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Metabolism and chemical composition of pelagic decapod shrimps: synthesis toward a global-bathymetric model

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Abstract

Respiration, ammonia excretion, chemical composition data [water content, ash, carbon (C), nitrogen (N) and C:N ratios] of 16–43 pelagic decapods from epipelagic through abyssopelagic zones of the world's oceans were compiled. For respiration, the independent variables including body dry mass, habitat temperature and sampling depth were all significant predictors of the empirical regression model, whereas the former two variables were significant predictors of the theoretical regression model. For ammonia excretion, body dry mass and habitat temperature were significant predictors of both regression models. Overall, these variables accounted for 68–87% of the variance in the data. Atomic O:N ratios (respiration : ammonia excretion) ranged from 9.1 to 91 (median: 16.4), and no appreciable effects of the three variables were detected. Body composition components were not significantly affected by the three variables, excepting positive effects of habitat temperature on ash and negative effects of sampling depth on N composition. As judged by C:N ratios, protein was considered to be the major organic component of most pelagic decapods. Some pelagic decapods from > 500 m depth exhibited high C:N ratios (8.6–10.2) suggesting a deposition of lipids in the body. Comparison of the present results with global-bathymetric models of euphausiids and mysids revealed great similarities among these pelagic crustacean taxa characterized by common behavioral and morphological features such as active swimming, developed compound eyes and respiratory gill organ.

1 Introduction

Pelagic decapods (shrimps) represent an important component of oceanic micronekton in midwater food webs linking zooplankton and large pelagic predators such as fish, cephalopods and cetaceans (Aizawa 1974; Omori 1974; Foxton and Roe 1974; Flock and Hopkins 1992; Hopkins et al. 1994). Many pelagic decapods living in 500–1000 m depth undertake diel vertical migrations (DVMs) (Foxton and Roe 1974; Kikuchi and Omori 1985; Flock and Hopkins 1992; Nishikawa et al. 2001), a behavior which is regarded as an important mechanism for the rapid vertical transport of materials in the pelagic realm of the ocean (Angel 1989; Hidaka et al. 2001).

Information about metabolism [respiration rates, ammonia excretion rates, and O:N (as NH_4-N) ratios] has proven to be useful in understanding the energy demand, major metabolic substrates and nutritional condition of marine zooplankton (cf. Ikeda et al. 2000). Although body mass and temperature have been regarded as the two major parameters for defining the metabolic characteristics of marine epipelagic animals (Ivleva 1980; Ikeda 1985), habitat depth has emerged as an additional parameter since metabolic rates decrease rapidly with depth for larger pelagic animals with image-forming eyes such as micronektonic fishes, crustaceans, and cephalopods, as a result from reduced selective pressure for high activities at depth (Childress 1995; Seibel and Drazen 2007). To date, the effect of habitat depth on respiration rates and O:N ratios of pelagic decapods has only been analyzed together with mysids, euphausiids and other crustacean taxa (Childress 1975; Quetin et al. 1980; Ikeda 1988; Torres et al. 1994); no analyses have been attempted for decapods as an individual taxon.

Chemical composition of the body of zooplankton in terms of carbon (C) and

nitrogen (N) composition on diverse taxa from tropical, subtropical, temperate and subarctic waters has been studied by Ikeda (1974). Båmstedt (1986) compiled voluminous data on proximate composition and elemental C and N of pelagic copepods from high, intermediate and low latitude seas and from surface and deep. With regard to the effect of habitat depth on proximate and/or C and N composition, Childress and Nygaard (1974) and Morris and Hopkins (1983) made comprehensive surveys on various pelagic crustaceans off Southern California and in the eastern Gulf of Mexico, respectively. Recently, Ikeda et al. (2006a) reported C and N composition of copepods living in the epipelagic through abyssopelagic zones in the subarctic Pacific. While all these results contributed to our better understanding of global-bathymetric characteristics of body chemical composition of copepods and other pelagic crustaceans, no comparable data is presently available for pelagic decapods.

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

2 Materials and methods

91 2.1 The data compilation

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

93 1. Data represented post-larvae (juveniles and adults) collected from the field and used

94 for experiments without considerable time delay (< 24 h) with exceptions of 2–3 days

95 delay (Cowles et al. 1990) or unspecified (Childress 1975).

96 2. Measurements were made in the absence of food at near *in situ* temperatures in the

97 dark [and at normal pressure (1 atm) for deep-sea decapods on the premise that the

98 hydrostatic pressure has little effect on the metabolic rates of deep-sea pelagic

99 crustaceans, cf. review of Ikeda et al. (2000)]. This practice, combined with the criterion

100 above, makes it possible to compare the data of various decapods for which information

101 about feeding conditions in the field prior to the experiments is not available. The

102 metabolic rate thus measured on pelagic animals at uncontrolled but minimum motor

103 activity is defined as “routine” metabolism (Ikeda et al. 2000). The data from *in situ*

104 incubations of a deep-sea decapod (*Acanthephyra eximia*) by means of autonomus

105 landers (Bailey et al. 2005) were assumed to be comparable to those from above

106 mentioned procedures.

107 3. O:N ratios were computed from simultaneous measurements of respiration rates and

108 ammonia excretion rates.

109 4. Body mass in terms of wet mass (WM), dry mass (DM), carbon (C) or nitrogen (N)

110 units were given together with metabolic data (note: body mass specific rates without

111 body mass data are not useful).

112 5. The depth of sampling of decapods was described or deducible.

113 6. Body composition (water content, ash, C and N) were derived with standard methods

114 (Omori and Ikeda 1984; Postel et al. 2000) together with the records of sampling depth

and body mass.

As a result, a total of 55 datasets on 43 decapods, and 17 datasets on16 decapods were selected in the present study, and analyzed for respiration and ammonia excretion rate, respectively (Table 1). The same decapods but from different locations or seasons were treated as independent data sets, though mere repetition of the data on the same decapods was carefully avoided. For body composition, 37 datasets of water content were available on 34 decapods, 36 datasets of ash on 32 decapods, and 18 datasets of C, N and C:N ratios on 17 decapods (Table 2). Missing habitat temperature data in some studies in Table 2 were substituted by data from the World Ocean Atlas of the National Oceanography Data Center (NODC) Homepage by the use of known location, season and depth. Study sites of all decapods are plotted on the world map (Fig. 1) to illustrate the worldwide coverage of the data sets in the present study.

2.2 Regression models for metabolism

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

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

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

where Y is respiration rate ($\mu l O_2$ ind.$^{-1}$ h^{-1}) or ammonia excretion rate ($\mu g N$ ind.$^{-1}$ h^{-1}), X_1 is body mass, X_2 is habitat temperature (K for the theoretical model, and ^{o}C for the empirical model), and X_3: is mid-sampling depth (m). As body mass, wet mass (WM)

139 or dry mass (DM) has been used almost exclusively for decapods in the literature. In
140 order to make between-taxa comparison of marine zooplankton with diversified body
141 composition possible, dry mass (DM) was used in the present analyses. For the data sets
142 in which body mass was reported as WM without information about water content, DM
143 was estimated assuming water content of 73.9% of WM (see “Chemical composition”
144 below). It is noted that a_1 was 0.75 (= 3/4, cf. Brown et al. 2004) and a_2 was $-Ea/k$ [k:
145 Bolzman’s constant (8.62×10^{-5} eV/K)] for the theoretical model. As indices of
146 temperature effects, *E*a of the theoretical model and Q_{10} of empirical model could be
147 computed as $Ea = a_2 \times 1000 \times 8.62 \times 10^{-5}$ and $Q_{10} = \exp(10 \times a_2)$, respectively. The
148 attributes of these variables were analyzed simultaneously by using stepwise multiple
149 regression (forward selection) method (Sokal and Rohlf 1995). Independent variables
150 were added and removed at the p = 0.05.The calculation was conducted using SYSTAT
151 version 10.2.
152
153 **3 Results**
154 3.1 Metabolic rates
155 Of the decapods considered in the present study, *Lucifer* sp. (0.014 mgDM) and
156 *Notostomus elegans* (5944 mgDM) were the smallest and largest species, respectively
157 (Table 2). Respiration rates at *in situ* temperature ranged from 1.9 μlO_2 ind.$^{-1}$ h^{-1}
158 (*Acanthephyra quadrispinosa*) to 677 μlO_2 ind.$^{-1}$ h^{-1} (*Notostomus elegans*), and
159 ammonia excretion rates from 0.036 μgN ind.$^{-1}$ h^{-1} (*Lucifer* sp.) to 15 μgN
160 ind.$^{-1}$ h^{-1}(*Acanthephyra curtirostris* off South California) (Table 2).
161 Prior to the stepwise multiple regression analyses, a preliminary analysis was
162 performed to test the effects of temperature and sampling depth on the rates of

