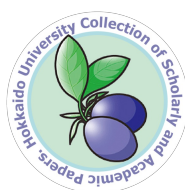




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Metabolism and chemical composition of marine pelagic amphipods: synthesis toward a global-bathymetric model

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ABSTRACT

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

1 Introduction

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

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

Information about metabolism [respiration rates, ammonia excretion rates, O:N (as $\text{NH}_4\text{-N}$) ratios] has proved to be useful to provide a wide perspective for understanding the energy demand, major metabolic substrates and nutritional condition of marine zooplankton (cf. Ikeda et al. 2000). Metabolic rates of zooplankton living in the epipelagic zones have been documented as a function of body mass and habitat temperature (Ivleva 1980; Ikeda 1985). Although body mass and temperature have been regarded as two major determinants of the metabolic characteristics of marine pelagic animals, habitat depth has also emerged as an additional parameter of importance since the observation that metabolic rates decrease rapidly with depth for large pelagic animals with developed visual perception systems (eyes) such as micronektonic fishes, crustaceans, and cephalopods (Childress 1995; Seibel and Drazen 2007). To date, the effect of habitat depth on respiration rates and O:N ratios of amphipods has been analyzed within “crustaceans” group, together with mysids, decapods and other crustacean taxa (Childress 1975; Quetin et al. 1980; Ikeda 1988; Torres et al. 1994), and no analyses have attempted for amphipods as a taxon.

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

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

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

2 Materials and methods

2.1 The data compilation

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

seawater for a certain period and the decrease of oxygen or increase in ammonia during the period (several hours to a day) is monitored throughout, or determined at the end of the incubation (Ikeda et al. 2000). Laval (1980) suggested the sealed chamber method overestimated metabolism of hyperiid amphipods because of the lack of a gelatinous substratum for the animals to attach to during the experiment. The magnitude of possible error due to methodological constraints is discussed in Discussion section. For the present analyses, the data compiled were those which met the following criteria:

1. Data are on fresh specimens collected from the field and used for experiments without a considerable time delay (< 24 h).
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 amphipods on the premise that the hydrostatic pressure has minimal 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 amphipods for which information about feeding conditions in the field prior to the experiments is not available.
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), C or N units were given together with metabolic data (note: body mass specific rates without body mass data are not useful).
5. Body composition (water contents, ash, C and N) were derived with standard methods (Omori and Ikeda 1984; Postel et al. 2000).

In cases where multiple literature sources (including those of my own) were

available on the same species from similar regions, preference was given to mine to reduce possible between-workers bias in the data. As a result, a total of 41 data sets on 32 amphipods (21 hyperiids and 11 gammarids) were selected, amongst which 22 were of simultaneous measurements of respiration and ammonia excretion rates, 18 were of respiration rates only, and 1 was ammonia excretion rates only (Table 1). Of the 32 amphipods used metabolic measurements, 17–18 data sets of water content and ash were available on 18 amphipods, and 36 data sets of C and N composition and C:N ratios on 28 amphipods (Table 2). Both genus and species names in the literatures were updated according to Vinogradov et al (1982) and Schneppenheim and Weigmann-Haass (1986). Amongst the gammarids, *Eusirus* spp. were difficult to judge whether they were pelagic or non-pelagic (sympagic), but have been considered as primarily pelagic after Krapp et al. (2008). The same amphipod species from different locations or studies were treated as independent data sets, though mere repetition of the data on the same amphipods was avoided carefully. The data expressed in the form of regression equations only were converted to the respiration rates of a specimen at mid-range of body mass. Study sites of all amphipods are plotted on the world map (Fig. 1) to facilitate graphical perception of worldwide coverage of the data sets in the present study.

