

Notes and Comments

Pelagic Tunicates: Why Gelatinous?

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Neutrally buoyant zooplankton are virtually free from the gravitational forces acting on terrestrial organisms, which allows for their adoption of large, watery bodies (Harbison 1992). Although this morphological trait is present in several phyla and is nearly ubiquitous in marine systems, the reasons for its great success remain an evolutionary mystery. From a top-down perspective, a transparent, gelatinous body may offer effective concealment from predators (Johnsen 2000) and may deter predation because of its low nutritive value (Verity and Smetacek 1996). However, the light-deprived depths of the deep sea teem with gelatinous life, many gelatinous animals exhibit bioluminescence, and some are not transparent (see Harbison 1992), which casts serious doubts on the transparency hypothesis. Moreover, there are predators specialized in gelatinous plankton (see Harbison 1998 for a comprehensive account of salp predators). Last, from a bottom-up perspective, a gelatinous body may allow survival at the low food concentrations prevailing in the open ocean (see Harbison 1992 for this and other hypotheses related to gelatinous bodies).

Salps, appendicularians, pyrosomas, and doliolids, collectively known as pelagic tunicates, are extremely watery animals that filter from very small colloids to large phytoplankton chains. They serve as prey for a host of marine animals, including fish, and under benign food conditions, they exhibit population growth rates that rank at the top among the metazoans (Bone 1998*b*). This allows them to

develop dense populations that mediate massive fluxes of fecal material from the surface to the deep sea, thus amplifying the oceans' role as an atmospheric carbon sink (Bone 1998*b*). Pelagic tunicates have successfully colonized the surface waters of coastal areas as well as the ultraoligotrophic cores of the great oceanic gyres and the abyssal depths, where levels of suspended particulate matter are critically low. Although they have the energy requirements of any other zooplankton of similar carbon content (Ikeda 1985; Schneider 1992) and do not store reserves (Deibel et al. 1992; Pond and Sargent 1998), pelagic tunicates maintain normal feeding and swimming activities in the nutritionally poor blue waters of the world oceans and during the seasonal periods of food scarcity in temperate seas without developing diapause eggs or dormant stages. The biological basis for their remarkable adaptation to low food concentrations is far from clear.

The notion that a large, gelatinous body may involve some feeding advantage at very low concentrations dates back at least to Harbison (1992), who pointed out the fact that gelatinous zooplankton can develop large and delicate feeding structures due to reduced gravitational and turbulent shear stresses in their natural environment. A similar argumentation, based on the costs of filter feeding, has been used by Lampert (1994) to explain why daphniid crustaceans have larger filtering combs when food is scarce (Kozá and Kořinek 1985). Here I will follow a semi-empirical approach using filtration theory and physiological allometry to support this contention as applied to pelagic tunicates, that is, to suggest that pelagic tunicates are normal animals that fake giants to endure food dilution. The argument is rooted on the biomechanical basis of filter feeding and substantiated on real data from a typical blue-water tunicate. It is, in principle, restricted to pelagic tunicates because they are theoretically and practically the most accessible case study. However, as our knowledge on the fluid mechanics of particle capture grows, the mechanism proposed may prove to be of sufficient generality to explain the gelatinous strategy in many other gelatinous organisms.

All pelagic tunicates screen the water using mucous fil-

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ters made of overlapping orthogonal arrays of parallel fibers. Most of the filter-feeding literature (e.g., Lehman 1976) describes the filtration activity of animals in terms of the filtration rate (P , volume/time) because it is easily measured in the laboratory and because the short-term filtration behavior of filter feeders can be adequately described using this variable. Accordingly, the total energy gain (G) from operation of the filter can be calculated as $G = PCe\beta$, where C is food concentration, e is the food assimilation efficiency, and β is the particle retention efficiency. However, I will decompose P as surface area of the filter (S) multiplied by through-filter flow velocity (U); therefore,

$$G = SUCe\beta. \quad (1)$$

This theoretical investigation stems from this slight modification because it allows consideration of the evolutionary adjustment of flow velocity and filter architecture. Obviously, a viable filter-feeding strategy implies that G is larger than the energy required to move water through the filter (condition 1) and the minimum metabolic requirements of the filter feeder (condition 2). As we shall see, positive net energy gain from the filter depends on the ultrastructure and flow regime through the filter, while scaling of the energy gain to the animal's needs depends on the filter surface.

