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Respiration and ammonia excretion of euphausiid crustaceans: synthesis toward a global-bathymetric model

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Running head: Global-bathymetric model of euphausiid metabolism

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ABSTRACT

Respiration and ammonia excretion rates of 19–24 euphausiids from the epipelagic through bathypelagic zones of the world's oceans were compiled. Body mass (expressed in terms of dry mass, carbon or nitrogen), habitat temperature and sampling depth were designated as parameters in multiple regression analysis. Results suggested that the three parameters were highly significant, contributing 71–89 % of the variance in respiration rates and 69–81% of the variance in ammonia excretion rates. Atomic O:N ratios derived from simultaneous measurements of respiration and ammonia excretion rates ranged from 11 to 90 (median: 27), and no appreciable effects of the three parameters on O:N ratios were detected. If global-bathymetric models for the metabolism and chemical composition of copepods and chaetognaths are compared with those of euphausiids, it becomes evident that euphausiids are unique in that they maintain high metabolic rates and accumulate moderate amounts of energy reserves (lipids).

Introduction

The order Euphausiacea (euphausiids) has 85 species and is distributed from epipelagic to bathypelagic depths in the world's oceans (Mauchline 1980). Euphausiids are an important link between primary production and production of fish, squids, marine mammals and seabirds (Mauchline and Fisher 1969; Mauchline 1980). Moreover, they are a major contributor to world plankton community biomass (21%), second only to copepods (47%), in terms of their total organic carbon (Longhurst 1985). Many euphausiids undertake diel vertical migrations (DVMs) of 400-500 m (Brinton 1967), a behavior which is regarded as an important mechanism of rapid vertical transport of materials in the pelagic realm of the ocean (Longhurst et al. 1990; Hidaka et al. 2001).

Information about metabolism [respiration rates, ammonia excretion rates, and O:N (as NH_4-N) ratios] has proven to be useful in understanding the energy demand, major metabolic substrates and nutritional condition of marine zooplankton (cf. Ikeda et al. 2000). Although body mass and temperature have been regarded as the two major parameters for defining the metabolic characteristics of marine epipelagic animals (Ivleva 1980; Ikeda 1985), habitat depth has emerged as an additional parameter since the observation that metabolic rates decrease rapidly with depth for larger pelagic animals with image-forming 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 euphausiids has only been analyzed together with mysids, decapods and other crustacean taxa (Childress 1975; Quetin et al.1980; Ikeda 1988; Torres et al. 1994); no analyses have attempted for euphausiids as an individual taxon.

To evaluate global-bathymetric patterns in the metabolism of euphausiids, I

compiled published and unpublished data of respiration, ammonia excretion and O:N ratios of euphausiids living at various depths in polar, temperate and tropical/subtropical seas, and significant parameters affecting the variance were explored. Body mass, habitat temperature, sampling depth and ambient oxygen saturation have been used as determinants of metabolic rates as in the global-bathymetic model for pelagic copepods and chaetognaths (Ikeda et al. 2007; Ikeda and Takahashi 2012). Finally, the present results were compared with those of copepods and chaetognaths to highlight any unique global-bathymetric features of euphausiids.

Materials and methods

The data

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). In most studies on euphausiid metabolism, no attempts have been made to relate the metabolic data to the level of activity on the premise that the measured rates are close to routine metabolism (Ikeda et al. 2000). As a notable exception, Torres and Childress (1983) established the relationship between respiration rates and swimming speed in the migrating euphausiid *Euphausia pacifica*. To date, intensive studies of the metabolic rates have been made on some euphausiids, including *E. pacifica* in the northern North Pacific (Ross 1982 and citations therein), *E. superba* in the Southern Ocean (Clarke and Morris 1983) and *Meganyctiphanes norvegica* in the northern North Atlantic (Saborowski et al. 2002). However, available information about metabolism on the other euphausiids is scarce and widely spread in the literature. For the present

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

1. Data represented post-larvae (juveniles and adults) collected from the field and used for experiments without considerable time delay (< 24 h).

2. Measurements were made in the absence of food at near *in situ* temperatures in the dark [and at normal pressure (1 atm) for deep-sea euphausiids on the premise that the hydrostatic pressure affects little to the metabolic rates of deep-sea pelagic crustaceans, cf. review of Ikeda et al. (2000)]. This practice, combined with the criterion above, makes it possible to compare the data of various euphausiids 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), carbon (C) or nitrogen (N) units were given together with metabolic data (note: body mass specific rates without body mass data are not useful).

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

In cases where multiple papers (including those of the present author) were available on the same species from similar regions, preference was given to mine to reduce possible between-workers bias in the data. As a result, a total of 39 data sets from 24 euphausiids for respiration rates, and 31 data sets from 19 euphausiids were selected and analyzed in the present study (Table 1). Data sets were separated into juveniles, females, gravid females, and males if the information was available. The same euphausiids but from different locations were treated as independent data sets, though mere repetition of the data on the same euphausiids was carefully avoided. The data expressed in the form of regression equations only were converted to the

