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Functional differences in the allometry of the water, carbon and nitrogen content of gelatinous organisms

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We have supplemented available, concurrent measurements of fresh weight (*W*, g) and body carbon (C, g) (46 individuals, 14 species) and nitrogen (N, g) (11 individuals, 9 species) of marine gelatinous animals with data obtained during the global ocean MALASPINA 2010 Expedition (totalling 267 individuals and 33 species for the *W* versus C data; totalling 232 individuals and 31 species for the N versus C data). We then used those data to test the allometric properties of the *W* versus C and N versus C relationships. Overall, gelatinous organisms contain 1.13 ± 1.57% of C (by weight, mean ± SD) in their bodies and show a C:N of 4.56 ± 2.46, respectively, although estimations can be improved by using separate conversion coefficients for the carnivores and the filter feeders. Reduced major axis regression indicates that *W* increases isometrically with *C* in the carnivores (cnidarians and ctenophores), implying that their water content can be described by a single conversion coefficient of 173.78 gW(g C)$^{-1}$, or a C content of 1.17 ± 1.90% by weight, although there is much variability due to the existence of carbon-dense species. In contrast, *W* increases more rapidly than C in the filter feeders (salps and doliolids), according to a power relationship $W = 446.68C^{1.54}$. This exponent is not significantly different from 1.2, which is consistent with the idea that the watery bodies of gelatinous animals represent an evolutionary response towards increasing food capture surfaces, i.e. a bottom-up rather than a top-down mechanism. Thus, the available evidence negates a bottom-up mechanism in the carnivores, but supports it in the filter feeders. Last, N increases isometrically with C in both carnivores and filter

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feeders with C:N ratios of 3.89 ± 1.34 and 4.38 ± 1.21, respectively. These values are similar to those of compact, non-gelatinous organisms and reflect a predominantly herbivorous diet in the filter feeders, which is confirmed by a difference of one trophic level between filter feeders and carnivores, according to stable N isotope enrichment data.

KEYWORDS: gelatinous organisms; allometry; carbon content; water content; body weight

INTRODUCTION

Marine pelagic and neustonic animals tend to display either low (i.e. crustaceans, gastropods, larval fish) or high (i.e. ctenophores, cnidarians, tunicates) water contents in their bodies, with comparatively few species occupying an intermediate position (i.e. chaetognaths, pteropod molluscs, polychaetes) (Vinogradov, 1953; Kiørboe, 2013). Such a gap between alternative body plans, and the sheer taxonomic diversity of gelatinous organisms, points to some fundamental cause for their evolution (Kiørboe, 2013). According to top-down explanations, gelatinous bodies have evolved as a strategy to evade predation, due to their transparency, low nutritive value and large relative size (Hamner *et al.*, 1975; Verity and Smetacek, 1996; Johnsen and Widder, 1998; Johnsen, 2000). The alternative, bottom-up explanation, proposes the existence of a functional difference in food-gathering strategy among gelatinous and non-gelatinous animals (Harbison, 1992; Acuña, 2001; Acuña *et al.*, 2011; Kiørboe, 2013). While non-gelatinous animals would be capable of remote sensorial detection of their prey, gelatinous animals would depend upon direct contact with several types of feeding surfaces. Such process may be passive, and depend solely on the motility of the prey (as in many siphonophores, some scyphozoans and ctenophores), or may depend on the active generation of water currents which bring the prey into contact with the feeding surfaces (as in the filter-feeding salps and cruising scyphozoans and ctenophores). Theoretical consideration of the costs and benefits of filter feeding (Acuña, 2001) and cruising predation (Acuña *et al.*, 2011) suggests that the typically low prey densities of the ocean would require exceedingly large feeding surfaces, hence a need for a large, gelatinous sustaining structure.

A low metabolic rate has also been suggested as one of the main advantages of gelatinous bodies (e.g. Alldredge and Madin, 1982). Certainly, because of their high water content and low concentration of metabolizing organic substances, gelatinous organisms exhibit much lower metabolic rates than those of non-gelatinous animals of similar linear or volumetric dimension (e.g. Acuña *et al.*, 2011; Pitt *et al.*, 2013). However, earlier studies showed that carbon-specific excretion and respiration rates did not differ significantly among gelatinous and non-gelatinous organisms, suggesting that C may be a better proxy for body size than W, the body volume, the dry weight or the concentration of biological macromolecules (Schneider, 1990, 1992). Further work has shown that such normalization works particularly well for the respiration rate (R), where the allometric power relationship $R = aC^b$ has similar coefficients for both gelatinous and non-gelatinous animals (Acuña *et al.*, 2011; Pitt *et al.*, 2013). Allometric regressions for the excretion and the growth rates also preserve the value of the power exponent b, although excretion rates are 10 times lower and growth rates 2 times higher in gelatinous than in non-gelatinous animals (i.e. there is a difference in the coefficient a; Pitt *et al.*, 2013). Such discrepancies are likely due to fundamental, ecophysiological differences between gelatinous and non-gelatinous organisms (Pitt *et al.*, 2013). Consequently, C rather than W is usually the variable of interest when building ecophysiological, population or ecosystem energy budgets.

In non-gelatinous animals, body carbon content can be reasonably estimated from the dry weight or by CHN analysis of dried samples (Schneider, 1992; Postel *et al.*, 2000; Kiørboe, 2013), but dried gelatinous animals tend to contain large amounts of salt and residual water (Larson, 1986), and their preparation for CHN analysis requires a cumbersome drying process. Furthermore, unplanned encounter with swarms of gelatinous animals may require tools for simple estimation of individual carbon from measurements of the individual fresh weight, which could be easily achieved with appropriate equations to estimate individual C from W. All of the studies comparing the allometry of gelatinous and non-gelatinous animals (e.g. Schneider, 1990, 1992; Acuña *et al.*, 2011; Kiørboe, 2013; Pitt *et al.*, 2013) have relied on the same set of published coefficients to transform the different body size units to a common carbon currency for each species or recognizable taxonomic group [a compilation of most of those coefficients can be visited in Lucas *et al.* (Lucas *et al.*, 2011)]. Those studies have shown that W in gelatinous organisms (or the body volume) scales isometrically with C, that is, $W = aC^b$, where $b = 1$ (Kiørboe, 2013; Pitt *et al.*, 2013). This means that, as in the non-gelatinous organisms, the water content of gelatinous organisms (or the quotient W/C) is independent of the body carbon C, which has been interpreted as a symptom that some evolutionary limit on the water

content of a gelatinous body plan has been reached (Kiørboe, 2013). It also means that the body carbon can be easily estimated for a given taxon by multiplying the body volume or W by certain, taxon-specific coefficient (Kiørboe, 2013). Unfortunately, this important and useful allometric generalization rests on a limited and taxonomically biased data set, with the tunicates as the only group with sufficient concurrent individual observations of both W and C ($n = 38$) to produce a meaningful regression (Kiørboe, 2013). In addition, a majority of those concurrent observations of W and C rely on conversion coefficients to estimate either W or C, which involves some degree of pseudoreplication.

