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

5

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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 NH<sub>4</sub>-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 ( $8.62 \times 10^{-5}$  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  $\mu\text{O}_2$   
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  $\geq 500$  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  $10^\circ\text{C}$ ) of the medusae and ctenophores from these sampling depths ( $< 500$  m +  $\geq 500$  m),  
218 which were plotted against the mid-sampling depth (Fig. 3). The standardized rates ( $R_0$   
219 or  $E_0$  at  $10^\circ\text{C}$ ) 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 ( $\pm 11.8$ , 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 ( $\pm 0.7$ , SD), ash from 30.1 (*P. haeckeli*) to 81.6% of DM

257 (*Solmissus incisus*) with a grand mean of 68.6 ( $\pm 10.9$ ), 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 ( $\pm 7.1$ ),  
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 ( $\pm 1.9$ ), C:N ratios from 2.5  
261 (*Liriope tetraphylla*) to 7.7 (*Agmayeria tortugensis*) with a grand mean of 3.8 ( $\pm 0.8$ ).  
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 ( $a_1 = 0.5-1.1$ , 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  $\mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ ) are the lowest, with those of euphausiids and mysids (15.2–17.1  $\mu\text{LO}_2$   
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:  $0.192 \text{ d}^{-1}$ ) 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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## 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 from 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.
- Kjørboe, 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 leidy*. *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.
- Lucas, 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
- Marshallones, 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, semaestomae). *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 Bay. *Mar. Biol.* 116, 451–458.
- Nival, P., Nival, S., Palazzoli, I., 1972. Données sur la respiration de différents 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 cypid 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 *Phyllorhiza 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 advantages 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 ctenophores 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  $\geq 500$  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 ( $\geq 500$  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  $10^{\circ}\text{C}$  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 ( $\geq 500$  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 ( $\geq 500$  m), respectively. <sup>NS</sup>  $p > 0.05$ .

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 Skjoldal (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	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)						
			TC24	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Chlress (1994)						
			TC25	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  $\pm$  SD. 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 <sup>-1</sup> )	Respiration rate ( $\mu\text{O}_2 \text{ ind}^{-1} \text{ h}^{-1}$ )	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] <sup>a</sup>	[0.96] <sup>b</sup>	
	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] <sup>f</sup>	0.38 $\pm$ 0.20			[95.8] <sup>f</sup>		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] <sup>f</sup>	0.90 $\pm$ 0.40			[95.8] <sup>f</sup>		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] <sup>f</sup>	2.84 $\pm$ 1.48			[95.8] <sup>f</sup>		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] <sup>b</sup>	[2.4] <sup>b</sup>	
	24	1	15	2	5.0 $\pm$ 0.4	1.70 $\pm$ 0.70					[11.8] <sup>f</sup>	[3.4] <sup>b</sup>	
	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] <sup>f</sup>	[4.9] <sup>b</sup>	
	27	15 (0-30)	26	8	[4.7] <sup>f</sup>	14.50	0.75	24.2			[8.7] <sup>f</sup>	[2.3] <sup>f</sup>	
	27	15 (0-30)	26	8	[47.4] <sup>f</sup>	60	5.0	15.0			[8.7] <sup>f</sup>	[2.3] <sup>f</sup>	
	27	15 (0-30)	26	8	[47.4] <sup>f</sup>	300	30	12.5			[8.7] <sup>f</sup>	[2.3] <sup>f</sup>	
	28	1650 (1200-2100)	1		1252						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] <sup>f</sup>	1.4	
	30a	1	30	27	[7583] <sup>f</sup>	2488					[8.7] <sup>f</sup>	[2.3] <sup>f</sup>	
	30b	1	24	40	[7583] <sup>f</sup>	3504					[8.7] <sup>f</sup>	[2.3] <sup>f</sup>	
	31	1	25		[90762] <sup>f</sup>						[0.67] <sup>f</sup>	[0.18] <sup>f</sup>	
	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] <sup>f</sup>	[0.48] <sup>b</sup>	
	35a	200	18	4	147.9	151				56.6	[10.6] <sup>f</sup>	[3.0] <sup>b</sup>	
	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] <sup>f</sup>	[9.5] <sup>b</sup>	
	37c	1300	3	1	214.9	25.8	5.45	5.9			[22.8] <sup>f</sup>	[5.9] <sup>b</sup>	
	38	1	30	1	2050	2460					[2.0] <sup>f</sup>	[0.58] <sup>b</sup>	
	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] <sup>f</sup>	[2.5] <sup>f</sup>		
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] <sup>f</sup>	[0.79] <sup>b</sup>		
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 <sup>f</sup>	8.2 <sup>f</sup>	14 <sup>f</sup>	95.5		[6.5] <sup>f</sup>	[1.6] <sup>b</sup>		
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					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] <sup>f</sup>	[2.5] <sup>f</sup>		
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] <sup>f</sup>	[0.83] <sup>b</sup>		
59	767 (685-850)	9	5	18400 $\pm$ 5880	276 $\pm$ 156	27.3 $\pm$ 51.2	17.5 $\pm$ 9.3	96.0 $\pm$ 0.1		0.51	0.16	3.3	
B	TC1	800	5		[212] <sup>f</sup>	21.0			[95.8] <sup>f</sup>		[5.5] <sup>f</sup>	[1.4] <sup>b</sup>	
	TC2	600	5		[55.9] <sup>f</sup>	4.17			[95.8] <sup>f</sup>		[8.9] <sup>f</sup>	[2.3] <sup>b</sup>	
	TC3	300	5		[206] <sup>f</sup>	10.0			[95.8]				

