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Synthesis toward a global model of metabolism and chemical composition of medusae and ctenophores

Tsutomu Ikeda*
16-3-1001 Toyokawa-cho, Hakodate, 040-0065 Japan
ikeda.tutomu@sepia.plala.or.jp
Tel: +81-138-22-5612

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ABSTRACT

Respiration and ammonia excretion data and chemical composition data [water content, ash, carbon (C), nitrogen (N) and C:N ratios] of a total of 28–72 species of hydromedusae, scyphomedusae, siphonophores and ctenophores from various depths of the world's oceans were compiled. Multiple regression analyses revealed that body mass and habitat temperature but habitat depth were significant predictors for respiration and ammonia excretion rates. The scale exponents of body mass (0.66–1.05) and temperature coefficients (1.7–3.1 as Q_{10}) of the empirical regression models varied greatly by the choice of body mass units (DM, C or N). The O:N ratios (median: 15.0) were independent of these parameters. Body C and N compositions (% of DM) decreased with the increase in either DM or habitat temperature, showing a stable C:N ratio of 3.8 (by mass). Comparison of the present results with global-bathymetric features of chaetognaths, copepods, euphausiids and mysids revealed that the medusae and ctenophores are unique in that they maintain high metabolic rates per unit body N, the lack of significant effects of habitat depth on metabolic rates, high specific growth rates, and little accumulation of energy reserves (lipids) in the body.

1. Introduction

Medusae of the phylum Cnidaria (hydromedusae, siphonophores, scyphomedusae) and the phylum Ctenophora are collectively often called “jellyfish” and they are typical members of the gelatinous zooplankton which occurs in coastal waters and at various depth horizons of the world’s oceans (Raymont, 1983). Medusae and ctenophores are planktonic predators, feeding on diverse zooplankton taxa (especially crustaceans) and they have been described as apex predators for “low-energy” food chains (small flagellates–jellyfish) in contrast to traditional “high-energy” food chains (large diatoms–fish) (Purcell, 1991; Mills, 1995; Parsons and Lalli, 2002). Since 1960s, blooms of medusae and/or ctenophores have been reported from many locations of the world (Purcell et al., 2007; Brotz et al., 2012). The reasons for jellyfishes blooms (leading to “low-energy” food chains) has been linked to human activities associated with pollution, eutrophication, overfishing, construction, and climate change but causes remain unresolved. Jellyfish is characterized by high water content, and have long been considered that their physiological rate processes per body mass are low. However, recent studies have shown that jellyfish exhibit foraging capacity and growth potential similar to or even greater than those of other zooplankton or fish of equivalent body carbon (Acuña et al., 2011; Pitt et al., 2013).

Information about metabolism (respiration rates, ammonia excretion rates, and O:N as NH_4-N ratios) has proved useful in understanding the energy demand, metabolic substrates and nutritional condition of marine zooplankton (Ikeda et al., 2000). Historically body mass and temperature have been regarded as the two major parameters for defining the metabolic characteristics of marine epipelagic animals (Ivleva, 1980; Ikeda, 1985), yet habitat depth has emerged as an additional parameter

since metabolic rates decrease rapidly with depth for larger pelagic animals with image-forming eyes such as micronektonic fishes, crustaceans, and cephalopods (Childress, 1995; Seibel and Drazen, 2007). Reduced metabolic rates have also been reported on deep-living copepods and chaetognaths which lack functional eyes (Ikeda et al., 2006a; Ikeda and Takahashi, 2012; Brey, 2010; Kruse et al., 2010). For medusae and ctenophores, data are available in the literature on the effects of body mass and temperature within and between species (Biggs, 1977; Kremer et al., 1986; Larson, 1987a; Pitt et al., 2009; Scolardi et al., 2006; Purcell, 2009 and others), but data on the effect of habitat depth on metabolism are currently limited (Thuesen and Childress, 1994; Bailey et al., 1994a, 1995).

Accumulation of lipids in the body is a widespread phenomenon across marine zooplankton taxa (such as copepods and euphausiids) living in the cold temperature regimes of high latitudes and the deep sea, and lipids are considered an important energy reserve for coping with food scarcity, for reproduction or energy savings while swimming via neutral buoyancy (Lee et al., 2006). Deep-living micronektonic crustaceans and pelagic copepods are characterized by low protein or N content, suggesting reduced musculature for locomotion (Childress and Nygaard, 1974; Ikeda et al., 2006b). Reduced locomotion at depth may reflect reduction in predation pressure with depth (Childress, 1995; Ikeda et al., 2006b). Larson (1986) described the chemical composition (water content, ash, C and N) of shallow-water medusae, and Larson and Harbison (1989) surveyed visible lipid droplets for Arctic and Antarctic medusae and ctenophores and they discussed the origin and fate of lipids under starved conditions. Bailey et al. (1995) and Clarke et al. (1992) reported proximate composition and C and N composition of 5 mesopelagic and bathypelagic species of medusae and 2 species of

ctenophores off Cape Hatteras, North Carolina, USA, and 4 medusae from the Southern Ocean. Lucus et al. (2011) compiled published data of proximate and elemental composition of a total of 102 species of medusae, ctenophores and thaliaceans. Although these results have contributed substantially to our understanding of body chemical composition of medusae and ctenophores, no attempt has been made to analyze these data within the context of global-bathymetric models.

As part of the project to establish metabolic and body compositional responses of major marine zooplankton/micronekton taxa, therefore, I have compiled published data of metabolism (respiration, ammonia excretion, and O:N ratios) and chemical composition (water content, ash, C, N and C:N ratios) of medusa and ctenophore species living at various depths in polar, temperate and tropical/subtropical seas, and significant parameters affecting the variance were explored. The present results are compared with those of the global-bathymetric models reported previously for pelagic copepods (Ikeda et al., 2007), chaetognaths (Ikeda and Takahashi, 2012; Kruse et al., 2010), euphausiids (Ikeda, 2013a), mysids (Ikeda, 2013b) and amphipods (Ikeda, 2013c) to highlight unique features of medusae and ctenophores.

2. Materials and methods

2.1. The data compilation

For the present analyses, the data compiled were those which met the following criteria: 1. Data represented post-larvae collected from the field and used for experiments without considerable time delay (< 24 h) with exceptions of < 8 days delay (Morand et al., 1987), 4–5 days delay (Ikeda and Hirakawa, 1998) or unspecified (Thuesen and Childress, 1994).

114 2. Measurements were made in the absence of food at near *in situ* temperatures in the
115 dark or under natural light regimes for epipelagic or shallow-living medusae and
116 ctenophores. For delicate deep-sea species, the data were those derived from *in situ*
117 capture and incubations by the use of submersibles (Smith, 1982; Bailey et al., 1944a,
118 1995). For robust deep-sea species, the data are those recovered to the surface (1 atom)
119 on the premise that hydrostatic pressure affects little to the metabolism of deep-sea
120 medusae and ctenophores (Childress and Thuesen, 1993; Thuesen and Childress, 1994).
121 The metabolic rate measured on pelagic animals at uncontrolled but minimum motor
122 activity is defined as “routine metabolism” (Ikeda et al., 2000). The ratio of “routine
123 metabolism” to “standard metabolism” (anaesthetized immobile specimens) has been
124 reported as 2.1 for a scyphomedusa *Pelagia noctiluca* (Davenport and Trueman, 1985),
125 2 for *Stomolophus meleagris* (Larson, 1987a) and 4.5 for a ctenophore *Beroe ovata*
126 (Svetlichny et al., 2004).
127 3. O:N ratios were computed from simultaneous measurements of respiration rates and
128 ammonia excretion rates.
129 4. Body mass in terms of wet mass (WM), dry mass (DM), carbon (C), nitrogen (N) or
130 protein (PRO) units were given alone, or together with metabolic data. (Note: body
131 mass specific rates without body mass data are not useful).
132 5. The depth of sampling of specimens was described or deducible (the depth of near
133 surface collections was assigned as 1 m for regression analyses).
134 6. Body composition (water content, ash, C and N) were derived with standard methods
135 (Omori and Ikeda, 1984; Postel et al., 2000) (Note: percent composition without body
136 mass data is not useful).
137 As a result, a total of 93 datasets on 72 species (55 and 18 species from datasets A

and B, respectively) plus 3 size categories of siphonophores, and 38 datasets on 30 species plus 3 size categories of siphonophores were selected in the present study, and these were analyzed for respiration and ammonia excretion rates (Table 1). For siphonophore data, a colony was treated as an individual based on experimental observations on colonial ascidians (Nakaya et al., 2005). The same medusae or ctenophores but from different locations or seasons (when differences in thermal conditions were appreciable) were treated as independent datasets, though mere repetition of the data on the same species from the same or nearly habitats was carefully avoided. The data expressed in the form of regression equations only were converted to the metabolic rates of a specimen at mid-body mass ranges (= geometric means). For chemical composition, 47 datasets of water content, 38 datasets of ash, and 61–62 datasets of C, N and C:N ratios were available on 35, 28 and 44 medusae and ctenophores, respectively (Table 2). Missing habitat temperature data in some of the literature in Table 2 were substituted by those in the World Ocean Atlas of the National Oceanography Data Center (NODC) Homepage by knowing location, season and depth. Study sites of all medusae and ctenophores are plotted on the world map (Fig. 1) to illustrate the worldwide coverage of the datasets in the present study.

Thuesen and Childress's (1994) data (Dataset B, Table 2) were treated separately from the other published datasets because their "minimum-depth of occurrence" (MDO; below which 90% of the population can be found) is difficult to translate to the sampling depth (= habitat depth) because of the broad vertical distribution of each medusa or ctenophores. For comparative purposes, MDO was assumed to be equivalent to mid-sampling depth, and body WM was converted to DM, C or N by using appropriate conversion equations established in the present study (see "3.3. Chemical

composition" section below).

2.2. Regression models

To analyze metabolic data, two regression models were adopted according to the mathematical form of the temperature and body mass effects. One was a theoretical model characterized by the Arrhenius relationship and the other was empirical (or log/linear) model characterized by the Van't Hoff rule (Q_{10}) (Ikeda et al., 2007; Ikeda and Takahashi, 2012; Ikeda, 2013a,b,c);

Theoretical model: $\ln Y = a_0 + a_1 \ln X_1 + a_2(1000X_2^{-1}) + a_3 \ln X_3 + a_4 X_{SC} + a_5 X_{SI} + a_6 X_{HY}$

Empirical model: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 X_{SC} + a_5 X_{SI} + a_6 X_{HY}$

where, Y is respiration rate ($\mu l O_2$ ind.$^{-1}$ h^{-1}) or ammonia excretion rate ($\mu g N$ ind.$^{-1}$ h^{-1}), X_1 is body mass, X_2 is habitat temperature (1000/K for the theoretical model, and ^{o}C for the empirical model), X_3: is mid-sampling depth (m), and X_{SC}, X_{SI} and X_{HY} are dummy variables on scyphomedusae, siphonophores and hydromedusae, respectively (for the definitions of these dummy variables, see Appendix). In order to make between-taxa comparison of marine zooplankton with diversified body composition possible, DM, C or N was used in the present analyses. For the datasets in which body mass was reported as WM without information about water content, DM was estimated assuming a grand mean of water content obtained in the present study (96.0 % of WM), then converted to C or N mass by means of conversion equations established in the present study (see "3.3. Chemical composition" below). It is noted that a_1 was 0.75 (= 3/4, cf. Gillooly et al., 2001) and a_2 was $-E_a/(k \times 1000)$ [E_a: activation energy, k:

185 Bolzman's constant (8.62×10^{-5} eV/K)] for the theoretical model. As an index of
186 temperature effects, Q_{10} of empirical model could be computed as $Q_{10} = \exp(10 \times a_2)$.
187 The attributes of these variables were analyzed simultaneously by using stepwise
188 multiple regression (forward selection) method (Sokal and Rohlf, 1995). Independent
189 variables were added and removed at the $p = 0.05$.The calculation was conducted using
190 SYSTAT version 10.2.
191 As regression models of body composition components, percent data of water,
192 ash, C and N (Table 2) were converted to mg per specimen, then were substituted into
193 the stepwise multiple regression model (empirical model) mentioned above to explore
194 significant variables (body mass, habitat temperature, sampling depth and taxa) which
195 affect them.
196
197 **3. Results**
198 *3.1. Metabolic rates*
199 Of the medusae and ctenophores considered in the present study, *Diphyes* sp. (0.48
200 mgDM) and *Catostylus mosaicus* (86440 mgDM) were the smallest and largest species,
201 respectively (Table 2). Respiration rates at *in situ* temperature ranged from 0.46 μlO_2
202 $ind.^{-1}\,h^{-1}$ (*Crossota* sp. from western subarctic Pacific) to 3504 μlO_2 $ind.^{-1}\,h^{-1}$
203 (*Cassiopea xamachana*), and ammonia excretion rates from 0.019 μgN $ind.^{-1}\,h^{-1}$
204 (*Diphyes antarctica*) to 1787 μgN $ind.^{-1}\,h^{-1}$(*C. mosaicus*) (Table 2).
205 Prior to the stepwise multiple regression analyses, a preliminary analysis was
206 performed to test the effects of temperature and sampling depth on the rates of
207 respiration (R) and ammonia excretion (E) by first plotting the rates standardized to 1
208 mg DM ($R_0 = R \times DM^{-0.75}$ or $E_0 = E \times DM^{-0.75}$) against temperature (1000/K or ^oC)

where the scale coefficient of body mass was assumed as 0.75 (as in the theoretical model) (Fig. 2). No appreciable differences were seen between Datasets A and B. To facilitate the analysis, the data (Dataset A) were separated into two groups depending on the depth of sampled (< 500 m and ≥ 500 m). Since the effect of sampling depth to respiration or ammonia excretion rates was unclear at this stage, only the data of <500 m were used for the analysis of temperature effects on R_0 or E_0. The resultant slope (–4.672 for respiration rates, and –5.569 for ammonia excretion rates, Fig. 2) of the regression lines was used to compute R_0 or E_0 at a given temperature (designated as 10°C) of the medusae and ctenophores from these sampling depths (< 500 m + ≥ 500 m), which were plotted against the mid-sampling depth (Fig. 3). The standardized rates (R_0 or E_0 at 10°C) of these medusae and ctenophores were correlated negatively with the sampling depth ($p < 0.01$ or 0.05), and this result was not affected with or without the addition of the dataset B of Thuesen and Childress (1994) for R_0. From these results, Dataset A and B were combined in the following regression analyses of respiration rates.