In this paper, we revise the W, C and N content of gelatinous organisms using only those sources where both W and C or N and C have been measured concurrently, thus not being estimated from conversion coefficients. To increase the sample size, and to achieve a more balanced taxonomic representation, we have sampled gelatinous neuston and plankton along the track of the global MALASPINA 2010 Expedition (Fig. 1), and processed those samples using a standard protocol. We then focused our analysis on examination of the allometric properties of the W versus C and N versus C relationship. For the exploration, we partitioned the data into taxonomic categories (Phyla), trophic guilds (TG) (carnivores versus filter feeders) or feeding mechanisms (FMs) (filter feeders, ambush predators, cruising predators). Carnivores capture larger prey using external collection surfaces, while filter feeders capture smaller prey using internal collection filters. Since smaller prey tend to be more abundant, and usually contain a larger proportion of phytoplankton, we expect differences in C and N content among carnivores and filter feeders. At a finer functional level, the energy spent in prey collection depends greatly on prey availability in the ambush predators, which wait for the prey, and less in the cruising predators, which swim constantly to search for prey. As a means to characterize differences in the trophic position among these functional groups, we conducted a stable isotope analysis. Last, we tested whether the water content of these taxonomic or functional categories is independent of size (i.e. whether the exponent of the power functions relating W or N with C is 1) or instead increases with size, in which case it would lend support to current theories on the origin of gelatinous bodies (see next section on theoretical considerations).

SOME THEORETICAL CONSIDERATIONS ON THE ALLOMETRY OF THE W VERSUS C RELATIONSHIP

We will assume that the allometry of the fresh body weight of gelatinous animals is adequately described by the power relationship

$$W = a\mathrm{C}^b, \tag{1}$$

where a and b are parameters. All published evidence points to the idea that W increases isometrically with C, that is, $b = 1$ (Pitt *et al.*, 2013; Kiørboe, 2013). This exponent is perfectly valid from an empirical point of view, but we are also concerned with its consistency with current theories to explain the evolution of gelatinous bodies. In particular, the bottom-up approach contends that the heavily inflated bodies of gelatinous organisms may represent a structural adaptation to support large collection surfaces in endemically low food environments (i.e. Harbison, 1992; Acuña, 2001; Acuña *et al.*, 2011; Kiørboe, 2013). The question is what value of b should we expect if this theory were true? To follow is a brief allometric derivation showing that a value of $b \sim 1.2$ is what best conforms to the bottom-up theory.

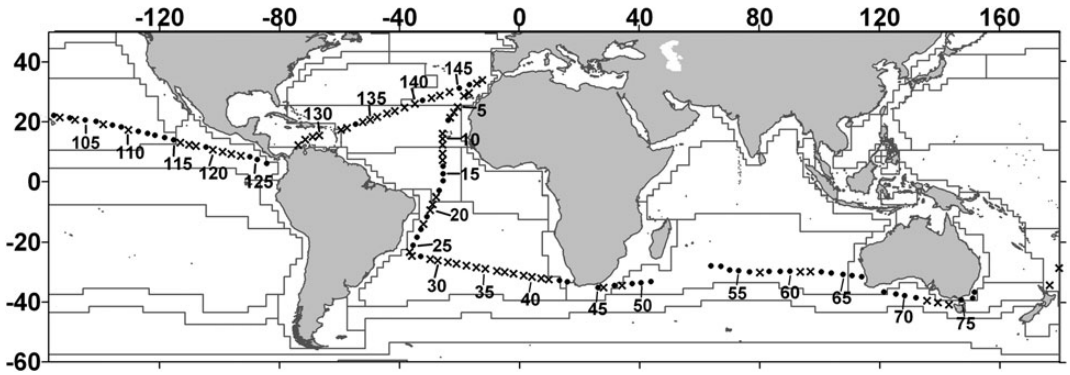

Fig. 1. Geographic location of the MALASPINA 2010 Expedition stations, indicating those where gelatinous neuston were (dots) and were not (crosses) collected for C, N and W analysis (see Table I for correspondence between species and stations).

According to this theory, the energy intake E is directly proportional to the total feeding surface S, thus $E \propto S$. The feeding surface is sustained by a body structure, thus larger bodies should sustain larger surfaces. Such dependence can be expressed by a power relationship between the feeding surface S and the body volume V of the kind $S \propto V^x$. Last, in a watery organism, the body volume should be directly proportional to the body fresh weight W, and the body fresh weight should depend on a power function of the body carbon such that $V \propto W \propto C^b$. The above considerations can be summarized as

$$E \propto S \propto V^x \propto W^x \propto C^{bx}. \quad (2)$$

In addition, previous research indicates that the metabolic demand, described by the respiration rate, is best expressed as a power function of the carbon content.

$$R \propto C^y. \quad (3)$$

The bottom-up theory to explain the evolution of high body water content in gelatinous animals indicates that the energy intake E, given in equation (2), should at least fulfil the metabolic demand R given in equation (3), that is $E \propto R$. If this is true, we can combine the right-hand terms of equations (2) and (3) and arrive at $C^{bx} \propto C^y$ which, in turn, implies that $bx = y$. Solving for b, we have

$$b = \frac{y}{x}, \quad (4)$$

where b is the slope of the power allometric function relating the fresh body weight W with the body carbon C.

Thus, the actual value of b according to equation (3) will depend on the values of y and x. In principle, x could vary between 2/3 (that is, $S \propto V^{2/3}$) if the feeding surface is flat, to 1 (that is, $S \propto V$) if the feeding surface has a space-filling, fractal geometry (Mandelbrot, 1983). However, the feeding surfaces of pelagic tunicates (Acuña, 2001), scyphozoans and ctenophores (Colin *et al.*, 2010; Acuña *et al.*, 2011) are typically flat, thus $x \sim 2/3$. Moreover, according to reviews on the respiration rates of gelatinous organisms, we know that $y \sim 0.8$ (Acuña *et al.*, 2011; Pitt *et al.*, 2013). Therefore, according to equation (4), $b = y/x = 0.8/(2/3) = 1.2$.

