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

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11 Running head: Global-bathymetric model of metabolism and body composition of
12 medusae/ctenophores

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15 ratio, respiration

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18 ABSTRACT

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

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42 **1. Introduction**

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

60 Information about metabolism (respiration rates, ammonia excretion rates, and
61 O:N as NH₄-N ratios) has proved useful in understanding the energy demand, metabolic
62 substrates and nutritional condition of marine zooplankton (Ikeda et al., 2000).
63 Historically body mass and temperature have been regarded as the two major
64 parameters for defining the metabolic characteristics of marine epipelagic animals
65 (Ivleva, 1980; Ikeda, 1985), yet habitat depth has emerged as an additional parameter

66 since metabolic rates decrease rapidly with depth for larger pelagic animals with
67 image-forming eyes such as micronektonic fishes, crustaceans, and cephalopods
68 (Childress, 1995; Seibel and Drazen, 2007). Reduced metabolic rates have also been
69 reported on deep-living copepods and chaetognaths which lack functional eyes (Ikeda et
70 al., 2006a; Ikeda and Takahashi, 2012; Brey, 2010; Kruse et al., 2010). For medusae
71 and ctenophores, data are available in the literature on the effects of body mass and
72 temperature within and between species (Biggs, 1977; Kremer et al., 1986; Larson,
73 1987a; Pitt et al., 2009; Scolardi et al., 2006; Purcell, 2009 and others), but data on the
74 effect of habitat depth on metabolism are currently limited (Thuesen and Childress,
75 1994; Bailey et al., 1994a, 1995).

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

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

96 As part of the project to establish metabolic and body compositional responses of
97 major marine zooplankton/micronekton taxa, therefore, I have compiled published data
98 of metabolism (respiration, ammonia excretion, and O:N ratios) and chemical
99 composition (water content, ash, C, N and C:N ratios) of medusa and ctenophore
100 species living at various depths in polar, temperate and tropical/subtropical seas, and
101 significant parameters affecting the variance were explored. The present results are
102 compared with those of the global-bathymetric models reported previously for pelagic
103 copepods (Ikeda et al., 2007), chaetognaths (Ikeda and Takahashi, 2012; Kruse et al.,
104 2010), euphausiids (Ikeda, 2013a), mysids (Ikeda, 2013b) and amphipods (Ikeda,
105 2013c) to highlight unique features of medusae and ctenophores.

106

107 **2. Materials and methods**

108 *2.1. The data compilation*

109 For the present analyses, the data compiled were those which met the following criteria:

110 1. Data represented post-larvae collected from the field and used for experiments
111 without considerable time delay (< 24 h) with exceptions of < 8 days delay (Morand et
112 al., 1987), 4–5 days delay (Ikeda and Hirakawa, 1998) or unspecified (Thuesen and
113 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 atm)
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

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

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

162 composition” section below).

163

164 2.2. Regression models

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

170 Theoretical model: $\ln Y = a_0 + a_1 \ln X_1 + a_2 (1000 X_2^{-1}) + a_3 \ln X_3 + a_4 X_{SC} + a_5 X_{SI}$
171 $+ a_6 X_{HY}$

172 Empirical model: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 X_{SC} + a_5 X_{SI} + a_6 X_{HY}$
173 where, Y is respiration rate ($\mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) or ammonia excretion rate ($\mu\text{gN ind.}^{-1} \text{ h}^{-1}$),
174 X_1 is body mass, X_2 is habitat temperature (1000/K for the theoretical model, and °C
175 for the empirical model), X_3 : is mid-sampling depth (m), and X_{SC} , X_{SI} and X_{HY} are
176 dummy variables on scyphomedusae, siphonophores and hydromedusae, respectively
177 (for the definitions of these dummy variables, see Appendix). In order to make
178 between-taxa comparison of marine zooplankton with diversified body composition
179 possible, DM, C or N was used in the present analyses. For the datasets in which body
180 mass was reported as WM without information about water content, DM was estimated
181 assuming a grand mean of water content obtained in the present study (96.0 % of WM),
182 then converted to C or N mass by means of conversion equations established in the
183 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 Boltzman'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 μO_2
202 $\text{ind.}^{-1} \text{h}^{-1}$ (*Crossota* sp. from western subarctic Pacific) to 3504 $\mu\text{O}_2 \text{ ind.}^{-1} \text{h}^{-1}$
203 (*Cassiopea xamachana*), and ammonia excretion rates from 0.019 $\mu\text{gN ind.}^{-1} \text{h}^{-1}$
204 (*Diphyes antarctica*) to 1787 $\mu\text{gN ind.}^{-1} \text{h}^{-1}$ (*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 ($R_0 = R \times \text{DM}^{-0.75}$ or $E_0 = E \times \text{DM}^{-0.75}$) against temperature ($1000/\text{K}$ or $^{\circ}\text{C}$)

209 where the scale coefficient of body mass was assumed as 0.75 (as in the theoretical
210 model) (Fig. 2). No appreciable differences were seen between Datasets A and B. To
211 facilitate the analysis, the data (Dataset A) were separated into two groups depending on
212 the depth of sampled (< 500 m and ≥ 500 m). Since the effect of sampling depth to
213 respiration or ammonia excretion rates was unclear at this stage, only the data of <500
214 m were used for the analysis of temperature effects on R_0 or E_0 . The resultant slope
215 (-4.672 for respiration rates, and -5.569 for ammonia excretion rates, Fig. 2) of the
216 regression lines was used to compute R_0 or E_0 at a given temperature (designated as
217 10°C) of the medusae and ctenophores from these sampling depths (< 500 m + ≥ 500 m),
218 which were plotted against the mid-sampling depth (Fig. 3). The standardized rates (R_0
219 or E_0 at 10°C) of these medusae and ctenophores were correlated negatively with the
220 sampling depth ($p < 0.01$ or 0.05), and this result was not affected with or without the
221 addition of the dataset B of Thuesen and Childress (1994) for R_0 . From these results,
222 Dataset A and B were combined in the following regression analyses of respiration
223 rates.

