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Metabolism and chemical composition of marine pelagic amphipods: synthesis toward a global-bathymetric model

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ABSTRACT

Respiration and ammonia excretion data and chemical composition data [water content, ash, carbon (C), nitrogen (N) and C:N ratios] of 18–32 amphipods (hyperiids and gammarids) from the epipelagic through bathypelagic zones of the world's oceans were compiled. The independent variables including body mass, habitat temperature and mid-sampling depth were all significant predictors of respiration, accounting for 65–83% of the variance in the data, while the former two variables were significant predictor of ammonia excretion, accounting 64–77% of the variance. Atomic O:N ratios (respiration : ammonia excretion) ranged from 11 to 74 (median: 21.5). C composition was negatively correlated with habitat temperature, but water contents ash, N and the C:N ratio were uncorrelated with the three independent variables. As judged by C:N ratios, protein was considered to be the major organic component of most pelagic amphipods. However, some amphipods from > 500 m depth exhibited high C:N ratios (> 10) suggesting a large deposition of lipids in the body.

1 Introduction

Amphipods are a common component of marine zooplankton communities throughout the world, though their contribution to the zooplankton biomass is usually low (Longhurst 1985). There are two suborders (Hyperiidea and Gammaridea) of pelagic amphipods; species in the former are exclusively pelagic (often associated with gelatinous zooplankton as commensals, parasites or predators), and the latter contains benthic and bentho-pelagic species, with a few pelagic forms (Vinogradov 1968; Laval 1980; Raymont 1983). Pelagic hyperiids (such as genus *Themisto*) are numerous in the upper layers of higher latitude seas (Shih 1982), whereas pelagic gammarids are largely inhabitants of the deep-sea (Vinogradov 1968). Both are primarily considered to be carnivores (Sheader and Evans 1975; Hopkins 1985; Pakhomov and Perissinotto 1996; Haro-Garay 2004).

The importance of pelagic amphipods, however, has long been overlooked in the study of energy flow and matter cycling in pelagic marine ecosystems. This is partly due to their low contributions to the total zooplankton biomass, usually less than 0.5% (cf. Longhurst 1985). However, recent studies suggest that amphipod populations (mostly *Themisto* spp.) exert significant predation pressure (30–70%) on secondary production in the waters around South Georgia in the southern Ocean (Pakhomov and Perrissinotto 1996) and in the southern Japan Sea (Ikeda and Shiga 1999). In the pelagic zone of the Kerguelen waters, in the southern Indian Ocean, *Themisto gaudichaudii* have been reported to have an integral role in zooplankton-seabird couplings (Bocher et al. 2001). In the central Strait of Georgia, Canada, *Themisto pacifica* and *Cyphocaris challengeri* predominated the zooplankton communities as a possible consequence of the 1997 El Nino, and they appear to be important prey of juvenile salmon (Haro-Garay 2008).

Information about metabolism [respiration rates, ammonia excretion rates, O:N (as NH_4-N) ratios] has proved to be useful to provide a wide perspective for understanding the energy demand, major metabolic substrates and nutritional condition of marine zooplankton (cf. Ikeda et al. 2000). Metabolic rates of zooplankton living in the epipelagic zones have been documented as a function of body mass and habitat temperature (Ivleva 1980; Ikeda 1985). Although body mass and temperature have been regarded as two major determinants of the metabolic characteristics of marine pelagic animals, habitat depth has also emerged as an additional parameter of importance since the observation that metabolic rates decrease rapidly with depth for large pelagic animals with developed visual perception systems (eyes) such as micronektonic fishes, crustaceans, and cephalopods (Childress 1995; Seibel and Drazen 2007). To date, the effect of habitat depth on respiration rates and O:N ratios of amphipods has been analyzed within “crustaceans” group, together with mysids, decapods and other crustacean taxa (Childress 1975; Quetin et al.1980; Ikeda 1988; Torres et al. 1994), and no analyses have attempted for amphipods as a taxon.

Comparing carbon (C) and nitrogen (N) composition of diverse zooplankton taxa from tropical, subtropical, temperate and subarctic waters, Ikeda (1974) noted a general increase in C composition toward higher latitude seas. Båmstedt (1986) compiled voluminous data on the chemical composition (proximate composition and elemental C and N) of pelagic copepods from high, intermediate and low latitude seas and from surface and deep, and confirmed higher C and lower N composition for those living in lower temperature habitats (= high latitude seas and deep waters). Higher C and lower N composition of zooplankton living in high latitude seas have been interpreted as resulting from an accumulation of energy reserves (lipids) to compensate for unstable

97 food supply. According to a recent study on pelagic copepods from the surface to 5000
98 m depth in the subarctic Pacific where the vertical change in temperature is less
99 pronounced, the chemical composition of deeper living copepods is characterized by
100 stable C composition but low N composition, possibly because of reduced musculature
101 reduced swimming activities in dark environments (Ikeda et al. 2006a). For pelagic
102 amphipods, analysis of the data to reveal global and bathymetric trends has not yet been
103 attempted.

104 In order to evaluate global-bathymetric patterns of metabolism and chemical
105 composition of amphipods I compiled published data of respiration, ammonia excretion,
106 O:N ratio, water content, ash, C, N and C:N ratio of amphipods from various
107 bathymetric levels of polar, temperate and tropical/subtropical seas, and significant
108 parameters attributing to the variance were explored. Body mass, habitat temperature,
109 sampling depth and ambient oxygen saturation have been used as determinants of
110 metabolic rates as in the global-bathymetic model for pelagic copepods and
111 chaetognaths (Ikeda et al. 2007; Ikeda and Takahashi 2012). Finally, the present results
112 are compared with those of copepods and chaetognaths to highlight any unique
113 global-bathymetric features of pelagic amphipods.

114

115 **2 Materials and methods**

116 2.1 The data compilation

117 As indices of metabolism, respiration rates represent total metabolism, and
118 ammonia excretion rates represent nitrogen metabolism. Presently available respiration
119 and ammonia excretion data for pelagic amphipods are those derived from the sealed
120 chamber method, in which specimens are confined in containers filled with filtered

121 seawater for a certain period and the decrease of oxygen or increase in ammonia during
122 the period (several hours to a day) is monitored throughout, or determined at the end of
123 the incubation (Ikeda et al. 2000). Laval (1980) suggested the sealed chamber method
124 overestimated metabolism of hyperiid amphipods because of the lack of a gelatinous
125 substratum for the animals to attach to during the experiment. The magnitude of
126 possible error due to methodological constraints is discussed in Discussion section. For
127 the present analyses, the data compiled were those which met the following criteria:
128 1. Data are on fresh specimens collected from the field and used for experiments
129 without a considerable time delay (< 24 h).
130 2. Measurements were made in the absence of food at near *in situ* temperatures in the
131 dark [and at normal pressure (1 atm) for deep-sea amphipods on the premise that the
132 hydrostatic pressure has minimal effect on the metabolic rates of deep-sea pelagic
133 crustaceans, cf. review of Ikeda et al. (2000)]. This practice, combined with the criterion
134 above, makes it possible to compare the data of various amphipods for which
135 information about feeding conditions in the field prior to the experiments is not
136 available.
137 3. O:N ratios were computed from simultaneous measurements of respiration rates and
138 ammonia excretion rates.
139 4. Body mass in terms of wet mass (WM), dry mass (DM), C or N units were given
140 together with metabolic data (note: body mass specific rates without body mass data are
141 not useful).
142 5. Body composition (water contents, ash, C and N) were derived with standard
143 methods (Omori and Ikeda 1984; Postel et al. 2000).
144 In cases where multiple literature sources (including those of my own) were