2.2 Regression models for metabolism

In addition to the 2 conventional independent variables (X_1 : body mass; and X_2 : habitat temperature) used in the previous global respiration model for marine epipelagic crustaceans (Ivleva 1980; Ikeda 1985), 2 new independent variables (X_3 : mid-sampling

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

Two regression models were adopted according to the mathematical form of the temperature and body mass effects. One was a theoretical model characterized by the Arrhenius relationship ($R = R_0 M^{3/4} e^{-E_a/kT}$ or $E = E_0 M^{3/4} e^{-E_a/kT}$, where R ($\mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) is respiration rate, E ($\mu\text{gNH}_4\text{-N ind.}^{-1} \text{ h}^{-1}$) is ammonia excretion rate, M (mg) is body mass, T is absolute temperature, $3/4$ is theoretical body mass exponent, E_a (eV) is an average activation energy for the rate-limiting enzyme-catalyzed biochemical reactions of metabolism, k is Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$) and R_0 or E_0 is a normalization constant (cf. Gillooly et al. 2001) and the other was empirical (or log/linear) model characterized by the Van't Hoff rule (Q_{10}) (Ikeda 1985; Ikeda and

Takahashi 2012);

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

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

It is noted that a_1 was 0.75 (= 3/4) for the theoretical model. As indices of temperature effects, E_a of the theoretical model and Q_{10} of empirical model could be computed as $E_a = a_2 \times 1000 \times 8.62 \times 10^{-5}$ and $Q_{10} = \exp(10 \times a_2)$, respectively. The attributes of these variables were analyzed simultaneously using the 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 pelagic amphipods considered in the present analyses, *Themisto gaudichaudii* (1.0 mgDM) and *Eusirus perdentatus cornuta* (344 mgDM) were the smallest and largest species, respectively (Table 2). Respiration rates at *in situ* temperature ranged from $0.37 \mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (*Cyphocaris* sp. B) to $68.4 \mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (*Cyphocaris faueri*), and ammonia excretion rates from $0.049 \mu\text{gN ind.}^{-1} \text{ h}^{-1}$ (*Cyphocaris challengerii* from the eastern subarctic Pacific Ocean) to $4.76 \mu\text{gN ind.}^{-1} \text{ h}^{-1}$ (*Oxycephalus clausi* from tropical Indian Ocean) (Table 2).

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 the rate of specimens weighing 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 analysis, the data were separated into two groups depending on the depth of amphipods sampled (< 500 m and ≥ 500 m). It is clear that the rates values for the species from ≥ 500 m depth distribute well below the rate values <500 m at equivalent inverse temperature or temperature. From this result, only the data of < 500 m were used for the analysis of temperature effect on R_0 or E_0 . The resultant slope (−4.582 for respiration rates, and −5.408 for ammonia excretion rates) of the regression lines was used to compute R_0 or E_0 at a given temperature (designated as 10°C) of the amphipods from these sampling depths (< 500 m + ≥ 500 m), which were plotted against the mid-sampling depth (Fig. 3). The standardized R_0 or E_0 at 10°C of these amphipods were correlated negatively with the sampling depth, but the correlation was significant ($p < 0.01$) in the former only.

The overall results of stepwise multiple regressions showed that the new variable X_3 (sampling depth) was significant ($p < 0.005$) irrespective of the choice of the theoretical or empirical model for respiration rates. For ammonia excretion rates, the data for *Paracallisoma coecus* were considered outliers and therefore omitted in the following analyses. In contrast to the results for respiration rates, the new variable X_3 (sampling depth) was not significant in both theoretical and empirical models ($p > 0.18$) for ammonia excretion rates. As judged by R^2 values, the empirical model was superior to the theoretical model, accounting for 79.6–83.1% and 64.7–68.2% of variance, respectively, for the respiration rates, and the reverse was the case of ammonia excretion rates (63.9–67.9% and 73.1–76.8%, respectively) (Table 3). There was no consistent pattern in the performance of the various body mass units to yield best fit in

the models of respiration rates and ammonia excretion rates.

