J. Exp. Mar. Biol. Ecol. 445: 79–87 (2013)

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 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 musculaturr 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-bathymetic 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 *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);

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

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 ^{o}C for the empirical model), and X_3: is mid-sampling depth (m).

166 It is noted that a_1 was 0.75 (= 3/4) for the theoretical model. As indices of temperature
167 effects, Arrhenius activation energy (E_a) of the theoretical model and Q_{10} of empirical
168 model could be computed as $E_a = a_2 \times 1000 \times 8.62 \times 10^{-5}$ and $Q_{10} = \exp(10 \times a_2)$,
169 respectively. The attributes of these variables were analyzed simultaneously by using
170 stepwise multiple regression (forward selection) method (Sokal and Rohlf 1995).
171 Independent variables were added and removed at the $p = 0.05$. The calculation was
172 conducted using SYSTAT version 10.2.
173 The effects of body mass, habitat temperature and sampling depth to the chemical
174 composition data were analyzed by the same stepwise multiple regression method,
175 substituting water content, ash, C, N or C:N ratios into Y of the empirical model.
176
177 **Results**
178 **Metabolic rates**
179 Of the mysids considered in the present analyses, the smallest and largest species
180 were *Anisomysis pelewensis* (0.07 mgDM) and *Gnathophausia ingens* (1040 mgDM),
181 respectively. Respiration rates at *in situ* temperature ranged from 0.37 μlO_2 $ind.^{-1}\,h^{-1}$ (*A.*
182 *pelewensis*) to 235 μlO_2 $ind.^{-1}\,h^{-1}$ (*G. ingens*), and ammonia excretion rates from 0.10
183 μgN $ind.^{-1}\,h^{-1}$ (*Hemimysis speluncola)* to 13.8 μgN $ind.^{-1}\,h^{-1}$(*Gnathophausia gracilis*)
184 (Table 2).
185 A preliminary analysis was performed to test the effects of temperature and
186 sampling depth on the rates of respiration (R) and ammonia excretion (E) by first
187 plotting the rates standardized to the rate of specimens weighing 1 mg DM ($R_0 = R \times$

188 $DM^{-0.75}$ or $E_0 = E \times DM^{-0.75}$) against temperature (1000/K or ^oC) where the scale
189 coefficient of body mass was assumed as 0.75 (as in the theoretical model) (Fig. 2). To
190 facilitate analysis, the data were separated into two groups depending on the depth of
191 mysids sampled (< 500 m and ≥ 500 m). Within < 500 m data sets, no marked deviation
192 of the two freshwater data sets from those of marine data sets was obvious. Only the
193 data of < 500 m were used for the analysis of temperature effect on R_0 or E_0. The
194 resultant slope (–6.788 for respiration rates, and –6.634 for ammonia excretion rates) of
195 the regression lines was used to compute R_0 or E_0 at a given temperature (designated as
196 10°C) of the mysids from these sampling depths (< 500 m + ≥ 500 m), which were
197 plotted against the mid-sampling depth (Fig. 3). The standardized R_0 or E_0 at 10°C of
198 these mysids were correlated negatively with the sampling depth ($p < 0.01$).
199 The results of stepwise multiple regressions showed that the variable X_3
200 (sampling depth) was significant ($p < 0.05$) irrespective of the choice of the theoretical
201 or empirical model for respiration rates. For ammonia excretion rates, the variable X_3
202 was not significant in both theoretical and empirical models ($p = 0.074–0.163$), which
203 contrast to the results in Fig 3 where the data were standardized by body mass and
204 temperature (e.g., R_0 or E_0 at 10^oC, respectively) and grouped based on a single
205 criterion (mid-sampling depth). As judged by R^2 values, the empirical model was
206 superior to the theoretical model, attributing 85.0% and 73.5%, respectively, for the
207 respiration rates, but models yielded similar results (85.2% and 85.6%, respectively) for
208 ammonia excretion rates (Table 3).
209
210 **O:N ratios**
211 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 ($R^2 = 0.377$) (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 11.5of 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^{o}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^{o}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 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, phytoplankton, microzooplanktin 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

