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Disentangling the counteracting effects of water content and carbon mass on zooplankton growth

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Zooplankton vary widely in carbon percentage (carbon mass as a percentage of wet mass), but are often described as either gelatinous or non-gelatinous. Here we update datasets of carbon percentage and growth rate to investigate whether carbon percentage is a continuous trait, and whether its inclusion improves zooplankton growth models. We found that carbon percentage is continuous, but that species are not distributed homogenously along this axis. To assess variability of this trait *in situ*, we investigated the distribution of biomass across the range of carbon percentage for a zooplankton time series at station L4 off Plymouth, UK. This showed separate biomass peaks for gelatinous and crustacean taxa, however, carbon percentage varied 8-fold within the gelatinous group. Species with high carbon mass had lower carbon percentage, allowing separation of the counteracting effects of these two variables on growth rate. Specific growth rates, g (d^{-1}) were negatively related to carbon percentage and carbon mass, even in the gelatinous taxa alone, suggesting that the trend is not driven by a categorical difference between these groups. The addition of carbon percentage doubled the explanatory power of growth models based on mass alone, demonstrating the benefits of considering carbon percentage as a continuous trait.

KEYWORDS: water content; zooplankton; gelatinous; carbon percentage; growth

INTRODUCTION

Gelatinous zooplankton are a phylogenetically broad and ecologically important group of taxa found throughout the world's oceans. Their prey range from bacteria to fish (Sutherland *et al.*, 2010) and they exhibit an equally diverse range of life history strategies and body compositions. The high water content characteristic of this group can be expressed as carbon percentage (carbon mass as % of wet mass), with some taxa having carbon mass as low as 0.01% of their wet mass (Clarke *et al.*, 1992; Harbison, 1992; Lucas *et al.*, 2011; Kiørboe, 2013).

Interest in gelatinous zooplankton is linked to a growing appreciation of their impact on pelagic ecosystems and human activities (Richardson *et al.*, 2009; Purcell, 2012, Gibbons and Richardson, 2013). For example, the introduction of the ctenophore, *Mnemiopsis leidyi* to the Black Sea has had considerable financial implications for fisheries in the area (Shiganova and Bulgakova, 2000). Research on gelatinous zooplankton has grown apace with basic ecological interest in the physiology, trophic ecology and bloom dynamics of this group (Møller and Riisgård, 2007; Condon *et al.*, 2013; Gemmell *et al.*, 2013).

Based on a compilation of zooplankton body composition, Kiørboe (2013) found that most zooplankton species are either gelatinous (~0.5%) or non-gelatinous (5–10%), with comparatively few intermediates. Indeed, much research has been directed toward comparing and contrasting gelatinous versus non-gelatinous zooplankton. For example, compared to other planktonic animals, gelatinous zooplankton have higher carbon mass-specific feeding rates (Hamner *et al.*, 1975; Acuña, 2001; Acuña *et al.*, 2011), lower locomotion costs and higher specific growth rates (Hirst *et al.*, 2003; Pitt *et al.*, 2013). Indeed, gelatinous taxa such as salps are amongst the fastest growing metazoans (Bone, 1998).

The use of a categorical approach to zooplankton body composition (i.e. gelatinous versus non-gelatinous) contrasts with the treatment of carbon mass (Peters, 1983), which is used as a continuous variable in many models of growth (Hansen *et al.*, 1997; Gillooly *et al.*, 2002, Hirst *et al.* 2003). However, the carbon percentage of zooplankton species also varies widely, even among gelatinous taxa (Molina-Ramirez *et al.* 2015). A recent review suggested that water content was second only to body size in determining key aspects of the biology of zooplankton (Andersen *et al.*, 2015b). So far, empirical models of zooplankton growth use equations that are specific to various taxonomic groups (Hirst *et al.* 2003; Kiørboe and Hirst, 2014) and these equations have not yet been unified. As carbon mass and carbon percentage are both variable traits, it is important to consider them together in empirical models of zooplankton growth. Furthermore, quantifying the relationship between growth rate and carbon percentage may help to explain how carbon percentage functions as an evolutionary trait, and, e.g. why there are gelatinous representatives from six phyla found in the plankton.

In this study we have used both a meta-analyses approach and an *in situ* time series of zooplankton from weekly sampling at the Plymouth L4 time series (Smyth *et al.* 2015). We had three objectives. The first was to quantify the degree of variability in carbon percentage both in 'trait space' from the meta-analysis dataset and in a natural plankton assemblage, to gauge whether it was appropriate to treat water content as a continuous variable. The second aim was to investigate the degree of collinearity between carbon mass and carbon percentage, again both in a meta-assemblage and in the L4 assemblage. Dependent on the outcome of these two objectives, the third aim was to construct a simple empirical model of zooplankton growth that combines carbon mass and carbon percentage.

METHOD

Carbon percentage data

Ratios of wet mass to carbon mass were combined from a series of recent compilations (Kiørboe, 2013; Pitt *et al.*, 2013; Molina-Ramirez *et al.*, 2015). The amalgamated dataset with their sources is presented in Supplementary Information 1 online. Only concurrent measurements of carbon and wet mass of the same individual were used to calculate carbon percentage.