224 The overall results of stepwise multiple regression analyses showed that X_1 (body
225 mass) and X_2 (habitat temperature) were significant variables regardless the choice of
226 models or body mass unit. The new variable X_3 (sampling depth) was not significant (p
227 > 0.05) for respiration rates and ammonia excretion rates (Table 3). Higher respiration
228 and ammonia excretion of scyphomedusae than those of hydromedusae, siphonophores
229 and ctenophores were evident in both theoretical and empirical models when body mass
230 was expressed by DM units. Conversely, lower respiration rates of hydromedusae were
231 the case in the theoretical models when body mass was expressed by C and N. For
232 either respiration rates or ammonia excretion rates, the regression coefficient a_2 of the

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

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

245

246 3.2. O:N ratios

247 A total of 32 O:N ratios ranged from 5.9 (*Poralia rufescens* off south California) to 67.5
248 (*Diphyes antarctica*) (Table 2). A scatter diagram of the O:N ratios and habitat
249 temperature is shown in Fig. 4. Simple correlation analyses indicated that none of the
250 three independent variables was significantly correlated with the O:N ratios (Pearson
251 correlation coefficients > 0.50). Mean and median O:N ratio were 18.0 (± 11.8 , SD) and
252 15.0, respectively.

253

254 3.3. Chemical composition

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

257 (*Solmissus incisus*) with a grand mean of 68.6 (± 10.9), C from 0.37 (*Bathocyroe fosteri*
258 off Cape Hatteras, USA) to 37.7% of DM (*P. haeckeli*) with a grand mean of 8.8 (± 7.1),
259 N from 0.10 (*B. fosteri* off Cape Hatteras, USA) to 11.0 of DM (*Aglantha digitale* from
260 Usujiri coast, Hokkaido, Japan) with a grand mean of 2.3 (± 1.9), C:N ratios from 2.5
261 (*Liriope tetraphylla*) to 7.7 (*Agmayeria tortugensis*) with a grand mean of 3.8 (± 0.8).
262 Stepwise multiple regression analyses demonstrated that 82.4–99.6% of the variance in
263 water, ash, C and N were contributed by body mass (represented by DM), habitat
264 temperature, sampling depth and taxa, though these variables contributed only 21.9% of
265 the variance of C:N ratios (Table 4). Among significant variables, the standardized
266 partial regression coefficients indicated body mass to be the prominent importance
267 while importance of sampling depth and taxa were modest or minor. The scale
268 coefficient of body mass (a_2) was significantly greater than 1.0 for ash ($p < 0.05$), but
269 significantly less than 1.0 for C ($p < 0.001$) and N ($p < 0.001$). The scale coefficient did
270 not significantly differ from 1.0 for water ($p > 0.50$) and the sum of ash, C and N ($p >$
271 0.50) (Table 4). These results for C and N were consistent with those analyzed in Fig 5
272 in which C and N were expressed as percent values of DM and grouped based on single
273 criterion (body mass and habitat temperature) and where the sampling depth and
274 taxonomic groups were treated as random variables.

275

276 **4. Discussion**

277 *4.1. Respiration and ammonia excretion*

278 While rates of respiration and ammonia excretion of marine zooplankton are well
279 documented as a power function of body mass in general (Ikeda, 1985), the previous
280 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 ($a_1 = 0.5\text{--}1.1$, 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

305 species. Acclimated $Q_{10} >$ adapted Q_{10} and this has been described as an “evolutionary
306 trade-off” by Clarke and Fraser (2004). From this view, acclimated Q_{10} values for
307 individual medusae and ctenophores are 1.9–3.7 (excluding the data of 1.7–25.3 of 11
308 siphonophore species, Table 5) which partially overlap adapted Q_{10} values (1.8–2.8,
309 depending choice of body mass units) derived from the global model for the medusae
310 and ctenophores of the present study. The evolutionary trade-off hypothesis
311 characterized by adapted $Q_{10} < 2.0$ has been supported by the global compilation of the
312 data of teleost fishes (1.8, Clarke and Johnston, 1999), pelagic copepods (1.9, Ikeda et
313 al., 2007), chaetognaths (1.7, Ikeda and Takahashi, 2012) and euphausiids (1.7, Ikeda,
314 2013a), but this is true for medusae and ctenophores only when their body mass was
315 expressed by DM unit (1.8, this study). The only exception to this in the world literature
316 is from Purcell et al. (2010) who reported no significant temperature effects on the
317 respiration rates of 16 scyphomedusa species. Perhaps, the effects of temperature are
318 masked in their analyses of the data characterized by the broad body mass range (5
319 orders of magnitude, which is comparable to the datasets of the present study) but
320 relatively narrow temperature range (7–30°C, as compared with –2 to 30°C of the
321 present study). In the analyses of metabolism–body size (in terms of WM, C and
322 equivalent body diameter) of jellyfish, Acuña et al. (2011) and Pitt et al. (2013)
323 standardized the metabolic data at an inverse absolute temperature (K^{-1}) of 0 by
324 adopting the activation energy [$E_a = 0.65\text{eV}$, Gillooly et al. (2001)] of aquatic
325 invertebrates. The E_a value is equivalent to $Q_{10} = 2.5 [\exp(10 \times 0.65/(k \times (273-2) \times$
326 $(273+30)))]$, where k is Boltzmann’s constant, cf. Ivleva (1980)] for the temperature
327 range of –2.0 to 30°C, which fall within the range of 1.8–2.8, depending on the choice
328 of body mass units (DM, C or N), of the present study.

329 As judged by R^2 values, the empirical models are superior to the theoretical
330 models for the prediction of respiration rates or ammonia excretion rates of the medusae
331 and ctenophores (Table 3). Among the three empirical models in which body mass was
332 expressed by DM, C, or N, the best fit to the model was the case for DM for respiration
333 rates but was C for ammonia excretion rates. The difference between C and N was small
334 in both respiration rates ($R^2 = 0.797$ versus 0.799) and ammonia excretion rates ($R^2 =$
335 0.855 versus 0.849). The advantage of the use of C or N unit is the omission of a
336 dummy variable (X_{SC} : scyphomedusae) which was significant when DM units were
337 used as body mass unit for the prediction of respiration rates and ammonia excretion
338 rates. Among the hydromedusae, siphonophores, scyphomedusae and ctenophores
339 treated as dummy variables in the present analyses, scyphomedusae were selected as a
340 distinct taxon characterized by higher respiration and ammonia excretion rates (Table 3),
341 which may be due to their greater C and N composition than the rest of the three taxa
342 (Table 4). Hydromedusae were a significant taxon in the prediction of respiration rates
343 from the theoretical models based on C and N, but no immediate reason for this is seen
344 in their C and N composition data as compared with these of the other taxa.