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

3.2 O:N ratios

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

3.3 Chemical composition

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

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

4 Discussion

4.1 Methodological issues in measuring metabolic rates

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

substratum. For *Themisto* (formerly *Euthemisto*) *pacifica*, King et al. (1975) adopted the sealed-chamber method to measure R and determined ETS/R ratio as 2.0 (original ETS data were multiplied by 3.3 to standardize to the sensitivity of the Owens and King's assay), which is similar to those of free-living crustaceans of the same study (2.1 for a decapods *Pleurocodes planipes*, 2.4–2.5 for euphausiids *Euphausia pacifica* and *Nematoscelis atlantica*). This result suggests that the majority of *T. pacifica* are almost exclusively free-living, and that the extra energy needed for swimming is relatively less as compared with that for the standard metabolism as discussed in the following.

While no information about the relationship between R and swimming activities is presently available for hyperiid amphipods, Halcrow and Boyd (1967) determined the relationship on an intertidal gammarid amphipod *Gammarus oceanicus*, and calculated factorial scopes [FS; the ratio between activity metabolism (R at maximum activity) to standard metabolism (R at rest)] as 3–4, depending on temperature (5–20°C). The FSs of *G. oceanicus* are the same order of magnitude (3.1) to that of a planktonic copepod *Dioithona oculata* (Buskey 1998) and that (6.1) of a euphausiid *Euphausia pacifica* at 8°C and normal pressure (1 atm) (Torres and Childress 1983), but are much less than 10–20 in salmon (Brett, 1964) and 50–200 in flying insects (cf. Prosser 1961).

Clearly, the gap in our knowledge about the metabolism of partly parasitic hyperiid amphipods needs to be filled by developing new methodology in the future. Nevertheless, presently available information of ETS:R ratios and FSs suggests that the magnitude of possible errors due to the current methodological constraints in measuring metabolic rates of pelagic hyperiids are sufficiently small to allow the broad comparison of metabolic data in the present study.

4.2 Body mass and habitat temperature as traditional predictors

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

The effect of temperature on metabolism has been studied in individual amphipod species at graded temperatures within the range of their habitats. 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). The activation energy (E_a) or Q_{10} values thus obtained for acclimated amphipod species by previous workers are 0.44–0.64 eV or 1.9–2.69 for respiration rates (Table 4). Similar intra-specific Q_{10} values (2–3) are

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

4.3 Habitat (= sampling) depth as a new predictor

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

analyses (see Fig. 3).

The negative effects of habitat depth on respiration rates of pelagic amphipods are consistent with those of micronektonic crustaceans, fishes and cephalopods with image-forming eyes (Torres et al. 1994; Childress 1995; Seibel and Drazen 2007), and zooplankton such as copepods (Ikeda et al. 2006, 2007) and chaetognaths (Kruse et al. 2011; Ikeda and Takahashi 2012). For the reduction in respiration rates for deeper-living pelagic animals, the “visual-interactions hypothesis” (Childress 1995) or “predation-mediated selection hypothesis” (Ikeda et al. 2007) have been proposed. These two hypotheses are similar in that both interpret the phenomena as a result of lowered selective pressure for high activity at depth because of the decrease in visual predators in the dark. However, the former hypothesis applies strictly to micronekton with functional eyes, and the latter to both micronekton and zooplankton irrespective of presence/absence of functional eyes. In terms of size-based classification, most pelagic amphipods in the present study belong to zooplankton rather than micronekton (> 20 mm body length, cf. Omori and Ikeda 1984) though they possess 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, in the Gulf of Mexico, off Hawaii and in Antarctic waters. According to their results, the respiration rates [standardized to a body size of 1 mg wet mass by using the scale 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 the pelagic amphipods based on the present results (theoretical models in Table 3) showed that the reduction was 0.3–0.4

times, depending on the choice of DM, C or N body mass unit, which fall within the range of the mixed crustacean taxa by Torres et al. (1994).