METHOD

Data set

Our data set consists of concurrent measurements such as W, C and N in individuals or groups of individuals of several species of ctenophores, tunicates and cnidarians. Table I offers a summary of data and sources, pooled for the lowest level of taxonomic identification (the full data set can be consulted in the Supplementary Material, Table SI). We did not include semi-gelatinous zooplankton as tunicate appendicularians and thecosomate pteropods, because they do not have gelatinous bodies, although their strategy of expanding large, gelatinous food collection structures is essentially the same as that of true gelatinous organisms (Acuña, 2001; Kiørboe, 2013). Part of the data originate from published articles and data compilations (46 individuals, 14 species for the W versus C data; 11 individuals, 10 species for the N versus C data), and we refer to the original articles for details on methods (Table I). The rest of data were collected during the global MALASPINA 2010 Expedition, for which we next provide detailed information (totalling 267 individuals and 33 species for the W versus C data, and 232 individuals and 31 species for the N versus C data).

Sampling methods

The MALASPINA 2010 Expedition took place aboard the Spanish research vessel "*BIO Hespérides*" *A33* from 15 December 2010 to 11 July 2011 in the Atlantic, Indian and Pacific Oceans (Fig. 1, Table I). Gelatinous neustonic and planktonic specimens were sampled with a neuston net made of a rectangular stainless-steel frame attached to two longitudinal floats at its sides, with a mouth opening of 80 × 30 cm, of which ~10 cm remained above sea level. The mesh had a pore size of 200 μm and was equipped with a General Oceanics™ flowmeter to estimate the volume of water filtered. At each station, the net was towed from a crane at 2 knots for 10 min at a distance of 5 m from the starboard side of the hull. Two tows were done at each station, before sunrise (4:00 a.m.) and at noon.

Gelatinous specimens retained in the cod-end were quickly collected with a 5 mm mesh size sieve cup, transferred to a jar filled with filtered seawater and placed inside a cooler for at least 1 h to allow for defecation of their gut contents. They were then placed on a tray and sorted into morphologically distinct categories, which we considered separate taxa. The first specimen of a given taxon was preserved in formalin for taxonomic analysis. The following two, if available, were preserved in absolute ethanol for genetic analysis (data not presented here). Any remaining specimens used in a destructive analysis of wet weight and elemental composition. Each of those animals was photographed on a Kaiser RE PRO 5602 motorized reprography column with a Canon EOS Mark III DSLR camera using a transparent polycarbonate stands to allow inferior illumination by an Elinchrome 600 W flash unit. The animal was then placed on a 200 μm mesh sieve which was blotted on desiccant paper until no trace of excess water was left, placed on small pre-weighted aluminium trays, and

Table I: List of the species for which we found or collected concurrent information on individual wet weight and carbon content or of individual nitrogen and carbon content