145 available on the same species from similar regions, preference was given to mine to
146 reduce possible between-workers bias in the data. As a result, a total of 41 data sets on
147 32 amphipods (21 hyperiids and 11 gammarids) were selected, amongst which 22 were
148 of simultaneous measurements of respiration and ammonia excretion rates, 18 were of
149 respiration rates only, and 1 was ammonia excretion rates only (Table 1). Of the 32
150 amphipods used metabolic measurements, 17–18 data sets of water content and ash
151 were available on 18 amphipods, and 36 data sets of C and N composition and C:N
152 ratios on 28 amphipods (Table 2). Both genus and species names in the literatures were
153 updated according to Vinogradov et al (1982) and Schneppenheim and
154 Weigmann-Haass (1986). Amongst the gammarids, *Eusirus* spp. were difficult to judge
155 whether they were pelagic or non-pelagic (sympagic), but have been considered as
156 primarily pelagic after Krapp et al. (2008). The same amphipod species from different
157 locations or studies were treated as independent data sets, though mere repetition of the
158 data on the same amphipods was avoided carefully. The data expressed in the form of
159 regression equations only were converted to the respiration rates of a specimen at
160 mid-range of body mass. Study sites of all amphipods are plotted on the world map (Fig.
161 1) to facilitate graphical perception of worldwide coverage of the data sets in the present
162 study.
163
164 2.2 Regression models for metabolism
165 In addition to the 2 conventional independent variables (X_1: body mass; and X_2:
166 habitat temperature) used in the previous global respiration model for marine epipelagic
167 crustaceans (Ivleva 1980; Ikeda 1985), 2 new independent variables (X_3: mid-sampling

depth, X_4: oxygen saturation) were introduced in an early stage of the present analyses。 X_1 was expressed as DM, C or N since the choice of the body mass unit is known to cause somewhat different results (Ivleva 1980; Ikeda 1985). X_4 was expressed as a fraction of saturation (full saturation = 1.00). Missing oxygen saturation and/or habitat temperature data were substituted by those in the World Ocean Atlas of the National Oceanography Data Center (NODC) Homepage by knowing location, season and depth. Preliminary analyses indicated high correlation between X_3 and X_4 ($R = –0.797$, $df = 39$, $p < 0.01$) therefore the latter was omitted in the following analyses to avoid errors due to multicollinearity. For the species on which C and/or N composition data are not reported, the missing values were substituted by those of the same species studied by the other workers, or grand mean values of those of the same genera of the present study were used.

Two regression models were adopted according to the mathematical form of the temperature and body mass effects. One was a theoretical model characterized by the Arrhenius relationship ($R = R_0M^{3/4}e^{-Ea/kT}$ or $E = E_0M^{3/4}e^{-Ea/kT}$, where R (μlO_2 ind.$^{-1}$ h^{-1}) is respiration rate, E (μgNH_4-N ind.$^{-1}$ h^{-1}) is ammonia excretion rate, M (mg) is body mass, T is absolute temperature, 3/4 is theoretical body mass exponent, E_a (eV) is an average activation energy for the rate-limiting enzyme-catalyzed biochemical reactions of metabolism, k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}) and R_0 or E_0 is a normalization constant (cf. Gillooly et al. 2001) and the other was empirical (or log/linear) model characterized by the Van't Hoff rule (Q_{10}) (Ikeda 1985; Ikeda and

189 Takahashi 2012);

190 Theoretical model: $\ln Y = a_0 + a_1 \ln X_1 + a_2(1000 X_2^{-1}) + a_3 \ln X_3$

191 Empirical model: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3$

192 It is noted that a_1 was 0.75 (= 3/4) for the theoretical model. As indices of
193 temperature effects, *E*a of the theoretical model and Q_{10} of empirical model could be
194 computed as $Ea = a_2 \times 1000 \times 8.62 \times 10^{-5}$ and $Q_{10} = \exp(10 \times a_2)$, respectively The
195 attributes of these variables were analyzed simultaneously using the stepwise multiple
196 regression (forward selection) method (Sokal and Rohlf 1995). Independent variables
197 were added and removed at the p = 0.05. The calculation was conducted using SYSTAT
198 version 10.2.
199
200 **3 Results**
201 3.1 Metabolic rates
202 Of the pelagic amphipods considered in the present analyses, *Themisto*
203 *gaudichaudii* (1.0 mgDM) and *Eusirus perdentatus cornuta* (344 mgDM) were the
204 smallest and largest species, respectively (Table 2). Respiration rates at *in situ*
205 temperature ranged from 0.37 μlO_2 ind.$^{-1}$ h^{-1} (*Cyphocaris* sp. B) to 68.4 μlO_2 ind.$^{-1}$ h^{-1}
206 (*Cyphocaris faueri*), and ammonia excretion rates from 0.049 μgN ind.$^{-1}$ h^{-1}
207 (*Cyphocaris challengeri* from the eastern subarctic Pacific Ocean) to 4.76 μgN
208 ind.$^{-1}$ h^{-1}(*Oxycephalus clausi* from tropical Indian Ocean) (Table 2).
209 A preliminary analysis was performed to test the effects of temperature and
210 sampling depth on the rates of respiration (R) and ammonia excretion (E) by first
211 plotting the rates standardized to the rate of specimens weighing 1 mg DM ($R_0 = R \times$

212 $DM^{-0.75}$ or $E_0 = E \times DM^{-0.75}$) against temperature (1000/K or ^oC) where the scale
213 coefficient of body mass was assumed as 0.75 (as in the theoretical model) (Fig. 2). To
214 facilitate analysis, the data were separated into two groups depending on the depth of
215 amphipods sampled (< 500 m and ≥ 500 m). It is clear that the rates values for the
216 species from ≥ 500 m depth distribute well below the rate values <500 m at equivalent
217 inverse temperature or temperature. From this result, only the data of < 500 m were
218 used for the analysis of temperature effect on R_0 or E_0. The resultant slope (–4.582 for
219 respiration rates, and –5.408 for ammonia excretion rates) of the regression lines was
220 used to compute R_0 or E_0 at a given temperature (designated as 10°C) of the amphipods
221 from these sampling depths (< 500 m + ≥ 500 m), which were plotted against the
222 mid-sampling depth (Fig. 3). The standardized R_0 or E_0 at 10°C of these amphipods
223 were correlated negatively with the sampling depth, but the correlation was significant
224 ($p < 0.01$) in the former only.
225 The overall results of stepwise multiple regressions showed that the new variable
226 X_3 (sampling depth) was significant ($p < 0.005$) irrespective of the choice of the
227 theoretical or empirical model for respiration rates. For ammonia excretion rates, the
228 data for *Paracallisoma coecus* were considered outliers and therefore omitted in the
229 following analyses. In contrast to the results for respiration rates, the new variable X_3
230 (sampling depth) was not significant in both theoretical and empirical models ($p > 0.18$)
231 for ammonia excretion rates. As judged by R^2 values, the empirical model was superior
232 to the theoretical model, accounting for 79.6–83.1% and 64.7–68.2% of variance,
233 respectively, for the respiration rates, and the reverse was the case of ammonia
234 excretion rates (63.9–67.9% and 73.1–76.8%, respectively) (Table 3). There was no
235 consistent pattern in the performance of the various body mass units to yield best fid in

236 the models of respiration rates and ammonia excretion rates.

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

242

243 3.2 O:N ratios

244 A total of 22 O:N ratios from 19 amphipods ranged from 10.8 (*Oxycephalus*
245 *clausi* from tropical Indian Ocean) to 73.9 (*Cyphocaris* sp. A) (Table 2). The O:N ratio
246 data were separated into two depth groups (< 500 m and ≥ 500 m) and plotted against
247 habitat temperature of the amphipods (Fig. 4). The number of data of the ≥ 500 m group
248 was limited to only one. The multiple regression analysis of the O:N ratios (pooled data
249 of the two depth groups) on body mass (represented by DM), habitat temperature and
250 mid-sampling depth revealed that neither body mass ($p = 0.916$) nor habitat temperature
251 ($p = 0.599$) were significant. The O:N ratios were correlated with sampling depth ($p <$
252 0.05), which was contributed to 36.0% of the variance in the O:N ratios ($R^2 = 0.36$) (Fig.
253 4). Mean and median O:N ratio were 30.2 (± 21.3, SD) and 21.5, respectively.

