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3 Metabolism and chemical composition of mysid crustaceans: synthesis toward a
4 global-bathymetric model

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14 Running head: Global-bathymetric model of amphipod metabolism

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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 13–32 mysids from freshwater, coastal littoral, epipelagic and abyssopelagic zones of the world's oceans were compiled. The independent variables including body mass, habitat temperature and sampling depth were all significant predictors of respiration, accounting for 74–85% of the variance in the data, while the former two variables were significant predictors of ammonia excretion, accounting for 85–86% of the variance. Atomic O:N ratios (respiration : ammonia excretion) ranged from 7.9 to 44.8 (median: 18.7), indicating protein-oriented metabolism. Body water content and ash were not correlated with habitat temperature and sampling depth, but C and N composition increased and decreased with the increase of sampling depth. As judged by C:N ratios, protein was considered to be the major organic component of most mysids. Some mysids from > 500 m depth exhibited high C:N ratios (8.6–10.6) suggesting a deposition of lipids in the body.

Introduction

Mysidacea (Crustacea, Malacostraca) includes approximately 1000 species and is distributed to freshwater, coastal littoral, epipelagic and abyssopelagic zones of the world's oceans (Mauchline and Murano 1977; Mauchline and Fisher 1980; Meland and Willassen 2007). As plankton or hyperbenthos, mysids feed on a wide range of preys including detritus, phytoplankton, microzooplankton and mesozooplankton, and are preyed upon by a variety of fishes (Mauchline and Fisher 1980).

From global viewpoints, the importance of mysids has long been overlooked in the study of energy flow and matter cycling in aquatic ecosystems. This is particularly true in the marine pelagic realm where their contributions to the total zooplankton abundance and biomass are low (0.17% and 0.01%, respectively, Longhurst 1985). From regional viewpoints, however, mysid populations have been reported to exert variable feeding impacts; 33–154% on secondary production in a tropical lagoon along the Gulf of Guinea shoreline (Kouassi et al. 2006), 1% on zooplankton production in the top 1000 m of the eastern Gulf of Mexico (Hopkins et al. 1994), and < 21% of detrital sedimentation in a coral reef lagoon in the Great Barrier Reef (Carleton and McKinnon 2007).

Information about metabolism [respiration rates, ammonia excretion rates, O:N (as $\text{NH}_4\text{-N}$) ratios] has proved to be useful in understanding the energy demand, major metabolic substrates and nutritional condition of marine zooplankton (cf. Ikeda et al. 2000). While body mass and temperature have been regarded as two major parameters for defining the metabolic characteristics of marine pelagic animals (Ivleva 1980; Ikeda 1985), the habitat depth has emerged as an additional parameter since the observation that metabolic rates decrease rapidly with depth for large pelagic animals with

functional 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 mysids has only been analyzed as a group “crustaceans” together with amphipods, decapods and other crustacean taxa (Childress 1975; Quetin et al.1980; Ikeda 1988; Torres et al. 1994); no analyses have attempted for mysids as an individual taxon.

The metabolic rate of animals is defined with respect to the activity of animals as ‘standard’ or ‘basal’ metabolism (maintenance only), ‘routine’ (uncontrolled but minimum motor activity), and ‘active’ metabolism (enforced activity at a maximal level). Presently available metabolic data of mysids are those derived from 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) are monitored throughout, or determined at the end of the incubation (Ikeda et al. 2000). Thus obtained respiration and ammonia excretion data of mysids without control of their activities are considered to be close to routine metabolism (Ikeda et al. 2000). It is noted that Cowles and Childress (1988) and Buskey (1998) established the relationship between respiration rates and swimming speed in *Mysidium columbiae* and *Gnathophausia ingens*, respectively. According to their results, active metabolism is 2.7 times greater than routine metabolism and routine metabolism is 1.7 times greater than standard metabolism for *M. columbiae*, and respective values were 1.9 and 1.4 times for *G. ingens* (calculated from Fig.3 of Cowles and Childress 1988).

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 results 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 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 or reduced swimming activities in dark environments (Ikeda et al. 2006a). For mysids, 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 mysids I compiled published data of respiration, ammonia excretion, O:N ratio, water content, ash, C, N and C:N ratio of mysids from various bathymetric levels of polar, temperate and tropical/subtropical seas and inland freshwater lakes, and significant parameters attributing to the variance were explored. Body mass, habitat temperature, sampling depth have been used as determinants of metabolic rates as in the global-bathymetric model for pelagic copepods, chaetognaths and euphausiids (Ikeda et al. 2007; Ikeda and Takahashi 2012; Ikeda in press).

Materials and methods

The data compilation

Because of high diversity in habitats, information about metabolism on mysids is widely spread in the literature. 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 considerable time delay (< 24 h).
2. Measurements were made in the absence of food at near *in situ* temperatures and salinities in the dark. For deep-sea mysids, experiments were those undertaken at normal pressure (1 atm) since hydrostatic pressure is known to affect little to the metabolic rates of deep-sea pelagic crustaceans [cf. review of Ikeda et al. (2000)]. This practice, combined with the criterion above, make it possible to compare the data of various mysids 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).

As exceptions, the respiration data of *Gnathophausia ingens* which maintained at near *in situ* temperature for 5–11 days in the laboratory after capture, and those of *Metamysidopsis elongata* raised in the laboratory were included in the present analyses. In case where multiple papers were available on the same species from similar regions, one or two representative data were chosen. Data sets were separated into males and

females if the information was available. *Eucopia grimaldii* (= *E. australis*, cf. Krygier and Murano 1988) and *Meterythropsis microphthalma* were separated into two size-groups (small and large). As a result, a total 38 mysids (including 2 freshwater species) was selected, including 32 species for metabolism data, amongst which simultaneous measurements of respiration and ammonia excretion rates were available on 13 mysids (Table 1). Eighteen data sets of water content and ash, and 24 data sets of C, N and C:N ratios were those on 14 and 20 mysids, respectively (Table 2). Missing habitat temperature data in some literatures in Table 2 were substituted by those in the World Ocean Atlas of the National Oceanography Data Center (NODC) Homepage by knowing location, season and depth. Study sites of all mysids are plotted on the world map (fig. 1) to illustrate the worldwide coverage of the data sets in the present study.