116 respiration rates of a specimen at mid-body mass ranges. Study sites of all euphausiids
117 are plotted on the world map (Fig. 1) to illustrate the worldwide coverage of the data
118 sets in the present study.
119
120 **Regression model**
121 In addition to the 2 conventional independent variables (X_1: body mass; and X_2:
122 habitat temperature) used in the previous global respiration model for marine epipelagic
123 crustaceans (Ivleva 1980; Ikeda 1985), one new independent variables (X_3:
124 mid-sampling depth) were introduced to the present analyses。X_1 was expressed as DM,
125 C or N since the choice of the body mass unit is known to affect the results (Ivleva
126 1980; Ikeda 1985). Initially, ambient oxygen saturation was introduced as an another
127 new independent variable, but removed in the following analyses because of high
128 correlation (R = –0.758) with the sampling depth. For the species on which C and/or N
129 composition data are not reported, the missing values were substituted with those of the
130 same species studied by other workers, or with grand mean values for all euphausiids of
131 the present study.
132 Two regression models were adopted according to the mathematical form of the
133 temperature and body mass effects. One was a theoretical model characterized by the
134 Arrhenius relationship ($R = R_0M^{3/4}e^{-Ea/kT}$ or $E = E_0M^{3/4}e^{-Ea/kT}$, where R is respiration
135 rate, E is ammonia excretion rate, M is body mass, T is absolute temperature, 3/4 is
136 theoretical body mass exponent, *E*a is an average activation energy for the rate-limiting
137 enzyme-catalyzed biochemical reactions of metabolism, *k* is Boltzmann's constant (8.62
138 $\times 10^{-5}$ eV K^{-1}) and R_0 or E_0 is a normalization constant (cf. Gillooly et al. 2001) and the

other was empirical (or log/linear) model characterized by the Van't Hoff rule (Q_{10}) (Ikeda 1985; Ikeda and Takahashi 2012);

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

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

It is noted that a_1 was 0.75 (= 3/4) for the theoretical model. As indices of temperature effects, *E*a of the theoretical model and Q_{10} of empirical model could be computed as $Ea = a_2 \times 1000 \times 8.62 \times 10^{-5}$ and $Q_{10} = \exp(10 \times a_2)$, respectively The attributes of these variables were analyzed simultaneously by using stepwise multiple regression (forward selection) (Sokal and Rohlf 1995). Independent variables were added and removed at $p = 0.05$. The calculation was conducted using SYSTAT version 10.2.

Results

Metabolic rates

Of the euphausiids considered in the present study, the smallest and largest species were *Euphausia krohnii* (0.29 mgDM) and *Thysanopoda cornuta* (1405 mgDM), respectively (Table 2). Respiration rates at *in situ* temperature ranged from 0.43 μlO_2 ind.$^{-1}$ h^{-1} (*Thysanoessa macrura* from the Scotia Sea) to 109 μlO_2 ind.$^{-1}$ h^{-1} (*Thysanopoda cornuta*), and ammonia excretion rates from 0.026 μgN ind.$^{-1}$ h^{-1} (*Thysanoessa macrura* juveniles from the Scotia Sea) to 7.44 μgN ind.$^{-1}$ h^{-1}.(*Euphausia superba* gravid females off Wilkes Land, Antarctica) (Table 2).

Prior to the stepwise multiple regression analyses, preliminary analysis was made for the effects of temperature and sampling depth on the rates of respiration (R) and

ammonia excretion (E) by first plotting the rates standardized to 1 mg DM ($R_0 = R \times DM^{-0.75}$ or $E_0 = E \times DM^{-0.75}$) against temperature (1000/K or ^oC) 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 euphausiids sampled (< 500 m and ≥ 500 m). It is clear that the values for species from ≥ 500 m depth distribute well below the rates <500 m at equivalent inverse temperature or temperature. Because of this result, only the data of <500 m were used for the analysis of temperature effects on R_0 or E_0. The resultant slope (–4.119 for respiration rates, and –5.214 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 euphausiids from these sampling depths (< 500 m + ≥ 500 m), which were plotted against the mid-sampling depth (Fig. 3). The standardized rates (R_0 or E_0 at 10°C) of these euphausiids were correlated negatively with the sampling depth ($p < 0.01$).

The overall results of stepwise multiple regressions showed that the three independent variables were highly significant (*F*-test, $p < 0.001$). As judged by R^2 values, the empirical model was superior to the theoretical model, accounting for 85.7–89.0% vs 71.2–74.0%, respectively, of the variability in respiration, and 78.2–80.6% vs 69.0–70.6%, respectively, for the ammonia excretion rates (Table 3). As a body mass unit, N yielded the best fit, excepting the theoretical model of ammonia excretion rates for which C yielded the best fit. Overall, the choice of body mass units affected little to R^2 values.

The multiple regression analyses yielded results similar to those of the simple regression analyses (Figs. 2, 3) in which respiration rates or ammonia excretion rates were standardized by body mass and temperature (e.g., R_0 or E_0 at 10^oC, respectively)

and grouped based on a single criterion (mid-sampling depth or ambient oxygen saturation).

O:N ratios

The atomic ratio of oxygen consumption rate to ammonia-nitrogen excretion rate (O:N ratio) has been used as an index of the proportion of protein in the diet of marine zooplankton (Mayzaud and Conover 1988; Ikeda et al. 2000). When only protein is metabolized, the O:N ratio is 7 (Table 10.3 in Ikeda et al. 2000). When protein and lipid or carbohydrate are catabolized in equal quantities O:N ratios are calculated as 21 or 13. Hence, O:N ratios of 7–17 (mid-point of 21 and 13) may be used as an index of protein-oriented metabolism and ratios of >17 as lipid/carbohydrate-oriented metabolism.

A total of 31 O:N ratios from 19 euphausiids ranged from 11 (*Euphausia mutica*) to 90 (*Euphausia pacifica* female from the western subarctic Pacific). The O:N data were separated into two depth groups (< 500 m and ≥ 500 m) and plotted against habitat temperature of the euphausiids (Fig. 4). While the number of data from the ≥ 500 m group were limited to only two, they fall well within the range of those of the < 500 m group (*U*-test, $p = 0.904$). The correlation between the O:N ratios (pooled data of the two depth groups) and temperature was significant ($p < 0.05$) but the contribution of temperature to the variance in the O:N ratios was only 15% (R^2). Mean and median O:N ratio were 30.0 (± 17.4, SD) and 27.1, respectively.