4.4 O:N ratios

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 total metabolites in 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 is catabolized in equal quantities at the same time, O:N ratios are calculated between 13 and 21. Hence, O:N ratios of 7–17 (mid-point of 13 and 21) may be used as an index of protein-oriented metabolism and the ratios of > 17 as lipid/carbohydrate-oriented metabolism. As carnivores, the O:N ratio of the 19 pelagic amphipods compiled in the present study (Table 2) varied from one species to the next (11–74, Table 2), with a median of 21.5. The somewhat greater than expected O:N ratios for the pelagic amphipods may be due to methodological constraints of the incubation of specimens in filtered seawater (no food), a typical design of the sealed-chamber method (Ikeda et al. 2000). Ammonia excretion is more susceptible to food deprivation than respiration, hence high O:N ratios in starved amphipods have been documented in *Phronima sedentaria* (Ikeda 1974) and *Themisto pacifica* (Ikeda 1977). The same phenomenon has also been observed in a bathypelagic mysid *Gnathophausia ingens* (Quetin et al. 1980; Hiller-Adams and Childress 1983) and an epipelagic euphausiid *Euphausia superba* (Ikeda and Dixon 1984).

In addition to food deprivation, N composition of diets is known to affect O:N ratios of marine invertebrates (cf. Ikeda and McKinnon 2012). As carnivores,

progressive increase in the O:N ratios of the pelagic amphipods downward (Fig. 4) may be a result from N-poor and/or C-rich prey animals at depth. Copepods are the major prey components of pelagic amphipods (Shedder and Evans 1975; Pakhomov and Perissinotto 1996; Haro-Garay 2004) and their depth-related patterns in chemical composition are characterized by a gradual decline in N composition and increase in C:N ratio toward great depth (Ikeda et al. 2006a). As an alternative explanation, the increase in body C:N ratios of deeper-living pelagic amphipods themselves may also be considered. However, this explanation is not consistent with the insignificant correlation between the C:N ratios and sampling depth in the pelagic amphipods (Table 4).

4.5 Chemical composition

Ikeda (1974), analyzing C and N compositions of various zooplankton taxa from tropical to subarctic waters, showed that high C composition and C:N ratios are characteristics of those inhabiting cold habitats. Båmstedt (1986) noted also high C and low N (thus leading to high C:N) for copepods from cold thermal regimes (high latitude seas and deep sea) as compared with counterparts from warm thermal regimes (low latitude seas). A recent study on copepods living in the epipelagic through abyssopelagic zones of the western subarctic Pacific Ocean revealed a gradual decline in the N content and an increase in C:N ratios downward (Ikeda et al. 2006a). The present results on pelagic amphipods are consistent with the results of these previous studies in that C composition was negatively correlated with habitat temperature (Fig. 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 the pelagic amphipods were 3.4–7.9 (mean = 6.0, Table 2), indicating protein dominated composition. As exceptions, the three amphipods from the mesopelagic/abyssopelagic zones exhibited C:N ratios beyond the range (10.9 for *Chuneola spinifera*, 12.7 for Gammaridea sp., and 13.0 for *Cyphocaris* sp., Table 2), indicating lipid dominated composition. Little has been studied on the function of lipids in pelagic amphipods, with a notable exception of the study of Percy (1993) who demonstrated that the hyperiid amphipod *Themisto libellula* utilized lipid reserves in the body for metabolic needs when starved. For copepods and euphausiids, the function of large lipid deposits (mostly as wax esters, triacylglycerols or phospholipids) is considered as an energy reserve for coping with temporal food scarcity and reproduction, or energy saving for swimming by achieving neutral buoyancy (Lee et al. 2006).

In conclusion, global-bathymetric models designed in the present study could explain 65–83% of the variance in respiration rates and 64–77% of the variance in

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

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Figure captions

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

Fig. 2. Pelagic amphipods. 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 the specimens from shallow (open circles; < 500 m) and deep layers (closed triangles; ≥ 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. **: $p < 0.01$.