Regression models

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 in press);

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

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

Common to these models, Y is respiration rate ($\mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) or ammonia excretion rate ($\mu\text{gN ind.}^{-1} \text{ h}^{-1}$), X_1 is body mass (mgDM), 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).

It is noted that a_1 was 0.75 (= 3/4) for the theoretical model. As indices of temperature effects, Arrhenius activation energy (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 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.

The effects of body mass, habitat temperature and sampling depth to the chemical composition data were analyzed by the same stepwise multiple regression method, substituting water content, ash, C, N or C:N ratios into Y of the empirical model.

Results

Metabolic rates

Of the mysids considered in the present analyses, the smallest and largest species were *Anisomysis pelewensis* (0.07 mgDM) and *Gnathophausia ingens* (1040 mgDM), respectively. Respiration rates at *in situ* temperature ranged from 0.37 $\mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (*A. pelewensis*) to 235 $\mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (*G. ingens*), and ammonia excretion rates from 0.10 $\mu\text{gN ind.}^{-1} \text{ h}^{-1}$ (*Hemimysis speluncola*) to 13.8 $\mu\text{gN ind.}^{-1} \text{ h}^{-1}$ (*Gnathophausia gracilis*) (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 mysids sampled (< 500 m and ≥ 500 m). Within < 500 m data sets, no marked deviation of the two freshwater data sets from those of marine data sets was obvious. Only the data of < 500 m were used for the analysis of temperature effect on R_0 or E_0 . The resultant slope (−6.788 for respiration rates, and −6.634 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 mysids 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 mysids were correlated negatively with the sampling depth ($p < 0.01$).

The results of stepwise multiple regressions showed that the variable X_3 (sampling depth) was significant ($p < 0.05$) irrespective of the choice of the theoretical or empirical model for respiration rates. For ammonia excretion rates, the variable X_3 was not significant in both theoretical and empirical models ($p = 0.074$ – 0.163), which contrast to the results in Fig 3 where the data were standardized by body mass and temperature (e.g., R_0 or E_0 at 10°C, respectively) and grouped based on a single criterion (mid-sampling depth). As judged by R^2 values, the empirical model was superior to the theoretical model, attributing 85.0% and 73.5%, respectively, for the respiration rates, but models yielded similar results (85.2% and 85.6%, respectively) for ammonia excretion rates (Table 3).

O:N ratios

The O:N ratios ranged from 7.9 (*Rhopalophthalmus africana* adult) to 44.8

(*Gnathophausia gigas* from Prydz Bay, Antarctica) (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 mysids (Fig. 4). The multiple regression analysis of the O:N ratios (pooled data of the two depth groups) on body mass, habitat temperature and mid-sampling depth revealed that neither body mass ($p = 0.916$) nor sampling depth ($p > 0.760$) were significant. The O:N ratios were correlated with habitat temperature ($p = 0.015$), which accounted for 37.7% of the variance in the O:N ratios ($R^2 = 0.377$) (Fig. 4). Mean and median O:N ratio were $20.3 (\pm 10.6, \text{SD})$ and 18.7, respectively.

Chemical composition

Water content varied from 63.0 to 83.4% of WM (mean; 77.6), and ash from 8.9 to 22.9% of DM (13.6), C from 36.8 to 58.1% of DM (46.0), N from 4.8 to 11.5% of DM (8.8), C:N ratios from 3.2 to 11.6 (5.8) (Table 4). Multiple regression analyses between these chemical components and designated parameters (body mass, habitat temperature and mid-sampling depth) revealed that the contribution of these parameters to the variation in water content and ash was insignificant. Among the three parameters, the sampling depth was the only parameter affecting C, N and C:N ratios. Deeper-living mysids exhibited higher C and lower N (Fig. 5), resulting higher C:N ratios.

Discussion

Body mass and habitat temperature as traditional parameters

While no information is currently available for ammonia excretion rates, the respiration rates has been reported as a power function of body mass for many individual mysid species (Table 5). The scale exponent of body mass varied from 0.38

(at 10°C) for *Hemimysis speluncola* to 0.78 for *Neomysis intermedia*, which partially overlaps the 95% CI (0.65–0.86) of that computed from inter-specific data of 31 mysids of the present study. Small differences in the scale exponents may be not important since a large marginal error is associated with it derived from small body mass (DM) ranges. In this regard, the mean scale exponent (0.75 for respiration, and 0.69 for ammonia excretion) computed from inter-specific data (DM range: 4 orders of magnitude) of the present study can be taken as a typical for mysids, as all previous data are from intra-specific data of narrow DM ranges (1 or 2 orders of magnitude). The inter-specific scale exponent of DM body mass of the mysids (0.754) is similar or near similar 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 mysid 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 Q_{10} values thus obtained for acclimated mysid species by previous workers are 1.6–3.3 for respiration rates, and 1.8–4.0 for ammonia excretion rate (Table 5). 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). Inter-specific Q_{10} values (2.1 for respiration rates, and 3.0 for ammonia excretion rates) derived from global data sets of adapted mysids of the

present study overlap these intra-specific Q_{10} values. Taking into account a wide marginal errors (1.5–2.6), Q_{10} value for respiration rates of mysids does not differ significantly from 1.9 for copepods (Ikeda et al. 2007), 1.7 for chaetognaths (Ikeda and Takahashi 2012), and 1.7 for euphausiids (Ikeda in press).

Habitat (= sampling) depth as a new parameter

The effect of habitat depth was significant for respiration rates but not for ammonia excretion rates in mysids 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 multiple regression analyses (see Fig. 3).