254

255 3.3 Chemical composition

256 Water content varied from 60.9 to 93.3% of WM (mean; 77.9), and ash from 9.1 to
257 47.5% of DM (24.8), C from 23.0 to 59.8% of DM (39.1), N from 4.0 to 10.1of DM
258 (6.9), C:N ratios from 3.4 to 13.0 (6.0)(Table 2). Simple correlation analyses between
259 these chemical components and designated parameters [mid-sampling depth, body mass

(represented by DM) and habitat temperature] revealed that mid-sampling depth positively affected C composition and C:N ratios, and habitat temperature negatively affected C composition (Table 4). The scatter diagram of C composition and habitat temperature is showed in Fig. 5. Since mid-sampling depth and habitat temperature are inter-correlated ($R = -0.687$, $p < 0.01$), the effect of the depth was re-analyzed by comparing the > 500 m data and the < 500 m data within the same temperature regimes (< 5.5^{o}C; the maximum temperature of the > 500 m data sets). The results of this re-analyses showed no significant differences in C composition and C:N ratios between < 500 m and > 500 m data set groups (U-test, $p = 0.797$). Thus, it became clear that habitat temperature alone exerts the greatest effect on the chemical composition of the pelagic amphipods.

4 Discussion

4.1 Methodological issues in measuring metabolic rates

Enzyme assay of intermediary metabolism is another measure of respiration rates (R): a measure that is almost free from the problems associated with swimming performance in nature. This follows from the premise that the amounts of enzymes in a specimen do not vary appreciably over a short time (see Ikeda et al. 2000). Activities of ETS are measured under saturating conditions of substrates and cofactors so that they estimate potential respiration rates (V_{max} of the Michaelis-Menten equation). The theoretical ETS:R ratio is 2 (Owens and King 1975) and shows little effect of temperature or the body mass of zooplankton (King and Packard, 1975). On this basis, ETS:R ratios of hyperiids would be less than the theoretical value (2) when R is overestimated by the sealed-chamber method without the inclusion of a gelatinous

284 substratum. For *Themisto* (formerly *Euthemisto*) *pacifica*, King et al. (1975) adopted the
285 sealed-chamber method to measure R and determined ETS/R ratio as 2.0 (original ETS
286 data were multiplied by 3.3 to standardize to the sensitivity of the Owens and King's
287 assay), which is similar to those of free-living crustaceans of the same study (2.1 for a
288 decapods *Pleurocodes planipes*, 2.4–2.5 for euphausiids *Euphausia pacifica* and
289 *Nematoscelis atlantica*). This result suggests that the majority of *T. pacifica* are almost
290 exclusively free-living, and that the extra energy needed for swimming is relatively less
291 as compared with that for the standard metabolism as discussed in the following.
292 While no information about the relationship between R and swimming activities
293 is presently available for hyperiid amphipods, Halcrow and Boyd (1967) determined the
294 relationship on an intertidal gammarid amphipod *Gammarus oceanicus*, and calculated
295 factorial scopes [FS; the ratio between activity metabolism (R at maximum activity) to
296 standard metabolism (R at rest)] as 3–4, depending on temperature (5–20^{o}C). The FSs
297 of *G. oceanicus* are the same order of magnitude (3.1) to that of a planktonic copepod
298 *Dioithona oculata* (Buskey 1998) and that (6.1) of a euphausiid *Euphausia pacifica* at
299 8^{o}C and normal pressure (1 atm) (Torres and Childress 1983), but are much less than
300 10–20 in salmon (Brett, 1964) and 50–200 in flying insects (cf. Prosser 1961).
301 Clearly, the gap in our knowledge about the metabolism of partly parasitic
302 hyperiid amphipods needs to be filled by developing new methodology in the future.
303 Nevertheless, presently available information of ETS:R ratios and FSs suggests that the
304 magnitude of possible errors due to the current methodological constraints in measuring
305 metabolic rates of pelagic hyperiids are sufficiently small to allow the broad comparison
306 of metabolic data in the present study.
307

308 4.2 Body mass and habitat temperature as traditional predictors

309 The effects of body mass and temperature on respiration and ammonia rates of
310 pelagic amphipods have been studied in *Themisto* spp., *Cyphocaris challengeri* and
311 *Primno abyssalis*, all inhabiting high latitude seas (Hirsche 1984; James and Wilkinson
312 1988; Ikeda 1991; Yamada and Ikeda 2003) (Table 4). The results of these earlier
313 studies showed that the rates are a power or linear function of body mass (a_2 =
314 0.70–1.37). Small differences in the scale exponents (a_2) of body mass (DM) may be
315 not important since a large marginal error is associated with a_2 derived from small body
316 mass (DM) ranges. In this regard, a_2 (0.742 for respiration rates, and 0.763 for ammonia
317 excretion rates) computed from inter-specific data (DM range: 3 orders of magnitude)
318 can be taken as typical for pelagic amphipods, as all previous intra-specific data are
319 from narrow DM ranges (1 or 2 orders of magnitude). The inter-specific a_2 based on the
320 DM body mass unit of the pelagic amphipods (0.745) is comparable to 0.750 for pelagic
321 copepods (Ikeda et al. 2007) and 0.753 for euphausiids (Ikeda unpublished data), both
322 derived from global-bathymetric models based on the broad body mass (DM) ranges of
323 animals (4 orders of magnitude). The scale exponents have been reported as 0.7–0.8 for
324 diverse animal phyla (Zeuthen 1947).

325 The effect of temperature on metabolism has been studied in individual amphipod
326 species at graded temperatures within the range of their habitats. According to the
327 definition by Clarke (1987), this is “acclimation” (adjustment of an organism to a new
328 temperature in the laboratory), in contrast to “adaptation” (the evolutionary adjustment
329 of an organism’s physiology to environment). The activation energy (E_a) or Q_{10} values
330 thus obtained for acclimated amphipod species by previous workers are 0.44–0.64 eV or
331 1.9–2.69 for respiration rates (Table 4). Similar intra-specific Q_{10} values (2–3) are

typical for the respiration rates measured at graded temperatures within the ranges of natural habitats of acclimated aquatic fishes and crustaceans living in arctic and tropical regions (Scholander et al. 1953). On the other hand, inter-specific E_a (0.26) or Q_{10} values (1.45) derived from global data sets of adapted amphipods are less than these intra-specific values. Analyzing the effect of temperature on 69 teleost fishes from polar to tropical regions, Clarke and Johnston (1999) noted that a Q_{10} = 1.83 derived from inter-specific data over the temperature range 0–30^{o}C was smaller than typical intra-specific acclimated Q_{10} values in the literature (median: 2.40, N = 138), as is the case for pelagic amphipods of the present study. Those results suggest that evolutionary temperature adaption has produced an inter-specific relationship that has a lower thermal sensitivity than is typical of intra-specific relationships (cf. Clarke and Johnston 1999). While no comparable information about intra-specific data of ammonia excretion rates is currently available for pelagic amphipods, the present results showed that the 95% CIs of E_a or Q_{10} for ammonia excretion rates overlap those of respiration rates Table 4).

4.3 Habitat (= sampling) depth as a new predictor

The effect of habitat depth was significant for respiration rates but not for ammonia excretion rates in pelagic amphipods in the present study (Table 2). The present results contrast with those of Quetin et al. (1980) and Ikeda (1988), who compared ammonia excretion rates of various pelagic crustaceans (including amphipods) and found a pattern of reduction in the rates with increasing the depth of occurrence. Perhaps, the effect of habitat depth on ammonia excretion rates may be masked by a large scatter of the data together with fewer data sets in the present

356 analyses (see Fig. 3).

357 The negative effects of habitat depth on respiration rates of pelagic amphipods are
358 consistent with those of micronektonic crustaceans, fishes and cephalopods with
359 image-forming eyes (Torres et al. 1994; Childress 1995; Seibel and Drazen 2007), and
360 zooplankton such as copepods (Ikeda et al. 2006, 2007) and chaetognaths (Kruse et al.
361 2011; Ikeda and Takahashi 2012). For the reduction in respiration rates for deeper-living
362 pelagic animals, the “visual-interactions hypothesis” (Childress 1995) or
363 “predation-mediated selection hypothesis” (Ikeda et al. 2007) have been proposed.
364 These two hypotheses are similar in that both interpret the phenomena as a result of
365 lowered selective pressure for high activity at depth because of the decrease in visual
366 predators in the dark. However, the former hypothesis applies strictly to micronekton
367 with functional eyes, and the latter to both micronekton and zooplankton irrespective of
368 presence/absence of functional eyes. In terms of size-based classification, most pelagic
369 amphipods in the present study belong to zooplankton rather than micronekton (> 20
370 mm body length, cf. Omori and Ikeda 1984) though they possess functional eyes.