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 ( $X_1$ :  $\text{mg ind.}^{-1}$ ), 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)	
	C	38	2	25.904	0.75	-7.641					0.481 (0.466)	
			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.<sup>-1</sup>), 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 <sup>2</sup>	p for t-test H <sub>0</sub> : a <sub>1</sub> = 1.0	
		a <sub>0</sub>	a <sub>1</sub>	a <sub>2</sub>	a <sub>3</sub>	a <sub>4</sub>	a <sub>5</sub>			a <sub>6</sub>
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)		
<b>Respiration</b>								
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 <sup>a</sup>	10–15	Larson (1987a)	
Siphonophores	11 species	0.79 ± 0.26	PRO	4.4–436	1.7–25.3 <sup>b</sup>	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 <sup>c</sup>	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			
<b>Ammonia excretion</b>								
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			Nemazee 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			Nemazee 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			

<sup>a</sup> Three species

<sup>b</sup> *Forskalia* spp.

<sup>c</sup> 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	
<b>Metabolism</b>						
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 $30^\circ\text{C}$ (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) <sup>a</sup>	
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 ( $20^\circ\text{C}$ , $\text{O}_2$ saturation = 100%)						
T-model	29.4 <sup>b</sup> , 15.4 <sup>c</sup>	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 <sup>d</sup>					
Pitt et als.' model	32.4 <sup>d</sup>					
Predicted rate for a specimen of 1 mgN body mass inhabiting 500 m depth ( $5^\circ\text{C}$ , $\text{O}_2$ saturation = 10%)						
T-model	8.7 <sup>b</sup> , 4.6 <sup>c</sup>	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 <sup>d</sup>					
Pitt et als.' model	8.1 <sup>d</sup>					
<b>O:N ratio (by atoms)</b>						
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)	
<b>Growth</b>						
Weight specific rate ( $\text{day}^{-1}$ )						
Range	$-0.069$ to $0.078$ <sup>e</sup>	$-0.013$ to $0.41$ <sup>e</sup>	$0.000$ – $1.62$ <sup>f</sup>	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)			
<b>Body composition component, and regression coefficients of body mass (<math>a_2</math>), habitat temperature (<math>a_3</math>) and depth (<math>a_4</math>)</b>						
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) <sup>g</sup>	36 (27)	18 (14)
	% of WM, mean (SD)	95.8 (0.7)	90.8 (2.9)	81.4 (5.1) <sup>g</sup>	76.9 (3.7)	77.6 (5.4)
C	$a_2$ , mean ( $\pm$ SD)	0.635 (0.052) <sup>h</sup>	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) <sup>h</sup>	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)
<b>C:N (by mass)</b>						
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)	