The negative effects of habitat depth on respiration rates of mysids 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 with no such eyes including copepods (Ikeda et al. 2006b, 2007), 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. 2006b) have been proposed. These two hypotheses are similar as 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, 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. In terms of size-based classification, most mysids 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 mysids based on the present results (theoretical models in Table 3) showed that the reduction was 0.5 times, which fall within the range of the mixed crustacean taxa by Torres et al. (1994).

O:N ratios

The theoretical minimum O:N ratio is 7 when protein alone catabolized in a zooplankton (Mayzaud and Conover 1988; Ikeda et al. 2000). When protein and lipid or carbohydrate are catabolized in equal quantities at the same time, O:N ratios are calculated as 21 or 13 (mid-point: 17). Thus, the O:N ratio is highly sensitive to the N content of the diets. From this view, the between-species variation (7.9–44.8, Table 2) and median O:N ratio (18.7) of 13 mysids may reflect their diverse food sources (detritus, phytoplankton, microzooplankton and mesozooplankton), yet suggesting the importance of protein as a metabolite. For grazing copepods and euphausiids living high

latitude seas, the O:N ratios have been reported to vary greatly with season [around 8 during active feeding spring season to > 100 during food poor winter season (Conover and Corner 1968; Ikeda and Kirkwood 1989) . While no comparable information is available for shallow-living mysids, Hillar-Adams and Childress (1983) reported no marked seasonal variations in specific respiration and ammonia excretion rates and O:N ratios (mean: 44.3) for the bathypelagic mysid *Gnathophausia ingens* off Southern California, implying that the seasonality in food supply to deep-sea is less marked.

Generalization of the O:N ratio-habitat temperature relationship of the 13 mysids requires a caution because of smaller data sets (N = 15) and regionally biased trophic features of the mysids. Among the three tropical mysids used in the analysis, *Rhopalophthalmus africana* (O:N = 7.9–8.5) and *Siriella thompsoni* (14.4) have been documented as highly carnivorous, based on selective feeding experiments (Kouassi et al. 2006) and stable isotope analyses (Richoux and Froneman 2009), respectively. No information about food habit of *Siriella media* (O:N = 19.6) is not available at present. From the analysis of comprehensive data sets (N = 607), the effect of habitat temperature on O:N ratios has been reported insignificant for diverse zooplankton taxa from the world's oceans (Ikeda 1985).

Chemical composition

Habitat depth was identified as only parameter affecting chemical composition of mysids. With the increase in habitat depth, N composition declined and C composition increased, resulting the increase in C:N ratios (Table 4, Fig. 5). Similar results have already been reported on various marine zooplankton taxa (Ikeda 1974) and copepods

(Båmstedt 1986; Ikeda et al. 2006a). The reduction in N composition in deeper-living mysids implies the decrease in musculature (= protein) in the body or sluggish swimming activity, which is consistent with their lowered respiration rates discussed above.

Based on 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 planktonic crustaceans. On this basis, body C:N ratios of the majority of the mysids in Table 2 of the present study fell into the range of protein-dominated composition. As exceptions, some mysids from > 500 m depth (*Boreomysis californica*, *B. intermedia*, *Eucopia grimaldii*, *Gnathophausia gigas* and *Longithorax fuscus*) exhibited C:N ratios of 8.6–10.6, indicating lipid dominated composition. According to Ikeda (2012), the C:N ratio as high as 13 has been recorded on deep-sea copepods and amphipods. Major lipid classes in *Gnathophausia* spp. have been known as triacylglycerols (Lee et al. 2006), but little has been studied on the function of lipids in deep-sea mysids. 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 74–85% of the variance in respiration rates and 85–86% of the variance in ammonia excretion rates. The scale exponents of body mass and temperature coefficients (Q_{10}) for single mysid species by previous studies overlapped those derived from the global-bathymetric models. The O:N ratios of the mysids suggested that protein is of prime importance as a metabolic substrate in them. Deeper-living mysids were characterized by lower N and higher C composition (result in higher C:N ratios). As judged by body C:N ratios, protein was the major organic component of the body of most mysids (C:N = 3.3–8.4). However, some mysids from > 500 m depth exhibited high C:N ratios (8.6–10.6) indicating a deposition of C-rich organic matter (lipids) in the body.

Acknowledgments

References

- Båmstedt U (1979) Seasonal variation in the respiratory rate and ETS activity of deep-water zooplankton from the Swedish west coast. In: Naylor E, Hartnoll RG (eds.), *Cyclic Phenomena in Marine Plants and Animals*. Pergamon Press, Oxford, pp 267–274
- Båmstedt U (1986) Chemical composition and energy content. In: Corner EDS, O'Hara SCM (eds), *The biological chemistry of marine copepods*. Clarendon Press, Oxford, pp 1–58
- Buskey EJ (1998) Energetic costs of position-holding behavior in the planktonic mysid *Mysidium columbiae*. *Mar Ecol Prog Ser* 172: 139–147
- Carleton JH, McKinnon AD (2007) Resident mysids: secondary production, consumption, and trophic role in a coral reef lagoon. *Mar Ecol Prog Ser* 336: 89–98
- Childress JJ (1975) The respiratory rates of midwater crustaceans as a function of depth occurrence and relation to the oxygen minimum layer off Southern California. *Comp Biochem Physiol A* 50: 787–799
- Childress JJ (1995) Are there physiological and biochemical adaptation of metabolism in deep-sea animals? *Trends Ecol Evol* 10: 30–36
- Clarke A (1987) The adaptation of aquatic animals to low temperatures. In: Grout BWW, Morris GJ (eds), *The effects of low temperatures on biological systems*, Edward Arnold, London, pp 315–348
- Clutter RI, Theilacker GH (1971) Ecological efficiency of a pelagic mysid shrimp; estimates from growth, energy budget, and mortality studies. *Fish Bull* 69: 93–115