The overall results of stepwise multiple regression analyses showed that X_1 (body mass) and X_2 (habitat temperature) were significant variables regardless the choice of models or body mass unit. The new variable X_3 (sampling depth) was not significant ($p > 0.05$) for respiration rates and ammonia excretion rates (Table 3). Higher respiration and ammonia excretion of scyphomedusae than those of hydromedusae, siphonophores and ctenophores were evident in both theoretical and empirical models when body mass was expressed by DM units. Conversely, lower respiration rates of hydromedusae were the case in the theoretical models when body mass was expressed by C and N. For either respiration rates or ammonia excretion rates, the regression coefficient a_2 of the

empirical models significantly differed from unity (1.0) when body mass was expressed by DM units, but the difference was not significant when body mass was expressed by C or N. As judged by R^2 values, the empirical model was superior to the theoretical model, accounting for 78.6–85.6% and 36.1–46.5%, respectively, of the variance in respiration and ammonia excretion (Table 3). As body mass units, C followed by N and DM yielded best fit in the theoretical models, but such the performance of the body mass units was not clear in the empirical models.

Thus, with regard to the effect of sampling depth, the results from the multiple regression analyses were dissimilar to those of the simple regression analyses (Figs. 2, 3) for respiration rates and ammonia excretion rates, in which both rates standardized by body mass and temperature (e.g., R_0 or E_0 at 10^oC, respectively) were grouped based on a single criterion (mid-sampling depth).

3.2. O:N ratios

A total of 32 O:N ratios ranged from 5.9 (*Poralia rufescens* off south California) to 67.5 (*Diphyes antarctica*) (Table 2). A scatter diagram of the O:N ratios and habitat temperature is shown in Fig. 4. Simple correlation analyses indicated that none of the three independent variables was significantly correlated with the O:N ratios (Pearson correlation coefficients > 0.50). Mean and median O:N ratio were 18.0 (± 11.8, SD) and 15.0, respectively.

3.3. Chemical composition

Water content varied from 92.6 (*Pantachogon haeckeli*) to 97.6% of WM (*Beroe ovate*) with a grand mean of 95.8 (± 0.7, SD), ash from 30.1 (*P. haeckeli*) to 81.6% of DM

(*Solmissus incises*) with a grand mean of 68.6 (± 10.9), C from 0.37 (*Bathocyroe fosteri* off Cape Hatteras, USA) to 37.7% of DM (*P. haeckeli*) with a grand mean of 8.8 (± 7.1), N from 0.10 (*B. fosteri* off Cape Hatteras, USA) to 11.0 of DM (*Aglantha digitale* from Usujiri coast, Hokkaido, Japan) with a grand mean of 2.3 (± 1.9), C:N ratios from 2.5 (*Liriope tetraphylla*) to 7.7 (*Agmayeria tortugensis*) with a grand mean of 3.8 (± 0.8). Stepwise multiple regression analyses demonstrated that 82.4–99.6% of the variance in water, ash, C and N were contributed by body mass (represented by DM), habitat temperature, sampling depth and taxa, though these variables contributed only 21.9% of the variance of C:N ratios (Table 4). Among significant variables, the standardized partial regression coefficients indicated body mass to be the prominent importance while importance of sampling depth and taxa were modest or minor. The scale coefficient of body mass (a_2) was significantly greater than 1.0 for ash ($p < 0.05$), but significantly less than 1.0 for C ($p < 0.001$) and N ($p < 0.001$). The scale coefficient did not significantly differ from 1.0 for water ($p > 0.50$) and the sum of ash, C and N ($p > 0.50$) (Table 4). These results for C and N were consistent with those analyzed in Fig 5 in which C and N were expressed as percent values of DM and grouped based on single criterion (body mass and habitat temperature) and where the sampling depth and taxonomic groups were treated as random variables.

4. Discussion

4.1. Respiration and ammonia excretion

While rates of respiration and ammonia excretion of marine zooplankton are well documented as a power function of body mass in general (Ikeda, 1985), the previous results on single or mixed species of hydromedusae, siphonophores, scyphomedusae

281 and ctenophores suggest that the rates are either a power or linear function of body mass
282 (a_1 = 0.5–1.1, Table 5), and the dual functions are seen between-species as well during
283 ontogeny within a species (*Aurelia aurita*; Kinoshita et al., 1997; *Beroe ovate*;
284 Svetlichny et al., 2004). The linear relationship may be an artifact (but see Glazier,
285 2006), often due to the data sets characterized by narrow body mass ranges (typically
286 1–2 orders of magnitude); as was the case in earlier studies in euphausiids (Ikeda,
287 2013a) and amphipods (Ikeda, 2013c). However, the same line of explanation is not
288 applicable to the results summarized in Table 5, as body mass ranges that span 2–4
289 orders of magnitude are sufficient to yield valid rate–body mass relationships. Multiple
290 regression analyses of the present study, in which the attributes by habitat temperature
291 and the other variables are taken in account, showed that respiration and ammonia
292 excretion rates of medusae and ctenophores are a power function ($a_1 < 1.0$) of DM mass
293 but a linear function of C or N mass ($a_1 = 1.0$). Such changes in the scale exponent (a_1)
294 by the choice of body mass units (WM, DM, ash-free DM, C or N) have never been
295 observed in the broad analyses of the relationship between metabolic rates and body
296 mass of non-gelatinous or largely non-gelatinous zooplankton (Ivleva, 1980; Ikeda,
297 1985).

298 The effect of temperature on metabolism has been studied in individual medusa
299 and ctenophore species at graded temperatures within the range of their natural habitats
300 (Table 5). According to the definition by Clarke (1987), this is “acclimation”
301 (adjustment of an organism to a new temperature in the laboratory) in contrast to
302 “adaptation” (the evolutionary adjustment of an organism’s physiology to environment).
303 Acclimated Q_{10} is interpreted as reflecting the acute thermodynamic effect of
304 temperature whereas adapted Q_{10} is presumably the evolutionary optimization of each

species. Acclimated Q_{10} > adapted Q_{10} and this has been described as an "evolutionary trade-off" by Clarke and Fraser (2004). From this view, acclimated Q_{10} values for individual medusae and ctenophores are 1.9–3.7 (excluding the data of 1.7–25.3 of 11 siphonophore species, Table 5) which partially overlap adapted Q_{10} values (1.8–2.8, depending choice of body mass units) derived from the global model for the medusae and ctenophores of the present study. The evolutionary trade-off hypothesis characterized by adapted Q_{10} < 2.0 has been supported by the global compilation of the data of teleost fishes (1.8, Clarke and Johnston, 1999), pelagic copepods (1.9, Ikeda et al., 2007), chaetognaths (1.7, Ikeda and Takahashi, 2012) and euphausiids (1.7, Ikeda, 2013a), but this is true for medusae and ctenophores only when their body mass was expressed by DM unit (1.8, this study). The only exception to this in the world literature is from Purcell et al. (2010) who reported no significant temperature effects on the respiration rates of 16 scyphomedusa species. Perhaps, the effects of temperature are masked in their analyses of the data characterized by the broad body mass range (5 orders of magnitude, which is comparable to the datasets of the present study) but relatively narrow temperature range (7–30^{o}C, as compared with –2 to 30^{o}C of the present study). In the analyses of metabolism–body size (in terms of WM, C and equivalent body diameter) of jellyfish, Acuña et al. (2011) and Pitt et al. (2013) standardized the metabolic data at an inverse absolute temperature (K^{-1}) of 0 by adopting the activation energy [E_a = 0.65eV, Gillooly et al. (2001)] of aquatic invertebrates. The E_a value is equivalent to Q_{10} = 2.5 [exp(10 × 0.65/(k × (273–2) × (273+30))), where k is Boltzmann's constant, cf. Ivleva (1980)] for the temperature range of –2.0 to 30^{o}C, which fall within the range of 1.8–2.8, depending on the choice of body mass units (DM, C or N), of the present study.

As judged by R^2 values, the empirical models are superior to the theoretical models for the prediction of respiration rates or ammonia excretion rates of the medusae and ctenophores (Table 3). Among the three empirical models in which body mass was expressed by DM, C, or N, the best fit to the model was the case for DM for respiration rates but was C for ammonia excretion rates. The difference between C and N was small in both respiration rates (R^2 = 0.797 versus 0.799) and ammonia excretion rates (R^2 = 0.855 versus 0.849). The advantage of the use of C or N unit is the omission of a dummy variable (X_{SC}: schyphomedusae) which was significant when DM units were used as body mass unit for the prediction of respiration rates and ammonia excretion rates. Among the hydromedusae, siphonophores, scyphomedusae and ctenophores treated as dummy variables in the present analyses, scyphomedusae were selected as a distinct taxon characterized by higher respiration and ammonia excretion rates (Table 3), which may be due to their greater C and N composition than the rest of the three taxa (Table 4). Hydromedusae were a significant taxon in the prediction of respiration rates from the theoretical models based on C and N, but no immediate reason for this is seen in their C and N composition data as compared with these of the other taxa.

For the progressive decline in respiration rates in deeper-living micronekton and zooplankton, the “visual-interactions hypothesis” (Childress, 1995) or “predation-mediated selection hypothesis” (Ikeda et al., 2006a) have been proposed respectively. These two hypotheses are similar as both interpret the phenomena as a result of lowered selective pressure for high activity at depth because of the decrease in visual predation in the dark. However, these two hypotheses are different in that the former applies strictly to micronekton with functional eyes whereas the latter applies to both micronekton and zooplankton irrespective of presence/absence of functional eyes.

353 The present results showing no significant depression effects of habitat depth on
354 respiration rates and ammonia excretion rates of the medusae and ctenophores (Table 3)
355 are consistent with those of Thuesen and Childress (1994), and can be interpreted by the
356 absence of functional eyes in them (visual-interactions hypothesis), or very weak
357 predation pressure on them (predation-mediated selection hypothesis).
358
359 *4.2. O:N ratios*
360 The atomic ratio of oxygen consumption rate to ammonia-nitrogen excretion rate
361 (O:N ratio) has been used as an index of the proportion of protein in the diet of marine
362 zooplankton (Mayzaud and Conover, 1988; Ikeda et al., 2000). When only protein is
363 metabolized, the O:N ratio is 7 (Table 10.3 in Ikeda et al., 2000). When protein and lipid
364 or carbohydrate are catabolized in equal quantities O:N ratios are calculated as 21 or 13,
365 respectively (mid-point: 17). Hence, O:N ratios of 7–17 may be used as an index of
366 protein-oriented metabolism and ratios of >17 as lipid/carbohydrate-oriented
367 metabolism. Metabolic O:N ratios (median; 15.0) of the medusae and ctenophores favor
368 protein-oriented metabolism in general. It is noted that the O:N ratios of the medusae
369 and ctenophores listed in Table 2 are derived from experiments in which they were
370 placed in filtered seawater, a common practice when using the sealed-chamber method
371 (Ikeda et al. 2000). Use of filtered seawater is imperative to determine the rates of
372 respiration and ammonia excretion accurately without any corrections for complex
373 uptake/release of oxygen and ammonia by food organisms, but starvation of animals has
374 been reported to reduce the normal metabolism of various zooplankton taxa (Ikeda et al.,
375 2000). Ammonia excretion is more susceptible to food deprivation than respiration,
376 hence high O:N ratios in starved animals have been documented in *Pleurobrachia*

377 *pileus* (Ikeda, 1977) and *Mnemiopsis mccradyi* (Kremer, 1982). The same phenomenon
378 has also been noted in the global-bathymetric models of the metabolism of euphausiids,
379 mysids and amphipods (Ikeda, 2013a,b,c).
380
381 *4.3. Chemical composition*
382 According to Larson and Harbison (1989), medusae and ctenophores inhabiting
383 Arctic and Antarctic waters do contain visible lipid droplets in the lumen of the
384 gastrovascular system. However, the amount of lipids (max 6–22% of DM, Larson and
385 Harbison, 1989) is considerably less than those being found in the copepods and
386 euphausiids in high latitude seas (51–71% of DM, Lee et al., 2006). The present results
387 of non-significant relationships between body C:N ratios (as an index of the ratio of
388 lipids to proteins) and habitat temperatures in medusae and ctenophores (Fig. 6) suggest
389 that lipid deposition is not marked in these gelatinous zooplankton, as was noted already
390 by Pitt et al. (2013). The C:N ratios (grand mean: 3.8) of the medusae and ctenophores
391 is close to those (3.3) for crustacean plankton protein (Ventura, 2006) and that (3.1) for
392 protein derived from an average amino acid composition (Gnaiger and Bitterlich, 1984).
393 The predominance of protein in the organic matter has been confirmed by the proximate
394 composition analyses on jellyfish (Hoeger, 1983; Larson, 1986; Arai et al., 1989; Clarke
395 et al., 1992; Doyle et al., 2007). At the same time, these proximate composition analyses
396 revealed the presence of a significant amount of bound water [lost at 450–500^{o}C (ash
397 measurement) but not at 50–60^{o}C] and unmeasured N-compounds (a glycoprotein or an

398 amino-polysaccharide). These rather unique components may be derived from the
399 mesoglea (composed of water and collagen-like protein) which present in large
400 quantities in these animals (cf. Arai, 1997).

401 C and N compositions decreased with the increase in body mass for the medusae
402 and ctenophores (Fig. 5, Table 4). The decreases in C and N in larger specimens are
403 replaced by the increase in ash since the sum of C, N and ash is independent of body
404 mass (Table 4). The decline in percent C and N composition with the increase in body
405 mass, which emerged from between-species comparison in the present study, has
406 already been noted within-species of some ctenophores (Kremer et al., 1986, Reeve et
407 al., 1989; Kasuya et al., 2000; Finenko et al., 2006) and salps (Iguchi and Ikeda, 2004).