345 For the progressive decline in respiration rates in deeper-living micronekton and
346 zooplankton, the “visual-interactions hypothesis” (Childress, 1995) or
347 “predation-mediated selection hypothesis” (Ikeda et al., 2006a) have been proposed
348 respectively. These two hypotheses are similar as both interpret the phenomena as a
349 result of lowered selective pressure for high activity at depth because of the decrease in
350 visual predation in the dark. However, these two hypotheses are different in that the
351 former applies strictly to micronekton with functional eyes whereas the latter applies to
352 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°C (ash
397 measurement) but not at 50–60°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 $E_a = 0.65\text{eV}$ (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 using 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°C), predicted
441 respiration rates from the theoretical or empirical model of the medusae/ctenophores
442 (22.4–29.4 $\mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$, excluding 15.4 $\mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ for hydromedusae from the

443 theoretical model) are the highest, and those of chaetognaths and copepods (8.4–14.8
444 $\mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) are the lowest, with those of euphausiids and mysids (15.2–17.1 μO_2
445 $\text{ind.}^{-1} \text{ h}^{-1}$) 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°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 (Kjørboe 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 euphausiids and mysids (16.9–27.1) may be interpreted 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.

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

504

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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 : $^{\circ}\text{C}$) 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 $\text{NH}_4\text{-N}$) 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						
A	Cnidaria	Hydrozoa	1	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)						
			2	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			3a	Usujiri coast, Hokkaido, Japan	May 1971	Ikeda (1974)						
			3b	Barrett's Sea	May/June 1987	Ikeda and Skjoldhal (1989)						
			3c	W. subarctic Pacific Ocean	Mar 2006	Ikeda (unpublished data)						
			3d	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			4	Off Sweeting Cay, the Bahamas	Dec 1990, Mar 1991	Bailey et al. (1994a)						
			5	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)						
			6	North Inlet, S Carolina, USA	Jan, Jul 2006	Marshall and Pinckney (2007)						
			7a	Off Enderby Land, Antarctica	Oct 1985	Ikeda (unpublished data)						
			7b	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)						
			8	North Inlet, S Carolina, USA	Jan, Jul 2006	Marshall and Pinckney (2007)						
			9	off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)						
			10	W. subarctic Pacific Ocean	Dec 2004	Ikeda (2012)						
			11a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			11b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			12	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			13	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			14	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			15	Tropical Indian/Atlantic Ocean	Nov/Dec 1971	Ikeda (1974)						
			16	North Inlet, S Carolina, USA	Jan, Jul 2006	Marshall and Pinckney (2007)						
			17	W. subarctic Pacific Ocean	Mar 2003	Ikeda (2012)						
			18a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			18b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			19	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			20	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			21	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)						
			22a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			22b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)						
			23	Villefranche-sur-Mer, France	Jul 1960, Jul–Oct 1970	Nival et al. (1972)						
			24	Villefranche-sur-Mer, France	Jul, Oct 1970	Nival et al. (1972)						
			25a	Off Enderby Land, Antarctica	Oct 1985	Ikeda (unpublished data)						
			25b	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)						
			26	Cape Ferguson Coast, N Queensland, Australia	May 1978	Ikeda (unpublished data)						
			27	Subtropical N Atlantic Ocean		Biggs (1977)						
			Siphonophora	Siphonophora	Siphonophora	28	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)			
						29a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)			
						29b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)			
						29c	Seto Inland Sea, Japan	Jul–Aug 1991, May–Jun 1992	Uye and Shimauchi (2005)			
						29d	Kiel Bight, W. Baltic Sea	Mar–Oct 1982, 1983, 1984	Schneider (1989)			
						30a	Florida Keys, Florida, USA	Sep 1992	Verde and McCloskey (1998)			
						30b	Florida Keys, Florida, USA	Jan 1993	Verde and McCloskey (1998)			
						31	Smiths Lake, NSW, Australia	Feb 2003	Pitt et al. (2005)			
						32	Chesapeake Bay, Maryland, USA	May–Oct 1990	Nemazizadeh et al. (1993)			
						33a	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)			
						33b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)			
						33c	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)			
						34	Eil Malk, Jellyfish Lake, Palau	Feb–Mar 1982	McCloskey et al. (1994)			
						35a	Off W Africa	Aug 1983	Davenport and Trueman (1985)			
						35b	W. Mediterranean Sea	Jan–Dec 1984, 1985	Morand et al. (1987)			
						36	Lurefjorden, W coast of Norway	Mar, Nov 1999	Youngbladh and Bärnstedt (2001)			
						37a	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)			
						37b	Off S. California, USA		Smith (1982)			
						37c	Off S. California, USA		Smith (1982)			
						38	NE Gulf of Mexico, USA		Larson (1987b)			
						Ctenophora	Ctenophora	Ctenophora	39	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
									40a	Bahamian waters, WN Atlantic Ocean	May, Sept, Oct 1983, 1984	Youngbladh et al. (1988)
									40b	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
									40c	Off Sweeting Cay, the Bahamas	Dec 1990, Mar 1991	Bailey et al. (1994a)
41	S. Japan Sea	Nov 1991							Ikeda and Hirakawa (1998)			
42a	Oshoro Bay, Hokkaido, Japan	Jul 1970							Ikeda (1974)			
42b	Oshoro Bay, Hokkaido, Japan	Jun 1970							Ikeda (1974)			
42c	Kosterfjorden, W. Sweden	Jul 1981							Bärnstedt (1985)			
43a	Bahamian waters, WN Atlantic Ocean	1982–1984							Kremer et al. (1986)			
43b	Black Sea	Sep–Nov 1999							Finenko et al. (2001)			
44	Off Wilkes Land, Antarctica	Jan 1980							Ikeda and Michel (1982)			
45	Prydz Bay, Antarctica	Nov 1989							Ikeda and Bruce (1986)			
46	Gulf of Maine, USA	Sep 1989							Bailey et al. (1994b)			
47	Tateyama Bay, Chiba, Japan	Jul–Dec 1992, Oct–Nov 1993	Kasuya et al. (2000)									
48	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)									
49	Marguerite Bay, Antarctica	Apr–May 2001, 2002, Jul–Aug 2001, Jul–Sep 2002	Scolardi et al. (2006)									
