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

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Running head: Global-bathymetric model of amphipod metabolism

Keywords: ammonia excretion, CN composition, global-bathymetric model, mysids, O:N ratio, respiration
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, microzooplanktin 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 NH$_4$-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 Drazan 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 columbiana* 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. columbiana*, 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 musculaturrr 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 ingesns which maintained at near in situ temperature for 5–11 days in the laboratory after capture, and those of Metamysis 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 microphthalmia* 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);

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

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

Common to these models, \( Y \) is respiration rate (\( \mu L O_2 \) ind.\(^{-1}\) h\(^{-1}\)) or ammonia excretion rate (\( \mu g N \) ind.\(^{-1}\) h\(^{-1}\)), \( X_1 \) is body mass (mgDM), \( X_2 \) is habitat temperature (K for the theoretical model, and °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 μlO₂ ind.⁻¹ h⁻¹ (*A. pelewensis*) to 235 μlO₂ ind.⁻¹ h⁻¹ (*G. ingens*), and ammonia excretion rates from 0.10 μgN ind.⁻¹ h⁻¹ (*Hemimysis speluncola*) to 13.8 μgN ind.⁻¹ 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 (*Rhopalophthaalmus 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 (R² = 0.377) (Fig.
4). Mean and median O:N ratio were 20.3 (± 10.6, 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 posses
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 Q10 = 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
zooplankter (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, phyto plankton, 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
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


Ikeda T (1988) Metabolism and chemical composition of crustaceans from the Antarctic