408 With regard to the effect of habitat depth to the chemical composition of jellyfish,
409 Bailey et al. (1995) compared the data of 5 medusae and 2 ctenophores from the
410 mesopelagic zone off Cape Hatteras, North Carolina, USA, with epipelagic counterparts.
411 From this comparison, they concluded that several mesopelagic species were more
412 robust than epipelagic species, but there were no appreciable differences between the
413 two. In the present analyses, habitat depth was not a significant variable affecting the C
414 and N composition of the jellyfish (Table 4). Habitat depth, together with body mass,
415 was a significant variable contributing to the majority of the variance of ash (R^2 =
416 0.993). As judged by the standardized partial regression coefficients, the contribution of
417 habitat depth to the variance of ash content was much less relative to that of body mass,
418 however. Thus, the present results are consistent with those of Bailey et al. (1995) and
419 confirmed that habitat depth is a minor variable affecting chemical composition of

420 jellyfish. From the “predation-mediated selection” hypothesis, these results, combined
421 with insignificant effects of habitat depth on metabolism mentioned above, underpin
422 possible relaxation of jellyfish from predation pressure in the marine pelagic realm as
423 compared with non-gelatinous zooplankton and micronekton.
424
425 *4.4. Medusae and ctenophores as compared with other zooplankton taxa*
426 Previous metabolic comparison of jellyfish with other zooplankton or fish has been
427 made on the bases of equivalent C as a body mass unit and at standardized temperature
428 assuming a common Q_{10} = 2 (Schneider, 1990) or E_a = 0.65eV (Acuña et al., 2011; Pitt
429 et al., 2013). These comparisons revealed that the respiration rate of a jellyfish is nearly
430 comparable to that of other zooplankton or fish. Ikeda (2008) argued that N instead of C
431 is an appropriate body mass unit since N represents proteins which are of prime
432 importance of for living systems.
433 Defining body mass by N units, and usng taxon-specific Q_{10} values revealed in
434 the present analyses, physiological features of medusae and ctenophores were compared
435 with those of global-bathymetric models of chaetognaths, copepods, euphausiids and
436 mysids (Table 6). Among these taxa, the significant depth-related decline in respiration
437 has been observed for all the taxa excepting for the medusae/ctenophores. Adapted Q_{10}
438 value (2.66) of the medusae/ctenophores is the highest among the other zooplankton
439 taxa compared. For a specimen with similar body mass (1 mg N) living in the epipelagic
440 zone (10 m depth, and 100% oxygen saturation) of temperate latitudes (20^{o}C), predicted
441 respiration rates from the theoretical or empirical model of the medusae/ctenophores
442 (22.4–29.4 μlO_2 ind.$^{-1}$ h^{-1}, excluding 15.4 μlO_2 ind.$^{-1}$ h^{-1} for hydromedusae from the

443 theoretical model) are the highest, and those of chaetognaths and copepods (8.4–14.8
444 μlO_2 ind.$^{-1}$ h^{-1}) are the lowest, with those of euphausiids and mysids (15.2–17.1 μlO_2
445 ind.$^{-1}$ h^{-1}) being intermediate. Previous body C- based models (Acuña et al., 2011; Pitt
446 et al., 2013), converted to body N-based models by using the C:N ratios of 3.8, yielded
447 high respiration rates of the specimen comparable to those of the present results (Table
448 6). For the specimen living in the mesopelagic zone (500 m, 5^{o}C and 10% oxygen
449 saturation), similar calculations showed that the high-low orders of respiration rates
450 among the five taxa remained the same.
451 As compared with those of other zooplankton or fish of equivalent body C,
452 jellyfish have been evaluated to exhibit slow swimming speeds but near identical or
453 greater mass specific growth rates (Acuña et al., 2011; Pitt et al., 2013). My own
454 calculations based on the data of Hirst et al. (2003) confirmed that specific growth rates
455 of medusae and ctenophores (mean: 0.192 d^{-1}) were much greater than that (0.143) of
456 copepods and that (0.103) of chaetognaths. No comparable growth rate data are
457 presently available for euphausiids and mysids. Protein synthesis requires the highest
458 energy among the processes involved in the formation of new body mass in zooplankton
459 (Kiørboe et al., 1985; Thor, 2000). To achieve fast growth, jellyfish must capture and
460 ingest prey animals efficiently. A recent analysis revealed that jellyfish are indeed a
461 group of animals that evolved large, watery bodies that enhance prey contact rates and
462 could exhibit clearance rates as high as fish competitor of equivalent C mass (Acuña et
463 al., 2011).
464 As a metabolic quotient, large standard deviations (SD) associated with the mean
465 O:N ratios of the medusae/ctenophores and the other zooplankton taxa suggest
466 non-normal distribution of the O:N data. Thus, the medians rather than means are

467 thought to provide better index of the central trend. Somewhat lower median O:N ratios
468 of the medusae/ctenophores and chaetognaths (15.0 and 12.2) than those of copepods,
469 euphausids and mysids (16.9–27.1) may be interpret by the taxon-specific feeding
470 habits; e.g. the former group is a typical carnivore characterized by protein-oriented
471 metabolism (O:N ratio = 7–17) while the latter group is a mixture of herbivores,
472 omnivores and carnivores characterized by protein- and lipid/carbohydrate-oriented
473 metabolism (O:N ratio = 7–∞).

474 In terms of chemical body composition, the medusae/ctenophores contrast to the
475 three crustacean taxa by extremely high water content (mean: 95.8% vs. 76.9–81.4%),
476 but much lower C (8.7% vs. 42.6–50.6%) and N (2.3% vs. 8.8–10.1%) compositions
477 and C:N ratios (mean: 3.8 vs. 4.2–5.8) (Table 6). The data of chaetognaths fall between
478 these two extremes. Apart from these between-taxa differences in body composition, an
479 important finding of the present study is the progressive decline in C and N composition
480 (expressed as % of DM, Table 4) in the medusae/ctenophores; a phenomenon never
481 been observed in chaetognaths, copepods, euphausiids and mysids. Implications gained
482 from this result are that; one, in addition to taxonomic similarities, body size and habitat
483 temperature are needed to take into account to convert WM or DM to C and N for
484 jellyfish; two, large jellyfish are advantageous to maintain the same WM or DM mass
485 specific growth rate to that of small ones by lower cost of organic matter under identical
486 environmental conditions. In other words, the benefit of large, watery body of jellyfish
487 is not limited to enhance foraging capacity (Acuña et al., 2011) but also to achieve same
488 growth by lesser amount of organic matter input.

In conclusion, multiple-regression analyses of metabolic rates and body composition data in medusae and ctenophores from various depth horizons of the world's oceans revealed that not only the rates of respiration and ammonia excretion but also C and N compositions were a function of body mass and habitat temperature. No significant effects of habitat depth on the metabolic rates and body composition were detected. From global-bathymetric comparisons of the present results with those of chaetognaths, copepods, euphausiids and mysids, medusae and ctenophores are shown to be unique in that they exhibit at higher respiration rates per unit body N, no-significant depth-related reduction in metabolic rates, higher specific growth rates, significant decline in body C and N composition with increasing in body mass and habitat temperature, and no appreciable accumulation of energy reserves (lipids) in the body. Because of body mass-dependence of the C and N composition, the scale exponents of body mass (0.66–1.05) and temperature coefficients (1.7–3.1 as Q_{10}) in the empirical regression models of their respiration rates and ammonia excretion rates varied greatly by the choice of body mass units (DM, C or N).

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References

Acuña, J.L., López-Urrutia, A., Colin, S., 2011. Faking giants: the evolution of high prey clearance rates in jellyfishes. Science 333, 1627–1629.

Arai, M.N., 1997. A functional biology of Scyphozoa. Chapman & Hall, London.

Arai, M.N., Ford, J.A., Whyte, J.N.C., 1989. Biochemical composition of fed and starved *Aequorea victoria* (Murbach et Shearer, 1902)(Hydromedusa). J. Exp. Mar. Biol. Ecol. 127, 289–299.

Bailey, T.G., Torres, J.J., Youngbluth, M.J., Owen, G.P., 1994a. Effect of decompression on mesopelagic gelatinous zooplankton: a comparison of in situ and shipboard measurements of metabolism. Mar. Ecol. Prog. Ser. 113, 13–27.

Bailey, T.G., Youngbluth, M.J., Owen, G.P., 1994b. Chemical composition and oxygen consumption rates of the ctenophore *Bolinopsis infundibulum* from the Gulf of Maine. J. Plankton Res. 16, 673–689.

Bailey, T.G., Youngbluth, M.J., Owen, G.P., 1995. Chemical composition and metabolic rates of gelatinous zooplankton from midwater and benthic boundary layer environments off Cape Hatteras, North Carolina, USA. Mar. Ecol. Prog. Ser. 122, 121-134.

Båmstedt, U., 1985. Seasonal excretion rates of macrozooplankton from the Swedish west coast. Limnol. Oceanogr. 30, 607–617.

Båmstedt, U. 1986. Chemical composition and energy content. In: Corner, E.D.S., O'Hara, S.C.M. (Eds.), The biological chemistry of marine copepods. Clarendon Press, Oxford, pp. 1–58.

Biggs, D.C., 1977. Respiration and ammonia excretion by open ocean gelatinous zooplankton. Limnol. Oceanogr. 22, 108-117.

Brey,T., 2010. An empirical model for estimating aquatic invertebrate respiration. Method. Ecol. Evol. 1, 92–101.

Brotz, L., Cheung, W.W.L., Kleisner, K., Pakhomov, E., Pauly, D., 2012. Increasing jellyfish populations: trends in Large Marine Ecosystems. Hydrobiologia 690, 3–20.

Childress, J.J., 1995. Are there physiological and biochemical adaptation of metabolism in deep-sea animals? Trends Ecol. Evol. 10, 30–36.

Childress, J.J., Nygaard, M., 1974. The chemical composition and relative buoyancy of midwater crustaceans as a function of depth off Southern California. Mar. Biol. 27, 225–238.

Childress, J.J., Thuesen, E.V., 1993. Effects of hydrostatic pressure on metabolic rates of six species of deep-sea gelatinous zooplankton. Limnol. Oceanogr. 38, 665–670.

Clarke, A., 1987. The adaptation of aquatic animals to low temperatures. In: Grout, B.W.W., Morris, G.J. (Eds.), The effects of low temperatures on biological systems. Edward Arnold, London, pp. 315–348.

Clarke, A., Fraser, K.P.P., 2004. Why does metabolism scale with temperature? Functional Ecol. 18, 243–251.

Clarke, A., Holmes, L.J., Gore, D.J., 1992. Proximate and elemental composition of gelatinous zooplankton from the Southern Ocean. J. Exp. Mar. Biol. Ecol. 155, 55–68.

Clarke, A., Johnston, N.M., 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. J. Anim. Ecol. 68, 893–905.

Costello, J., .1991. Complete carbon and nitrogen budgets for the hydromedusa

Cladonema californicum (Anthomedusa: Cladonemidae). Mar. Biol. 108, 119–128.

Davenport, J., Trueman, E.R., 1985. Oxygen uptake and buoyancy in zooplanktonic organisms from the tropical eastern Atlantic. Comp. Biochem. Physiol. 81A, 857–863.

Doyle, T.K., Houghton, J.D.R., McDevitt, R., Davenport, J., Hays, G.C. 2007. The energy density of jellyfish: Estimates from bomb-calorimetry and proximate-composition. J. Exp. Mar. Biol. Ecol, 343, 239–252.

Finenko, G.A., Anninsky, B.E., Romanova, Z.A., Abolmasova, G.I., Kideys, A.E., 2001. Chemical composition, respiration and feeding rates of the new alien ctenophore, *Beroe ovata*, in the Black Sea. Hydrobiologia 451, 177–186.

Finenko, G.A., Kideys, A.E., Anninsky, B.E., Shiganova, T.A., Roohi, A., Tabari, M.R., Rostami, H., Bagheri, S., 2006. Invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea: feeding, respiration, reproduction and predatory impact on the zooplankton community. Mar. Ecol. Prog. Ser. 314, 171–185.

Gillenberg, G., Greve, W., 1979. Studies on oxygen uptake in ctenophores. Ann. Zool. Fennici. 16, 44–49.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of size and temperature on metabolic rate. Science 293, 2248–2251.

Glazer, D.S., 2006. The 3/4-power law is not universal: Evolution of isometric, ontogenetic metabolic scaling in pelagic animals. BioScience 56, 325–332.

Gnaiger, E., Bitterlich, G., 1984. Proximate biochemical composition and caloric content calculated from elemental CHN analysis: a stoichiometric concept. Oecologia (Berlin) 62, 289-298.

Hirst, A.G., Roff, J.C., Lampitt, R.S., 2003. A synthesis of growth rates in marine epipelagic invertebrate zooplankton. Adv. Mar. Sci. 44, 1–142.

Hoeger, U., 1983. Biochemical composition of ctenophores. J. Exp. Mar. Biol. Ecol. 72, 251–261.

Iguchi, N., Ikeda, T., 2004. Metabolism and elemental composition of aggregate and solitary forms of *Salpa thompsoni* (Tunicata: Thaliacea) in waters off the Antarctic Peninsula during austral summer 1999. J. Plankton Res. 26, 1025–1037.

Ikeda, T., 1974. Nutritional ecology of marine zooplankton. Mem. Fac. Fish. Hokkaido Univ. 22, 1–97.

Ikeda, T., 1977. The effect of laboratory conditions on the extrapolation of experimental measurements to the ecology of marine zooplankton. IV. Changes in respiration and excretion rates of boreal zooplankton species maintained under fed and starved conditions. Mar. Biol. 41, 241–252.

Ikeda, T., 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Mar. Biol. 85, 1–11.

Ikeda, T., 2008. Metabolism in mesopelagic and bathypelagic copepods: Reply to Childress et al. (2008). Mar. Ecol. Prog. Ser. 373, 193–196.

Ikeda, T., 2012. Metabolism and chemical composition of zooplankton fro0m 500 to 5,000 m depth of the western subarctic Pacific Ocean. J. Oceanogr. 68, 641–649.

Ikeda, T., 2013a. Respiration and ammonia excretion of euphausiid crustaceans: synthesis towards a global-bathymetric model. Mar. Biol. 160, 251–262.

Ikeda, T., 2013b. Synthesis toward a global-bathymetric model of metabolism and chemical composition of mysid crustaceans. J. Exp. Mar. Biol. Ecol. 445, 79–87.

Ikeda, T., 2013c. Metabolism and chemical composition of marine pelagic amphipods: synthesis towards a global-bathymetric model. J. Oceanogr. 69, 339–355.

Ikeda, T., Bruce, B., 1986. Metabolic activity and elemental composition of krill and other zooplankton from Prydz Bay, Antarctica, during early summer (November-December). Mar. Biol. 92, 545–555.

Ikeda, T., Hirakawa, K., 1998. Metabolism and body composition of zooplankton in the cold mesopelagic zone of the southern Japan Sea. Plankton Biol. Ecol. 45, 31-44.

Ikeda, T., Mitchell, A.W., 1982. Oxygen uptake, ammonia excretion, and phosphate excretion of krill and other Antarctic zooplankton, in relation to their body size and chemical composition. Mar. Biol.71, 283–298.

Ikeda, T., Skjoldal, H.R., 1989. Metabolism and elemental composition of zooplankton from the Barents Sea during early arctic summer. Mar. Biol. 100, 173–183.