163 respiration (R) and ammonia excretion (E) by first plotting the rates standardized to 1
164 mg DM ($R_0 = R \times DM^{-0.75}$ or $E_0 = E \times DM^{-0.75}$) against temperature (1000/K or ^oC)
165 where the scale coefficient of body mass was assumed as 0.75 (as in the theoretical
166 model) (Fig. 2). To facilitate the analysis, the data were separated into two groups
167 depending on the depth of decapods sampled (< 500 m and ≥ 500 m). Since the values
168 for species from ≥ 500 m depth distribute well below the rates < 500 m at equivalent
169 inverse temperature or temperature, only the data of < 500 m were used for the analysis
170 of temperature effects on R_0 or E_0. The resultant slope (–5.654 for respiration rates, and
171 –5.778 for ammonia excretion rates, Fig. 2) of the regression lines was used to compute
172 R_0 or E_0 at a given temperature (designated as 10°C) of the decapods from these
173 sampling depths (< 500 m + ≥ 500 m), which were plotted against the mid-sampling
174 depth (Fig. 3). The standardized rates (R_0 or E_0 at 10°C) of these decapods were
175 correlated negatively with the sampling depth ($p < 0.01$).
176 The overall results of stepwise multiple regressions for respiration rates showed
177 that the new variable X_3 (sampling depth) was significant for the empirical model ($p <$
178 0.001) but not for the theoretical model ($p = 0.991$) (Table 3). As an index of the
179 magnitude of multicolinearity among independent variables, the variation inflation
180 factors (VIF) of X_3 were computed as 1.681 for the empirical model. Since the VIF
181 value is < 5, multicolinearity between the variable (X_3) and others is considered to be
182 not serious (cf. Kutner et al. 2004). For ammonia excretion rates, the data for
183 *Systellapsis braueri* and *Lucifer* sp. were considered outliers and therefore omitted in
184 the following analyses. Furthermore, Pearson correlation matrix among the independent
185 variables for ammonia excretion indicated that X_2 (habitat temperature) and X_3 were
186 closely inter-related (correlation coefficient $R = 0.965$, $p < 0.001$). To avoid errors due

187 to multicolinearity, X_3 was removed for stepwise multiple regression of ammonia
188 excretion data. For ammonia excretion rates, X_1 and X_2 (empirical model) or X_2
189 (theoretical model) were highly significant. As judged by R^2 values, the empirical
190 model was superior to the theoretical model, accounting for 85.4–87.1% and
191 68.2–69.5%, respectively, of the variance in respiration and ammonia excretion (Table
192 3).
193 Thus, with regard to the effect of sampling depth for respiration rates, the results
194 from the multiple regression analyses were nearly identical to those of the simple
195 regression analyses (Figs. 2, 3) in which the rates standardized by body mass and
196 temperature (e.g., R_0 at 10^oC) were grouped based on single criteria (mid-sampling
197 depth). However, the effect of sampling depth on ammonia excretion rates was unable
198 to resolve by the multiple regression analyses in the present study because of its close
199 correlation with habitat temperature.
200
201 3.2 O:N ratios
202 A total of 15 O:N ratios from 14 decapods ranged from 9.1 (*Systellaspis cristata*)
203 to 91 (*Parapsdiphaea sulcatifrons*) (Table 2). A scatter diagram of the O:N ratios and
204 habitat temperature is shown in Fig. 5. Simple correlation analyses indicated that none
205 of the three independent variables was significantly correlated with the O:N ratios
206 (Pearson correlation coefficients > 0.50). Mean and median O:N ratio were 24.3 (± 20.8,
207 SD) and 16.4, respectively.
208
209 3.3 Chemical composition
210 Water content varied from 63.8 to 91.3% of WM (mean; 73.9), and ash from 4.8 to

25.0% of DM (13.7), C from 32.9 to 60.6% of DM (46.1), N from 5.9 to 12.1of DM (8.6), C:N ratios from 3.5 to 10.2 (5.7). Simple correlation analyses between these chemical components and designated parameters [mid-sampling depth, body mass (DM) and habitat temperature] revealed that habitat temperature and sampling depth were significant parameters affecting ash and N composition, respectively, but none of the parameters significantly affected water content, C composition and C:N ratios (Table 4). The scatter diagram of N composition and sampling depth is showed in Fig. 5.

4 Discussion

4.1 Body mass and temperature as traditional parameters

The effects of DM mass on respiration rates of pelagic decapods have been little studied, and the only information presently available is for *Pasiphaea scotiae* from the Weddell Sea, Antarctica (Donnelly et al. 2004). Since the scale coefficient of DM mass of *P. scotiae* was derived from fewer data sets (N = 6), the comparison with the present results from interspecific data sets (N = 55) may not be meaningful (Table 5). Taking into account a wide 95% CI (0.766–0.978), the mean scale coefficient of body DM of pelagic decapods (0.872) is similar to or less than those of global-bathymetric models for zooplankton taxa; e.g. 0.750 for copepods (Ikeda et al. 2007), 0.833 for chaetognaths (Ikeda and Takahashi 2012), 0.753 for euphausiids (Ikeda 2013a), 0.743 for pelagic amphipods (Ikeda 2013b) and 0.755 for mysids (Ikeda 2013c). The scale coefficient of DM mass is highly sensitive to the magnitude of the ranges of DM mass analyzed. In this light, the DM mass ranges of these zooplankton taxa are nearly comparable to each other (3–5 orders of magnitude). The scale exponents have been reported as 0.55–0.95

235 for diverse animal phyla (Prosser 1961).

236 The effect of temperature on metabolism in terms of activation energy (*E*a)
237 derived from the theoretical model established in the present study (Table 3) is 0.755 eV
238 (95% CI = 0.615–0.895) for respiration rates and 0.572eV (0.356–0.787) for ammonia
239 excretion rates, both of which partially overlap the theoretical value (0.6–0.7eV, cf.
240 Brown et al. 2004). Temperature effects on respiration rates have been studied
241 exclusively in terms of Q_{10} in individual decapod species at graded temperatures within
242 the range of those occurring in their natural habitats (Table 5). According to the
243 definition by Clarke (1987), this is “acclimation” (adjustment of an organism to a new
244 temperature in the laboratory), in contrast to “adaptation” (the evolutionary adjustment
245 of an organism’s physiology to environment). Acclimated Q_{10} is interpreted as
246 reflecting the acute thermodynamic effect of temperature, adapted Q_{10} as an
247 evolutionary optimization of each species, and acclimated Q_{10} > adapted Q_{10} (the
248 evolutionary trade-off hypothesis, Clarke and Fraser 2004). From this view, acclimated
249 Q_{10} values for individual pelagic decapods are 1.8–3.8, with most values between 2.0
250 and 3.0, within which adapted Q_{10} values (2.7) derived from the global-bathymetric
251 model of the pelagic decapods of the present study fall. The evolutionary trade-off
252 hypothesis characterized by adapted Q_{10} < 2.0 has been supported by the global
253 compilation of the data of teleost fishes (1.8, Clarke and Johnston 1999), pelagic
254 copepods (1.9, Ikeda et al. 2007), chaetognaths (1.7, Ikeda and Takahashi 2012),
255 euphausiids (1.7, Ikeda 2013a) and pelagic amphipods (1.5, Ikeda 2013b), but this is not
256 the case for mysids (2.1, Ikeda 2013c) and the pelagic decapods (2.7, this study). The
257 large scatter in the data of the pelagic decapods is evidenced by the relationship between
258 respiration rates standardized to a body mass of 1 mg DM and habitat temperature [R^2 =