50	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)									
51	Frobisher Bay, Baffin Island, Canada	Aug 1984	Percy (1988)									
52	Prydz Bay, Antarctica	Nov 1982	Ikeda and Bruce (1986)									
53a	Narragansett Bay, Rhode Island, USA		Kremer (1977)									
53b	Chesapeake Bay, Maryland, USA	May–Oct 1990	Nemazizadeh et al. (1993)									
54	N. Biscayne Bay, Florida, USA	Nov 1979	Kremer (1982)									
55	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)									
56	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)									
57a	Usujiri coast, Hokkaido, Japan	May 1971	Ikeda (1974)									
57b	Kosterfjorden, W. Sweden	Jul 1981	Bärnstedt (1985)									
58	Cape Ferguson Coast, N Queensland, Australia	May 1979	Ikeda (unpublished data)									
59	Off Sweeting Cay, the Bahamas	Dec 1990, Mar 1991	Bailey et al. (1994a)									
B	Cnidaria	Hydrozoa	TC1	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC2	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC3	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC4	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC5	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC6	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC7	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC8	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC9	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC10	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC11	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC12	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC13	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC14	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC15	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC16	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC17	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC18	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
Scyphozoa	Scyphozoa	Scyphozoa	TC14	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC15	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC16	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC17	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC18	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC19	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC20	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC21	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC22	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC23	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (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 \pm 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 (Thøgersen 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 (μO_2 ind ⁻¹ h ⁻¹)	Ammonia excretion rate ($\mu\text{gN ind}^{-1}\text{h}^{-1}$)	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 \pm 30	49.0 \pm 21.6				95.6 \pm 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 \pm 0.58	4.74 \pm 0.91	0.24 \pm 0.057	24.8 \pm 1.1				30.2	11.0	2.7
	3b	150 (0-400)	1.1	8	14.0 \pm 6.3	2.27 \pm 0.80	0.08 \pm 0.05	44.2 \pm 28.3		94.7 \pm 0.1	56.5 \pm 0.0	16.7	4.3	3.9
	3c	125	3	8	5.74 \pm 3.67	0.52 \pm 0.34				95.7 \pm 0.1	60.3 \pm 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 \pm 100	114 \pm 61	9.2 \pm 9.6	17.8 \pm 7.5		95.3 \pm 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 \pm 0.27] ^f	0.38 \pm 0.20				[95.8] ^f		11.3	3.60	3.1
	7a	100 (0-200)	-0.7	5	136.0 \pm 24.1	1.7 \pm 0.4	0.15 \pm 0.06	17.6 \pm 11.8		95.7 \pm 0.3	68.3 \pm 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 \pm 0.32] ^f	0.90 \pm 0.40				[95.8] ^f		9.6	3.04	3.2
	9	600 (430-760)	6	3	660 \pm 120	65.3 \pm 15.5				95.2 \pm 0.1	63.7	16.9	4.4	3.8
	10	750 (500-1000)	3	9	6.22 \pm 8.51	0.46 \pm 0.43				95.2 \pm 0.5	59.7 \pm 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 \pm 0.51	1.31 \pm 0.71	0.09 \pm 0.04	18.7 \pm 2.6				7.2	2.9	2.5
	16	1 (0.5-1.5)	12	22	[5.05 \pm 2.62] ^f	2.84 \pm 1.48				[95.8] ^f		14.3	4.04	3.5
	17	1125 (500-1500)	3	3	38.78 \pm 7.83	4.19 \pm 3.28				92.6 \pm 0.1	30.1 \pm 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 \pm 790	322 \pm 575				95.9 \pm 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 \pm 2.9	3.1 \pm 0.8						[8.5] ^b	[2.4] ^b	
	24	1	15	2	5.0 \pm 0.4	1.70 \pm 0.70						[11.8] ^f	[3.4] ^b	
	25a	100 (0-200)	-0.7	2	37.10 \pm 2.18	0.96 \pm 0.14	0.019	67.5 \pm 29.4		95.7 \pm 0.3	64.0 \pm 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 \pm 0.11	1.08 \pm 0.37	0.07 \pm 0.02	19.4 \pm 3.3				[15.6] ^f	[4.9] ^b	
	27	15 (0-30)	26	8	[4.7] ^f	14.50	0.75	24.2				[8.7] ^f	[2.3] ^f	
	27	15 (0-30)	26	8	[47.4] ^f	60	5.0	15.0				[8.7] ^f	[2.3] ^f	
	27	15 (0-30)	26	8	[47.4] ^f	300	30	12.5				[8.7] ^f	[2.3] ^f	
	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	25200	2862				96.4		3.7	1.0	3.7
	29d	1	surface	15	12	6054		182				[5.2] ^f	1.4	
	30a	1	30	27	[7583] ^f	2488						[8.7] ^f	[2.3] ^f	
	30b	1	24	40	[7583] ^f	3504						[8.7] ^f	[2.3] ^f	
	31	1	25		[90762] ^f		1787 ^g					[0.67] ^f	[0.18] ^f	
	32	1	surface	23	195			12.4				11.1	2.8	4.0
	33a	600 (430-760)	6	4	6710 \pm 3740	470 \pm 280				95.5 \pm 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] ^f	[0.48] ^b	
	35a	200	18	4	147.9	151					56.6	[10.6] ^f	[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 \pm 16850	3495 \pm 7495				96.0 \pm 0.0	73.1	0.59	0.14	4.2
	37b	1300	3	1	59.6	11.3	0.94	15.0				[36.4] ^f	[9.5] ^b	
	37c	1300	3	1	214.9	25.8	5.45	5.9				[22.8] ^f	[5.9] ^b	
	38	1	30	1	2050	2460						[2.0] ^f	[0.58] ^b	
	39	600 (430-760)	6	5	2520 \pm 3000	302				95.2 \pm 0.7	48.1	19.5	2.5	7.7
	40a	615 (530-700)	11	23, 20	444	9.3	0.37	31.2 \pm 3.8				0.74	0.20	3.7
40b	600 (430-760)	6	4	980 \pm 450	213 \pm 253				96.0 \pm 0.0	81.5	0.37	0.10	3.7	
40c	767 (685-850)	9	3	1900 \pm 1510	144 \pm 142	13.7 \pm 45.8	17.8 \pm 11.3		96.1 \pm 0.3		0.43	0.14	3.2	
41	550 (400-700)	0.5	2	63.6 \pm 31.3	2.3 \pm 1.0	0.81	10.6		96.0 \pm 0.4	65.3 \pm 0.0	11.2	3.0	3.7	
42a	2	15	2	3.43 \pm 0.81	3.02 \pm 0.70						11.3	3.7	3.1	
42b	2	15	3	52.1 \pm 18.9	15.8 \pm 2.9	1.2 \pm 0.4	17.2 \pm 2.9				11.3	3.7	3.1	
42c	100 (0-200)	6	2	14.3	0.1						[9.3] ^f	[2.5] ^f		
43a	10 (0-20)	25	22	76	20.6						3.7	1.0	3.8	
43b	5 (0-10)	21		100	31.1				97.6		[2.8] ^f	[0.79] ^b		
44	2	-0.8	1	401.6	15.4 \pm 4.7	2.21 \pm 0.24	8.70 \pm 24.8				9.0	2.3	3.8	
45	1	-1.6	11	1362 \pm 1192	24.8 \pm 14.9	2.26 \pm 1.27	14.9 \pm 6.0		96.1 \pm 0.2	72.8 \pm 0.7	5.6	1.5	3.6	
46	180 120-240	6	10	1921 \pm 291	104 \pm 40				96.2		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 \pm 329	42.7	2.6	20.2 \pm 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] ^f	[1.6] ^b		
52	1	-1.6	8	93.7 \pm 53.7	12.1 \pm 6.26	0.76 \pm 0.58	24.2 \pm 9.0		95.8 \pm 0.4	66.3 \pm 1.3	11.2	2.4	4.7	
53a	1	surface?	20	30	300	30.5	2.9	13.0 \pm 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 \pm 2.40	1.1 \pm 0.06						11.3	3.7	3.1	
57b	100 (0-200)	6	5	5.2		0.19					[9.3] ^f	[2.5] ^f		
58	2	25	6	52.3 \pm 70.4	8.0 \pm 11.1	0.88 \pm 1.18	11.2 \pm 2.1				[2.8] ^f	[0.83] ^b		
59	767 (685-850)	9	5	18400 \pm 5880	276 \pm 156									