The energy spent in filtration (F) is conventionally calculated as $F = \alpha P\Delta p$, where P is filtration rate, Δp is pressure drop (i.e., Vogel 1994), and α is a coefficient added to convert energy units to organic carbon units. As for G in equation (1), I have expressed P as $P = SU$; therefore, $F = \alpha SU\Delta p$. According to the modified Darcy's equation (Silvester 1983),

$$\Delta p = kU,$$

where

$$k = 8\pi\mu/h_e\Lambda_e,$$

$$h_e = wl/(w + l),$$

$$\Lambda_e = 1 - 2 \ln \tau + (\tau^2/6) - (\tau^4/144) + (\tau^6/1,080),$$

$$\tau = \pi f/h_0,$$

$$h_0 = wl/(w^2 + l^2)^{1/2}$$

and μ is the dynamic viscosity of the water, w is the pore width, l is the pore length, and f is the fiber diameter. Thus, k depends on ultrastructural properties of the filter mesh and water viscosity. Accordingly, the energy spent in filtration can be calculated as $F = \alpha SU\Delta p = \alpha kSU^2$.

It follows that the net energy gain (N) obtained from the operation of the filter will thus be the difference between food assimilation (eq. [1]) and F , that is,

$$N = G - F = SUCe\beta - \alpha kSU^2. \quad (2)$$

The quadratic term in equation (2) has important implications. Because G grows linearly while F grows quadratically with U , there is a maximum through-filter flow velocity (U_m) above which the net energy gain N becomes negative and the filter delivers less energy than it consumes in filtration. Thus, U has to be smaller than U_m to keep condition 1 true. This means that it is always possible to obtain positive net energy gain, no matter how low the food concentration is, as long as U is kept below U_m . Moreover, maximum net energy profit will occur when the filter feeder adopts an intermediate optimal flow velocity (U_o). The value of U_m can be found by setting $N = 0$ in equation (2) and solving for U . The value of U_o can be found by setting $dN/dU = 0$ and solving for U . Calculated in this way, it is clear that both U_o and U_m depend on the filter ultrastructure and the food concentration but not on filter surface:

$$U_o = \frac{e\beta}{2\alpha k} C,$$

$$U_m = \frac{e\beta}{\alpha k} C. \quad (3)$$

The tunicate salp *Pegea confoederata* is one of the best-studied inhabitants of the ultraoligotrophic cores of the great oceanic gyres (fig. 1). In contrast to many species of crustacean zooplankton, *P. confoederata* meets its minimum energy requirements at extremely low average food concentrations, while it experiences serious mechanical problems when feeding at moderate food concentrations (Harbison et al. 1986). *Pegea confoederata* filters particles $>2 \mu\text{m}$ in size (Kremer and Madin 1992; see table 1) with an across-filter flow velocity of 0.17 cm s^{-1} (Bone et al. 1991). Combination of equation (3) with parameter values from the literature (table 1) confirms that this filter velocity would correspond to minimum food concentrations of 0.37 and $0.74 \mu\text{g C L}^{-1}$ should the animal adopt a maximum or an optimal across-filter flow velocity, respectively (see lines 1 and 2 in fig. 2). These concentrations are below $5.1 \mu\text{g C L}^{-1}$, the minimum concentration of particles $>2 \mu\text{m}$ observed by Buck et al. (1996) in 53 stations regularly spaced along a transect in the North Atlantic from 5°S to 61°N in summer 1993 (fig. 2). Therefore, equation (3) allows prediction of minimum food concentrations from knowledge of filter ultrastructure and flow velocity (i.e., parameters k and U), and this prediction seems consistent