259 0.612 (Fig. 2, this study) as compared with R^2 = 0.804 for the copepods (Fig. 2A, Ikeda
260 et al. 2007), 0.882 for chaetognaths (Fig. 2, Ikeda and Takahashi 2012), 0.833 for
261 euphausiids (Ikeda 2013a) and 0.784 for pelagic amphipods (Ikeda 2013b)] may partly
262 be responsible for a discrepancy between the pelagic decapods and the other pelagic
263 animals.
264
265 4.2 Habitat (sampling) depth as a new parameter
266 The present results from the empirical model (Table 3) demonstrate depression
267 effects of habitat depth on respiration rates of pelagic decapods to those of larger
268 pelagic animals with image-forming eyes such as micronektonic crustaceans,
269 cephalopods and fishes (Torres et al. 1994; Childress 1995; Seibel and Drazen 2007),
270 and zooplankton with no such eyes including copepods (Ikeda et al. 2006, 2007) and
271 chaetognaths (Kruse et al. 2010; Ikeda and Takahashi 2012). Two explanations have
272 been proposed for the progressive decline in respiration rates in deeper-living
273 micronekton and zooplankton; the “visual-interactions hypothesis” (Childress 1995) and
274 the “predation-mediated selection hypothesis” (Ikeda et al. 2006b). These two
275 hypotheses are similar in that both interpret the phenomenon as a result of lowered
276 selective pressure for high activity at depth because of the decrease in visual predators
277 in the dark. However, these two hypotheses are different in that the former applies
278 strictly to micronekton with functional eyes, and the latter to both micronekton and
279 zooplankton irrespective of presence/absence of functional eyes.
280 Torres et al. (1994) compiled the relationship between respiration rates and the
281 depth of occurrence for pelagic crustaceans (amphipods, decapods, euphausiids, isopods,
282 mysids and ostracods) off California, the Gulf of Mexico, off Hawaii and Antarctic

283 waters. According to their results, the respiration rates [standardized to a body size of 1
284 mg wet mass by using the body mass exponent of 0.75 (equivalent to the theoretical
285 model adopted in the present study), and at 0.5^{o}C by assuming Q_{10} = 2.0)], the
286 reduction in the rates of a specimen due to the increase of its habitat depth from 1 m to
287 1000 m depth is in the order of 0.1–0.5 times. Similar calculations for pelagic decapods
288 based on the present results (the empirical model in Table 3) showed that the reduction
289 was 0.4 times, which is close to the upper range of the values for the mixed crustacean
290 taxa by Torres et al. (1994).
291
292 4.3 Ammonia excretion and O:N ratios
293 While no global-bathymetric model is presently available for ammonia excretion
294 rates of pelagic decapods, global ammonia excretion models with two parameters (body
295 mass, habitat temperature) for mixed epipelagic zooplankton taxa (Ikeda 1985) and for
296 epipelagic copepods (Ikeda et al. 2001) yielded a body mass exponent and Q_{10} similar
297 to those for respiration rates. With regard to the effect of habitat depth, lowered
298 ammonia excretion rates have already been reported on some deeper-living decapods
299 species off Southern California (Quetin et al. 1980) and Pridz Bay, Antarctica (Ikeda
300 1988). In the present study, regression analyses of ammonia excretion rates on body
301 mass, habitat temperature and sampling depth for the pelagic decapods were not
302 amenable due to close inter-correlation of sampling depth with habitat temperature
303 (Table 3). Considering the large scatter of ammonia excretion data evident in the
304 presence of outliers (two data), the number of data sets (N = 15) available to the present
305 analyses was too few to build a robust model. While further investigations are needed to
306 prove a likely parallel change in respiration and ammonia excretion rates in pelagic

307 decapods, O:N ratios were observed to be rather stable across the 14 pelagic decapods
308 considered in this study (median: 16.4). Insignificant effects of body mass and habitat
309 temperature on O:N ratios have already been reported on mixed epipelagic zooplankton
310 taxa (Ikeda 1985) and epipelagic copepods (Ikeda et al. 2001).
311 The atomic ratio of oxygen consumption rate to ammonia-nitrogen excretion rate
312 (O:N ratio) has been used as an index of the proportion of protein in the diet of marine
313 zooplankton (Mayzaud and Conover 1988; Ikeda et al. 2000). When only protein is
314 metabolized, the O:N ratio is 7 (Table 10.3 in Ikeda et al. 2000). When protein and lipid
315 or carbohydrate are catabolized in equal quantities O:N ratios are calculated as 21 or 13,
316 respectively (mid-point: 17). Hence, O:N ratios of 7–17 may be used as an index of
317 protein-oriented metabolism and ratios of >17 as lipid/carbohydrate-oriented
318 metabolism. The high metabolic O:N ratios (median; 16.4) of pelagic decapods favor
319 protein-oriented metabolism on average. It is noted that the O:N ratios of pelagic
320 decapods listed in Table 2 are derived from experiments in which they were placed in
321 filtered seawater, a common practice when using the sealed-chamber method (Ikeda et
322 al. 2000). The use of filtered seawater is imperative to determine the rates of respiration
323 and ammonia excretion accurately without any corrections for complex uptake/release
324 of oxygen and ammonia by food organisms, but starvation of decapods may influence
325 their normal metabolism. While no data are presently available for pelagic decapods,
326 Ikeda and Dixon (1984) examined the effect of methodological problems associated
327 with the sealed chamber method on the euphausiid *Euphausia superba*. According to
328 their results, respiration and ammonia excretion rates of wild *E. superba,* in which daily
329 ration is 5%, are 1.6 and 4.5 times the rates of non-feeding krill in 24 h laboratory
330 experiments. From these results, the O:N ratios of wild *E. superba* are calculated as

331 0.36 (= 1.6/4.5) times those of the non-feeding *E. superba*. Generalization of the results
332 of *E. superba* to pelagic decapods requires caution since no comparable data are
333 available for the other pelagic crustaceans.
334
335 4.4 Chemical composition
336 Among pelagic crustacean taxa, global-bathymetric features of body chemical
337 composition (water content, ash, C, N and C:N) have been well documented for pelagic
338 copepods (Ikeda 1974; Båmstedt 1986; Ikeda et al. 2004, 2006b), and can be
339 summarized as follows; first, most species from cold thermal regimes (high latitude seas
340 and deep sea) are characterized by the accumulation of lipids which reflects higher C
341 and lower N composition (thus leading to higher C:N) as compared with counterparts
342 from warm thermal regimes (low latitude seas); second, shallow and deep-sea species at
343 higher latitudes are similar in that both exhibit high C composition but different in that
344 the latter exhibit much reduced N composition (reduced protein or musculature); and
345 third, lipid or C-rich species are often accompanied by correspondingly low water
346 content and ash content. Depth-related reduction in protein has also been reported on
347 mixed pelagic crustacean taxa (Morris and Hopkins 1983; Childress and Nygaard
348 1974).
349 The present results for pelagic decapods (Table 4) showed that the effects of
350 habitat temperature and sampling depth on C and N composition and C:N ratios were
351 similar to those of copepods mentioned above. However, the effect of sampling depth

