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Abstract

I compiled literature on zooplankton body composition, from protozoans to gelatinous plankton, and report allometric relations and average body composition. Zooplankton segregate into gelatinous and non-gelatinous forms, with few intermediate taxa (chaetognaths, polychaetes, and pteropods). In most groups body composition is size independent. Exceptions are protozoans, chaetognaths, and pteropods, where larger individuals become increasingly watery. I speculate about the dichotomy in body composition and argue that differences in feeding mechanisms and predator avoidance strategies favor either a watery or a condensed body form, and that in the intermediate taxa the moderately elevated water content is related to buoyancy control and ambush feeding.

The chemical body composition is a significant property of an organism's body plan and hence an important organismal trait. It varies dramatically between different groups of zooplankton, mainly segregating zooplankton into gelatinous and non-gelatinous forms. The gelatinous plankton have an inflated volume and a low dry mass to body volume ratio compared to non-gelatinous forms (Vinogradov 1953) and this difference has significant implications for the functional ecology of the respective groups (Hamner et al. 1975; Acuña et al. 2011). The body composition may also vary within taxonomic groups, as documented for protozoans (Menden-Deuer and Lessard 2000) as well as for some phytoplankton (Strathmann 1967), and such size-dependent variation likewise has implications for nutrient acquisition (Thingstad et al. 2005) and other aspects of the organism's ecology (Kiørboe 2008).

Vital rates—metabolism, growth, feeding—constitute other important characteristics of an organism, and they are all related to body size. Comparisons of vital rates between and within taxa must be made using common and relevant body mass units. Carbon (C) is the primary structural component of zooplankton and hence is often chosen as the common unit, and C and nitrogen (N) are the most commonly used currencies of biogeochemical ocean models and in assessments of zooplankton biomass. Despite the need for a common unit, body masses of zooplankton are reported in a variety of units: volume, wet mass, dry mass, ash-free dry mass, C, or N.

There are many reports on the body composition of zooplankton in the primary literature, including several compilations focusing on specific groups, such as jellyfish (Lucas et al. 2011), copepods (Båmstedt 1986), and protists (Menden-Deuer and Lessard 2000), but to my knowledge there are no extensive compilations that examine and compare patterns in body composition across a broader range of taxa. Also, most previous papers report bulk composition and—implicitly—assume that the relative body composition is size independent, which we know in some cases is not the case (e.g., protozoans; Menden-Deuer and Lessard 2000). Here, I compile data on zooplankton body composition, from flagellates to jellyfish and euphausiids, with two purposes. The first is to examine how the body composition trait varies as a function of size and between taxonomic groups, and particularly to see how groups segregate. Although it is well known that gelatinous plankton have a high water content compared to most other zooplankton, the questions are whether the water content is similar or different among the taxonomically and functionally very different gelatinous groups (Cnidarians, Ctenophores, Tunicates), and whether other groups segregate with respect to content of water or other constituents. Such information will allow speculation about the functionality of body composition. The other purpose of the compilation is to facilitate the comparison of vital rates between groups by providing body mass conversion factors, although such comparisons themselves are beyond the scope of this paper.

Methods

Data collection—I collected data on body composition from original papers and supplemented with compilations produced by others (mainly Lucas et al. 2011 for gelatinous plankton). Only observations including simultaneous measurements of two or more measurements of body mass in zooplankton were included. The metrics were body volume, wet weight, dry weight, ash content, C content, and N content. Wet weight and volume were assumed to be equivalent measures, i.e., a density of 1 g cm^{-3}, with the exception of organisms with a heavy shell (snails). The body composition of some organisms varies seasonally; such variation was ignored.

