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

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Running head: Global-bathymetric model of pelagic decapod metabolism

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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 $\text{NH}_4\text{-N}$) 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

2.1 The data compilation

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

1. Data represented post-larvae (juveniles and adults) collected from the field and used for experiments without considerable time delay (< 24 h) with exceptions of 2–3 days delay (Cowles et al. 1990) or unspecified (Childress 1975).

2. Measurements were made in the absence of food at near *in situ* temperatures in the dark [and at normal pressure (1 atm) for deep-sea decapods on the premise that the hydrostatic pressure has little effect on the metabolic rates of deep-sea pelagic crustaceans, cf. review of Ikeda et al. (2000)]. This practice, combined with the criterion above, makes it possible to compare the data of various decapods for which information about feeding conditions in the field prior to the experiments is not available. The metabolic rate thus measured on pelagic animals at uncontrolled but minimum motor activity is defined as “routine” metabolism (Ikeda et al. 2000). The data from *in situ* incubations of a deep-sea decapod (*Acantheephyra eximia*) by means of autonomous landers (Bailey et al. 2005) were assumed to be comparable to those from above mentioned procedures.

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

4. Body mass in terms of wet mass (WM), dry mass (DM), carbon (C) or nitrogen (N) units were given together with metabolic data (note: body mass specific rates without body mass data are not useful).

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

6. Body composition (water content, ash, C and N) were derived with standard methods (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 on 16 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);

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

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

where Y is respiration rate ($\mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) or ammonia excretion rate ($\mu\text{gN ind.}^{-1} \text{ h}^{-1}$), X_1 is body mass, X_2 is habitat temperature (K for the theoretical model, and $^{\circ}\text{C}$ for the empirical model), and X_3 is mid-sampling depth (m). As body mass, wet mass (WM)

or dry mass (DM) has been used almost exclusively for decapods in the literature. In order to make between-taxa comparison of marine zooplankton with diversified body composition possible, dry mass (DM) was used in the present analyses. For the data sets in which body mass was reported as WM without information about water content, DM was estimated assuming water content of 73.9% of WM (see “Chemical composition” below). It is noted that a_1 was 0.75 (= 3/4, cf. Brown et al. 2004) and a_2 was $-Ea/k$ [k: Boltzman’s constant (8.62×10^{-5} eV/K)] for the theoretical model. As indices of temperature effects, Ea of the theoretical model and Q_{10} of empirical model could be computed as $Ea = a_2 \times 1000 \times 8.62 \times 10^{-5}$ and $Q_{10} = \exp(10 \times a_2)$, respectively. The attributes of these variables were analyzed simultaneously by using stepwise multiple regression (forward selection) method (Sokal and Rohlf 1995). Independent variables were added and removed at the $p = 0.05$. The calculation was conducted using SYSTAT version 10.2.

3 Results

3.1 Metabolic rates

Of the decapods considered in the present study, *Lucifer* sp. (0.014 mgDM) and *Notostomus elegans* (5944 mgDM) were the smallest and largest species, respectively (Table 2). Respiration rates at *in situ* temperature ranged from $1.9 \mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (*Acantheephyra quadrispinosa*) to $677 \mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (*Notostomus elegans*), and ammonia excretion rates from $0.036 \mu\text{gN ind.}^{-1} \text{ h}^{-1}$ (*Lucifer* sp.) to $15 \mu\text{gN ind.}^{-1} \text{ h}^{-1}$ (*Acantheephyra curtirostris* off South California) (Table 2).

Prior to the stepwise multiple regression analyses, a preliminary analysis was performed to test the effects of temperature and sampling depth on the rates of

respiration (R) and ammonia excretion (E) by first plotting the rates standardized to 1 mg DM ($R_0 = R \times DM^{-0.75}$ or $E_0 = E \times DM^{-0.75}$) against temperature (1000/K or °C) where the scale coefficient of body mass was assumed as 0.75 (as in the theoretical model) (Fig. 2). To facilitate the analysis, the data were separated into two groups depending on the depth of decapods sampled (< 500 m and ≥ 500 m). Since the values for species from ≥ 500 m depth distribute well below the rates < 500 m at equivalent inverse temperature or temperature, only the data of < 500 m were used for the analysis of temperature effects on R_0 or E_0 . The resultant slope (-5.654 for respiration rates, and -5.778 for ammonia excretion rates, Fig. 2) of the regression lines was used to compute R_0 or E_0 at a given temperature (designated as 10°C) of the decapods from these sampling depths (< 500 m + ≥ 500 m), which were plotted against the mid-sampling depth (Fig. 3). The standardized rates (R_0 or E_0 at 10°C) of these decapods were correlated negatively with the sampling depth ($p < 0.01$).