352 was significant only for N composition ($p < 0.05$) and the effect of habitat temperature
353 was less pronounced ($p = 0.277$ for C, $p = 0.212$ for N and $p = 0.199$ for C:N). Positive
354 correlations between habitat temperature and water content and ash are also in line with
355 those of copepods, though the correlation between habitat temperature and water
356 content was not significant ($p > 0.5$).
357 Analyzing chemical composition data on 182 zooplankton species (mostly
358 crustaceans), Ventura (2006) calculated average C and N composition of protein to be
359 52.8% and 16.0%, and lipids (represented by wax esters) to be 81.0% and 0%. With
360 these results, the C:N ratio is calculated as 3.3 for protein alone and 8.4 for organic
361 matter composed of equal amounts of protein and lipid. Carbohydrate in zooplankton
362 has been reported to be < 8.5% of DM (Ventura 2006) and is therefore omitted in this
363 calculation. Then, C:N ratios of 3.3–8.4 and > 8.4 can be used as indices of protein- and
364 lipid-dominated composition, respectively, for zooplankton. On this basis, body C:N
365 ratios of most of the pelagic decapods were 3.5 to 10.2 (mean = 5.7, Table 4), indicating
366 protein-dominated composition. As exceptions, the two mesopelagic decapods exhibited
367 C:N ratios beyond the range (8.6 and 9.8 for *Hymenodora frontalis* off Southern
368 California and the western subarctic Pacific, and 10.2 for *Pasiphaea scotiae* from Prydz
369 Bay, Antarctica, Table 2), indicating lipid dominated composition. Little has been
370 studied on the function of lipids in pelagic decapods. For copepods and euphausiids, the
371 function of large lipid deposits (mostly as wax esters, triacylglycerols or phospholipids)
372 is considered to be an energy reserve for coping with temporal food scarcity and

reproduction, or to save energy for swimming by achieving neutral buoyancy (Lee et al. 2006).

4.5 Pelagic decapods as compared with euphausiids and mysids

The global-bathymetric model for pelagic decapods derived from the present study was compared with those of euphausiids and mysids (Table 6). For a specimen with similar body mass (1 mg N) living in the epipelagic zone (100 m depth) of temperate latitudes (20^{o}C), predicted respiration rates from the theoretical or empirical model of decapods (23.7 or 16.5 μlO_2 ind.$^{-1}$ h^{-1}) are somewhat different from those of euphausiids (13.1 or 13.0 μlO_2 ind.$^{-1}$ h^{-1}) and mysids (15.0 or 14.4 μlO_2 ind.$^{-1}$ h^{-1}). However, the difference would not be significant if one takes into account the wide 95% CIs of the estimates of the decapods. Taxon-specific respiration rates are less marked for the specimen living in the bathypelagic zone (1000 m, 5^{o}C). The results may be regarded as reasonable, since all of them are active swimmers with well developed compound eyes and respiratory organs (gills). Large standard deviations (SD) associated with the mean O:N ratios of the three taxa suggest non-normal distribution of the O:N data. Thus, the medians rather than means are thought to provide better index of the central trend. The median O:N ratio of the decapods (16.4) is less than those (18.7–27.1) of euphausiids and mysids, possibly reflecting increased importance of protein-oriented metabolism in decapods (omnivores or carnivores) as compared with lipids or carbohydrate-oriented metabolism in euphausiids and mysids (herbivores, omnivores or carnivores (see the Chapter 4.3 “Ammonia excretion and O:N ratios” above).

With regard to chemical composition of the body, the decapods are similar to

mysids rather than euphausiids in terms of C and N composition (Table 6). Compared with euphausiids, somewhat higher C composition and lower N composition, which is reflected in their higher C:N ratios, suggest a larger capacity in lipid storage in the body of the two taxa. Water content component exhibited taxon-specific differences among decapods, euphausiids and mysids. Nevertheless, these differences in C and N composition and water content are too small to regard as unique features of pelagic decapods.

Ash content is the only component for which taxon-specific differences were not seen. The ecological implication of ash (or ash-free DM or energy content) has been explored in conjunction with adaptive traits for planktonic versus benthic life, and the former is considered to be characterized by increased energy content (or decreased ash level) to cope with patchy food resources in time or space as well as on an evolutionary scale (Norrbin and Båmstedt 1984). In support of this view, the overall range of ash content of pelagic decapods, eupahusiids and mysids (12.9–13.6%) is much less than with those of benthic crustaceans (36–53%, Norrbin and Båmstedt 1984, Company and Sardà 1998).

In conclusion, global-bathymetric models designed in the present study could explain 68–85% of the variance in respiration rates and 70–87% of the variance in ammonia excretion rates. The O:N ratios of the pelagic decapods suggested relative importance of protein rather than lipid and/or carbohydrate rather during short-term starvation. As components of body chemical composition, significant positive effects of habitat temperature on ash and significant negative effects of sampling depth on N composition were seen. As judged by body C:N ratios, protein was the major organic component of the body of most pelagic decapods (C:N = 3.5–7.8). However, some

pelagic decapods from > 500 m depth exhibited high C:N ratios (8.6–10.2) indicating a deposition of C-rich organic matter (lipids) in the body. Overall global-bathymetric features of pelagic decapods discussed above are very similar to those of euphausiids and mysids, all of which are phylogenetically close (belonging to the same class Malacotraca), and active swimmers with developed functional eyes and respiratory gill organ..

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605 **Figure captions**

606 Fig. 1. Study sites of metabolic rates and chemical composition of pelagic decapods.
607 The number and associated character alongside the symbol correspond to the code of
608 each decapod listed in Table 1.

609 Fig. 2. Relationship between the respiration rate (top) or ammonia excretion rate
610 (bottom) standardized to a body size of 1 mg body DM (R_0 or E_0) and temperature
611 (T^{-1}: 1000/K, or T: ^{o}C) of pelagic decapods from shallow (< 500 m) and deep layers
612 (≥ 500 m). The data points represent means from the data sets in Table 2, and the
613 regression line is derived from shallow layer species only. * $p < 0.05$, ** $p < 0.01$.

614 Fig. 3. Relationship between respiration rates (top) or ammonia excretion rates (bottom)
615 standardized to a body size of 1 mgDM (R_0 or E_0) at 10°C of pelagic decapods and
616 mid-sampling depth. The data points represent means derived from the data sets in
617 Table 2. Open circles and closed triangles denote the data of the species from shallow
618 (< 500 m) and deep layers (≥ 500 m), respectively. ** $p < 0.01$.

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

623 Fig. 5. Relationship between N composition of pelagic decapods and sampling depth
624 from various regions of the world's oceans. The data points represent the data sets in
625 Table 2. Open circles and closed triangles denote the data of the species from shallow
626 (< 500 m) and deep layers (≥ 500 m), respectively. ** $p < 0.01$.

