



Size-Specific Growth of Filter-Feeding Marine Invertebrates

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Abstract: Filter-feeding invertebrates are found in almost all of the animal classes that are represented in the sea, where they are the necessary links between suspended food particles (phytoplankton and free-living bacteria) and the higher trophic levels in the food chains. Their common challenge is to grow on the dilute concentrations of food particles. In this review, we consider examples of sponges, jellyfish, bryozoans, polychaetes, copepods, bivalves, and ascideans. We examine their growth with the aid of a simple bioenergetic growth model for size-specific growth, i.e., in terms of dry weight (W), $\mu = (1/W) dW/dt = aW^{b}$, which is based on the power functions for rates of filtration ($F \approx W^{b1}$) and respiration ($R \approx W^{b2}$). Our theory is that the exponents have (during the evolution) become near equal ($b_1 \approx b_2$), depending on the species, the stage of ontogeny, and their adaptation to the living site. Much of the compiled data support this theory and show that the size-specific rate of growth (excluding spawning and the terminal phase) may be constant (b = 0) or decreasing with size (b < 0). This corresponds to the growth rate that is exponential or a power function of time; however, with no general trend to follow a suggested 3/4 law of growth. Many features are common to filter-feeding invertebrates, but modularity applies only to bryozoans and sponges, implying exponential growth, which is probably a rather unique feature among the herein examined filter feeders, although the growth may be near exponential in the early ontogenetic stages of mussels, for example.

Keywords: filtration; respiration; bioenergetic growth model; exponential growth; power function growth

1. Introduction and Growth Model

Filter-feeding (or suspension-feeding) marine invertebrates are important animals in the food chains of the sea [1,2]. They trap food particles, such as phytoplankton and bacteria, from a feeding current that is created by their own pumping device or by the ambient, and the mechanisms that are used in order to capture and transport the particles to be ingested reflect various secondary adaptations to filter feeding among species [3]. The rate of growth of individuals is of interest in estimating the population grazing impact at a particular site, hence its ecological significance. However, the growth rates may also be of commercial interest, e.g., in mussel farming [4].

Here, we focus on the somatic growth of filter-feeding marine invertebrates under favorable conditions and exclude the release of biomass that is associated with spawning and terminal growth. We consider sponges (*Halichondria panicea*), jellyfish (*Aurelia aurita*), bryozoans (*Electra pilosa* and *Celleporella hyalina*), polychaetes (*Nereis diversicolor* and *Sabella spallanzanii*), crustaceans (calanoid copepods), bivalves (*Mytilus edulis*), and ascideans (*Ciona intestinalis*). Among these, only *N. diversicolor* is a facultative filter feeder that may switch to surface deposit feeding or scavenging.

Filter feeding in all marine invertebrates is a secondary adaptation. The blue mussel, *Mytilus edulis*, is a well-known example where the gills have become the water-pumping and particle-capturing organ, while the original function as gills has become superfluous [1,5]. In crustaceans, the secondary adaptation to filter feeding has evolved independently in many groups, and often filter feeding is only one of several feeding methods



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). that are adopted by one species. A common feature is that the filter-feeding process is true sieving, where the mesh size of the filter determines the size of the captured food particles [6]. However, a secondary adaptation to filter feeding must have involved the development of a filter pump that can cover the need for food energy in order to cover the respiration requirements. When the respiration (*R*) increases with increasing body mass, the filtration (*F*) must necessarily follow and, therefore, our theory is that the exponents in the equation $F = a_1 W^{b_1}$ and $R = a_2 W^{b_2}$ have (during their evolution) become near equal ($b_1 \approx b_2$), depending on the species, the stage of ontogeny, and their adaptation to the living site.