394 Conover RJ, Corner EDS (1968) Respiration and nitrogen excretion by some marine
 395 zooplankton in relation to their life cycles. J Mar Biol Ass UK, 48: 49–75
 396 Cowles DL, Childress JJ (1988) Swimming speed and oxygen consumption in the
 397 bathypelagic mysid *Gnathophausia ingens*. Biol Bull 175: 111–121
 398 Donnelly J, Kawall H, Geiger P, Torres JJ (2004) Metabolism of Antarctic
 399 micronektonic crustacea across a summer ice-edge bloom: respiration,
 400 composition, and enzymatic activity. Deep-Sea Res II 51: 2225–2245
 401 Gaudy R, Guérin JP, Pagano M (1980) Écophysiologie comparée des mysidaciés
 402 *Hemimysis speluncola* Ladoyer (cavernicole) et *Leptomysis lingvula* G.O. Sars
 403 (non cavernicole). Respiration et excrétion. J Exp Mar Biol Ecol 44: 24–46
 404 Gorsky G, Dallot S, Sardou J, Fenaux R, Carré C, Palazzoli I (1988) C and N
 405 composition of some northwestern Mediterranean zooplankton and
 406 micronekton species. J Exp Mar Biol Ecol 124: 133–144
 407 Hiller-Adams P, Childress JJ (1983) Effects of season on the bathypelagic mysid
 408 *Gnathophausia ingens*: water content, respiration and excretion. Deep-Sea Res
 409 30: 629–638
 410 Hopkins TL, Flock ME, Gartner JV, Torres JJ (1994) Structure and trophic ecology of a
 411 low latitude midwater decapods and mysid assemblage. Mar Ecol Prog Ser 109:
 412 143–156
 413 Ikeda T (1974) Nutritional ecology of marine zooplankton. Mem Fac Fish Hokkaido
 414 Univ 22: 1–97
 415 Ikeda T (1985) Metabolic rates of epipelagic marine zooplankton as a function of body
 416 mass and temperature. Mar Biol 85: 1–11
 417 Ikeda T (1988) Metabolism and chemical composition of crustaceans from the Antarctic

418 mesopelagic zone. Deep-Sea Res 35: 1991–2002

419 Ikeda T (1991) Ecological and physiological features of the mesopelagic mysid,
 420 *Meterythrops microphthalma*, in the Japan Sea. J Oceanogr Soc Japan 47:
 421 94–103

422 Ikeda T (2012) Metabolism and chemical composition of zooplankton from 500 to
 423 5,000 m depth of the western subarctic Pacific Ocean. J Oceanogr 68: 641–649

424 Ikeda T Respiration and ammonia excretion of euphausiid crustaceans: synthesis
 425 towards a global-bathymetric model. Mar Biol (in press)

426 Ikeda T, Bruce B (1986) Metabolic activity and elemental composition of krill and other
 427 zooplankton from Prydz Bay, Antarctica, during early summer
 428 (November–December). Mar Biol. 92: 545–555

429 Ikeda T, Kirkwood R (1989) Metabolism and body composition of two euphausiid
 430 (*Euphausia superba* and *E. crystallorophias*) collected from under the
 431 pack-ice off Enderby Land, Antarctica. Mar Biol 100: 301–308

432 Ikeda T, Mckinnon DA (2012) Metabolism and chemical composition of zooplankton
 433 and hyperbenthos from the Great Barrier Reef waters, North Queensland,
 434 Australia. Plankton Benthos Res 7: 8–19

435 Ikeda T, Takahashi T. (2012) Synthesis towards a global-bathymetric model of
 436 metabolism and chemical composition of marine pelagic chaetognaths. J Exp
 437 Mar Biol Ecol 424–425: 78–88

438 Ikeda T, Torres JJ, Hernández-León S, Geiger SP (2000) Metabolism. In: Harris RP,
 439 Wiebe PH, Lenz J, Skjoldal HR, Huntley M (eds), ICES zooplankton
 440 methodology manual. Academic Press, San Diego, pp 455–532

441 Ikeda T, Yamaguchi A, Matsuishi T (2006a) Chemical composition and energy content

442 of deep-sea calanoid copepods in the western North Pacific Ocean. Deep-Sea
 443 Res I 53: 1791–1809

444 Ikeda T, Sano F, Yamaguchi A, Matsuishi T (2006b) Metabolism of mesopelagic and
 445 bathypelagic copepods in the western North Pacific Ocean. Mar Ecol Prog Ser
 446 322:199-211

447 Ikeda T, Sano F, Yamaguchi A (2007) Respiration in marine pelagic copepods: a
 448 global-bathymetric model. Mar Ecol Prog Ser 339: 215–219

449 Ivleva IV (1980) The dependence of crustacean respiration rate on body mass and
 450 habitat temperature. Int Revue ges Hydrobiol 65: 1–47

451 Jawd M (1973) Effects of environmental factors and body size on rates of oxygen
 452 consumption in *Archaeomysis grebnitzkii* and *Neomysis awatschensis*
 453 (Crustacea: Mysidae). Mar Biol 21: 173–179

454 Kouassi E, Pagano M, Saint-Jean L, Sorbe JC (2006) Diel vertical migrations and
 455 feeding behavior of the mysid *Rhopalophthalmus Africana* (Crustacea:
 456 Mysidacea) in a tropical lagoon (Ebrié, Côte d'Ivoire). Estuar Coast Shelf Sci
 457 67: 355–368

458 Krygier EE, Murano M (1988) Vertical distribution and zoogeography of oceanic
 459 mysids from the northeastern Pacific Ocean. Bull Ocean Res Inst Univ Tokyo
 460 26: 109–122

461 Kruse S, Brey T, Bathmann U (2010) Role of midwater chaetognaths in Southern
 462 Ocean pelagic energy flow. Mar Ecol Prog Ser.416: 105–113