Ikeda, T., Takahashi, T., 2012. Synthesis towards a global-bathymetric model of metabolism and chemical composition of marine pelagic chaetognaths. J. Exp. Mar. Biol. Ecol. 424–425, 78–88.

Ikeda, T., Sano, F., Yamaguchi, A., Matsuishi, T., 2006a. Metabolism of mesopelagic and bathypelagic copepods in the western North Pacific Ocean. Mar. Ecol. Prog. Ser. 322, 199-211.

Ikeda, T., Yamaguchi, A., Matsuishi, T., 2006b. Chemical composition and energy content of deep-sea calanoid copepods in the western North Pacific Ocean. Deep-Sea Res. I 53, 1791–1809.

Ikeda, T., Torres, J.J., Hernández-León, S., Geiger, S.P., 2000. Metabolism. In: Harris,

R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), ICES zooplankton methodology manual. Academic Press, San Diego, pp. 455–532.

Ikeda, T., Sano, F., Yamaguchi, A., 2007. Respiration in marine pelagic copepods: a global-bathymetric model. Mar. Ecol. Prog. Ser. 339, 215–219.

Ivleva, I.V., 1980. The dependence of crustacean respiration rate on body mass and habitat temperature. Int. Revue ges. Hydrobiol. 65, 1–47.

Kasuya, T., Ishimaru, T., Murano, M., 2000. Metabolic characteristics of the lobate ctenophore *Bolinopsis midado* (Moser) Plankton Biol. Ecol. 47, 114–121.

Kinoshita, J., Hiromi, J., Kadota, S., 1997. Do respiratory metabolic rates of the scyphomedusa *Aurelia aurita* scale isometrically throughout ontogeny in a sexual generation? Hydrobiologia, 347, 51–55.

Kiørboe, T., Møhlenberg, F., Hamburger, K., 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. Mar. Ecol. Prog. Ser. 26, 85–97.

Kremer, P., 1977. Respiration and excretion by the ctenophore *Mneopiopsis leidyi*. Mar. Biol. 44, 43–50.

Kremer, P., 1982. Effect of food availability on the metabolism of the ctenophore *Mnemiopsis mccradyi*. Mar. Biol. 71, 149–156.

Kremer, P., Canino, M.F., Gilmer, R.W., 1986. Metabolism of epipelagic tropical ctenophore. Mar. Biol. 90, 403–412.

Kruse, S., Brey, T., Bathmann, U., 2010. Role of midwater chaetognaths in Southern Ocean pelagic energy flow. Mar. Ecol. Prog. Ser. 416, 105–113.

Larson, R.J., 1986. Water content, organic content, and carbon and nitrogen composition of medusa from the Northeast Pacific. J. Exp. Mar. Biol. Ecol. 99, 107–120.

Larson, R.J., 1987a. Respiration and carbon turnover rates of medusae from the NE Pacific. Comp. Biochem. Physiol. 87A, 93–100.

Larson, R.J., 1987b. Costs of transport for the scyphomedusa *Stomolophus meleagris* L. Canadian J. Zool. 65, 2690–2695.

Larson, R.J., Harbison, G.R., 1989. Source and fate of lipids in polar gelatinous zooplankton. Arctic 42, 339–346.

Lee, R.F., Hagen, W., Kattner, G., 2006. Lipid storage in marine zooplankton. Mar. Ecol. Prog. Ser. 307, 273–306.

Lucus, C.H., Pitt, K.A., Purcell, J.E., Lebrato, M., Condon, R.H., 2011. What's in a jellyfish? Proximate and elemental composition and biometric relationships for use in biogeochemical studies. Ecology 92, 1704. Ecological Archives E092–144–D1

Marshalones, D., Pinckney, J.L., 2007. Respiration rates of dominant hydromedusae in the North Inlet tidal estuary during winter and summer. J. Plankton Res. 29, 1031–1040.

Mayzaud, P., Conover, R.J., 1988. O:N atomic ratio as a tool to describe zooplankton metabolism. Mar. Ecol. Prog. Ser. 45, 289–302.

McCloskey, L.R., Muscatine, L., Wilkerson, F.P., 1994. Daily photosynthesis, respiration, and carbon budgets in a tropical jellyfish (*Mastigias* sp.). Mar. Biol. 119, 13–22.

Mills, C.E., 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. ICES J. Mar. Sci. 52, 575–581.

Møller, L.F., Riisgård, H.U., 2007. Respiration in the scyphozoan jellyfish *Aurelia aurita* and two hydromedusae (*Sarsia tubulosa* and *Aequorea vitrina*): effect of

size, temperature and growth. Mar. Ecol. Prog. Ser. 330, 149–154.

Morand, P., Carre, C., Biggs, D.C., 1987. Feeding and metabolism of the jellyfish *Pelagia noctiluca* (scyphomedusae, semaeostomae). J. Plankton Res. 9, 651–665.

Nakaya, F., Saito, Y., Motokawa, T., 2005. Experimental allometry: effect of size manipulation on metabolic rate of colonial ascidians. Proc. R. Soc. B 272, 1963–1969.

Nemazie, D.A., Purcell, J.E., Gilbert, P.M., 1993. Ammonium excretion by gelatinous zooplankton and their contribution to the ammonium requirements of microplankton in Chesapeake By. Mar. Biol. 116, 451–458.

Nival, P., Nival, S., Palazzoli, I., 1972. Données sur la respiration de différent organismes communs dans le plankton de Villefranche-sur-Mer. Mar. Biol. 17, 63–76.

Omori, M., Ikeda, T., 1984. Methods in marine zooplankton ecology. John Wiley and Sons Inc., USA.

Parsons, T.R., Lalli, C.M., 2002. Jellyfish population explosions: Revisiting a hypothesis of possible causes. La Mer 40, 111–121.

Percy, J.A., 1988. Influence of season, size, and temperature on the metabolism of an arctic cyppid ctenophore, *Mertensia ovum* (Fabricius). Sarsia 73, 61–70.

Pitt, K.A., Koop, K., Rissik, D., 2005. Contrasting contributions to norganic nutrient recycling by the co-occurring jellyfishes, *Catostylus mosaicus* and *Phyllorihiza punctata* (Scyphozoa, Rhizostomeae). J. Exp. Mar. Biol. Ecol. 315, 71–86.

Pitt, K.A., Welsh, D.T., Condon, R.H., 2009. Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. Hydrobiologia 616,

133–149.

Pitt, K.A., Duarte, C.M., Lucas, C.H., Sutherland, K.R., Condon, R.H., Mianzan, H., Purcell, J.E., Robinson, K.L., Uye, S., 2013. Jellyfish body plans provide allometric advantates beyond low carbon content. PloS One 8, 2–10.

Postel, L., Fock, H., Hagen, W., 2000. Biomass and abundance. In: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), ICES zooplankton methodology manual. Academic Press, San Diego, pp. 83–192.

Purcell, J.E., 1991. A review of cridarians and ctenophores feeding on competitors in the plankton. Hydrobiologia 216/217, 335–342.

Purcell, J.E., 2009. Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. Hydrobiologia 616, 23–50.

Purcell, J.E., Uye, S., Lo, W-T., 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar. Ecol. Prog. Ser. 350, 153–174.

Purcell, J.E., Fuentes, V., Atienza, D., Tilves, U., Astorga, D., Kawahara, M., Hays, G., 2010. Use of respiration rates of scyphozoan jellyfish to estimate their effects on the food web. Hydrobiologia 645, 135–152.

Raymont, J.E.G., 1983. Plankton and productivity in the oceans. Vol 2. Zooplankton. Pergamon Press, Oxford.

Reeve, M.R., Syms, M.A., Kremer, P., 1989. Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply. I. Carbon biomass, feeding, egg production, growth and assimilation efficiency. J. Plankton Res. 11, 535–552.

Schneider, G., 1989. The common jellyfish *Aurelia aurita*: standing stock, excretion

and nutrient regeneration in the Kiel Bight, Western Baltic. Mar. Biol. 100, 507–514.

Schneider, G., 1990. A comparison of carbon based ammonia excretion rates between gelatinous and non-gelatinous zooplankton: implications and consequences. Mar. Biol. 106, 219–225.

Scolardi, K.M., Daly, K.L., Pakhomov, E.A., Torres, J.J., 2006. Feeding ecology and metabolism of the Antarctic cydippid ctenophore *Callianira antarctica*. Mar. Ecol. Prog. Ser. 317, 111–126.

Seibel, B.A., Drazen, J.C., 2007. The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. Phil. Trans. R. Soc. B 362, 2061–2078.

Shimauchi, H., Uye, S., 2007. Excretion and respiration rates of the scyphomedusa *Aurelia aurita* from the inland sea of Japan. J. Oceanogr. 63, 27–34.

Smith, K.L.Jr, 1982. Zooplankton of a bathyal benthic boundary layer: In situ rates of oxygen consumption and ammonium excretion. Limnol. Oceanogr. 27, 461–471.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. The principles and practice of statistics in biological research. Freeman, New York.

Svetlichny, L.S., Abolmasova, G.I., Hubareva, E.S., Finenko, G.A., Bat, L., Kideys, A.E., 2004. Respiration rates of *Beroe ovata* in the Black Sea. Mar. Biol. 145, 585–593.

Thor, P., 2000. Relationship between specific dynamic action and protein deposition in calanoid copepods. J. Exp. Mar. Biol. Ecol. 245, 171–182.

Thuesen, E.V., Childress, J.J., 1994. Oxygen consumption rates and metabolic enzyme activities of oceanic California medusae in relation to body size and habitat

depth. Biol. Bull. 187, 84–98.

Uye, S., Shimauchi, H., 2005. Population biomass, feeding, respiration and growth rates, and carbon budgets of the scyphomedusa *Aurelia aurita* in the Inland Sea of Japan. J. Plankton Res. 27, 237–248.

Ventura, M., 2006. Linking biochemical and elemental composition in freshwater and marine crustacean zooplankton. Mar. Ecol. Prog. Ser. 327, 233–246.

Verde, E.A., McCloskey, L.R., 1998. Production, respiration, and photophysiology of the mangrove jellyfish *Cassiopea xamachana* symbiotic with zooxanthellae: effect of jellyfish size and season. Mar. Ecol. Prog. Ser. 168, 147–162.

Youngbluth, M.J., Båmstedt, U., 2001. Distribution, abundance, behavior and metabolism of *Periphylla periphylla*, a mesopelagic coronate medusa in a Norwegian fjord. Hydrobiologia 451, 321–333.

Youngbluth, M.J., Kremer, P., Bailey, T.G., Jacoby, C.A., 1988. Chemical composition, metabolic rates and feeding behavior of the midwater ctenophore *Bathocyroe fosteri*. Mar. Biol. 98, 87–94.

Figure captions

Fig. 1. Study sites of metabolic rates and chemical composition of medusae and ctenophores. The number and associated character alongside the symbol correspond to the code of each medusa and ctenophore species listed in Table 1. Open stars denote samplings from < 500 m depth, and closed stars from ≥ 500 m depth. Enveloped by hatched lines in the subtropical North Atlantic Ocean are study areas of Biggs (1977).

Fig. 2. Relationship between the respiration rate (A) or ammonia excretion rate (B) of medusae and ctenophores standardized to a body size of 1 mg body DM (R_0 or E_0) and temperature (T^{-1}: 1000/K, or T: ^{o}C) of the specimens from shallow (< 500 m) and deep layers (≥ 500 m). The data points represent means from the datasets in Table 2, and the regression line is derived from shallow layer species only. ** $p < 0.01$.

Fig. 3. Relationship between respiration rates (A) or ammonia excretion rates (B) of medusae and ctenophores standardized to a body size of 1 mgDM (R_0 or E_0) at 10°C and mid-sampling depth. The data points represent means derived from the datasets in Table 2. Open circles and closed triangles denote the data of the species from shallow (< 500 m) and deep layers (≥ 500 m), respectively. ** $p < 0.01$.

Fig. 4. Relationships between O:N (as NH_4-N) ratios and habitat temperature (T) of medusae and ctenophores from various regions of the world's oceans. The data points represent means in Tables 2. Open circles and closed triangles denote the data of the species from shallow (< 500 m) and deep layers (≥ 500 m), respectively. ^{NS} $p > 0.05$.

Fig. 5. Relationship between C and N composition and body mass (A) or habitat temperature T (B) of medusae and ctenophores from various regions of the world's oceans. The data points represent the datasets in Table 2. ** $p < 0.01$.

Fig. 6. Relationship between C:N ratios and body mass (A) or habitat temperature T (B) of medusae and ctenophores from various regions of the world's oceans. The data points represent the datasets in Table 2. ** $p < 0.01$.