<sup>a</sup> Substituted by the DM-based data

<sup>b</sup> For siphonophores, scyphomedusae and ctenophores

<sup>c</sup> For hydromedusae

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

<sup>e</sup> Calculated from the data in Hirst et al. (2003)

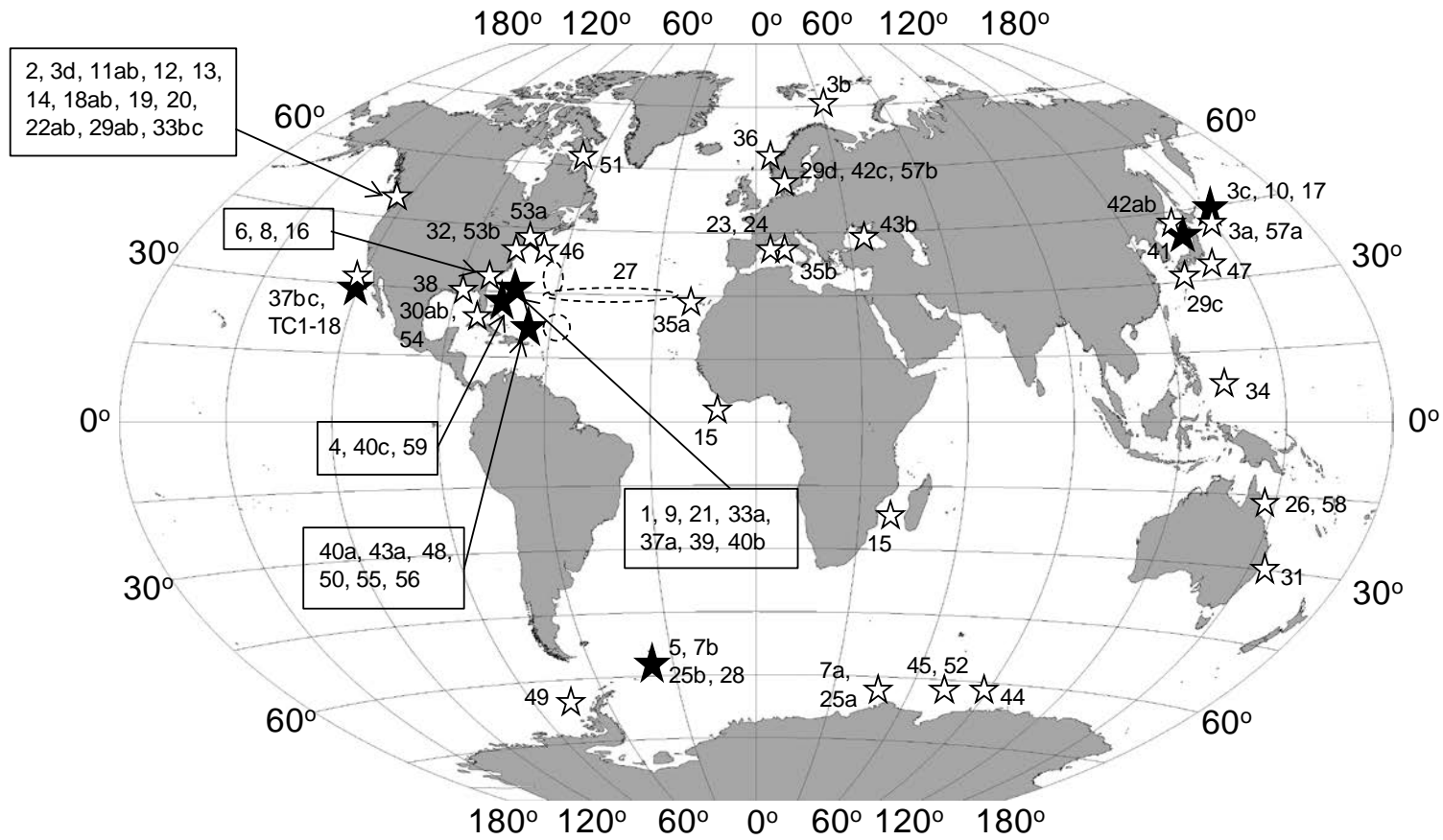
<sup>f</sup> From Hirst et al. (2003)