Here, *Mytilus edulis* is a good example as $b_1 \approx 1$ in very small juvenile mussels but decreases to $b_1 = 0.66$ in larger mussels [7]. This makes the bioenergetic growth model [8,9] particularly simple, expressing the growth rate as $G = aW^{b1}$ and the weight-specific growth rate as follows:

$$\mu \equiv (1/W) \, \mathrm{d}W/\mathrm{d}t = aW^{b}; b = b_1 - 1, \tag{1}$$

where the coefficient $a = (C \times AE \times a_1 - a_2)/a_0$ depends on the food concentration (*C*), the assimilation efficiency (*AE*), and the cost of growth (R_g/G), i.e., the metabolic cost of synthesizing new biomass, being the equivalent fraction of $a_0 - 1$ of the growth itself. Because the proportion of the biomass with a low metabolism (e.g., lipid and glycogen store, gonads) may increase with the body size, the weight-specific respiration may concurrently decrease due to a negative exponent ($b = b_1 - 1$).

Depending on the species that is investigated, the growth parameter of the dry body weight (W) could be the tissue volume (V) (sponges), the area (A) or number (N) of zooids in an encrusting colony (bryozoans), or a characteristic length (ascidians). Furthermore, it is of interest to note that the growth function W(t) may take two specific forms that are simply related to the specific growth rate, i.e., exponential growth, as follows:

$$W(t) \sim \exp(at), \ \mu = a, \tag{2}$$

and power function growth as follows:

$$W(t) \sim t^{d}, \mu \sim W^{-1/d}.$$
 (3)

If $b_1 \approx b_2 \approx 1$, hence b = 0 in a filter-feeding animal, then $\mu = a$, and the growth is exponential, but otherwise the weight-specific growth rate will decrease with increasing body size.

The present theory of near-equal *b*-exponents forms the underlying basis of this review, where we consider examples of filter-feeding invertebrates and examine if their growth functions are exponential or power functions of time. The *b*-exponents of rates of filtration and respiration that have been found for the examined filter feeders are compiled in Table 1, from which it appears that, in many cases, $b_1 \approx b_2$ in support of the theory, and the typical growth rates are listed in Table 2.

Filter Feeder	b	1	b	2
Sponges Halichondria panicea, small	~2/3	[10]	~2/3	[10]
Halichondria panicea, large	~1.0	[11]	~1.0	[11]
Jellyfish Aurelia aurita	0.78	[12]	0.86	[13]
Bryozoans Electra pilosa				
Polychaetes Nereis diversicolor	1.0	[14]	1.2	[15]
Crustaceans calanoid copepods	0.84	[16]	0.78	[16]
Bivalves <i>Mytilus edulis</i> , W < 10 mg	0.887	[7]	1.03	[7]
<i>Mytilus edulis,</i> W > 10 mg	0.663	[7]	0.66	[7]
Ascidians Ciona intestinalis	0.68	[17]	0.831	[18]

Table 1. *b*-exponents of rates of filtration b_1 (in $F = a_1 W^{b_1}$) and respiration b_2 (in $R = a_2 W^{b_2}$) of some filter-feeding invertebrates. *Halichondria panicea*, "small" = single osculum sponge explant; "large" = multi-oscula sponge.

Table 2. Specific growth rates of some filter-feeding marine invertebrates. Growth is measured as the change in size of the following: (W) = dry weight, (A) = colony area, (N) = number of zooids, (L) = body length. Cost of growth = R_g/G .

Specimen	μ (% d ⁻¹)		Comment	Cost of C	Cost of Growth	
Sponges Halichondria panicea	0.6 to 1.18 (W)	[11,19]	$\max = 4\% d^{-1}$ [11]	1.39	[11]	
Jellyfish Aurelia aurita	24.4 (W) to 6.28 (W)	[20,21]	2.2 mg to 115–1887 mg	0.2	[19]	
Bryozoans Electra pilosa	9 (A), 11 (N)	[22]				
Celleporella hyalina	10 (A), 12 (N)	[22]				
5 cheilostome species	12 (N) to 4 (N)	[23]	100 to 600 zooids			
Polychaetes Nereis diversicolor	3.1 to 3.9 (W)	[24]	fed on algea	0.08	[15]	
Nereis diversicolor	7 (W)	[15]	fed on scrimp meat	0.26	[15]	
Sabella spallanzanii	0.74~1 (W)	[25]				
Crustaceans calanoid copepods	4 to 135 (W)	[26]	$L = 50 \text{ to } 80 \ \mu \text{m}$			
Bivalves Mytilus edulis	7.8 to 1.6 (W)	[19]	W = 0.01 g to 1 g	0.12	[19]	
Ascidians Ciona intestinalis	1.4 to 3 (L), 7.7 (W)	[27,28]		0.21 - 0.23	[27]	