In the source papers, body volumes were estimated from linear dimensions or measured by Coulter counter (protozoans), C and N were measured by C–hydrogen–N elemental analyzers or by wet oxidation (for C), ash content by weighing the residual after combusting the sample at typically 500°C, and wet and dry mass by weighing the fresh and dried sample, respectively. Mass, C, and N measurements were considered only for unpreserved (or frozen) animals. Body volumes (protozoa) were mainly measured on live specimens; when measurements were taken on preserved specimens, no correction for shrinkage

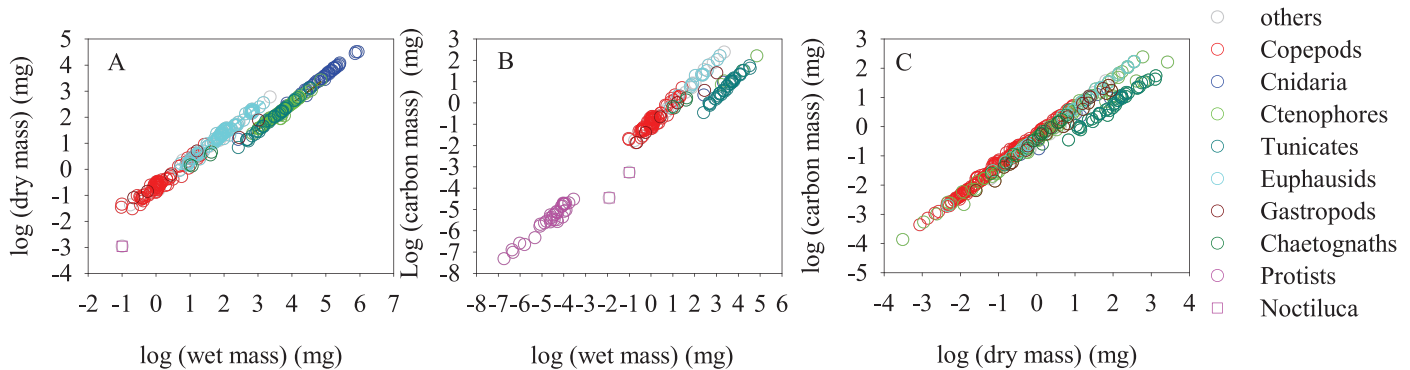* Corresponding author: tk@aqua.dtu.dk

Fig. 1. Individual zooplankter content of (A) dry matter and (B) C relative to wet mass, and of (C) C relative to dry mass.

was attempted (Menden-Deuer and Lessard 2000). Although the measurements of wet and dry mass may seem trivial, there are substantial sources of error that one needs to be aware of when interpreting the results. Typically specimens or samples are blotted prior to estimating the wet weight, but the amount of attached water may vary. A large data set was excluded from this data compilation because the animals were not explicitly blotted prior to weighing and the wet : dry mass ratios reported were significantly and systematically higher than found in all other studies for similar species. Dry masses are measured following drying "to constant weight," which may be up to several days for large gelatinous forms. Drying temperature is typically 50–70°C. Samples are typically, but not always, rinsed in distilled water prior to drying to remove salt. Independent of drying duration and method, a substantial amount of water bound to tissues does not disappear on drying, only after combustion of the sample. The amount of "hydration water" is highly correlated to the water content of the live animal: it is high in gelatinous forms, up to 50% or more of the ash-free dry weight, and small (a few percent) in the more "dense" zooplankton (Madin et al. 1981). Also, both the internal concentration of salt and the amount of hydration water is known to increase with increasing ambient salinity in the jellyfish *Aurelia aurita*, leading to a factor of up to 2 variation in ash content and dry mass relative to wet mass for a salinity range between 10 and 32 (Hirst and Lucas 1998). This implies that the dry mass may be significantly overestimated in gelatinous forms, and that the conversion from dry mass to, e.g., C content may depend on the ambient salinity. Following Lucas et al. (2011) no attempt was made to correct for these factors because the dependency on ambient salinity is known in only a few species.

Data were of two kinds: measurements made on individuals of known size or groups of individuals of similar sizes, which allowed examination of allometric relations between parameters, reported here for several groups for the first time; and measurements made on bulk material from animals of either unknown size or a mixture of sizes, which allowed only examination of bulk body composition. Data were either read from tables or digitized from graphs. For estimates of bulk composition, multiple

observations on the same species were combined into one average estimate per species or stage. These estimates also included those made on individuals of known size. Multiple measurements made on organisms that were not determined to species, e.g., "Brachyuran zoea" or "*Pyrosoma* sp.," were considered one unit. Appendicularians were not included because of the difficulty of defining size, depending on whether or not the "house" was included. Altogether, the compilation resulted in 1130 sets of observations, representing 350 species and 3200 measurements of body mass. All raw data and sources are reported in Web Appendix (www.aslo.org/lo/toc/vol_58/issue_5/1843a.html) Tables A1 (individual measurements), A2 (bulk measurements, raw data), and A3 (species-specific average bulk composition).