The degree of tissue dilution of zooplankton taxa has been expressed previously as body carbon content (Molina-Ramirez *et al.*, 2015). However, to avoid confusion with carbon mass, throughout this article it is referred to as 'carbon percentage' (carbon mass as a percentage of wet mass). For our comparisons the levels of taxonomic organization were selected based on functional diversity and body form (e.g. phylum for Chaetognatha, but orders Cydippida and Lobata).

In situ analysis

To investigate how species biomass was distributed along the spectrum of carbon percentage an *in situ* community, the L4 zooplankton time series (Western Channel Observatory, Plymouth) was used. The L4 sampling site is approximately 15 km south–west of Plymouth and undergoes seasonal stratification (Harris, 2010). Sampling at the L4 site consists of a pair of vertical hauls with a 200 μm WP-2 zooplankton net from 50 m to the surface (maximum depth 54 m). The nets are retrieved at 20 cm s^{-1} and are immediately fixed in 4% formaldehyde solution (Maud *et al.*, 2015). The zooplankton are then subsampled, counted and identified (Eloire *et al.* 2010). This zooplankton abundance times series has high resolution both temporally (weekly sampling) and taxonomically, with many taxa consistently identified to species level since 2009. To determine zooplankton biomass, a total of 3780 individuals from the formalin-preserved catches at L4 taken throughout 2014 and 2015 were measured. From standard length measurements (e.g. cnidarian bell height or diameter, copepod prosome length), length-carbon mass relationships from the literature were used to estimate carbon mass per individual. These length measurements were then aggregated into seasons, namely spring (March–May), summer (June–August), autumn (September–November) and winter (December–February) to account for the high intraspecific variability in length observed at L4 (Atkinson *et al*., 2015). This allowed us to derive season-specific mean carbon masses per individual, which were multiplied by numerical densities to estimate biomass density (mg C m^{-3}). Previously measured, L4-specific seasonal values of individual carbon biomass were used, when available (e.g. *Calanus helgolandicus;* Pond *et al.* 1996).

Of the approximately 189 taxa recorded at L4, only 22 contributed more than 0.5% to the total biomass for all species. To examine how biomass was distributed across the spectrum of carbon percentage, these taxa were assigned to $\log_2$ classes (0.1–0.2%, 0.2–0.4%, 0.4–0.8%, 0.8–1.6%, 1.6–3.2%, 3.2–6.4%, 6.4–12.8%, >12.8%) using the carbon percentage data in Supplementary Information 1 online. The distribution of carbon biomass in each carbon percentage category across the seasons was then calculated.

Growth rate data

Using the references from the appendices of Kiørboe and Hirst (2014) as a starting point, zooplankton growth rate data were extracted from the original sources and augmented by searching the literature. All growth rate data used here are in Supplementary Information 2 online.

To improve comparability of source data we restricted the meta-analysis to data from laboratory incubations with food available in high (assumed non-limiting) concentrations. By using only data collected under these conditions we suggest that the measurements are more directly comparable, with the observed patterns more likely to reflect the intrinsic biology of the species than external factors.

Published growth rates are normally expressed either as increase in length or body mass over time. When organism size was expressed as length, published length-mass regressions were used to convert to body carbon mass (Hirst, 2012; Kiørboe and Hirst, 2014). To express growth rates in the terms commonly used for zooplankton (as an exponential rate; see Hirst and Forster 2013), the mass-specific growth rate, g (d^{-1}) was determined as follows:

$$g = (\ln M_t - \ln M_0)/d$$

where M_t is mass at time, t, M_0 is mass at the previous time point, and d is the time period between the two measurements of mass (in days).

Growth data were temperature-corrected to 15°C using a Q_{10} of 2.8 (following Hansen *et al.*, 1997; Kiørboe and Hirst, 2014). General linear models (GLMs) were constructed in R (R Core Team, 2014) to determine the relationships between growth rate, carbon percentage and carbon mass. To determine whether there was collinearity between the predictor variables we examined the condition indices for the variables in the model using the *colldiag* function in the *perturb* package in R (Hendrickx, 2012). A condition index of greater than 30 is considered large (Belsley *et al.*, 1980) and suggests that the variable should be removed from the model.

When growth data were available for a species but carbon percentage values were not, the latter was estimated using the mean value for the highest level of taxonomic relatedness available. For instance, if composition values for a species were not available, then the composition values for all other species within the genus were averaged and used as an estimate. The estimates were typically at the genus level but no lower relatedness than family (38% estimated at family level, primarily for copepods).

Growth rate analysis

Four analyses were performed; the first two were based on mean and maximum growth rates for all zooplankton taxa in the dataset, the second two as above but for the classical gelatinous taxa only (Cnidaria, Ctenophora and Thaliacea). Maximum growth values were defined as the highest temperature-adjusted growth rate value available for each species. Issues of non-independence between data were avoided by using single growth rate values per species per study. For illustrative purposes only (i.e. the plots in Fig. 4), we adjusted all growth rates to a fixed body carbon mass of 1 mg C after correcting to 15°C. This mass correction was performed assuming $\log_{10}$ mass-specific growth (g) scales against $\log_{10}$ mass with a slope of −0.25 (Brown *et al.* 2004).