463 Lasenby DC, Langford RR (1972) Growth, life history, and respiration of *Mysis relicta*
 464 in an Arctic and temperate Lake. J Fish Res Bd Canada 29: 1701–1708

465 Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol

466 Prog Ser 307: 273–306
 467 Longhurst AR (1985) The structure and evolution of plankton communities. Prog
 468 Oceanogr 15: 1–35
 469 Mauchline J, Fisher LR (1967) The biology of euphausiids. Adv Mar Biol 7: 1–454
 470 Mauchline J, Murano M (1977) World list of the Mysidacea, Crustacea. J Tokyo Univ
 471 Fish 64: 39–88
 472 Meland K, Willassen E (2007) The disunity of “Mysidacea” (Crustacea). Mol
 473 Phylogenet Evol 44: 1083–1104
 474 Mayzaud P, Conover RJ (1988) O:N atomic ratio as a tool to describe zooplankton
 475 metabolism. Mar Ecol Prog Ser 45: 289–302
 476 Morioka Y, Nakamura J, Kimoto K (1987) Oxygen consumption and biological
 477 productivity of mysid population in a small inlet of Kyushu. Bull Seikai Reg
 478 Fish Res Lab 65: 115–123
 479 Morris MJ, Hopkins TL (1983) Biochemical composition of crustacean zooplankton
 480 from the eastern Gulf of Mexico. J Exp Mar Biol Ecol 69: 1–19
 481 Ogonowski M, Andersson K, Hansson S (2012) A weight- and temperature-dependent
 482 model of respiration in *Praunus flexuosus* (Cruatacea, Mysidacea) J Plankton
 483 Res 34: 642–645
 484 Omori M (1969) Weight and chemical composition of some important oceanic
 485 zooplankton in the North Pacific Ocean. Mar Biol 3: 4–10
 486 Omori, M. & T. Ikeda 1984. *Methods in marine zooplankton ecology*. John Wiley and
 487 Sons Inc., USA, 332pp
 488 Postel L, Fock H, Hagen W (2000) Biomass and abundance. In: Harris RP, Wiebe PH,
 489 Lenz J, Skjoldal HR, Huntley M (eds), ICES zooplankton methodology manual.

Academic Press, San Diego, pp 83–192

Quetin LB, Ross RM, Uchio K (1980) Metabolic characteristics of midwater zooplankton: ammonia excretion, O:N ratios, and the effect of starvation. *Mar Biol* 59: 201–209

Ranta E, Hakala I (1978) Respiration of *Mysis relicta* (Crustacea, Malacostraca). *Arch Hydrobiol* 83: 515–523

Raymont JEG, Conover RJ (1961) Further investigations on the carbohydrate content of marine zooplankton. *Limnol Oceanogr* 6: 154–164

Richoux NB, Froneman PW (2009) Plankton trophodynamics at the subtropical convergence, Southern Ocean *J Plankton Res* 31: 1059–1073

Scholander PF, Flagg W, Walters V, Irving L (1953) Climatic adaptation in arctic and tropical poikilotherms. *Physiol Zool* 26: 67–92

Seibel, BA, Drazen JC (2007) The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. *Phil Trans.R Soc B* 362: 2061–2078

Sokal RR, Rohlf FJ (1995) *Biometry. The principles and practice of statistics in biological research*. Freeman, New York

Toda H, Arima T, Takahashi M, Ichimura S (1987) Physiological evaluation of temperature effect on the growth processes of the mysid, *Neomysis intermedia* Czerniawsky. *J Plankton Res* 9: 51–63

Torres JJ, Aarset AV, Donnelly J, Hopkins TL, Lancraft TM, Ainley DJ (1994) Metabolism of Antarctic micronektonic Crustacea as a function of depth of occurrence and season. *Mar Ecol Prog Ser* 113: 207–219

Ventura M (2006) Linking biochemical and elemental composition in freshwater and

514 marine crustacean zooplankton. Mar Ecol Prog Ser 327: 233–246
 515 Vilas C, Drake P, Pascual E (2006) Oxygen consumption and osmoregulatory capacity
 516 in *Neomysis integer* reduce competition for resources among mysid shrimp in a
 517 temperate estuary. Physiol Biochem Zool 79: 866–877
 518 Weisse T, Rudstam LG (1989) Excretion and respiration rates of *Neomysis integer*
 519 (Mysidaceae): effects of temperature, sex and starvation. Hydrobiol 178:
 520 253–258
 521 Zeuthen E (1947) Body size and metabolic rate in the Animal Kingdom with special
 522 regard to the marine microfauna. C r Trav Lab. Carlsberg (Sér chim) 26: 17–161
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Figure captions

Fig. 1. Study sites of metabolic rates and chemical composition of mysids. The sites were separated into three groups depending on freshwater (FW) and marine (M) habitats and the latter divided further into shallow (< 500 m) and deep (> 500 M). The number and associated character alongside the symbol corresponds to the code of each mysid listed in Table 1.

Fig. 2. Mysids. 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 : °C) of the specimens from shallow (open triangles; freshwater, open circles; marine from < 500 m) and deep layers (closed triangles; marine from $\geq$ 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. Mysids. 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°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. Mysids. Relationship between O:N (as $\text{NH}_4\text{-N}$) ratios and habitat temperatures. The data points represent means in Tables 2. For symbols see Fig. 2. *: $p < 0.05$

Fig. 5. Mysids. Relationship between N composition and mid-sampling depth. The data points represent means in Tables 2. For symbols see Fig. 2. **: $p < 0.01$.