The overall results of stepwise multiple regressions for respiration rates showed that the new variable X_3 (sampling depth) was significant for the empirical model ($p < 0.001$) but not for the theoretical model ($p = 0.991$) (Table 3). As an index of the magnitude of multicollinearity among independent variables, the variation inflation factors (VIF) of X_3 were computed as 1.681 for the empirical model. Since the VIF value is < 5 , multicollinearity between the variable (X_3) and others is considered to be not serious (cf. Kutner et al. 2004). For ammonia excretion rates, the data for *Systellapsis braueri* and *Lucifer* sp. were considered outliers and therefore omitted in the following analyses. Furthermore, Pearson correlation matrix among the independent variables for ammonia excretion indicated that X_2 (habitat temperature) and X_3 were closely inter-related (correlation coefficient $R = 0.965$, $p < 0.001$). To avoid errors due

to multicollinearity, X_3 was removed for stepwise multiple regression of ammonia excretion data. For ammonia excretion rates, X_1 and X_2 (empirical model) or X_2 (theoretical model) were highly significant. As judged by R^2 values, the empirical model was superior to the theoretical model, accounting for 85.4–87.1% and 68.2–69.5%, respectively, of the variance in respiration and ammonia excretion (Table 3).

Thus, with regard to the effect of sampling depth for respiration rates, the results from the multiple regression analyses were nearly identical to those of the simple regression analyses (Figs. 2, 3) in which the rates standardized by body mass and temperature (e.g., R_0 at 10°C) were grouped based on single criteria (mid-sampling depth). However, the effect of sampling depth on ammonia excretion rates was unable to resolve by the multiple regression analyses in the present study because of its close correlation with habitat temperature.

3.2 O:N ratios

A total of 15 O:N ratios from 14 decapods ranged from 9.1 (*Systellaspis cristata*) to 91 (*Parapsdiphaea sulcatifrons*) (Table 2). A scatter diagram of the O:N ratios and habitat temperature is shown in Fig. 5. Simple correlation analyses indicated that none of the three independent variables was significantly correlated with the O:N ratios (Pearson correlation coefficients > 0.50). Mean and median O:N ratio were 24.3 (± 20.8 , SD) and 16.4, respectively.

3.3 Chemical composition

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 12.1 of 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

for diverse animal phyla (Prosser 1961).

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

0.612 (Fig. 2, this study) as compared with $R^2 = 0.804$ for the copepods (Fig. 2A, Ikeda et al. 2007), 0.882 for chaetognaths (Fig. 2, Ikeda and Takahashi 2012), 0.833 for euphausiids (Ikeda 2013a) and 0.784 for pelagic amphipods (Ikeda 2013b)] may partly be responsible for a discrepancy between the pelagic decapods and the other pelagic animals.

4.2 Habitat (sampling) depth as a new parameter

The present results from the empirical model (Table 3) demonstrate depression effects of habitat depth on respiration rates of pelagic decapods to those of larger pelagic animals with image-forming eyes such as micronektonic crustaceans, cephalopods and fishes (Torres et al. 1994; Childress 1995; Seibel and Drazen 2007), and zooplankton with no such eyes including copepods (Ikeda et al. 2006, 2007) and chaetognaths (Kruse et al. 2010; Ikeda and Takahashi 2012). Two explanations have been proposed for the progressive decline in respiration rates in deeper-living micronekton and zooplankton; the “visual-interactions hypothesis” (Childress 1995) and the “predation-mediated selection hypothesis” (Ikeda et al. 2006b). These two hypotheses are similar in that both interpret the phenomenon as a result of lowered selective pressure for high activity at depth because of the decrease in visual predators in the dark. However, these two hypotheses are different in that the former applies strictly to micronekton with functional eyes, and the latter to both micronekton and zooplankton irrespective of presence/absence of functional eyes.

Torres et al. (1994) compiled the relationship between respiration rates and the depth of occurrence for pelagic crustaceans (amphipods, decapods, euphausiids, isopods, mysids and ostracods) off California, the Gulf of Mexico, off Hawaii and Antarctic

waters. According to their results, the respiration rates [standardized to a body size of 1 mg wet mass by using the body mass exponent of 0.75 (equivalent to the theoretical model adopted in the present study), and at 0.5°C by assuming $Q_{10} = 2.0$], the reduction in the rates of a specimen due to the increase of its habitat depth from 1 m to 1000 m depth is in the order of 0.1–0.5 times. Similar calculations for pelagic decapods based on the present results (the empirical model in Table 3) showed that the reduction was 0.4 times, which is close to the upper range of the values for the mixed crustacean taxa by Torres et al. (1994).