371 Torres et al. (1994) compiled the relationship between respiration rates and the
372 depth of occurrence for pelagic crustaceans (amphipods, decapods, euphausiids, isopods,
373 mysids and ostracods) off California, in the Gulf of Mexico, off Hawaii and in Antarctic
374 waters. According to their results, the respiration rates [standardized to a body size of 1
375 mg wet mass by using the scale exponent of 0.75 (equivalent to the theoretical model
376 adopted in the present study), and at 0.5^{o}C by assuming Q_{10} = 2.0)], the reduction in the
377 rates of a specimen due to the increase of its habitat depth from 1 m to 1000 m depth is
378 in the order of 0.1–0.5 times. Similar calculations for the pelagic amphipods based on
379 the present results (theoretical models in Table 3) showed that the reduction was 0.3–0.4

380 times, depending on the choice of DM, C or N body mass unit, which fall within the
381 range of the mixed crustacean taxa by Torres et al. (1994).
382
383 4.4 O:N ratios
384 The atomic ratio of oxygen consumption rate to ammonia-nitrogen excretion rate
385 (O:N ratio) has been used as an index of the proportion of protein in total metabolites in
386 marine zooplankton (Mayzaud and Conover 1988; Ikeda et al. 2000). When only protein
387 is metabolized, the O:N ratio is 7 (Table 10.3 in Ikeda et al. 2000). When protein and
388 lipid or carbohydrate is catabolized in equal quantities at the same time, O:N ratios are
389 calculated between 13 and 21. Hence, O:N ratios of 7–17 (mid-point of 13 and 21) may
390 be used as an index of protein-oriented metabolism and the ratios of > 17 as
391 lipid/carbohydrate-oriented metabolism. As carnivores, the O:N ratio of the 19 pelagic
392 amphipods compiled in the present study (Table 2) varied from one species to the next
393 (11–74, Table 2), with a median of 21.5. The somewhat greater than expected O:N ratios
394 for the pelagic amphipods may be due to methodological constraints of the incubation
395 of specimens in filtered seawater (no food), a typical design of the sealed-chamber
396 method (Ikeda et al. 2000). Ammonia excretion is more susceptible to food deprivation
397 than respiration, hence high O:N ratios in starved amphipods have been documented in
398 *Phronima sedentalia* (Ikeda 1974) and *Themisto pacifica* (Ikeda 1977). The same
399 phenomenon has also been observed in a bathypelagic mysid *Gnathophausia ingens*
400 (Quetin et al. 1980; Hiller-Adams and Childress 1983) and an epipelagic euphausiid
401 *Euphausia superba* (Ikeda and Dixon 1984).
402 In addition to food deprivation, N composition of diets is known to affect O:N
403 ratios of marine invertebrates (cf. Ikeda and McKinnon 2012). As carnivores,

404 progressive increase in the O:N ratios of the pelagic amphipods downward (Fig. 4) may
405 be a result from N-poor and/or C-rich prey animals at depth. Copepods are the major
406 prey components of pelagic amphipods (Sheader and Evans 1975; Pakhomov and
407 Perissinotto 1996; Haro-Garay 2004) and their depth-related patterns in chemical
408 composition are characterized by a gradual decline in N composition and increase in
409 C:N ratio toward great depth (Ikeda et al. 2006a). As an alternative explanation, the
410 increase in body C:N ratios of deeper-living pelagic amphipods themselves may also be
411 considered. However, this explanation is not consistent with the insignificant correlation
412 between the C:N ratios and sampling depth in the pelagic amphipods (Table 4).
413
414 4.5 Chemical composition
415 Ikeda (1974), analyzing C and N compositions of various zooplankton taxa from
416 tropical to subarctic waters, showed that high C composition and C:N ratios are
417 characteristics of those inhabiting cold habitats. Båmstedt (1986) noted also high C and
418 low N (thus leading to high C:N) for copepods from cold thermal regimes (high latitude
419 seas and deep sea) as compared with counterparts from warm thermal regimes (low
420 latitude seas). A recent study on copepods living in the epipelagic through abyssopelagic
421 zones of the western subarctic Pacific Ocean revealed a gradual decline in the N content
422 and an increase in C:N ratios downward (Ikeda et al. 2006a). The present results on
423 pelagic amphipods are consistent with the results of these previous studies in that C
424 composition was negatively correlated with habitat temperature (Fig. 5).

425 Analyzing chemical composition data on 182 zooplankton species (mostly
426 crustaceans), Ventura (2006) calculated average C and N composition of protein to be
427 52.8% and 16.0%, and lipids (represented by wax esters) to be 81.0% and 0%. With
428 these results, the C:N ratio is calculated as 3.3 for protein alone and 8.4 for organic
429 matter composed of equal amounts of protein and lipid. Carbohydrate in zooplankton
430 has been reported to be < 8.5% of DM (Ventura 2006) and is therefore omitted in this
431 calculation. Then, C:N ratios of 3.3–8.4 and > 8.4 can be used as indices of protein- and
432 lipid-dominated composition, respectively, for zooplankton. On this basis, body C:N
433 ratios of most the pelagic amphipods were 3.4–7.9 (mean = 6.0, Table 2), indicating
434 protein dominated composition. As exceptions, the three amphipods from the
435 mesopelagic/abyssopelagic zones exhibited C:N ratios beyond the range (10.9 for
436 *Chuneola spinifera*, 12.7 for Gammaridea sp., and 13.0 for *Cyphocaris* sp., Table 2),
437 indicating lipid dominated composition. Little has been studied on the function of lipids
438 in pelagic amphipods, with a notable exception of the study of Percy (1993) who
439 demonstrated that the hyperiid amphipod *Themisto libellula* utilized lipid reserves in the
440 body for metabolic needs when starved. For copepods and euphausiids, the function of
441 large lipid deposits (mostly as wax esters, triacylglycerols or phospholipids) is
442 considered as an energy reserve for coping with temporal food scarcity and reproduction,
443 or energy saving for swimming by achieving neutral buoyancy (Lee et al. 2006).
444 In conclusion, global-bathymetric models designed in the present study could
445 explain 65–83% of the variance in respiration rates and 64–77% of the variance in

ammonia excretion rates of pelagic amphipods. From the comparison of the scale exponents of body mass and temperature coefficients (E_a and Q_{10}) derived from the global-bathymetric models and those of previous regional models based on single amphipod species, the differences in the magnitude of the ranges of the data were considered as a prime source of dissimilar results. As carnivores, the O:N ratios of the pelagic amphipods were somewhat greater than expected, to which methodological constraints (incubation without food) are suggested. Although the C composition was negatively correlated with habitat temperature, none of the other variables (water contents, ash, N and the C:N ratio) were correlated with body mass, habitat temperature and sampling depth. As judged by body C:N ratios, protein was considered to be the major organic component of most of the pelagic amphipods. As exceptions, some pelagic amphipods from > 500 m depth exhibited very high C:N ratios (> 10) indicating a large deposition of C-rich organic matter (lipids) in the body.

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635 **Figure captions**

636 Fig. 1. Study sites of metabolic rates of pelagic amphipods. The sites were separated
637 into two groups depending on the depth where amphipods collected (< 500 m and ≥
638 500 m). The number and associated character alongside the symbol corresponds the
639 code of each amphipod listed in Table 1.

640 Fig. 2. Pelagic amphipods. Relationship between the respiration rate (top) or ammonia
641 excretion rate (bottom) standardized to a body size of 1 mg body DM (R_0 or E_0) and
642 temperature (T^{-1}: 1000/K, or T: ^oC) of the specimens from shallow (open circles; <
643 500 m) and deep layers (closed triangles; ≥ 500 m). The data points represent means
644 from the data sets in Table 2, and the regression line is derived from shallow layer
645 species only. **: $p < 0.01$.