2. Sponges

Sponges are one of the earliest evolved and simplest groups of animals [29]. They are multicellular filter feeders that actively pump volumes of water, which are equivalent to about six times their body volume per minute, through their canal system by means of flagellated choanocytes that are arranged in choanocyte chambers. They feed on free-living bacteria that are trapped on the array of microvilli of the collars of their choanocytes, and on larger phytoplankton cells that are drawn into the inhalant canal system, where they are captured and phagocytosed [30–35]. The water enters the sponge body through numerous small inhalant openings (ostia) and passes through incurrent canals, the choanocyte chambers, and through excurrent canals to be expelled as a jet through an exhalant opening (osculum). The water flow also ensures a supply of oxygen for respiration via diffusive oxygen uptake [36].

The experimental results that were summarized in [19] for the demosponge *Hali-chondria panicea* show the exponential growth at rates of $\mu = 0.6\%$ to 1.18% d⁻¹, and the maintenance food concentration (at no growth) was estimated for a given specimen to be $C_m = 25.1 \ \mu g \ C \ L^{-1}$. The highest reported growth rate of *H. panicea* of 4% d⁻¹ [11] corresponds to an available total carbon biomass (TCB) of $C = 8 \ C_m$, i.e., eight times that of the maintenance food concentration. The growth rate may thus be expected to increase linearly with *C* to a maximal value that is not exceeded, irrespective of how high *C* becomes.

In fair agreement with the observed exponential growth of *Halichondria panicea*, [11] found that exponents of the power functions of the filtration and respiration rates were $b_1 = 0.914$ and $b_2 = 0.927$, while [37] found that $b_1 \approx b_2 \approx 1$ for three larger tropical marine sponges. It is, therefore, of interest to see how the filtration rates of sponges depend on their size, which was summarized in [38] and approximated by the power function

 $F/V = a_3 V^{b3}$, because this implies that $b_3 = b_1 - 1 = b$ of Equation (1), assuming that the dry weight was proportional to the volume (*V*). Many values of the exponents b_3 , which have been reported by various authors that were cited in [38], suggest that $b \approx 0$, implying exponential growth. However, in other cases, b < -0.2, and as low as -0.7, implying power function growth, which, however, is subject to the uncertainty of the assumption $V \sim W$ for larger sponges.

Related to these considerations of volume-specific filtration rate is a recent discussion of its possible scaling to the size of demosponges. Here, according to [10], demosponges are modular filter feeders where the early stages of single-osculum aquiferous modules have volume-specific pumping rates that scale as $F/V = a_3 V^{b3}$, $b_3 \approx -1/3$ (hence $b_2 = 1 + b_3 = 2/3$, Table 1), as measured for small explants of *Halichondria panicea* [39,40]. Such modules only grow to a certain size [41,42], such that new modules will be formed for a growing sponge. Larger multi-oscular sponges consist mainly of single-oscular modules that have reached their maximal size, hence $b_3 \approx 0$, as noted for some species that were mentioned in [38]. A similar situation may be expected for large pseudo-oscular sponges (e.g., *Xestospongia muta* [43,44]), provided that the volumes were taken to be that of structural tissue and not the total volume that includes the large atrium volume of water. In summary, these considerations and $b_1 \approx b_2$ suggest that $b \approx -1/3$ for growing single-osculum demosponges and $b \approx 0$ for multi-oscula sponges, according to Equation (1).

3. Jellyfish

Medusae of the common jellyfish *Aurelia aurita* are voracious predators that filter feed on zooplankton. They occur in many coastal ecosystems where they can be very abundant and so exert a considerable predation impact on the zooplankton; thus, they play an important role as a key organism in the ecosystem [45]. The predation impact can be evaluated when the population density and the individual clearance rate of the jellyfish are known. The weight-specific growth rate μ can be determined from the time interval collection, measuring their umbrella diameters, and converting that to dry weight.