4.3 Ammonia excretion and O:N ratios

While no global-bathymetric model is presently available for ammonia excretion rates of pelagic decapods, global ammonia excretion models with two parameters (body mass, habitat temperature) for mixed epipelagic zooplankton taxa (Ikeda 1985) and for epipelagic copepods (Ikeda et al. 2001) yielded a body mass exponent and Q_{10} similar to those for respiration rates. With regard to the effect of habitat depth, lowered ammonia excretion rates have already been reported on some deeper-living decapods species off Southern California (Quetin et al. 1980) and Pridz Bay, Antarctica (Ikeda 1988). In the present study, regression analyses of ammonia excretion rates on body mass, habitat temperature and sampling depth for the pelagic decapods were not amenable due to close inter-correlation of sampling depth with habitat temperature (Table 3). Considering the large scatter of ammonia excretion data evident in the presence of outliers (two data), the number of data sets ($N = 15$) available to the present analyses was too few to build a robust model. While further investigations are needed to prove a likely parallel change in respiration and ammonia excretion rates in pelagic

decapods, O:N ratios were observed to be rather stable across the 14 pelagic decapods considered in this study (median: 16.4). Insignificant effects of body mass and habitat temperature on O:N ratios have already been reported on mixed epipelagic zooplankton taxa (Ikeda 1985) and epipelagic copepods (Ikeda et al. 2001).

The atomic ratio of oxygen consumption rate to ammonia-nitrogen excretion rate (O:N ratio) has been used as an index of the proportion of protein in the diet of marine zooplankton (Mayzaud and Conover 1988; Ikeda et al. 2000). When only protein is metabolized, the O:N ratio is 7 (Table 10.3 in Ikeda et al. 2000). When protein and lipid or carbohydrate are catabolized in equal quantities O:N ratios are calculated as 21 or 13, respectively (mid-point: 17). Hence, O:N ratios of 7–17 may be used as an index of protein-oriented metabolism and ratios of >17 as lipid/carbohydrate-oriented metabolism. The high metabolic O:N ratios (median; 16.4) of pelagic decapods favor protein-oriented metabolism on average. It is noted that the O:N ratios of pelagic decapods listed in Table 2 are derived from experiments in which they were placed in filtered seawater, a common practice when using the sealed-chamber method (Ikeda et al. 2000). The use of filtered seawater is imperative to determine the rates of respiration and ammonia excretion accurately without any corrections for complex uptake/release of oxygen and ammonia by food organisms, but starvation of decapods may influence their normal metabolism. While no data are presently available for pelagic decapods, Ikeda and Dixon (1984) examined the effect of methodological problems associated with the sealed chamber method on the euphausiid *Euphausia superba*. According to their results, respiration and ammonia excretion rates of wild *E. superba*, in which daily ration is 5%, are 1.6 and 4.5 times the rates of non-feeding krill in 24 h laboratory experiments. From these results, the O:N ratios of wild *E. superba* are calculated as

0.36 (= 1.6/4.5) times those of the non-feeding *E. superba*. Generalization of the results of *E. superba* to pelagic decapods requires caution since no comparable data are available for the other pelagic crustaceans.

4.4 Chemical composition

Among pelagic crustacean taxa, global-bathymetric features of body chemical composition (water content, ash, C, N and C:N) have been well documented for pelagic copepods (Ikeda 1974; Båmstedt 1986; Ikeda et al. 2004, 2006b), and can be summarized as follows; first, most species from cold thermal regimes (high latitude seas and deep sea) are characterized by the accumulation of lipids which reflects higher C and lower N composition (thus leading to higher C:N) as compared with counterparts from warm thermal regimes (low latitude seas); second, shallow and deep-sea species at higher latitudes are similar in that both exhibit high C composition but different in that the latter exhibit much reduced N composition (reduced protein or musculature); and third, lipid or C-rich species are often accompanied by correspondingly low water content and ash content. Depth-related reduction in protein has also been reported on mixed pelagic crustacean taxa (Morris and Hopkins 1983; Childress and Nygaard 1974).

The present results for pelagic decapods (Table 4) showed that the effects of habitat temperature and sampling depth on C and N composition and C:N ratios were similar to those of copepods mentioned above. However, the effect of sampling depth

was significant only for N composition ($p < 0.05$) and the effect of habitat temperature was less pronounced ($p = 0.277$ for C, $p = 0.212$ for N and $p = 0.199$ for C:N). Positive correlations between habitat temperature and water content and ash are also in line with those of copepods, though the correlation between habitat temperature and water content was not significant ($p > 0.5$).