Table 1. A list of medusa and ctenophore species of which metabolic and chemical composition data were analyzed

Data set	Phylum/Class	Genus and species	Code	Collection site	Date	Reference
	Cnidaria					
A	Hydrozoa	*Aeginura grimaldii*	1	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		Aequorea victoria	2	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Aglantha digitale	3a	Usujiri coast, Hokkaido, Japan	May 1971	Ikeda (1974)
		Aglantha digitale	3b	Barents Sea	May/Jun 1987	Ikeda and Skjoldal (1989)
		Aglantha digitale	3c	W. subarctic Pacific Ocean	Mar 2006	Ikeda (unpublished data)
		Aglantha digitale	3d	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Benthocodon pedunculata	4	Off Sweeting Cay, the Bahamas	Dec 1990, Mar 1991	Bailey et al. (1994a)
		Botrynema brucei	5	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)
		Bougainvillia muscus	6	North Inlet, S Carolina, USA	Jan, Jul 2006	Marshalonis and Pinckney (2007)
		Calycopsis borchgrevinki	7a	Off Enderby Land, Antarctica	Oct 1985	Ikeda (unpublished data)
		Calycopsis borchgrevinki	7b	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)
		Clytia hemisphaerica	8	North Inlet, S Carolina, USA	Jan, Jul 2006	Marshalonis and Pinckney (2007)
		Colobonema sericeum	9	off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		Crossota sp.	10	W. subarctic Pacific Ocean	Dec 2004	Ikeda (2012)
		Earleria cellularia (formerly *Mitrocoma cellularia)*	11a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Earleria cellularia (formerly *Mitrocoma cellularia)*	11b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Eperetmus typus	12	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Eutonina indicans	13	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Gonionemus vertens	14	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Liriope tetraphylla	15	Tropical Indian/Atlantic Ocean	Nov/Dec 1971	Ikeda (1974)
		Nemopsis bachei	16	North Inlet, S Carolina, USA	Jan, Jul 2006	Marshalonis and Pinckney (2007)
		Pantachogon haeckeli	17	W. subarctic Pacific Ocean	Mar 2003	Ikeda (2012)
		Phialidium gregarium	18a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Phialidium gregarium	18b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Phialidium lomae	19	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Sarsia princeps	20	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Solmissus incisus	21	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		Stomotoca atra	22a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Stomotoca atra	22b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
	Siphonophora	*Abylopsis tetragona*	23	Villefranche-sur-Mer, France	Jul 1960, Jul–Oct 1970	Nival et al. (1972)
		Chelophyes appendiculata	24	Villefranche-sur-Mer, France	Jul, Oct 1970	Nival et al. (1972)
		Diphyes antarctica	25a	Off Enderby Land, Antarctica	Oct 1985	Ikeda (unpublished data)
		Diphyes antarctica	25b	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)
		Diphyes sp.	26	Cape Ferguson Coast, N Queensland, Australia	May 1978	Ikeda (unpublished data)
		19 species	27	Subtropical N Atlantic Ocean		Biggs (1977)
	Scyphozoa	*Atolla wyvillei*	28	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)
		Aurelia aurita	29a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Aurelia aurita	29b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Aurelia aurita	29c	Seto Inland Sea, Japan	Jul–Aug 1991, May–Jun 1992	Uye and Shimauchi (2005)
		Aurelia aurita	29d	Kiel Bight, W. Baltic Sea	Mar–Oct 1982, 1983. 1984	Schneider (1989)
		Cassiopea xamachana	30a	Florida Keys, Florida, USA	Sep 1992	Verde and McCloskey (1998)
		Cassiopea xamachana	30b	Florida Keys, Florida, USA	Jan 1993	Verde and McCloskey (1998)
		Catostylus mosaicus	31	Smiths Lake, NSW, Australia	Feb 2003	Pitt et al. (2005)
		Chrysaora quinquecirrha	32	Chesapeake Bay, Maryland, USA	May–Oct 1990	Nemazie et al. (1993)
		Cyanea capillata	33a	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		Cyanea capillata	33b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Cyanea capillata	33c	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		Mastigias sp.	34	Eil Malk Jellyfish Lake, Palau	Feb–Mar 1982	McCloskey et al. (1994)
		Pelagia noctiluca	35a	Off W Africa	Aug 1983	Davenport and Trueman (1985)
		Pelagia noctiluca	35b	W. Mediterranean Sea	Jun–Dec 1984, 1985	Morand et al. (1987)
		Periphylla periphylla	36	Lurefjorden, W coast of Norway	Mar, Nov 1999	Youngbluth and Båmstedt (2001)
		Poralia rufescens	37a	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		Poralia rufescens	37b	Off S. California, USA		Smith (1982)
		Poralia rufescens	37c	Off S. California, USA		Smith (1982)
		Stomolophus meleagris	38	NE Gulf of Mexico, USA		Larson (1987b)
	Ctenophora	*Agmayeria tortugensis*	39	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		Bathocyroe fosteri	40a	Bahamian waters, WN Atlantic Ocean	May, Sept, Oct 1983, 1984	Youngbluth et al. (1988)
		Bathocyroe fosteri	40b	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		Bathocyroe fosteri	40c	Off Sweeting Cay, the Bahamas	Dec 1990, Mar 1991	Bailey et al. (1994a)
		Beroe abyssicola (formaly *Beroe* sp.)	41	S. Japan Sea	Nov 1991	Ikeda and Hirakawa (1998)
		Beroe cucumis	42a	Oshoro Bay, Hokkaido, Japan	Jul 1970	Ikeda (1974)
		Beroe cucumis	42b	Oshoro Bay, Hokkaido, Japan	Jun 1970	Ikeda (1974)
		Beroe cucumis	42c	Kosterfjorden, W. Sweden	Jul 1981	Båmstedt (1985)
		Beroe ovata	43a	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)
		Beroe ovata	43b	Black Sea	Sep/Nov 1999	Finenko et al. (2001)
		Beroe sp. A	44	Off Wilkes Land, Antarctica	Jan 1980	Ikeda and Mitchell (1982)
		Beroe sp. B	45	Prydz Bay, Antarctica	Nov 1982	Ikeda and Bruce (1986)
		Bolinopsis infundibulum	46	Gulf of Maines, USA	Sep 1989	Bailey et al. (1994b)
		Bolinopsis mikado	47	Tateyama Bay, Chiba, Japan	Jul–Dec 1992, Oct–Nov 1993	Kasuya et al. (2000)
		Bolinopsis vitrea	48	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)
		Callianira antarctica	49	Marguerite Bay, Antarctica	Apr–May 2001, 2002, Jul–Aug 2001, Jul–Sep 2002	Scolardi et al. (2006)
		Eurhamphaea vexilligera	50	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)
		Mertensia ovum	51	Frobisher Bay, Baffin Island, Canada	Aug 1984	Percy (1988)
		Mertensiidae sp.	52	Prydz Bay, Antarctica	Nov 1982	Ikeda and Bruce (1986)
		Mnemiopsis leidyi	53a	Narragansett Bay, Rhode Island, USA		Kremer (1977)
		Mnemiopsis leidyi	53b	Chesapeake Bay, Maryland, USA	May–Oct 1990	Nemazie et al. (1993)
		Mnemiopsis mccradyi	54	N. Biscayne Bay, Florida, USA	Nov 1979	Kremer (1982)
		Ocyropsis maculata	55	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)
		Ocyropsis spp.	56	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)
		Pleurobrachia pileus	57a	Usujiri coast, Hokkaido, Japan	May 1971	Ikeda (1974)
		Pleurobrachia pileus	57b	Kosterfjorden, W. Sweden	Jul 1981	Båmstedt (1985)
		Pleurobrachia sp.	58	Cape Ferguson Coast, N Queensland, Australia	May 1979	Ikeda (unpublished data)
		UC–1	59	Off Sweeting Cay, the Bahamas	Dec 1990, Mar 1991	Bailey et al. (1994a)
	Cnidaria					
B	Hydrozoa	*Aegina citrea*	TC1	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Botrynema brucei	TC2	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Colobonema sericeum	TC3	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Crossota alba	TC4	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Crossota rufobrunnea	TC5	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Crossota sp. A	TC6	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Eirene mollis	TC7	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Haliscera bigelowi	TC8	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Halitrephes maasi	TC9	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Pantachogon sp. A	TC10	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Tetrorchis erythrogaster	TC11	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Vallentinia adherens	TC12	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Vampyrocrossota childressi	TC13	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
	Scyphozoa	*Atolla vanhoeffeni*	TC14	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Atolla wyvillei	TC15	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Nausithoe rubra	TC16	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Paraphyllina ransoni	TC17	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		Periphylla periphylla	TC18	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)

Table 2. Sampling depth, temperature, body mass, rates of respiration and ammonia excretion, O:N ratios, water content, ash, C, N and C:N ratios of medusae and ctenophores. Values are means or means ± 1SD. For species codes, see Table 1. *Italic* values for sampling depth denote "minimum depth of occurrence"defined as the depth below which 90% of the population found (Thuesen and Childress, 1994). When the number of replicates (N) is different for respiration and ammonia excretion rates, respective numbers are given. Blank = no data.

Data set	Species Code	Mid-sampling depth (range) (m)	T (°C)	N	Body mass (mg DM ind.$^{-1}$)	Respiration rate (μlO_2 ind.$^{-1}$h^{-1})	Ammonia excretion rate (μgN ind^{-1}h^{-1})	O:N ratio (by atoms)	Body chemical composition: Water (% of WM)	Ash (% of DM)	C (% of DM)	N (% of DM)	C:N (by mass)
A	1	600 (430–760)	6	6	80 ± 30	49.0 ± 21.6			95.6 ± 0.4	72.0	6.7	1.7	4.0
	2	1	10	45	290	31.9			96.5	77.0	[3.6][a]	[0.96][b]	
	3a	2	8.5	2	3.39 ± 0.58	4.74 ± 0.91	0.24 ± 0.057	24.8 ± 1.1			30.2	11.0	2.7
	3b	150 (0–400)	1.1	8	14.0 ± 6.3	2.27 ± 0.80	0.08 ± 0.05	44.2 ± 28.3	94.7 ± 0.1	56.5 ± 0.0	16.7	4.3	3.9
	3c	125	3	8	5.74 ± 3.67	0.52 ± 0.34			95.7 ± 0.1	60.3 ± 0.0	13.6	3.9	3.5
	3d	1	10	22	6	5.58			95.3	58.0	16.0	4.7	3.4
	4	767 (685–850)	9	17, 8	200 ± 100	114 ± 61	9.2 ± 9.6	17.8 ± 7.5	95.3 ± 0.1		8.2	2.7	3.1
	5	1100 (1000–1200)	2		136.0				95.8	73.2	5.6	1.6	3.4
	6	1 (0.5–1.5)	28	15	[0.70 ± 0.27][d]	0.38 ± 0.20			[95.8][d]		11.3	3.60	3.1
	7a	100 (0–200)	–0.7	5	136.0 ± 24.1	1.7 ± 0.4	0.15 ± 0.06	17.6 ± 11.8	95.7 ± 0.3	68.3 ± 0.0	9.5	2.5	3.9
	7b	595 (190–1000)	2		135.0				95.3	67.2	10.8	2.6	4.2
	8	1 (0.5–1.5)	28	3	[1.08 ± 0.32][d]	0.90 ± 0.40			[95.8][d]		9.6	3.04	3.2
	9	600 (430–760)	6	3	660 ± 120	65.3 ± 15.5			95.2 ± 0.1	63.7	16.9	4.4	3.8
	10	750 (500–1000)	3	9	6.22 ± 8.51	0.46 ± 0.43			95.2 ± 0.5	59.7 ± 0.0	19.8	3.7	5.4
	11a	1	10	32	280	25.2			96.4	81.0	2.8	0.80	3.5
	11b	1	15	20	310	49.6			96.4	81.0	2.8	0.80	3.5
	12	1	10	11	99	24.8			96.0	69.0	8.6	2.5	3.4
	13	1	10	25	43	12.0			96.2	77.0	8.9	2.5	3.6
	14	1	10	12	31	18.0			95.4	52.0	13.7	4.1	3.3
	15	2	27	2	2.27 ± 0.51	1.31 ± 0.71	0.09 ± 0.04	18.7 ± 2.6			7.2	2.9	2.5
	16	1 (0.5–1.5)	12	22	[5.05 ± 2.62][d]	2.84 ± 1.48			[95.8][d]		14.3	4.04	3.5
	17	1125 (500–1500)	3	3	38.78 ± 7.83	4.19 ± 3.28			92.6 ± 0.1	30.1 ± 0.0	37.7	7.4	5.1
	18a	1	10	24	16	4.16			96.1	77.0	9.4	2.5	3.8
	18b	1	15	20	14	6.44			96.1	77.0	9.4	2.5	3.8
	19	1	15	25	7	2.45			96.3	79.0	6.8	1.7	4.0
	20	1	10	8	15	2.40			96.2	64.0	6.7	1.8	3.7
	21	600 (430–760)	6	4	1040 ± 790	322 ± 575			95.9 ± 0.1	81.6	1.5	0.42	3.6
	22a	1	10	14	15	3.90			95.7	75.0	9.6	2.6	3.7
	22b	1	15	13	24	7.44			95.7	75.0	9.6	2.6	3.7
	23	1	15	5	12.5 ± 2.9	3.1 ± 0.8					[8.5][a]	[2.4][b]	
	24	1	15	2	5.0 ± 0.4	1.70 ± 0.70					[11.8][a]	[3.4][b]	
	25a	100 (0–200)	–0.7	2	37.10 ± 2.18	0.96 ± 0.14	0.019	67.5 ± 29.4	95.7 ± 0.3	64.0 ± 0.0	9.9	3.2	3.1
	25b	2050 (1800–2300)	0.5		34.20				95.4	60.0	9.2	2.6	3.5
	26	2	25	3	0.48 ± 0.11	1.08 ± 0.37	0.07 ± 0.02	19.4 ± 3.3			[15.6][a]	[4.9][b]	
	27	15 (0–30)	26	8	[4.7][c]	14.50	0.75	24.2			[8.7][c]	[2.3][c]	
	27	15 (0–30)	26	8	[47.4][c]	60	5.0	15.0			[8.7][c]	[2.3][c]	
	27	15 (0–30)	26	8	[474][c]	300	30	12.5			[8.7][c]	[2.3][c]	
	28	1650 (1200–2100)	1		1252				95.1		15.6	4.0	3.9
	29a	1	10	18	490	68.6			96.2	79.0	4.3	1.3	3.3
	29b	1	15	26	470	113			96.2	79.0	4.3	1.3	3.3
	29c	1 surface	20	24	25200	2862			96.4		3.7	1.0	3.7
	29d	1 surface	15	12	6054		182				[5.2][d]	1.4	
	30a	1	30	27	[7583][c]	2488					[8.7][c]	[2.3][c]	
	30b	1	24	40	[7583][c]	3504					[8.7][c]	[2.3][c]	
	31	1	25		[90762][d]		1787[e]				[0.67][d]	[0.18][d]	
	32	1 surface	23		195		12.4				11.1	2.8	4.0
	33a	600 (430–760)	6	4	6710 ± 3740	470 ± 280			95.5 ± 0.1	68.5	10.0	2.5	4.0
	33b	1	10	16	240	115			95.8	68.6	12.8	3.7	3.5
	33c	1	15	7	130	114			95.8	68.6	12.8	3.7	3.5
	34	1	29		4000	1177					[1.6][a]	[0.48][b]	
	35a	200	18	4	147.9	151				56.6	[10.6][a]	[3.0][b]	
	35b	1 surface	21	13	597	154	26.0	7.4			11.4	2.9	3.9
	36	200 (0–400)	7	162	279	95.3			96.8		19.6	2.9	6.8
	37a	600 (430–760)	6	4	12010 ± 16850	3495 ± 7495			96.0 ± 0.0	73.1	0.59	0.14	4.2
	37b	1300	3	1	59.6	11.3	0.94	15.0			[36.4][a]	[9.5][b]	
	37c	1300	3	1	214.9	25.8	5.45	5.9			[22.8][a]	[5.9][b]	
	38	1	30	1	2050	2460					[2.0][a]	[0.58][b]	
	39	600 (430–760)	6	5	2520 ± 3000	302			95.2 ± 0.7	48.1	19.5	2.5	7.7
	40a	615 (530–700)	11	23, 20	444	9.3	0.37	31.2 ± 3.8			0.74	0.20	3.7
	40b	600 (430–760)	6	4	980 ± 450	213 ± 253			96.0 ± 0.0	81.5	0.37	0.10	3.7
	40c	767 (685–850)	9	3	1900 ± 1510	144 ± 142	13.7 ± 45.8	17.8 ± 11.3	96.1 ± 0.3		0.43	0.14	3.2
	41	550 (400–700)	0.5	2	63.6 ± 31.3	2.3 ± 1.0	0.81	10.6	96.0 ± 0.4	65.3 ± 0.0	11.2	3.0	3.7
	42a	2	15	2	3.43 ± 0.81	3.02 ± 0.70					11.3	3.7	3.1
	42b	2	15	3	52.1 ± 18.9	15.8 ± 2.9	1.2 ± 0.4	17.2 ± 2.9			11.3	3.7	3.1
	42c	100 (0–200)	6	2	14.3		0.1				[9.3][c]	[2.5][c]	
	43a	10 (0–20)	25	22	76	20.6	2.4	10.7			3.7	1.0	3.8
	43b	5 (0–10)	21		100	31.1			97.6		[2.8][a]	[0.79][b]	
	44	2	–0.8	1	401.6	15.4 ± 4.7	2.21 ± 0.24	8.70 ± 24.8			9.0	2.3	3.8
	45	1	–1.6	11	1362 ± 1192	24.8 ± 14.9	2.26 ± 1.27	14.9 ± 6.0	96.1 ± 0.2	72.8 ± 0.7	5.6	1.5	3.6
	46	180 120–240	6	10	1921 ± 291	104 ± 40			96.2	80.7	2.2	0.45	4.8
	47	1 surface	22	14, 11	224	11.7	0.95	15.4			1.1	0.34	3.2
	48	10 (0–20)	25	56	56.30	3.8	0.27	17.6			0.60	0.12	5.0
	49	5 (0-10)	1		232 ± 329	42.7	2.6	20.2 ± 18.4	95.7		8.4	1.8	4.6
	50	10 (0–20)	25	47, 52	202	12.7	1.3	12.2			0.88	0.24	3.7
	51	15 (10–20)	0	115	300	94[f]	8.2[f]	14[f]	95.5		[6.5][a]	[1.6][b]	
	52	1	–1.6	8	93.7 ± 53.7	12.1 ± 6.26	0.76 ± 0.58	24.2 ± 9.0	95.8 ± 0.4	66.3 ± 1.3	11.2	2.4	4.7
	53a	1 surface?	20	30	300	30.5	2.9	13.0 ± 0.9	96.6		1.7	0.50	3.4
	53b	1 surface	23		52.3		3.1				5.1	1.3	3.9
	54	1	22		720	70.2	7.1	12.4			1.4	0.37	3.9
	55	10 (0–20)	25	3, 2	1263	150	15.9	11.8			2.3	0.64	3.5
	56	10 (0–20)	25	16	141	17.8	1.4	15.8			1.2	0.30	3.9
	57a	2	7.3	2	5.80 ± 2.40	1.1 ± 0.06					11.3	3.7	3.1
	57b	100 (0–200)	6	5	5.2		0.19				[9.3][c]	[2.5][c]	
	58	2	25	6	52.3 ± 70.4	8.0 ± 11.1	0.88 ± 1.18	11.2 ± 2.1			[2.8][a]	[0.83][b]	
	59	767 (685–850)	9	5	18400 ± 5880	276 ± 156	27.3 ± 51.2	17.5 ± 9.3	96.0 ± 0.1		0.51	0.16	3.3
B	TC1	*800*	5		[212][c]	21.0			[95.8][d]		[5.5][a]	[1.4][b]	
	TC2	*600*	5		[55.9][c]	4.17			[95.8][d]		[8.9][a]	[2.3][b]	
	TC3	*300*	5		[206][c]	10.0			[95.8][d]		[5.5][a]	[1.4][b]	
	TC4	*100*	5		[25.1][c]	4.46			[95.8][d]		[11.9][a]	[3.2][b]	
	TC5	*500*	5		[24.0][c]	1.97			[95.8][d]		[12.1][a]	[3.2][b]	
	TC6	*1100*	5		[5.74][c]	0.51			[95.8][d]		[20.5][a]	[5.5][b]	
	TC7	*10*	15		[10.8][c]	4.53			[95.8][d]		[8.9][a]	[2.5][b]	
	TC8	*800*	5		[28.5][c]	1.95			[95.8][d]		[11.4][a]	[3.0][b]	
	TC9	*500*	5		[850][c]	20.9			[95.8][d]		[3.3][a]	[0.84][b]	
	TC10	*800*	5		[22.8][c]	3.15			[95.8][d]		[12.4][a]	[3.3][b]	
	TC11	*600*	5		[18.3][c]	1.15			[95.8][d]		[13.4][a]	[3.6][b]	
	TC12	*10*	15		[1.40][c]	1.44			[95.8][d]		[18.8][a]	[5.5][b]	
	TC13	*750*	5		[14.7][c]	1.10			[95.8][d]		[14.5][a]	[3.9][b]	
	TC14	*450*	5		[25.3][c]	2.72			[95.8][d]		[44.1][a]	[11.8][b]	
	TC15	*500*	5		[366][c]	26.2			[95.8][d]		[16.6][a]	[4.3][b]	
	TC16	*1100*	5		[285][c]	33.3			[95.8][d]		[18.2][a]	[4.7][b]	
	TC17	*800*	5		[11.2][c]	1.99			[95.8][d]		[59.5][a]	[16.0][b]	
	TC18	*650*	5		[948][c]	47.6			[95.8][d]		[11.8][a]	[3.0][b]	