Table 3. Stepwise (forward selection, $p_{in} = p_{out} = 0.05$) multiple regression statistics of theoretical and empirical models of respiration rates (Y : $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) or ammonia excretion rates (Y : $\mu\text{gN ind.}^{-1} \text{ h}^{-1}$) of medusae and ctenophores on body mass (X_1 : mg ind.^{-1}), habitat temperature (X_2 : re-defined as 1000/K for the former, °C for the latter), depth sampled (X_3 : m), and taxa (X_{SC} , X_{SI} and X_{HY} are dummy variables on scyphomedusae, 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:						R^2 (adjusted R^2)	p for t-test $H_0: a_1 = 1.0$	
				$\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 \ln X_{SC} + a_5 X_{SI} + a_6 \ln X_{HY}$	a_0	a_1	a_2	a_3	a_4			a_5
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)	
			2	25.904	0.75	-7.641					0.481 (0.466)	
	C	38	2	26.529	0.75	-7.543					0.464 (0.449)	
			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 : °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 coefficients as a measure of relative contribution to the variance. * $p < 0.05$, ** $p < 0.01$

Body component	N	Regression equation:						Adjusted R ²	p for t -test H ₀ : a ₁ = 1.0	
		a ₀	a ₁	a ₂	a ₃	a ₄	a ₅			a ₆
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	<i>Aequorea vitrina</i>	1.02	DM	2–800			Møller and Rieggård (2007)	
	<i>Cladonema californicum</i>	0.74	DM	0.01–0.52			Costello (1991)	
	<i>Sarsia tubulosa</i>	0.91	DM	0.3–5			Møller and Rieggård (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	<i>Aurelia aurita</i>	1.06	WM	440–35400			Shimauchi and Uye (2007)	
	<i>Aurelia aurita</i>	1.01	DM	20–8000	3.1	7–22	Møller and Rieggård (2007)	
	<i>Aurelia aurita</i> (15°C)	0.63	DM	0.06–10			Kinosita et al. (1997)	
	<i>Aurelia aurita</i> (15°C)	0.93	DM	10–1100			Kinosita et al. (1997)	
	<i>Cassiopea xamachana</i> (Jan)	0.74	PRO	100–13080			Verde and McCloskey (1998)	
	<i>Cassiopea xamachana</i> (Sep)	0.85	PRO	100–6366			Verde and McCloskey (1999)	
	<i>Pelagia noctiluca</i>	0.95	VOL	306–1163			Morand et al. (1987)	
	<i>Periphylla periphylla</i>	0.589	C	100–6366			Youngbluth and Bänstedt (2001)	
	2 species	0.97 ± 0.06	DM	12–16200	2.9 ^c	10–15	Larson (1987a)	
	Ctenophores	<i>Beroë gracilis</i>				3.56	8–20	Gylleberg and Greve (1979)
		<i>Beroë ovata</i>	0.90	DM	10–561			Kremer et al. (1986)
<i>Beroë ovata</i>		0.58	WM	0.03–91			Svetlichny et al. (2004)	
<i>Beroë ovata</i>		1.04	WM	91–23400	2.17	10–28	Svetlichny et al. (2004)	
<i>Beroë ovata</i>		1.04	DM	10–1000			Finenko et al. (2001)	
<i>Bolinopsis infundibulum</i>					3.73	8–20	Gylleberg and Greve (1979)	
<i>Bolinopsis infundibulum</i>		0.67	DM	100–4800			Bailey et al. (1995)	
<i>Bolinopsis mikado</i>		1.015	DM	50–2000	1.9	16–24	Kasuya et al. (2000)	
<i>Bolinopsis vitrea</i>		0.64	DM	45–2778			Kremer et al. (1986)	
<i>Callianira antarctica</i>		0.707	DM	2.8–1049			Scolardi et al. (2006)	
<i>Eurhamphaea vexilligera</i>		1.12	DM	16–257			Kremer et al. (1986)	
<i>Mertensia ovum</i> (summer)		0.655	DM	10–1000			Percy (1988)	
<i>Mertensia ovum</i> (winter)		0.744	DM	40–700			Percy (1988)	