352 considered as an energy reserve for coping with temporal food scarcity and reproduction,
353 or energy saving for swimming by achieving neutral buoyancy (Lee et al. 2006).
354 In conclusion, global-bathymetric models designed in the present study could
355 explain 74–85% of the variance in respiration rates and 85–86% of the variance in
356 ammonia excretion rates. The scale exponents of body mass and temperature
357 coefficients (Q_{10}) for single mysid species by previous studies overlapped those derived
358 from the global-bathymetric models. The O:N ratios of the mysids suggested that
359 protein is of prime importance as a metabolic substrate in them. Deeper-living mysids
360 were characterized by lower N and higher C composition (result in higher C:N ratios).
361 As judged by body C:N ratios, protein was the major organic component of the body of
362 most mysids (C:N = 3.3–8.4). However, some mysids from > 500 m depth exhibited
363 high C:N ratios (8.6–10.6) indicating a deposition of C-rich organic matter (lipids) in
364 the body.
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366 Acknowledgments
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538 **Figure captions**

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

544 Fig. 2. Mysids. Relationship between the respiration rate (top) or ammonia excretion
545 rate (bottom) standardized to a body size of 1 mg body DM (R_0 or E_0) and
546 temperature (T^{-1}: 1000/K, or T: ^oC) of the specimens from shallow (open triangles;
547 freshwater , open circles; marine from < 500 m) and deep layers (closed triangles;
548 marine from ≥ 500 m). The data points represent means from the data sets in Table 2,
549 and the regression line is derived from shallow layer species only. **: $p < 0.01$.

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

554 Fig. 4. Mysids. Relationship between O:N (as NH_4-N) ratios and habitat temperatures.
555 The data points represent means in Tables 2. For symbols see Fig. 2. *: $p < 0.05$

556 Fig. 5. Mysids. Relationship between N composition and mid-sampling depth. The data
557 points represent means in Tables 2. For symbols see Fig. 2. **: $p < 0.01$.
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Table 1. A list of mysid species of which metabolic and chemical composition data were analyzed.

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

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.

									Body chemical composition				
	Subcode	Mid-sampling depth (range)	T		Body mass	Respiration	Ammonia excretion	O:N ratio	Water	Ash	C	N	C:N
Code	(size)	(m)	(°C)	N	(mg DM ind.$^{-1}$)	(μlO_2 ind.$^{-1}h^{-1}$)	(μgN ind$^{-1}h^{-1}$)	(by atoms)	(% of WM)	(% of DM)	(% of DM)	(% of DM)	(by mass)
1		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		*1*	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		*1*	14	2	0.8 ± 0.3	1.6 ± 0.0	0.10 ± 0.02	21.1 ± 5.1					
20a		*1*	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		*1*	20		0.6	2.4							
23a		*1*	15.2		0.3	0.55				12.5	36.8	11.5	3.2
23b		*1*	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		*10*	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		*1*	10	10	2.0	7.4							
29a		*1*	20		3.2	7.9							
29b		*1*	16		4.2	9.7	0.59	20.5					
29c		*1*	16		2.9	8.4	0.47	22.5					
30		*1*	15	14	1.0	2.0			82.4		45.2	11.3	4.0
31		*1*	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		*1*	20		5.3	10.8							
34		*1* 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: µl O_2 ind.$^{-1}$h^{-1}) or ammonia excretion rates (Y: µgN ind.$^{-1}$h^{-1}) of mysids on body mass (X_1: mgDM ind.$^{-1}$), habitat temperature (X_2: 1000/K for the former, ^{o}C for the latter) and depth sampled (X_3: m).

