specific growth rate (μ) as a function of time (d) in growth experiment with sponge explants in the inlet to Kerteminde Fjord, Denmark. Data used for calculation of μ are from [6].

Time (d)	Day of Year	WW (g)	W (mg)	W_{avg} (mg)	μ (% d ⁻¹)
0	96	11.0	989		
9	105	12.2	1094	1040	
14	110	11.9	1073	1083	0.45
22	118	11.7	1052	1062	-0.39
29	125	12.7	1146	1098	0.41
36	132	13.6	1224	1184	1.08
50	146	15.0	1353	1287	1.19
71	167	15.6	1404	1378	0.49
78	174	17.0	1530	1466	0.29
83	179	18.6	1672	1599	1.25
90	186	18.7	1679	1675	0.93
97	193	19.5	1759	1719	0.36
104	200	20.0	1796	1777	0.48
118	214	21.8	1966	1879	0.79
125	221	23.1	2078	2021	0.52
Mean					0.62

Table A2. *Halichondria panicea*. Development of sponge biomass (AFDW) and temperature obtained by replotting data from [34] based on a field experiment at Boknis Eck, Western Baltic Sea, at 10 m and used here for calculation of the weight-specific growth rate (μ).

Time (d)	AFDW (g)	AFDW _{avg} (g)	μ (% d ⁻¹)	T (°C)
14	99.8			1.8
45	115.8	107.5	0.480	3.0
71	123.2	119.5	0.236	4.7
98	147.9	135.0	0.664	7.5
134	241.0	188.8	1.365	13.8
Average			0.69	7.26

Table A3. *Halichondria panicea*. Development of biomass (AFDW) in natural sponge populations at Boknis Eck, Western Baltic Sea, at 3 different water depths of 6, 8 and 10 m obtained by replotting data from [35]. Day zero = 1 January 1984.

6 m depth			
Day of 1984 (d)	AFDW (g m ⁻²)	AFDW _{avg} (g m ⁻²)	μ (% d ⁻¹)
148	21.9		
184	27.2	24.4	0.61
205	40.7	33.3	1.85
Average			1.23
8 m depth			
119	3.5		

Table A3. Cont.

147	6.9	4.95	2.41
183	16.0	10.54	2.34
204	22.5	18.99	1.58
		Average	2.11
10 m depth			
47	10.4	4.32	2.54
66	9.1	9.71	0.20
94	9.6	9.31	
148	16.6	12.59	1.03
183	18.2	17.35	0.27
204	24.5	21.13	1.41
		Average	1.09

Table A4. *Neopetrosia* sp. Growth data in terms of specimen length obtained by replotting data from [36].

Time	Length	L_{avg}	μ_L
(d)	(cm)	(cm)	(% d ⁻¹)
46	6.9		
59	7.8	7.32	0.86
74	8.4	8.07	0.51
87	9.3	8.83	0.78
104	10.5	9.89	0.75
113	11.1	10.81	0.58
129	12.7	11.86	0.84
		Average	0.72

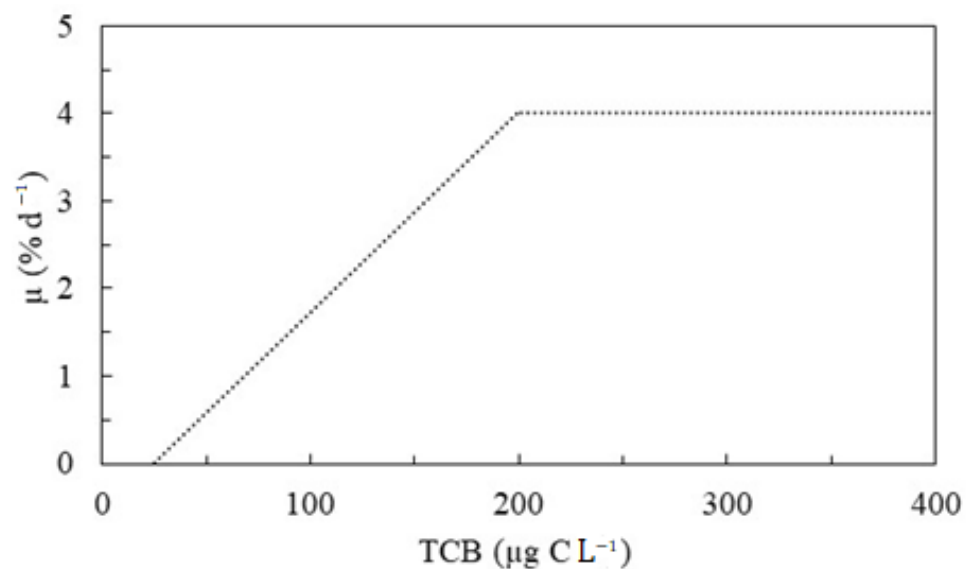


Figure A1. *Halichondria panicea*. Estimated weight-specific growth rate as a function of TCB (total sponge-available carbon biomass) according to Equation (7) and suggested maximum possible growth rate $\mu = 4\% \text{ d}^{-1}$ at $C_{max} = 200 \mu\text{g C L}^{-1} = 8 \times C_m$ (maintenance TCB). The increase in specific growth rate is linear between C_m and C_{max} .

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