Biomass-to-volume ratio as a central continuous functional trait for marine zooplankton

Lemoine, Julie; Ayata, Sakina Dorothée; Jaspers, Cornelia; Lombard, Fabien

Published in:
Limnology and Oceanography

Link to article, DOI:
10.1002/lno.70171

Publication date:
2025

Document Version
Publisher's PDF, also known as Version of record

LIMNOLOGY and OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 70, 2025, 2673–2687

doi: 10.1002/lno.70171

RESEARCH ARTICLE

Biomass-to-volume ratio as a central continuous functional trait for marine zooplankton

Julie Lemoine [1*], **Sakina-Dorothée Ayata** [2,3], **Cornelia Jaspers** [4], **Fabien Lombard** [1,3]

[1]CNRS, Laboratoire d'Océanographie de Villefranche (LOV), Sorbonne Université, Villefranche-sur-Mer, France; [2]MNHN, CNRS, IRD, Laboratoire d'Océanographie et du Climat: Expérimentations et Approches Numériques, Sorbonne Université, Paris, France; [3]Institut Universitaire de France (IUF), Paris, France; [4]Centre for Gelatinous Plankton Ecology & Evolution, Technical University of Denmark, Charlottenlund, Denmark

Abstract

Gelatinous zooplankton are an important component of many ecosystems and important for ecosystem structure and carbon cycling. However, this group is generally not considered in biogeochemical models. Here we investigate the biomass-to-volume ratio as an underappreciated "master trait" that allows for the incorporation of a large diversity of zooplankton groups into modeling exercises. By considering the biomass-to-volume ratio as a continuum, we investigate the potential trade-offs between body composition and physiological (e.g., clearance, respiration, carbon mass-specific growth, assimilation) as well as ecological (e.g., predator–prey size ratio, feeding modes) traits. We find that a low carbon composition has a positive effect on the organism's fitness, as more prey could be captured for the same active mass. Thus, taking the biomass-to-volume ratio into account could improve the estimation of physiological rates. Additionally, we show that gelatinous feeding-current feeders (e.g., tunicata, *Mnemiopsis* spp., *Rhizostoma* spp.) have an ability to catch smaller prey over a wider size range than non-gelatinous feeding-current feeding organisms (gelatinous feeding-current feeders min–max: 10^2–10^6 $\mu m_{predator}$ μm_{prey}^{-1}; non-gelatinous feeding-current feeders min–max: 5×10^0–8×10^1 $\mu m_{predator}$ μm_{prey}^{-1}). However, results are only valid for the respective feeding mode, highlighting new trade-offs. This allows us to re-evaluate the functional role of certain organisms, such as larvaceans (appendicularians), which were previously considered to be super-filters, or pteropods, which remain understudied. This study contributes to a wider representation of the complexity of the zooplankton community in size-structured models. We highlight that the biomass-to-volume ratio, along with size, is the most important parameter required to represent the full diversity of zooplankton.

Marine plankton, though unable to counter ocean currents, regulate their vertical position and exhibit fine-scale behaviors. Their short lifespans and direct exposure to environmental conditions make them highly responsive to climate change (Ibarbalz et al. 2019; d'Elbée 2016). Shifts in temperature and circulation patterns have already altered their biogeography (Beaugrand 2005; Borkman and Smayda 2009). As key drivers of oceanic biogeochemical cycles and major contributors to the global carbon sink (Turner 2015), plankton are recognized as essential ocean and climate variables (Bax et al. 2019). However, their immense diversity and complex interactions are often oversimplified in models, limiting our understanding of ecosystem responses to global change (Guidi et al. 2016).

To better represent the complexity of plankton functional types are used in biogeochemical models, grouping species by distinct ecological roles (Quere et al. 2005). However, for each new functional group that is added to models, new parameters have to be determined, making the models more complex, and increasing their uncertainty. A way forward is the functional trait-based approach, which uses one or more individual properties or traits of organisms (Martini et al. 2021) to cover a large diversity of organisms. This allows for reducing the number of parameters required to capture the entire plankton

*Correspondence: julie.lemoine@imev-mer.fr

Associate editor: Joseph Warren

community (Kiørboe et al. 2018). Many models adopt size as the key trait (e.g., Heneghan et al. 2020; Serra-Pompei et al. 2020; Negrete-García et al. 2022), though they still rely on plankton functional types to reflect taxonomic and functional variability, including feeding strategies.

The size trait is defined as a master trait of zooplankton communities by Litchman et al. (2013), meaning that it is a primary trait impacting the fitness of an organism (e.g., growth, reproduction, feeding, and survival) and that it affects many other functional traits. The biomass-to-volume ratio refers to the carbon content of an organism and can be used to differentiate between gelatinous and non-gelatinous plankton. It has also been defined as having an impact on various ecological functions of zooplankton organisms as well (Litchman et al. 2013; Martini et al. 2021).

Compared to other groups, gelatinous zooplankton exhibit higher carbon mass-specific feeding rates (Hamner et al. 1975; Acuña et al. 2011), lower locomotion costs (Pitt et al. 2013), and higher specific growth rates (Hirst et al. 2003; Pitt et al. 2013; McConville et al. 2016). They exploit a broad prey size spectrum, from viruses to fish (Sutherland et al. 2010; Jaspers et al. 2023), making them a highly competitive group. In some systems, overfishing has led to shifts from fish to gelatinous dominance (Kawasaki 1993; Lynam et al. 2006; Brodeur et al. 2008). Their contribution to carbon fluxes is increasingly recognized (Henschke et al. 2016; Luo et al. 2020), highlighting their often-overlooked role in biogeochemical cycles. As a result, research interest in their physiology, trophic ecology, and population dynamics has grown (Purcell 2012; Gibbons and Richardson 2013; Condon et al. 2013).

However, gelatinous zooplankton span the entire tree of life and show wide variation in biomass-to-volume ratios, from 0.01% to 19.02% of the total wet mass (Molina-Ramírez et al. 2015; McConville et al. 2016). Therefore, we here suggest that the biomass-to-volume ratio could be considered as a continuous variable across large taxonomic ranges (McConville et al. 2016) to facilitate incorporation into diverse modeling exercises. This approach could enhance biogeochemical models by more accurately reflecting zooplankton diversity and improving predictions of carbon fluxes under climate change.

Thus, in this study, we test the hypotheses that (1) the biomass-to-volume ratio can be considered as a continuum and (2) it impacts other physiological and ecological traits. To investigate this, we compile experimental data on various physiological and ecological traits and conduct statistical analyses. We quantify the impact of the biomass-to-volume ratio on these rates and provide equations that can be applied in size-structured models. Our results raise new hypotheses and underscore the value of using biomass-to-volume ratios to enhance the representation of all key zooplankton functional groups in biogeochemical models.

Materials and methods

Compilation of physiological rates and trait data

In this study, we explored different types of traits (morphological, physiological, and behavioral) which have an influence on critical ecological processes (feeding, growth, reproduction, and survival) in order to obtain the most complete analysis of the trade-offs involved in biomass-to-volume ratios (Litchman et al. 2013).

We compiled data on four physiological parameters: (1) carbon mass-specific growth rate, (2) clearance rate, (3) respiration rate, and (4) assimilation rate, along with two functional traits: (1) predator–prey size ratio and (2) feeding mode. The aim was to collect data on 11 taxonomic categories of zooplankton used in the study of McConville et al. (2016): Ctenophores (Lobata, Cydippida, and Nuda), Cnidarians (Scyphozoa and Hydrozoa), Thaliacea, Polychaeta, Chaetognatha, Mollusca, Crustacea (other than copepods), and Copepoda. In addition to this taxon list, we also considered larvaceans (appendicularians), not studied in McConville et al. (2016). The selection of the different taxonomic levels is based on the functional and morphological diversity within each taxonomic category (e.g., phylum for Chaetognatha, but order for Cydippida and Lobata within Ctenophora).

We then compiled the following datasets: Hirst et al. (2003) for growth, Kiørboe and Hirst (2014) for growth, respiration, and clearance, Acuña et al. (2011) for respiration and clearance, and Boyce et al. (2015) for predator–prey size ratios. In order to complete these datasets, 67 other sources were used. The datasets and their sources are summarized in Supporting Information Table S1 and are stored in the GitHub repository (https://github.com/lemoinejulie/database_zooplankton_traits). In addition to the predator–prey size ratios, when available, a percentage of efficiency has been added to catch the optimal prey size of each organism (Hansen et al. 1994).

For physiological rates, with the exception of assimilation because this rate is not influenced by temperature, the effect of temperature was corrected for each measurement, so the values of physiological rates are the values at a reference temperature of 15°C. To do this, following the work of Kiørboe and Hirst (2014), a Q10 value of 2.8 was chosen (Hansen et al. 1997). For some analyses, in order to study the influence of other factors, the effect of physiological rate measurements was normalized by the respective body mass (carbon or wet mass). To do so, we used the power relationship $Y = bW^a$, with Y being the physiological rate and W the carbon or wet weight. The parameters b and a are the values from the allometric curve specific for each physiological rate (Table 1).