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


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


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


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


Zeuthen E (1947) Body size and metabolic rate in the Animal Kingdom with special regard to the marine microfauna. C r Trav Lab.Carlsberg (Sér chim) 26: 17–161
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 (R₀ or E₀) 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 ≥ 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 (R₀ or E₀) 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 NH₄-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.
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<td>Glaucophasia gracilis</td>
<td>OES, California, USA</td>
<td>Oceanic</td>
<td>1976-1977</td>
<td>Quetin et al. (1980)</td>
</tr>
<tr>
<td>18</td>
<td>Homophylus abbrevicala</td>
<td>Kostenfjorden, W. Sweden</td>
<td>Litoral</td>
<td>Dec-Sep ?</td>
<td>Bimand (1979)</td>
</tr>
<tr>
<td>19</td>
<td>Homophylus gradiscus</td>
<td>Submarine cave, Gulf of Marseille, Mediterranean</td>
<td>Litoral</td>
<td>Apr 1977</td>
<td>Guntay et al. (1980)</td>
</tr>
<tr>
<td>20a</td>
<td>Lepasophthea longiprora</td>
<td>Gulf of Marseille, Mediterranean</td>
<td>Neritic</td>
<td>May, Oct 1977</td>
<td>Guntay et al. (1980)</td>
</tr>
<tr>
<td>21</td>
<td>Longithorax fuscus</td>
<td>W. subarctic Pacific Ocean</td>
<td>Oceanic</td>
<td>Dec 2004</td>
<td>Ikeda (2012)</td>
</tr>
<tr>
<td>23a</td>
<td>Metaphyllosomus elonga, female</td>
<td>Off La Eil, California</td>
<td>Litoral</td>
<td>Clutter &amp; Theilacker (1971)</td>
<td></td>
</tr>
<tr>
<td>23b</td>
<td>Metaphyllosomus elonga, male</td>
<td>Off La Eil, California</td>
<td>Litoral</td>
<td>Clutter &amp; Theilacker (1971)</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>Mygale gryllus</td>
<td>Hikado Island, Kyushu, Japan</td>
<td>Neritic</td>
<td>Jan 1985</td>
<td>Morita et al. (1987)</td>
</tr>
<tr>
<td>26a</td>
<td>Mysis relicta</td>
<td>Char Lake, N.W.T., Canada</td>
<td>Freshwater</td>
<td>Feb-Oct 1976</td>
<td>Ranta &amp; Hakala (1978)</td>
</tr>
<tr>
<td>26b</td>
<td>Mysis relicta</td>
<td>Lake Pääjärvi, S. Finland*</td>
<td>Freshwater</td>
<td>Aug 1959</td>
<td>Baynton &amp; Coverett (1961)</td>
</tr>
<tr>
<td>27</td>
<td>Neomysis americana</td>
<td>Cape Cod Bay, USA</td>
<td>Freshwater</td>
<td>Spring/Summer 1970</td>
<td>Jawed (1973)</td>
</tr>
<tr>
<td>29a</td>
<td>Neomysis integer, female</td>
<td>Guadeloupe, SW Spain</td>
<td>Litoral</td>
<td>Sep 1984</td>
<td>Weise &amp; Rasmussen (1989)</td>
</tr>
<tr>
<td>29b</td>
<td>Neomysis integer, female</td>
<td>Northern Baltic coast, Sweden</td>
<td>Litoral</td>
<td>Sep 1984</td>
<td>Weise &amp; Rasmussen (1989)</td>
</tr>
<tr>
<td>30</td>
<td>Neomysis intermedia</td>
<td>Lake Kasumigaura, Japan</td>
<td>Freshwater</td>
<td>Oct 1982</td>
<td>Toda et al. (1987)</td>
</tr>
<tr>
<td>32a</td>
<td>Rhaphidophthalmus africana, juvenile</td>
<td>Ebrie lagoon, Ivory-Coast</td>
<td>Litoral</td>
<td>Oct-Nov 1997</td>
<td>Kremer et al. (2006)</td>
</tr>
<tr>
<td>33</td>
<td>Rhaphidophthalmus mediterraneus, female</td>
<td>Guadeloupe, SW Spain</td>
<td>Litoral</td>
<td>May 2001, Jan 2003</td>
<td>Vila et al. (2006)</td>
</tr>
<tr>
<td>34</td>
<td>Savigilus aequatorialis</td>
<td>NW Pacific Ocean</td>
<td>Oceanic</td>
<td>Dec 1967</td>
<td>Oono (1968)</td>
</tr>
<tr>
<td>35</td>
<td>Savigilus armatus</td>
<td>NW Mediterranean</td>
<td>Oceanic</td>
<td>Mar-May 1985</td>
<td>Geredy et al. (1988)</td>
</tr>
<tr>
<td>37</td>
<td>Savigilus sp.</td>
<td>Uonpi, SW Hokkaido, Japan</td>
<td>Neritic</td>
<td>May 1971</td>
<td>Ikeda (1974)</td>
</tr>
<tr>
<td>38a</td>
<td>Savigilus thompsoni</td>
<td>Tropical Indian Ocean</td>
<td>Oceanic</td>
<td>Nov 1971</td>
<td>Ikeda (1974)</td>
</tr>
<tr>
<td>38b</td>
<td>Savigilus thompsoni</td>
<td>E Gulf of Mexico</td>
<td>Oceanic</td>
<td>Summer 1978</td>
<td>Morris &amp; Houghton (1983)</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Subcode</th>
<th>T (°C)</th>
<th>N (mg DM ind.−1)</th>
<th>Respiration (μl O₂ ind.−1 h−1)</th>
<th>Ammonia excretion (μg N ind.−1 h−1)</th>
<th>O:N ratio (by atoms)</th>
<th>Water (°W)</th>
<th>Ash (%)</th>
<th>C (%)</th>
<th>N (%)</th>
<th>C:N</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>17</td>
<td>2.0 ± 1.0</td>
<td>2.2 ± 0.9</td>
<td>0.3 ± 0.5</td>
<td>18 ± 1.1</td>
<td>21 ± 0.3</td>
<td>25 ± 0.5</td>
<td>28 ± 0.3</td>
<td>32 ± 0.5</td>
<td>67 ± 0.7</td>
</tr>
<tr>
<td>2</td>
<td>20</td>
<td>1.5 ± 0.2</td>
<td>3.4 ± 1.2</td>
<td>0.2 ± 0.1</td>
<td>12 ± 1.2</td>
<td>18 ± 0.3</td>
<td>25 ± 0.5</td>
<td>28 ± 0.3</td>
<td>32 ± 0.5</td>
<td>67 ± 0.7</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
<td>4.5 ± 2.0</td>
<td>2.3 ± 1.0</td>
<td>0.3 ± 0.1</td>
<td>15 ± 1.1</td>
<td>20 ± 0.3</td>
<td>25 ± 0.5</td>
<td>28 ± 0.3</td>
<td>32 ± 0.5</td>
<td>67 ± 0.7</td>
</tr>
<tr>
<td>4</td>
<td>18</td>
<td>3.5 ± 1.0</td>
<td>4.6 ± 2.0</td>
<td>0.1 ± 0.1</td>
<td>13 ± 1.1</td>
<td>18 ± 0.3</td>
<td>25 ± 0.5</td>
<td>28 ± 0.3</td>
<td>32 ± 0.5</td>
<td>67 ± 0.7</td>
</tr>
<tr>
<td>5</td>
<td>24</td>
<td>5.5 ± 3.0</td>
<td>7.2 ± 3.5</td>
<td>0.0 ± 0.1</td>
<td>10 ± 1.1</td>
<td>18 ± 0.3</td>
<td>25 ± 0.5</td>
<td>28 ± 0.3</td>
<td>32 ± 0.5</td>
<td>67 ± 0.7</td>
</tr>
<tr>
<td>6</td>
<td>30</td>
<td>7.5 ± 4.0</td>
<td>9.3 ± 4.5</td>
<td>0.0 ± 0.1</td>
<td>8 ± 1.1</td>
<td>18 ± 0.3</td>
<td>25 ± 0.5</td>
<td>28 ± 0.3</td>
<td>32 ± 0.5</td>
<td>67 ± 0.7</td>
</tr>
</tbody>
</table>