RESULTS

Variability in carbon percentage across the zooplankton

The range in body volume for two animals of equal carbon mass but at either end of the carbon percentage spectrum is show in Fig. 1. For the compiled dataset, the range in carbon percentage extended over four orders of magnitude, from 0.01% in the lobate ctenophore, *Bathycyroe fosteri*, to 19.02% in the copepod, *Calanus hyperboreus* (Figs 1 and 2a, Supplementary Information 1 online). The intervals between adjacent ranked species were small relative to the range covered (Fig. 2a), suggesting that water content could be considered as a continuous variable. The largest interval between species coincided with the shift from the classic gelatinous taxa to other zooplankton (i.e. from Thaliacea to Chaetognatha). However, this difference between species constituted a relatively small fraction of the total range (6.8%). In addition, there was overlap of classic gelatinous and non-gelatinous groups. For example, some chaetognaths were within the traditional gelatinous range (1.27 and 1.35% for *Pseudosagitta lyra (as P. scrippsae)* and *Pseudosagitta* (as *Sagitta) gazellae* respectively), whereas one tunicate had a carbon percentage which lay within the non-gelatinous range (3.87% for *Doliolum denticulatum*). This overlap of taxonomic groups was extensive across the spectrum of water content, as can be seen by the mixing of colour across Fig. 2. This was particularly the case among the Ctenophora and Thaliacea with the range of both taxa approaching two orders of magnitude in carbon percentage.

The wide variation in body carbon percentage observed at a species level in Fig. 1a is also summarized at the broader taxon level in Fig. 2b. Median values for groups do loosely cluster into gelatinous and non-gelatinous taxa following the bimodal distribution of species suggested by Kiørboe (2013). The ranges of all adjacent taxa (excluding lobate ctenophores) overlapped, with Thaliacea and Chaetognatha bridging the gap between the classical gelatinous and non-gelatinous taxa. The variability within groups was greater for gelatinous taxa, with the greatest range in the scyphomedusae, closely followed by the thaliaceans. The gelatinous taxa sort into their respective phyla when ranked (i.e. Lobata, Nuda, Cydippida for the Ctenophora, then Hydromedusae and Scyphomedusae for Cnidaria) suggesting that taxa within phyla are on average more similar to each other than with other phyla.

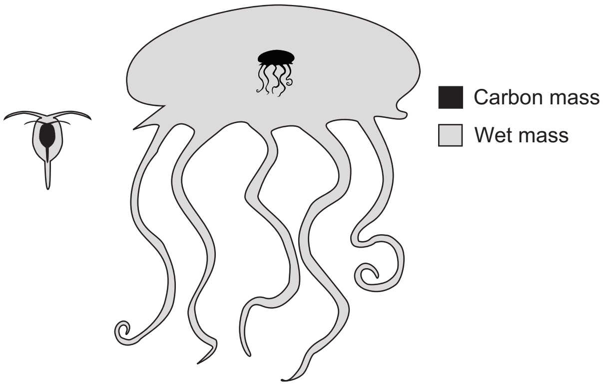

Fig. 1. Comparison of the relative carbon (black) and wet masses (grey) of *Calanus hyperboreus* (left, carbon percentage = 19.02%) and *Bathycyroe fosteri* (right, carbon percentage = 0.01%). The relative area of each shade is scaled as volume so the silhouettes are representative of true size.

In the natural assemblage sampled at the Plymouth L4 site (Figure 3) we have an alternative picture, namely how biomass is distributed along this spectrum of carbon percentage. At L4, biomass is distributed bimodally. The biomass is primarily concentrated in the categories that are either highly gelatinous (carbon mass 0.1–0.8% of wet mass) or non-gelatinous (6.4–>12.8%) However, there is considerable variability within the carbon percentage categories, as some gelatinous taxa are as much as 8 times larger in wet mass for the same carbon mass as others. The biomass in the intermediate categories (0.8–1.6 and 1.6–3.2%) was very low and below our threshold for inclusion. This area of the spectrum is populated by thaliaceans and large rhizostome scyphomedusae, which are either not commonly recorded at L4 (thaliaceans) or are rarely or poorly sampled by the 0.57 cm diameter nets used. Gelatinous taxa comprise a greater proportion of biomass in summer than the other seasons. In winter, chaetognaths (3.56%) have similar total biomass to the dominant copepods. There is also a broad trend of increasing carbon percentage through the year within the gelatinous taxa. In spring, the cydippids (the most gelatinous group frequently encountered at L4) are dominant, followed by Nuda (Beroe) in summer and finally hydromedusae and siphonophores in autumn.