<i>Mnemiopsis leidyi</i>		0.96	DM	35–562	3.67	16–25	Kremer (1977)	
<i>Ocyropsis</i> sp.		0.97	DM	996–1575			Kremer et al. (1986)	
<i>Pleurobrachia pileus</i>					2.72	2–24	Gylleberg and Greve (1979)	
Scyphomedusae(Semeaostomeae)		7 species	1.09	WM	320–1259000			
Schypomedusae (Rhizostomeae)	6 species	0.917	WM	160–7943000			Purcell et al. (2010)	
Schypomedusae	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				
Hydromedusae/scyphomedusae/ctenophores	40 species	0.79	C	0.01–1000			Acuña et al. (2001)	
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	<i>Cladonema californicum</i>	1.41	DM	0.01–0.52			Costello (1991)	
Siphonophores	11 species	0.80±0.18	PRO	4.4–436			Biggs (1977)	
Scyphomedusae	<i>Aurelia aurita</i>	0.93	WM	1836–19962			Schneider (1989)	
	<i>Aurelia aurita</i>	1.09	WM	440–35400			Shimauchi and Uye (2007)	
	<i>Chrysaora quinquecirrha</i>	0.974	DM	13–2826			Nemazie et al. (1993)	
	<i>Pelagia noctiluca</i>	0.90	VOL	306–1163	3.8	15–25	Morand et al. (1987)	
	<i>Beroë ovata</i>	0.82	DM	10–561			Kremer et al. (1986)	
	<i>Bolinopsis mikado</i>	1.147	DM	50–1000	4.1	16–24	Kasuya et al. (2000)	
Ctenophores	<i>Bolinopsis vitrea</i>	0.76	DM	45–2778			Kremer et al. (1986)	
	<i>Callianira antarctica</i>	0.487	DM	2.8–1049			Scolardi et al. (2006)	
	<i>Eurhamphaea vexilligera</i>	0.93	DM	16–257			Kremer et al. (1986)	
	<i>Mertensia ovum</i> (summer)	0.623	DM	10–1000			Percy (1988)	
	<i>Mertensia ovum</i> (winter)	0.546	DM	40–700			Percy (1988)	
	<i>Mnemiopsis leidyi</i>	0.89	DM	35–562	3.73	16–25	Kremer (1977)	
	<i>Mnemiopsis leidyi</i>	0.604	DM	7–391			Nemazie et al. (1993)	
	<i>Ocyropsis</i> 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 components 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 ($\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$)						
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 1 mgN 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 als.' model	28.4 ^d					
Pitt et als.' model	32.4 ^d					
Predicted rate for a specimen of 1 mgN 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 als.' model	7.1 ^d					
Pitt et als.' model	8.1 ^d					
O:N ratio (by atoms)						
Range	5.9–67.5	6.8–36	4.8–49	11–142	8–45	
Mean (\pm 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 (\pm 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 (\pm SD)	0.997 (0.011)	1.128 (0.055)	ND	1.002 (0.007)	0.953 (0.033)
	a_3 , mean (\pm SD)	0.16 (0.003)	NS	ND	NS	NS
	a_4 , mean (\pm 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 (\pm 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 (\pm SD)	-0.060 (0.013)	NS	-0.003 (0.001)	NS	NS
	a_4 , mean (\pm SD)	NS	NS	NS	NS	NS
	N (Nsp)	57 (42)	27 (18)	253 (108)	41 (28)	24 (20)
	% of DM, mean (\pm 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 (\pm 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 (\pm SD)	-0.054 (0.013)	NS	NS	NS	NS
	a_4 , mean (\pm 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 (\pm 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 (\pm 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)

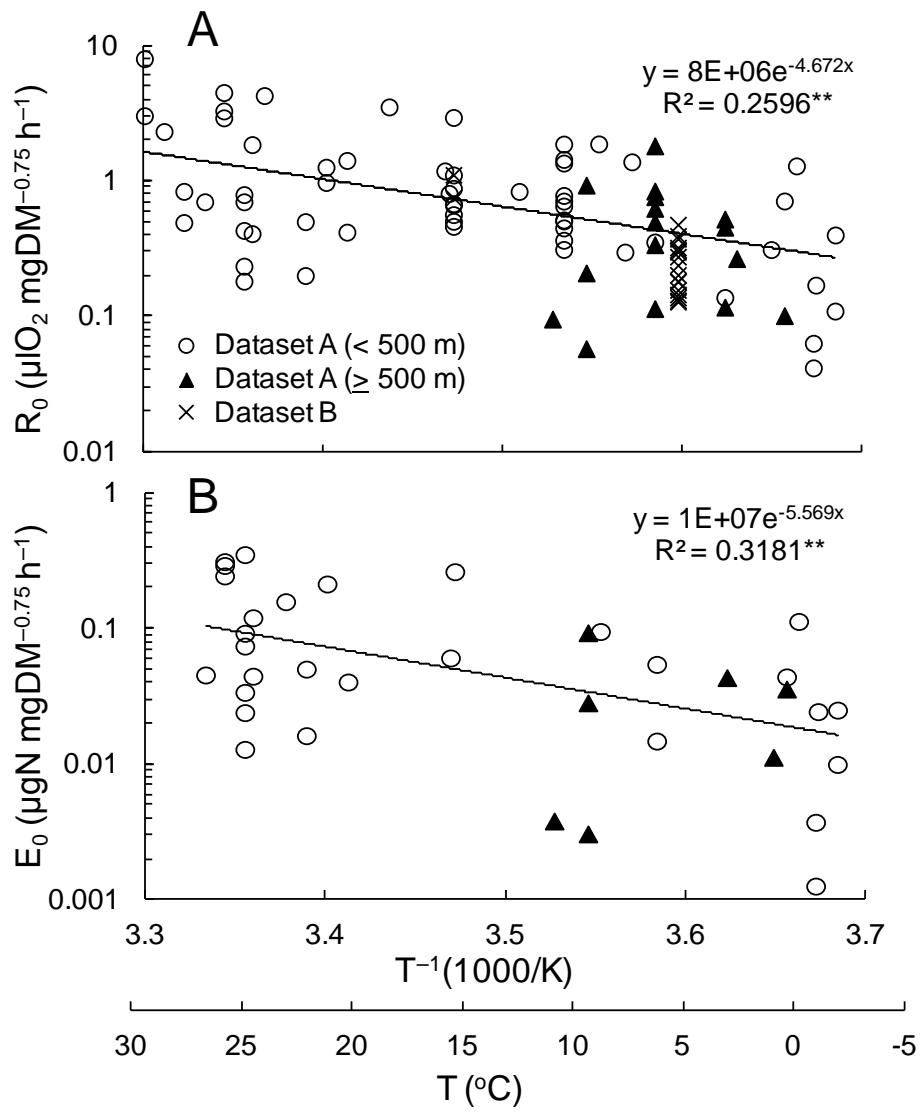
^f From Hirst et al. (2003)