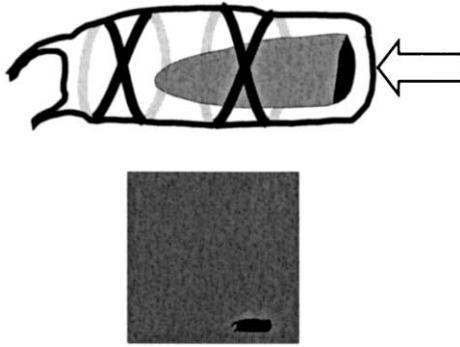


Figure 1: Schematic diagram of a 4-cm-long solitary generation *Pegea confoederata* (actual size; based on figure 1 in Bone et al. 1991; see Bone 1998a for salp anatomy). Essentially, a salp is a hollow, gelatinous cylinder open at both ends through which water is pumped (direction of water stream shown by arrow) by circular muscles (*black crossed stripes* and *lighter stripes* underneath) similar to the iron bands that keep tight the wooden boards of a barrel. The muscles are abundantly irrigated by a complex of blood sinuses that are nearly absent from the gelatinous matrix (Bone 1998a). This matrix is basically physiologically inert, watery tissue. Thus, it is hard not to interpret this morphology as the large, outstretched body of a small organism. The filter (*shaded area*) is a hemiellipsoidal structure open at the base (*dark area*). The shaded square below has the same surface as the filter of the salp above (4.4 cm²; Bone et al. 1991). The small black shape in the lower right corner of the square corresponds to a salp having exactly the same relative dimensions as the salp above but scaled down as if it had the volume to carbon proportion of many other zooplankton organisms (0.0079 m³ [kg C]⁻¹; Hansen et al. 1997) instead of the normal volume to carbon proportion of *P. confoederata* (5 m³ [kg C]⁻¹).

with the average food conditions that this species encounters in nature.

Filtration with an across-filter flow velocity U_o corresponds to an optimal strategy that maximizes net energy gain while producing an intermediate food assimilation rate (G_o) only partly devoted to filtration. Filtration with an across-filter flow velocity U_m corresponds to a wasteful strategy, which leads to a maximum assimilation rate (G_m) that is entirely devoted to making water flow through the filter. The G_o and G_m values can be calculated by substituting U in equation (1) with U_o and U_m from equation (3):

$$\begin{aligned} G_o &= \frac{e^2\beta^2}{2\alpha k} SC^2, \\ G_m &= \frac{e^2\beta^2}{\alpha k} SC^2. \end{aligned} \quad (4)$$

The variable G_m represents the maximum total energy gain that guarantees fulfillment of condition 1. The variable G_o also meets condition 1, but it is, in addition, the most profitable and biologically sound strategy. According

to condition 2, G_o and G_m must suffice the minimum energy requirements of the animal. An approximation to these requirements is given by the visible respiration rate (R), which depends on body carbon (W), according to the power function

$$R = rW^s, \quad (5)$$

where r and s are scaling coefficients. Setting the right-hand side of equation (4) equal to the right-hand term of equation (5) and solving for S , we obtain

$$\begin{aligned} S_o &= \frac{2\alpha kr}{e^2\beta^2} W^s C^{-2}, \\ S_m &= \frac{\alpha kr}{e^2\beta^2} W^s C^{-2}, \end{aligned} \quad (6)$$

where S_o and S_m represent the minimum filter surfaces that suffice the respiratory demand of an animal filtering with optimal and maximum strategies, respectively.