Controlled laboratory experiments have used brine shrimp *Artemia* sp. as prey, for which the retention efficiency (60%) [46] is much higher and well defined than for natural prey, such as copepods, probably due to a lack of escape behavior. A study [20] found a typical growth rate of $\mu = 10\%$ d⁻¹ and the exponent b = -0.2 in Equation (1) for fully fed larger specimens (W = 154 mg, d = 56.9 mm umbrella diameter) with a diet of five *Artemia* L⁻¹. A value of b = -0.2 is in fair agreement with the values $b_1 = 0.78$ and $b_2 = 0.86$, which were determined earlier [12,13]. For smaller specimens (W = 2.2 mg, d = 12.7 mm), the growth rate was $\mu = 24.4\%$ d⁻¹, which was in good agreement with the growth model of Equation (1) for b = -0.2. Similar experiments [21] showed b = -0.24 and a mean growth rate of $\mu = 6.28\%$ d⁻¹ over a size range of 115 to 1887 mg. According to the growth model of Equation (1), μ increases from zero (at the maintenance concentration, 1.23 *Artemia* L⁻¹) linearly with the prey concentration, but only to a maximal value (at about five times that of the maintenance concentration), above which there is no further increase, and such maximal values depend on the size, see [45].

The growth rates from the field data, as indicated by the values of b = -0.43 to -0.84, which are summarized in [45], decrease much more with increasing size than those from the laboratory, which were close to the suggested theoretical value of b < -0.2. This difference can be explained by the lower retention efficiency and the fluctuating prey concentrations.

4. Bryozoans

Bryozoans are sessile, colonial filter feeders that mainly feed on phytoplankton that are drawn in with the flow into the tentacle crown (lophophore) by the cilia on the tentacles, which act as pumps and help to retain and transfer the prey to the mouth. In encrusting bryozoans, the filtered water flows under the lophophore canopy in order to escape at the edges of the colony or as jets from 'chimneys' inside of the colony, which, as a biomixing process, may help to prevent re-filtration. Encrusting bryozoans may form colonies of essentially identical zooids, which have the same filtration rates, and hence may be considered to be modules of an 'organism', the colony [19]. The growth occurs by adding zooid modules along the periphery and may be measured by the increase with time of the area (*A*) or the number (*N*) of zooids in the colony. By denoting the area of one zooid as A_z , the relation for incremental growth may be written as $dA = A_z dN$. If A_z remains constant during the growth, the specific growth rates - μ_A and μ_N would be equal, but if A_z decreased with growth, we expect $\mu_A < \mu_N$.

The growth rates of colonies of *Electra pilosa* and *Celleporella hyalina* that were placed on microscope slides in both field and laboratory tests were measured in [22]. For the laboratory tests at an algal concentration of about 5000 *Rhodomonas* cells mL⁻¹, representing well-fed conditions, the growth was found to be exponential, with specific growth rates for *E. pilosa* being $\mu_A = 0.09 \pm 0.02 d^{-1}$ and $\mu_N = 0.11 \pm 0.02 d^{-1}$, and for *C. hyaline* being $\mu_A = 0.10 \pm 0.01 d^{-1}$ and $\mu_N = 0.12 \pm 0.01 d^{-1}$. From the ratio of number-to-area, the density was in the range of five to eight zooids per mm². The higher growth rate, which was based on the number of zooids, implies an increasing density of zooids with increasing colony size. The field data for *C. hyaline* (genotype H) showed similar exponential growth rates but had slightly smaller specific growth rates, which was likely due to the larger zooid size and the lower algal concentration (<1500 cells mL⁻¹). The absence of the influence of the current velocity was ascribed to the fact that the thin layer of encrusting bryozoans is well within the low velocity viscous sublayer.

Among the 23 laboratory and field data sets for different species [22] the average specific growth rates were $\mu_A \sim 0.09$ to 0.14 d^{-1} , while some lower and higher values could be caused by high algal concentrations (> 5000 cells mL⁻¹). The low values (0.06–0.08 d⁻¹) were observed for the natural colonies that were feeding on macroalgae. This study gives the orders of magnitude of specific growth rates and indicates the growth rate to be exponential.