646 Fig. 3. Pelagic amphipods. Relationship between respiration rates (top) or ammonia
647 excretion rates (bottom) standardized to a body size of 1 mgDM (R_0 or E_0) at 10°C
648 and mid-sampling depth. The data points represent means derived from the data sets
649 in Table 2. For symbols see Fig. 2. **: $p < 0.01$.

650 Fig. 4. Pelagic amphipods. Relationship between O:N (as NH_4-N) ratios and
651 mid-sampling depth of specimens from various regions of the world's oceans. The
652 data points represent means in Tables 2. For symbols see Fig. 2. *: $p < 0.05$.

653 Fig. 5. Pelagic amphipods. Relationship between C composition and habitat temperature.
654 The maximum temperature for > 500 m data (5.5^oC) was superimposed (a vertical
655 hatched line). The data points represent means in Tables 2. For symbols see Fig. 2.
656 **: $p < 0.01$.

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Table 1. A list of pelagic amphipod species of which metabolic and chemical composition data were analyzed.

Code	Species	Region	Date	Reference
Hyperiidea				
1	*Chuneola spinifera*	W. subarctic Pacific Ocean	Aug 2004	Ikeda (2012)
2	*Cyllopus lucasii*	Scotia/Wedddell Sea	Nov–Dec 1983, Mar 1986, Jun–Aug 1988	Torres et al. (1994)
3	*Hemityphis tenuimanus*	Tropical Atlantic Ocean	Jan 1972	Ikeda (1974)
4	*Hyperia galba*	Gulf of Maine, USA	Dec 1959	Conover (1960)
5	*Hyperia gaudichaudii*	Off Wilkes Land, Antarctica	Jan 1980	Ikeda & Mitchell (1982)
6	*Lanceola loveni*	W. subarctic Pacific Ocean	Jun 2002	Ikeda (2012)
7a	*Oxycephalus clausi*	Coral Sea	May 2010	Ikeda & McKinnon (2012)
7b	*Oxycephalus cluasi* (formerly *O. porcellus*)	Tropical Indian Ocean	Oct 1971	Ikeda (1974)
8a	*Phronima sedentaria*	Tropical Indian Ocean	Oct 1971	Ikeda (1974)
8b	*Phronima sedentaria*	Subtropical Atlantic Ocean	Nov 1971	Ikeda (1974)
8c	*Phronima sedentaria*	W. subarctic Pacific Ocean	Jun 2003	Ikeda (2012)
9a	*Primno abyssalis* F	S. Japan Sea	Nov 1991	Ikeda & Hirakawa (1998)
9b	*Primno abyssalis*	W. subarctic Pacific Ocean	Jul 2000	Yamada & Ikeda (2003)
10	*Primno macropa*	Scotia/Wedddell Sea	Nov–Dec 1983, Mar 1986, Jun–Aug 1988	Torres et al. (1994)
11	*Scina borealis*	W. subarctic Pacific Ocean	Mar 2004	Ikeda (2012)
12	*Scina crassicornis* (formerly *S. cornigera*)	Subtopical Pacific Ocean	Mar 1972	Ikeda (1974)
13	*Thamneus rostratus* (formerly *Thamneus platyrrhynchus*)	Tropical Indian Ocean	Oct 1971	Ikeda (1974)
14	*Themisto compressa* (formerly *T. gaudichaudii*)	Gulf of Maine, USA	Sep 1966	Conover & Corner (1968)
15a	*Themisto gaudichaudii*	Off Wilkes Land, Antarctica	Jan 1980	Ikeda & Mitchell (1982)
15b	*Themisto gaudichaudii*	Scotia/Wedddell Sea	Nov–Dec 1983, Mar 1986, Jun–Aug 1988	Torres et al. (1994)
15c	*Themisto gaudichaudii*	E. Cook Strait, NZ	Mar–Apr 1983	James & Wilkinson (1988)
16a	*Themisto japonica*	Off SW Hokkaido, Japan	May 1971	Ikeda (1974)
16b	*Themisto japonica*	W. subarctic Pacific Ocean	May–Dec 2000	Yamada & Ikeda (2003)
16c	*Themisto japonica* F	S. Japan Sea	Sept 1990	Ikeda & Hirakawa (1998)
17	*Themisto libellula*	Barents Sea	Jun 1987	Ikeda & Skjoldal (1989)
18	*Themisto pacifica*	W. subarctic Pacific Ocean	Jul-Aug 2000	Yamada & Ikeda (2003)
19	*Vibilia* sp.	Tropical Indian Ocean	Nov 1971	Ikeda (1974)
20	*Vibilia propinqua*	Off Wilkes Land, Antarctica	Jan 1980	Ikeda & Mitchell (1982)
21	*Vibilia stebbingi*	Scotia/Wedddell Sea	Nov–Dec 1983, Mar 1986, Jun–Aug 1988	Torres et al. (1994)
Gammaridea				
22a	*Cyphocaris challengeri*	E. subarctic Pacific Ocean	Jul 1975	Ikeda, unpublished data
22b	*Cyphocaris challengeri*	W. subarctic Pacific Ocean	Oct 2000–Apr 2001	Yamada & Ikeda (2003)
23	*Cyphocaris faueri*	Scotia/Wedddell Sea	Nov–Dec 1983, Mar 1986, Jun–Aug 1988	Torres et al. (1994)
24	*Cyphocaris richardi*	Scotia/Wedddell Sea	Nov–Dec 1983, Mar 1986, Jun–Aug 1988	Torres et al. (1994)
25	*Cyphocaris* sp. A	Prydz Bay, Antarctica	Jan 1985	Ikeda (1988)
26	*Cyphocaris* sp. B	W. subarctic Pacific Ocean	Jun 2003	Ikeda (2012)
27	*Eusirus antarcticus*	Scotia/Wedddell Sea	Nov–Dec 1983, Mar 1986, Jun–Aug 1988	Torres et al. (1994)
28	*Eusirus microps*	Prydz Bay, Antarctica	Nov 1982	Ikeda, unpublished data
29	*Eusirus perdentatus*	South Georgia	Feb 1976	Opalinski & Jazdzewski (1978)
30	Gammaridea sp.	W. subarctic Pacific Ocean	Jun 2003	Ikeda (2012)
31a	*Paracallisoma coecus*	Off S. California	1969–1972	Childress (1975)
31b	*Paracallisoma coecus*	Off S. California	1976–1977	Quetin et al. (1980)
32	*Parandania boecki*	Scotia/Wedddell Sea	Nov–Dec 1983, Mar 1986, Jun–Aug 1988	Torres et al. (1994)

Table 2. Sampling depth, ambient oxygen saturation, temperature, body mass, rates of respiration and ammonia excretion, O:N ratios, water content, ash, C, N and C:N ratios of pelagic amphipods. For codes, see Table 1. *Italic* values for sampling depth are those estimated by the present author. Values in parentheses are those assumed for the multiple regression analyses. Blank = no data.