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

Code	Species	Collection site	Habitat	Date	Reference
1	<i>Acanthomysis pseudomacropsis</i>	Oshoro Bay, W Hokkaido, Japan	Neritic	Jul 1970	Ikeda (1974)
2	<i>Acanthomysis</i> sp.A	Usujiri, SW Hokkaido, Japan	Neritic	May 1971	Ikeda (1974)
3	<i>Acanthomysis</i> sp.B	W. subarctic Pacific Ocean	Oceanic	Mar 2005	Ikeda (2012)
4	<i>Anisomysis lamellicauda</i>	Great Barrier Reef, Australia	Neritic	Jul 1980–May 1981	Carleton & McKinnon (2007)
5	<i>Anisomysis pelewensis</i>	Hidado Island, Kyushu, Japan	Neritic	Jul 1985	Morioka et al. (1987)
6	<i>Antarctomysis maxima</i>	Prydz Bay, Antarctica	Oceanic	Nov 1982	Ikeda & Bruce (1986)
7	<i>Archaeomysis grebnitzkii</i>	San Juan Island, Washington, USA	Littoral	Spring/summer 1970	Jawed (1973)
8	<i>Boreomysis arctica</i>	Kosterfjorden, W. Sweden	Oceanic	Dec–Sep ?	Båmstedt (1979)
9a	<i>Boreomysis californica</i>	Off S. California, USA	Oceanic	1969–1972	Childress (1975)
9b	<i>Boreomysis californica</i>	W. subarctic Pacific Ocean	Oceanic	May 2005	Ikeda (unpublished data)
10	<i>Boreomysis intermedia</i>	W. subarctic Pacific Ocean	Oceanic	May 2005	Ikeda (unpublished data)
11	<i>Boreomysis rostrata</i>	Weddell Sea, Antarctica	Oceanic	Nov–Dec 1993	Donnelly et al. (2004)
12	<i>Charalaspidium</i> sp.	Off S. California, USA	Oceanic	1976–1977	Quetin et al. (1980)
13	<i>Eucopia hanseii</i>	NW Mediterranean	Oceanic	Mar–May 1985	Gorskey et al. (1988)
14	<i>Eucopia grimaldii</i>	W. subarctic Pacific Ocean	Oceanic	Dec 2004, Mar 2005, 2006	Ikeda (2012)
15a	<i>Gnathophausia gigas</i>	Prydz Bay, Antarctica	Oceanic	Dec 1984–Feb.1985	Ikeda (1988)
15b	<i>Gnathophausia gigas</i>	Scotia/Weddell Sea	Oceanic	Nov–Dec 1983, Jun–Aug 1988	Torres et al. (1994)
16	<i>Gnathophausia gracilis</i>	Off S. California, USA	Oceanic	1976–1977	Quetin et al. (1980)
17	<i>Gnathophausia ingens</i>	Off S. California, USA	Oceanic	Sep 1980, Jan 1981, Jul 1981	Hilker-Adams & Childress (1983a)
18	<i>Hemimysis abyssicola</i>	Kosterfjorden, W. Sweden	Neritic	Dec–Sep ?	Båmstedt (1979)
19	<i>Hemimysis speluncola</i>	Submarine cave, Gulf of Marseille, Mediterranean	Neritic	Apr, Oct 1977	Gaudy et al. (1980)
20a	<i>Leptomysis lingvura</i>	Gulf of Marseille, Mediterranean	Neritic	May, Oct 1977	Gaudy et al. (1980)
20b	<i>Leptomysis lingvura</i>	NW Mediterranean	Neritic	Mar–May 1985	Gorskey et al. (1988)
21	<i>Longithorax fuscus</i>	W. subarctic Pacific Ocean	Oceanic	Dec 2004	Ikeda (2012)
22	<i>Mesopodopsis slabberi, female</i>	Guadaluquivir estuary, SW Spain	Littoral	May 2001, Jun 2003	Vilas et al. (2006)
23a	<i>Metamysidopsis elongata, female</i>	Off La Jolla, California	Littoral		Clutter & Theilacker (1971)
23b	<i>Metamysidopsis elongata, male</i>	Off La Jolla, California	Littoral		Clutter & Theilacker (1971)
24	<i>Meterythropsis microphthalma</i>	S Japan Sea	Oceanic	May 1989	Ikeda (1991)
25	<i>Mysidopsis surugae</i>	Hidado Island, Kyushu, Japan	Neritic	Jun 1985	Morioka et al. (1987)
26a	<i>Mysis relicta</i>	Char Lake, N.W.T., Canada	Freshwater		Larsenby & Langford (1972)
26b	<i>Mysis relicta</i>	Lake Pääjärvi, S. Finland*	Freshwater	Feb–Oct 1976	Ranta & Hakala (1978)
27	<i>Neomysis americana</i>	Cape Cod Bay, USA	Neritic	Aug 1959	Raymont & Conover (1961)
28	<i>Neomysis awatschensis</i>	San Juan Island, Washington, USA	Littoral	Spring/summer 1970	Jawed (1973)
29a	<i>Neomysis integer, female</i>	Guadaluquivir estuary, SW Spain	Littoral	May 2001, Jun 2003	Vilas et al. (2006)
29b	<i>Neomysis integer, female</i>	Northern Baltic coast, Sweden	Littoral	Sept 1984	Weisse & Rudstam (1989)
29c	<i>Neomysis integer, male</i>	Northern Baltic coast, Sweden	Littoral	Sept 1984	Weisse & Rudstam (1989)
30	<i>Neomysis intermedia</i>	Lake Kasumigaura, Japan	Freshwater	Apr, Oct 1982	Toda et al. (1987)
31	<i>Praunus flexuosus</i>	N Baltic Sea	Littoral	Sep–Oct 2009	Ogonowski et al. (2012)
32a	<i>Rhopalophthalmus africana, juvenile</i>	Ebrie lagoon, Ivory-Coast	Neritic	Oct–Nov 1997	Kouassi et al. (2006)
32b	<i>Rhopalophthalmus africana, adult</i>	Ebrie lagoon, Ivory-Coast	Neritic	Oct–Nov 1997	Kouassi et al. (2006)
33	<i>Rhopalophthalmus mediterraneus, female</i>	Guadaluquivir estuary, SW Spain	Neritic	May 2001, Jun 2003	Vilas et al. (2006)
34	<i>Siriella aequiremis</i>	NW Pacific Ocean	Oceanic	Dec 1967	Omori (1969)
35	<i>Siriella armata</i>	NW Mediterranean	Oceanic	Mar–May 1985	Gorskey et al. (1988)
36	<i>Siriella media</i>	Great Barrier Reef, Australia	Neritic	Dec 2009	Ikeda & McKinnon (2012)
37	<i>Siriella</i> sp.	Usujiri, SW Hokkaido, Japan	Neritic	May 1971	Ikeda (1974)
38a	<i>Siriella thompsoni</i>	Tropical Indian Ocean	Oceanic	Nov 1971	Ikeda (1974)
38b	<i>Siriella thompsoni</i>	E Gulf of Mexico	Oceanic	Summer 1978	Morris & Hopkins (1983)