Statistical methods—Comparison of body composition between groups were made by one-way analysis of variance (ANOVA; using the parametric *F*-statistic) and parametric two-sample *t*-tests or by their nonparametric equivalents when normality and/or variance homogeneity tests failed (Kruskal-Wallis one-way ANOVA on ranks and Mann-Whitney rank sum test, respectively). For these analyses, one average value per species was used as the basis of comparisons. 95% confidence levels (95% CLs) were also computed to facilitate comparisons between individual groups, because non-overlapping confidence intervals can be taken as (conservative) evidence for a statistical difference at $p < 5\%$ (in all cases verified by ANOVA or two-sample tests). Size dependency of body content was examined using type II linear regressions of log-transformed metrics of body mass; for these regressions, individual measurements, not averages, were used.

Results

Water and C content—Dry matter and C content (relative to live weight) segregate most zooplankton into two distinct groups, the gelatinous group (tunicates, cnidarians, and ctenophores + the dinoflagellate *Noctiluca scintillans*), and the rest (Figs. 1A,B, 2; Table 1). The gelatinous group converges on an average dry matter content of about 4–5% of the live weight and a C content of
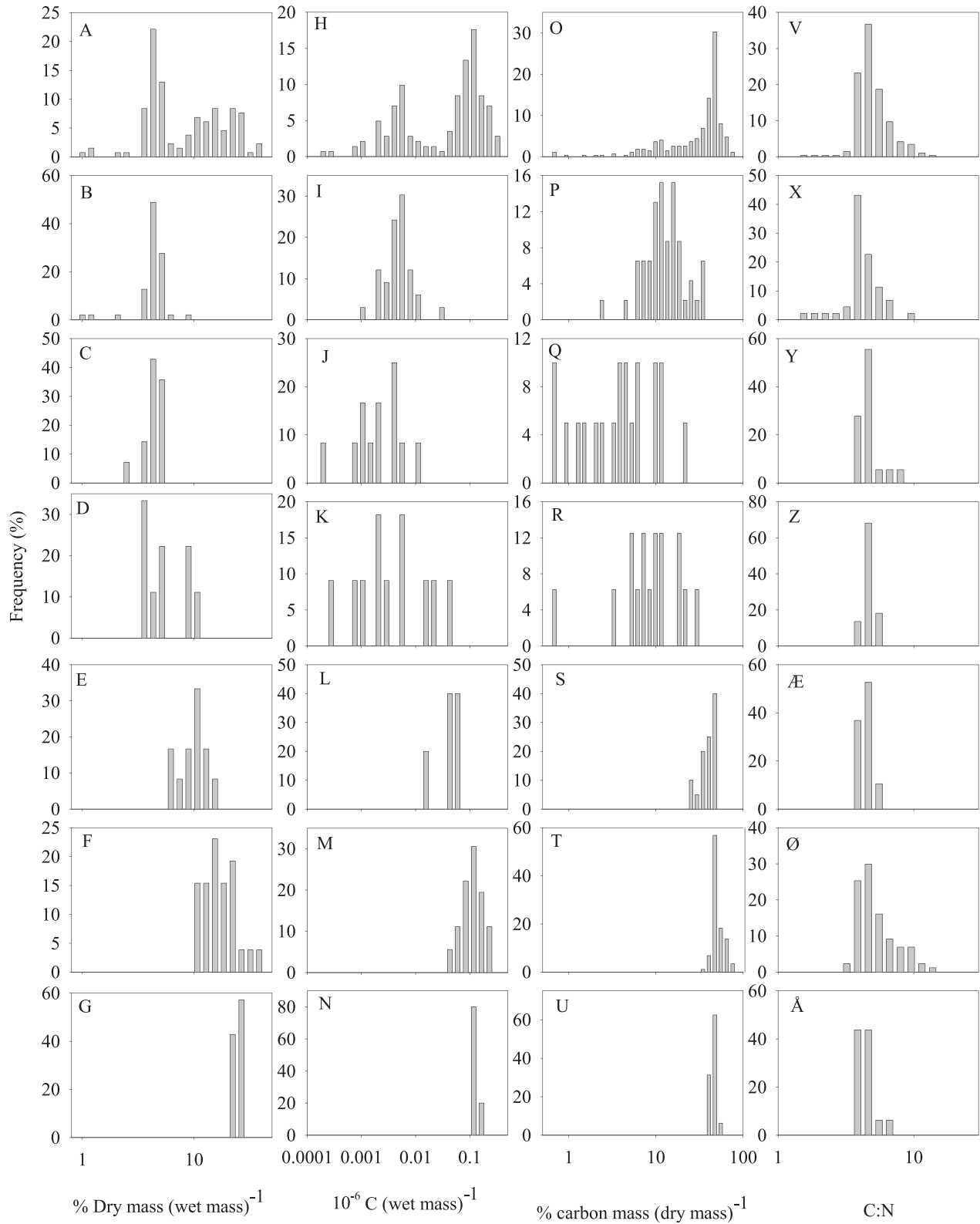
Fig. 2. Frequency distributions of body composition ratios of major taxonomic groups. One entry per species. All species (A, H, O, V), cnidarians (B, I, P, X), ctenophores (C, J, Q, Y), tunicates (D, K, R, Z), chaetognaths (E, L, S, Æ), copepods (F, M, T, Ø), and euphausiids (G, N, U, Å). For number of species and average values for each group, *see* Table 1. The frequency distribution of the entire data set (panels A, H, O, V) reflects the number of species examined in the different groups.