<sup>g</sup> 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

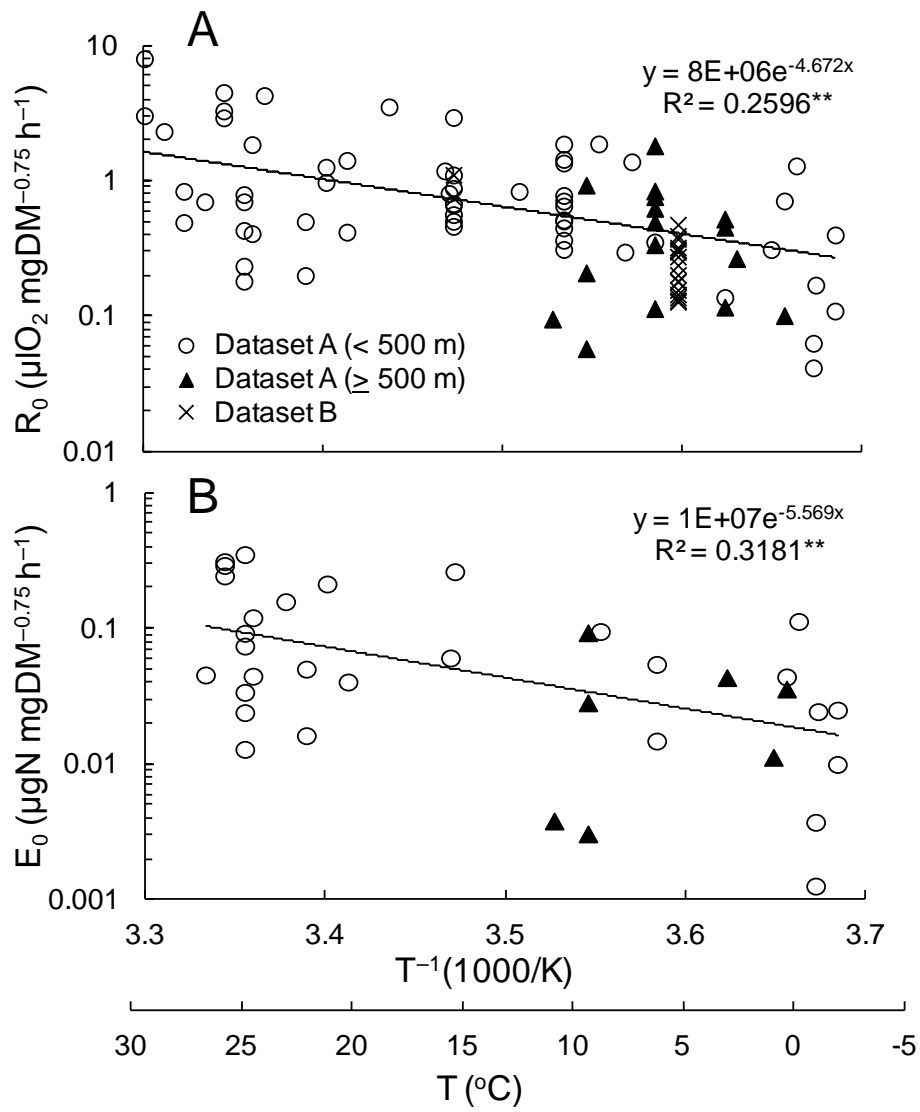
<sup>h</sup> Null hypothesis:  $a_2 = 1.0$  was rejected ( $p < 0.01$ ), suggesting progressive decline in % C or %N in DM with increasing DM