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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 mysids. For codes, see Table 1. Code 11 and 21 were separated into two size groups (S: small, L: large). *Italic* values for sampling depth were those not described, and estimated for the present analyses. Blank = no data.

Code	Subcode (size)	Mid-sampling depth	T (°C)	N	Body mass (mg DM ind. ⁻¹)	Respiration (μlO ₂ ind. ⁻¹ h ⁻¹)	Ammonia excretion (μgN ind. ⁻¹ h ⁻¹)	O:N ratio (by atoms)	Body chemical composition				
		(range) (m)							Water (% of WM)	Ash (% of DM)	C (% of DM)	N (% of DM)	C:N (by mass)
1		2 (0–5)	14.9	2	2.9 ± 0.7	4.4 ± 0.1	0.63 ± 0.10	8.6 ± 1.8			44.3	11.3	3.9
2		2 (0–5)	10	1	1.9	3.1	0.13 ±	29.8 ±			41.4	10.7	3.9
3		750 (500–1000)	3	1	12.9	1.3			72.3	8.9	55.1	7.2	7.7
4		10 (8–11)	28.8	15	0.3 ± 0.1	3.0 ± 1.0							
5		6 (5–7)	20	2	0.071 ± 0.001	0.37 ± 0.02							
6		60 (0–120)	-1.6	8	171 ± 52	29.4 ± 8.2	1.97 ± 0.77	19.5 ± 3.5	76.5	13.6	44.1	10.5	4.2
7		<i>I</i>	10	10	1.0	1.4							
8		100 (0–200)	5.5	8	19.2	4.0							
9a		650 (400–900)	5.5	6	12.2	13.4 ± 1.7			82.6	19.0	43.4	7.9	5.5
9b		4000 (3000–5000)	1.5		53.1				81.6	14.4	52.3	5.8	9.1
10		4000 (3000–5000)	1.5		53.8				76.2	11.4	55.2	5.3	10.4
11		100 (0–200)	0.5	1	589	51.4			63.0	5.3			
12		600 (400–800)	5.5	2	280 ± 80	51.2 ± 0.6	3.3 ± 0.1	20.0 ± 0.4					
13		800	13								43.1	7.3	5.9
14	S	750 (500–1000)	3	11	19.9 ± 11.6	1.6 ± 0.8			78.3	9.0	58.0	6.5	8.9
	L	1250 (1000–1500)	2.4	7	82.0 ± 47.3	5.1 ± 2.1			77.4	10.2	58.1	6.5	9.0
15a		600 (200–1000)	0.15	4	127 ± 156	19.2 ± 19.6	0.61 ± 0.61	40.7 ± 21.3	83.4	22.9	41.3	7.3	5.7
15b		500 (0–1000)	0.5	3	131 ± 62	22.3 ± 5.0			71.2	17.8	51.1	4.8	10.6
16		600 (400–800)	5.5	3	930 ± 470	164 ± 34	13.8 ± 3.4	15.0 ± 1.6					
17		550 (400–700)	5.5	3 ^a	1040 ± 135	235 ± 23	6.56 ± 0.52	44.8 ± 1.8	79.2	14.3 ^b	49.2 ^b	6.3 ^b	7.8 ^b
18		100 (0–200)	5.5	1	3.3	1.4							
19		<i>I</i>	14	2	0.8 ± 0.3	1.6 ± 0.0	0.10 ± 0.02	21.1 ± 5.1					
20a		<i>I</i>	14	3	1.7 ± 0.8	3.4 ± 0.8	0.27 ± 0.08	15.6 ± 5.9					
20b		15	15								37.5	11.1	3.4
21		750 (500–1000)	3	1	24.6	2.0			82.9	9.9	55.6	6.5	8.6
22		<i>I</i>	20		0.6	2.4							
23a		<i>I</i>	15.2		0.3	0.55				12.5	36.8	11.5	3.2
23b		<i>I</i>	13.8		0.3	1.1							
24	S	550 (400–700)	0.5	13	5.2 ± 1.7	2.6 ± 1.1			80.3	18.2	40.5	10.0	4.0
	L	550 (400–700)	0.5	20	18.1 ± 4.0	6.9 ± 2.7			79.5	15.2	43.6	9.6	4.6
25		6 (5–7)	20	1	0.607	1.11							
26a		<i>I</i>	2		0.3	0.41							
26b		40	5	209	4.6 ^c	3.4							
27		100	4	2	1.5 ± 0.0	2.0 ± 0.1							
28		<i>I</i>	10	10	2.0	7.4							
29a		<i>I</i>	20		3.2	7.9							
29b		<i>I</i>	16		4.2	9.7	0.59	20.5					
29c		<i>I</i>	16		2.9	8.4	0.47	22.5					
30		<i>I</i>	15	14	1.0	2.0			82.4		45.2	11.3	4.0
31		<i>I</i>	8.2	17	6.2 ± 1.1	3.5 ± 0.7							
32a		2 (0–4.5)	28.5	14	0.16 ± 0.06	3.3 ± 1.3	0.49 ± 0.18	8.5 ± 2.4					
32b		2 (0–4.5)	28.5	16	1.3 ± 0.2	13.3 ± 2.3	2.10 ± 0.53	7.9 ± 2.1					
33		<i>I</i>	20		5.3	10.8							
34		<i>I</i> surface	30		0.98				81.3		42.2	11.0	3.9
35		15	15								43.1	11.4	3.8
36		1 surface	28.5	6	4.1 ± 0.4	16.5 ± 1.1	1.12 ± 0.29	19.6 ± 5.0	69.8	14.2	43.8	10.9	4.0
37		2 (0–5)	9	1	1.1	2.8					39.3	10.9	3.6
38a		2 (0–5)	27.8	2	1.5 ± 0.2	7.5 ± 2.8	0.64 ± 0.15	14.4 ± 2.1			40.3	10.1	4.0
38b		8 (0–15)	28		0.65				79.5	15.3			