* grand mean of Sept, Jul, and Jan means

5. after Childress & Nygaard (1974)

6. converted from AFDM, assuming ash to be 13.6% of DM (grand mean of this table)
Table 3. Stepwise (forward selection) multiple regression statistics of theoretical and empirical models of respiration rates \((\text{Y}: \mu l O_2 \text{ind.}^{-1} \text{h}^{-1})\) or ammonia excretion rates \((\text{Y}: \mu gN \text{ind.}^{-1} \text{h}^{-1})\) of mysids on body mass \((X_1: \text{mgDM ind.}^{-1})\), habitat temperature \((X_2: 1000/K \text{ for the former, } ^\circ\text{C for the latter})\) and depth sampled \((X_3: \text{m})\).

Regression equation:
\[
\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 X_4
\]

<table>
<thead>
<tr>
<th>Regression model</th>
<th>N</th>
<th>Step No.</th>
<th>(a_0)</th>
<th>(a_1)</th>
<th>(a_2)</th>
<th>(a_3)</th>
<th>(a_4)</th>
<th>(R^2) (adjusted (R^2))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Respiration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Theoretical</td>
<td>42</td>
<td>1</td>
<td>0.75</td>
<td>-8.221</td>
<td></td>
<td></td>
<td></td>
<td>0.712</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>22.611</td>
<td>0.75</td>
<td>-6.227</td>
<td>-0.108</td>
<td>0.748</td>
<td>(0.735)</td>
</tr>
<tr>
<td>Empirical</td>
<td>42</td>
<td>1</td>
<td>0.481</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.641</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.698</td>
<td>0.092</td>
<td></td>
<td></td>
<td></td>
<td>0.842</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>-0.157</td>
<td>0.755</td>
<td>0.075</td>
<td>-0.115</td>
<td></td>
<td>0.861 (0.850)</td>
</tr>
<tr>
<td>Ammonia excretion</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Theoretical</td>
<td>15</td>
<td>1</td>
<td>33.592</td>
<td>0.75</td>
<td>-10.163</td>
<td></td>
<td></td>
<td>0.866 (0.856)</td>
</tr>
<tr>
<td>Empirical</td>
<td>15</td>
<td>1</td>
<td>0.374</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>-3.272</td>
<td>0.691</td>
<td>0.111</td>
<td></td>
<td></td>
<td>0.873 (0.852)</td>
</tr>
</tbody>
</table>
Table 4. Multiple regression statistics of chemical composition (Y: water content, ash, C, N or C:N ratio) of mysids on body mass (X₁: mgDM ind.⁻¹), habitat temperature (X₂: °C) and depth sampled (X₃: m). NS p > 0.05, * p < 0.05, ** p < 0.01

<table>
<thead>
<tr>
<th>Y</th>
<th>N</th>
<th>Regression equation:</th>
<th>Adjusted R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water (% of WM)</td>
<td>18</td>
<td>Y = a₀ + a₁lnX₁ + a₂X₂ + a₃lnX₃</td>
<td>0.100</td>
</tr>
<tr>
<td>Ash (% of DM)</td>
<td>18</td>
<td>NS</td>
<td>0.000</td>
</tr>
<tr>
<td>C (% of DM)</td>
<td>24</td>
<td>NS</td>
<td>0.409</td>
</tr>
<tr>
<td>N (% of DM)</td>
<td>24</td>
<td>NS</td>
<td>0.778</td>
</tr>
<tr>
<td>C:N (by mass)</td>
<td>24</td>
<td>NS</td>
<td>0.605</td>
</tr>
</tbody>
</table>
Table 5. Effects of body mass (as the scale exponent of body mass = a2 of the regression model adopted in the present study) and temperature (= a3) on respiration and ammonia excretion rates of mysids. The a3 was assessed as Q10 of Van’t Hoff rule. Values in parentheses denote the range of 95% CI.