Ref. [23] analyzed the datasets from [47] for the growth rate of five fouling marine cheilostome colony species and found the growth rate to follow power functions ($N = a_{\rm D} t^{\rm d}$), with exponent $d = 2.266 \pm 0.214 \text{ d}^{-1}$ as the average of 10 groups. Apparently, the rate of asexual zooid replication increases with the colony size in many bryozoan species, hence the switch from exponential growth to power function growth. Thus, according to Equation (3), the number-specific growth rate ($\mu_N = (1/N) dN/dt = d a_p^{1/d} N^{-1/d}$) decreases with increasing colony size as $\mu_N \sim N^{-0.44}$, according to the data for July to August of [23] from $\mu_N = 0.12 \text{ d}^{-1}$ at N = 100 zooids to $\mu_N = 0.041 \text{ d}^{-1}$ at N = 600 zooids. Interestingly, the first value of the specific growth rate is close to that observed in [22] for a growth up to a size of about 100 zooids, however, it became smaller in the larger colonies. This trend is similar to that observed for the blue mussel and may be ascribed to a change in the composition of the biomass. Although it is not supported by explicit data, it is possible that the rates of both filtration and respiration may be proportional to the number of zooids in a smaller growing colony of modules of developed zooids, which would imply $b_1 = b_2 \approx 1$, hence b = 0 in the bioenergetics model of Equation (1), implying exponential growth, as found in [22]. However, for the larger colonies, the growth follows a power function, as found in [23].

5. Polychaetes

The facultative filter-feeding polychaete *Nereis diversicolor* can feed by pumping water through a mucus net-bag that is attached to the entrance of its U-shaped burrow in the sediment. The retained food particles in the net are then ingested with the rolled-up net. Switching from surface deposit feeding to filter feeding in *N. diversicolor* is an adaptation that is useful for the near-bottom dweller in shallow waters, where the concentration of suspended food particles varies widely. Filter feeding, in place of surface deposit feeding or scavenging/predation, is preferred when there is a sufficient concentration of suspended algal cells; however, the full growth potential of the polychaete is not always achieved near to the bottom due to food depletion in the absence of efficient vertical mixing. Field growth studies [24] were therefore carried out with the worms placed in glass tubes at 15 cm above the bottom. This showed the weight-specific growth rates increasing to $\mu = 3.9\%$ d⁻¹ for an increasing concentration of Chl *a* of available algal cells, which is comparable to the results from the laboratory studies showing $\mu = 3.1\%$ d⁻¹, and the cost of growth was estimated to be only 8% of the total growth. Later laboratory studies [15] showed a growth rate of $\mu = 3.0\%$ d⁻¹ for a *Rhodomonas* algal diet but $\mu = 7\%$ d⁻¹ for a shrimp meat diet, and in both cases the weight-specific respiration (*R*/*W*) increased linearly with the specific-growth rate μ . This increase, which is also called 'specific dynamic action', indicated an energy cost of growth that was equivalent to 26% of the total growth, which is similar to some of the other filter feeders that are shown in Table 2. These studies show the effect of the nutritional value of the diet, from algae to shrimp meat, apparently raising both the weight-specific growth by the same factor of approximately two.

The obligate filter-feeding polychaete *Sabella spallanzanii* lives in a tube from which it extends its feeding organ that consists of a filament crown with closely spaced pinnules whose rows of compound latero-frontal cilia pump the water through the space between the pinnules and retain the food particles. It lives in patches and [25] recorded a density of 150 ind. m⁻² and observed the growth in terms of the mean length of the tubes from L = 10 to 18 cm during the period from April to August of 1992, implying a mean length-specific growth rate of $\mu_L = 100 \times \ln(18/10)/120 = 0.49\% d^{-1}$. They also reported an increase in the biomass (that we assume is proportional to the dry mass of the animals) from 60 g m⁻² to 75 g m⁻² for one month, which may be interpreted as a mean weight-specific growth rate over that period of $\mu = (1/W) dW/dt = 100 \times \ln(75/60)/30 = 0.74\% d^{-1}$. The relationship between these specific growth rates agrees with the relationship between the biomass *W*(g) and the total worm length *L*(cm) that is given approximately as $W = 0.0021 L^2 - 0.0098 L$, which is derived from [25].