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

Order	Species	Code	Collection site	Date	Reference
Caridea	*Acanthephyra acutifrons*	1	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Acanthephyra curitirostris	2a	Off S. California	1976–1977	Quetin et al. (1980)
	Acanthephyra curtirostris	2b	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Acanthephyra curtirostris	2c	Off S. California	1969–1972	Childress (1975)
	Acanthephyra eximia	3	E. Mediterranean	Jun 2002	Bailey et al. (2005)
	Acanthephyra purpurea	4a	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Acanthephyra purpurea	4b	Off Bermuda/Sargasso Sea	?	Teal (1971)
	Acanthephyra quadrispinosa	5	W. subarctic Pacific Ocean	Mar 2005	Ikeda (2012)
	Acanthephyra smithi	6	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Hymenodora frontalis	7a	Off S. California	1976–1977	Quetin et al. (1980)
	Hymenodora frontalis	7b	W. subarctic Pacific Ocean	2002–2005	Ikeda (2012)
	Hymenodora frontalis	7c	Off S. California	1969–1972	Childress (1975)
	Janicella spinicauda	8	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Nematocarcinus lanceopes	9	Weddell Sea, Antarctica	Nov–Dec 1993	Donnelly et al. (2004)
	Notostomus elegans	10	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Notostomus gibbosus	11	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Notostomus sp.	12	Off S. California	1969–1972	Childress (1975)
	Oplophorus gracilirostris	13a	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Oplophorus gracilirostris	13b	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Oplophorus spinosus	14a	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Oplophorus spinosus	14b	Off Bermuda/Sargasso Sea	?	Teal (1971)
	Parapandalus richardi	15a	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Parapandalus richardi	15b	Off Bermuda/Sargasso Sea	?	Teal (1971)
	Parapasiphaea sulcatifrons	16	Off S. California	1976–1977	Quetin et al. (1980)
	Pasiphaea chacei	17a	Off S. California	1976–1977	Quetin et al. (1980)
	Pasiphaea chacei	17b	Off S. California	1969–1972	Childress (1975)
	Pasiphaea emarginata	18a	Off S. California	1976–1977	Quetin et al. (1980)
	Pasiphaea emarginata	18b	Off S. California	1969–1972	Childress (1975)
	Pasiphaea japonica	19	Toyama Bay, S. Japan Sea	Dec 1991	Ikeda, unpublished data
	Pasiphaea multidentata	20	Kosterfjorden, W. Sweden	Neritic	Båmstedt (1979)
	Pasiphaea scotiae	21a	Prydz Bay, Antarctica	Jan 1985	Ikeda (1988)
	Pasiphaea scotiae	21b	Weddell Sea, Antarctica	Nov–Dec 1993	Donnelly et al. (2004)
	Systellaspis braueri	22	Off S. California	1976–1977	Quetin et al. (1980)
	Systellaspis cristata	23a	Off S. California	1976–1977	Quetin et al. (1980)
	Systellaspis cristata	23b	Off S. California	1969–1972	Childress (1975)
	Systellaspis debilis	24a	Off W Africa	Aug 1983	Davenport & Trueman (1985)
	Systellaspis debilis	24b	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Systellaspis debilis	24c	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Systellaspis debilis	24d	Off Bermuda/Sargasso Sea	?	Teal (1971)
Penaeroidea	*Funchalia villosa*	25	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Gennadas capensis	26	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Gennadas kempi	27a	Weddell Sea, Antarctica	Nov–Dec 1993	Donnelly et al. (2004)
	Gennadas kempi/Petalidium foliaceum	27b	Prydz Bay, Antarctica	Jan 1985	Ikeda (1988)
	Gennadas propinquus	28a	Off S. California	1976–1977	Quetin et al. (1980)
	Gennadas propinquus	28b	Off S. California	1969–1972	Childress (1975)
	Gennadas scutatus	29	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Gennadas valens	30	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
Sergestoidea	*Acetes sibogae australis*	31a	N Queensland coast, Australia	May 1978	Ikeda and Skjoldal (1980)
	Acetes sibogae australis	31b	N Queensland coast, Australia	Feb 2010	Ikeda and McKinnon (2012)
	Eusergestes similis (formerly *Sergestes similis*)	32a	Off S. California	1976–1977	Quetin et al. (1980)
	Eusergestes similis (formerly *Sergestes similis*)	32b	Off Oregon, USA	Mar 1966, Jan–Feb 1967	Pearcy and Small (1968)
	Eusergestes similis	32c	W. subarctic Pacific Ocean	Mar 2006	Ikeda, unpublished data
	Lucifer faxoni	33	E. Gulf of Mexico	Summer 1978	Morris and Hopkins (1983)
	Lucifer typus (formerly *L. reynaudii)*	34	W. North Pacific Ocean	Sept 1967	Omori (1969)
	Lucifer sp.	35	N Queensland coast, Australia	Feb 1977	Ikeda et al. (1982)
	Parasergestes armatus (formerly *Sergestes armatus*)	36	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Petalidium foliaceum	37	Weddell Sea, Antarctica	Nov–Dec 1993	Donnelly et al. (2004)
	Seosergestes corniculum (formerly *Sergestes corniculum*)	38	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Sergestes atlanticus	39	Coral Sea	Nov 2009	Ikeda and McKinnon (2012)
	Sergia bisulcata (formerly *Sergestes bisulcatus*)	40	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Sergia splendens (formerly *Sergestes crassus*)	41	Off Bermuda/Sargasso Sea	?	Teal (1971)
	Sergia fulgens (formerly *Sergestes fulgens*)	42	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Sergia phorca (formerly *Sergestes phorcus*)	43a	Off S. California	1976–1977	Quetin et al. (1980)
	Sergia phorca (formerly *Sergestes phorcus*)	43b	Off S. California	1969–1972	Childress (1975)
	Sergia tenuiremis (formerly *Sergestes tenuiremis*)	44	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
	Sergestes tenuroides	45	Off S. California	1976–1977	Quetin et al. (1980)
	Sergia grandis	46	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Sergia robusta (formerly *S. robustus*)	47	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Sergia splendens	48	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
	Sergia talismani	49	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly and Torres (1988)
Galatheidae	*Pleuroncodes planipes*	50	Off S. California	1969–1972	Childress (1975)

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 pelagic decapods. For species codes, see Table 1. *Italic* values for sampling depth were those not described, and estimated for the present analyses. For body mass data given as WM only, DM was computed by using a grand mean water content of other pelagic decapods (73.3% of WM). Blank = no data.