Table 1.   Bulk body composition of major zooplankton groups (average ± 95% CL). The data entering the computation are both bulk measurements and measurements on individuals but all data were combined into one average value per species for each parameter before computing taxon averages. n = number of species; CV = coefficient of variation (standard deviation/mean). Raw data are in Web Appendix, Tables A1 and A2.

Group	Dry (% wet)	Ash (% dry)	C (% dry)	C (% wet)	N (% dry)	C:N (by weight)
Ctenophores	4.0±0.4	72.9±4.6	5.1±2.2	0.26±0.15	1.1±0.5	4.4±0.5
	(n=14; CV=0.17)	(n=13; CV=0.11)	(n=20; CV=0.96)	(n=12; CV=0.96)	(n=18; CV=0.84)	(n=18; CV=0.22)
Tunicates	5.4±1.9	63.5±8.1	10.3±3.9	0.72±0.66	1.9±0.7	4.3±0.2
	(n=9; CV=0.46)	(n=10; CV=0.18)	(n=16; CV=1.37)	(n=11; CV=1.37)	(n=13; CV=0.66)	(n=22; CV=0.10)
Cnidarians	4.1±0.3	52.4±6.4	13.2±2.1	0.48±0.13	3.7±0.9	4.0±0.4
	(n=47; CV=0.28)	(n=34; CV=0.35)	(n=46; CV=0.54)	(n=33; CV=0.77)	(n=85; CV=0.83)	(n=84; CV=0.31)
Chaetognaths	9.3±1.6	24.5±10.2	36.7±3.1	3.6±1.8	9.2±0.9	4.0±0.2
	(n=12; CV=0.27)	(n=8; CV=0.65)	(n=20; CV=0.18)	(n=5; CV=0.41)	(n=19; CV=0.20)	(n=19; CV=0.13)
Polychaetes	13.4±1.7	15.2±6.3	37.0±3.6	5.2±1.4	8.8±0.7	4.2±0.0
	(n=3; CV=0.11)	(n=3; CV=0.18)	(n=2; CV=0.06)	(n=2; CV=0.07)	(n=2; CV=0.08)	(n=2; CV=0.04)
Pteropods	23.0±19.4	30.9±93.1	28.9±4.8	5.3±5.5	5.7±1.5	5.9±1.2
	(n=4; CV=0.53)	(n=2; CV=0.27)	(n=14; CV=0.29)	(n=3; CV=0.57)	(n=14; CV=0.47)	(n=14; CV=0.34)
Copepods	16.2±2.4	7.6±1.8	48±1.4	9.95±1.49	10.2±0.4	5.1±0.4
	(n=26; CV=0.37)	(n=31; CV=0.63)	(n=88; CV=0.14)	(n=36; CV=0.44)	(n=87; CV=0.29)	(n=87; CV=0.38)
Euphausids	22.8±1.4	12.1±3.6	41.9±4.1	10.7±3.2	10.4±0.4	4.1±0.3
	(n=7; CV=0.07)	(n=5; CV=0.32)	(n=16; CV=0.10)	(n=5; CV=0.24)	(n=16; CV=0.08)	(n=16; 0.16)
Amphipods	23.9±9.0	20.7±6.7	34.5±3.2	8.41±1.38	6.8±0.6	5.1±0.3
	(n=5; CV=0.30)	(n=8; CV=0.39)	(n=27; CV=0.24)	(n=6; CV=0.15)	(n=27; CV=0.23)	(n=27; CV=0.18)
All crustaceans	18.3±1.9	11.5±2.4	43.5±1.3	9.61±1.01	9.3±0.3	4.9±0.2
	(n=45; CV=0.34)	(n=47; CV=0.71)	(n=162;CV=0.19)	(n=56; CV=0.39)	(n=161;CV=0.24)	(n=161;CV=0.32)
Protozoa	—	—	—	15.4±3.1	—	5.3±0.7
				(n=14; CV=0.39)		(n=14; CV=0.21)