[a] lnC = –0.635 + 0.633lnDM - 0.060T (+ 1.313 for scyphomedusae)

[b] lnN = –1.950 + 0.619lnDM - 0.054T (+ 1.328 for scyphomedusae)

[c] calculated from protein (PRO); N = 0.218 PRO (Bailey et al., 1995), C = 3.8 N (this study), DM = N/0.023 (this study)

[d] Original body WM data were converted to DM, C or N by using these conversion factors detrived from the data set A

[e] nighttime data

[f] summer data

Table 3. Stepwise (forward selection, $p_{in} = p_{out} = 0.05$) multiple regression statistics of theoretical and empirical models of respiration rates (Y: µl O_2 ind.$^{-1}$h^{-1}) or ammonia excretion rates (Y: µgN ind.$^{-1}$h^{-1}) of medusae and ctenophores on body mass (X_1: mg ind.$^{-1}$), habitat temperature (X_2: re-defined as 1000/K for the former, ^{o}C for the latter), depth sampled (X_3: m), and taxa (X_{SC}, X_{SI} and X_{HY} are dummy variables on scyphomeduase, siphonophores and hydromedusae, respectively). The coefficient $a_2 = 1$ was tested for the empirical model. ** $p < 0.001$.

Regression model	Body mass unit	N	Step No.	Regression equation: $\ln Y = a_0 + a_1\ln X_1 + a_2 X_2 + a_3\ln X_3 + a_4\ln X_{SC} + a_5 X_{SI} + a_6\ln X_{HY}$ a_0	a_1	a_2	a_3	a_4	a_5	a_6	R^2 (adjusted R^2)	p for t-test H_0: $a_1 = 1.0$
Respiration												
Theoretical	DM	93	1		0.75	–5.186					0.282	
			2	16.380	0.75	–4.875		0.865			0.396 (0.383)	
	C	93	1		0.75	–7.650					0.379	
			2	26.155	0.75	–6.956				–0.604	0.426 (0.414)	
	N	93	1		0.75	–7.330					0.354	
			2	25.863	0.75	–6.587				–0.645	0.410 (0.397)	
Empirical	DM	93	1		0.817						0.776	
			2		0.822	0.063					0.841	
			3	–1.436	0.754	0.059		0.854			0.861 (0.856)	–6.000**
	C	93	1		0.862						0.641	
			2	–0.132	0.950	0.102					0.802 (0.797)	–0.962
	N	93	1		0.893						0.654	
			2	1.150	0.972	0.098					0.803 (0.799)	–0.528
Ammonia excretion												
Theoretical	DM	38	1		0.75	–4.953					0.246	
			2	13.341	0.75	–4.755		1.380			0.396 (0.361)	
	C	38	2	25.904	0.75	–7.641					0.481 (0.466)	
	N	38	2	26.529	0.75	–7.543					0.464 (0.449)	
Empirical	DM	38	1		0.792						0.676	
			2		0.800	0.061					0.756	
			3	–3.917	0.718	0.058		1.461			0.804 (0.786)	–3.570**
	C	38	1		0.913						0.622	
			2	–2.891	1.072	0.109					0.863 (0.855)	0.960
	N	38	1		0.924						0.621	
			2	–1.496	1.080	0.108					0.857 (0.849)	1.026

Table 4. Final multiple regression equations derived from stepwise (forward selection, $P_{in} = P_{out} = 0.05$) multiple regression analyses of body components (Y: water, ash, C or N, all in mg; and C:N ratio with no dimension) of medusae and ctenophores on body mass (X_1: mgDM ind.$^{-1}$), habitat temperature (X_2: ^{o}C), depth sampled (X_3: m), and taxa (X_{SC}, X_{SI} and X_{HY} are dummy variables on scyphomeduase, siphonophores and hydromedusae, respectively). Values in parentheses denote standardized partial regression coefficnets as a measure of relative contribution to the variance. * $p < 0.05$, ** $p < 0.01$

Body component	N	Regression equation: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 X_{SC} + a_5 X_{SI} + a_6 X_{HY}$								p for *t* -test
		a_0	a_1	a_2	a_3	a_4	a_5	a_6	Adjusted R^2	H_0: $a_1 = 1.0$
Water	47	3.087	0.997 (0.981)	0.016 (0.044)				–0.100 (–0.023)	0.996	–0.273
Ash	38	–0.469	1.034 (1.001)		–0.027 (–0.042)				0.993	2.267*
C	61	–0.649	0.635 (0.735)	–0.060 (–0.250)		1.31 (0.271)			0.824	–7.019**
N	62	–1.964	0.622 (0.735)	–0.054 (–0.226)		1.317 (0.282)			0.835	–7.560**
C:N	61	1.257			0.035 (0.482)				0.219	
Ash+C+N	36	4.359	0.999 (1.001)	0.006 (0.015)					0.999	–0.200

Table 5. Effects of body mass (as the scale exponent of body mass = a_2 of the regression model adopted in the present study) and temperature (= a_3) on respiration rates of medusae and ctenophores. The a_3 was assessed as Q_{10} of Van't Hoff rule. For body mass units, VOL = body volume, WM = wet mass, DM = dry mass, PRO = protein, and C = carbon..

Taxonomic group	Species, or the number of species pooled	Body mass effect			Temperature effect		Reference
		a_2	Mass unit	Range (mgDM equivalent)	Q_{10}	Range (°C)	
Respiration							
Hydromedusae	*Aequorea vitrina*	1.02	DM	2–800			Møller and Riisgård (2007)
	Cladonema californicum	0.74	DM	0.01–0.52			Costello (1991)
	Sarsia tubulosa	0.91	DM	0.3–5			Møller and Riisgård (2007)
	11 species	1.02 ± 0.19	DM	1–1900	2.6 ± 1.0[a]	10–15	Larson (1987a)
Siphonophores	11 species	0.79 ± 0.26	PRO	4.4–436	1.7–25.3[b]	16–25.5	Biggs (1977)
Scyphomedusae	*Aurelia aurita*	1.06	WM	440–35400			Shimauchi and Uye (2007)
	Aurelia aurita	1.01	DM	20–8000	3.1	7–22	Møller and Riisgård (2007)
	Aurelia aurita (15°C)	0.63	DM	0.06–10			Kinosita et al (1997)
	Aurelia aurita (15°C)	0.93	DM	10–1100			Kinosita et al (1997)
	Cassiopea xamachana (Jan)	0.74	PRO	100–13080			Verde and McCloskey (1998)
	Cassiopea xamachana (Sep)	0.85	PRO	100–6366			Verde and McCloskey (1999)
	Pelagia noctiluca	0.95	VOL	306–1163			Morand et al. (1987)
	Periphylla periphylla	0.589	C	100–6366			Youngbluth and Båmstedt (2001)
	2 species	0.97 ± 0.06	DM	12–16200	2.9[c]	10–15	Larson (1987a)
Ctenophores	*Beroe gracilis*				3.56	8–20	Gylleberg and Greve (1979)
	Beroe ovata	0.90	DM	10–561			Kremer et al. (1986)
	Beroe ovata	0.58	WM	0.03–91			Svetlichny et al. (2004)
	Beroe ovata	1.04	WM	91–23400	2.17	10–28	Svetlichny et al. (2004)
	Beroe ovata	1.04	DM	10–1000			Finenko et al. (2001)
	Bolinopsis infundibulum				3.73	8–20	Gylleberg and Greve (1979)
	Bolinopsis infundibulum	0.67	DM	100–4800			Bailey et al. (1995)
	Bolinopsis mikado	1.015	DM	50–2000	1.9	16–24	Kasuya et al. (2000)
	Bolinopsis vitrea	0.64	DM	45–2778			Kremer et al. (1986)
	Callianira antarctica	0.707	DM	2.8–1049			Scolardi et al. (2006)
	Eurhamphaea vexilligera	1.12	DM	16–257			Kremer et al. (1986)
	Mertensia ovum (summer)	0.655	DM	10–1000			Percy (1988)
	Mertensia ovum (winter)	0.744	DM	40–700			Percy (1988)
	Mnemiopsis leidyi	0.96	DM	35–562	3.67	16–25	Kremer (1977)
	Ocyropsis sp.	0.97	DM	996–1575			Kremer et al. (1986)
	Pleurobrachia pileus				2.72	2–24	Gylleberg and Greve (1979)
Scyphomedusae(Semeaostomeae)	7 species	1.09	WM	320–1259000			
Schyphomedusae (Rhizostomeae)	6 species	0.917	WM	160–7943000			Purcell et al. (2010)
Schyphomedusae	16 species	0.917	C	0.03–100000	1.0	7–30	
Hydromedusae/scyphomedusae	19 species	0.78	WM	1–926			Thuesen and Childress (1994)
Hydromedusae/scyphomedusae/ siphonophores/ctenophores	26 species	0.78	WM	5–1000000			Acuña et al. (2001)
		0.79	C	0.01–1000			
Hydromedusae/scyphomedusae/ ctenophores	40 species	0.82	C	0.03–14330			Pitt et al. (2013)
Hydromedusae/scyphomedusae/ siphonophores/ctenophores	71 species + 3 size groups of siphonophores	0.754	DM	0.5–25200	1.80		
		0.950	C	0.075–932	2.77	–2 to 30	This study
		0.972	N	0.024–252	2.66		
Ammonia excretion							
Hydromedusae	*Cladonema californicum*	1.41	DM	0.01–0.52			Costello (1991)
Siphonophores	11 species	0.80±0.18	PRO	4.4–436			Biggs (1977)
Scyphomedusae	*Aurelia aurita*	0.93	WM	1836–19962			Schneider (1989)
	Aurelia aurita	1.09	WM	440–35400			Shimauchi and Uye (2007)
	Chrysaora quinquecirrha	0.974	DM	13–2826			Nemazie et al. (1993)
	Pelagia noctiluca	0.90	VOL	306–1163	3.8	15–25	Morand et al. (1987)
Ctenophores	*Beroe ovata*	0.82	DM	10–561			Kremer et al. (1986)
	Bolinopsis mikado	1.147	DM	50–1000	4.1	16–24	Kasuya et al. (2000)
	Bolinopsis vitrea	0.76	DM	45–2778			Kremer et al. (1986)
	Callianira antarctica	0.487	DM	2.8–1049			Scolardi et al. (2006)
	Eurhamphaea vexilligera	0.93	DM	16–257			Kremer et al. (1986)
	Mertensia ovum (summer)	0.623	DM	10–1000			Percy (1988)
	Mertensia ovum (winter)	0.546	DM	40–700			Percy (1988)
	Mnemiopsis leidyi	0.89	DM	35–562	3.73	16–25	Kremer (1977)
	Mnemiopsis leidyi	0.604	DM	7–391			Nemazie et al. (1993)
	Ocyropsis sp.	1.06	DM	996–1575			Kremer et al. (1986)
Hydromedusae/scyphomedusae/ ctenophores		0.84	C	0.14–69780			Pitt et al. (2013)
Hydromedusae/scyphomedusae/ siphonophores/ctenophores	29 species + 3 size groups of siphonophores	0.718	DM	0.658–1050	1.79		
		1.07	C	0.075–608	2.97	–2 to 27	This study
		1.08	N	0.024–163	2.94		

[a] Three species

[b] *Forskalia* spp.