Species	Ph	FM	TG	*N*	C (*g*)	N (*g*)	*W* (g)	C:N	C:*W*	δ^{15}N	TL	Data source
Mnemiopsis leidyi	cte	cp	ca	16	4.10×10^{-2}	7.91×10^{-3}	2.41×10^{1}	5.53	1.70×10^{-3}	8.38	2.6	Mutlu (2009), ME (123*)
Pleurobrachia pileus	cte	ap	ca	9	3.76×10^{-2}	NA	6.41×10^{1}	NA	5.86×10^{-4}	NA	NA	Mutlu (2009)
Beroe sp.	cte	ap	ca	2	1.95×10^{-2}	5.00×10^{-3}	6.91	3.90	2.82×10^{-3}	NA	NA	Clarke *et al.* (1992), Ikeda and Bruce (1986)
Beroe ovata	cte	ap	ca	4	1.89×10^{-2}	NA	1.06×10^{1}	NA	1.77×10^{-3}	NA	NA	Fineko *et al.* (2003), Mutlu (2009)
Mertensia sp.	cte	ap	ca	1	1.05×10^{-2}	2.00×10^{-4}	2.28	4.64	4.61×10^{-3}	NA	NA	Ikeda and Bruce (1986)
Aurelia aurita	cni	cp	ca	10	1.62×10^{-1}	NA	1.78×10^{2}	NA	9.12×10^{-4}	NA	NA	Bamstedt (1990), Hirst and Lucas (1998), Mutlu (2009); Uye and Shimauchi (2005)
Nemopilema nomurai	cni	cp	ca	1	2.20×10^{2}	4.40×10^{1}	4.00×10^{4}	4.99	5.49×10^{-3}	NA	NA	Uye cited in Lucas *et al* (2011)
Rhopilema esculentum	cni	cp	ca	2	6.05×10^{1}	1.10×10^{1}	5.00×10^{3}	4.99	1.21×10^{-2}	NA	NA	Uye cited in Lucas *et al* (2011)
Rhopilema hipsidium	cni	cp	ca	2	3.04×10^{1}	7.60	4.00×10^{3}	5.64	7.59×10^{-3}	NA	NA	Uye cited in Lucas *et al* (2011)
Mastigias papua	cni	cp	ca	1	2.35×10^{-1}	3.50×10^{-2}	3.50×10^{1}	6.72	6.71×10^{-3}	NA	NA	Uye cited in Lucas *et al* (2011)
Atolla sp.	cni	cp	ca	1	1.92×10^{-1}	4.90×10^{-2}	2.50×10^{1}	3.89	7.68×10^{-3}	NA	NA	Clarke *et al.* (1992)
Botrynema brucei	cni	cp	ca	1	1.18×10^{-5}	3.46×10^{-6}	5.00×10^{-3}	3.42	2.36×10^{-3}	NA	NA	Clarke *et al.* (1992)
Prayidae sp.	cni	cp	ca	11	7.34×10^{-3}	4.29×10^{-3}	5.54×10^{-1}	1.71	1.32×10^{-2}	9.85	2.8	ME (8, 10, 15, 23, 45, 58, 69*, 74, 145)
Physophora sp.	cni	ap	ca	4	NA	NA	NA	NA	NA	10.10	2.9	ME (125*, 126, 141)
Physalia physalis	cni	ap	ca	18	2.51×10^{-1}	6.61×10^{-2}	2.78	3.79	9.02×10^{-2}	NA	NA	ME (45, 49*, 50*, 52*, 53*, 65*, 66*, 67*, 105*, 106*, 111*, 113*, 125, 126*, 141)
Diphyes antarctica	cni	cp	ca	1	3.13×10^{-3}	9.06×10^{-4}	7.50×10^{-1}	3.46	4.17×10^{-3}	NA	NA	Clarke *et al.* (1992)
Athorybia sp.	cni	cp	ca	3	6.20×10^{-3}	7.00×10^{-3}	3.85	9.02×10^{-1}	1.61×10^{-3}	7.10	2.3	ME (124*, 125)
Apolemia sp.	cni	cp	ca	1	3.90×10^{-3}	1.18×10^{-3}	2.50×10^{-1}	3.29	1.56×10^{-2}	NA	NA	ME (72)
Abyla sp.	cni	cp	ca	5	2.52×10^{-3}	7.16×10^{-4}	4.94×10^{-1}	3.52	5.11×10^{-3}	NA	NA	ME (76)
Pegantha sp.	cni	cp	ca	2	5.15×10^{-2}	1.60×10^{-2}	1.17×10^{1}	3.28	4.39×10^{-3}	NA	NA	ME (44)
Velella velella	cni	cp	ca	15	1.82×10^{-2}	5.08×10^{-3}	2.88	3.58	6.32×10^{-3}	NA	NA	ME 54, 55, 60, 65*, 66*, 67*, 69*, 70*, 71*, 77, 101, 145, 146)
Porpita porpita	cni	cp	ca	2	8.44×10^{-2}	2.50×10^{-2}	2.24×10^{-1}	3.42	3.77×10^{-1}	NA	NA	ME (24,25)
Calycopsis borchgrevinki	cni	cp	ca	1	2.26×10^{-5}	5.43×10^{-6}	5.00×10^{-3}	4.16	4.53×10^{-3}	NA	NA	Clarke *et al.* (1992)
Thalia sp.	cho	ff	ff	3	1.09×10^{-1}	2.55×10^{-2}	1.50×10^{1}	4.28	7.26×10^{-3}	10.19	2.2	ME (111*)
Thalia rhomboides	cho	ff	ff	8	1.30×10^{-1}	2.68×10^{-2}	8.76	4.84	1.48×10^{-2}	10.20	2.1	ME (108, 109, 110, 111*, 112*)
Thalia democratica	cho	ff	ff	4	9.60×10^{-2}	6.27×10^{-3}	5.47	1.53×10^{1}	1.76×10^{-2}	1.80	1.2	ME (51*,65*,76,77)
Thethys vagina	cho	ff	ff	4	7.07×10^{-2}	1.49×10^{-2}	1.57×10^{1}	4.75	4.51×10^{-3}	9.90	2.2	ME (69*,71*)
Salpa thompsoni	cho	ff	ff	2	4.28×10^{-2}	4.84×10^{-3}	3.09	8.84	1.38×10^{-2}	NA	NA	Dubischar *et al.* (2006)
Salpa sp.	cho	ff	ff	1	3.33×10^{-2}	6.94×10^{-3}	NA	4.80	NA	5.12	1.3	ME (113*)
Salpa fusiformis	cho	ff	ff	6	4.70×10^{-2}	9.43×10^{-3}	2.32	4.98	2.02×10^{-2}	3.47	1.6	ME (16,51*,74,78*,115)
Pegea confedertata	cho	ff	ff	1	3.11×10^{-2}	5.63×10^{-3}	2.71	5.52	1.15×10^{-2}	3.70	1.5	ME (64*)
Ihlea racovitzai	cho	ff	ff	98	4.41×10^{-2}	9.66×10^{-3}	5.00	4.57	8.82×10^{-3}	3.80	1.2	ME (49*, 50*, 51*, 56*, 59*, 63*, 64*, 66*, 67*)
Iasis zonaria	cho	ff	ff	11	4.32×10^{-2}	8.48×10^{-3}	2.68	5.09	1.61×10^{-2}	6.18	1.6	ME (17, 47, 50, 78*, 103*, 111*, 112*)
Cyclosalpa affinis	cho	ff	ff	5	7.04×10^{-2}	1.62×10^{-2}	1.00×10^{1}	4.35	7.04×10^{-3}	NA	NA	ME (43,51*,74)
Doliolum sp.	cho	ff	ff	11	1.31×10^{-1}	2.70×10^{-2}	2.25×10^{1}	4.85	5.82×10^{-3}	6.60	1.5	ME (45,70*)

Symbols stand for: Phylum (PH): Ctenophora (cte), Cnidaria (cni), Chordata (cho); feeding mechanism (FM): filter feeder (ff); cruising predator (cp), ambush predator (ap); trophic guild (TG): carnivore (ca), filter feeder (ff); number of individuals (*n*). For each species, we provide the geometric mean of the individual carbon (C), nitrogen (N) and wet weight (*W*), and the C:*W*, C:N ratios, δ^{15}N and trophic level (TL). Sources of data: ME means that some or all of the data have been obtained during the MALASPINA 2010 Expedition (sampling stations as referred in Fig. 1 are given in brackets and stations with stable isotopes sample are marked with an *).

weighed using one of five Pesola® Micro-Line Spring scales, models 20010, 20030, 20060, 20100 and 20300, which measured up to 10, 30, 60, 100 and 300 g with precisions of 0.10, 0.25, 0.50, 1.00 and 2 g. In a selected set of stations, we weighed each specimen five times, to examine the influence of sea roughness on the variability of weight determinations. The coefficient of variation of weight did not vary significantly with sea roughness [one-way analysis of variance comparison among the subjective sea states "calm", "moderate" and "rough", $F_{2,27} = 0.981$, $P = 0.38$; the average ($\pm$SD) coefficient of variation was 0.068 ± 0.099].

Specimens inside the aluminium trays were then dried in an oven at 60°C for 48 h. Our own preliminary tests using the scyphozoan *Aurelia aurita* and some unidentified salps (data not shown) revealed that after 24 h of desiccation, the sample reached an asymptotic minimum weight. The aluminium trays with the dried specimens were stored inside plastic bags to which silica gel was added until analysis on shore. The dried specimens were weighed again in the laboratory using a Mettler Toledo® UMT2 microbalance with a precision of 1 μg, ground using a mortar pestle and a subsample of between 1 and 10 mg of the powder was set aside for CHN analysis using an EA 1108 FISONS elemental analyzer, with absolute precision and reproducibility of <0.3 and 0.2%, respectively.