<table>
<thead>
<tr>
<th>Amphipod species</th>
<th>Body mass effect</th>
<th>Temperature effect</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a2</td>
<td>Range (mgDM)</td>
<td>Q10</td>
</tr>
<tr>
<td>Mixed (31 species)</td>
<td>0.754 (0.645–0.861)</td>
<td>0.3–1040</td>
<td>2.12 (1.47–2.60)</td>
</tr>
<tr>
<td>Archaeomysis grebnitzkii</td>
<td>0.70</td>
<td>0.20–1.97</td>
<td>Jawed (1973)</td>
</tr>
<tr>
<td>Hemimysis spelancola</td>
<td>0.38–0.70</td>
<td>0.58–1.07</td>
<td>2.52–2.62*</td>
</tr>
<tr>
<td>Leptomysis linguva</td>
<td>0.56–0.72</td>
<td>0.91–2.40</td>
<td>1.62–1.94*</td>
</tr>
<tr>
<td>Mesopodopsis slabbert</td>
<td>0.692b</td>
<td>0.06–0.58</td>
<td>Vås et al. (2006)</td>
</tr>
<tr>
<td>Metamysidopsis elongata</td>
<td>0.680</td>
<td>0.03–0.66</td>
<td>Clutter &amp; Theilacker (1971)</td>
</tr>
<tr>
<td>Mysis relicta</td>
<td>0.75</td>
<td>0.04–0.9</td>
<td>Laserly &amp; Langford (1972)</td>
</tr>
<tr>
<td>Neomysis awatschensis</td>
<td>0.62</td>
<td>0.48–4.37</td>
<td>Jawed (1973)</td>
</tr>
<tr>
<td>Neomysis integer</td>
<td>0.505b</td>
<td>0.08–3.19</td>
<td>Vås et al. (2006)</td>
</tr>
<tr>
<td>Neomysis integer, female</td>
<td>3.3d</td>
<td>6–16</td>
<td>Weisse &amp; Rudstam (1989)</td>
</tr>
<tr>
<td>Neomysis integer, male</td>
<td>3.1d</td>
<td>6–16</td>
<td>Weisse &amp; Rudstam (1989)</td>
</tr>
<tr>
<td>Neomysis intermedia</td>
<td>0.778</td>
<td>0.07–6.0</td>
<td>1.86</td>
</tr>
<tr>
<td>Praunus flexuosus</td>
<td>0.597</td>
<td>5–7e</td>
<td>Ogonowski et al. (2012)</td>
</tr>
<tr>
<td>Rhopalophthalmus mediterraneus</td>
<td>0.772b</td>
<td>0.08–5.29</td>
<td>Vås et al. (2006)</td>
</tr>
</tbody>
</table>

Ammonia excretion

<table>
<thead>
<tr>
<th>Amphipod species</th>
<th>Body mass effect</th>
<th>Temperature effect</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a2</td>
<td>Range (mgDM)</td>
<td>Q10</td>
</tr>
<tr>
<td>Mixed (12 species)</td>
<td>0.691 (0.522–0.860)</td>
<td>0.8–1040</td>
<td>3.03 (1.92–4.80)</td>
</tr>
<tr>
<td>Hemimysis spelancola</td>
<td></td>
<td>2.08–4.01*</td>
<td>10–20</td>
</tr>
<tr>
<td>Leptomysis linguva</td>
<td></td>
<td>1.79–1.90a</td>
<td>10–20</td>
</tr>
<tr>
<td>Neomysis integer, female</td>
<td>2.1c</td>
<td>6–16</td>
<td>Weisse &amp; Rudstam (1989)</td>
</tr>
<tr>
<td>Neomysis integer, male</td>
<td>2.9c</td>
<td>6–16</td>
<td>Weisse &amp; Rudstam (1989)</td>
</tr>
</tbody>
</table>

* 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
Legend:
Depth collected: < 500 m
Depth collected: > 500 m

Ikeda Fig. 1
y = 1E+10e^{-7.316x}
R² = 0.7534**

y = 1E+13e^{-9.115x}
R² = 0.8061**
Ikeda Fig. 3

\[ y = 6.158148x^{-0.499} \]
\[ R^2 = 0.5957** \]

\[ y = 1.0285x^{-0.647} \]
\[ R^2 = 0.5383** \]
y = 27.779e^{-0.03x}
R^2 = 0.3767^*
Ikeda Fig. 5

\[ y = -0.65 \ln(x) + 11.543 \]
\[ R^2 = 0.7475^{**} \]

\[ y = 1.38 \ln(x) + 40.241 \]
\[ R^2 = 0.4199^{**} \]