										Body chemical composition				
	Sampling depth (range)		Oxygen saturation	T		Body mass	Respiration rate	Ammonia excretion rate	O:N ratio	Water	Ash	C	N	C:N
Code	(m)		(1.00=100%)	(°C)	N	(mg DM ind.$^{-1}$)	(μlO_2 ind.$^{-1}h^{-1}$)	(μgN ind.$^{-1}h^{-1}$)	(atomic)	(% of WM)	(% of DM)	(% of DM)	(% of DM)	(by mass)
1	4000	(3000–5000)	0.45	1.5	1	239	6.40					49.4	4.6	10.9
2	*100*		0.9	0.5	5	61.8 18.5	29.4 4.5			68.7	16.5	44.9	5.7	7.9
4	2	(0–5)	1.00	26.4	2	1.62 ± 0.02	3.23 ± 0.25	0.26 ± 0.01	15.9 ± 1.7			25.1	4.6	5.5
5	125	(0–250)	0.80	5.6	4	6.63 ± 3.09	3.30 ± 1.10					(29.3)[a]	(5.0)[a]	
6	3	(0–5)	1.00	-0.8	3	105.3 ± 49.63	22.33 ± 7.44	2.64 ± 2.25	14.4 ± 7.6			46.8	7.1	6.6
7	1500	(1000–2000)	0.20	2	4	5.16 ± 3.25	0.63 ± 0.52					31.9	9.3	3.4
8a	1	surface	1.00	27.5	1	13.98	26.61	2.44	13.7	85.2	43	25.5	6.2	4.1
8b	2	(0–5)	1.00	27.4	1	17.67	40.97	4.76	10.8			24.1	5.5	4.4
9a	2	(0–5)	1.00	27.4	2	9.48 ± 3.70	32.39 ± 16.18	3.11 ± 1.34	12.8 ± 1.0			23.8	5.1	4.7
9b	2	(0–5)	1.00	19.7	2	7.29 ± 0.01	10.05 ± 0.31	0.73 ± 0.05	17.4 ± 1.7			23.8	5.1	4.7
9c	750	(500–1000)	0.13	3	3	7.57 ± 9.23	1.44			93.3	47.5	23.0	5.6	4.1
10a	550	(400–700)	0.75	0.5	14	14.82 ± 3.26	5.71 ± 1.74			82.6	25.3	39.0	9.4	4.2
10b	250	(0–500)	0.50	5	18	6.15 ± 4.45	5.09 ± 3.92	0.20 ± 0.17	40.8 ± 25.2			53.3	7.6	7.1
11	*100*		0.90	0.5	6	37.9 ± 2.1	19.1 ± 5.8			70.6	21.3	41.7	6.6	6.3
12	1500	(1000–2000)	0.20	2	1	8.74	1.56			81.0	29.6	35.6	7.8	4.6
13	2	(0–5)	1.00	22.4	2	2.99 ± 0.01	5.50 ± 0.65	0.14 ± 0.17	20.3 ± 11.8			41.7	10.1	4.1
13	2	(0–5)	1.00	27.4	2	2.44 ± 0.48	10.11 ± 5.09	0.50 ± 0.29	26.3 ± 2.5			24.1	4.0	6.0
14	250	(0–500)	0.60	4	2	2.13	2.02	0.087	29.1			(46.1)	9.4	(4.9)[b]
15a	2	(0–5)	1.00	-0.9	22	7.06 ± 5.48	3.71 ± 2.05	0.42 ± 0.32	13.7 ± 5.5			37.9	8.2	4.6
15b	*100*		0.90	0.5	2	60.5 ± 6.0	17.0 ± 4.1			80.7	24.5	(37.9)[c]	(8.2)[c]	
15c	*2*		1.00	15	11–17	*1.00*	1.70	0.13	16.2			38.2	8.0	4.8
16a	2	(0–5)	1.00	8.7	9	2.90 ± 1.95	4.30 ± 2.85	0.30 ± 0.17	24.2 ± 6.6			41.2	7.9	5.2
16b	250	(0–500)	0.50	5	41	2.65 ± 3.02	2.42 ± 1.92	0.24 ± 0.19	14.1 ± 6.0			46.3	8.8	5.3
16c	550	(400–700)	0.75	0.5	8	3.14 ± 0.64	2.04 ± 0.50			85.9	25.6	37.1	8.9	4.2
17	90	(35–150)	1.00	-0.1	11	2.98 ± 0.63	2.53 ± 0.63	0.05 ± 0.02	69.3 ± 32.0	82.5	26.6	38.3	8.1	4.7
18	250	(0–500)	0.50	5	20	1.18 ± 0.75	1.71 ± 1.01	0.10 ± 0.10	29.8 ± 16.5			47.9	8.3	5.8
19	2	(0–5)	1.00	27.8	2	1.24 ± 0.03	5.68 ± 1.52	0.31 ± 0.06	22.7 ± 2.0			35.1	7.1	4.9
20	2	(0–5)	1.00	-1.1	5	12.14 ± 0.96	6.07 ± 0.46	0.43 ± 0.11	18.4 ± 3.8			40.3	8.1	5.0
21	*100*		0.9	0.5	2	24.2 0.6	17.3 ± 0.5			79.2	24.3	34.7	7.4	4.7
22a	2	(0–5)	1.00	13	2	3.96 ± 0.22	2.84 ± 0.76	0.05 ± 0.06	73.1 ± 64.6			41.0	8.0	5.1
22b	250	(0–500)	0.50	5	36	5.90 ± 3.61	2.53 ± 1.73	0.07 ± 0.08	66.9 ± 37.9			36.8	6.8	5.4
23	*100*		0.90	0.5	8	293.2 ± 94.3	68.4 ± 8.6			76.4	21.8	39.3	5.1	7.7
24	*500*		0.60	0.5	5	127.2 43.8	47.0 ± 8.6			74.8	23.4	38.3	5.9	6.5
25	600	(200–1000)	0.60	0.2	12	81.42 ± 38.53	17.89 ± 9.79	0.58 ± 0.86	73.9 ± 58.0	75.8	18.8	47.3	7.0	6.8
26	750	(500–1000)	0.13	3	1	1.23	0.37			78.9		56.1	4.3	13.0
27	*100*		0.90	0.5	26	18.4 ± 3.5	6.44 ± 1.27			60.9	15.5	(45.3)[d]	(6.3)[d]	
28	55	(0–110)	1.00	-1.6	3	193.1 ± 37.28	24.13 ± 4.25	0.94 ± 0.67	40.8 ± 19.6	73.9	19.6	45.3	6.3	7.2
29	290	(0–580)	0.60	–1.0	20	344.0 ± 13.8	39.2 ± 4.1					(45.3)[d]	(6.3)[d]	
30	750	(500–1000)	0.13	3	1	4.01	0.81			67.6	9.1	59.8	4.7	12.7
31a	*600*		0.05	5.5	1	31.8	4.50					57.4	8.8	6.5
31b	600	(400–800)	0.05	5.5	2	50 ± 20		0.056 ± 0.056				(57.4)[a]	(8.8)[a]	
32	*500*		0.60	0.5	6	75.9 19.1	19.1 ± 7.4			83.7	29.1	36.2	5.7	

[a] after Childress and Nygaard (1974)

[b] mean of *Themisto* spp. of this study

[c] after Ikeda and Mitchell (1982)

[d] assumed the same to those of *Eusirus microps* in this Table

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Table 3. Stepwise (forward selection) multiple regression statistics of theoretical and empirical models of respiration rates (Y: µl O_2 ind.$^{-1}$h^{-1}) or ammonia excretion rates (Y: µgN ind.$^{-1}$h^{-1}) of pelagic amphipods on body mass (X_1: mg ind.$^{-1}$), habitat temperature (X_2: 1000/K for the former, ^{o}C for the latter) and depth sampled (X_3: m).

				Regression equation: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 X_4$				
Regression model	Body mass unit	N	Step No.	a_0	a_1	a_2	a_3	R^2 (adjusted R^2)
Respiration								
Theoretical	DM	41	1		0.75		–0.266	0.576
			2	11.561	0.75	–3.050	–0.167	0.665 (0.647)
	C	41	1		0.75	–6.434		0.599
			2	15.483	0.75	–3.940	–0.171	0.698 (0.682)
	N	41	1		0.75	–5.860		0.605
			2	16.203	0.75	–3.808	–0.141	0.687 (0.671)
Empirical	DM	41	1		0.572			0.553
			2		0.683		–0.254	0.795
			3	0.407	0.743	0.037	–0.165	0.833 (0.820)
	C	41	1		0.511			0.474
			2		0.652		–0.278	0.752
			3	1.066	0.740	0.048	–0.169	0.812 (0.797)
	N	41	1		0.576			0.532
			2		0.808	0.077		0.804
			3	2.217	0.793	0.051	–0.136	0.843 (0.830)
Ammonia excretion								
Theoretical	DM	22	1		0.75	–5.642		0.550
			2	11.911	0.75	–4.398		0.782 (0.760)
	C	22	1		0.75	–6.778		0.610
			2	16.628	0.75	–5.527		0.790 (0.768)
	N	22	1		0.75	–6.357		0.586
			2	16.769	0.75	–5.191		0.757 (0.731)
Empirical	DM	22	1		0.570			0.383
			2	–3.070	0.763	0.070		0.710 (0.679)
	C	22	1		0.452			0.260
			2	–2.668	0.762	0.084		0.674 (0.639)
	N	22	1		0.502			0.289
			2	–1.338	0.796	0.081		0.685 (0.652)

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Table 4. Spearman correlation coefficients (R) between body chemical components (water, ash, C, N and C:N) and body mass [ln DM (mg)], habitat temperature [T (^{o}C)], and mid-sampling depth [ln Depth (m)], of pelagic amphipods. DF = degree of freedom, * $p < 0.05$, ** $p < 0.01$, ^{NS} $p > 0.05$.