Table 2. Taxa-specific relationships between dry mass (mg) and wet mass (mg), and between C mass (mg) and wet mass of individual zooplankters as described by log-log type II regressions. Parameter estimates are given with 95% CLs. n = number of observations. * = significantly different from 1.0 ($p < 0.05$). Raw data are in Web Appendix, Table A1.

	Log(dry mass)=a+b×log(wet mass)				Log(C mass)=a+b×log(wet mass)			
	a	b	n	R^2	a	b	n	R^2
Ctenophores	−1.40±0.08	0.98±0.02	130	0.98				
Tunicates	−1.77±0.08	1.08±0.03*	40	1.00	−2.78±0.14	1.01±0.04	38	0.99
Cnidarians	−1.33±0.11	0.99±0.02	49	0.99				
Chaetognaths	−0.68±0.40	0.79±0.30	4	0.97	−0.88±0.51	0.66±0.38	4	0.94
Gastropods	−0.55±0.24	0.80±0.13*	6	0.98	−1.17±0.22	0.83±0.14*	6	0.98
Copepods	−0.67±0.03	0.96±0.06	76	0.93	−0.93±0.04	0.95±0.08	76	0.89
Euphausiids	−0.69±0.05	1.03±0.03	95	0.99	−1.02±0.22	1.01±0.10	13	0.98
Amphipods	−0.57±0.19	0.92±0.30	6	0.92	−0.99±0.18	0.92±0.15	6	0.98
Protozoans					−1.37±0.33	0.88±0.07*	36	0.95

~ 0.5% of the live weight, whereas the non-gelatinous plankton scatter around 15–25% and 5–10%, respectively. The gelatinous zooplankters not only have a high water content, they also have a low C content relative to their dry matter content and they contain a high fraction of minerals (ash; Fig. 1C; Table 1). The low C content relative to dry matter is partly artificial because of the relatively high fraction of hydration water in gelatinous forms that does not disappear on drying.

Although they are similar in dry matter content, there are statistically significant differences within the gelatinous group, with the cnidarians having the highest C and N content and the ctenophores the lowest, and the pelagic tunicates in between (ANOVA: C% dry mass: $p < 0.001$; N% dry mass: $p < 0.001$).

There are also significant differences in body composition between taxa within the non-gelatinous group, and even between the different crustacean taxa. In fact, most groups differ statistically in most of the properties as revealed by ANOVA or two-sample tests and further identified by non-overlapping 95% CLs in Table 1.

Three groups are intermediate, i.e., they have body compositions that are between the gelatinous and the non-gelatinous groups, namely the gastropods, the chaetognaths, and the polychaetes. The gastropods have a relatively high dry matter and ash content (because of the shell), but an intermediate C content. The chaetognaths are intermediate with respect to all measures. Despite the scarcity of data for these groups, the differences are statistically significant from the two other groups for many of the properties (non-overlapping 95% CL in Table 1; significant differences confirmed by two-sample tests).