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

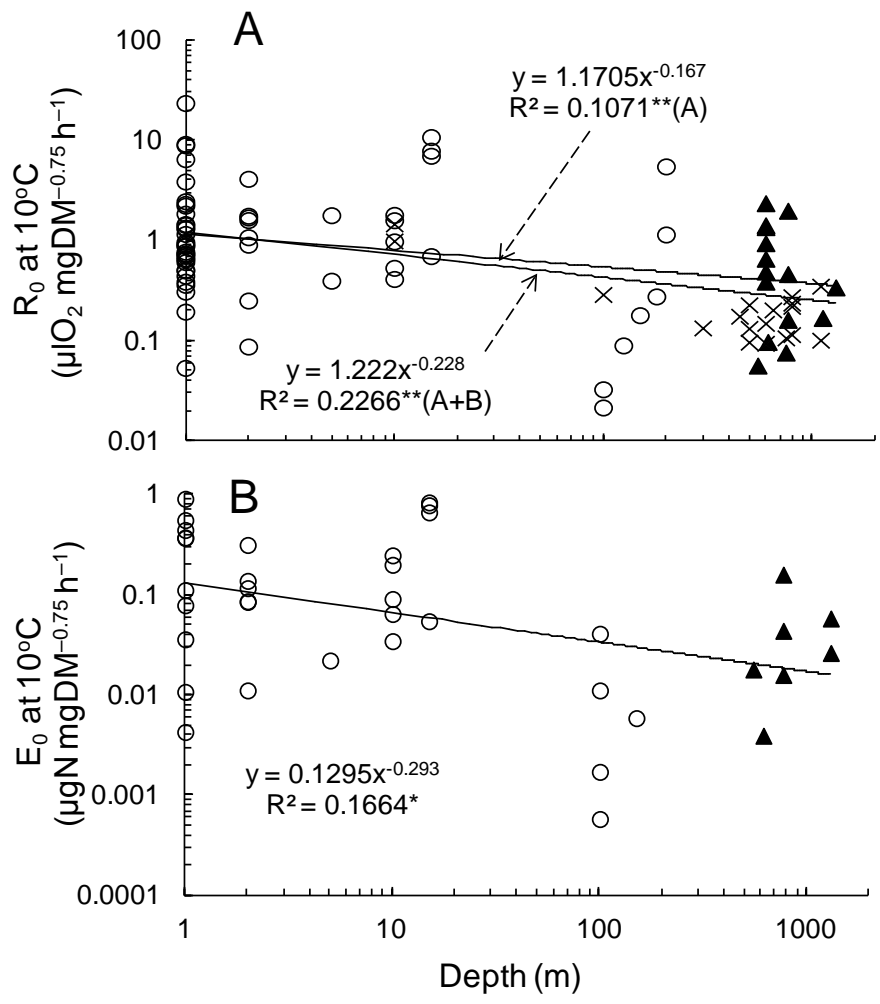
Taxon category	$X_{SC}$	$X_{SI}$	$X_{HY}$
Scyphozoa	1	0	0
Siphonophora	0	1	0
Hydrozoa	0	0	1
Ctenophora	0	0	0