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

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

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

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

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

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

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

^a after Childress and Nygaard (1974)

^b mean of *Themisto* spp. of this study

^c after Ikeda and Mitchell (1982)

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

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Table 3. Stepwise (forward selection) multiple regression statistics of theoretical and empirical models of respiration rates (Y : $\mu\text{l O}_2 \text{ ind.}^{-1}\text{h}^{-1}$) or ammonia excretion rates (Y : $\mu\text{gN ind.}^{-1}\text{h}^{-1}$) of pelagic amphipods on body mass (X_1 : mg ind.^{-1}), habitat temperature (X_2 : 1000/K for the former, $^{\circ}\text{C}$ for the latter) and depth sampled (X_3 : m).

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

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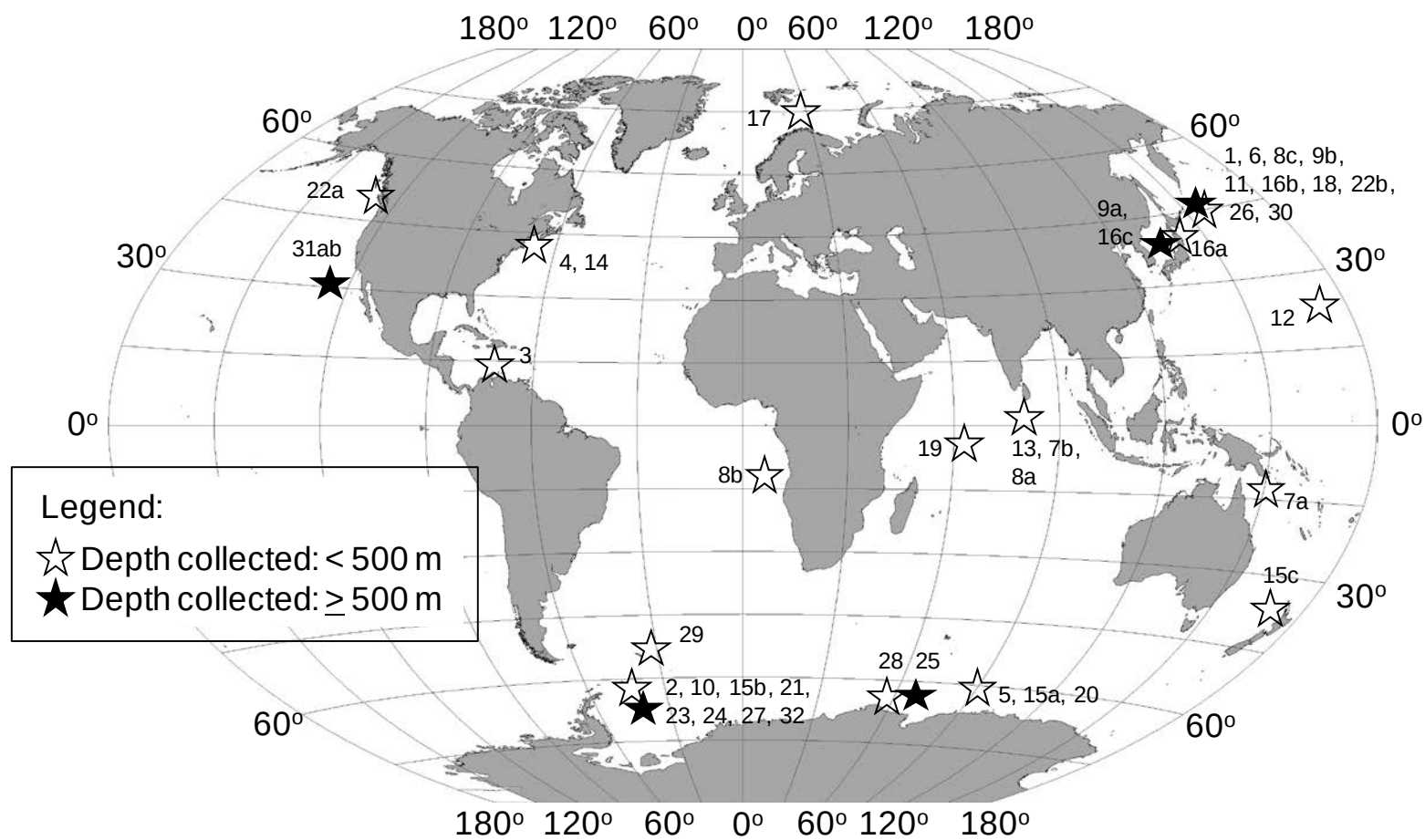
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Table 4. Spearman correlation coefficients (R) between body chemical components (water, ash, C, N and C:N) and body mass [ln DM (mg)], habitat temperature [T (°C)], and mid-sampling depth [ln Depth (m)], of pelagic amphipods. DF = degree of freedom,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