Allometry—Dry matter and C content are size independent for most zooplankton groups, and slopes of log-log regressions of C or dry-matter content vs. live weight are not significantly different from 1.0 (Table 2). This warrants expressing body composition as taxon-specific averages. Two groups are significantly different, i.e., the protozoans and the gastropods, which both have declining dry matter and C content with increasing size. The chaetognaths show a similar trend, but the scarcity of data prevents a significant result. For these groups, average bulk body composition (Table 1) is not meaningful and size-dependent conversion factors should be preferred (Table 2).

C:N ratios—C and N contents are in most cases closely related, and the overall C:N ratio of all zooplankton is 4.9 and size independent as estimated from the regression between N and C contents (Fig. 3). Despite the similarity in C:N ratios between groups, they are significantly different (one-way ANOVA on both untransformed and
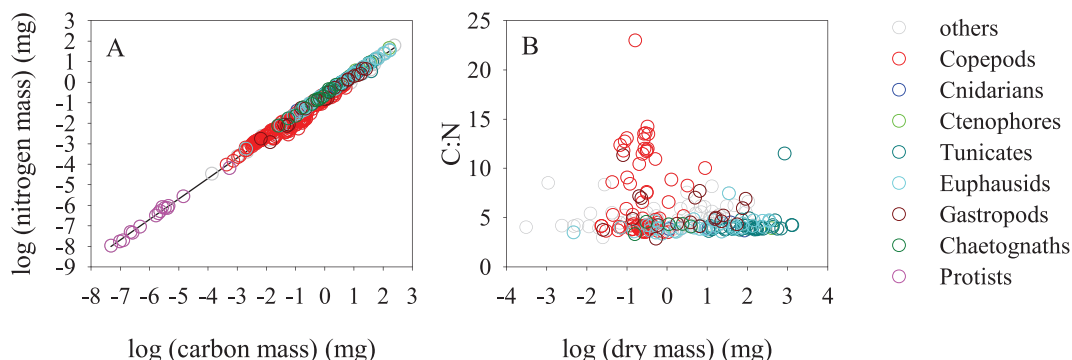

Fig. 3. (A) N content (mg) as a function of C content (mg) of individual zooplankton, and (B) C:N ratio as a function of size (dry mass, mg). The regression line is log N (mg) = −069 + 1.00 log C (mg); $R^2 = 0.99$.

log-transformed data, $p < 0.0001$). They are similarly low in the gelatinous forms and the chaetognaths, and higher but more variable among the crustaceans and other groups.

Discussion

It is striking that the frequency distributions of zooplankton body compositions are bimodal (Figs. 1, 2) with most organisms converging on either a gelatinous or a non-gelatinous body plan, and with relatively few organisms with an intermediate body composition. This finding confirms and substantiates earlier observations (Vinogradov 1953). The frequency distributions, of course, reflect the number of species examined in each group, but that, in turn, reflects also to a large extent the relative abundances of these organisms in the ocean. Chaetognaths, gastropods, and pelagic polychaetes are not rare, but they normally contribute a relatively minor fraction of the zooplankton biomass. Why do groups of very different taxonomy and functional ecology segregate into these two contrasting body plans and why are intermediate strategies apparently less successful, at least as judged from their abundances in the ocean?