Relationship between carbon mass and carbon percentage

There were negative relationships between carbon mass and carbon percentage, both in the meta-dataset (Fig. 4a) and in the *in situ* dataset (Fig.4b). While the more gelatinous taxa tended to have higher carbon mass there was considerable variability, with some organisms of similar carbon mass differing 100-fold in carbon percentage (Fig. 4). To ensure that collinearity was not influencing the growth model the condition

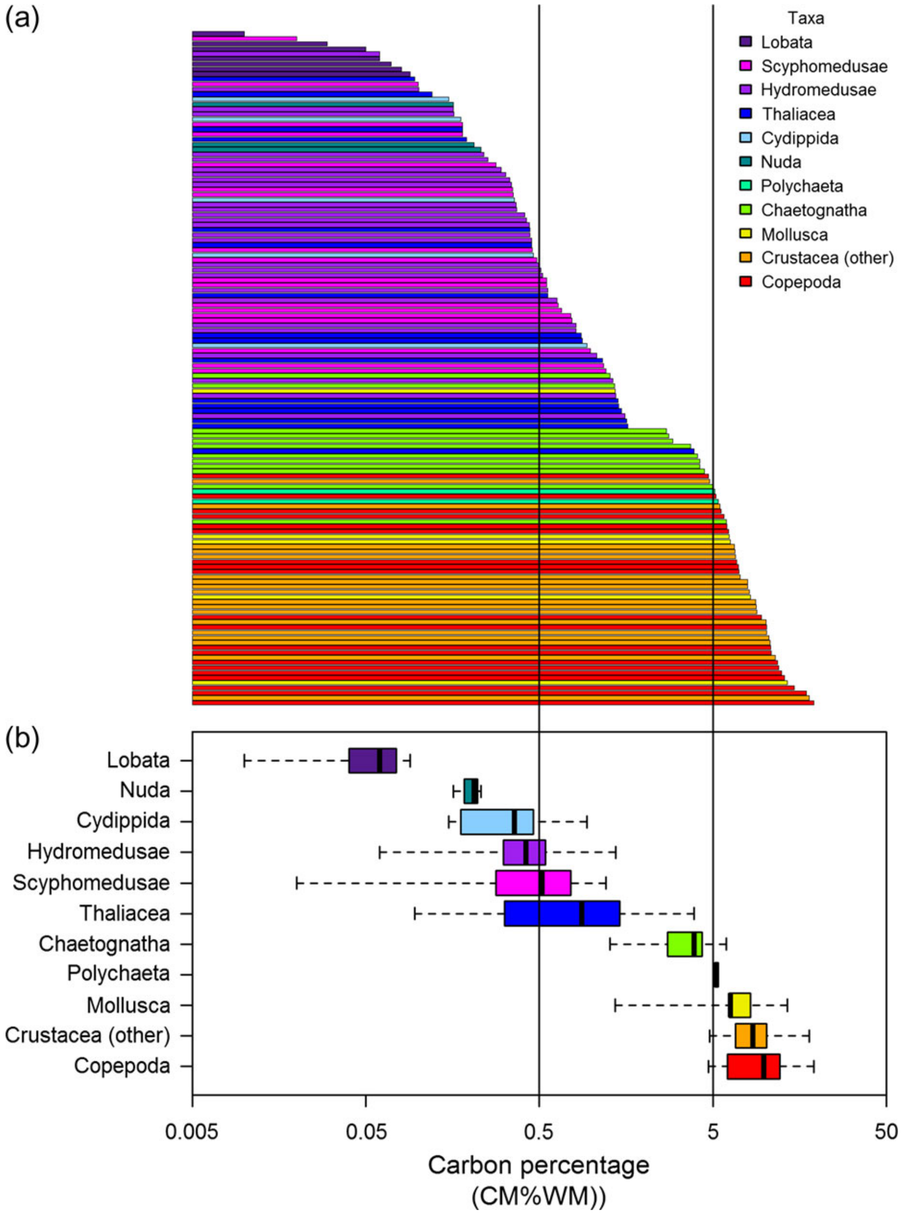

Fig. 2. (**a**) Zooplankton species ranked according to their carbon percentage (CM%WM; $\log_{10}$ scale), each horizontal bar represents a single species. Colours indicate taxonomic groups as detailed in the legend. (**b**) Zooplankton taxonomic groups ranked according to their carbon mass (as % of wet mass; $\log_{10}$ scale). Boxes indicate median, lower and upper quartiles with whiskers showing the range. (Vertical lines at 0.5 and 5 CM%WM represent the composition of the gelatinous and non-gelatinous taxa defined by Kiørboe (2013).).

indices for the variables were inspected. The highest condition index observed was 3.05, lower than the threshold of 30 suggested by Belsley *et al.* (1980) confirming that carbon mass and carbon percentage can be used in combination in models of zooplankton growth. As gelatinous and small organisms tend to grow fastest, the tendency for more gelatinous taxa to have higher carbon mass underlines the need to include both as covariates in our growth model.