^a grand mean of Sept, Jul, and Jan means

^b after Childress & Nygaard (1974)

^c converted from AFDM, assuming ash to be 13.6% of DM (grand mean of 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 mysids on body mass ($X_1: \text{mgDM ind.}^{-1}$), habitat temperature ($X_2: 1000/\text{K}$ for the former, $^{\circ}\text{C}$ for the latter) and depth sampled ($X_3: \text{m}$).

Regression model	N	Step No.	Regression equation:				
			$\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 X_4$				
			a_0	a_1	a_2	a_3	R^2 (adjusted R^2)
Respiration							
Theoretical	42	1		0.75	-8.221		0.712
		2	22.611	0.75	-6.227	-0.108	0.748 (0.735)
Empirical	42	1		0.481			0.641
		2		0.698	0.092		0.842
		3	-0.157	0.755	0.075	-0.115	0.861 (0.850)
Ammonia excretion							
Theoretical	15	1	33.592	0.75	-10.163		0.866 (0.856)
Empirical	15	1		0.374			0.59
		2	-3.272	0.691	0.111		0.873 (0.852)

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Table 4. Multiple regression statistics of chemical composition (Y: water content, ash, C, N or C:N ratio) of mysids on body mass (X_1 : mgDM ind.⁻¹), habitat temperature (X_2 : °C) and depth sampled (X_3 : m). *NS* $p > 0.05$, * $p < 0.05$, ** $p < 0.01$

Y	N	Regression equation: $Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3$				Adjusted R ²
		a_0	a_1	a_2	a_3	
Water (% of WM)	18	78.575**	<i>NS</i>	<i>NS</i>	<i>NS</i>	0.100
Ash (% of DM)	18	12.946*	<i>NS</i>	<i>NS</i>	<i>NS</i>	0.000
C (% of DM)	24	36.529**	<i>NS</i>	<i>NS</i>	1.760*	0.409
N (% of DM)	24	12.805**	<i>NS</i>	<i>NS</i>	-0.674**	0.778
C:N (by mass)	24	<i>NS</i>	<i>NS</i>	<i>NS</i>	0.687*	0.605

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

Amphipod species	Body mass effect		Temperature effect		Reference
	a ₂	Range (mgDM)	Q ₁₀	Range (°C)	
Respiration					
Mixed (31 species)	0.754 (0.645–0.861)	0.3–1040	2.12 (1.47–2.60)	–1.6 to 28.8	This study
<i>Archaeomysis grebnitzkii</i>	0.70	0.20–1.97			Jawed (1973)
<i>Hemimysis speluncola</i>	0.38–0.70	0.58–1.07	2.52–2.62 ^a	10–20	Gaudy et al. (1980)
<i>Leptomysis lingvura</i>	0.56–0.72	0.91–2.40	1.62–1.94 ^a	10–20	Gaudy et al. (1980)
<i>Mesopodopsis slabberi</i>	0.692 ^b	0.06–0.58			Vilas et al. (2006)
<i>Metamysidopsis elongata</i>	0.680	0.03–0.66			Clutter & Theilacker (1971)
<i>Mysis relicta</i>	0.75	0.04–0.9	2.45 ^c	0–8	Lasenby & Langford (1972)
<i>Neomysis awatschensis</i>	0.62	0.48–4.37			Jawed (1973)
<i>Neomysis integer</i>	0.505 ^b	0.08–3.19			Vilas et al. (2006)
<i>Neomysis integer</i> , female			3.3 ^d	6–16	Weisse & Rudstam (1989)
<i>Neomysis integer</i> , male			3.1 ^d	6–16	Weisse & Rudstam (1989)
<i>Neomysis intermedia</i>	0.778	0.07–6.0	1.86	5–25	Toda et al. (1987)
<i>Praunus flexuosus</i>	0.597	5–7 ^e	2.05	3.1–18.7	Ogonowski et al. (2012)
<i>Rhopalophthalmus mediterraneus</i>	0.772 ^b	0.08–5.29			Vilas et al. (2006)
Ammonia excretion					
Mixed (12 species)	0.691 (0.522–0.860)	0.8–1040	3.03 (1.92–4.80)	–1.6 to 28.5	This study
<i>Hemimysis speluncola</i>			2.08–4.01 ^a	10–20	Gaudy et al. (1980)
<i>Leptomysis lingvura</i>			1.79–1.90 ^a	10–20	Gaudy et al. (1980)
<i>Neomysis integer</i> , female			2.1 ^c	6–16	Weisse & Rudstam (1989)
<i>Neomysis integer</i> , male			2.9 ^c	6–16	Weisse & Rudstam (1989)

^a range of seasonal variations

^b at optimal salinity

^c calculated from their data

^d data from 6 h starvation

^e The means of the DMs of the specimens used in the experiments at 4 temperatures

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Ikeda Fig. 1

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Ikeda Fig. 2

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Ikeda Fig. 3

Ikeda Fig. 4

Ikeda Fig. 5