The gelatinous body plan—The gelatinous plankton are taxonomically and functionally diverse. Their inflated volume allows them a common trait in the form of a large prey capture cross section or filtering area and, hence, high potential clearance rates as compared to non-gelatinous plankton (Hamner et al. 1975; Acuña 2001; Acuña et al. 2011). They acquire prey by a variety of mechanisms and feed on very different prey. The cnidarians are either passive ambush feeders that use the tentacles as fishing lines and wait for zooplankton prey to randomly encounter a line; or they generate a feeding current through a curtain of tentacles by pulsating their umbrella, and capture zooplankton prey strained by the tentacles or other structures (Costello et al. 2008). The pelagic tunicates are truly filter feeders that retain nano-sized plankton on a large filter with very fine pores. The feeding current is driven either by cilia (doliolids, pyrosomes) or by muscles (salps and appendicularians; Sutherland et al. 2010; Deibel and Lowen 2012). The ctenophores either swim slowly and generate a weak but spatially extended ciliary feeding current that entrains zooplankton prey that are captured when they—too late—try to escape (Colin et al. 2010), or they are ambush feeders that capture prey on plumose tentacles (Greene et al. 1986). Finally, the protozoan "jelly," *N. scintillans*, uses buoyancy regulation to ascend or descend in the water column in order to scavenge phytoplankton prey (Kiørboe and Titelman 1998). Obviously, large size is essential to high clearance rates in all these feeding modes. This applies also to *N. scintillans* in that ascending and descending velocity and, therefore, prey encounter rate increases with cell diameter squared (Stokes' law).

Many gelatinous and intermediate zooplankters may further increase their prey capture size and clearance rate by the use of external mucus feeding webs and structures (Hamner et al. 1975), and this "pseudo-inflation" is not captured by the observed body composition parameters. The appendicularians have elaborate, disposable mucus house filters with a large filter area that allows high clearance rates on small prey (Alldredge and Madin 1982). Larvae of the polychaete *Loimia medusa* secrete a simple mucus barrel around themselves and generate a feeding current through the structure by peristaltic movements of the body (Hamner et al. 1975; Martin et al. 1996), and many mollusk larvae produce mucus strings that function as a drift anchor and increase the efficiency of the ciliary feeding current (Fenchel and Ockelmann 2002). The protozoan *N. scintillans* secretes mucus strings that collect prey (Omori and Hamner 1982; Kiørboe and Titelman 1998), and many pteropods produce very large feeding webs that passively capture particles (Gilmer and Harbison 1986). Thus, a functional gelatinous life form can arise both as the result of an inflated body and as the result of disposable external feeding webs.

The gelatinous body plan offers yet another advantage in that it makes the animals transparent and therefore difficult to see for potential predators (Hamner et al. 1975; Johnsen and Widder 1998). The watery body further makes them unattractive prey to most predators, and their inflated body may make gelatinous plankton difficult to grasp and swallow. A gelatinous body plan therefore provides partial protection from predation. The dual advantage of an inflated body—enhanced feeding and predator protection—is also found among several unicellular osmotrophs (Thingstad et al. 2005). Osmotrophs and unicellular zooplankton "diffusion feeders" (many of the protozoans) become increasingly nutrient limited the larger they are because diffusive delivery of nutrients or prey increases with the radius, not the volume, of the cell (Kiørboe 2008). The decreasing C : volume ratio of protozoans (Table 2) and phytoplankton (Menden-Deuer and Lessard 2000) with increasing size may be considered an adaptation to compensate for this effect of size and at the same time offers partial protection from predation.

However, there must be an upper limit to how inflated an organism can be. Diatoms need a costly silicate wall to suspend the central watery vacuole, and gelatinous plankters need structures to distribute resources and maintain the integrity of the organism, e.g., in the face of ambient turbulence. Pseudo-inflation by external mucus webs is also expensive. Appendicularians, for example, may discard the equivalent of three times their body C as mucus houses every day (Hopcroft and Roff 1998; Sato et al. 2001, 2003). In addition, an inflated body reduces the maximum swimming speed and/or increases the cost of swimming, simply because a larger body implies a larger drag. This is compensated by a substantially lower cost of transportation (specific energy consumption per distance covered) in jellyfish compared to, e.g., crustacean zooplankton (Larson 1987). The low transportation cost is feasible because of the near neutral buoyancy of the gelatinous plankton and of its ability to efficiently regulate its buoyancy (Mills 1984; Newton and Potts 1993) but it has the implication that typical cruise velocities are about an order of magnitude less than cruise velocities of crustacean zooplankters of similar wet body mass (Acuña et al. 2011). The largest

diatoms have a volume : C ratio about 10 times that of other phytoplankton (Menden-Deuer and Lessard 2000), and gelatinous plankton have volume : C ratios that are 20–100 times those of non-gelatinous forms (Table 1), and these may be the limits where the costs and disadvantages exceed the advantage of further inflation and, hence, the optimal ''jelliness'' that gelatinous plankton converge on. The small differences in body composition within the gelatinous group are difficult to explain. They are, for example, unrelated to the main mode of propulsion and feeding current generation: cnidarians and salps both use muscles for propulsion and feeding current generation, doliolids (tunicates) and ctenophores use both muscles and cilia, and pyrosomes (tunicates) use only cilia.