Pegea confoederata that are 4 cm long have 4.4 cm² of filter surface (Bone et al. 1991; fig. 1). According to equation (6), this filter surface should allow survival of *P. confoederata* at minimum food concentrations between 0.84 and 2.17 $\mu\text{g C L}^{-1}$ (lines 3–6 in fig. 2), depending on choice of filtration strategy and respiration parameters. These concentrations are close to the minimum food concentrations as predicted from equation (3) (0.37 and 0.74 $\mu\text{g C L}^{-1}$). Therefore, equation (6) allows prediction of the minimum target food concentrations of a filter feeder just from knowledge of its filter morphometry (i.e., fiber and pore size [parameter k] and filter surface [parameter S]), and these predictions are consistent with an independent estimate based on filter ultrastructure and flow velocity (i.e., parameters k and U ; eq. [3]). This suggests that the whole filter architecture and functioning in *P. confoederata* are finely tuned for survival at the lowest food concentrations that can be found in the ocean and, in turn, that the fluid mechanical reasoning presented here is sound.

Salps are extremely watery animals, with 5 m³ of body volume per kilogram of body carbon (calculated from a volume of 7.45×10^{-6} m³ and a carbon weight of 1.26×10^{-6} kg C per individual for a 4-cm-long cylindrical *P. confoederata*, estimated from a figure in Bone et al. [1991; see fig. 1] and an equation to convert salp length to carbon weight in Madin et al. [1981], respectively) as opposed to 0.0079 m³ [kg C]⁻¹ for most other nongelatinous zooplankton (Hansen et al. 1997). If *P. confoederata* had the same carbon but a normal water content, it would be hard to imagine how it could hold 4.4 cm² of functional filter (fig. 1). Thus, it is tempting

Table 1: Parameter values used in model calculations

Parameter	Value	Units	Definition
β	1	Proportion	Particle retention efficiency
e	.61	kg C assimilated [kg C ingested] ⁻¹	Food assimilation efficiency
α	1.82×10^{-8}	kg C J ⁻¹	Coefficient to convert from energy to carbon units
k	7.29×10^3	kg m ⁻² s ⁻¹	Parameter from Darcy's equation
W	1.26×10^{-6}	kg C individual ⁻¹	Body carbon weight
r	Coefficient of the power function relating respiration rate to body carbon weight
All zooplankton	6.84×10^{-8}	kg C individual ⁻¹ s ⁻¹	
Oceanic salps	3.95×10^{-7}	kg C individual ⁻¹ s ⁻¹	
s	Exponent of the power function relating respiration rate to body carbon weight
All zooplankton	.83	Nondimensional	
Oceanic salps	.87	Nondimensional	
a	1.15	m ²	Coefficient of the power function relating filter surface to body volume
b	Two-thirds	Nondimensional	Exponent of the power function relating filter surface to body volume