For stable isotope determination, dried samples were ground to a fine powder, packed in 3.3 × 5 mm tin capsules and processed in a Thermo Finnigan Mat Delta Plus isotope-ratio mass spectrometer coupled to a Carlo Erba CHNSO 1108 elemental analyzer. Stable isotope ratios ($^{15}N/^{14}N$) were expressed in $\delta^{15}N$ notation as the deviation from standards in parts per thousand (‰). Replicate measurements of internal laboratory standards indicate measurement errors of ± 0.15‰ for $\delta^{15}N$. The trophic level (TL) was estimated using the equation given by Vander Zanden and Rasmussen (Vander Zanden and Rasmussen, 2001):

$$TL = \frac{\delta^{15}N_{consumer} - \delta^{15}N_{baseline}}{3.4} + \lambda.$$

We adopted the commonly assumed trophic fractionation of 3.4, averaged over multiple trophic pathways (Minagawa and Wada, 1984). Nonetheless, trophic fractionation should be taken cautiously in gelatinous organisms because it is especially variable and difficult to predict (Pitt *et al.*, 2009). λ is the trophic position of the organism used as the $\delta^{15}N_{baseline}$. We used as a baseline representative of TL = 2 (i.e. zooplankton primary consumers), the $\delta^{15}N$ of the 40–200 μm fraction of plankton collected by means of vertical hauls from 200 m depth to the surface at each of the MALASPINA sampling stations (see Mompeán *et al.*, 2013 for details of sampling and analysis of plankton size fractions).

Data analysis

To study the relationship between *W* and C, and between N and C, we used log-log transformation, because it is methodologically adequate for the treatment and comparison of power allometric relationships [see equation (1) (Peters, 1983; Kerkhoff and Enquist, 2009)]. To fit the models, we have used reduced major axis (RMA) instead of ordinary least squares, because the dependent (*W* or N) and the independent (C) variables are measured with similar error. We also have an interest in the functional relationship between both variables, and it is both methodologically and theoretically convenient that the relationship is reversible (i.e. that there is consistency between the regression estimate for C versus *W* and that for *W* versus *C*) (Kaitaniemi, 2004; Smith, 2009). The different models were fitted by means of the SMATR package for R (Warton *et al.*, 2012). Those models include C as covariate (model 1, Tables II and IV) and one of the three different factors. One of them is the TG, with two possible levels: filter feeders and carnivores (models 2 and 3, Tables II and IV). Another factor is the FM, with three possible levels: ambush predators, cruising predators and filter feeders (models 6 and 7, Tables II and IV). Last is a taxonomic factor, the Phylum (P), with three levels: tunicates, cnidarians and ctenophores (models 4 and 5, Tables II and IV). We considered the effects of those factors only on the intercept and on both intercept and slope (when there is interaction between the factor and the covariate). The classification of the different species within the different levels of those factors is shown in Table I.

The models were ranked according to the second-order Akaike information criterion (AICc) (Burnham and Anderson, 2002). We also estimated the AICc weight, which provides a relative weight of evidence for each model. In this way, we inferred (i) the relative importance of the factors considered in the *W* versus C and N versus C content relationships and (ii) if the slopes were similar or different among the levels of each factor. In addition, we used the 95% confidence intervals (95% CIs) to examine (iii) the isometry of the slopes and (iv) in the case of *W* versus *C*, whether the slopes were significantly different from 1.2.

RESULTS

Allometry of the water content

The model including TG best described the relationship between log *W* and log C (model 3 in Table II, AICc = 114.76, AICw = 0.54; Fig. 2A). According to this model, the slope of the log *W* versus log C relationship for the carnivores [$b = 1.00$ (95% CI 0.85, 1.17)] is significantly different from 1.2 but not from 1 (i.e. the 95% CI

Table II: Summary of the RMA models for the fresh body weight (W)

Model	Model structure	Factor level	Rank	AICc	AICc w	*a*	*b*
1	$\log_{10}W = a + b\log_{10}C$		7	143.96	0.00	2.16	1.00 (0.88, 1.15)
2	$\log_{10}W = a(TG) + b\log_{10}C$		3	117.31	0.15		
		Carnivores				2.35	1.07 (0.91, 1.27)
		Filter feeders				2.07	1.07 (0.91, 1.27)
3	$\log_{10}W = a(TG) \times b(TG)\log_{10}C$		1	114.76	0.54		
		Carnivores				2.24	1.00 (0.85, 1.17)
		Filter feeders				2.65	1.54 (1.11, 2.13)
4	$\log_{10}W = a(PH) + b\log_{10}C$		2	116.86	0.19		
		Chordata				2.11	1.11 (0.92, 1.33)
		Cnidaria				2.25	1.11 (0.92, 1.33)
		Ctenophora				2.90	1.11 (0.92, 1.33)
5	$\log_{10}W = a(PH) \times b(PH)\log_{10}C$		4	117.99	0.11		
		Chordata				2.65	1.54 (1.11, 2.13)
		Cnidaria				2.08	0.98 (0.83, 1.17)
		Ctenophora				4.30	2.00 (0.88, 4.51)
6	$\log_{10}W = a(FM) + b\log_{10}C$		5	123.93	0.01		
		Ambush				2.48	1.06 (0.91, 1.26)
		Cruising				2.29	1.06 (0.91, 1.26)
		Filter feeders				2.05	1.06 (0.91, 1.26)
7	$\log_{10}W = a(FM) \times b(FM)\log_{10}C$		6	130.05	0.00		
		Ambush				−0.67	−1.14 (−4.47, −0.29)
		Cruising				2.19	0.99 (0.85, 1.16)
		Filter feeders				2.65	1.54 (1.11, 2.13)

Model 1 is a simple RMA of log *W* on log C. The rest of models also include as factors either the TG (two levels: filter feeders and carnivores; models 2 and 3), the FM (three levels: filter feeders, ambush predators and cruising predators; models 6 and 7) or the phylum (PH; three Phyla: tunicates, ctenophores and cnidarians; models 4 and 5). Models with factors are expressed as $\log_{10}W = a(\text{factor}) + b\log_{10}C$ when there is a common slope (*b*) but different intercepts [*a*(factor)] for each level of the factor, or $\log_{10}W = a(\text{factor}) + b(\text{factor})\log_{10}C$ when there are a distinct slopes [*b*(factor)] and intercepts [*a*(factor)] for each level of the factor. Where appropriate, estimates for the intercepts and the slopes are given for each level of the factor. 95% CI for the slopes are provided between parentheses for comparison with hypothesized values of 1 (isometry) and 1.2 (bottom-up theory). AICc, second-order Akaike information criteria; AICc w, second-order Akaike weight.

envelopes a value of 1 but not a value of 1.2, Table II). The fact that $W = 173.78C$ implies that, in the carnivores, the individual body water content (defined as W/C) and the percentage carbon (defined as $\%C = 100 \times C/W$) are approximately constant and independent of C (Table II). In contrast, the slope for the filter feeders [1.54 (95% CI 1.11, 2.13)] was significantly higher than 1 but statistically indistinguishable from 1.2 (Table II). This implies that, in the filter feeders, the body water content increases with C according to the power function $W = 443.68C^{1.54}$ (Fig. 2A, Table II) and therefore, the percentage carbon decreases with C as $\%C = 100 \times C/W = 100 \times C/(443.68C^{1.54}) = 100 \times (1/443.68)C^{(1-1.54)}$.