[c] One species

Table 6. Global-bathymetric comparisons of ecological and physiological features of medusae/ctenophores, pelagic chaetognaths, copepods, euphausiids and mysids living in world's oceans. For respiration rate, T and E denote Theoretical and Empirical models, respectively. For comparative purpose, the rates predicted from the models from Acuña et al. (2011) and Pitt et al. (2013) are included. Body compnents were compared based on the results from multiple regression analyses in which body mass, habitat temperature and depth were designated as independent variables (for the regression model, see Table 4). N is the number of data and Nsp the number of species. Modified from Ikeda (2013a,b,c). *NS* : Not significant ($p > 0.05$), ND: No data

Parameters	Medusae/ctenophores	Chaetognaths	Copepods	Euphausiids	Mysids
Food habit	Carnivore	Carnivore	Herbivore, omnivore, carnivore	Herbivore, omnivore, carnivore	Herbivore, omnivore, carnivore
Metabolism					
Respiration rate ($\mu l\ O_2\ ind.^{-1} h^{-1}$)					
Depression effect of habitat depth	Not significant	Significant	Significant	Significant	Significant
Body mass (mgN, range)	0.024–252	0.010–2.01	0.0005–2.38	0.029–149	0.008–66.0
Q_{10} for the temperature range of –1.8 to 30°C (based on body N)					
Mean (95% CI range)	2.66 (2.10–3.38)	2.05 (1.60–2.63)	1.92 (1.67–1.93)	1.60 (1.39–1.60)	2.12 (1.60–2.81)[a]
N (Nsp)	93 (72)	25 (17)	253 (108)	39 (24)	42 (38)
Predicted rate for a specimen of 1mgN body mass inhabiting 10 m depth (20°C, O_2 saturation = 100%)					
T-model	29.4[b], 15.4[c]	8.4	12.1	15.9	17.1
E-model	22.4	14.2	14.8	15.7	15.2
Acuña et al.s' model	28.4[d]				
Pitt et al.s' model	32.4[d]				
Predicted rate for a specimen of 1mgN body mass inhabiting 500 m depth (5°C, O_2 saturation = 10%)					
T-model	8.7[b], 4.6[c]	1.5	2.3	5.6	4.4
E-model	5.2	1.8	2.6	5.6	3.3
Acuña et al.s' model	7.1[d]				
Pitt et al.s' model	8.1[d]				
O:N ratio (by atms)					
Range	5.9–67.5	6.8–36	4.8–49	11–142	8–45
Mean (±SD)	18.0 (11.8)	15.6 (8.9)	20.7 (11.3)	30.1 (17.4)	20.3 (10.6)
Median	15.0	12.2	16.9	27.1	18.7
N (Nsp)	32 (25)	12 (10)	37 (29)	31 (19)	15 (13)
Growth					
Weight specific rate (day^{-1})					
Range	–0.069 to 0.078[e]	–0.013 to 0.41[e]	0.000–1.62[f]	ND	ND
Mean (±SD)	0.192 (0.198)	0.103 (0.125)	0.143 (0.209)		
N (Nsp)	103 (9)	87 (4)	2528 (69)		
Body composition component, and regression coefficients of body mass (a_2), habitat temperature (a_3) and depth (a_4)					
Water a_2, mean (±SD)	0.997 (0.011)	1.128 (0.055)	ND	1.002 (0.007)	0.953 (0.033)
a_3, mean (±SD)	0.16 (0.003)	*NS*	ND	*NS*	*NS*
a_4, mean (±SD)	*NS*	*NS*	ND	0.005 (0.004)	*NS*
N (Nsp)	47 (35)	18 (13)	93 (93)[g]	36 (27)	18 (14)
% of WM, mean (SD)	95.8 (0.7)	90.8 (2.9)	81.4 (5.1)[g]	76.9 (3.7)	77.6 (5.4)
C a_2, mean (±SD)	0.635 (0.052)[h]	0.957 (0.028)	1.045 (0.006)	1.011 (0.008)	1.038 (0.012)
a_3, mean (±SD)	–0.060 (0.013)	*NS*	–0.003 (0.001)	*NS*	*NS*
a_4, mean (±SD)	*NS*	*NS*	*NS*	*NS*	*NS*
N (Nsp)	57 (42)	27 (18)	253 (108)	41 (28)	24 (20)
% of DM, mean (±SD)	8.7 (7.3)	37.9 (7.3)	50.6 (6.7)	42.6 (4.4)	46.6 (6.6)
N a_2, mean (±SD)	0.622 (0.050)[h]	0.936 (0.027)	0.952 (0.011)	1.013 (0.012)	1.038 (0.012)
a_3, mean (±SD)	–0.054 (0.013)	*NS*	*NS*	*NS*	*NS*
a_4, mean (±SD)	*NS*	*NS*	–0.022 (0.006)	–0.028 (0.008)	*NS*
N (Nsp)	58 (42)	26 (18)	253 (108)	41 (28)	24 (20)
% of DM, mean (±SD)	2.3 (1.9)	9.6 (2.2)	8.8 (1.8)	10.1 (1.4)	8.8 (2.3)
C:N (by mass)					
Range	2.5–7.7	2.6–5.1	3.7–9.4	3.4–8.6	3.2-10.6
Mean (±SD)	3.8 (0.8)	4.0 (0.6)	5.4 (1.5)	4.2 (1.1)	5.8 (2.5)
N (Nsp)	57 (42)	32 (22)	94 (94)	41 (28)	24 (20)

[a] Substituted by the DM-based data

[b] For siphonophores, scyphomedusae and ctenophores

[c] For hydromedusae

d For a specimen weighing 3.8 mgC, which is equivalent to 1 mgN (C:N ratio = 3.8)

[e] Calculated from the data in Hirst et al. (2003)

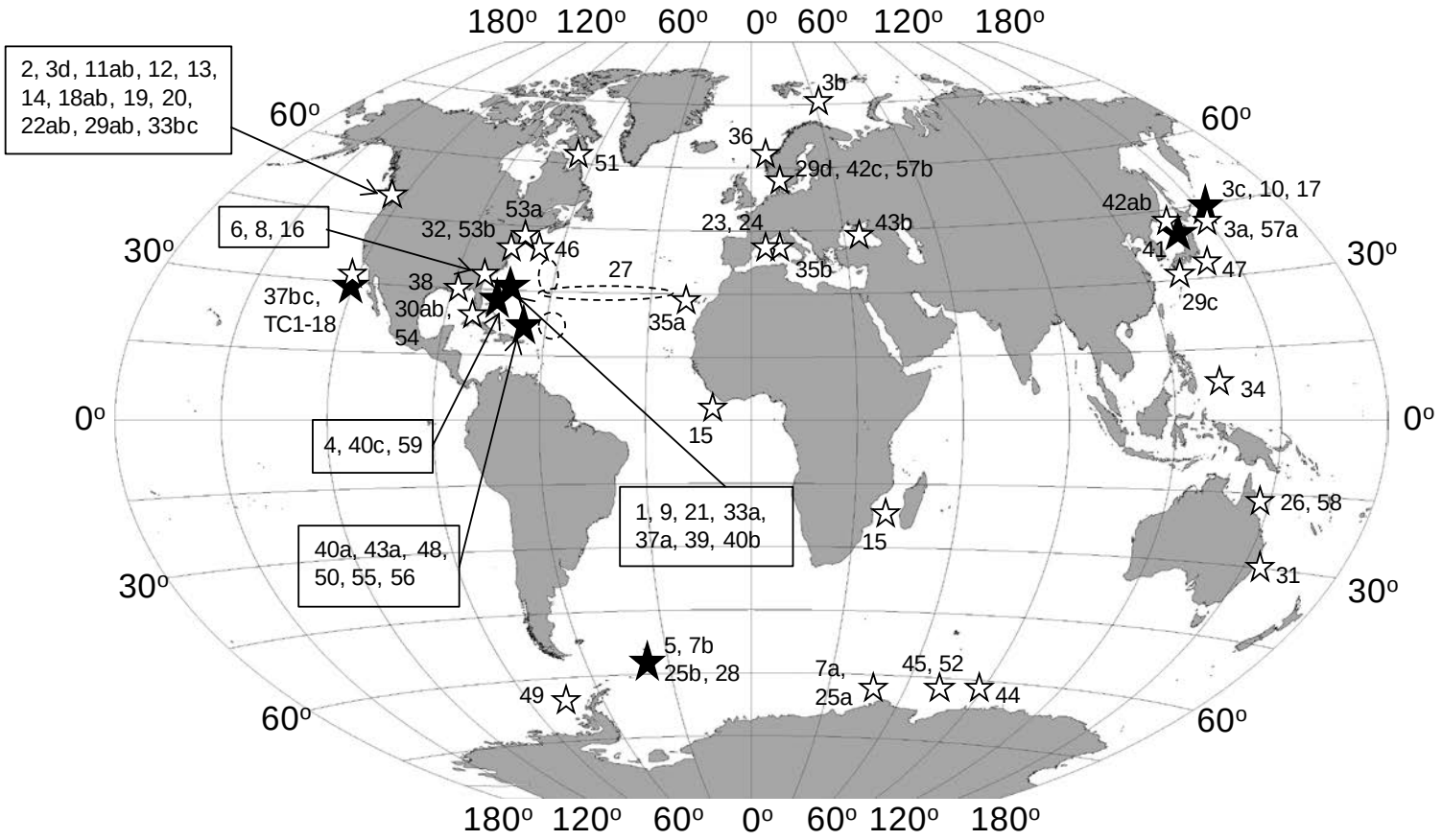
[f] From Hirst et al. (2003)

[g] From Båmstedt (1986). Means given for six groups (3 latitudes × 2 depths) were weighed by the number of data sets to derive a grand mean

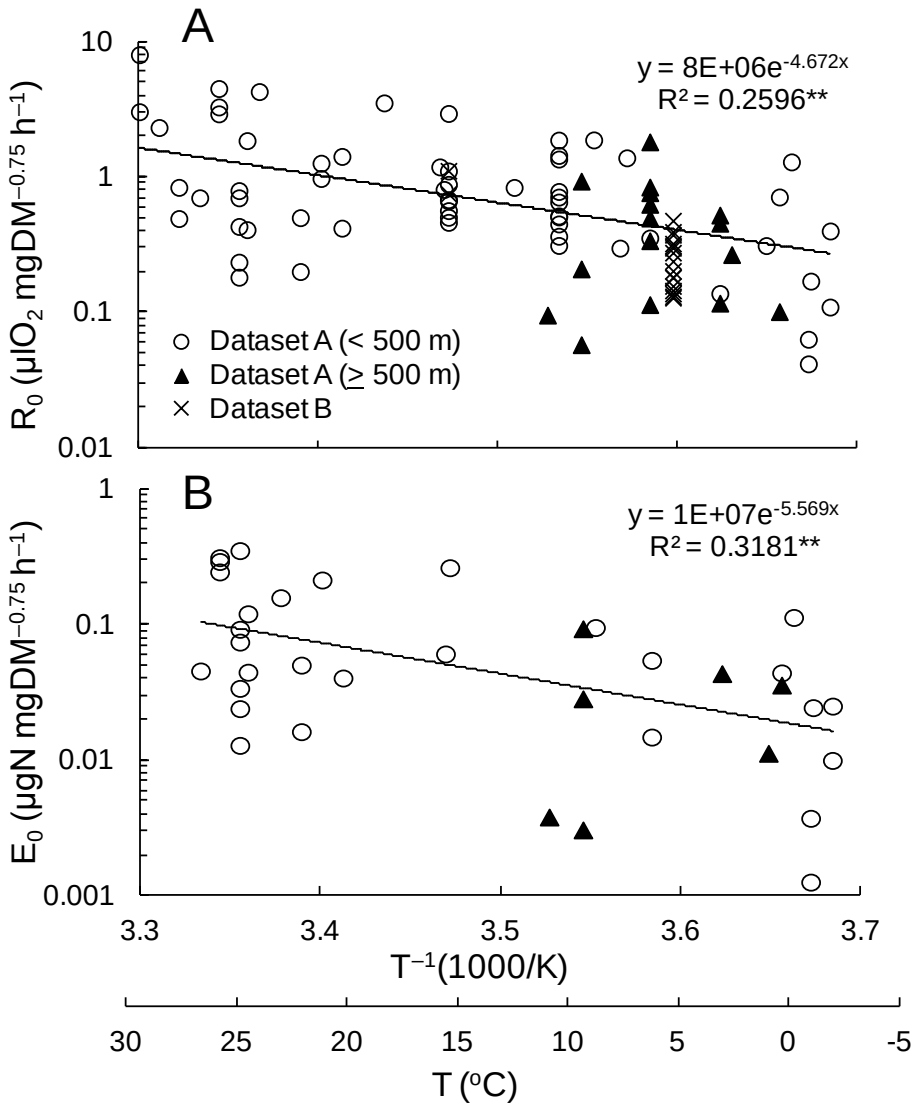
[h] Null hypothesis: $a_2 = 1.0$ was rejected ($p < 0.01$), suggesting progressive decline in % C or %N in DM with increasing DM

Appendix. Definitions of dummy variables. The taxa were categorized into Scyphozoa, Siphonophora, Hydrozoa and Ctenophora.