Feeding modes

Kiørboe's (2011) study distinguished four main feeding modes for zooplankton, which we will here refer to as feeding-current feeders, cruise feeders, passive ambush feeders, and active ambush feeders. Feeding-current feeders create a feeding

Table 1. Estimations of the regression parameters *a*, *b*, and *c* between variables *X*, *Y*, and *Z* with different types of model expressions (CM%WM: biomass-to-volume ratio (%)). The shaded equations are defined as the best for estimating physiological rates using carbon mass or wet mass on the basis of the significance of the equations. The results of the comparison of these equations are in the last four columns (R^2: coefficient of determination; AIC: Akaike Information Criterion; Δi: delta of the second-order Akaike criterion; ωi: Akaike weight).

	X	*Y*	*Z*	Type	*a*	*b*	*c*	R^2	AIC	Δi	ωi
Clearance	Carbon mass (g)	Clearance (L d^{-1})		$Y = X^a \times b$	0.84 ± 0.02	1199 ± 280		0.79	3010	581	6.77E-127
	Carbon mass (g)	Clearance (L d^{-1})	CM%WM	$Y = X^a \times b \times (10^c)^z$	0.82 ± 0.02	2109 ± 397	−0.09 ± 0.007	0.86	2429		1
	Wet mass (g)	Clearance (L d^{-1})		$Y = X^a \times b$	0.72 ± 0.02	13.46 ± 1.44		0.86	2480.1	1.98	0.27
	Wet mass (g)	Clearance (L d^{-1})	CM%WM	$Y = X^a \times b \times (10^c)^z$	0.75 ± 0.02	11.67 ± 1.36	−0.02 ± 0.008	0.86	2478.12		0.73
Respiration	Carbon mass (g)	Respiration (mmolO_2 d^{-1})		$Y = X^a \times b$	0.88 ± 0.01	2.55 ± 0.28		0.9	1607	19	4.97E-05
	Carbon mass (g)	Respiration (mmolO_2 d^{-1})	CM%WM	$Y = X^a \times b \times (10^c)^z$	0.87 ± 0.01	2.63 ± 0.29	−0.008 ± 0.003	0.9	1588		0.999
	Wet mass (g)	Respiration (mmolO_2 d^{-1})		$Y = X^a \times b$	0.60 ± 0.01	0.03 ± 0.002		0.78	3123	986	8.46E-215
	Wet mass (g)	Respiration (mmolO_2 d^{-1})	CM%WM	$Y = X^a \times b \times (10^c)^z$	0.73 ± 0.01	0.02 ± 0.001	0.08 ± 0.005	0.87	2137		1
Growth	Carbon mass (g)	Carbon mass specific growth (d^{-1})		$Y = X^a \times b$	−0.2 ± 0.02	0.01 ± 0.003		0.39	802.2	−0.7	0.58
	Carbon mass (g)	Carbon mass specific growth (d^{-1})	CM%WM	$Y = X^a \times b \times (10^c)^z$	−0.2 ± 0.02	0.01 ± 0.003	−0.004 ± 0.001	0.39	802.9		0.42
	Wet mass (g)	Carbon mass specific growth (d^{-1})		$Y = X^a \times b$	−0.15 ± 0.02	0.04 ± 0.006		0.33	877	37	6.42E-09
	Wet mass (g)	Carbon mass specific growth (d^{-1})	CM%WM	$Y = X^a \times b \times (10^c)^z$	−0.17 ± −0.02	0.04 ± 0.007	−0.02 ± 0.007	0.36	840		1

current that is subsequently scanned for prey organisms in multiple ways (e.g., tunicata, euphausiacea, *Mnemiopsis* spp., *Rhizostoma* spp.). In contrast, cruise feeders swim continuously and detect prey by visual or chemical cues, hydrodynamic signals, and encounter their prey (e.g., *Euchaeta* spp., *Clausocalanus furcatus*, *Metridia* spp.). Passive ambush feeders are non-motile and are feeding on motile prey by collision for example, via their inflated body structures such as tentacles (hydrozoa with siphonophores and hydromedusa such as *Sarsia* spp.) or mucus nets (pteropods) in order to intercept and capture their prey. Active ambush feeders, in contrast, are non-mobile until they detect and attack their prey using mechanical or chemical cues as signals (e.g., chaetognatha, *Beroe* spp., *Oithona* spp.). The conceptual figure (Fig. 6) shows these different feeding modes and their position on the biomass-to-volume ratio continuum.

Biomass-to-volume ratio

The biomass-to-volume ratio is the ratio of carbon mass to wet mass of an individual. It represents the degree of dilution of the organism's tissues. In the study by McConville et al. (2016), wet mass and carbon mass measurements of the same individual were used to calculate their biomass-to-volume ratio. This provides biomass-to-volume ratios for 133 species belonging to 11 taxa spanning the tree of life. As it is rare to find simultaneous wet mass and carbon mass measurements in the sources used for data compilation, a biomass-to-volume ratio was assigned to each individual using those defined by McConville et al. (2016). These estimates were made to the nearest relative (i.e., to the species if available, then to the genus), by averaging the biomass-to-volume ratios of all available species in this genus, then to the family, etc. The taxa level used for the biomass-to-volume ratio estimation is indicated in the accompanying database.

Larvacean (Appendicularia) biomass-to-volume ratio

Since the study by McConville et al. (2016) did not include larvaceans, their biomass-to-volume ratio had to be calculated differently. Larvaceans produce external filtering structures, called houses, enabling them to filter particulate material (Lombard et al. 2009). The gelatinous character of larvaceans is not attributed to their body, which is similarly carbon dense as copepods when considering their trunk lengths (Jaspers et al. 2023), but to the house they create. The house enables them to drastically increase their exchange surface. Three biomass-to-volume ratios were calculated for this taxon: the biomass-to-volume ratio of the body (as calculated in Jaspers et al. 2023), the biomass-to-volume ratio of the house, and the biomass-to-volume ratio of the body-house complex (explanatory schema; Supporting Information Fig. S1).

Initially, the following formula (Eq. 1; from Lombard et al. 2009) was used to estimate carbon mass of the body (CM_{body}; μgC) from trunk length (L_{trunk}; μm):

$$CM_{body} = 1.06 \times 10^{-7} \times L_{trunk}^{2.6} \times 10^{-6} \quad (1)$$

Using actual or estimated carbon mass values, body biovolume (BV_{body}; mm^3) can be determined using the following formula (Eq. 2; Lombard et al. 2009):

$$BV_{body} = \frac{CM_{body}}{47.66} \quad (2)$$

The wet mass of the bodies (WM_{body}) can be calculated by assuming that their density is equal to the density of seawater (dsw = 1.025 g cm^3) (Knutsen 2001) (Eq. 3):

$$WM_{body} = BV_{body} \times dsw \times 10^{-3} \quad (3)$$

The biomass-to-volume ratio of the body was calculated by dividing the carbon mass by the estimated wet mass. This gave a body biomass-to-volume ratio of around 4.65% for larvaceans (as reported in Jaspers et al. 2023).

Secondly, the formula given by the study of Lombard and Kiørboe (2010) was used to estimate the house diameter (D_{house}; μm) using actual or estimated trunk length values (Eq. 4):

$$D_{house} = 7.22 \times L_{trunk} - 595 \quad (4)$$

The house is assumed to be spherical, so the biovolume of the house (BV_{house}; mm^3) is calculated using the following formula (Eq. 5):

$$BV_{house} = \frac{(D_{house} \times 10^{-3})^3}{2} \times \pi \times \frac{4}{3} \quad (5)$$

As before, we can estimate the wet mass of a house using the density of seawater (Eq. 3).

The carbon mass of a house (CM_{house}; μm) is estimated from the carbon mass of the larvacean body according to the formula established by Sato et al. (2001) (Eq. 6):

$$CM_{house} = CM_{body} \times 0.153 \quad (6)$$

The biomass-to-volume ratio of the house was calculated in a similar way. This provided an average biomass-to-volume ratio for the house of 0.03%. Finally, the biomass-to-volume-ratio of the body-house complex was determined by calculating the sum of the carbon mass of the house and body over the sum of the wet mass of the house and body. This gave an average body-house biomass-to-volume ratio of 0.07%.

Statistical analyses

To determine the relationships between each trait, linear regressions (model II; Sokal and Rohlf 2012) followed by statistical tests (Pearson test) were carried out to test the significance of the observed trends. Furthermore, the clearance,

respiration, and carbon mass-specific growth rates obtained from two different equations were compared. The first type of equation only took the mass (carbon or wet) into account, while the second type of equation took the mass (carbon or wet) and the biomass-to-volume ratio into account. Three criteria were compared with (1) the coefficient of determination R^2, (2) the Akaike Information Criterion, where we assumed that the second type of equation was better when the delta was superior to 2 (delta is the difference between the Akaike Information Criterion values of each model) (Anderson and Burnham 2002), and (3) the Akaike weight, where a model with an Akaike value 10 times greater than the value of the other models was considered to be more significant (Royall 2017).

For the predator–prey size ratio, linear regression was weighted by the percentage of efficiency in order to calculate the optimal prey size as a function of biomass-to-volume ratio. Mean and standard deviation of the predator/prey size ratio for each species were calculated. We then calculated the maximum and minimum (corresponding to a normal distribution) using the mean, standard deviation, and the second quartile (corresponding to the optimal prey size). The scripts used for these analyses are freely available on GitHub (https://github.com/lemoinejulie/database_zooplankton_traits).