The model including the Phylum was the second best model (model 4 in Table II, AICc = 116.86, AICc w = 0.19; Fig. 2B). Its AICc is only ca. 2 units higher than that of the first model, a difference that can be explained by a higher number of parameters, not by a lower explanatory power (Burnham and Anderson, 2002). The model has a common slope of 1.11 (95% CI 0.92, 1.33), which is statistically indistinguishable from either 1.0 or 1.2, but has different intercepts for each Phylum (model 4, Table II; Fig. 2B). Accordingly, the relationship approaches isometry, the body water content (W/C) does not change appreciably with C, and the percentage carbon can be described by global averages of 1.04 ± 0.54, 0.23 ± 0.14 and 1.77 ± 2.44% for the tunicates, the ctenophores and the cnidarians, respectively (Table III). Models incorporating the FM (models 6 and 7 in Table II) were poorer than those including the TG or the Phylum, yet better than a simple log *W* versus log C regression (Table II).

Allometry of the N content

As for *W*, the best model for the relationship between log N and log C included the TG (model 2 in Table IV, AICc = 24.70, AICw = 0.40; Fig. 3). In this model, the guilds shared a common slope of 0.98 which is statistically undistinguishable from 1 (i.e. the 95% CI 0.95, 1.01). Therefore, the relationship is isometric, with N α C. Accordingly, the nitrogen content (expressed as C:N) is constant and independent of C (since C:N α C/N α C/C∼constant). However, each guild has a different intercept, which translates into a global C:N of 4.38 ± 1.21 and 3.89 ± 1.3 for filter feeders and carnivores, respectively (Table III). According to the $\delta^{15}N$ enrichment observations (Table I), there is a one trophic level difference between the carnivores (trophic level = 2.7 ± 0.3,

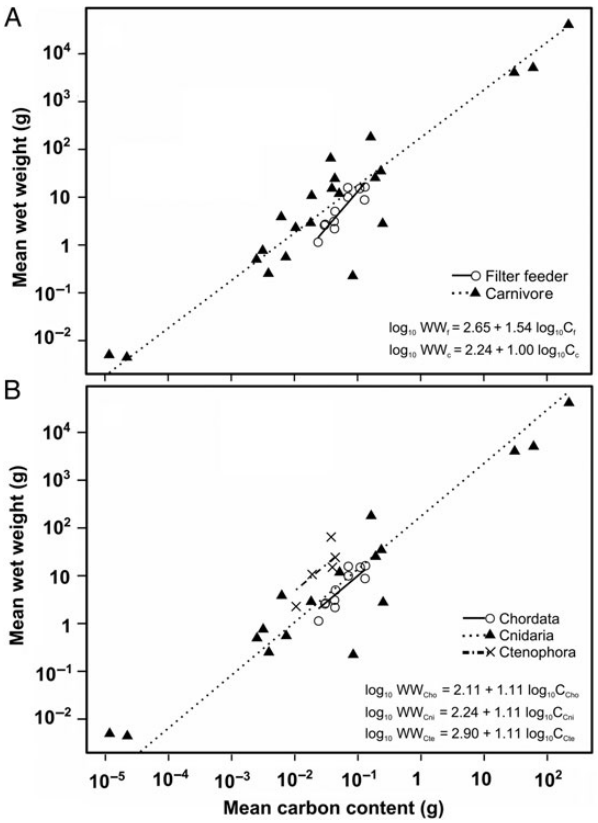

Fig. 2. Fitted RMA regression lines for W versus C separate regressions with different slope for either TG (**A**) or separate regressions with common slope for each Phylum (**B**). Each point corresponds to one species, from Table I.

$n = 11$) and the filter feeders (trophic level = 1.6 ± 0.4, $n = 130$).

DISCUSSION

Previous analyses of W and N as a function of C (Lucas *et al.*, 2011; Kiørboe, 2013) were based largely on conversion coefficients to estimate C and/or W from dry weight or other body size proxies. The use of dry weight for this kind of study is complicated by the presence of hydration water (Larson, 1986; Schneider, 1992; Hirst and Lucas, 1998; Kiørboe, 2013). This led Schneider (Schneider, 1992) to conclude that the individual biomass of gelatinous zooplankton is better expressed in terms of body carbon content. Here, we have used a data set that relies exclusively on direct, concurrent measurements of W and C and of N and C. In our data set, the average carbon content of the ctenophores (0.23% of the fresh body weight, Table III) is similar to that described by Kiørboe (Kiørboe, 2013) (0.26%). However, our average for the cnidarians is remarkably higher and more variable (1.77 ± 2.44%) than that in Kiørboe (Kiørboe, 2013) (0.48 ± 0.68%), due to our inclusion of some species which had high body carbon contents, like the man o'war *Physalia physalis* [9.02%, Table I; a high carbon content for this species was already mentioned in Beers (Beers, 1966)], the velellid *Porpita porpita* (3.75%), the siphonophore *Physophora* sp. (3.21%) or the scyphomedusa *Rophilema sculentum* (1.21%) pointing to a marked

Table III: Body nitrogen content (expressed as the ratio C:N) and body carbon content (expressed as percentage of the wet weight, that is 100 × C/W)