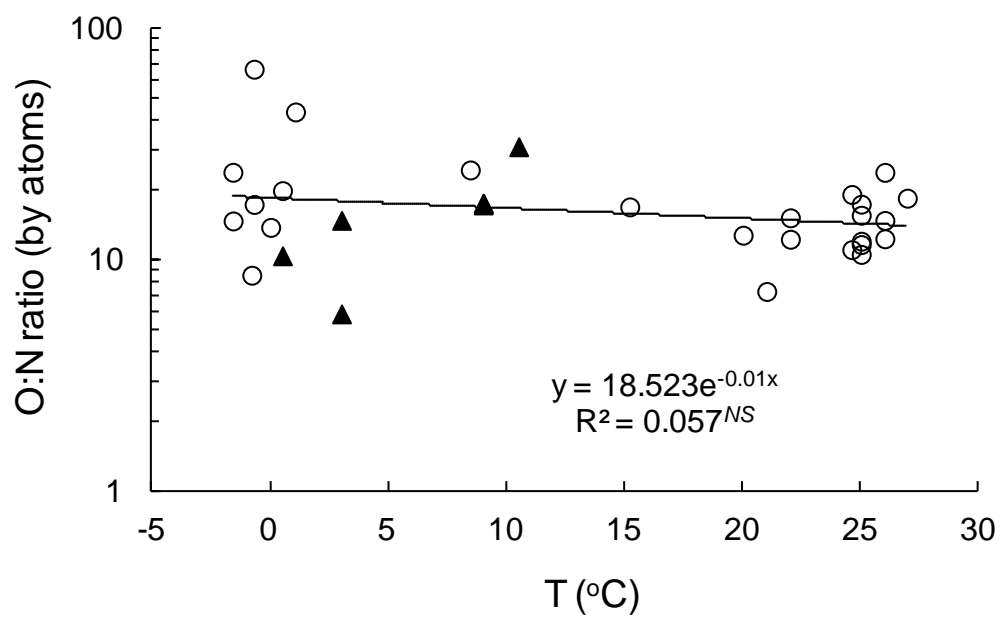
Ikeda Fig. 1



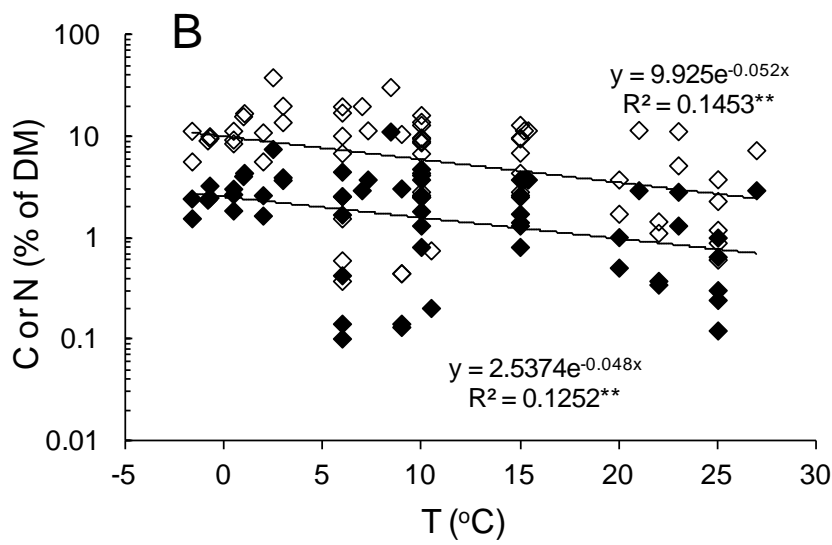
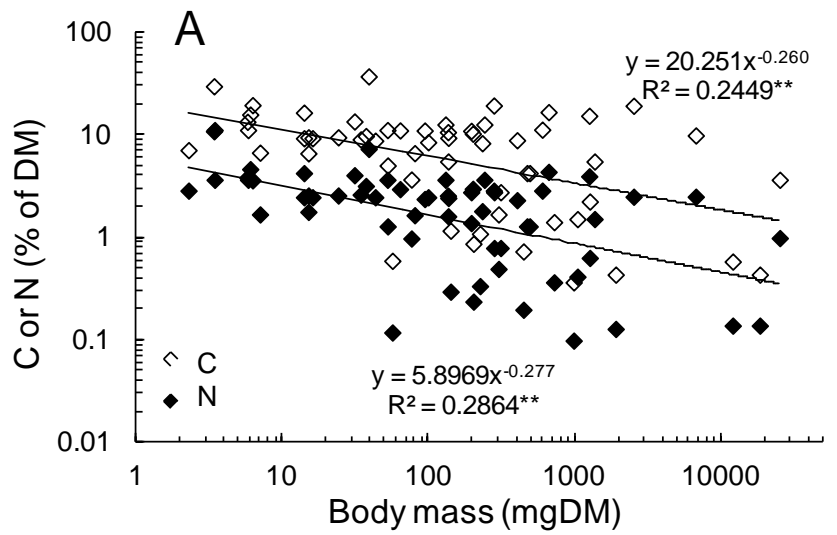
Ikeda Fig. 2