Discussion

Body mass and temperature as traditional parameters

The effects of body mass and temperature on respiration rates of euphausiids have been studied most intensively in *Euphausia pacifica*, an intermediate-sized species that is important throughout the North Pacific including west coast of North America (Small and Hebard 1967; Paranjape 1967; Ross 1982). Earlier studies showed that the respiration rates of *E. pacifica* were not a power function of body mass but scaled directly with it (e.g. a_3 = 1.0 in the regression models of the present study, cf. Table 3). Later, Ross (1982), working on a broader size range of *E. pacifica* specimens raised in the laboratory (0.01–3 mgC or 2 orders of magnitude as compared with 1–10 mg DM or 1 order of magnitude for the earlier workers), demonstrated that the rates were indeed a power function of body mass (a_3 = 0.7–0.8, as has been reported for diverse animal taxa (Zeuthern 1947). The range of DM for the 24 euphausiids considered in the present study was 4 orders of magnitude (Table 2) and resultant a_3 from the empirical models in which the attributes of body mass and ambient oxygen saturation were taken into account was 0.78–0.79 (depending on the choice of body mass units; DM, C or N) for respiration rates and 0.80–0.81 for ammonia excretion (Table 3).

The effect of temperature on metabolism has been studied in individual euphausiid species at graded temperatures within the range of their habitats. According to the definition by Clarke (1987), this is “acclimation” (adjustment of an organism to a new temperature in the laboratory), in contrast to “adaptation” (the evolutionary adjustment of an organism’s physiology to environment). The activation energy (*E*a) or Q_{10} values thus obtained for acclimated euphausiids by previous workers are 0.63–0.67 eV or 2.0–3.5 (Table 4). Similar intra-specific Q_{10} values (2–3) are typical for the respiration rates measured at graded temperatures within the ranges of natural habitats of acclimated aquatic fishes and crustaceans living in arctic and tropical regions

234 (Scholander et al. 1953). On the other hand, inter-specific *E*a or Q_{10} values (0.35 or 1.7)
235 derived from global data sets of adapted euphausiids are less than these intra-specific
236 values, but similar to those from global compilation of inter-specific data of adapted
237 pelagic copepods, chaetognaths, teleost fishes and crustaceans (Table 4). Analyzing the
238 effect of temperature on 69 teleost fishes from polar to tropical regions, Clarke and
239 Johnston (1999) noted that a Q_{10} = 1.83 derived from inter-specific data over the
240 temperature range 0–30^{o}C was smaller than typical intra-specific acclimated Q_{10} values
241 in the literature (median: 2.40, N = 138), as is the case for euphausiids of the present
242 study. Those results suggest that evolutionary temperature adaption has produced an
243 inter-specific relationship that has a lower thermal sensitivity than is typical of
244 intra-specific relationships (cf. Clarke and Johnston 1999).
245
246 **Habitat (sampling) depth as a new parameter**
247 The present results of negative effects of habitat depth on respiration rates of
248 euphausiids are consistent with those of larger pelagic animals with image-forming eyes
249 such as micronektonic crustaceans, cephalopods and fishes (Torres et al. 1994;
250 Childress 1995; Seibel and Drazen 2007), and zooplankton with no such the eyes
251 including copepods (Ikeda et al. 2006, 2007) and chaetognaths (Kruse et al. 2011; Ikeda
252 and Takahashi 2012). For the progressive decline in respiration rates in deeper-living
253 micronekton and zooplankton, the “visual-interactions hypothesis” (Childress 1995) or
254 “predation-mediated selection hypothesis” (Ikeda et al. 2007) have been proposed
255 respectively. These two hypotheses are similar as both interpret the phenomena as a
256 result of lowered selective pressure for high activity at depth because of the decrease in
257 visual predators in the dark. However, these two hypotheses are different in that the

former applies strictly to micronekton with functional eyes, and the latter to both micronekton and zooplankton irrespective of presence/absence of functional eyes.

Torres et al. (1994) compiled the relationship between respiration rates and the depth of occurrence for pelagic crustaceans (amphipods, decapods, euphausiids, isopods, mysids and ostracods) off California, the Gulf of Mexico, off Hawaii and Antarctic waters. According to their results, the respiration rates [standardized to a body size of 1 mg wet mass by using the body mass exponent of 0.75 (equivalent to the theoretical model adopted in the present study), and at 0.5^{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 euphausiids based on the present results (theoretical models in Table 3) showed that the reduction was 0.5–0.6 times, depending on the choice of DM, C or N body mass unit, which is close to the upper range of the values for the mixed crustacean taxa by Torres et al. (1994).

Accompanied with reduction in respiration rates, lowered swimming activity of deeper-living pelagic crustaceans has also been demonstrated by higher water, lower protein or lower N content (= reduced muscles) of their bodies (Childress and Nygaard 1973, 1974; Ikeda et al. 2006). For euphausiids only, presently available data are too small to allow precise analysis of depth-related patterns in the body chemical composition of this taxon.

Ammonia excretion and O:N ratios

While no global-bathymetric model is presently available for ammonia excretion rates of marine zooplankton including euphausiids, global ammonia excretion models with two parameters (body mass, habitat temperature) for mixed zooplankton taxa

(Ikeda 1985) and for planktonic copepods (Ikeda et al. 2001) yielded a body mass exponent and Q_{10} similar to those for respiration rates. With regard to the effect of habitat depth, lowered ammonia excretion rates of deep-sea euphausiids have already been reported on the bathypelagic *Bentheuphausia ambloyops* (Quetin et al. 1980) and mesopelagic *Euphausia tricantha* (Ikeda 1988). Parallel changes in respiration and ammonia excretion rates are anticipated in other species. In support of this hypothesis, O:N ratios (mean; 30.0 ± 17.4, median; 27.1) and body C:N ratios (4.0 ± 0.7, see below) were observed to be largely stable across the 24 euphausiids considered in this study (Table 2). Insignificant effects of body mass and habitat temperature on O:N ratios have already been reported on mixed zooplankton taxa (Ikeda et al. 2001) and pelagic copepods (1985).