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

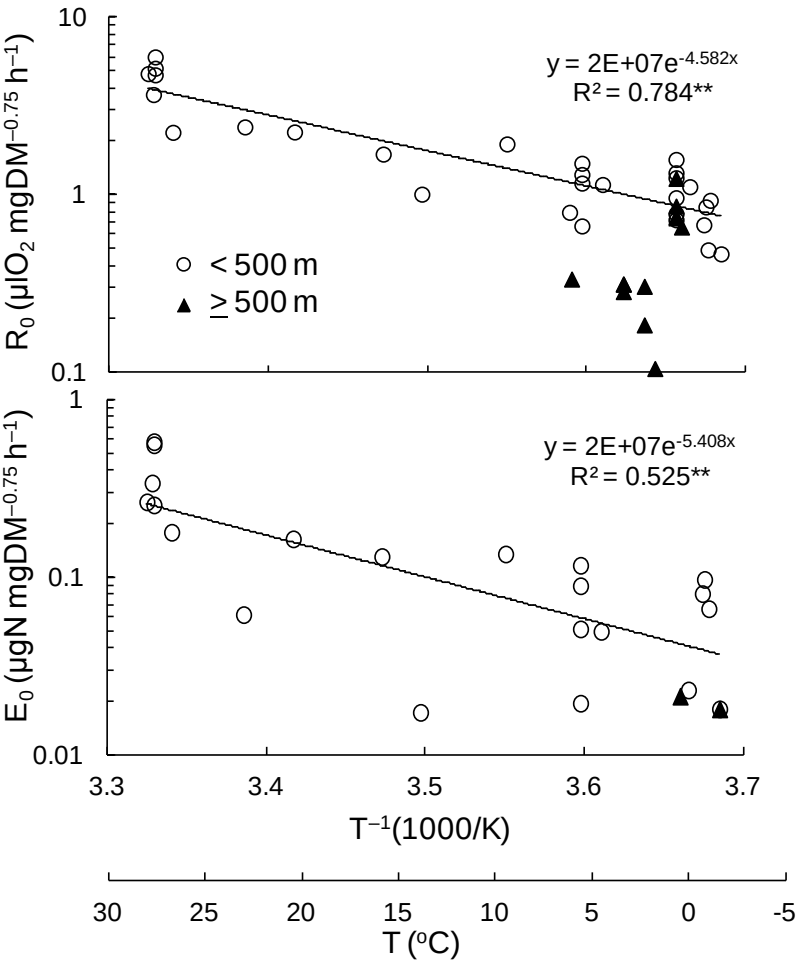
Table 5. Effects of body mass (as the scale exponent of body mass = a_2 of the regression model adopted in the present study) and temperature (= a_3) on respiration and ammonia excretion rates of pelagic amphipods. The a_3 was assessed as activation energy (E_a) of Arrhenius equation or Q_{10} of Van't Hoff rule on DM body mass. basis. Values in parentheses denote the range of 95% CI.