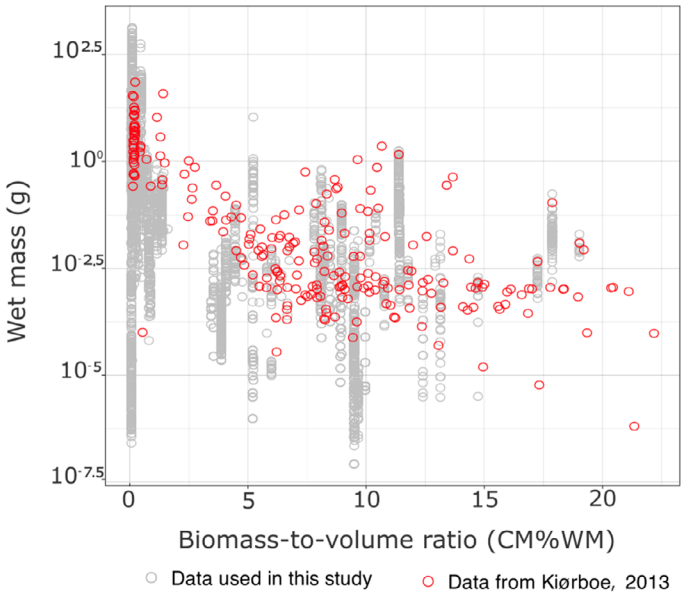

Fig. 1. Continuum of biomass-to-volume ratios in the planktonic kingdom. Wet mass (g) as a function of biomass-to-volume ratio (CM: carbon mass, WM: wet mass) based on all data from this study (gray circle), where biomass-to-volume ratio is assigned according to taxonomy following McConville et al. (2016). Data from Kiørboe (2013) (red circle), where carbon mass and wet mass were measured for the same individual, providing the actual biomass-to-volume ratio for each.

Results

Continuum of biomass-to-volume ratios

Across the planktonic kingdom (Supporting Information Fig. S2), all biomass-to-volume ratios appear to be represented (Fig. 1; red dots), reinforcing the idea that the biomass-to-volume ratio is a continuous variable. However, the dataset used in this study has some gaps, with intermediate carbon compositions being less represented compared to other body compositions (Fig. 1; gray dots).

Physiological traits

Our regression analyses confirmed that clearance and respiration rates increased significantly with carbon mass (Fig. 2a, b) as well as wet mass (Fig. 2d, e). Two groups of points composed of organisms with very different body compositions were clearly distinguishable by their carbon mass in the case of clearance rate (Fig. 2a) and by their wet mass in the case of respiration rate (Fig. 2e). Conversely, the carbon mass-specific growth rate decreased as a function of carbon mass (Fig. 2c) and wet mass (Fig. 2f), with greater variability than that observed in the relationships between respiration and clearance. The relationship between carbon mass-specific rate and biomass-to-volume ratio enabled a deeper investigation into the differences linked to biomass-to-volume ratios. Indeed, for the carbon-mass specific, only clearance (Fig. 3a) and respiration rates (Fig. 3b) changed significantly with biomass-to-volume ratio. For the wet mass-specific, only respiration (Fig. 3e) and growth (Fig. 3f) rates changed significantly with biomass-to-volume ratio. Nevertheless, the correlation coefficient and R^2 associated with the carbon-mass specific respiration rate and the wet-mass specific growth rate were very low.

While directly related to feeding, the assimilation efficiency seemed to be neither influenced by size nor carbon proportion of the organisms (Fig. 4).

Comparison equations

The addition of biomass-to-volume ratio to the models of respiration, clearance, and growth based on carbon mass and wet mass increased or did not alter the explanatory power (Table 1, R^2). Indeed, the delta of the second-order Akaike criterion (Table 1, Δi) was greater than 2 in the models that included biomass-to-volume ratio in addition to either wet or carbon mass in the majority of cases, indicating that adding biomass-to-volume ratio was relevant for estimating these rates (clearance, respiration, and growth). The Akaike Information Criterion was only less than 2 for the model including wet mass to estimate clearance rate and the model including carbon mass for estimating growth rate, suggesting that adding biomass-to-volume ratio was not relevant for estimating clearance rate when using wet mass or growth rate when using carbon mass. These results were confirmed by the Akaike weights (Table 1, ωi), which were approximately 10 times higher in the majority of models that included the biomass-to-volume ratio. Only for the models using wet mass vs. clearance rate and carbon mass vs. growth rate, the

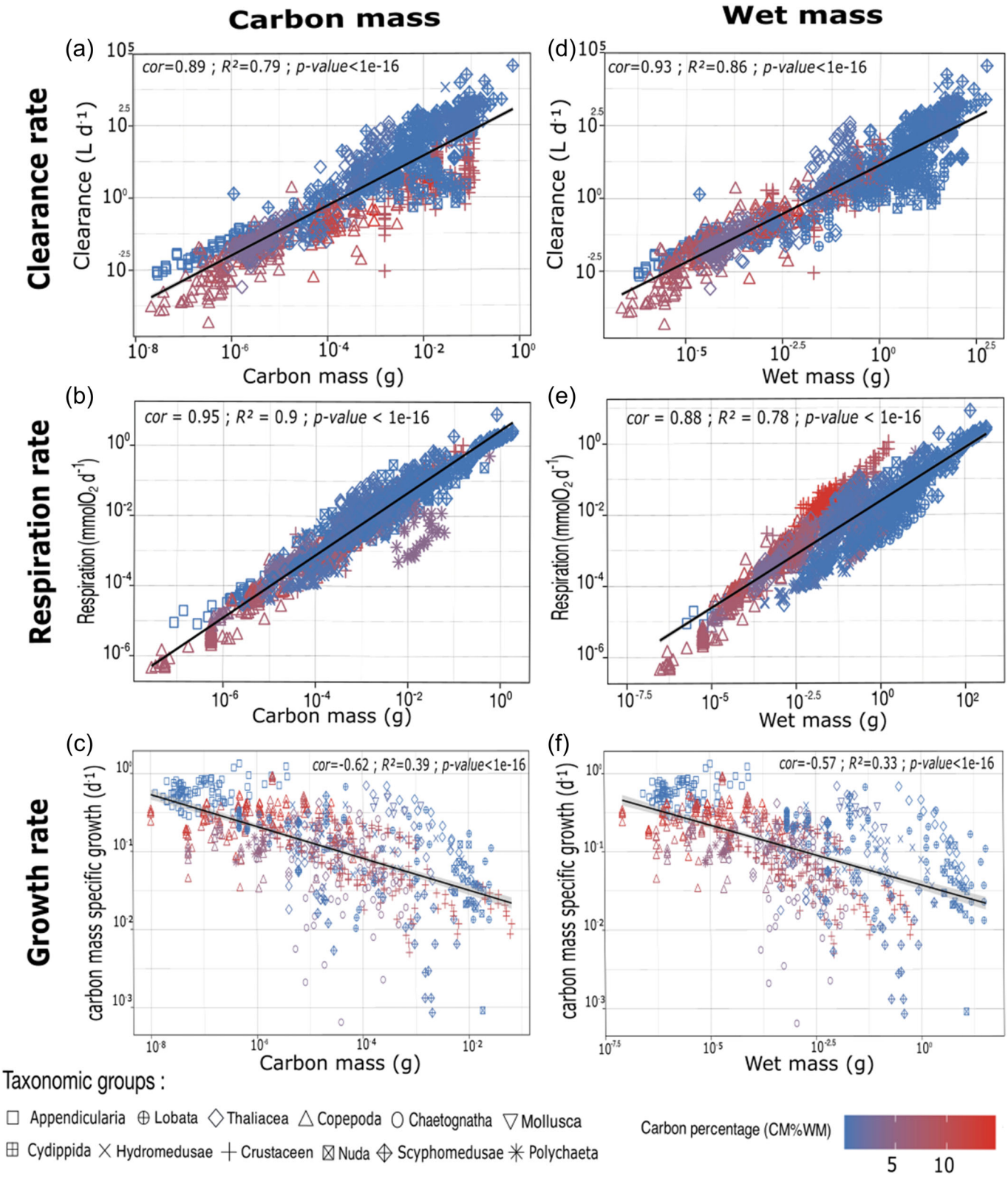

Fig. 2. Trade-offs between physiological rates and two types of mass (carbon and wet) (**a**) Clearance rate (L d^{-1}), (**b**) respiration rate (mmolO_2 d^{-1}), (**c**) carbon mass-specific growth rate (d^{-1}) as a function of carbon mass (g). (**d**) Clearance rate (L d^{-1}), (**e**) respiration rate (mmolO_2 d^{-1}), (**f**) carbon mass-specific growth rate (d^{-1}) as a function of wet mass (g). The shape corresponds to the taxonomic groups.