The condensed body plan—The contrasting strategy of a condensed body is related to different feeding and predator avoidance strategies. Feeding typically involves cruising through the water, creation of a scanning current, or ambushing, but, importantly, prey are typically sensed and captured individually in contrast to automatic filtering or random interception. Predator defense strategies similarly typically involve perception of approaching predators and subsequent very powerful escape responses (Kiørboe 2011*a,b*). We find this combination of strategies among planktonic crustaceans, cephalopods, and larval fish, for example, and even among evasive protozoans (Jakobsen 2001), that is, the dense zooplankton. Copepods and ciliates, for example, have peak escape speeds corresponding to 500 body lengths per second (Buskey et al. 2002; Fenchel and Hansen 2006), orders of magnitude higher than escape speeds reported for gelatinous zooplankters. The muscles or other power-generating structures necessary to achieve such high escape velocities imply a denser body and, in some cases, a consequential lower prey capture cross section and clearance rate, although the ability to remotely sense prey may partly compensate for that. But the denser body also makes these zooplankters attractive prey because of a high nutrient content. I argue that there must be a body plan—in terms of structural mass—where the tradeoffs between feeding and predator avoidance are optimized, and towards which non-gelatinous plankters converge. I am thus proposing that these contrasting strategies lead to the observed dichotomy of body plans among marine zooplankton.

Intermediate forms—What about the intermediate forms, e.g., the chaetognaths and the gastropods? The moderately inflated bodies in these groups do not imply increased prey capture areas, as in the truly gelatinous forms. The chaetognaths are ambush feeders, which perceive prey by means of mechanosensory setae, and the prey-encounter cross section is defined by the perception distance, rather than by the size of the chaetognath. The pteropods are also mainly ambush feeders that collect prey on a large blob of mucus, not by a body element (Gilmer and Harbison 1986). I suggest that the relatively low C content and consequently low density is an adaptation to ambush feeding, i.e., to reduce their sinking speeds while ambushing for prey. This is in particular relevant to the gastropods that need to

compensate for their heavy shells. This may also explain why in these groups the water content increases with size, as this may compensate for the sinking speed that otherwise would increase approximately with body size (length) squared. The mucus feeding webs of the pteropods may in addition function as a flotation device, and the relative size of the mucus web increases with the size of the animal (Kiørboe 2011*a*), similarly compensating for the otherwise elevated sinking speed. There are exceptions to this, e.g., actively hunting wing snails and pelagic polychaetes that may be difficult to explain in this framework. There are also ambush feeders among copepods, but these are restricted to small species, arguably because the larger species sink too fast (Kiørboe et al. 2010).

In conclusion, then, I am proposing that contrasting feeding and survival strategies lead to convergence on one or the other of the main zooplankton body plans and to size-independent body compositions, and that the intermediate and size-dependent water content of a few taxa is related to buoyancy control and an ambush feeding strategy.

Conversion factors—The conversion factors and relations between different body constituents reported here for various zooplankton groups may prove useful for the conversion of observed to preferred measures of body mass (Tables 1, 2). C and N are typically the preferred measures, and the ratio between the two is relatively constant (Fig. 3A). The relatively high within-group variation among the copepods (Fig. 3B) reflects the seasonally elevated lipid contents of hibernating copepods in high-latitude environments (Båmstedt 1986). However, C and N are also the most involved measures to achieve, in contrast to dry and wet mass that are the most frequently reported. For the dense zooplankton, dry mass is likely the most reproducible measure of the two, whereas hydration water and the dependency on ambient salinity makes dry mass (and ash-free dry mass) and the conversion to C and N more questionable in the gelatinous forms, where wet mass and the conversion to C and N, in contrast, is independent of ambient salinity (Hirst and Lucas 1998).

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