6. Copepods

Raptorial feeding is probably primary in copepods, whereas filter feeding is a specialized condition that has been developed within the order of calanoid copepods. For example, the calanoid copepod *Acartia tonsa* uses ambush feeding when it slowly sinks through the water with extended antennae that perceive motile prey, or it uses filter feeding by generating a feeding current with which phytoplankton cells are captured by a filter that is formed by setae on its appendages. Copepods need to consume a large number of phytoplankton per day in order to cover their nutritional needs. They are characterized by a relatively fast growth rate [48] and page 428 of [6].

The growth rates of three calanoid copepods were determined in [49]. The growth rates were low, particularly during the summer. The specific growth rates of the copepodites were moderately high for *Eurytemora affinis* in the spring as follows: 23% and 15% d⁻¹ for the early and late stages, respectively, and were low for *Pseudodiaptomus forbesi* in the summer as follows: 15% and 3% d⁻¹, respectively (not shown in Table 2).

Small copepods grow fast at high temperatures accompanied with an ample food supply, as shown in [26], which is a study from the East China Sea. Thus, the weight-specific growth rates ranged from 4% to 135% d⁻¹ in the 50 to 80 µm size fraction, and from 1% to 79% d⁻¹ in the 100 to 150 µm size fraction, showing that the growth rates were positively related to the temperature and were negatively related to the body size. The strong size dependence could imply a power function growth with a small negative *b*-value, as indicated by the exponent *b* of Equation (1), increasing from b = -0.88 to b = -0.32 for the two size fractions [26]. However, according to Table 1 of [16] for calanoid copepods, the exponents of the power functions of weight-specific rates of clearance and respiration take the following values: $b_1 = -0.16 + 1.0 = 0.84$, $b_2 = -0.22 + 1.0 = 0.78$, or $b_1 \approx b_2 \approx 0.8$, hence b = -0.2 for the weight-specific growth rate of Equation (1). The value of b = -0.2 may be compared with the somewhat higher value b = -0.06 in Table 1 of [16], both of which seem to suggest power-function growth.

7. Bivalves

Most filter-feeding bivalve species have flat gills and employ essentially the same feeding mechanism. There is a wide diversity of gill types, and two different principles are used for food capture, depending on the presence or absence of latero-frontal cirri (see reviews [3,50]). We can direct attention to the blue mussel, *Mytilus edulis*, because it is the most abundant and most studied, which is partly because of its role in commercial aqua farming. The pump that draws in the water through an inhalant mantel opening into the mantel cavity, through W-shaped gills, and discharges it through an exhalant siphon as a jet, is the lateral cilia on the sides of the gill filaments. The separation of the food particles from the pumped current and their retention is handled by the latero-frontal cirri, ensuring a near 100% retention of particles above about 4 μ m in size, which includes most phytoplankton. Filter feeding is a secondary adaptation where the gills have become greatly enlarged—far more than what is needed for respiration—which may be suggested to be 'evolutionary adapted' to the prevailing (often low) level of phytoplankton in the surrounding water [5].

The growth rates may change with the increasing size of the specimens. For *Mytilus edulis*, there is a shift at a dry weight of around W = 10 mg, corresponding to the shell length L = 10 mm, moving from the smaller post-metamorphic mussels of near-exponential growth to the larger juvenile specimens of power function growth. This is reflected by the following values of exponents for the rates of filtration and respiration, which are summarized in [51]: W < 10 mg: $b_1 = 1.03$ and $b_2 = 0.887$, or $b_1 \approx b_2 \approx 0.9$ and W > 10 mg: $b_1 \approx b_2 \approx 0.66$ (see Table 1).