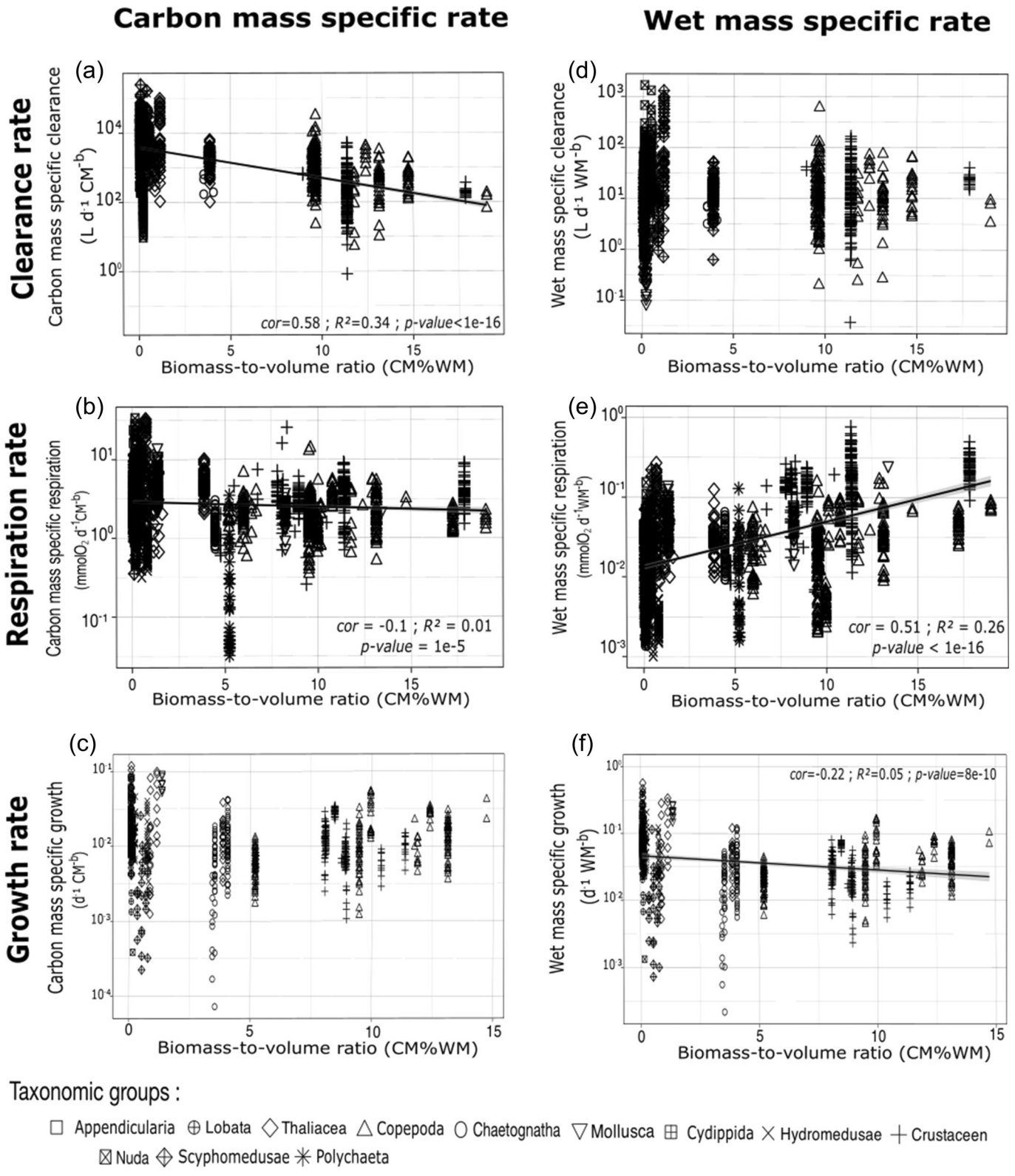

Fig. 3. Trade-offs between physiological rates and biomass-to-volume ratio by functional group. (**a**) Carbon-mass specific clearance rate (L $d^{-1}CM^{-b}$), (**b**) carbon-mass specific respiration rate ($mmolO_2$ d^{-1} CM^{-b}), (**c**) carbon-mass specific growth rate (d^{-1} CM^{-b}) as a function of biomass-to-volume ratio (carbon mass % wet mass). (**d**) Wet-mass specific clearance rate (L $d^{-1}WM^{-b}$), (**e**) wet-mass specific respiration rate ($mmolO_2$ $d^{-1}WM^{-b}$), (**f**) wet-mass specific growth rate (d^{-1} WM^{-b}) as a function of biomass-to-volume ratio (carbon mass % wet mass). The shape corresponds to the taxonomic groups.

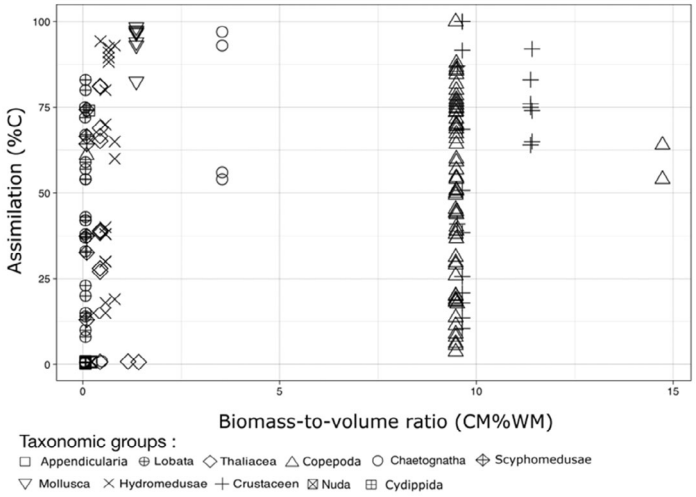

Fig. 4. Assimilation rate as a function of biomass-to-volume ratio (CM: carbon mass, CW: wet mass). The shape corresponds to the taxonomic groups.

addition of biomass-to-volume ratios did not improve the ωi criterion. This suggested that, except for wet mass vs. clearance and growth vs. carbon mass, models including biomass-to-volume ratio were significantly better than models based on either carbon or wet mass alone.

Ecological traits

Including biomass-to-volume ratios also helped represent the predator–prey size ratio, although this was impacted by the feeding mode. We analyzed two parameters: the optimal size of prey for each predator, obtained using the percentage of efficiency, and the range of prey sizes that predators were capable of capturing (minimum size – maximum size). For the feeding-current feeders, a significantly negative relationship between biomass-to-volume ratio and predator–prey size ratio was observed (Fig. 5a), indicating that the optimal prey size was significantly smaller for low-carbon-percentage organisms compared to that of high-carbon-percentage organisms. The range of catchable prey was higher for low-carbon than for high-carbon organisms, meaning that low-carbon organisms were able to catch prey over a larger size range than other organisms. While regression analyses reveal the relationship between the predator–prey size ratio and biomass-to-volume ratio, taxonomic differences seem to play a key role in shaping these relationships. They were driven by tunicates, whose predator–prey size ratio ranged between 10^1 and 10^6 $\mu m_{predator}$ $\mu m_{prey}{}^{-1}$, but this pattern was also valid for scyphomedusae, whose ratio ranged between 10^0 and 10^4 $\mu m_{predator}$ $\mu m_{prey}{}^{-1}$, which was greater than that of non-gelatinous organisms, ranging between 10^1 and 10^3 $\mu m_{predator}$ $\mu m_{prey}{}^{-1}$. Only lobate ctenophores and hydromedusae feeding-current feeders did not follow this relationship and displayed predator–prey size ratios between 10^0 and 10^2 $\mu m_{predator}$ $\mu m_{prey}{}^{-1}$.

For the passive ambush feeders, a significantly positive relationship between biomass-to-volume ratio and predator–prey size ratio was found (Fig. 5b), indicating that, in contrast to the feeding-current feeders, the optimal prey size was significantly smaller for intermediate body composition than for low-carbon organisms. Nevertheless, the range of catchable prey was not impacted by body composition for this feeding mode. This relationship also appears to be influenced by two distinct taxonomic groups: hydromedusae and pteropods. However, the limited data available for this feeding mode prevent a higher level of taxonomic resolution, making it unclear whether this relationship is driven solely by their biomass-to-volume ratios. For active ambush feeders (Fig. 5b), no significant relationship was found with the biomass-to-volume ratio. This indicated that there was no impact of body composition on the catchable and optimal prey size for this feeding mode. Finally, according to our knowledge, there is no gelatinous equivalent for the cruise feeding mode.