Ikeda Fig. 3

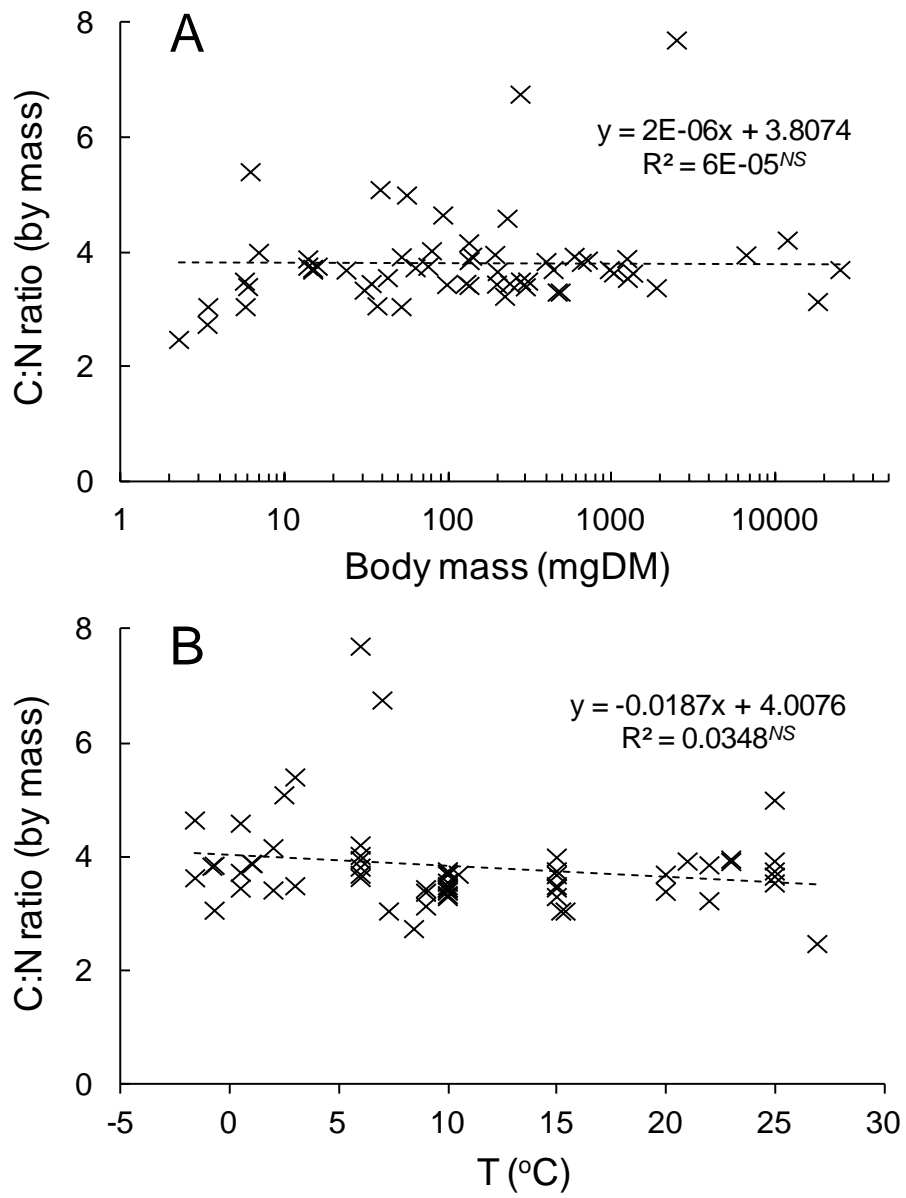


Ikeda Fig. 4



Ikeda Fig. 5





Ikeda Fig. 6