Note: Sources of these values: β , I am assuming that all particles are retained with 100% efficiency. Thus, the calculations reflect the minimum concentration of particles retained with 100% efficiency. Minimum particle size retained with 100% efficiency by most salps is between 2 and 4 μm (Harbison and McAlister 1979; Kremer and Madin 1992) and likely closer to 3 μm for *Pegea confoederata* if the available measurements in two individuals are correct. Since I am comparing model calculations against the biomass of particles >2 μm in size (from Buck et al. 1996; see fig. 2), this biomass represents a conservative overestimate of the actual food concentration experienced by *P. confoederata* in the ocean. Consideration of actual food concentrations would lead to reinforcement of the argument presented here, that is, organisms would need larger filter surfaces and more gelatinous bodies. e , Reasonable, given values of 0.61 for the salp *Cyclosalpa bakeri* (Madin and Purcell 1992) and of 0.64 for *Salpa fusiformis* (Andersen 1986). α , Calculated using approximate conversion coefficients from energy units to dry mass (4.55×10^{-8} kg dry mass J⁻¹) and from dry mass to carbon weight (0.4 kg C [kg dry mass]⁻¹) from Peters (1983). k , Calculated according to the dynamic viscosity of 35‰ salinity and 24°C seawater, $\mu = 0.99 \times 10^{-3}$ kg m⁻¹ s⁻¹, and fiber diameter of 5×10^{-8} m (Bone et al. 1991). Pore widths and lengths of the filter of *P. confoederata* seem to vary considerably depending on the exact location of the pore and the degree of stretching of the filter from highly rectangular pores $4.1 \times 0.7 \mu\text{m}$ in size (Bone et al. 1991; after assuming 20% shrinkage because of SEM fixation; see also fig. 7E in Bone et al. 2000) to nearly square pores $1.53 \pm 0.15 \times 1.36 \pm 0.14 \mu\text{m}$ in size (mean \pm SD of measurements of the three largest, intact, apparently not stretched pores in fig. 7F of Bone et al. [2000] and correcting for 20% shrinkage). I have assumed this later figure for the pore size because it seems to be closer to the operating morphology of the filter (Bone et al. 2000) and more consistent with the particle-size retention efficiency of salps (note that these pores are smaller than the minimum particle size retained with 100% efficiency) and because it leads to a conservative estimate of energy expenditure by the filter feeder and to lower calculated minimum concentrations. Use of smaller pore sizes would lead to reinforcement of the argument presented here, which implies that the organisms would need larger filter surfaces and more gelatinous bodies. Use of larger pores up to 3 μm in size does not significantly alter the conclusions reached here, even in the most conservative scenario (i.e., using Ikeda's [1985] respiration coefficients [see below], which lead to lower metabolic requirements; assuming an unlikely maximum-filter-feeding strategy, which implies minimum filter surface requirements; and comparing model calculations against the concentration of >2- μm particles, which overestimates actual food concentrations). W , Calculated for a 4-cm-long blastozoid of *P. confoederata* using the equation to convert salp length to carbon weight in Madin et al. (1981). r , s , Obtained from general allometric relationships for the respiration rate of zooplankton from Ikeda (1985) for a water temperature of 24°C, which is typical of subtropical regions in summer, where the lowest food concentrations of nano- and microplankton occur (Buck et al. 1996), and from the equation in Cetta et al. (1986) for measurements of the respiration rate of oceanic salps conducted at temperatures between 20° and 29°C in nearly all cases. Since all calculations have been adjusted to the typically high temperatures prevailing at the central oceanic gyres, the predictions presented here are necessarily biased at the lowest temperatures at which *P. confoederata* can live (10°C; Harbison and Campenot 1979). The dynamic viscosity (and the work needed to pump water) increases more slowly than the concomitant decrease in respiration rate with decreasing temperature (assuming a Q_{10} of 2). Therefore, at the same food concentration, the organisms would need to be less gelatinous in colder environments (or in higher latitudes). a , b , If we assume isometric growth in linear dimensions, then b is equal to two-thirds. Since $S = 4.4 \times 10^{-4}$ m² and $V = 7.45 \times 10^{-6}$ m³ for a 4-cm-long *P. confoederata* (from Bone et al. 1991), a can be solved from the equation $S = aV^{2/3}$; b was allowed to vary between 0.25 and 2.0 for calculations in figure 3.

to interpret the gelatinous body as an evolutionary strategy to increase the body size and the supportive structure for the filter while maintaining the same carbon content. As a matter of biomechanical speculation, it is interesting

to examine whether a scaled down version of a salp with the same body carbon and architecture but a normal water content (like the small salp in fig. 1) would be able to survive at normal food concentrations in the open