Discussion

The impacts of the biomass-to-volume ratio on physiological traits

Respiration rate is a function of metabolic expenditures varying from a fixed maintenance cost to variable costs due to various activities such as swimming, feeding, etc. (Ware 1978). These costs are related to the active mass of the organism for which carbon mass is supposed to represent a better proxy than wet mass (Acuña et al. 2011). In this study, respiration rates cannot be summarized solely in terms of fixed maintenance costs (basal respiration). The measured values are closer to metabolic expenditure since the experimental protocols cannot isolate basal respiration. Thus, results showed that metabolic expenditures seem to be more important for gelatinous organisms than for non-gelatinous organisms. This may be because gelatinous organisms have a larger total mass relative to their active mass, which increases their swimming costs as they need to move more mass through the water for each distance traveled compared to non-gelatinous organisms. For clearance rates, whatever strategy is used (using filtration current, chemosensing, etc.) finding food is directly dependent on the encounter probability of its prey. Here, the surface area interacting with the environment is key. For the same exchange surface, clearance rate is the same, no matter the body composition of the organism. Nevertheless, feeding for gelatinous organisms is more advantageous because a greater volume of water can be filtered for the same active mass compared to non-gelatinous organisms. For example, despite having a body carbon content similar to that of copepods, larvaceans exhibit significantly higher growth rates (Jaspers et al. 2023), a trait that could be attributed to the increased exchange surface provided by their house. Finally, for the same carbon mass, highly evolved visual predators such as fish achieve clearance rates comparable to those of gelatinous

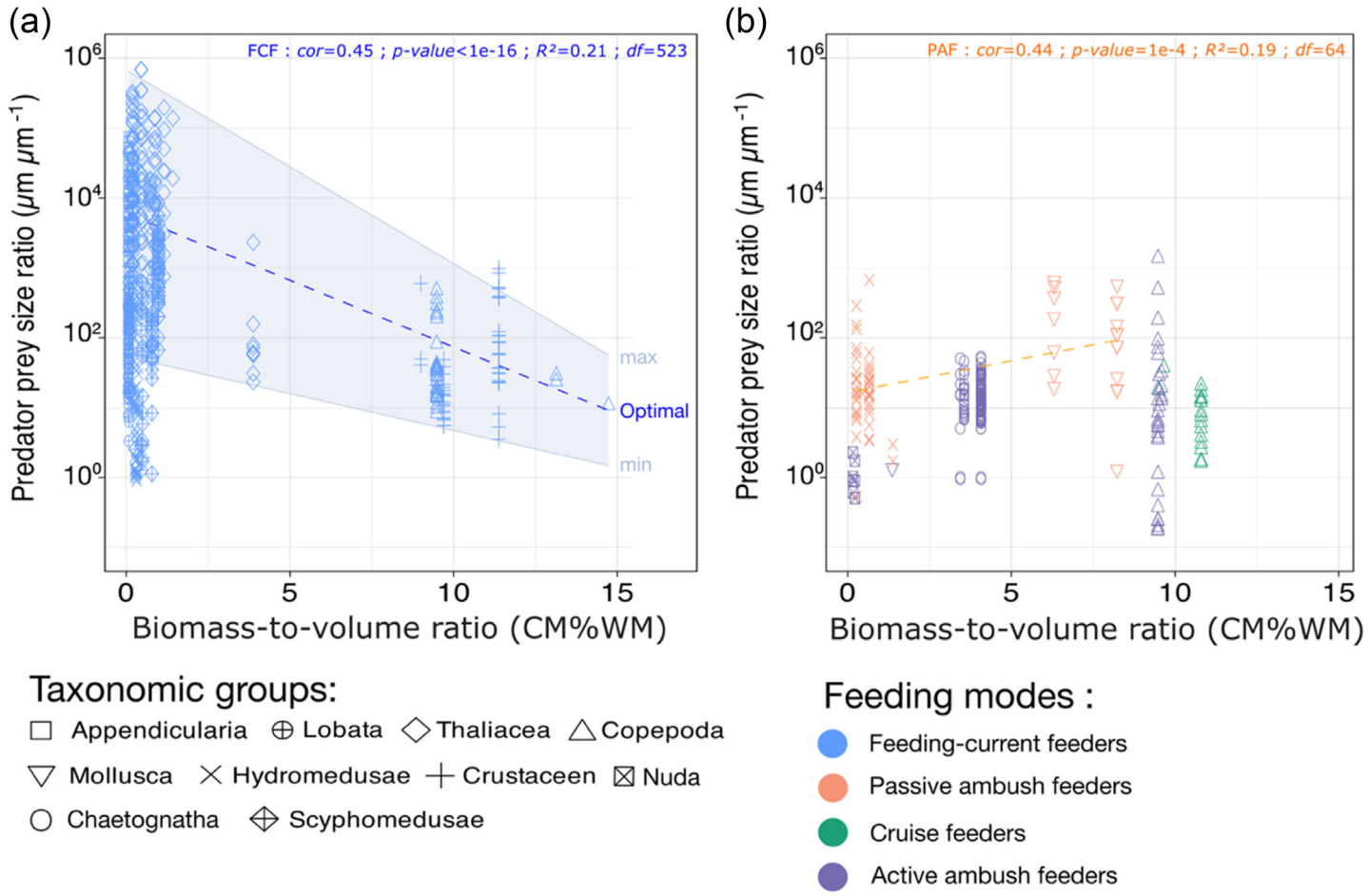

Fig. 5. Predator–prey size ratio as a function of biomass-to-volume ratio (CM%WM) for marine organisms spanning several orders of magnitude in size and prey size ratios, split by feeding mode with (**a**) feeding-current feeders (blue), and (**b**) passive ambush feeders (orange), active ambush feeders (purple) and cruise feeders (green). The dotted line represents the predicted optimal size of prey and interval represents the range of catchable prey following a normal distribution. The interval represents the maximum and minimum, shape corresponds to the taxonomic groups and colors represent feeding modes. Statistical parameters refer to the predicted optimal prey size (dotted line) for feeding-current feeders (FCF) and passive ambush feeders (PAF). CM: carbon mass. WM: wet mass.

organisms, highlighting the exceptional optimization of their feeding mechanisms (Acuña et al. 2011). Furthermore, the assimilation efficiency does not appear to be influenced by the size or the carbon content of the organisms. Directly linked to feeding, but occurring after the filtration process, is it possible that assimilation has not undergone any specific adaptation unlike the rate of clearance? Thus, this complementary analysis of the two biomass measures presented in this study underlines the importance of biomass-to-volume ratios of organisms for their overall fitness.

Several trade-offs are involved for growth rates

The impact of biomass-to-volume ratio on growth rate (defined as daily carbon mass gain) remains inconclusive. While McConville et al. (2016) reported a negative correlation with specific growth rate, our results show no significant relationship. Zooplankton communities typically cluster into gelatinous (~ 0.5% carbon) or non-gelatinous (5–10% carbon) forms, with few intermediate forms (Kiørboe 2013; McConville et al. 2016; Dölger et al. 2019), suggesting bimodality in terms of biomass. This may reflect two growth optima, with intermediate forms exhibiting lower growth rate than gelatinous and non-gelatinous organisms. Growth rate integrates multiple physiological processes (e.g., respiration, clearance, predator–prey size ratio), each involving trade-offs that obscure simple relationships with the biomass-to-volume ratio. Moreover, at the population level, growth rate includes both organismal growth rate and population growth (fecundity, fertilization, hatching success, etc.) and mortality rates, adding further complexity. Our study focused on 7 of 23 zooplankton traits described by Litchman et al. (2013), so unexamined trade-offs may help explain the bimodal success in the biomass-to-volume ratio.

In addition, according to Kiørboe (2013), this bimodality reflects a balance between feeding and survival. On the one

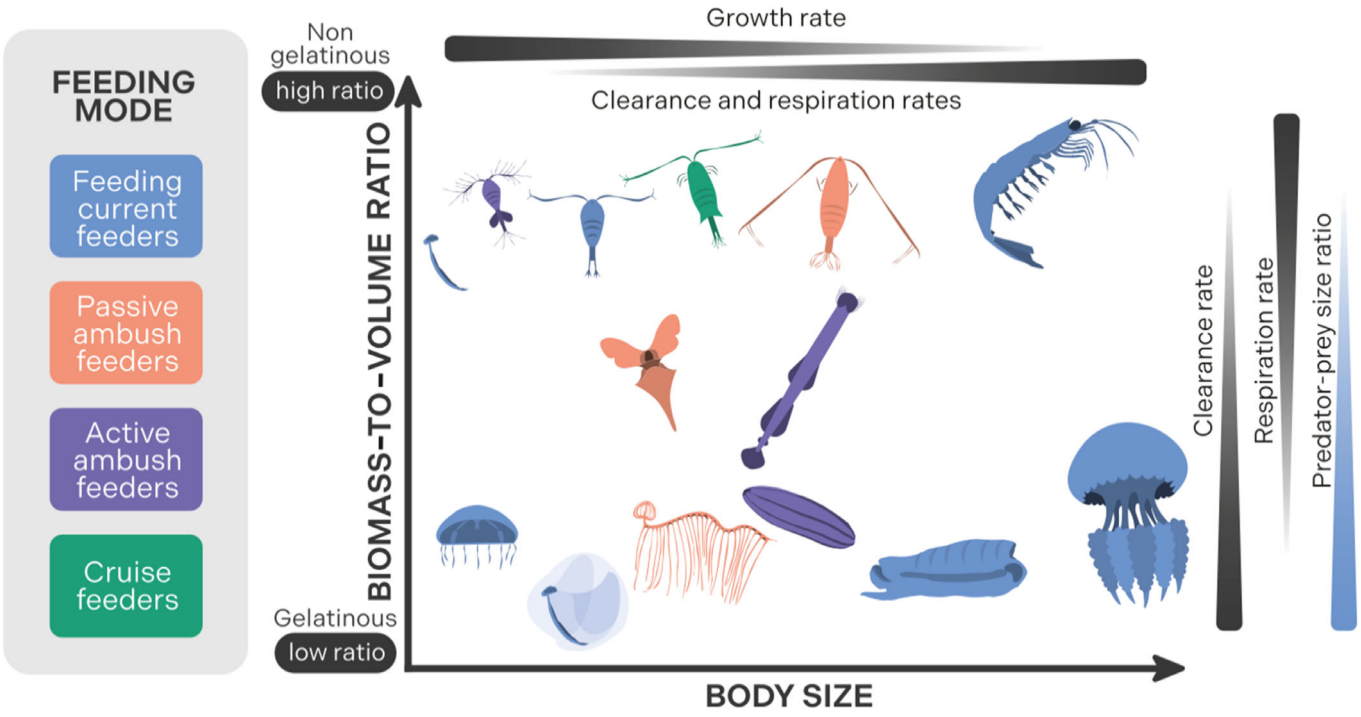

Fig. 6. Trade-offs among different functional traits of gelatinous and non-gelatinous zooplankton. Representation of zooplankton diversity using two quantitative variables: body size and biomass-to-volume ratio. Each organism uses a different feeding mode symbolized by the color in this diagram (blue: feeding current feeders, orange: passive ambush feeders, purple: Active ambush feeders, green: cruise feeders). The gray arrows represent the variation in different physiological parameters as a function of body size or biomass-to-volume ratio. The blue arrow represents the variation in the predator—prey size ratio as a function of biomass-to-volume ratio for feeding current feeders only. Schematic not to scale. Figure done by Thomas Boniface (Institut de la Mer de Villefranche (IMEV)).