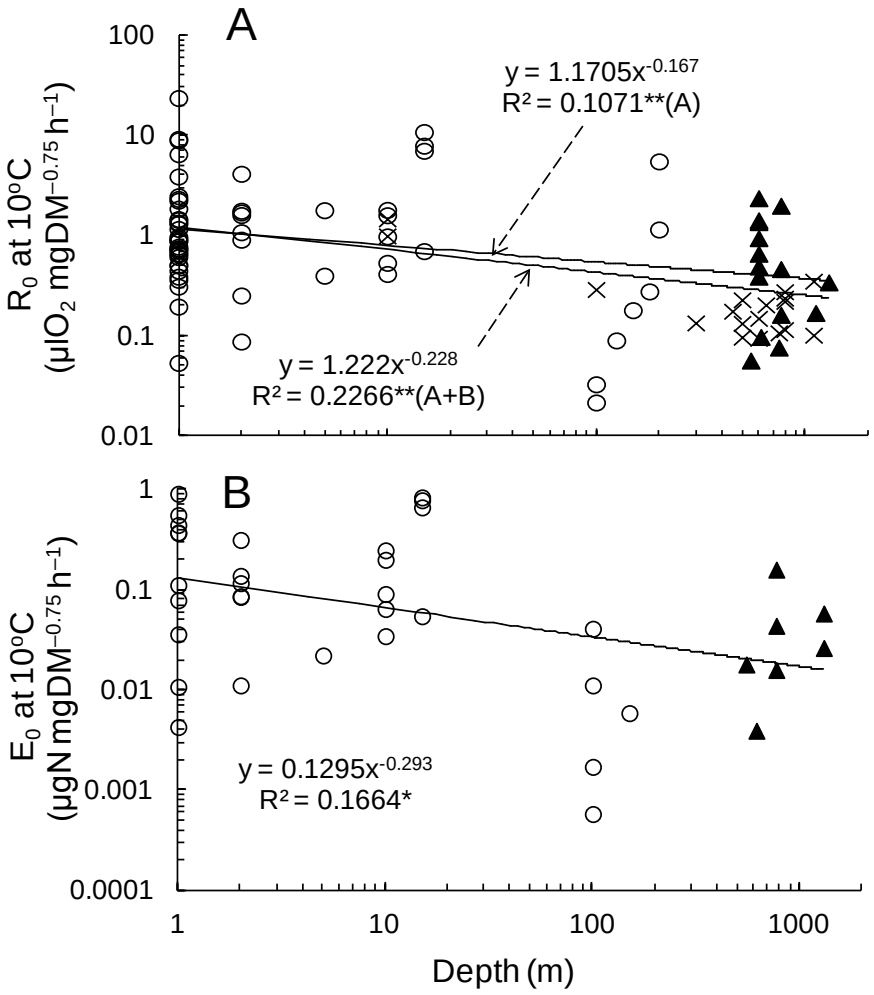
Taxon category	X_{SC}	X_{SI}	X_{HY}
Scyphozoa	1	0	0
Siphonophora	0	1	0
Hydrozoa	0	0	1
Ctenophora	0	0	0


180° 120° 60° 0° 60° 120° 180°
60°
30°
0°
30°
60°
2, 3d, 11ab, 12, 13, 14, 18ab, 19, 20, 22ab, 29ab, 33bc
6, 8, 16
37bc, TC1-18
4, 40c, 59
40a, 43a, 48, 50, 55, 56
1, 9, 21, 33a, 37a, 39, 40b
3b
36
29d, 42c, 57b
51
53a
32, 53b
46
38
30ab, 54
27
35a
23, 24
43b
35b
42ab
3c, 10, 17
3a, 57a
41
47
29c
34
15
26, 58
31
5, 7b
25b, 28
49
7a, 25a
45, 52
44

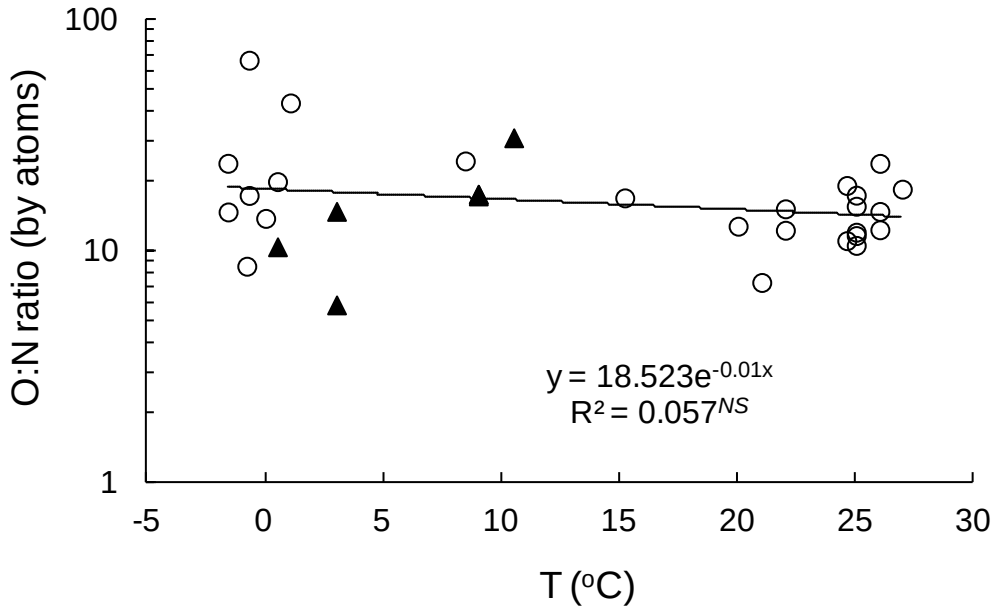
Ikeda Fig. 1


A
y = 8E+06e-4.672x
R² = 0.2596**
Dataset A (< 500 m)
Dataset A (≥ 500 m)
Dataset B
R0 (μlO2 mgDM−0.75 h−1)
10
1
0.1
0.01
B
y = 1E+07e-5.569x
R² = 0.3181**
E0 (μgN mgDM−0.75 h−1)
1
0.1
0.01
0.001
3.3
3.4
3.5
3.6
3.7
T−1(1000/K)
30
25
20
15
10
5
0
-5
T (°C)

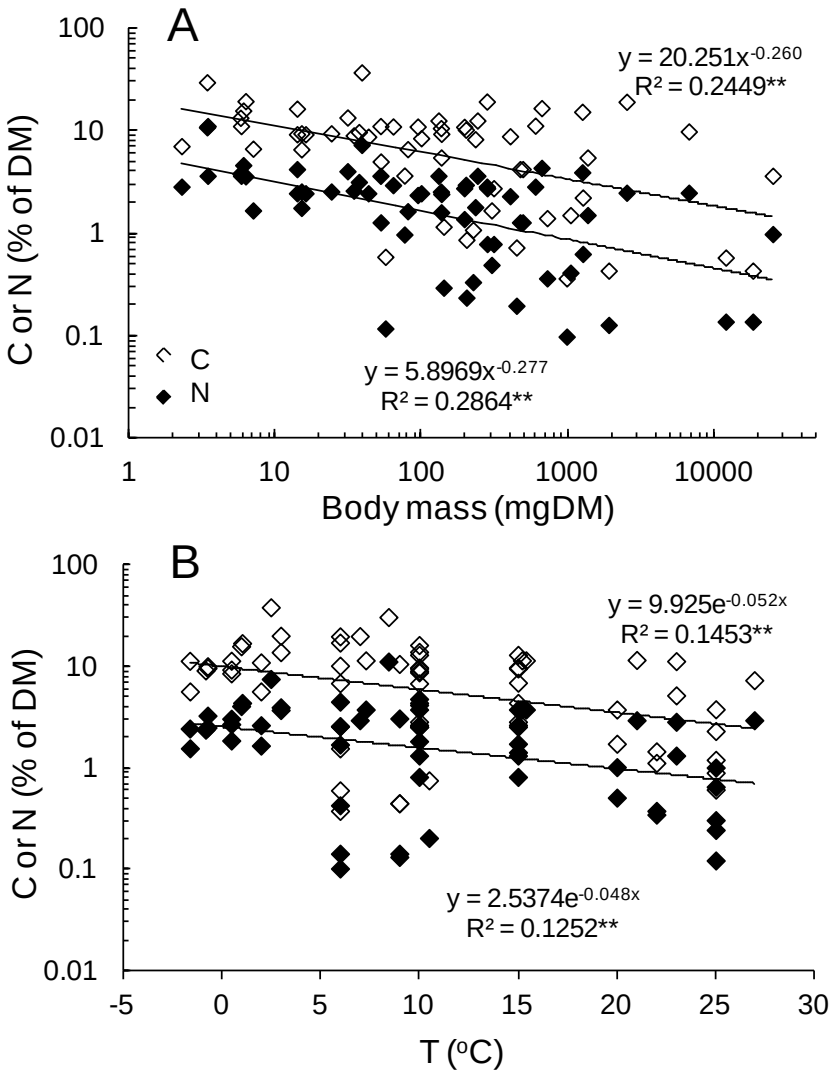
Ikeda Fig. 2


A
B
y = 1.1705x-0.167
R² = 0.1071**(A)
y = 1.222x-0.228
R² = 0.2266**(A+B)
y = 0.1295x-0.293
R² = 0.1664*
R0 at 10°C (µlO2 mgDM−0.75 h−1)
E0 at 10°C (µgN mgDM−0.75 h−1)
100
10
1
0.1
0.01
0.001
0.0001
1
10
100
1000
Depth (m)

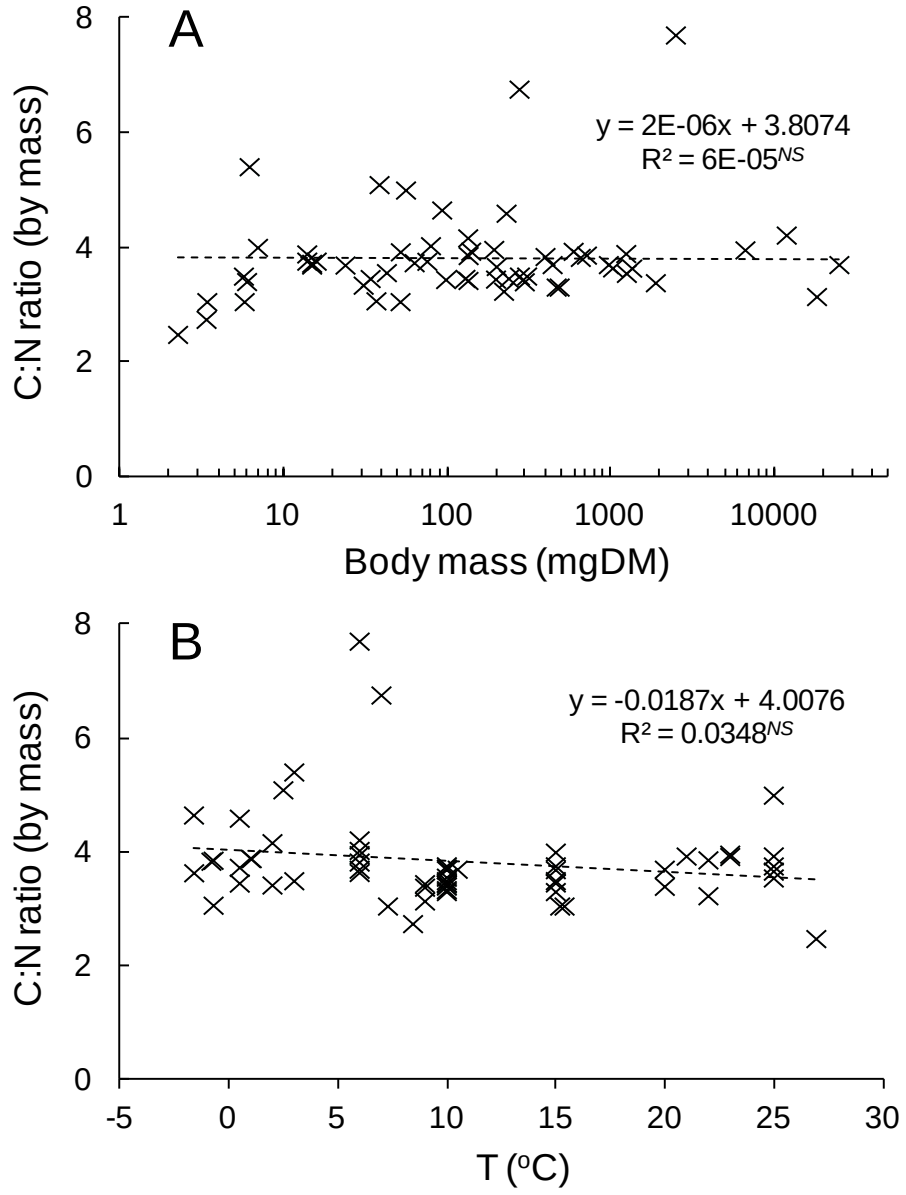
Ikeda Fig. 3


100
10
1
O:N ratio (by atoms)
-5
0
5
10
15
20
25
30
T (°C)
y = 18.523e-0.01x
R² = 0.057NS

Ikeda Fig. 4


A
100
10
1
0.1
0.01
C or N (% of DM)
y = 20.251x-0.260
R² = 0.2449**
C
N
y = 5.8969x-0.277
R² = 0.2864**
1
10
100
1000
10000
Body mass (mgDM)
B
100
10
1
0.1
0.01
C or N (% of DM)
y = 9.925e-0.052x
R² = 0.1453**
y = 2.5374e-0.048x
R² = 0.1252**
-5
0
5
10
15
20
25
30
T (ºC)

Ikeda Fig. 5


A
y = 2E-06x + 3.8074
R² = 6E-05NS
C:N ratio (by mass)
Body mass (mgDM)
B
y = -0.0187x + 4.0076
R² = 0.0348NS
C:N ratio (by mass)
T (°C)

Ikeda Fig. 6