In order to appreciate the influence of the food concentration on the weight-specific growth rate, Equation (1), with appropriate numerical coefficients (see [9]), takes the following form:

$$\mu \equiv (0.871 \times C - 0.986) W^{-0.34}; W > 0.01 \text{ g}, \tag{4}$$

where units are μ (% d⁻¹), *C* (µg Chl *a* L⁻¹), and *W*(g). The measured growth rates in the field at *C* = 2.8 µg to 3.6 µg Chl *a* L⁻¹ [4] are in good agreement with Equation (4), which also shows that starvation should occur at *C* ≤ 0.986/0.871 = 1.13 µg Chl *a* L⁻¹, while saturation has been found to occur at *C* ≈ 8 µg Chl *a* L⁻¹ [52]. For a typical value of *C* ≈ 3 µg Chl *a* L⁻¹, the growth rate decreases as μ = 7.8% to 1.6% d⁻¹ for a dry weight increase of *W* = 0.01 to 1.0 g.

The growth rates, in terms of the shell length, may be obtained from Equation (4) by the use of the allometric relation $W(\mu g) = 2.15 L(mm)^{3.40}$, which shows that W = 0.01 g to 1.0 g corresponds to L = 12 mm to 46 mm. Furthermore, Equation (1) may be integrated in time in order to show the time that it takes to grow a mussel of a certain size. Finally, the bioenergetic model of Equation (1) has been extended to include the effects of low temperature and low food concentration [53].

8. Ascidians

The benthic ascidian *Ciona intestinalis* may often exert a significant grazing impact because of its dense populations in shallow waters. It retains food particles, including free-living bacteria of $< 2 \mu m$, on its mucous net with 80% to 100% efficiency [54]. It is characterized by rapid growth, early maturation, and a high reproductive output.

The rate of oxygen consumption was found in [18] to be dependent on the dry weight to the power $b_2 = 0.831$, which would suggest power function growth according the bioenergetic model for $b_1 \approx b_2$ as $\mu \sim W^{-0.17}$. It is important to note, however, the lower value of $b_1 = 0.68$ in Table 1. However, growth can be exponential until it reaches a body length of 10 mm [55], which could suggest a switch from $\mu \sim \text{constant}$ for smaller specimens to a decreasing μ for large specimens.

The growth, in terms of length, has been reported to be 10 mm to 20 mm per month [56], 0.26 mm to 0.76 mm in diameter in seven days [57], or $0.7\% d^{-1}$, increasing to a maximum of 1.4% to 3% d⁻¹ [27]. The weight-specific growth rate increases with increasing temperature and algal concentration to about 7.7% d⁻¹ [17,56], and it appears that a condition index, which is defined as the ratio of the dry weight of the soft parts to the total dry weight, is a

good indicator of growth as it increases linearly with the weight-specific growth rate up to $8\% d^{-1}$ [27,28].

9. Adaptation to Filter Feeding

The present theory of near-equal *b*-exponents of filtration and respiration laws, which forms the underlying basis of the present review, is supported by the examples of filter-feeding invertebrates that are compiled in Table 1, from which it appears that $b_1 \approx b_2$. Furthermore, Figures 1A and 2A of [16] confirm this theory by showing that, for a large number of marine pelagic animals, $b_1 \approx b_2 \approx 1$ on the average, but with considerable scatter, and perhaps not $b_1 \approx b_2 \approx 3/4$, as was suggested by the authors. For a specific animal, however, the values of the exponents often take values that are different from 1 and 3/4, as seen from Table 1 of [16] and Table 1 herein, which suggests that there may not be a universal 3/4-law.

All obligate filter-feeding invertebrates (apart from predatory jellyfish) face the same challenge of growing on a thin soup of bacteria and phytoplankton. This fact suggests the existence of some common traits among these animals, which have been identified in [19], as at least the following two features: the magnitude of the filtration–respiration ratio (F/R) and the oxygen extraction efficiency (EE).