	Carnivores			Filter feeders	
	Ctenophores	Cnidarians	Total carnivores	Tunicates	Total
C:N this work	4.68 ± 0.81 [0.17] {4.64, 5.25–3.89} (31,3)	3.75 ± 1.34 [0.35] {3.52, 6.72–0.9} (73,17)	3.89 ± 1.3 [0.33] {2.6, 6.72–0.9} (104,20)	4.38 ± 1.21 [0.27] {4.73, 16–1.5} (155,7)	4.56 ± 2.46 [0.53] {4.36, 16–0.9} (255,30)
C:N (Steinberg and Sada, 2008)	3.86 ± 0.33 [0.08] {3.8, 4.4–3.5} (NA,5)	4.12 ± 1.41 [0.34] {3.8, 4.6–2.5} (NA,19)	4.08 ± 1.23 [0.3] {3.8, 4.6–2.5} (NA,24)	4.09 ± 1.21 [0.109] {4, 4.8–3.6} (NA,7)	4.07 ± 1.12 [0.27] {3.9, 9.6–2.5} (NA,31)
C:N (Kiørboe, 2013)	4.4 ± 0.5 [0.22] {3.93, 32–3.05} (45,20)	4.0 ± 0.4 [0.77] {3.74, 12.9–1.3} (84,17)	4.5 ± 0.51 [0.11] {3.49, 32–1.3} (129,37)	4.3 ± 0.2 [0.10] {3.41, 11.1–2.31} (85,18)	4.23 ± 0.2 [0.49] {3.91, 32–1.3} (214,55)
C:N (Ikeda, 2014)	3.82 ± 0.60 [0.15] {3.75, 5–1.5} (NA,14)	4.18 ± 2.51 [0.61] {3.63, 11.18–0.85} (NA,40)	4.07 ± 2.16 [0.53] {3.67, 11.18–0.85} (NA,52)	NA	3.8
% C (this work)	0.23 ± 0.14 [0.64] {0.23, 0.64–0.14} (32,4)	1.77 ± 2.44 [1.38] {0.67, 9.01–0.09} (82,19)	1.17 ± 1.9 [1.62] {0.58, 9.01–0.09} (114,23)	1.04 ± 0.54 [0.52] {1.01, 1.68} (155,12)	1.13 ± 1.57 [1.39] {0.68, 1.75–0.07} (271,36)
% C (Kiørboe, 2013)	0.26 ± 0.5 [0.22] {0.18, 0.94–0.007} (48,12)	0.48 ± 0.68 [0.17] {0.47,2.23–0.1} (84, 13)	0.27 ± 0.52 [0.22] {0.19,2.23–0.007} (132, 25)	0.72 ± 0.66 [1.37] {0.24, 3.18–0.02} (85, 11)	0.48 ± 0.23 [0.47] {0.24, 3.18–0–02} (217,36)

The statistics reported are the average ± SD, coefficient of variation (square brackets), median and range (braces) and number of individuals and number of species (parentheses). Statistics have been calculated with one datum per species.

Table IV: Summary of the RMA models for the individual body nitrogen (N)

Model	Model structure	Factor level	Rank	AICc	AICc w	*a*	*b*
1	$\log_{10}N = a + b\log_{10}C$		7	46.58	0.00	−0.66	0.98 (0.95, 1.01)
2	$\log_{10}N = a(TG) + b\log_{10}C$		1	23.96	0.58		
		Carnivores				−0.62	0.98 (0.95, 1.01)
		Filter feeders				−0.73	0.98 (0.95, 1.01)
3	$\log_{10}N = a(TG) \times b(TG)\log_{10}C$		2	24.70	0.40		
		Carnivores				−0.62	1.14 (0.94, 1.97)
		Filter feeders				−0.53	0.97 (0.94, 1.01)
4	$\log_{10}N = a(PH) + b\log_{10}C$		3	30.89	0.02		
		Chordata				−0.73	0.98 (0.95, 1.01)
		Cnidaria				−0.60	0.98 (0.95, 1.01)
		Ctenophora				−0.73	0.98 (0.95, 1.01)
5	$\log_{10}N = a(PH) \times b(PH)\log_{10}C$		5	40.89	0.00		
		Chordata				−0.53	1.14 (0.94, 1.37)
		Cnidaria				−0.61	0.97 (0.97, 1.01)
		Ctenophora				−0.86	0.90 (0.09, 8.76)
6	$\log_{10}N = a(FM) + b\log_{10}C$		4	37.44	0.00		
		Ambush				−0.71	0.98 (0.95, 1.01)
		Cruising				−0.60	0.98 (0.95, 1.01)
		Filter feeders				−0.72	0.98 (0.95, 1.01)
7	$\log_{10}N = a(FM) \times b(FM)\log_{10}C$		6	46.30	0.00		
		Ambush				−0.57	1.09 (0.27, 4.38)
		Cruising				−0.61	0.97 (0.94, 1.00)
		Filter feeders				−0.53	1.14 (0.94, 1.37)

Same conventions as in Table II.

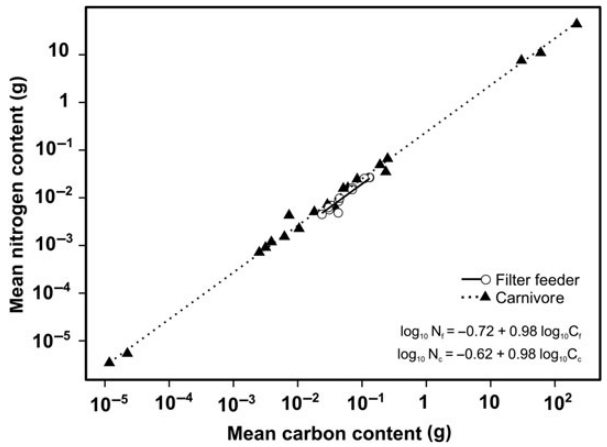

Fig. 3. Fitted RMA regression line for N versus C for TG with a common slope. Each point corresponds to one species, from Table I.

heterogeneity within the Phylum. Interestingly, all except *P. porpita* have a gelatinous appearance, which suggests that there may be special structures in their body plan that account for such high body carbon content, similar to the statoliths described in the moon jellyfish *A. aurita*, which are synthesized from carbonates (Spanberg and Beck, 1968). An interesting exercise would be to test for the presence of carbonates in jelly tissues by comparison of the dry weight before and after acidification. A similar heterogeneity in water content is apparent in the chordates, whose average carbon content in our data set (1.13%) was higher than that in Kiørboe (Kiørboe, 2013) (0.48%) due to inclusion of some carbon-dense species. The message implied is that no simple conversion coefficient should be used blindly and that the most sensible approach in the absence of conversions for a particular species is to use a coefficient from the phylogenetically closest relative [as was demonstrated by Lucas *et al.* (Lucas *et al.*, 2014) in their analysis of gelatinous carbon biomass], or a median (not mean) value for the Phylum if no species identification is possible. By comparison, the body C:N content is less variable, and a Phylum-wise or a global average seems adequate enough to estimate N from C (Table III), a similar conclusion to that of Steinberg and Saba (Steinberg and Saba, 2008) and Ikeda (Ikeda, 2014) using C contents estimated from dry weight.