Regression model	N	Step No.	Regression equation: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 X_4$				
			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: ^{o}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**	*NS*	*NS*	*NS*	0.100
Ash (% of DM)	18	12.946*	*NS*	*NS*	*NS*	0.000
C (% of DM)	24	36.529**	*NS*	*NS*	1.760*	0.409
N (% of DM)	24	12.805**	*NS*	*NS*	–0.674**	0.778
C:N (by mass)	24	*NS*	*NS*	*NS*	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 (^oC)	
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
Archaeomysis grebnitzkii	0.70	0.20–1.97			Jawed (1973)
Hemimysis speluncola	0.38–0.70	0.58–1.07	2.52–2.62[a]	10–20	Gaudy et al. (1980)
Leptomysis lingvura	0.56–0.72	0.91–2.40	1.62–1.94[a]	10–20	Gaudy et al. (1980)
Mesopodopsis slabberi	0.692[b]	0.06–0.58			Vilas et al. (2006)
Metamysidopsis elongata	0.680	0.03–0.66			Clutter & Theilacker (1971)
Mysis relicta	0.75	0.04–0.9	2.45[c]	0–8	Lasenby & Langford (1972)
Neomysis awatschensis	0.62	0.48–4.37			Jawed (1973)
Neomysis integer	0.505[b]	0.08–3.19			Vilas et al. (2006)
Neomysis integer, female			3.3[d]	6–16	Weisse & Rudstam (1989)
Neomysis integer, male			3.1[d]	6–16	Weisse & Rudstam (1989)
Neomysis intermedia	0.778	0.07–6.0	1.86	5–25	Toda et al. (1987)
Praunus flexuosus	0.597	5–7[e]	2.05	3.1–18.7	Ogonowski et al. (2012)
Rhopalophthalmus mediterraneus	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
Hemimysis speluncola			2.08–4.01[a]	10–20	Gaudy et al. (1980)
Leptomysis lingvura			1.79–1.90[a]	10–20	Gaudy et al. (1980)
Neomysis integer, female			2.1[c]	6–16	Weisse & Rudstam (1989)
Neomysis integer, 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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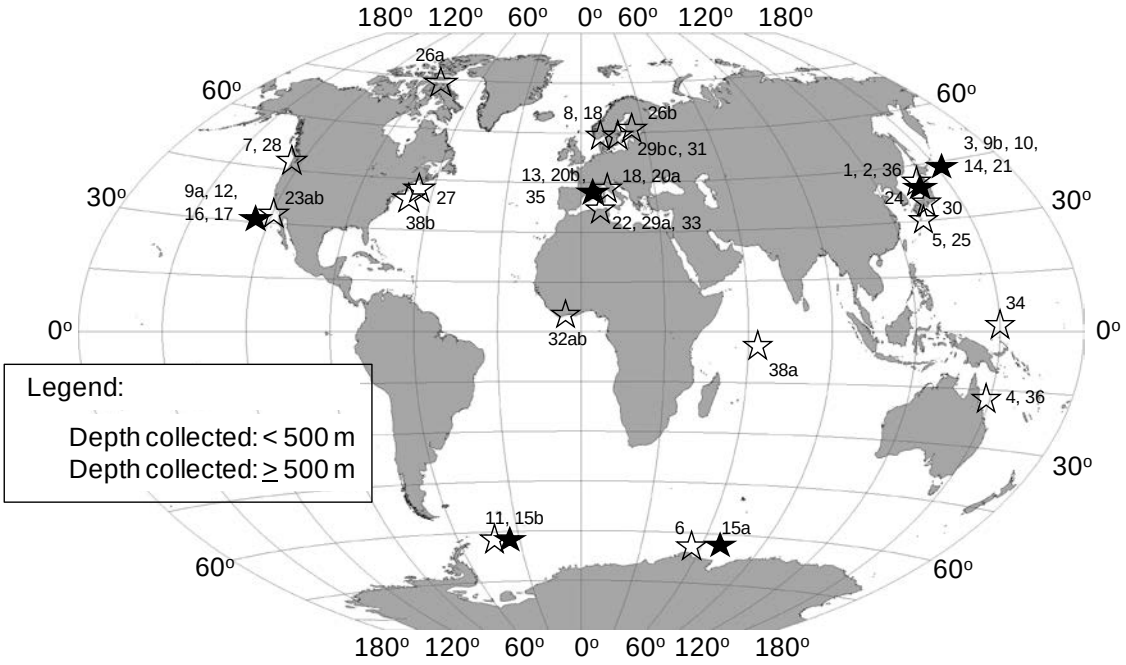
180° 120° 60° 0° 60° 120° 180°
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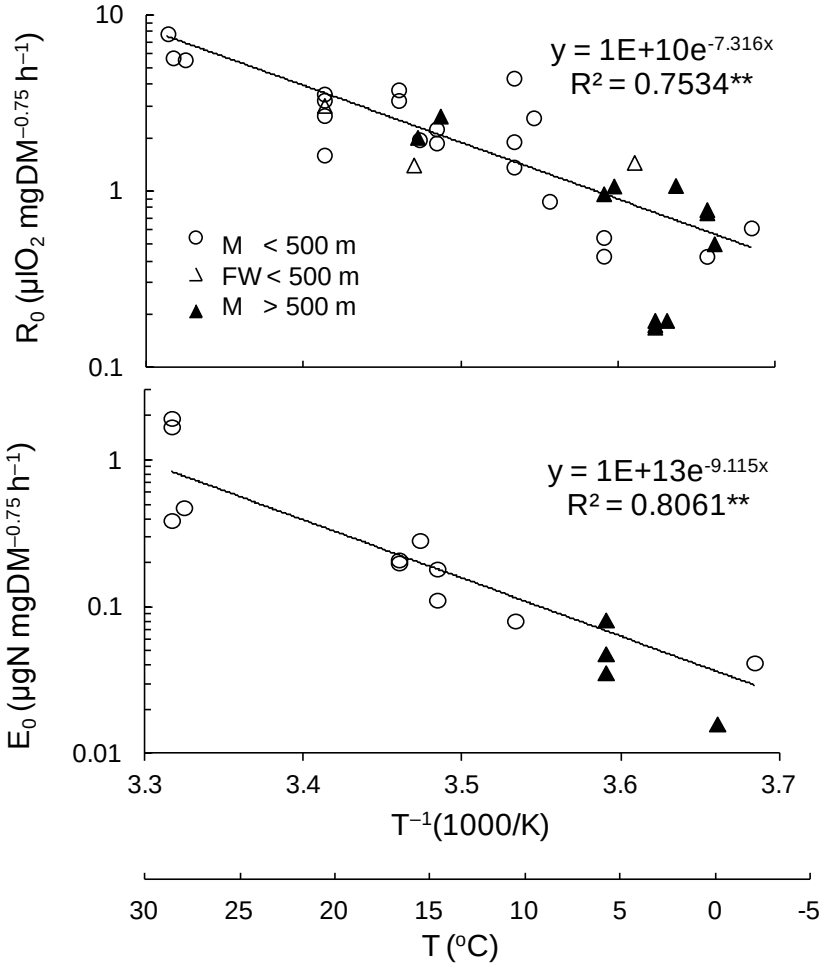
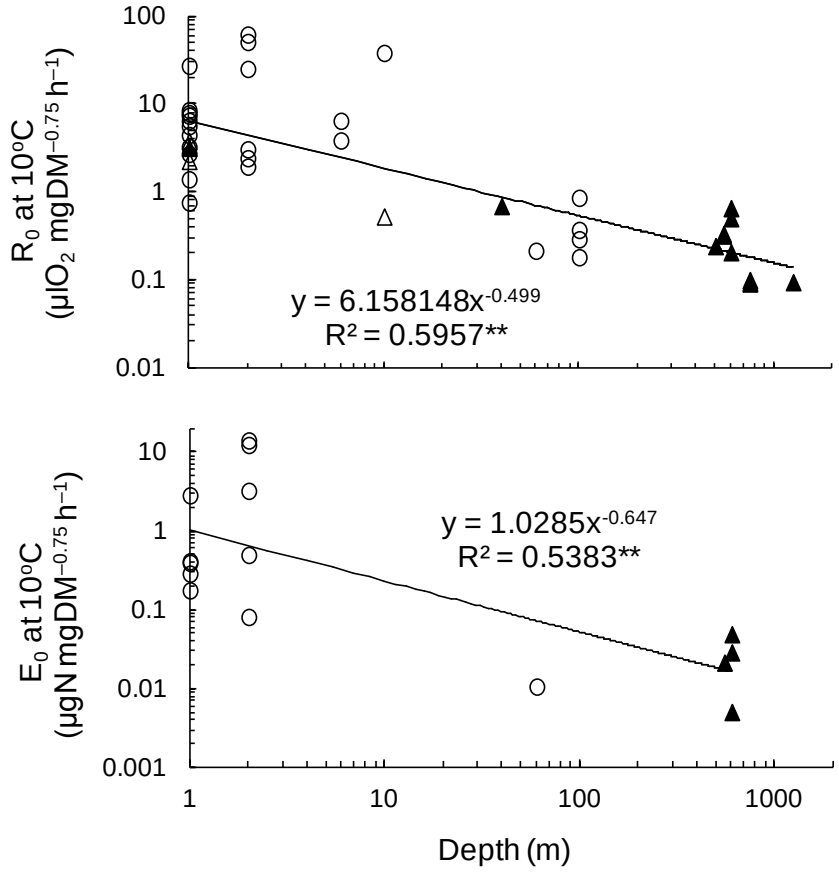
Legend:
Depth collected: < 500 m
Depth collected: ≥ 500 m