It is noted that the O:N ratios of euphausiids listed in Table 2 are derived from experiments in which they were placed in filtered seawater, a common practice when using the sealed-chamber method (Ikeda et al. 2000). Use of filtered seawater is imperative to determine the rates of respiration and ammonia excretion accurately without any corrections for complex uptake/release of oxygen and ammonia by food organisms, but starvation of euphausiids may influence their normal metabolism. Ikeda and Dixon (1984) examined the effect of methodological problems associated with the sealed chamber method on *Euphausia superba*. According to their results, respiration and ammonia excretion rates of wild *E. superba* in which daily ration is 5% are 1.6 and 4.5, respectively, times the rates of non-feeding krill in 24 h laboratory experiments. From these results, the O:N ratios of wild *E. superba* are calculated as 0.36 (= 1.6/4.5) times less than those of the non-feeding *E. superba.* Generalization of the results of *E. superba* to other euphausiids requires caution since no comparable data are available for

306 the other euphausiids.

307

308 **Euphausiids as compared with copepods and chaetognaths**

309 The present results for euphausiids can be put into a wider perspective if
310 compared with global-bathymetric models presented for pelagic copepods and
311 chaetognaths (Table 5). As an important group within the marine zooplankton,
312 euphausiids are different from copepods and chaetognaths in that they are active
313 swimmers, with well developed compound eyes and respiratory organs (gills). For a
314 specimen with similar body mass (1 mg N) living in the epipelagic zone (100 m depth,
315 and 100% oxygen saturation) of temperate latitudes (20^{o}C), predicted respiration rates
316 from the theoretical or empirical model (17.9 or 18.3 μlO_2 ind.$^{-1}$ h^{-1}) of euphausiids are
317 the greatest followed by that (10.2 or 12.3 μlO_2 ind.$^{-1}$ h^{-1}) of copepods and that (5.1 or
318 7.9 μlO_2 ind.$^{-1}$ h^{-1}) of chaetognaths. The rank of high to low remains unchanged but for
319 the specimen living in the bathypelagic zone (1000 m, 5^{o}C and 10% oxygen saturation).
320 Higher respiration rates of euphausiids may be related to their active swimming as
321 compared with copepods or chaetognaths. Large standard deviations (SD) associated
322 with the mean O:N ratios of the three taxa suggest non-normal distribution of the O:N
323 data. Thus, the medians rather than means are thought to provide better index of the
324 central trend. High metabolic O:N ratios (median; 27.1) of euphausiids are indicative of
325 their carbohydrate/lipid-oriented metabolism in contrast to protein-oriented metabolism
326 in chaetognaths (median; 12.2), which are consistent with the food habits of these taxa.
327 In terms of body chemical composition, chaetognaths are different from euphausiids and
328 copepods by their considerably higher water content (84–95% of WM) and low upper
329 range values of C:N ratios (< 5.1) as compared with respective values (< 84% of WM

330 and 8.6–9.4) of euphausiids and copepods. According to Ventura (2006), C:N ratio of
331 crustacean plankton protein is 3.3, and it is 8.4 for organic matter composed of equal
332 amounts of protein and lipids (as wax esters). Carbohydrate is omitted as it comprises <
333 8.5% of DM. On this basis, very high C:N ratios (3.7–9.4) of copepods are due to the
334 accumulation of lipids by species inhabiting cold thermal regimes (high latitude seas,
335 deep-seas) where they function as an energy reserve for coping with temporal food
336 scarcity, for reproduction or for achieving neutral buoyancy as is seen in diapausing
337 copepods (Lee et al. 2006). Judging from the C:N ratios, presently available data
338 suggest that the accumulation of lipids in the body of euphausiids is modest among the
339 three taxa (Table 5). To date, the maximum lipid content reported is as high as 70% of
340 DM or more for *Rhincalanus*, *Metridia*, *Calanus* and *Neocalanus* copepods (Lee et al.
341 2000), and is around 50% for *Thysanoessa* euphausiids (Lee et al. 2000; Harvey et al.
342 2012), all in high latitude seas. Major lipid class is wax esters for copepods while this is
343 phospholipids and triacylglycerols for euphausiids.
344 In conclusion, global-bathymetric compilation of respiration and ammonia
345 excretion rate data in 19–24 euphausiids revealed that the rates are a function of body
346 mass, habitat temperature and habitat depth. The O:N ratios were largely independent
347 from these parameters. The present results from inter-specific analyses of respiration
348 data are compared with those from intra-specific analyses by previous workers,
349 indicating similar body mass effects but dissimilar thermal sensitivities (lower E_a or Q_{10}
350 of the former than the latter). The reduction in metabolic rates of deeper-living
351 euphausiids was close to the upper range of those having been reported on pelagic
352 crustaceans. Global-bathymetric comparison of the present results with those of pelagic
353 copepods and chaetognaths revealed taxon-specific respiration rates and metabolic O:N,

as the possible reflect of dissimilar swimming patterns, food habits and body structures (water content, C:N ratios) among these taxa.

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Figure captions

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

Fig. 2. Euphausiids. 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: ^{o}C) of the specimens from shallow (< 500 m) and deep layers (≥ 500 m). The data points represent means from the data sets in Table 2, and the regression line is derived from shallow layer species only. **: $p < 0.01$.

Fig. 3. Euphausiids. 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. Euphausiids. Relationships between O:N (as NH_4-N) ratios and habitat temperature (T) of euphausiids from various regions of the world's oceans. The data points represent means in Tables 2. For symbols see Fig. 2. *: $p < 0.05$.