^g From Bänstedt (1986). Means given for six groups (3 latitudes \times 2 depths) were weighed by the number of data sets to derive a grand mean

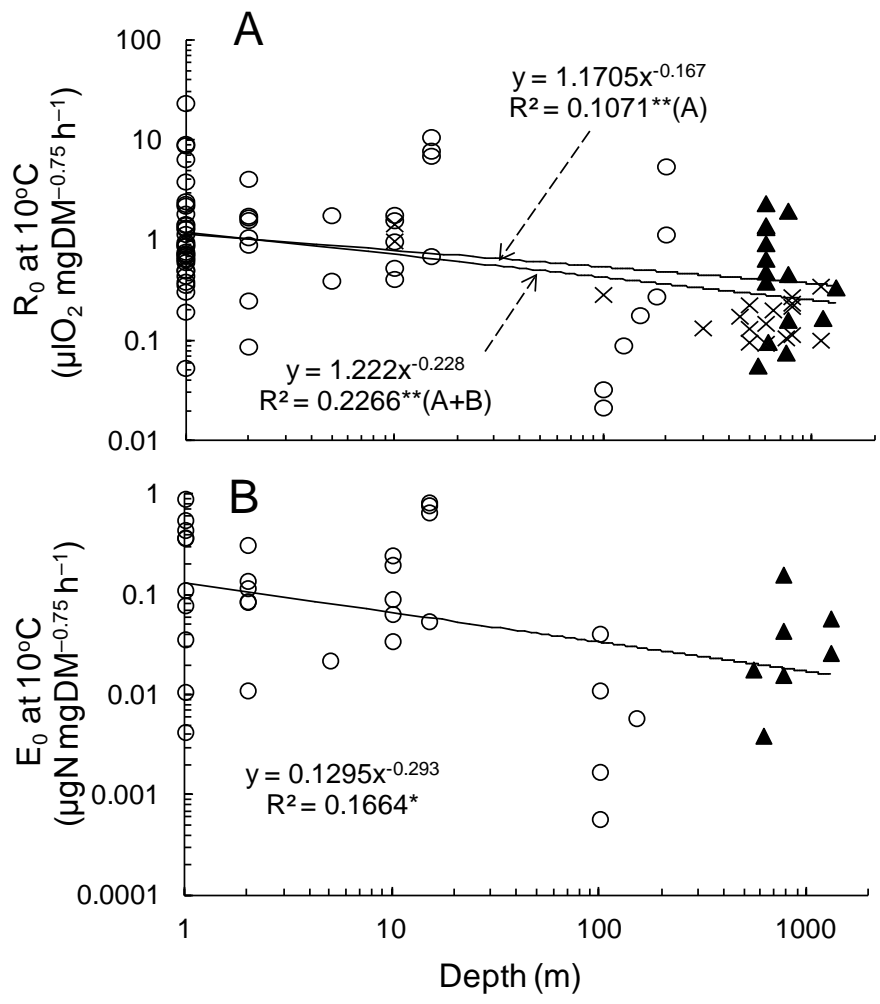
^h Null hypothesis: $a_2 = 1.0$ was rejected ($p < 0.01$), suggesting progressive decline in % C or %N in DM with increasing DM

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

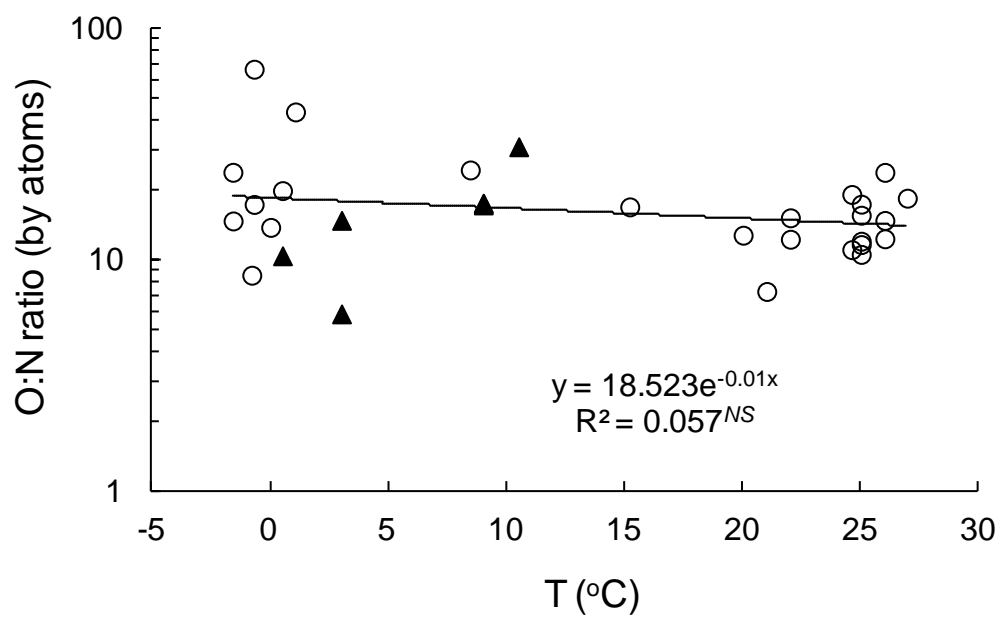
Taxon category	X_{SC}	X_{SI}	X_{HY}
Scyphozoa	1	0	0
Siphonophora	0	1	0
Hydrozoa	0	0	1
Ctenophora	0	0	0