Amphipod species	Body mass effect		Temperature effect				Reference
	a ₂	Range (mgDM)	E _a (eV)	Range (°C)	Q ₁₀	Range (°C)	
Respiration rates							
Mixed (32 species)	0.743 (0.626–0.860)	1–344	0.26 (0.10–0.43)	–1.6 to 28	1.45 (1.11–1.88)	–1.6 to 28	This study
<i>Cyphocaris challengerii</i>	0.880 (0.795–0.965)	0.60–12.66					Yamada & Ikeda (2003)
<i>Hyperia antarctica</i>			0.64	0–10	2.64 2.53	0–5 5–10	Hirsche (1984)
<i>Themisto gaudichaudii</i>	0.924 (0.695–1.154)	<10					James & Wilkinson (1988)
<i>Themisto gaudichaudii</i>	0.70 (0.69–0.71)	12–72					Opalinski & Jazdzewski (1978)
<i>Themisto gaudichaudii</i>			0.44	0–10	1.96 1.88	0–5 5–10	Hirsche (1984)
<i>Themisto japonica</i>					2.69 (1.47–4.93)	1–12	Ikeda (1991)
<i>Themisto japonica</i>	0.771 (0.694–0.848)	0.33–14.21					Yamada & Ikeda (2003)
<i>Themisto libellula</i>					2.01	0–5	Percy (1993)
<i>Themisto pacifica</i>	0.947 (0.794–1.099)	0.21–3.50					Yamada & Ikeda (2003)
<i>Primno abyssalis</i>	1.003 (0.815–1.190)	0.31–11.46					Yamada & Ikeda (2003)
Ammonia excretion rates							
Mixed (19 species)	0.763 (0.677–0.925)	1–193	0.49 (0.28–0.69)	–1.6 to 28	2.01 (1.47–2.75)	–1.6 to 28	This study
<i>Cyphocaris challengerii</i>	1.292 (1.080–1.503)	0.60–12.66					Yamada & Ikeda (2003)
<i>Themisto gaudichaudii</i>	0.807 (0.726–0.889)	<10					James & Wilkinson (1988)
<i>Themisto pacifica</i>	1.366 (1.059–1.674)	0.21–3.50					Yamada & Ikeda (2003)
<i>Themisto japonica</i>	1.005 (0.902–1.108)	0.33–14.21					Yamada & Ikeda (2003)
<i>Primno abyssalis</i>	1.045 (0.787–1.303)	0.31–11.46					Yamada & Ikeda (2003)