hand, dense-bodied zooplankton are efficient hunters but more visible and nutritious to predators. On the other hand, gelatinous zooplankton have efficient prey capture structures but poor escape abilities, which may potentially fully cancel the advantage of being large in escaping small predators. Indeed, a large number of small amphipods, copepods, or even decapods are known to specifically target gelatinous plankton as prey (Heron 1973; Diebel 1988; Kawaguchi and Takahashi 1996). Intermediate forms, typically ambush feeders, may benefit from lower density for buoyancy control but are constrained by their foraging mode (Kiørboe 2011, 2013).

The impacts of the biomass-to-volume ratio on ecological traits

Our results demonstrate that the biomass-to-volume ratio significantly influences prey size selection in feeding-current strategies. Feeding-current feeders, present across various planktonic taxa and sizes (Fig. 6), are generally adapted to feed on small, non-evasive prey, mainly phytoplankton, but also bacteria for some gelatinous organisms (Kiørboe 2011). Gelatinous feeding-current feeders tend to capture a broader range of prey sizes, with a preference for smaller organisms. This may be an adaptation to increase encounter rates, as smaller organisms are more abundant (Bodenheimer 1938; Sheldon et al. 1972), which is a trend seen in both terrestrial and marine environments (Cyr et al. 1997; White et al. 2007; Gjoni and Glazier 2020). Additionally, the delicate filtering structures of gelatinous filter feeders are better suited to capturing less-active prey, thereby reducing the risk of mechanical damage (Wirtz 2012).

In contrast, no clear relationship between predator–prey size ratio and body composition was observed in ambush feeding strategies, either active or passive, likely due to low taxonomic resolution. This may be because ambush feeders rely more on specialized appendages (e.g., mandibles, tentacles, teeth), whose size scales isometrically with body size (except for pteropods), leading to relatively constant predator–prey size ratios. For instance, chaetognaths are considered neutral predators due to this isometry (Wirtz 2012). Moreover, ambush feeding involves handling time, as these predators typically consume large, active prey. This necessitates strong, robust capture organs and limits the development of larger, yet more fragile, feeding structures. Gelatinous zooplankton face similar trade-offs requiring a balance between encounter and handling rates to optimize feeding efficiency (Hansson and Kiørboe 2006). For example, cnidarians use specialized stinging cells (cnidocytes) to subdue relatively large prey, including fish larvae and even small fish (Damian-Serrano et al. 2021).

On the other hand, feeding-current feeders rely on pump-generated flow to overcome head pressure and drive water through filtration structures (Kiørboe 2011). These structures vary across taxa, ranging from externally secreted mucus nets (e.g., tunicates, pteropods) to specialized appendages such as tentacles or maxillae (Rosenberg 1980). Filtration efficiency is governed by encounter rates and hydrodynamic factors (Dölger et al. 2019), and improves with larger filtering surfaces, which are typically found in organisms with low biomass-to-volume ratios (Acuña et al. 2011). The effectiveness of these systems depends on whether prey capture is mediated by cellular processes (e.g., secretion, cnidocytes) or specialized organs (e.g., mouthparts). Since metazoan cell size is relatively constant, generally around tens of microns (Machalek 2005), and organismal growth is primarily driven by increased cell number (Amodeo and Skotheim 2016), the prey size targeted by such mechanisms remains relatively unchanged with predator size. This may explain why gelatinous feeding-current feeders consistently capture smaller prey relative to their body size. These findings highlight the importance of biomass-to-volume ratio and feeding mode in prey selection, and suggest that incorporating prey specificity by functional group may reduce uncertainty in zooplankton grazing models, which has been shown as the greatest source of uncertainty in modeling exercises conducted to date (Sailley et al. 2013; Petrik et al. 2022; Rohr et al. 2023).

Repositioning larvaceans and pteropods in this continuity of biomass-to-volume ratios

Larvaceans have been termed as super-filters owing to their sophisticated filtration system (Conley et al. 2018; Jaspers et al. 2023). This enables them to prey over the widest range of predator–prey size ratios in the plankton (> 10,000 : 1 to less than 10 : 1) and to capture prey items as small as bacteria and large viruses (Conley et al. 2018; Jaspers et al. 2023). For calculating these predator–prey size ratios, the predator size is generally based on the trunk size of the larvacean only; hence, without taking the size of the tail or its house into account. This calculation has led larvaceans to be considered as different from other gelatinous zooplankton. Nevertheless, the house must be taken into account, as it amplifies the filtration surface and therefore the encounter rates with prey items. In this study, we considered the body and house as one complex (wet mass) and the body as the active mass (carbon mass) of the larvacean. By taking the body-house complex into account, we show that physiological rates are consistent with those observed in organisms of comparable body composition.

Similarly, pteropods utilize extensive mucous feeding webs, spanning 5–10 times their body diameter (Gilmer and Harbison 1986); thereby augmenting their exchange surface for prey capture akin to the larvacean house. However, due to limited data, we were unable to include the biomass-to-volume ratio of the body-mucus web complex for pteropods in our analyses. Future work incorporating these structures may reveal that their biomass-to-volume ratios are comparable to other gelatinous zooplankton, especially considering that pteropods can produce meter-scale webs from centimeter-scale bodies (Gilmer 1974).

Limitations and uncertainties

It is important to note that these analyses are subject to numerous limitations and uncertainties. One of the greatest uncertainties is that a significant bias can be found in relation to the biomass-to-volume ratio, as it has been attributed at least by species and not by individual. This variability, visible in all graphs where the biomass-to-volume ratio is used as an explanatory variable, reduces the certainty of the results. Nevertheless, this bias is difficult to reduce since only a few studies have simultaneously measured wet mass, carbon mass, and a physiological rate, providing the true biomass-to-volume ratio of each individual. However, the scarcity of such data represents an obstacle to understanding the trade-offs involved in the biomass-to-volume ratio. Efforts to measure wet mass and carbon mass at the same time as physiological rates at the individual level seem to be essential to better characterize the advantages and disadvantages implied by a low biomass-to-volume ratio.

Conclusion

Our different results are showing that inspecting two important traits, size and biomass-to-volume ratio simultaneously, allows in a large number of cases to simplify most observations of physiological rates to a single relationship. This massive influence on other traits has led the size to be considered as a "master trait" (Litchman et al. 2013; Martini et al. 2021). Here we propose the biomass-to-volume ratio as an additional "master trait," acting together with size and having a profound influence on other functional traits, at a point that the classical separation of organisms within discrete functional types vanished and could be resumed within their essential differences of size and carbon density. To this end, we propose equations to represent, as simply as possible, the diversity of zooplankton organisms and the trade-offs involved in being more or less gelatinous (Fig. 6). In general, models use a unique biomass (carbon or wet) to estimate all physiological rates (clearance, respiration, growth, etc.); nevertheless, this simplification leads to over- or under-estimations of rates depending on the body composition of planktonic organisms. Taking into account the right mass for the right process is the first step in integrating a gelatinous functional trait. We show that the incorporation of the biomass-to-volume ratio can correct the estimate of physiological rates when the biomass used for the estimates is not the one

involved in the process (e.g., the wet mass for estimating the respiration rate).

Furthermore, new trade-offs could be found if we continue to analyze the relationship between the biomass-to-volume ratio and other parameters. For example, decreasing the biomass-to-volume ratio could have an effect on mortality by increasing the chances of encountering a predator due to a larger surface area. Finally, the incorporation of the biomass-to-volume ratio in dynamical models will require special attention. Indeed, we have considered this ratio as a continuous variable because, in terms of diversity, every body composition can be found in the ecosystem. Nevertheless, in terms of biomass, planktonic organisms converge towards gelatinous or non-gelatinous with low intermediate biomass. Hence, biogeochemical models that want to include the biomass-to-volume ratio will have to be careful not to overestimate the biomass of intermediate body composition.