Table 1. A list of euphausiid species of which metabolic data were used for the present analyses. J = juveniles, M = males, F = females, FG = gravid females. Blank = no data.

Code	Species	Region	Date	Reference
1a	*Bentheuphausia amblyops*	W. subarctic Pacific	May 2005	Ikeda (2012)
1b	*Bentheuphausia amblyops*	Off S. California	1976–1978	Torres & Childress (1985)
1c	*Bentheuphausia amblyops*	Off S. California	1976–1977	Quetin et al. (1980)
2a	*Euphausia crystallorophias*	Prydz Bay, Antarctica	Nov–Dec 1982	Ikeda & Bruce (1986)
2b	*Euphausia crystallorophias* (J)	Off Enderby Land, Antarctica	Nov 1985	Ikeda & Kirkwood (1989)
3	*Euphausia diomedeae*	Tropical Atlantic	Nov 1971	Ikeda (1974)
4	*Euphausia distinquenda*	Tropical Pacific	Feb 1972	Ikeda (1974)
5	*Euphausia gibba*	Coral Sea	May 2010	Ikeda & McKinnon (2012)
6	*Euphausia gibboides*	Off W Africa	Aug 1983	Davenport & Trueman (1985)
7	*Euphausia krohnii*	Topical Atlantic	Nov 1971	Ikeda (1974)
8	*Euphausia lucens*	Off W. South Africa		Stuart (1986)
9	*Euphausia mutica*	Coral Sea	May 2010	Ikeda & McKinnon (2012)
10a	*Euphausia pacifica*	E. subarctic Pacific	July 1975	Ikeda, unpublished
10b	*Euphausia pacifica* (F)	W. subarctic Pacific	Mar–Apr 2007	Kim, Yamaguchi & Ikeda (2010)
10c	*Euphausia pacifica* (M)	W. subarctic Pacific	Mar–Apr 2007	Kim, Yamaguchi & Ikeda (2010)
11a	*Euphausia superba*	Off Wilkes Land, Antarctica	Jan 1980	Ikeda & Mitchell (1982)
11b	*Euphausia superba* (J)	Off Enderby Land, Antarctica	Nov 1985	Ikeda & Kirkwood (1989)
11c	*Euphausia superba* (FG)	Off Wilkes Land, Antarctica	Jan 1980	Ikeda & Mitchell (1982)
11d	*Euphausia superba* (FG)	Off Enderby Land, Antarctica	Nov 1985	Ikeda & Kirkwood (1989)
11e	*Euphausia superba* (M)	Off Enderby Land, Antarctica	Nov 1985	Ikeda & Kirkwood (1989)
12	*Euphausia tenera*	Tropical Indian & Atlantic	Oct–Dec 1971	Ikeda (1974)
13a	*Euphausia triacantha*	Off Wilkes Land, Antarctica	Jan 1980	Ikeda & Mitchell (1982)
13b	*Euphausia tricantha*	Prydz Bay, Antarctica	Dec 1984–Feb 1985	Ikeda (1988)
14a	*Meganyctiphanes norvegica*	Gulf of Maine	Jan–Mar 1966	Conover & Corner (1968)
14b	*Meganyctiphanes norvegica*	Mediterranean	Jan 1971	Mayzaud (1973)
14c	*Meganyctiphanes norvegica*	Kattegat Bay, Denmark	Jul 1996, Mar 1997	Saborowski et al. (2002)
15	*Nyctiphanes australis*	E. Cook Strait, NZ	Mar–Apr 1983	James & Wilkinson (1988)
16	*Tessarabrachion oculatus*	W. subarctic Pacific	Jun 2003	Ikeda (2012)
17	*Thysanoessa inermis*	Barents Sea	May–June 1987	Ikeda & Skjoldal (1989)
18a	*Thysanoessa macrura* (J)	Scotia Sea	Jan–Mar 1981	Ikeda, unpublished data
18b	*Thysanoessa macrura*	Prydz Bay, Antarctica	Nov–Dec 1982	Ikeda, unpublished data
18c	*Thysanoessa macrura*	Off Enderby Land, Antarctica	Sept–Dec 1985	Ikeda, unpublished data
19	*Thysanoessa raschii*	Gulf of St. Lawrence	June 1973	Sameoto (1976)
20	*Thysanoessa* spp.	Mid-Atlantic Bight	Aug–Sep 1980	Vidal & Whitledge (1982)
21a	*Thysanoessa spinifera* (F)	W. subarctic Pacific	Mar–Apr 2007	Kim, Yamaguchi & Ikeda (2010)
21b	*Thysanoessa spinifera* (M)	W. subarctic Pacific	Mar–Apr 2007	Kim, Yamaguchi & Ikeda (2010)
22	*Thysanopoda cornuta*	Off Hawaii, USA	July 1983, 1986, 1987	Cowles et al. (1991)
23	*Thysanopoda monocantha*	E. Gulf of Mexico	Jun 1981–July 1985	Donnelly & Torres (1988)
24	*Thysanopoda tricuspidata*	Coral Sea	Nov 2009	Ikeda & McKinnon (2012)

Table 2. Body mass, metabolic rates (oxygen consumption and ammonia excretion), O:N ratio and elemental composition (C, N) of euphausiids from various depths and regions of the world's oceans. For species codes, see Table 1. Values are means or means ± SD. *Italic* values for sampling depth are those estimated by the present author. Blank = no data.