One interpretation of the F/R ratio is its relation to food uptake. Here, the estimated F/R = 22.9 L of water per mL of O₂ consumed by a specimen of the demosponge Halichondria *panicea* [19] is well above the minimum value of $F/R_{\rm m} = 10$ L of water (mL O₂)⁻¹ [58] for a true filter feeder. Here, $F/R_m = 10$, being the maintenance value = $20/(0.8 \times 2.5)$, 20 J, i.e., the metabolic equivalent of 1 mL of O₂ and filtering water with a phytoplankton concentration of 1.5 μ g Chl *a* L⁻¹ (= 2.5 J L⁻¹) with 100% retention and an 80% assimilation efficiency. The minimum value of $F/R_{\rm m} = 10$ L water (mL O₂)⁻¹ was based on a phytoplankton concentration of 1.5 µg Chl a L⁻¹ (= 1.5 × 40) = 60 µg C L⁻¹. However, sponges also feed on free-living heterotrophic bacteria, cyanobacteria, and other small $(0.2-2 \mu m)$ picoplankton, as shown in [59], which measured F/R = 22.9 L of water per mL of O₂ for *H. panicea*, which appears to agree with the reported carbon concentrations of 40 μ g to 200 μ g C L⁻¹. Other values for demosponges, which were cited in [19], include 22.8 for Mycale sp. and 19.6 for *Tethya crypte,* which are of a similar magnitude. However, the much smaller value of 4.1 for Verongia gigante signifies a species that is not a true filter feeder, because it "consists of a tripartite community: sponge-bacteria-polychaete" [37]. [58] shows the F/R > 10 L of water per mL of O_2 values for most of the species that are mentioned of the following taxonomic groups: sponges, bryozoans, copepods, polychaetes, bivalves, ascidians, and lancelets. Thus, the F/R ratio is an indicator of the ability of a filter-feeding invertebrate to survive on a pure diet of phytoplankton of 1.5 Chl $a L^{-1}$. Any excess of the minimum for maintenance, 10 L water (mL O_2)⁻¹, is available for growth and reproduction, but if there is less than the minimum, there must be sources of food other than phytoplankton or it implies starvation.

Another interpretation of the *F*/*R*-ratio is related to the oxygen uptake. For example, the reciprocal of *F*/*R* = 22.9 L of water per mL of O₂, i.e., *R*/*F* = 0.044 mL O₂ (L water)⁻¹ may be compared to the actual O₂ content of water, which, at saturation, amounts to 6.3 mL O₂ (L water)⁻¹. The ratio, *EE* = 0.044/6.3 = 0.007 = 0.7% is denoted by the oxygen extraction efficiency. It is low for true filter feeders because the diffusive uptake readily provides the necessary oxygen, but it will increase if the flow is restricted by something, e.g., the reduced valve gape of mussels that occurs during periods of food depletion. The high value *EE* = 1/(4.1 × 6.3) = 0.039 = 3.9% of *Verongia gigante* signifies an atypically high O₂ uptake, which is demanded by the symbiotic bacterial community within the sponge.

Finally, the metabolic cost of growth (R_g/G) that enters the bioenergetic growth model in the coefficient a_0 and represents the cost of synthesizing new biomass, which is mainly macromolecular synthesis, is generally low (8% to 23%, Table 2) but is very high (139%) for the sponge *Halichondria panicea* [11]. The latter high value is probably due to the early evolutionary simple structure that is mainly composed of the choanocyte pumps so that

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energy that is used for maintenance only constitutes a small fraction of the energy that is required for growth.

10. Conclusions

For the filter-feeding invertebrates that are examined herein, the results in Table 1 show that the theory of $b_1 \approx b_2$ appears to be approximately satisfied. The values of these *b*-exponents range from 0.66 to 1.0, implying size-specific growth rates of $\mu \approx W^{-0.34}$ to W^0 = constant, i.e., from a power function growth that is decreasing with increasing size to exponential growth. Exponential growth is a feature of modularity, which among filter feeders only applies to some bryozoans and sponges. Here, the filtration rate of a bryozoan colony, for example, increases in proportion to its size, hence its number of individual zooids each have the same filtration rate. Similarly, the filtration rate and the growth increase in proportion to the size of a larger sponge if it is composed mostly of fully grown aquiferous units (modules) of an equal filtration rate. In addition to modularity, the growth may be near exponential in the early ontogenetic stages of filter-feeding invertebrates, such as mussels.

There seems to be no indication that *b*-exponents should take a suggested universal value of 3/4 [16], which is a trend that seems to appear when pooling data from a large number of organisms covering a large span of sizes [59,60]. The magnitude of size-specific growth rates range from less than $1\% d^{-1}$ to more than $100\% d^{-1}$ (Table 2), tending to be high for small organisms or those in the early stages of growth and decreasing with size.

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