Inspection of the allometric trends of W versus C and N versus C also reveals some interesting differences with the patterns found using other data sets. Perhaps the most striking signal is the existence of functional differences in the allometry of W versus C and of N versus C relationships among filter feeders and carnivores. The best model for the relationship W versus C was the one where carnivores and filter feeders had separate regression lines (model 3, Table II). The slope of the regression line for the carnivores indicates that their water content varies isometrically with their body carbon, that is, $W = aC^b$ where $b \sim 1$. This implies that $W \sim aC$, which rearranging leads to $W/C \sim a$. In other words, the water content

of gelatinous carnivores can be adequately encapsulated by a constant which is independent of the body carbon content C, and which has a value of 173.78 gW(g $C)^{-1}$. Therefore, bulk measurements of the total fresh weight of ctenophores and cnidarians in a sample can be combined with an average of the C percentage to arrive at an estimate of the total C content in the sample. Such measurements of the fresh body weight can be easily conducted during unexpected encounters with swarms of gelatinous organisms using affordable scales as in the MALASPINA 2010 Expedition (see the Method section). In contrast, the tunicate filter feeders exhibited a strictly allometric relationship with C, such that $W = aC^b$ where $b \sim 1.5$. This means that $W/C \sim aC^{1.5-1} \sim aC^{0.5}$ (model 3, Table II). In other words, the body water content increases with the individual body carbon (i.e. animals with larger body carbon are more watery). Determination of the total tunicate carbon in a sample will therefore require that we measure the fresh body weight W of every single individual in a subsample, use W in combination with a regression equation (i.e. Fig. 2) to calculate their corresponding individual body carbon content C and then sum up all Cs.

Here, we have attempted a test of two alternative hypotheses for the allometry of the carbon content of gelatinous animals. In one of them, the body water content is constant across all sizes and the power allometric relationship between W and C is isometric, with a slope of 1. There is no theoretical underpinning for this hypothesis, but it seems to apply to the gelatinous carnivores in our analysis (see model 3 in Table II) and is consistent with which we know from studies conducted to date (i.e. Pitt *et al.*, 2013). In the alternative hypothesis, gelatinous animals capture prey in proportion to their body surface, which should therefore increase with the body carbon at the same rate as the respiration requirements, leading to a W versus C power relationship with a slope close to 1.2 (see the theoretical considerations in the Introduction section). A 1.2 slope is inconsistent with previous reports of an isometric relationship between W and C in the tunicates that is, a slope of 1 [see Table II in Kiørboe (Kiørboe, 2013)], but is consistent with our observation for these animals (Table II). As such, the gelatinous filter feeders lend support, while the gelatinous carnivores negate the bottom-up, surface limitation hypothesis. This is unlikely due to a contrasting geometry of the capture surface, which seems planar in both cases and supporting a value for $x = 2/3$ in equations (2) and (4) for both types of organisms. However, the carnivores use an external, fixed collection structure (i.e. bell and tentacles in a medusoid cnidarian), while the tunicates use an internal pharyngeal filter which is continuously produced and ingested (Madin and Deibel, 1998). This involves a significant cost, which may explain why growth of the collection surface is more tightly coupled to the metabolic rates in the filter feeders, while other, scale-dependent factors may be at play in the carnivores, such as structural constraints to withstand ocean turbulence (Pitt *et al.*, 2013). In any case, more stringent tests of the hypothesis will require an expanded data set.

Differences in slope are only one of the aspects of the W versus C and N versus C relationships. Our data reveal that the log W versus log C regression line for the filter feeders is located in a lower position than the line for the carnivores (Fig. 2A). In other words, the bodies of gelatinous filter feeders contain slightly less water than the bodies of gelatinous carnivores. Tunicates exhibit maximum retention efficiencies for particles 1−2 μm in size, and are capable of capturing significant amounts of submicrometric or colloidal materials (Sutherland and Madin, 2010). In contrast, most ctenophores and scyphozoans feed on prey larger than several microns in size (Purcell and Arai, 2001). We also know that the biomass of particles in the ocean decreases rapidly with their size (Sheldon *et al.*, 1972). Accordingly, gelatinous carnivores experience a more diluted prey field than the gelatinous filter feeders and, potentially, a stronger selection pressure to develop larger prey capture surfaces, if we accept a bottom-up theory as initially posed by Harbison (Harbison, 1992). It is also likely that the diet of gelatinous filter feeders has a higher proportion of autotrophic prey, because phytoplankton tend to be microns to tens of microns in size, and because our stable isotope data support a difference of one trophic level between both groups of organisms (see the Results section). Autotrophic prey tend to contain less nitrogen than heterotrophic prey [see Table IV in Goñi and Hedges (Goñi and Hedges, 1995)], which may explain why the best of our regression models for the body nitrogen content (model 2, Table IV) separates the filter feeders with a slightly lower body N than the gelatinous carnivores.

In our analysis, a taxonomic classification among three Phyla (Chordata, Cnidaria and Ctenophora; model 4, Table II) was nearly as good as a broad functional classification (carnivores and filter feeders; model 3, Table II) in explaining variance in body water content. This is not surprising, since there is a marked overlap between both classifications: carnivores include ctenophores and cnidarians, while filter feeders correspond exactly with the tunicates in our data set. In other words, taxonomy and function are closely related. In addition, our limited and coarse taxonomic and functional categories do not represent the full existing diversity of taxa and feeding strategies. A proper analysis would require finer categories modelled according to a hierarchical factor arrangement. In this regard, we have tried to apply mixed modelling

analysis (Van de Pol and Wright, 2009) to establish the influence of different levels within the taxonomic hierarchy on the allometry of the water content, but unfortunately the sample size is not yet sufficient for this kind of analysis. Last, a classification among TG (model 3, Table II) was markedly better than a finer functional classification among feeding modes (model 7, Table II). This suggests that it is coarse functional characteristics, like the TG or the prey size rather than finer differences like the feeding mode, which really matters in terms of the water body content.

To summarize, C:N ratios in gelatinous organisms are well constrained and consistent among studies, with slight differences between gelatinous carnivores and filter feeders. In contrast, C:*W* ratios are more variable, and much of that variability is related to broad functional categories potentially intertwined with phylogenetic differences. Appropriate tests of hypothesis on the origins of such variability, and on the exact nature of the allometry between *C* and W will require expansion of the data set with more direct measurements of C and *W*. This can be fulfilled by incorporating relatively simple protocols prepared for serendipitous encounter with these organisms during open ocean oceanographic cruises or in coastal waters. Our experience during the MALASPINA 2010 Expedition demonstrates that the approach is feasible.

SUPPLEMENTARY DATA

Supplementary data can be found online at: http://plankt.oxfordjournals.org.

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