Code	Sampling depth (range) (m)		T (°C)	N	Body mass (mg DM ind.$^{-1}$)	Respiration consumption rate (µlO2 ind.$^{-1}$h^{-1})	Ammonia excretion rate (µgN ind.$^{-1}$h^{-1})	O:N ratio (atomic)	Elemental composition C (% of DM)	N (% of DM)	C:N
1a	4000	(3000–5000)	1.5	1	41.7	8.73			52.1	9.0	5.8
1b	1500	(500–2500)	3.5	16	27.9	3.82 ± 0.18			39.2	6.4	6.1
1c	600	(400–800)	5.5	1	60.0	10.0	0.30	41	[39.2][a]	[6.4][a]	
2a	10	(0–21)	–1.6	24	30.8 ± 18.9	16.4 ± 9.4	0.68 ± 0.61	42 ± 22	45.5	11.0	4.1
2b	5	(2–8)	–1.3	42	9.10 ± 5.17	4.68 ± 2.41	0.24 ± 0.21	35 ± 18	41.9	11.7	3.6
3	2	(0–<5)	26	2	1.89 ± 0.62	5.55 ± 0.21	0.42 ± 0.23	19 ± 10	41.3	10.6	3.9
4	2	(0–<5)	27	2	3.54 ± 2.23	15.6 ± 4.5	1.19 ± 0.11	16 ± 3	39.4	10.6	3.7
5	1	surface	28	7	3.29 ± 0.69	11.5 ± 1.7	0.70 ± 0.24	23 ± 7	41.7	11.3	3.7
6	*200*		18	3	5.10	12.7			[41.9][b]	[10.6][b]	
7	2	(0–<5)	20	2	0.29 ± 0.02	1.46 ± 0.16	0.13 ± 0.01	15 ± 1	40.7	10.0	4.1
8	40	(0–80)	13	28–40	5.00	10.5	0.85	15	40.4	10.8	3.7
9	1	surface	28	10	1.82 ± 0.66	5.88 ± 1.35	0.79 ± 0.48	11 ± 4	40.9	11.4	3.6
10a	2	(0–<5)	13	6	4.97 ± 1.71	6.03 ± 1.34	0.35 ± 0.12	23 ± 7	41.4	10.9	3.8
10b	100	(0–200)	5	39	12.8 ± 5.4	9.65 ± 3.82	0.18 ± 0.16	142 ± 148 (median: 90)	35.8	9.6	3.7
10c	100	(0–200)	5	19	11.5 ± 4.8	8.59 ± 3.10	0.15 ± 0.12	137 ± 138 (median: 76)	34.8	9.2	3.8
11a	35	(0–70)	–1.1	58	86.3 ± 57.8	35.5 ± 22.1	2.79 ± 1.56	17 ± 8	44.5	10.2	4.4
11b	3		–1.7	24	40.3 ± 11.1	20.0 ± 4.9	0.83 ± 0.42	34 ± 10	40.8	11.9	3.4
11c	35	(0–70)	–1.1	19	247.1 ± 96.7	94.2 ± 30.0	7.44 ± 3.48	17 ± 4	46.9	10.0	4.7
11d	3		–1.7	23	80.5 ± 30.1	34.6 ± 13.3	1.66 ± 0.93	29 ± 13	40.3	11.9	3.4
11e	3		–1.7	25	97.7 ± 36.1	42.8 ± 18.0	1.83 ± 0.82	32 ± 12	40.4	11.7	3.5
12	2	(0–<5)	27	9	0.77 ± 0.48	3.40 ± 2.51	0.31 ± 0.18	14 ± 5	40.2	10.1	4.0
13a	100	(0–200)	–0.8	15	23.0 ± 3.03	8.35 ± 1.43	0.86 ± 0.20	12 ± 2	41.2	11.6	3.5
13b	600	(200–1000)	0	9	82.8 ± 13.0	25.2 ± 6.3	1.27 ± 0.63	29 ± 12	47.3	10.7	4.4
14a	250	(0–500)	4	3–4	74.1	37.8	1.13	42	[35.0][c]	10.3	
14b	300	(0–600)	13	27	32.5 ± 2.7	41.3 ± 7.2	[11.04 ± 0.51][d]	[4.7][d]	39.4	11.5	3.4
14c	*50*		4	6–10	45.8	17.1	1.36	16	[37.2][e]	[10.9][e]	
15	*2*		15	21–31	2.00	4.71	0.27	22	43.5	11.6	3.8
16	750	(500–1000)	3	2	9.17 ± 0.23	4.07 ± 0.62			43.8	10.3	4.2
17	50	(0–100)	1	19	17.3 ± 16.2	7.64 ± 5.91	0.40 ± 0.44	44 ± 27	51.3	8.9	5.7
18a	2	(0–<5)	–0.4	27	0.47 ± 0.14	0.43 ± 0.13	0.026 ± 0.015	26 ± 16	42.6	11.2	3.8
18b	2	(0–<5)	–1.7	3	5.49 ± 0.36	4.46 ± 1.34	0.21 ± 0.08	27 ± 2	40.7	9.9	4.1
18c	300	(0–<1000)	–0.5	20	6.89 ± 2.32	3.21 ± 1.08	0.20 ± 0.10	22 ± 8	43.1	12.0	3.6
19	*25*		4	17	10.0	12.9			[41.9][b]	[10.6][b]	
20	15	(0–30)	20	9–13	5.00	8.59	0.33	32	[41.9][b]	[10.6][b]	
21a	100	(0–200)	5	34	12.2 ± 4.5	12.2 ± 4.5	0.40 ± 0.37	71 ± 82 (median: 42)	36.6	9.8	3.7
21b	100	(0–200)	5	32	7.02 ± 3.29	6.56 ± 2.04	0.24 ± 0.13	46 ± 27(median: 35)	37.1	10.1	3.7
22	650	(100–1200)	5	2	1405	109.3 ± 28.3			[41.9][b]	[10.6][b]	
23	500	(0–1000)	7	5	46.1	15.0 3.3			[41.9][b]	[10.6][b]	
24	1	surface	26	6	12.8 ± 3.5	32.3 ± 7.5	1.51 ± 0.76	31 ± 13	42.7	12.7	3.4

[a] after Torress and Childress (1985)

[b] grand mean values of 19 euphausiids in this table on which C and N compositions are determined; C = 41.9% (±3.8) of DM, N = 10.6% (±1.2) of DM.