Chemical components	DF	R		
		ln DM	T	ln Depth
Water	16	-0.270^{NS}	0.267^{NS}	0.053^{NS}
Ash	15	-0.229^{NS}	0.539^{NS}	-0.230^{NS}
C	34	0.138^{NS}	–0.566**	0.463**
N	34	-0.251^{NS}	-0.247^{NS}	0.036^{NS}
CN	34	0.222^{NS}	-0.292^{NS}	0.398*

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 and ammonia excretion rates of pelagic amphipods. The a_3 was assessed as activation energy (E_a) of Arrhenius equation or Q_{10} of Van't Hoff rule on DM body mass. basis. Values in parentheses denote the range of 95% CI.

Amphipod species	Body mass effect		Temperature effect				Reference
	a_2	Range (mgDM)	E_a (eV)	Range (^oC)	Q_{10}	Range (^oC)	
Respiration rates							
Mixed (32 species)	0.743 (0.626–0.860)	1–344	0.26 (0.10–0.43)	–1.6 to 28	1.45 (1.11–1.88)	–1.6 to 28	This study
Cyphocaris challengeri	0.880 (0.795–0.965)	0.60–12.66					Yamada & Ikeda (2003)
Hyperia antarctica			0.64	0–10	2.64	0–5	Hirsche (1984)
					2.53	5–10	
Themisto gaudichaudii	0.924 (0.695–1.154)	<10					James & Wilkinson (1988)
Themisto gaudichaudii	0.70 (0.69–0.71)	12–72					Opalinski & Jazdzewski (1978)
Themisto gaudichaudii			0.44	0–10	1.96	0–5	Hirsche (1984)
					1.88	5–10	
Themisto japonica					2.69 (1.47–4.93)	1–12	Ikeda (1991)
Themisto japonica	0.771 (0.694–0.848)	0.33–14.21					Yamada & Ikeda (2003)
Themisto libellula					2.01	0–5	Percy (1993)
Themisto pacifica	0.947 (0.794–1.099)	0.21–3.50					Yamada & Ikeda (2003)
Primno abyssalis	1.003 (0.815–1.190)	0.31–11.46					Yamada & Ikeda (2003)
Ammonia excretion rates							
Mixed (19 species)	0.763 (0.677–0.925)	1–193	0.49 (0.28–0.69)	–1.6 to 28	2.01 (1.47–2.75)	–1.6 to 28	This study
Cyphocaris challengeri	1.292 (1.080–1.503)	0.60–12.66					Yamada & Ikeda (2003)
Themisto gaudichaudii	0.807 (0.726–0.889)	<10					James & Wilkinson (1988)
Themisto pacifica	1.366 (1.059–1.674)	0.21–3.50					Yamada & Ikeda (2003)
Themisto japonica	1.005 (0.902–1.108)	0.33–14.21					Yamada & Ikeda (2003)
Primno abyssalis	1.045 (0.787–1.303)	0.31–11.46					Yamada & Ikeda (2003)

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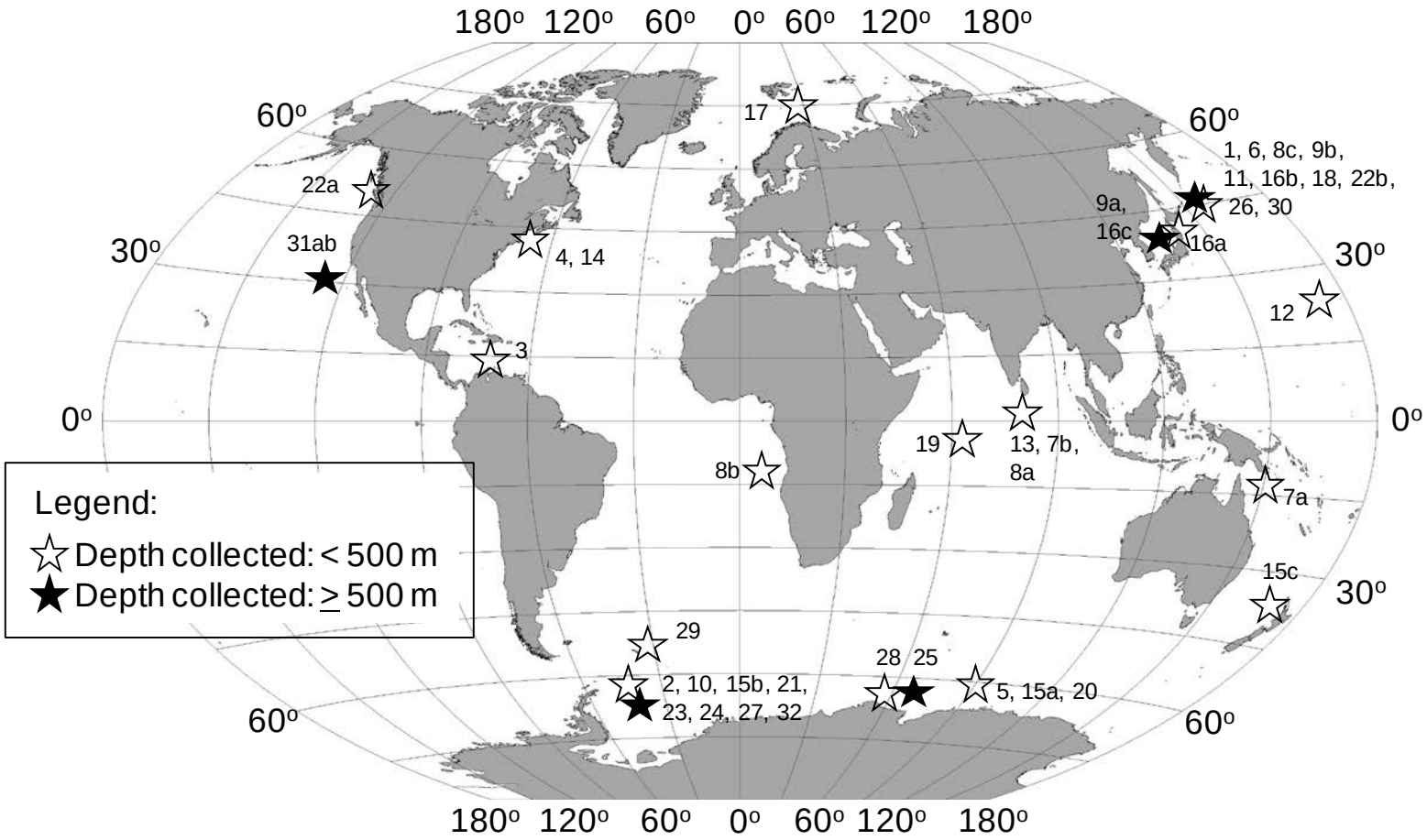