Relationship between carbon percentage and growth rate

We first conducted GLMs on the subset of data comprising the classical gelatinous taxa alone. These showed that mean growth rate declined with increasing mass and increasing body carbon percentage. The GLMs on the whole dataset established that $\log_{10}$ mass-specific mean and maximum growth rate was significantly correlated with both $\log_{10}$ carbon mass and $\log_{10}$ body

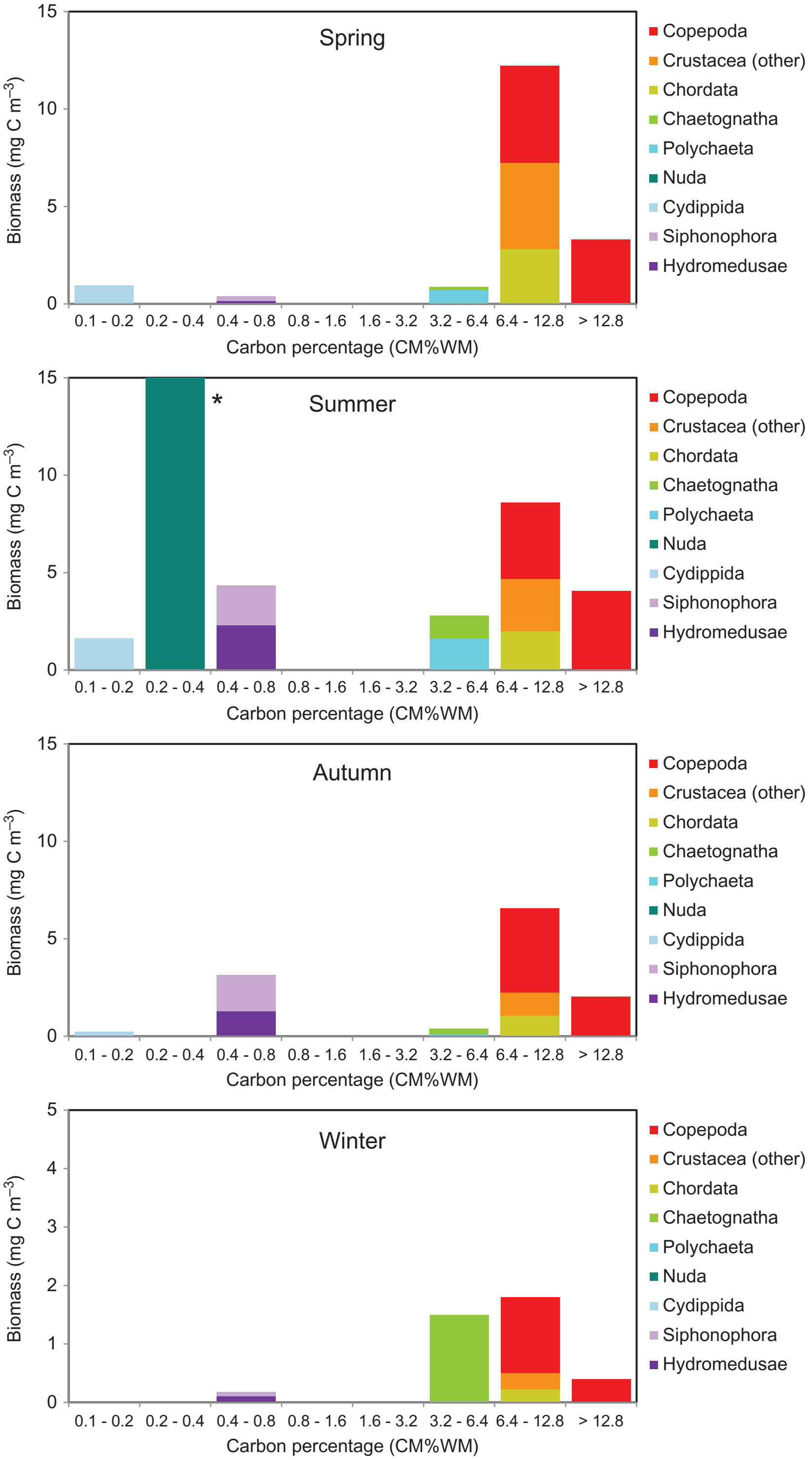

Fig. 3. Distribution of carbon biomass (mg C m^{-3}) between log$_2$ carbon percentage (CM%WM) categories through spring, summer, autumn and winter (2009–2015) at the L4 sampling site, Western Channel Observatory, Plymouth. The same colour coding of taxa is used as in Fig. 1—see legend. *Biomass value for the category 0.4–0.8 exceeds the scale in summer (34.4 mg C m^{-3}) as a result of 7 high abundance observations of *Beroe spp.* (of total 318 samples). Upper limit of biomass scale in winter is 5 mg C m^{3}.