Author Contributions

Julie Lemoine: methodology, software, writing—original draft preparation, review and editing, investigation, data curation, formal analysis. Sakina-Dorothée Ayata: formal analysis, discussion, feedback, writing—review and editing. Cornelia Jaspers: formal analysis, discussion and feedback, writing—review and editing. Fabien Lombard: conceptualization, formal analysis, discussion and feedback, writing—review and editing, funding acquisition, supervision.

Acknowledgments

This work has received funding from the European Union (GA#101059915—BIOcean5D) and received support through Schmidt Sciences via the Virtual Earth System Research Institute project CALISPO (Julie Lemoine, Fabien Lombard). Sakina-Dorothée Ayata acknowledges the support of the French Agence Nationale de la Recherche, under grant ANR-22-CE02-0023-1 (project TRAITZOO). Cornelia Jaspers was supported by Villum Fonden, Denmark (ID 25512). Views and opinions expressed are, however, those of the authors only and do not necessarily reflect those of the European Union. Neither the European Union nor the granting authority can be held responsible for them. A CC-BY public copyright license has been applied by the authors to the present document and will be applied to all subsequent versions up to the Author Accepted Manuscript arising from this submission, in accordance with the grant's open access conditions. We would like to thank Sean Colin for his expertise in jellyfish feeding modes and Thomas Boniface for drawing the illustrations.

Conflicts of Interest

None declared.

Data Availability Statement

In agreement with the FAIR principle for Open Science, the databases used for these analyses and the scripts generating the results presented in this article are stored in a GitHub repository (https://github.com/lemoinejulie/database_zooplankton_traits) and are publicly accessible under the CC-BY 4.0 license. Figure 6 by Thomas Boniface (Institut de la Mer de Villefranche (IMEV)) is licensed under CC-BY 4.0.

References

Acuña, J. L., Á. López-Urrutia, and S. Colin. 2011. "Faking Giants: The Evolution of High Prey Clearance Rates in Jellyfishes." *Science* 333: 1627–1629. https://doi.org/10.1126/science.1205134.

Amodeo, A. A., and J. M. Skotheim. 2016. "Cell-Size Control." *Cold Spring Harbor Perspectives in Biology* 8: a019083. https://doi.org/10.1101/cshperspect.a019083.

Anderson, D. R., and K. P. Burnham. 2002. "Avoiding Pitfalls When Using Information-Theoretic Methods." *Journal of Wildlife Management* 66: 912. https://doi.org/10.2307/3803155.

Bax, N. J., P. Miloslavich, F. E. Muller-Karger, et al. 2019. "A Response to Scientific and Societal Needs for Marine Biological Observations." *Frontiers in Marine Science* 6: 395. https://doi.org/10.3389/fmars.2019.00395.

Beaugrand, G. 2005. "Monitoring Pelagic Ecosystems Using Plankton Indicators." *ICES Journal of Marine Science* 62: 333–338. https://doi.org/10.1016/j.icesjms.2005.01.002.

Bodenheimer, F. S. 1938. Problems of Animal Ecology. Oxford University Press.

Borkman, D. G., and T. Smayda. 2009. "Multidecadal (1959–1997) Changes in Skeletonema Abundance and Seasonal Bloom Patterns in Narragansett Bay, Rhode Island, USA." *Journal of Sea Research* 61: 84–94. https://doi.org/10.1016/j.seares.2008.10.004.

Boyce, D. G., K. T. Frank, and W. C. Leggett. 2015. "From Mice to Elephants: Overturning the 'One Size Fits All' Paradigm in Marine Plankton Food Chains." *Ecology Letters* 18: 504–515. https://doi.org/10.1111/ele.12434.

Brodeur, R. D., M. B. Decker, L. Ciannelli, et al. 2008. "Rise and Fall of Jellyfish in the Eastern Bering Sea in Relation to Climate Regime Shifts." *Progress in Oceanography* 77: 103–111. https://doi.org/10.1016/j.pocean.2008.03.017.

Condon, R. H., C. M. Duarte, K. A. Pitt, et al. 2013. "Recurrent Jellyfish Blooms Are a Consequence of Global Oscillations." *Proceedings of the National Academy of Sciences* 110: 1000–1005. https://doi.org/10.1073/pnas.1210920110.

Conley, K. R., F. Lombard, and K. R. Sutherland. 2018. "Mammoth Grazers on the Ocean's Minuteness: A Review of Selective Feeding Using Mucous Meshes." *Proceedings of the Royal Society B: Biological Sciences* 285: 20180056. https://doi.org/10.1098/rspb.2018.0056.

Cyr, H., R. H. Peters, and J. A. Downing. 1997. "Population Density and Community Size Structure: Comparison of Aquatic and Terrestrial Systems." *Oikos* 80: 139. https://doi.org/10.2307/3546525.

d'Elbée, J. 2016. Mémento de planctonologie marine. Editions Quae.

Damian-Serrano, A., S. H. D. Haddock, and C. W. Dunn. 2021. "The Evolution of Siphonophore Tentilla for Specialized Prey Capture in the Open Ocean." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2005063118. https://doi.org/10.1073/pnas.2005063118.

Diebel, C.E. 1988. "Observations on the Anatomy and Behavior of Phronima sedentaria (Forskal) (Amphipoda: Hyperiidea)." *Journal of Crustacean Biology* 8: 79–90. https://doi.org/10.1163/193724088X00107.

Dölger, J., T. Kiørboe, and A. Andersen. 2019. "Dense Dwarfs Versus Gelatinous Giants: The Trade-Offs and Physiological Limits Determining the Body Plan of Planktonic Filter Feeders." *The American Naturalist* 194: E30–E40. https://doi.org/10.1086/703656.

Gibbons, M. J., and A. J. Richardson. 2013. "Beyond the Jellyfish Joyride and Global Oscillations: Advancing Jellyfish Research." *Journal of Plankton Research* 35: 929–938. https://doi.org/10.1093/plankt/fbt063.

Gilmer, R. W. 1974. "Some Aspects of Feeding in Thecosomatous Pteropod Molluscs." *Journal of Experimental Marine Biology and Ecology* 15: 127–144. https://doi.org/10.1016/0022-0981(74)90039-2.

Gilmer, R. W., and G. R. Harbison. 1986. "Morphology and Field Behavior of Pteropod Molluscs: Feeding Methods in the Families Cavoliniidae, Limacinidae and Peraclididae (Gastropoda: Thecosomata)." *Marine Biology* 91: 47–57. https://doi.org/10.1007/BF00397570.

Gjoni, V., and D. S. Glazier. 2020. "A Perspective on Body Size and Abundance Relationships across Ecological Communities." *Biology* 9: 42. https://doi.org/10.3390/biology9030042.

Guidi, L., S. Chaffron, L. Bittner, et al. 2016. "Plankton Networks Driving Carbon Export in the Oligotrophic Ocean." *Nature* 532: 465–470. https://doi.org/10.1038/nature16942.

Hamner, W. M., L. P. Madin, A. L. Alldredge, et al. 1975. "Underwater Observations of Gelatinous Zooplankton: Sampling Problems, Feeding Biology, and behavior: Gelatinous Zooplankton." *Limnology and Oceanography* 20: 907–917. https://doi.org/10.4319/lo.1975.20.6.0907.

Hansen, B., P. K. Bjornsen, and P. J. Hansen. 1994. "The Size Ratio between Planktonic Predators and Their Prey." *Limnology and Oceanography* 39: 395–403. https://doi.org/10.4319/lo.1994.39.2.0395.

Hansen, P. J., P. K. Bjørnsen, and B. W. Hansen. 1997. "Zooplankton Grazing and Growth: Scaling within the 2–2-μm Body Size Range." *Limnology and Oceanography* 42: 687–704. https://doi.org/10.4319/lo.1997.42.4.0687.

Hansson, L. J., and T. Kiørboe. 2006. "Prey-Specific Encounter Rates and Handling Efficiencies as Causes of Prey Selectivity in Ambush-Feeding Hydromedusae." *Limnology and Oceanography* 51: 1849–1858. https://doi.org/10.4319/lo.2006.51.4.1849.

Heneghan, R. F., J. D. Everett, P. Sykes, et al. 2020. "A Functional Size-Spectrum Model of the Global Marine Ecosystem that Resolves Zooplankton Composition." *Ecological Modelling* 435: 109265. https://doi.org/10.1016/j.ecolmodel.2020.109265.

Henschke, N., J. D. Everett, A. J. Richardson, and I. M. Suthers. 2016. "Rethinking the Role of Salps in the Ocean." *Trends in Ecology & Evolution* 31: 720–733. https://doi.org/10.1016/j.tree.2016.06.007.

Heron, A. C. 1973. "A Specialized Predator-Prey Relationship between the Copepod *Sapphirina angusta* and the Pelagic Tunicate *Thalia democratica*." *Journal of the Marine Biological Association of the United Kingdom* 53: 429–435. https://doi.org/10.1017/S0025315400022372.

Hirst, A. G., J. C. Roff, and R. S. Lampitt. 2003. "A Synthesis of Growth Rates in Marine Epipelagic Invertebrate Zooplankton." In Advances in Marine Biology, 1–142. Elsevier. https://doi.org/10.1016/S0065-2881(03)44002-9.