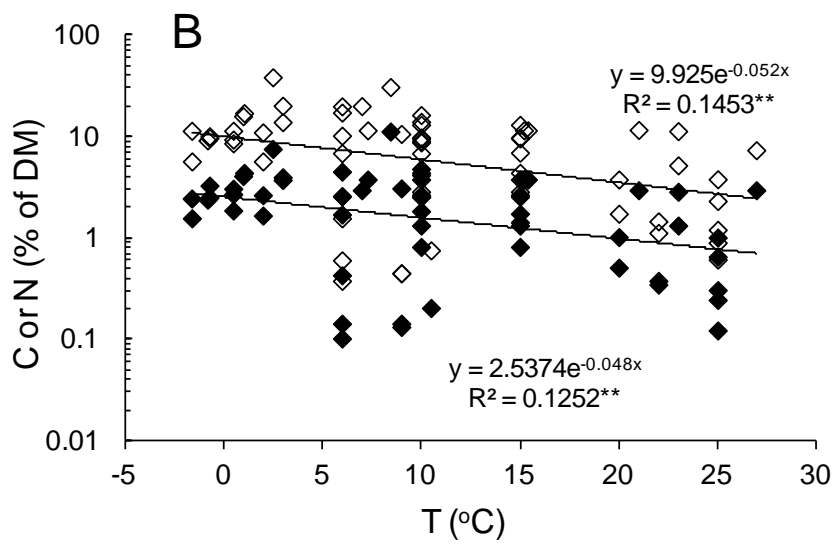
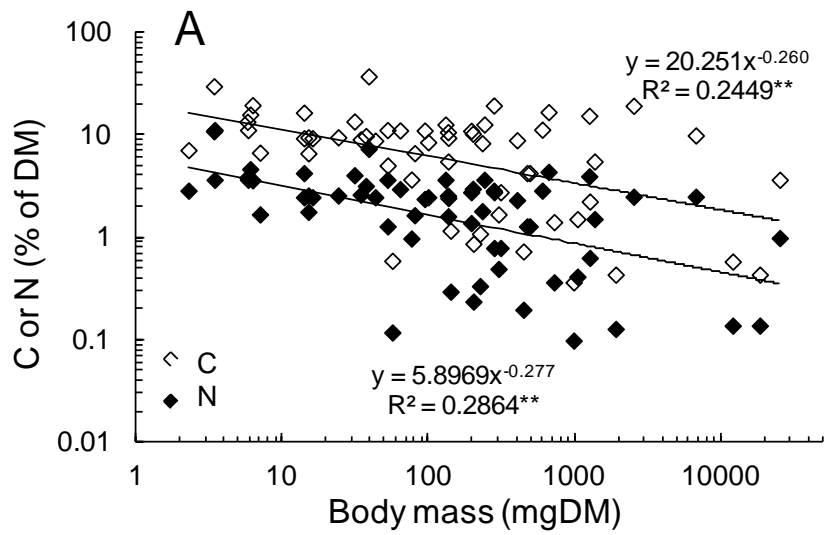
Ikeda Fig. 2



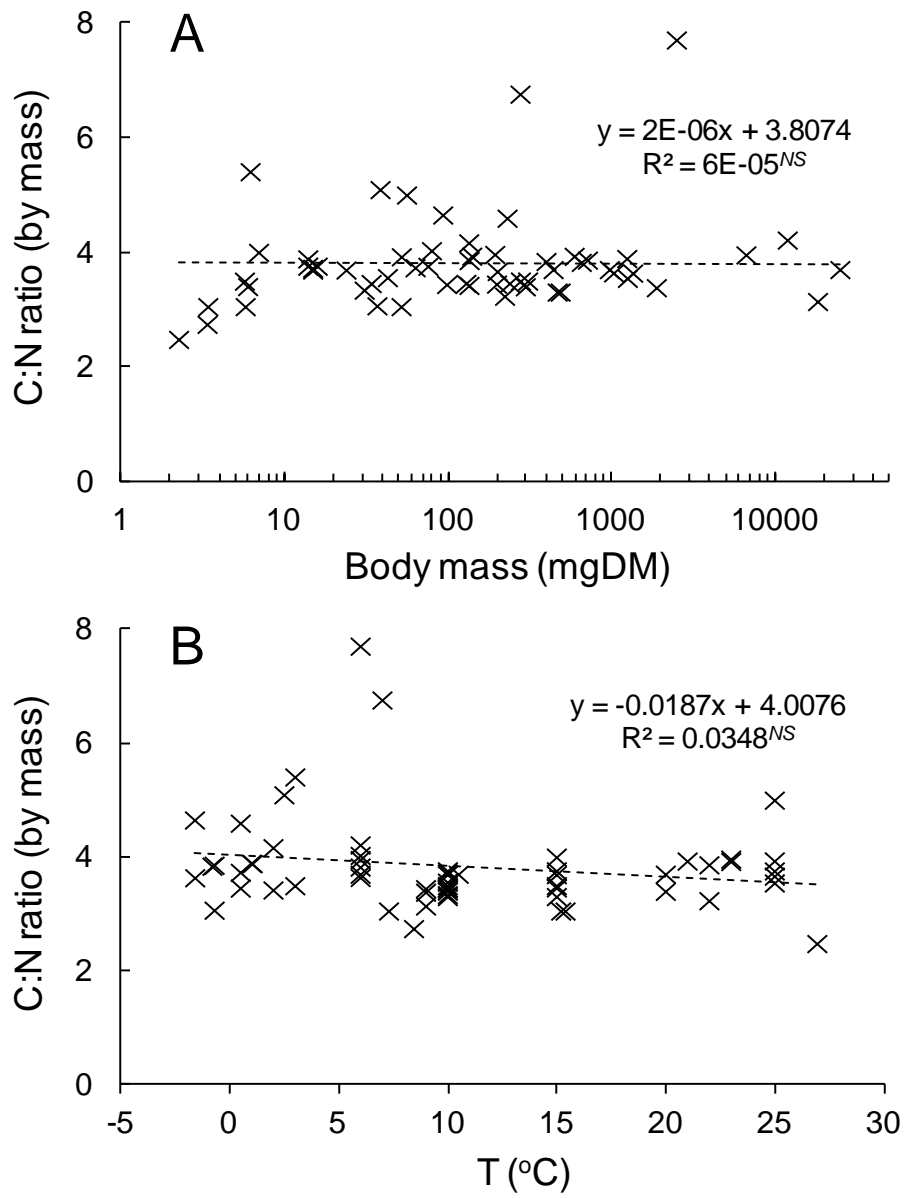
Ikeda Fig. 3



Ikeda Fig. 4



Ikeda Fig. 5



Ikeda Fig. 6