Species	Mid-sampling depth (range)	T		Body mass	Respiration rate	Ammonia excretion rate	O:N ratio	Body chemical composition				
								Water	Ash	C	N	C:N
Code	(m)	(°C)	N	(mg DM ind.$^{-1}$)	(μlO_2 ind.$^{-1}$h^{-1})	(μgN ind.$^{-1}$h^{-1})	(by atoms)	(% of WM)	(% of DM)	(% of DM)	(% of DM)	(by mass)
1	*650*	5	6	2278[a]	321.3 ± 67.7							
2a	600 (400–800)	5.5	10	840 ± 310		15.2 ± 2.4	14.9 ± 3.1[c]					
2b	*650*	5	10	604[a]	93.4 ± 12.8							
2c	650	5.5	9	651	98.0 ± 14.6			75.9	13.6	43.0	8.5	5.1
3	4200	14.5		786[a]	230							
4a	*300*	14	1	367	277 ± 85			73.6	20.4			
4b	*200*	10	7	448[a]	179							
5	1000	2.5	2	8.29	1.9 ± 1.2			74.3	4.8	51.2	8.0	6.4
6	*200*	10	13	1013[a]	404 ± 46							
7a	600 (400–800)	5.5	8	400 ± 40		3.21 ± 0.44	12.2[c]					
7b	750	3	3	22.8	2.3 ± 0.7			70.4	6.7	60.6	6.2	9.8
7c	650	5.5	4	290	18.6 ± 1.8			63.8	6.7	50.6	5.9	8.6
8	*200*	10	3	92.3[a]	39.6 ± 10.9							
9	*1*	0.5	3	68.5 ± 5.2	22.5 ± 12.3			77.8	14.0			
10	*650*	5	9	5944[a]	677 ± 81							
11	*650*	5	12	2742[a]	112 ± 9							
12	1100	4	1	800	54.3			91.3	15.3	32.9	7.8	4.2
13a	*100*	20	5	613	609 ± 167			69.5	19			
13b	*200*	10	6	681[a]	614 ± 81							
14a	*200*	10	5	770[a]	332 ± 105							
14b	*200*	10	9	105[a]	68							
15a	*200*	17	1	82.9	69.6 ± 2.8			70.8	17.3			
15b	*200*	10	8	52.7[a]	48							
16	600 (400–800)	5.5	6	520 ± 110		0.75 ± 0.13	91.0 ± 19.1[c]					
17a	*100*	5.5	24	340 ± 20		7.13 ± 0.78	17.3 ± 1.7[c]					
17b	200	7.5	3	195	106 ± 10			79.5	15.3	38.9	10.1	3.9
18a	600 (400–800)	5.5	18	790 ± 100		3.81 ± 0.43	21.4 ± 2.9[c]					
18b	650	5.5	6	116.5	10.3 ± 1.3			76.7	14.7	45.1	7.7	5.9
19	250 (0–500)	2	2	164 ± 24				75.6	14.8	41.7	11.3	3.7
20	100 (0–200)	5.5	7	56.16	21.3							
21a	600 (200–1000)	0.2	9	265 ± 136	36.4 ± 22.1	2.43 ± 1.50	32.5 ± 38.5[median: 21.4]	68.0	7.5	59.6	5.9	10.2
21b	100	0.5	6	957 ± 252	99.5 ± 38.1			67.3	7.6			
22	600 (400–800)	5.5	1	360		1.05						
23a	600 (400–800)	5.5	10	740 ± 120		10.2 ± 1.6	9.1 ± 1.2[c]					
23b	1100	5.5	4	884	107 ± 8			72.8	10.7	50.5	6.5	7.8
24a	200	18		353	533				18.0			
24b	*300*	14	3	318	174 ± 39			71.6	15.2			
24c	*200*	10	9	321[a]	118 ± 15							
24d	*200*	10	9	210[a]	72							
25	*100*	20	6	565	453 ± 106			72.9	13.4			
26	*700*	7	2	86.1	26.0 ± 0.3			67.5				
27a	500	0.5	2	561 ± 118	68.0 ± 1.8			69.5	10.9			
27b	600 (200–1000)	0.2	17	339 ± 144	48.2 ± 20.8	3.85 ± 2.11	19.3 ± 9.7[median: 15.5]	70.1	7.5	58.1	7.7	7.5
28a	600 (400–800)	5.5	14	140 ± 10		7.41 ± 1.15	10.3 ± 0.7[c]					
28b	650	5.5	4	140	16.4 ± 2.0			76.7	9.7	46.3	8.8	5.2
29	*100*	20	1	127	110 ± 9			75.2	16.2			
30	*300*	14	5	131	73.2 ± 13.9			75.5	14.3			
31a	1	24.5	6	6.49[b]	22.9 ± 8.2	1.22 ± 0.31	24.7 ± 5.2					
31b	1	30	8	26.7 ± 5.6	99.6 ± 20.9	2.80 ± 0.90	46.1 ± 10.4	75.8	13.3	42.4	12.1	3.5
32a	*100*	5.5	5	110 ± 5		3.10 ± 0.59	33 ± 4.8[c]					
32b	100	10	36	74	91.0 ± 32.6							
32c	100 (0–200)	2	1	85 ± 21				73.7	13.0	50.4	10.4	4.8
33	50	24	2	0.2				80.1	18.4			
34	50 (0–100)	25		0.16				86.7		41.1	9.3	4.4
35	1	28.5	11	0.0135 ± 0.0010		0.036 ± 0.010						
36	*300*	14	1	8.0	6.3 ± 1.0			72.3	15.1			
37	500	0.5	1	248	19.8			68.7	8.3			
38	*100*	20	1	86.9	48.3 ± 12.2			69.4	10.7			
39	1	27.5	3	23.5 ± 9.2	58.5 ± 12.3	5.40 ± 2.10	14.6 ± 5.0	73.1	16.2	40.1	10.9	3.7
40	*200*	10	5	670[a]	265 ± 68							
41	*200*	10	9	79.1[a]	46.5							
42	*200*	10	4	280[a]	163 ± 32							
43a	600 (400–800)	5.5	20	500 ± 30		13.5 ± 1.5	12.9 ± 0.8[c]					
43b	650	5.5	4	664	69.3 ± 8.6			77.5	13.8	42.8	10.3	4.1
44	*650*	5	4	688[a]	87.7 ± 14.0							
45	600 (400–800)	5.5	2	210 ± 80		3.81 ± 0.88	22.8 ± 2.1[c]					
46	*300*	14	1	170	113 ± 26			76.2	18.1			
47	*300*	14	5	409	284 ± 52			75.0	17.9			
48	*300*	14	1	84.1	53.5 ± 6.3			70.6	14.6			
49	*100*	20	3	51.1	53.1 ± 5.7			74.7	15.4			
50	200	15	1	812	330			75.4	25.0	34.9	7.3	4.8

[a] Converted from WM assuming water content of 73.9% (see Table 4).

[b] Converted from protein assuming a protein: DM ratio for subtropical pelagic decapods to be 0.432:1(Morris and Hopkins 1983)

[c] Data from separate experiments on the same species

Table 3. Stepwise (forward selection, $p_{in} = p_{out} = 0.05$) multiple regression statistics of theoretical and empirical models of respiration rates or ammonia excretion rates (Y: µl O_2 ind.$^{-1}$h^{-1} or µg N ind.$^{-1}$h^{-1}) of pelagic decapods on body mass (X_1: mgDM ind.$^{-1}$), habitat temperature (X_2: re-defined as 1000/K for the former, ^{o}C for the latter) and depth sampled (X_3: m).

Regression model	N	Step No.	Regression equation: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3$				R^2 (adjusted R^2)	F-ratio	df	p
			a_0	a_1	a_2	a_3				
Respiration										
Theoretical	55	1	31.257	0.75	–8.758		0.688 (0.682)	116.91	1, 53	< 0.001
Empirical	55	1		0.64			0.515			
		2		0.828	0.112		0.847			
		3	–0.718	0.872	0.099	–0.119	0.862 (0.854)	106.15	3, 51	< 0.001
Ammonia excretion										
Theoretical	15	1	21.214	0.75	–6.632		0.717 (0.695)	32.91	1, 13	< 0.001
Empirical	15	1		0.459			0.83			
		2	–2.089	0.608	0.051		0.889 (0.871)	48.07	2, 12	< 0.001

Table 4. Simple correlation between body chemical components (water, ash, C, N and C:N) of pelagic decapods and the logarithm of its body DM (lnDM), habitat temperature (T), and the logarithm of sampling depth (lnDepth). *NS* not significant, $p > 0.05$

Component	N	Mean	SD	Pearson correlation coefficient (R)		
				lnDM (mg)	T(^{o}C)	ln Depth (m)
Water (% of WM)	37	73.9 ±	5.2	-0.314^{NS}	0.197^{NS}	-0.136^{NS}
Ash (% of DM)	36	13.7 ±	4.4	0.020^{NS}	0.580**	-0.251^{NS}
C (% of DM)	18	46.1 ±	8.0	-0.058^{NS}	-0.475^{NS}	0.314^{NS}
N (% of DM)	18	8.6 ±	1.9	-0.254^{NS}	0.498^{NS}	–0.677*
C:N (by mass)	18	5.7 ±	2.1	0.116^{NS}	-0.503^{NS}	0.502^{NS}

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 pelagic decapods. The a_3 was assessed as Q_{10} of Van't Hoff rule. Values in parentheses denote the 95% CI.

Species	Body mass effect		Temperature effect		Reference
	a_2	Range (mgDM)	Q_{10}	Range (^{o}C)	
Mixed (46 species)	0.872 (0.766–0.978)	6.5–5944	2.69 (2.12–3.42)	0.2–30	This study
Pasiphaea scotiae	0.613	80–1458*			Donnelly et al. (2004)
Acanthephyra purpurea			2.0	5–15	Teal (1971)
Oplophorus spinosus			2.1	5–20	
Parapandalus richardi			2.1	5–20	
Sergia splendens (formerly *Sergestes crassus*)			1.9	5–20	
Systellaspis debilis			2.5	5–20	
Acanthephyra purpurea			3.37	7–14	Donnelly and Torres (1988)
Funchalia villosa			2.63	7–20	
Gennadas scutatus			2.12	7–20	
Oplophorus gracilirostris			2.44	7–20	
Parapandalus richardi			2.61	7–17	
Parasergestes armatus (formerly *Sergestes armatus*)			3.81	7–14	
Sergia grandis			2.14	14–20	
Sergia robusta (formerly *S. robustus*)			2.22	7–17	
Sergia splendens			2.61	7–20	
Sergia talismani			1.62	7–20	
Systellaspis debilis			1.79	7–20	

*Converted from WM assuming water content of 73.9% (see Table 4).

Table 6. Global-bathymetric comparisons of ecological and physiological characteristics of pelagic decapods (this study), euphausiids (Ikeda 2013a) and mysids (Ikeda 2013c) living in the world's oceans. For respiration rate, T and E denote Theoretical and Empiriacal models, respectively. Differences in chemical composition components among taxa were tested by 1-way ANOVA, combined with Bonferroni test for between means. N is the number of data and N_{sp} the number of species.