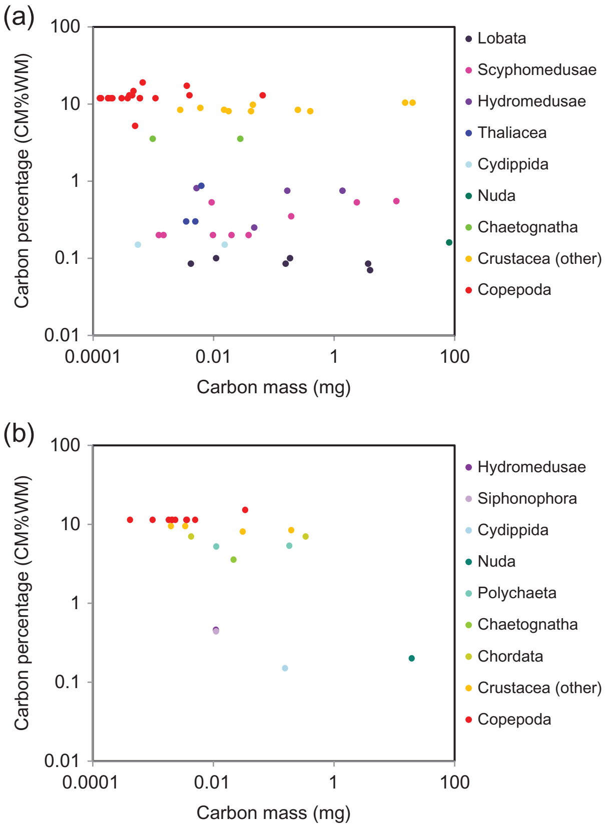

Fig. 4. Carbon percentage (CM%WM) as a function of carbon mass (mg) for the meta-analysis dataset (A, log carbon percentage = −0.26 * log carbon mass −0.18, $P = 0.0001$, $R^2 = 0.21$, df = 60) and the L4 assemblage (B, log carbon percentage = −0.34* log carbon mass −1.1, $P = 0.0026$, $R^2 = 0.3429$, df = 20). Taxonomic groups coloured as indicated in the legends.

carbon percentage (Fig. 5 and Table I). As expected, there was a negative relationship between $\log_{10}$ mass-specific growth rate (g), and $\log_{10}$ carbon mass, consistent with the results of Kiørboe and Hirst (2014). In the analyses of all zooplankton taxa, mean and maximum growth rate decreased with increasing carbon mass and carbon percentage.

In all analyses, the addition of body carbon percentage to models of growth based on carbon mass alone increased the explanatory power (Table II). The second order Akaike criterion, AICc, (Burnham and Anderson, 2002) was lower in the model including water content in all analyses, supporting the inclusion of this factor in analyses of zooplankton growth. In the maximum analysis including all taxa, Akaike weights (ω_i) were approximately 10 times higher in the models including body carbon percentage (mass $\omega_i = 0.08$, mass + carbon percentage $\omega_i = 0.92$). This suggests that these models were significantly better than models based on mass alone (Royall, 1997). A similar pattern was observed in the analysis of maximum growth rates of the gelatinous taxa however it was not observed for mean growth rates (mass $\omega_i = 0.02$, mass + GI $\omega_i = 0.98$).

DISCUSSION

Our study provides strong support for body carbon percentage being a continuous trait, for a negative relationship between body carbon percentage and growth rate, and for considerable increases in model predictive power as a result of inclusion of this trait for zooplankton. Below we discuss the implications of each of these findings in turn.

Kiørboe (2013) demonstrated that if zooplankton are arranged in a frequency distribution based on body composition, that most taxa are either gelatinous (carbon mass is ~0.5% of wet mass) or non-gelatinous (~5–10%), with little overlap. Our study would appear to contradict this, since we found a fairly continuous distribution of carbon percentage. However, this does not conflict with the findings of Kiørboe (2013), since in that study it was emphasized that most taxa are either highly gelatinous or non-gelatinous. Rather, we highlight that, while most species fall into one of these two groups, there is considerable variability in carbon percentage within each group and there are representatives across much of this spectrum. The distribution of zooplankton biomass at L4 supports both of these views. Biomass is clustered at either end of the spectrum as described previously, and this could suggest that the fitness landscape for this trait favours extremes. However, at either end of the spectrum there is considerable variability. The traditional gelatinous group alone spans an 8-fold range in carbon percentage, with implications for growth rate. For example, there is a trend of increasing carbon percentage among the gelatinous zooplankton through the year, with cydippids being replaced by beroids in summer and finally by hydromedusae and siphonophores in autumn.

In the meta-analysis compilation, the largest interval occurs between taxa typically considered as gelatinous and intermediate, between the pelagic tunicate, *Thalia* (as *Salpa*) *democratica* (1.6% body carbon percentage) and a chaetognath, *Eukrohnia hamata* (2.7 % body carbon percentage). Molina-Ramirez *et al.* (2015) stressed that considerable variation in carbon percentage existed even within the classic gelatinous taxa (Cnidaria, Ctenophora and Tunicata). Our results are in agreement, albeit with even higher degree of variability (at 350-fold). Taken together, the relatively small interval between values for gelatinous and non-gelatinous species and the high variability observed within the gelatinous