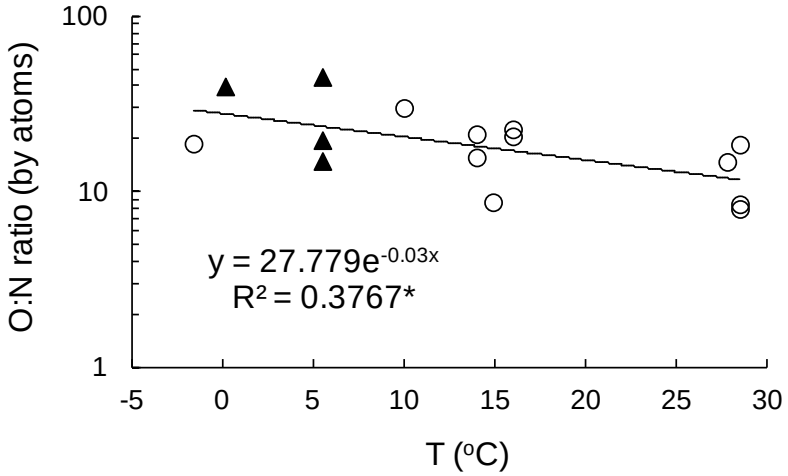
Ikeda Fig. 1


10
1
0.1
R_0 (μlO$_2$ mgDM$^{-0.75}$ h^{-1})
y = 1E+10e$^{-7.316x}$
R² = 0.7534**
M < 500 m
FW < 500 m
M > 500 m
1
0.1
0.01
E_0 (μgN mgDM$^{-0.75}$ h^{-1})
y = 1E+13e$^{-9.115x}$
R² = 0.8061**
3.3
3.4
3.5
3.6
3.7
T^{-1}(1000/K)
30
25
20
15
10
5
0
-5
T (°C)

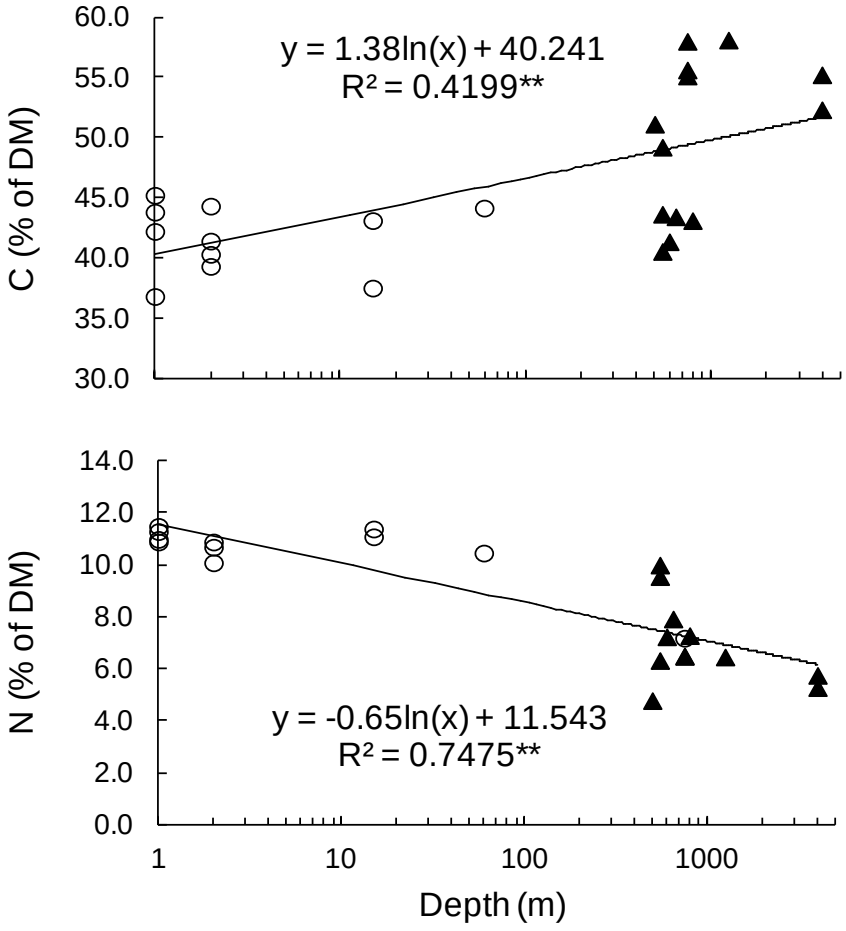
Ikeda Fig. 2


100
10
1
0.1
0.01
R_0 at 10°C
(µlO_2 mgDM$^{-0.75}$ h^{-1})
y = 6.158148x$^{-0.499}$
R² = 0.5957**
10
1
0.1
0.01
0.001
E_0 at 10°C
(µgN mgDM$^{-0.75}$ h^{-1})
y = 1.0285x$^{-0.647}$
R² = 0.5383**
1
10
100
1000
Depth (m)

Ikeda Fig. 3


100
10
1
O:N ratio (by atoms)
y = 27.779e-0.03x
R² = 0.3767*
-5
0
5
10
15
20
25
30
T (ºC)

Ikeda Fig. 4


y = 1.38ln(x) + 40.241
R² = 0.4199**
C (% of DM)
60.0
55.0
50.0
45.0
40.0
35.0
30.0
y = -0.65ln(x) + 11.543
R² = 0.7475**
N (% of DM)
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
1
10
100
1000
Depth (m)

Ikeda Fig. 5

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