Parameters	Decapods (De)	Euphausiids (Eu)	Mysids (My)	ANOVA H_0: DE = Eu = My
Behavior in the water column	active swimming	active swimming	active swimming	
Food habit	Omnivore, carnivore	Herbivore, omnivore, carnivore	Herbivore, omnivore, carnivore	
Metabolism				
Respiration rate (μl O_2 ind.$^{-1}$h^{-1})				
A specimen of 1mgN body mass (= 11.0[a] and 11.7[b] mgDM for decapods and mysids, respectively) inhabiting 100 m depth (20°C)				
T-model	23.7 [95%CI: 3.0–185]	13.1	15.0	
E-model	16.5 [95%CI: 4.6–59.1]	13.0	14.4	
A specimen of 1mgN body mass (=13.0[a] and 14.2[b] mgDM for decapods and mysids, respectively) inhabiting 1000 m depth (5°C)				
T-model	5.4 [95%CI: 0.7–40.9]	5.3	4.3	
E-model	3.3 [95%CI: 1.0–11.4]	5.3	4.2	
O:N ratio (by atms)				
Range	9–91	11–142	8–45	
Mean (±SD)	24.3 (20.8)	30.0 (17.4)	20.3 (10.6)	
Median	16.4	27.1	18.7	
N (Nsp)	15 (14)	31 (19)	15 (13)	
Body composition				
Water content (% of WM)				
Range	63.8–91.3	62.6–82.3	63.0–83.4	
Mean (±SD)	73.9 (5.2)	76.9 (3.7)	77.6 (5.4)	p = 0.002
N (Nsp)	37 (34)	36 (27)	18 (14)	My = Eu > De
Ash (% of DM)				
Range	4.8–25.0	9.4–17.7	5.3-22.9	
Mean (±SD)	13.7 (4.4)	12.9 (2.2)	13.6 (4.2)	p = 0.641
N (Nsp)	36 (32)	34(25)	18 (14)	
C (% of DM)				
Range	32.9–60.6	34.5–56.5	36.8-58.1	
Mean (±SD)	46.1 (8.0)	42.6 (4.4)	46.6 (6.6)	p = 0.007
N (Nsp)	18 (17)	41 (28)	24 (20)	De = My > Eu
N (% of DM)				
Range	5.9–12.1	6.4–12.7	4.8-11.5	
Mean (±SD)	8.6 (1.9)	10.4 (1.4)	8.8 (2.3)	p < 0.001
N (Nsp)	18 (17)	41 (28)	24 (20)	Eu > De = My
C:N (by mass)				
Range	3.5–10.2	3.4–8.6	3.2-10.6	
Mean (±SD)	5.7 (2.1)	4.2 (1.1)	5.8 (2.5)	p = 0.001
N (Nsp)	18 (17)	41 (28)	24 (20)	De = My > Eu

[a] estimated from the N compositon-habitat temperature relationship (Fig. 4) of this study

[b] estimated from the N compositon-sampling depth relationship of Ikeda (2013c)

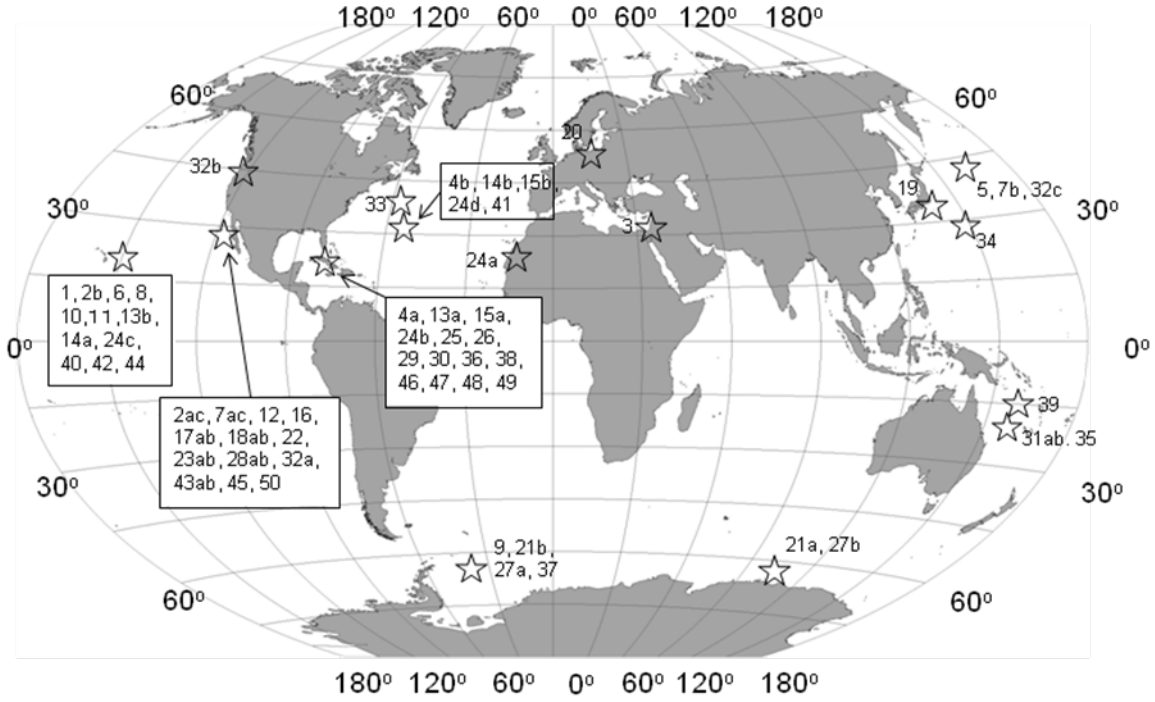
180° 120° 60° 0° 60° 120° 180°
60°
30°
0°
30°
60°
32b
33
4b, 14b, 15b
24d, 41
20
19
5, 7b, 32c
34
3
24a
1, 2b, 6, 8,
10, 11, 13b,
14a, 24c,
40, 42, 44
4a, 13a, 15a,
24b, 25, 26,
29, 30, 36, 38,
46, 47, 48, 49
2ac, 7ac, 12, 16,
17ab, 18ab, 22,
23ab, 28ab, 32a,
43ab, 45, 50
39
31ab, 35
9, 21b,
27a, 37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

Fig. 1 Ikeda

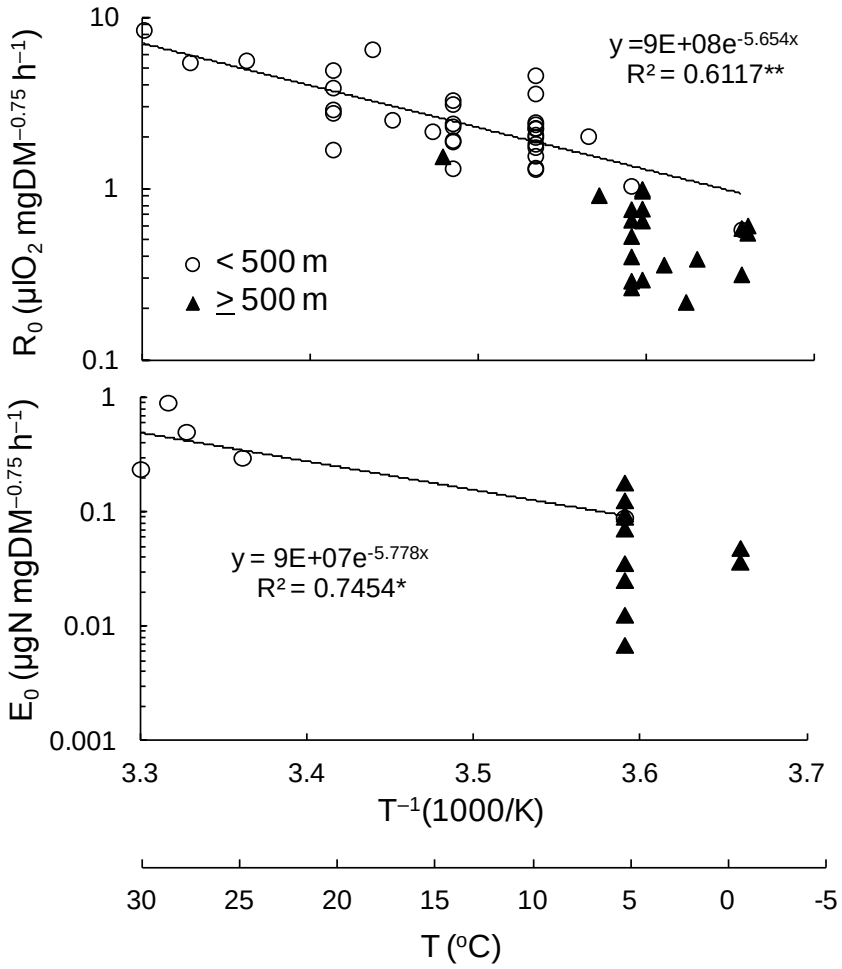
y =9E+08e-5.654x
R² = 0.6117**
< 500 m
≥ 500 m
R0 (μlO2 mgDM−0.75 h−1)
y = 9E+07e-5.778x
R² = 0.7454*
E0 (μgN mgDM−0.75 h−1)
T−1(1000/K)
T (°C)