[c] calculated from C:N ratio given by Mayzaud (1973)

[d] assumed as an artifact (cf. Mayzaud and Conover 1988) and excluded in the present analysis

[e] estimated from Conover and Corner (1968) and Mayzaud (1973)

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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 euphausiids on body mass (X_1: mg ind.$^{-1}$), habitat temperature (X_2: 1000/K for the former, ^{o}C for the latter) and depth sampled (X_3: m).

Regression model	Body mass unit	N	Step No.	Regression equation: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3$				R^2 (adjusted R^2)
				a_0	a_1	a_2	a_3	
Oxygen consumption								
Theoretical	DM	39	1		0.75	–4.628		0.628
			2	14.017	0.75	–3.717	–0.109	0.735 (0.720)
	C	39	1		0.75	–4.708		0.624
			2	14.971	0.75	–3.798	–0.109	0.727 (0.712)
	N	39	1		0.75	–4.530		0.679
			2	15.992	0.75	–3.818	–0.085	0.753 (0.740)
Empirical	DM	39	1		0.517			0.680
			2		0.690	0.051		0.837
			3	0.392	0.753	0.046	–0.107	0.877 (0.867)
	C	39	1		0.510			0.672
			2		0.684	0.052		0.830
			3	1.060	0.745	0.046	–0.105	0.868 (0.857)
	N	39	1		0.533			0.713
			2		0.707	0.052		0.874
			3	2.002	0.749	0.047	–0.082	0.899 (0.890)
Ammonia excretion								
Theoretical	DM	31	1		0.75	–5.346		0.633
			2	13.061	0.75	–4.248	–0.141	0.710 (0.690)
	C	31	1		0.75	–5.400		0.657
			2	14.142	0.75	–4.371	–0.132	0.726 (0.706)
	N	31	1		0.75	–5.293		0.668
			2	15.240	0.75	–4.407	–0.114	0.723 (0.703)
Empirical	DM	31	1		0.464			0.498
			2		0.729	0.064		0.753
			3	–2.606	0.788	0.056	–0.145	0.803 (0.782)
	C	31	1		0.466			0.508
			2		0.736	0.066		0.772
			3	–1.940	0.788	0.057	–0.136	0.817 (0.796)
	N	31	1		0.479			0.525
			2		0.750	0.066		0.792
			3	–0.927	0.790	0.058	–0.117	0.826 (0.806)

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Table 4. Temperature effects on respiration rates of various zooplankton taxa and eupahusiids in terms of activation energy (Ea) of Arrhenius equation and Q_{10} of Van't Hoff rule. Values are based on DM as a measure of body mass, and those in parentheses denote the range of 95% CI.

Data set type/zooplankton taxa	*E* a (eV)	Temp range (°C)	Q_{10}	Temp range (°C)	Reference
Global/interspecific					
Euphausiids (24 species)	0.35 (0.28–0.42)	–1.7 to 28	1.7 (1.5–1.9)	–1.7 to 28	This study
Copepods (108 species)	0.45 (0.36–0.54)	–1.7 to 28.5	1.9 (1.7–2.2)	–1.7 to 28.5	Ikeda et al (2007)
Chaetognaths (17 species)	0.38 (0.18–0.58)	–1 to 28	1.7 (1.4–2.4)	–1 to 28	Ikeda & Takahashi (2012)
Chaetognaths (14 species)	0.59	0–30			Kruse et al. (2010)
Teleost fishes (69 species)	0.43	–2 to 40	1.8	0–30	Clarke & Johnson (1999)
Crustaceans (many species**)	0.57*	0–30	2.1–2.4	0–30	Ivleva (1980)
Regional/intraspecific					
Euphausia superba	0.67*	0–5	2.8	0–5	Hirsche (1984)
Meganyctiphanes norvegica	0.63*	0–5	2.6	0–5	
Euphausia pacifica			2.2	1–20	Iguchi & Ikeda (1995)
Euphausia pacifica			2.4	5–15	Paranjape (1967)
Euphausia pacifica			2.8	5–15	Small & Hebard (1967)
Euphausia americana			2.3	15–25	Teal & Carey (1967)
Euphausia hemigibba			2.8	10–25	
Thysanopoda monocantha			2.5	10–20	
Thysanopoda obtusifrons			2.5	10–20	
Thysanopoda tricuspidata			3.5	10–20	
Meganyctiphanes norvegica			2.0	5–10	

*converted from μ (kcal $mole^{-1}$) by an equation *E* a = μ/23.06 (cf. Brown et al. 2004).

595 **some benthic species included

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Table 5. Global-bathymetric comparisons of ecological and physiological characteristics of euphausiids, copepods and chaetognaths living in the world's oceans. For respiration rate, T and E denote Theoretical and Empiriacal models, respectively. N is the number of data and N_{sp} the number of species.