Analyzing chemical composition data on 182 zooplankton species (mostly crustaceans), Ventura (2006) calculated average C and N composition of protein to be 52.8% and 16.0%, and lipids (represented by wax esters) to be 81.0% and 0%. With these results, the C:N ratio is calculated as 3.3 for protein alone and 8.4 for organic matter composed of equal amounts of protein and lipid. Carbohydrate in zooplankton has been reported to be $< 8.5\%$ of DM (Ventura 2006) and is therefore omitted in this calculation. Then, C:N ratios of 3.3–8.4 and > 8.4 can be used as indices of protein- and lipid-dominated composition, respectively, for zooplankton. On this basis, body C:N ratios of most of the pelagic decapods were 3.5 to 10.2 (mean = 5.7, Table 4), indicating protein-dominated composition. As exceptions, the two mesopelagic decapods exhibited C:N ratios beyond the range (8.6 and 9.8 for *Hymenodora frontalis* off Southern California and the western subarctic Pacific, and 10.2 for *Pasiphaea scotiae* from Prydz Bay, Antarctica, Table 2), indicating lipid dominated composition. Little has been studied on the function of lipids in pelagic decapods. For copepods and euphausiids, the function of large lipid deposits (mostly as wax esters, triacylglycerols or phospholipids) 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°C), predicted respiration rates from the theoretical or empirical model of decapods (23.7 or 16.5 $\mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) are somewhat different from those of euphausiids (13.1 or 13.0 $\mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) and mysids (15.0 or 14.4 $\mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$). 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°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, euphausiids 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 ($C:N = 3.5\text{--}7.8$). 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 Malacostraca), and active swimmers with developed functional eyes and respiratory gill organ..

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Figure captions

Fig. 1. Study sites of metabolic rates and chemical composition of pelagic decapods.

The number and associated character alongside the symbol correspond to the code of each decapod listed in Table 1.

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

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

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

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

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

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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 Code	Mid-sampling depth (range) (m)	T (°C)	N	Body mass (mg DM ind. ⁻¹)	Respiration rate (μlO ₂ l nd. ⁻¹ h ⁻¹)	Ammonia excretion rate (μgN ind. ⁻¹ h ⁻¹)	O:N ratio (by atoms)	Body chemical composition				
								Water (% of WM)	Ash (% of DM)	C (% of DM)	N (% of DM)	C:N (by mass)
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

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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 : $\mu\text{l O}_2 \text{ ind.}^{-1}\text{h}^{-1}$ or $\mu\text{g N ind.}^{-1}\text{h}^{-1}$) of pelagic decapods on body mass (X_1 : mgDM ind.^{-1}), habitat temperature (X_2 : re-defined as $1000/K$ for the former, $^{\circ}\text{C}$ 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(°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 ($^{\circ}$ C)	
Mixed (46 species)	0.872 (0.766–0.978)	6.5–5944	2.69 (2.12–3.42)	0.2–30	This study
<i>Pasiphaea scotiae</i>	0.613	80–1458*			Donnelly et al. (2004)
<i>Acanthephyra purpurea</i>			2.0	5–15	Teal (1971)
<i>Oplophorus spinosus</i>			2.1	5–20	
<i>Parapandalus richardi</i>			2.1	5–20	
<i>Sergia splendens</i> (formerly <i>Sergestes crassus</i>)			1.9	5–20	
<i>Systellaspis debilis</i>			2.5	5–20	
<i>Acanthephyra purpurea</i>			3.37	7–14	Donnelly and Torres (1988)
<i>Funchalia villosa</i>			2.63	7–20	
<i>Gennadas scutatus</i>			2.12	7–20	
<i>Oplophorus gracilirostris</i>			2.44	7–20	
<i>Parapandalus richardi</i>			2.61	7–17	
<i>Parasergestes armatus</i> (formerly <i>Sergestes armatus</i>)			3.81	7–14	
<i>Sergia grandis</i>			2.14	14–20	
<i>Sergia robusta</i> (formerly <i>S. robustus</i>)			2.22	7–17	
<i>Sergia splendens</i>			2.61	7–20	
<i>Sergia talismani</i>			1.62	7–20	
<i>Systellaspis debilis</i>			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 Empirical 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 atoms)				
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 (N _{sp})	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 (N _{sp})	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 (N _{sp})	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 (N _{sp})	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 (N _{sp})	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 (N _{sp})	18 (17)	41 (28)	24 (20)	De = My > Eu

^a estimated from the N composition-habitat temperature relationship (Fig. 4) of this study

^b estimated from the N composition-sampling depth relationship of Ikeda (2013c)

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Fig. 1 Ikeda

Fig. 2 Ikeda

Fig. 3 Ikeda

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Fig. 4 Ikeda

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Fig. 5 Ikeda

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