Fig. 2 Ikeda

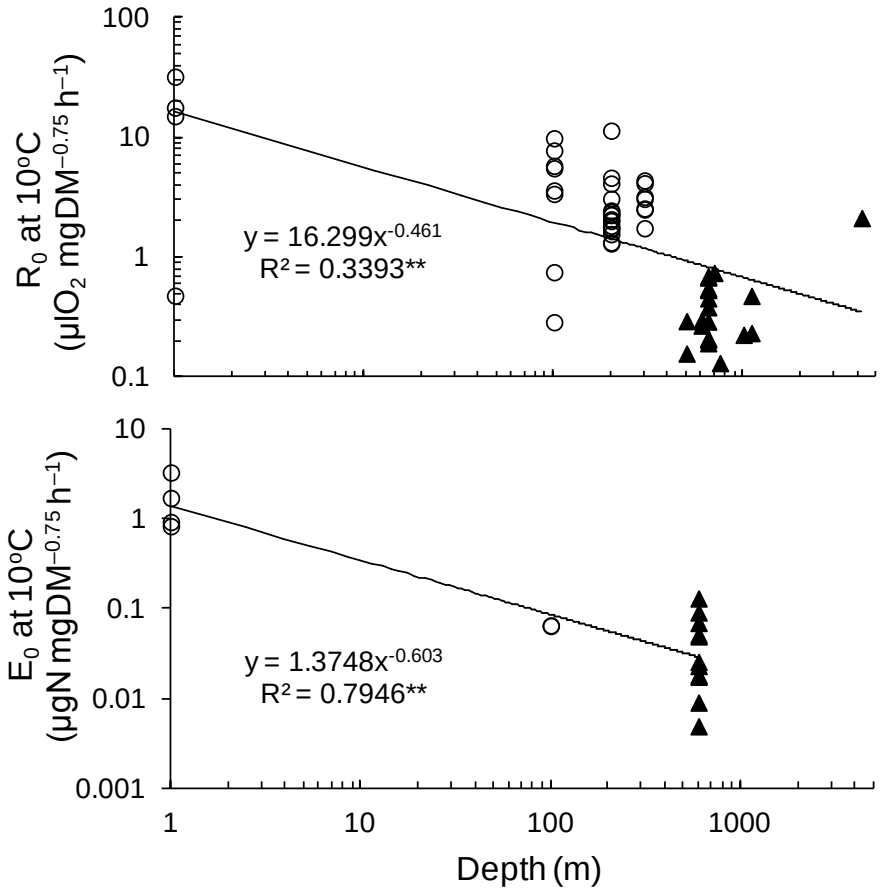
100
10
1
0.1
R_0 at 10°C
(μlO_2 mgDM$^{-0.75}$ h^{-1})
y = 16.299x$^{-0.461}$
R² = 0.3393**
10
1
0.1
0.01
0.001
E_0 at 10°C
(μgN mgDM$^{-0.75}$ h^{-1})
y = 1.3748x$^{-0.603}$
R² = 0.7946**
1
10
100
1000
Depth (m)

Fig. 3 Ikeda

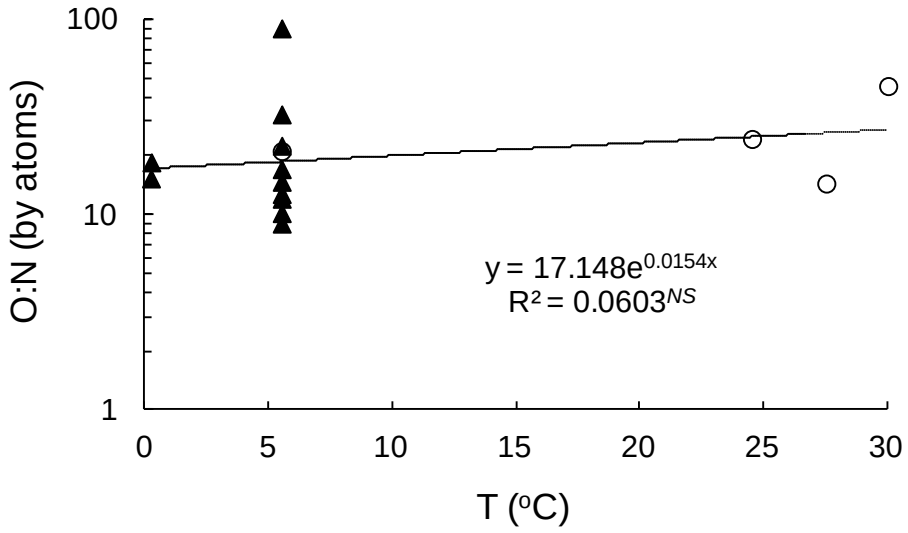
100
10
1
O:N (by atoms)
0
5
10
15
20
25
30
T (°C)
y = 17.148e0.0154x
R² = 0.0603NS

Fig. 4 Ikeda

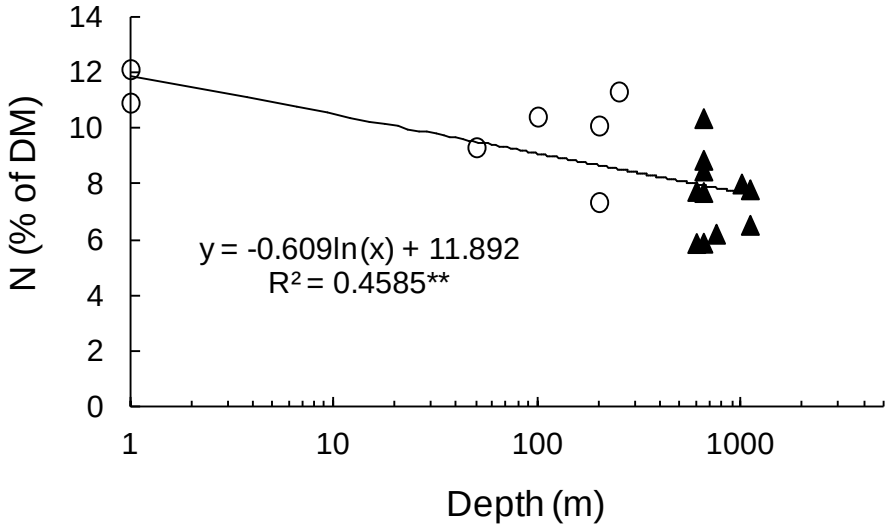
14
12
10
8
6
4
2
0
N (% of DM)
y = -0.609ln(x) + 11.892
R² = 0.4585**
1
10
100
1000
Depth (m)

Fig. 5 Ikeda