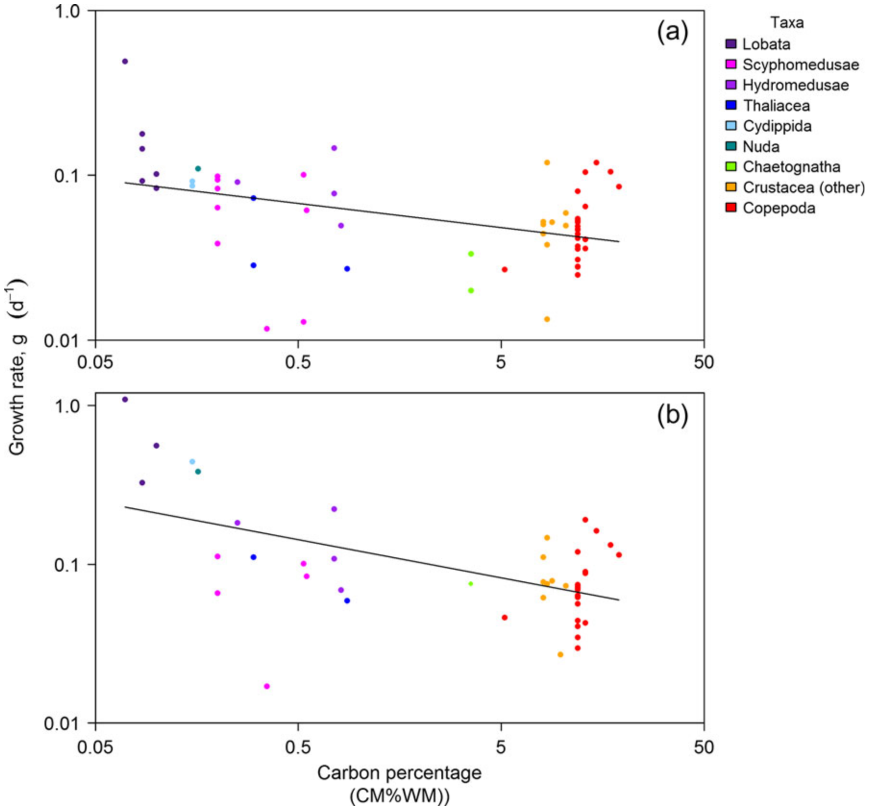

Fig. 5. Specific growth rate, *g* (d^{-1}) as a function of body carbon percentage (CM%WM). Growth values were temperature-adjusted to 15°C, mass adjusted to 1 mg C and then averaged for each species in each study. (**a**) Mean mass-specific growth rate values for each species in each study and (**b**) maximum specific growth rate values for each species.

Table I: General linear models predicting $\log_{10}$ mean specific and $\log_{10}$ maximum specific growth rate, g (d^{-1}), as a function of both $\log_{10}$ carbon mass (mg) and $\log_{10}$ body carbon percentage (100(CM/WM))*

Group		Factor	df	*P*	Slope	Intercept	Adj R^2
All zooplankton	Mean growth rate, *g*	$\log_{10}$ carbon mass	58	<0.0001	−0.17	−1.12	0.43
		$\log_{10}$ carbon percentage		0.036	−0.18		
	Max growth rate, *g*	$\log_{10}$ carbon mass	42	<0.0001	−0.16	−0.81	0.31
		$\log_{10}$ carbon percentage		0.013	−0.16		
Gelatinous taxa only	Mean growth rate, *g*	$\log_{10}$ carbon mass	22	0.027	−0.19	−1.18	0.33
		$\log_{10}$ carbon percentage		0.038	−0.17		
	Max growth rate, *g*	$\log_{10}$ carbon mass	13	0.011	−0.16	−1.15	0.42
		$\log_{10}$ carbon percentage		0.018	−0.72		

All models pertain to growth rate data that were first Q_{10}-adjusted to 15°C.

taxa suggest that growth models can indeed incorporate carbon percentage as a continuous trait.

When $\log_{10}$ mass-specific growth rate was regressed against $\log_{10}$ body carbon percentage as a continuous variable, a negative relationship was observed. Crucially, the pattern persisted when considering the gelatinous taxa alone (Table II). The existence of the relationship among the gelatinous taxa alone, is important as this demonstrates that the relationship is not due to a categorical difference between gelatinous organisms and non-gelatinous organisms.

One potential mechanism that could explain the relationship between body carbon percentage and growth rate is enhanced feeding rate (Acuña *et al.*, 2011). These authors suggested that the large dilute bodies of gelatinous zooplankton facilitate higher carbon-specific feeding rates than other zooplankton taxa of the same carbon mass. If this increased feeding rate drives faster growth,

Table II: Changes to measures of explanatory power of models of growth based solely on carbon mass when body carbon percentage (CC) was added as a factor

		R^2		AICc			ω_i	
Group	g	Mass	Mass + CC	Mass	Mass + CC	Δ_i	Mass	Mass + CC
All zooplankton	Mean	0.39	0.43	18.63	16.67	2.47	0.19	0.81
	max	0.22	0.31	21.99	17.57	4.42	0.076	0.92
Gelatinous taxa only	mean	0.33	0.33	18.51	19.96	1.44	0.54	0.46
	max	0.09	0.42	21.55	16.26	5.29	0.019	0.98

AICc is the corrected Akaike information criterion, Δ_i is the AIC difference, and ω_i is the Akaike weight. Models with Akaike weight values 10 times greater than that of the other models being compared are considered statistically significant as optimal models (mass + GI for mean and max all zooplankton and max gelatinous taxa only). All models pertain to growth data that were first Q_{10}-adjusted to $T = 15$°C.