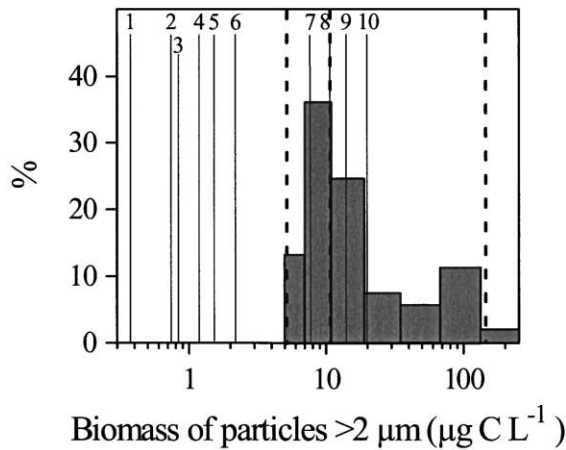


Figure 2: Frequency distribution (%) of measurements of biomass of particles $>2 \mu\text{m}$ (detrital fraction not included) conducted by Buck et al. (1996) in 53 stations regularly spaced along a transect in the Atlantic Ocean from 5°S to 61°N in summer 1993. These concentrations are used in this work as a proxy for the food concentration available for *Pegea confoederata*, although they likely represent an overestimate (table 1). Widths of biomass classes are arranged in an octave scale to facilitate representation. The dashed vertical lines indicate the minimum, median, and maximum biomasses observed. The thin vertical lines and numbers on top indicate predictions of minimum food concentrations according to the following: equation (3), maximum (line 1) and optimal (line 2) strategies; equation (6), assuming respiratory coefficients from all zooplankton (see table 1) for maximum (line 3) and optimal (line 4) strategies; equation (6), assuming respiratory coefficients from warm-water, oceanic salps (see table 1) for maximum (line 5) and optimal (line 6) strategies; equation (7), assuming normal body carbon density ($0.0079 \text{ m}^3 [\text{kg C}]^{-1}$, from Hansen et al. 1997), respiratory coefficients from all zooplankton, and isometric scaling (b equal to two-thirds; see table 1) for maximum (line 7) and optimal (line 8) strategies; equation (7), assuming normal body carbon density, respiratory coefficients from salps, and isometric scaling for maximum (line 9) and optimal (line 10) strategies. Parameter values for the calculations are given in table 1.

ocean. For this, it is necessary to model the water content of a filter-feeding animal.

Filter surface (S) should scale with body volume (V) or body carbon (W) according to power equations of the type $S = aV^b = a(\rho W)^b$, where a and b are scaling parameters and ρ is a coefficient that represents the total body volume per unit body carbon. Obviously, there is a direct relationship between ρ and body water content. The S_o and S_m variables in equation (6) can now be substituted by $a(\rho W)^b$, and solving for ρ , we obtain

$$\rho_o = \left(\frac{2\alpha kr}{e^2 \beta^2 a} \right)^{1/b} W^{(s-b)/b} C^{-(2/b)},$$

$$\rho_m = \left(\frac{\alpha kr}{e^2 \beta^2 a} \right)^{1/b} W^{(s-b)/b} C^{-(2/b)}. \quad (7)$$

Equation (7) specifies the minimum body volume : carbon conversion necessary to fulfill the minimum energy requirements as a function of body carbon and food concentration for a filter feeder that adopts an optimal (ρ_o) or a maximum (ρ_m) strategy.

If we assume isometric growth and respiratory parameters for zooplankton (i.e., b is equal to two-thirds and $s = 0.83$; table 1), then ρ should increase as a 0.25 power of W and decrease as the cube of C . Therefore, although larger animals (in carbon) should have higher water contents, clearly the determinative factor in driving a gelatinous strategy should be food concentration. Combination of equation (7) with parameter values from the literature (table 1) suggests that a scaled-down version of *P. confoederata* with the same carbon weight but a water content like that of other zooplankton ($\rho = 0.0079 \text{ m}^3 [\text{kg C}]^{-1}$; see the small salp in fig. 1) would hold enough filter surface to survive at minimum concentrations between 7.62 and $19.7 \mu\text{g C L}^{-1}$ (lines 7–10 in fig. 2; see also model calculations for b equal to two-thirds in fig. 3). These con-