Ibarbalz, F. M., N. Henry, M. C. Brandão, et al. 2019. "Global Trends in Marine Plankton Diversity across Kingdoms of Life." *Cell* 179: 1084–1097.e21. https://doi.org/10.1016/j.cell.2019.10.008.

Jaspers, C., R. R. Hopcroft, T. Kiørboe, et al. 2023. "Gelatinous Larvacean Zooplankton Can Enhance Trophic Transfer and Carbon Sequestration." *Trends in Ecology & Evolution* 38: 980–993. https://doi.org/10.1016/j.tree.2023.05.005.

Kawaguchi, S., and Y. Takahashi. 1996. "Antarctic krill (*Euphausia superba* Dana) eat salps." *Polar Biology* 16: 479–481. https://doi.org/10.1007/s003000050078.

Kawasaki, T. 1993. "Recovery and Collapse of the Far Eastern Sardine." *Fisheries Oceanography* 2: 244–253. https://doi.org/10.1111/j.1365-2419.1993.tb00139.x.

Kiørboe, T. 2011. "How Zooplankton Feed: Mechanisms, Traits and Trade-Offs." *Biological Reviews* 86: 311–339. https://doi.org/10.1111/j.1469-185X.2010.00148.x.

Kiørboe, T. 2013. "Zooplankton Body Composition." *Limnology and Oceanography* 58: 1843–1850. https://doi.org/10.4319/lo.2013.58.5.1843.

Kiørboe, T., A. Visser, and K. H. Andersen. 2018. "A Trait-Based Approach to Ocean Ecology." *ICES Journal of Marine Science* 75: 1849–1863. https://doi.org/10.1093/icesjms/fsy090.

Kiørboe, T., and A. G. Hirst. 2014. "Shifts in Mass Scaling of Respiration, Feeding, and Growth Rates across Life-Form Transitions in Marine Pelagic Organisms." *The American Naturalist* 183: E118–E130. https://doi.org/10.1086/675241.

Knutsen, T. 2001. "Determining the Mass Density of Marine Copepods and Their Eggs with a Critical Focus on Some of

the Previously Used Methods." *Journal of Plankton Research* 23: 859–873. https://doi.org/10.1093/plankt/23.8.859.

Litchman, E., M. D. Ohman, and T. Kiørboe. 2013. "Trait-Based Approaches to Zooplankton Communities." *Journal of Plankton Research* 35: 473–484. https://doi.org/10.1093/plankt/fbt019.

Lombard, F., and T. Kiørboe. 2010. "Marine Snow Originating from Appendicularian Houses: Age-Dependent Settling Characteristics." *Deep Sea Research, Part I: Oceanographic Research Papers* 57: 1304–1313. https://doi.org/10.1016/j.dsr.2010.06.008.

Lombard, F., F. Renaud, C. Sainsbury, A. Sciandra, and G. Gorsky. 2009. "Appendicularian Ecophysiology I." *Journal of Marine Systems* 78: 606–616. https://doi.org/10.1016/j.jmarsys.2009.01.004.

Luo, J. Y., R. H. Condon, C. A. Stock, et al. 2020. "Gelatinous Zooplankton-Mediated Carbon Flows in the Global Oceans: A Data-Driven Modeling Study." *Global Biogeochemical Cycles* 34: e2020GB006704. https://doi.org/10.1029/2020GB006704.

Lynam, C. P., M. J. Gibbons, B. E. Axelsen, et al. 2006. "Jellyfish Overtake Fish in a Heavily Fished Ecosystem." *Current Biology* 16: R492–R493. https://doi.org/10.1016/j.cub.2006.06.018.

Machalek, A. Z. 2005. "Chapter 1: An Owner's Guide to the Cell." In Inside the Cell. National Institute of General Medical Sciences.

Martini, S., F. Larras, A. Boyé, et al. 2021. "Functional Trait-Based Approaches as a Common Framework for Aquatic Ecologists." *Limnology and Oceanography* 66: 965–994. https://doi.org/10.1002/lno.11655.

McConville, K., A. Atkinson, E. S. Fileman, J. I. Spicer, and A. G. Hirst. 2016. "Disentangling the Counteracting Effects of Water Content and Carbon Mass on Zooplankton Growth." *Journal of Plankton Research* 39, no. 2: 246–256. https://doi.org/10.1093/plankt/fbw094.

Molina-Ramírez, A., C. Cáceres, S. Romero-Romero, et al. 2015. "Functional Differences in the Allometry of the Water, Carbon and Nitrogen Content of Gelatinous Organisms." *Journal of Plankton Research* 37: 989–1000. https://doi.org/10.1093/plankt/fbv037.

Negrete-García, G., J. Y. Luo, M. C. Long, K. Lindsay, M. Levy, and A. D. Barton. 2022. "Plankton Energy Flows Using a Global Size-Structured and Trait-Based Model." *Progress in Oceanography* 209: 102898. https://doi.org/10.1016/j.pocean.2022.102898.

Petrik, C. M., J. Y. Luo, R. F. Heneghan, J. D. Everett, C. S. Harrison, and A. J. Richardson. 2022. "Assessment and Constraint of Mesozooplankton in CMIP6 Earth System Models." *Global Biogeochemical Cycles* 36: e2022GB007367. https://doi.org/10.1029/2022GB007367.

Pitt, K. A., C. M. Duarte, C. H. Lucas, et al. 2013. "Jellyfish Body Plans Provide Allometric Advantages beyond Low Carbon Content." *PLoS One* 8: e72683. https://doi.org/10.1371/journal.pone.0072683.

Purcell, J. E. 2012. "Jellyfish and Ctenophore Blooms Coincide with Human Proliferations and Environmental Perturbations." *Annual Review of Marine Science* 4: 209–235. https://doi.org/10.1146/annurev-marine-120709-142751.

Quere, C. L., S. P. Harrison, I. Colin Prentice, et al. 2005. "Ecosystem Dynamics Based on Plankton Functional Types for Global Ocean Biogeochemistry Models." *Global Change Biology* 0: 051013014052005. https://doi.org/10.1111/j.1365-2486.2005.1004.x.

Rohr, T., A. J. Richardson, A. Lenton, M. A. Chamberlain, and E. H. Shadwick. 2023. "Zooplankton Grazing Is the Largest Source of Uncertainty for Marine Carbon Cycling in CMIP6 Models." *Communications Earth & Environment* 4: 212. https://doi.org/10.1038/s43247-023-00871-w.

Rosenberg, G. G. 1980. "Filmed Observations of Filter Feeding in the Marine Planktonic Copepod *Acartia clausii*." *Limnology and Oceanography* 25: 738–742. https://doi.org/10.4319/lo.1980.25.4.0738.

Royall, R. 2017. Statistical Evidence: A Likelihood Paradigm. 1st ed. Routledge. https://doi.org/10.1201/9780203738665.

Sailley, S. F., M. Vogt, S. C. Doney, et al. 2013. "Comparing Food Web Structures and Dynamics across a Suite of Global Marine Ecosystem Models." *Ecological Modelling* 261: 43–57. https://doi.org/10.1016/j.ecolmodel.2013.04.006.

Sato, R., Y. Tanaka, and T. Ishimaru. 2001. "House Production by *Oikopleura dioica* (Tunicata, Appendicularia) under Laboratory Conditions." *Journal of Plankton Research* 23: 415–423. https://doi.org/10.1093/plankt/23.4.415.

Serra-Pompei, C., F. Soudijn, A. W. Visser, T. Kiørboe, and K. H. Andersen. 2020. "A General Size- and Trait-Based Model of Plankton Communities." *Progress in Oceanography* 189: 102473. https://doi.org/10.1016/j.pocean.2020.102473.

Sheldon, R. W., A. Prakash, and W. H. Sutcliffe. 1972. "The Size Distribution of Particles in the Ocean: Particles in the Ocean." *Limnology and Oceanography* 17: 327–340. https://doi.org/10.4319/lo.1972.17.3.0327.

Sokal, R. R., and F. J. Rohlf. 2012. Biometry: The Principles and Practice of Statistics in Biological Research. 4th ed. W. H. Freeman.

Sutherland, K. R., L. P. Madin, and R. Stocker. 2010. "Filtration of Submicrometer Particles by Pelagic Tunicates." *Proceedings of the National Academy of Sciences* 107: 15129–15134. https://doi.org/10.1073/pnas.1003599107.

Turner, J. T. 2015. "Zooplankton Fecal Pellets, Marine Snow, Phytodetritus and the Ocean's Biological Pump." *Progress in Oceanography* 130: 205–248. https://doi.org/10.1016/j.pocean.2014.08.005.

Ware, D. M. 1978. "Bioenergetics of Pelagic Fish: Theoretical Change in Swimming Speed and Ration with Body Size." *Journal of the Fisheries Research Board of Canada* 35: 220–228. https://doi.org/10.1139/f78-036.

White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. "Relationships between Body Size and Abundance in Ecology." *Trends in Ecology & Evolution* 22: 323–330. https://doi.org/10.1016/j.tree.2007.03.007.

Wirtz, K. 2012. "Who Is Eating Whom? Morphology and Feeding Type Determine the Size Relation between Planktonic Predators and Their Ideal Prey." *Marine Ecology Progress Series* 445: 1–12. https://doi.org/10.3354/meps09502.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 15 November 2024
Revised 23 April 2025
Accepted 30 July 2025