then this might explain the relationship of increasing growth rate with decreasing carbon percentage (Fig. 2). As many gelatinous taxa are filter or ambush feeders that rely on capture surfaces to feed, assuming that feeding rate scales with surface area, then we may expect the scaling exponent between surface area and body carbon percentage to match the exponent for growth rate and body carbon percentage. To investigate this we used a simple geometric calculation. Assuming isomorphic growth, surface area (SA) scales with body volume with a power of 0.67. By altering degree of gelatinousness for a fixed amount of body carbon, SA then scales with carbon percentage with a power of −0.67. Hence, with an assumption that growth rate is a fixed proportion of feeding rate, this would give the same slope of −0.67 for $\log_{10}$ mass-specific growth versus $\log_{10}$ carbon percentage (Fig. 2). The exponents that we determined empirically across the various zooplankton taxa are less steeply negative than −0.67 (at −0.18 and −0.16 for mean and maximum respectively), i.e. increasingly gelatinous organisms increase their growth rate less rapidly than these surface considerations would predict. This could indicate a potential feeding inefficiency associated with decreasing carbon percentage or that factors additional to surface area may also be important.

In common with Ikeda (2014), we found that species with larger total carbon mass also tended to be more watery. Furthermore, as the larger organisms are typically more watery the effects of carbon mass and carbon percentage tend to counteract, underscoring the need to include these variables together in order to better predict growth. Molina-Ramirez *et al.* (2015) found a similar result for tunicates but found that body carbon percentage was invariant with increasing mass for cnidarians and ctenophores. The authors suggested that this might be due to differences between internal filter feeding in tunicates and external ambush or cruise feeding in the other groups. It has been suggested that feeding modes decrease in efficiency with increasing size (Kiørboe, 2011), so high water content may help to mitigate this decrease in efficiency and maintain relatively higher carbon-specific feeding rate at large carbon masses. This is supported by the findings of Acuña *et al.* (2011), suggesting that gelatinous plankton had higher carbon-specific feeding rates than other zooplankton of a similar carbon mass. Together with higher growth rates, these factors could help to explain how gelatinous zooplankton are capable of forming such high localized increases in species biomass (blooms).

While the increase in capture surface area and associated feeding and growth rates is one potential advantage of the gelatinous body form, there are other implications. There are potential negative implications also, especially with regard to limited swimming speed and escape responses. While medusae have potential defences in the form of nematocysts, many gelatinous taxa such as ctenophores do not, and may have limited ability to escape from potential predators as a result of their large dilute bodies (Acuña *et al.* 2011). Understanding why some taxa are gelatinous is not always straightforward. The most gelatinous mollusc in this analysis is *Clione limacina*, a gymnosome predator that feeds on almost exclusively on *Limacina helicina*. *Clione* does not rely on large capture surfaces or on generating a feeding current as it ambushes individual, relatively large prey items. In this case, water content does not appear to be a derived trait to increase body volume relative to carbon for feeding, suggesting that this may not be the only driver of high water content in zooplankton. It has been suggested that potential other causes include physical or ecological factors such as transparency to impair visual predation (Hamner *et al.*, 1975) or the efficiency of neutral buoyancy (Kiørboe, 2013). Together these factors may help to explain why semi-gelatinous bodies are observed in at least six major planktonic phyla (Cnidaria, Ctenophora, Chordata, Annelida, Chaetognatha, Mollusca, see Supplementary Information 1).

CONCLUSIONS

Body size is often described as a master-trait, and is frequently used as the sole intrinsic variable in empirical and simulation models involving zooplankton growth (Kiørboe and Hirst, 2014; Andersen *et al.*, 2015a). But what do we mean by 'body size'? Carbon mass is often used as the unit for size, but both our meta-analysis and the real assemblage data show that carbon percentage also varies greatly. It may even vary negatively with carbon mass, levering an opposing effect on growth. We argue that carbon mass and carbon percentage are both key traits, both are intrinsic to the zooplankton and since they are possible to estimate, then we should disentangle their separate effects in a unified growth model. By including carbon percentage in models of growth based on carbon mass alone, we substantially increased their explanatory power, with smaller body masses and lower body carbon percentages leading to higher specific growth rates. Building on the work of previous publications (Kiørboe, 2013; Pitt *et al.*, 2013; Molina-Ramirez *et al.*, 2015) we provide a carbon percentage dataset in Supplementary Table 1. By using these source data alongside carbon mass, the maximum growth rate equation in Table 1 may then be used as a starting point to estimate growth rates attainable by zooplankton.

Alongside the 'size' based simplifications used for modelling, there has also been an increase in 'trait-based' modelling in which categorical variables or functional groups are allowed to vary continuously. A purpose of this article is to allow water content also to be used as a continuous trait; to facilitate its inclusion alongside carbon mass and other traits such as feeding mode (Litchman *et al.*, 2013; Andersen *et al.* 2015a; Hérbert *et al.*, 2016). Since we found that growth rate depended on carbon percentage even among the gelatinous taxa alone, we hope that considering and modelling water content as a continuous trait will reveal the ecological and evolutionary factors that influence the water content of zooplankton.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Plankton Research* online.

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