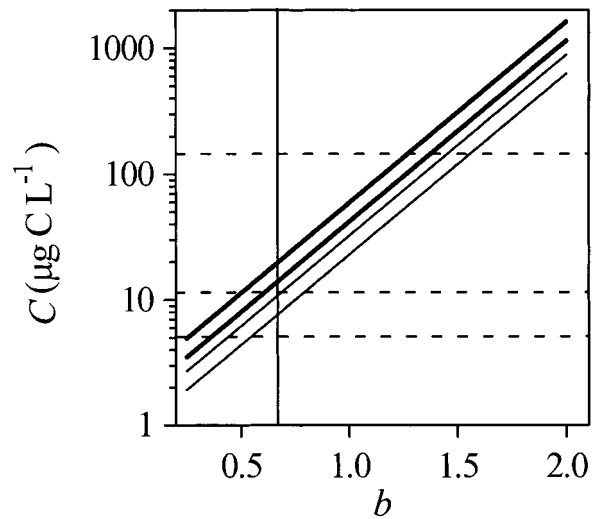


Figure 3: Minimum food concentration (C) attainable by a hypothetical ancestor with the same body carbon as *Pegea confoederata* but a normal water content as a function of the exponent of the surface-volume power law (b). In the predictions, equation (7) was used in combination with parameter values from the literature (table 1), while b was allowed to vary between 0.25 and 2. For every value of b , the coefficient a was calculated from the equation $S = aV^b$ using values of S and V for a 4-cm-long *P. confoederata* (table 1). The calculations were done assuming optimal (*upper thin diagonal line*) and maximum (*lower thin diagonal line*) strategies in combination with respiration parameters for all zooplankton or optimal (*upper thick diagonal line*) and maximum (*lower thick diagonal line*) strategies in combination with respiration parameters for oceanic salps (table 1). The vertical line depicts a value of b equal to two-thirds. The dashed horizontal lines indicate the minimum, median, and maximum biomass of particles $>2 \mu\text{m}$ observed by Buck et al. (1996) in the summer North Atlantic (see fig. 2).

centrations are close to the median concentration of ingestible particles in the North Atlantic during summer ($11.4 \mu\text{g C L}^{-1}$; Buck et al. 1996; fig. 2). In other words, such a salp would starve in nearly 50% of the latitudinal range in the North Atlantic. Since the lowest food concentrations occur at the extensive ocean surface of the low latitudes and the biomass of $>2\text{-}\mu\text{m}$ particles represents an overestimate of the actual food concentration (fig. 2; table 1), a hypothetical *P. confederata* with normal water content would likely starve in a large fraction of the world's oceans.

Although my assumption of isometric growth in the previous calculation represents the simplest hypothesis of the value for the surface-volume law exponent (b is equal to two-thirds; table 1), actual values for b are likely larger than two-thirds. Natural selection operating toward increasing filter surfaces should not only favor increasing tissue water contents but also better (e.g., more hollow) body architectures, which would lead to allometric growth of filter surface with b larger than two-thirds. The fact that salps are extremely hollow organisms and that most of their active tissue is spatially restricted to the inner wall of the tunica (Madin and Deibel 1998) is strongly suggestive that there has been an evolution of body morphologies. Unfortunately, it is also very likely that we will remain ignorant of the actual value for b given our lack of fossil record for pelagic tunicates. Nevertheless, we do know one point of the surface-volume relationship for *P. confederata* (i.e., we know the filter surface and body volume of one individual 4 cm long; see table 1). We can use this data point in combination with equation (7) to simulate the effect of different values of b on the predicted minimum food concentration attainable by a hypothetical ancestor with the same carbon but normal water content (fig. 3). As expected, values of b smaller than two-thirds render the gelatinous strategy nearly useless because an ancestor with normal water content would almost manage to survive at the lowest food concentrations that it can encounter in nature (fig. 3). However, a value of $b = 1$ would imply that an ancestor with normal water content would survive at minimum concentrations between 22 and $59 \mu\text{g C L}^{-1}$, depending on choice of filtration strategy and respiration parameters, that is, a minor fraction of the world's oceans during summer (fig. 3).