Ikeda Fig. 1

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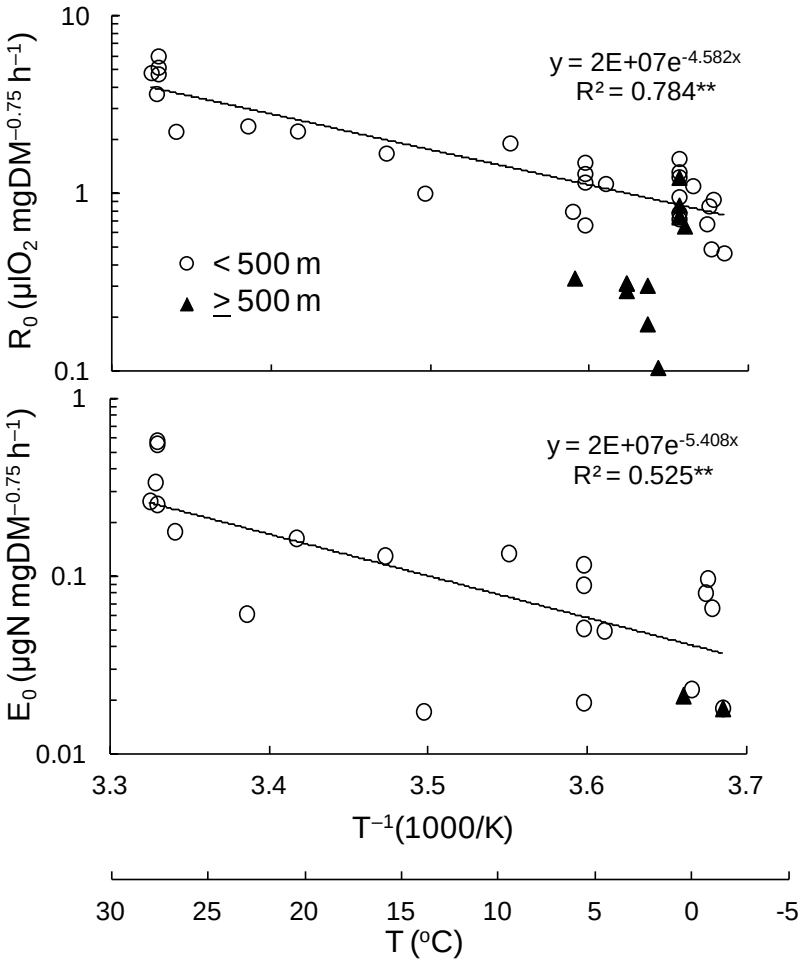
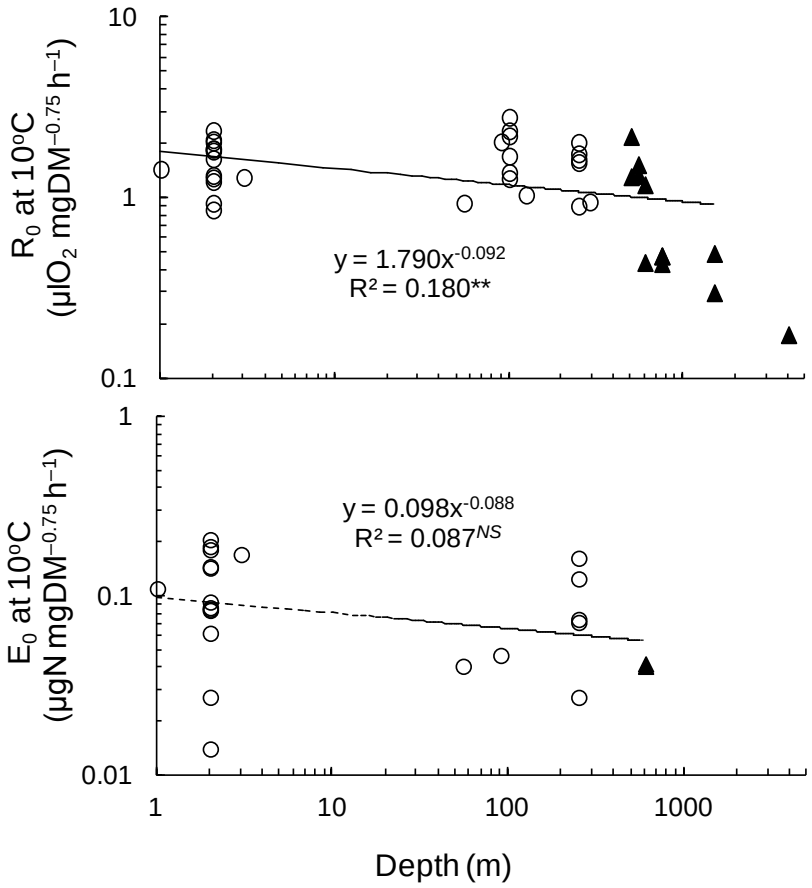
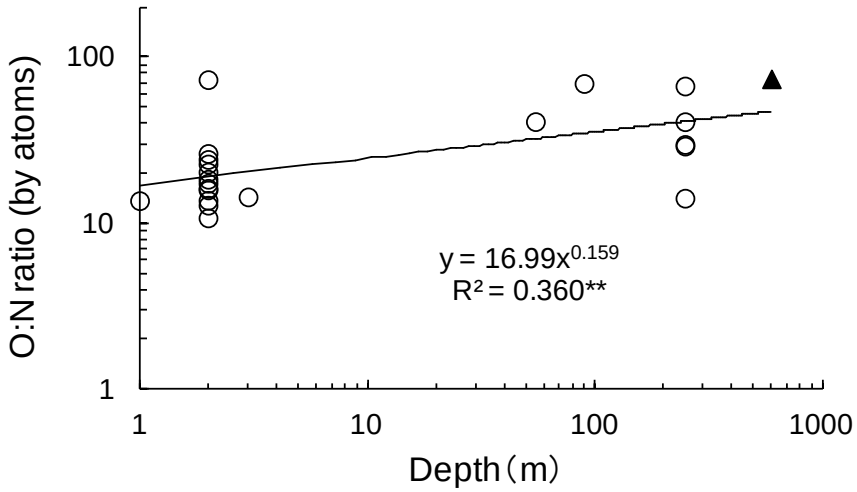

10
1
0.1
R_0 (μlO$_2$ mgDM$^{-0.75}$ h^{-1})
y = 2E+07e$^{-4.582x}$
R² = 0.784**
< 500 m
≥ 500 m
1
0.1
0.01
E_0 (μgN mgDM$^{-0.75}$ h^{-1})
y = 2E+07e$^{-5.408x}$
R² = 0.525**
3.3
3.4
3.5
3.6
3.7
T^{-1}(1000/K)
30
25
20
15
10
5
0
-5
T (°C)

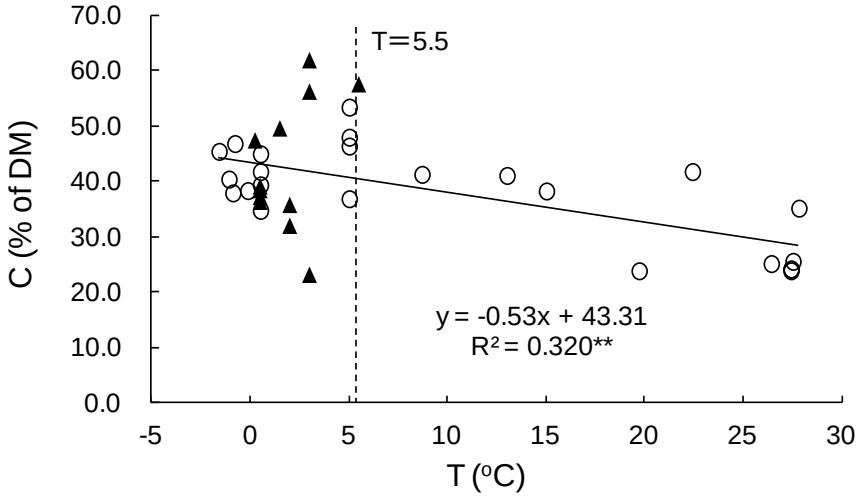
Ikeda Fig. 2


10
1
0.1
R_0 at 10°C
(µlO_2 mgDM$^{-0.75}$ h^{-1})
y = 1.790x$^{-0.092}$
R^2 = 0.180**
1
0.1
0.01
E_0 at 10°C
(µgN mgDM$^{-0.75}$ h^{-1})
y = 0.098x$^{-0.088}$
R^2 = 0.087^{NS}
1
10
100
1000
Depth (m)

Ikeda Fig. 3


O:N ratio (by atoms)
100
10
1
1
10
100
1000
Depth（m）
y = 16.99x^0.159
R² = 0.360**

Ikeda Fig. 4


70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
C (% of DM)
T=5.5
y = -0.53x + 43.31
R² = 0.320**
-5
0
5
10
15
20
25
30
T (°C)

Ikeda Fig. 5