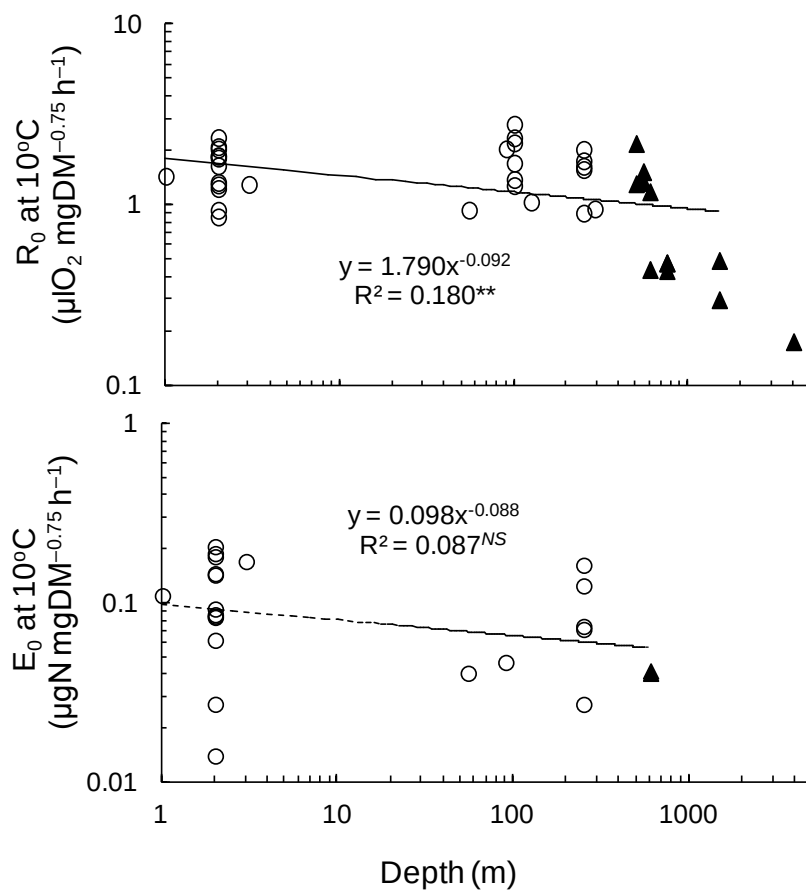
Ikeda Fig. 1

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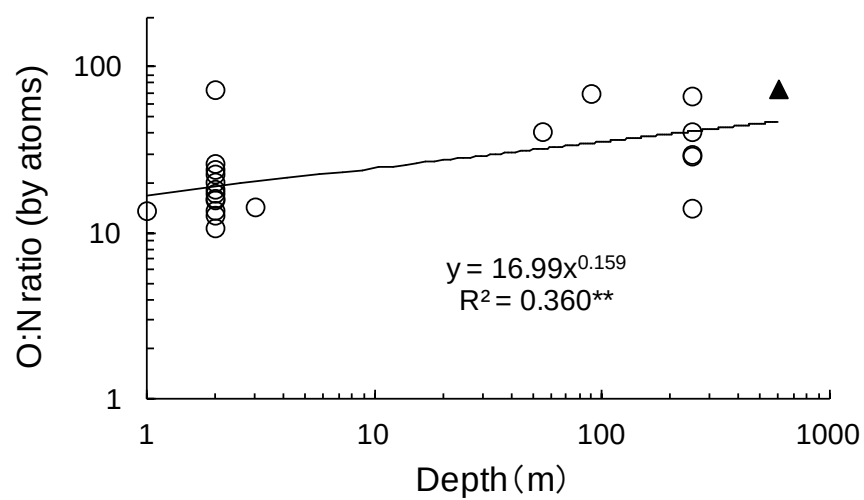
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Ikeda Fig. 2



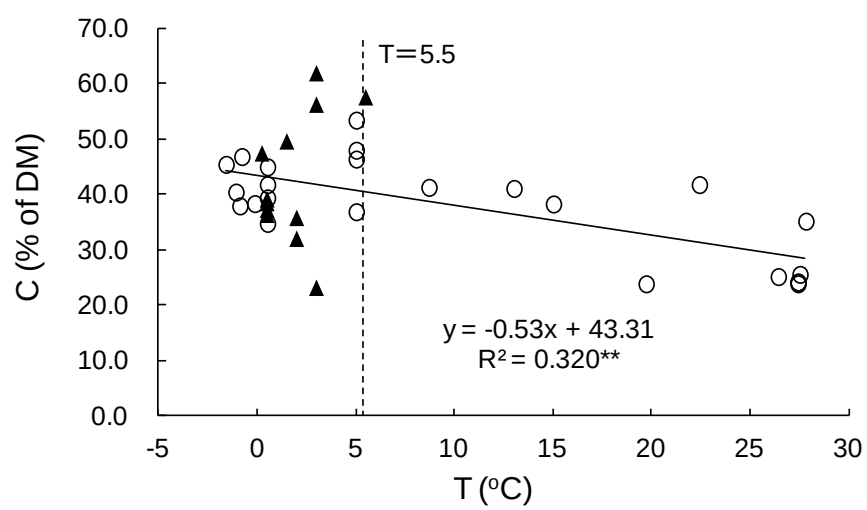
Ikeda Fig. 3

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Ikeda Fig. 4

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Ikeda Fig. 5