Clearly, there is much to gain from a gelatinous strategy, from colonization of a vast, predator-free space (Harbison et al. 1986) to continuous monitoring of the environment to ensure an opportunistic response to favorable food conditions. In this regard, the interpretation of the gelatinous body of salps as an evolutionary response to extreme food dilution is by no means inconsistent with the fact that salps may develop dense populations as a response to episodic or seasonal phytoplankton blooms in low-latitude, temper-

ate, polar, or coastal regions. However, the theory stresses the importance of periods of food scarcity in these environments and their potential bottleneck effects on zooplankton populations. In addition, equations (6) and (7) give similar results when applied to the ultrastructure of the food-concentrating filter of appendicularian tunicates (Deibel and Powell 1987), although I have not presented these results because of our incomplete knowledge of filter surfaces. Whereas in salps, the filter is an internal structure sustained by a large, watery body, the food-concentrating filter of appendicularians is held within a mucous bubble or filter house surrounding the body of the animal (Flood 1998). This suggests that the watery body of salps and the filter house of appendicularians are radically different versions of the same conceptual solution to life in endemically or episodically poor environments. It also suggests that the ascidian ancestors of pelagic tunicates had the morphological plasticity to cope with the severe increases in water content required by the gelatinous strategy. Interestingly, freshwater daphniids have larger filtering combs at low food concentrations (Koza and Kofinek 1985), which has been explained because costs of filtration increase linearly with filter surface but quadratically with flow velocity (Lampert 1994; like term F in eq. [2]). Although this is fully consistent with the mechanism proposed here, the chitinous carapace of crustacean zooplankton may not have been the best start for adoption of the gelatinous strategy. This raises the old question, though from a quite different perspective, of the extent to which crustacean zooplankton are true filter feeders or sensory-driven, raptorial feeders (for a seminal version of this question, see Koehl and Strickler 1981). Clearly, if the tunicate body and filter architecture has an optimal design, which we do not yet know, the present theory suggests that the distribution of true filter feeders of normal water content should be restricted to areas of moderate productivity. Alternatively, they could colonize poor, open ocean waters by making opportunistic use of seasonal phytoplankton blooms through a temporal/spatial migration strategy or by developing highly efficient, sensory-driven raptorial mechanisms in conjunction with very low body carbon. In this regard, sensory-driven crustacean copepods of small size seem to have colonized the open ocean more successfully than larger, filter-feeding copepods (Paffenhöfer and Stearns 1988).

The argument presented here might help to elucidate the reasons for the watery body of other gelatinous plankton, although we may need some theory to model their particle-capture mechanisms and more knowledge of model parameters. Much evidence points to limited lipid storage in herbivorous or carnivorous gelatinous zooplankton (see references in Deibel et al. 1992), and, to my knowledge, most of these animals lack resistance forms or cysts. However, many of them screen the water for food

using arrays of tentacles, large parachute filters, or their own body. Since for most collectors particle capture should increase linearly while energy expenditure should increase faster than linearly with flow velocity (like in eq. [2]; Lehman 1976; Vogel 1994), it is reasonable to expect an upper limit for the flow velocity beyond which the net energy profit is negative. This would leave increasing collector surface as the only strategy for survival under food limitation without spatial/temporal migration mechanisms and would provide further theoretical support for Harbison's (1992) early contention on the advantages of gelatinous bodies. Perhaps in the near future we will interpret the gelatinous strategy as a broad-ranging adaptive syndrome to food dilution, just as we now clearly see the logic behind the fusiform bodies of swimming organisms. Meanwhile, our rudiments of filtration biomechanics suggest that it is always possible to obtain profit from filter feeding, no matter how low the food concentration, provided that the filter feeder is structurally prepared to support a large filtering device.

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