Ecological/physiological characteristics		Euphausiids	Copepods	Chaetognaths
Behavior in the water column		active swimming	suspended, up-and-down or continuous gliding	suspended
Food habit		Herbivore, omnivore, carnivore	Herbivore, omnivore, carnivore	Carnivore
Respiration rate ($\mu l\ O_2\ ind.^{-1}h^{-1}$)				
A specimen of 1 mgN body mass inhabiting 100 m depth (20°C, O_2 saturation = 1.0)	T-model	13.1[a]	10.2[b]	5.1[c]
	E-model	13.0[a]	12.3[b]	7.9[c]
A specimen of 1 mgN body mass inhabiting 1000 m depth (5°C, O_2 saturation = 0.1)	T-model	5.3[a]	2.2[b]	1.3[c]
	E-model	5.3[a]	2.5[b]	1.5[c]
Metabolic O:N ratio (by atms)	Range	11–142[a]	4.8–49[d]	6.8–36[e]
	Mean (±SD)	30.0 (17.4)	20.7(11.3)	15.6(8.9)
	Median	27.1	16.9	12.2
	N (N_{sp})	31(19)	37(29)	12(10)
Body water content (% of WM)	Range	62.6–82.3[f]	78.3–83.8[g]	83.7–94.7[c]
	Mean (±SD)	76.9 (3.7)		90.4 (3.0)
	N (N_{sp})	36(27)	93(93)	19(14)
Body C:N (by mass)	Range	3.4–8.6[f]	3.7–9.4[g]	2.6–5.1[c]
	Mean (±SD)	4.2 (1.1)		4.0 (0.7)
	N (N_{sp})	41(26)	94(94)	30(24)

[a] calculated from the equations in Table 3 of this study

[b] calculated from the equations in Ikeda et al. (2007). Note that ambient oxygen saturation is a parameter for the model of copepods, but not for those of chaetognaths and euphausiids

[c] calculated from the equations in Ikeda and Takahashi (2012)

[d] from Ikeda et al. (2001)

[e] from literatures listed in Table 2 of Ikeda and Takahashi (2012) in which both respiration and ammonia excretion rates determined simultaneously

[f] from Table 2 of this study supplimented by those of Nemoto et al. (1972), Lindley et al. (1999), Morris and Hopkins (1983) and Harvey et al. (2012)

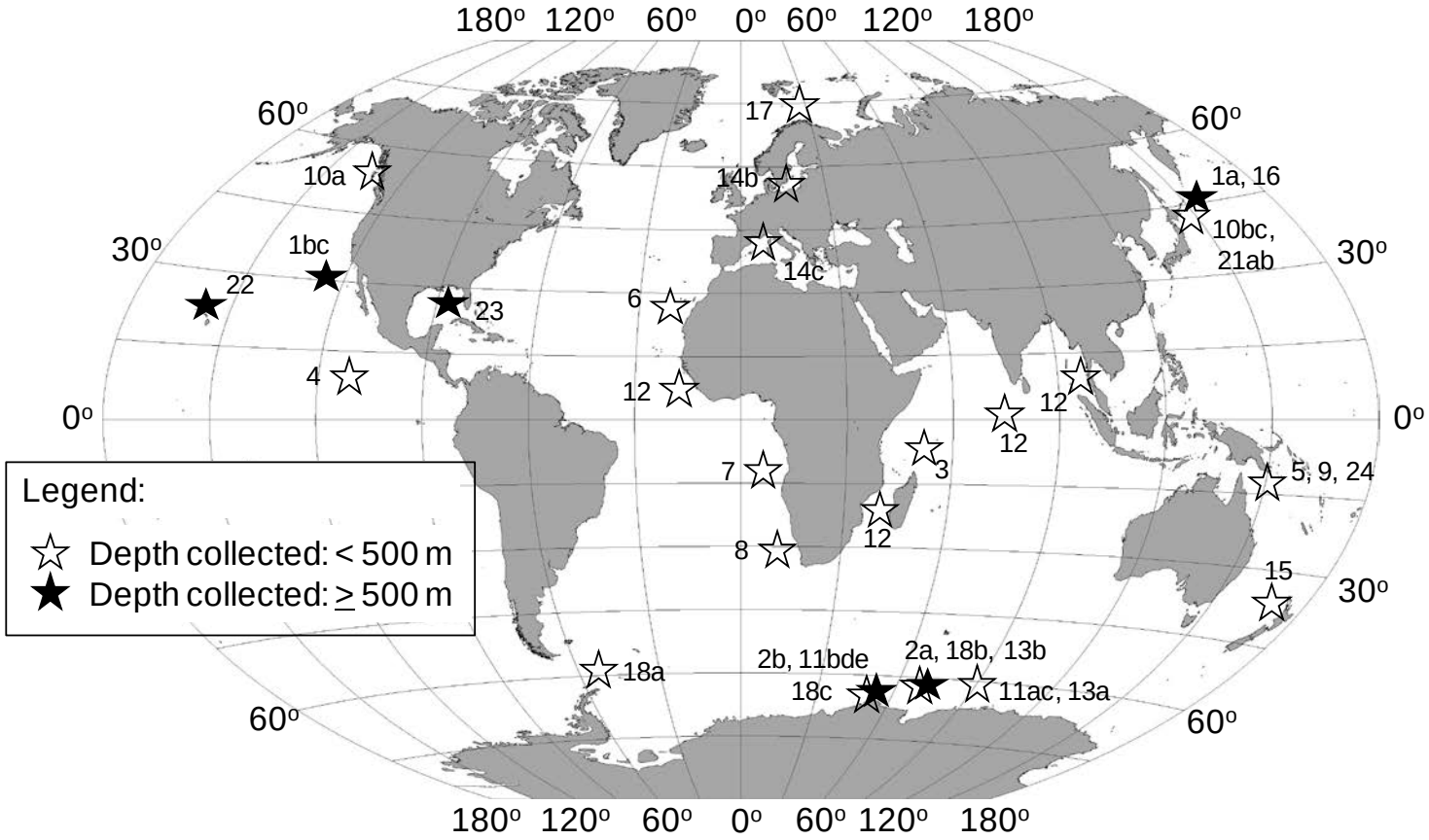
603 [g] from Båmstedt (1986)

604

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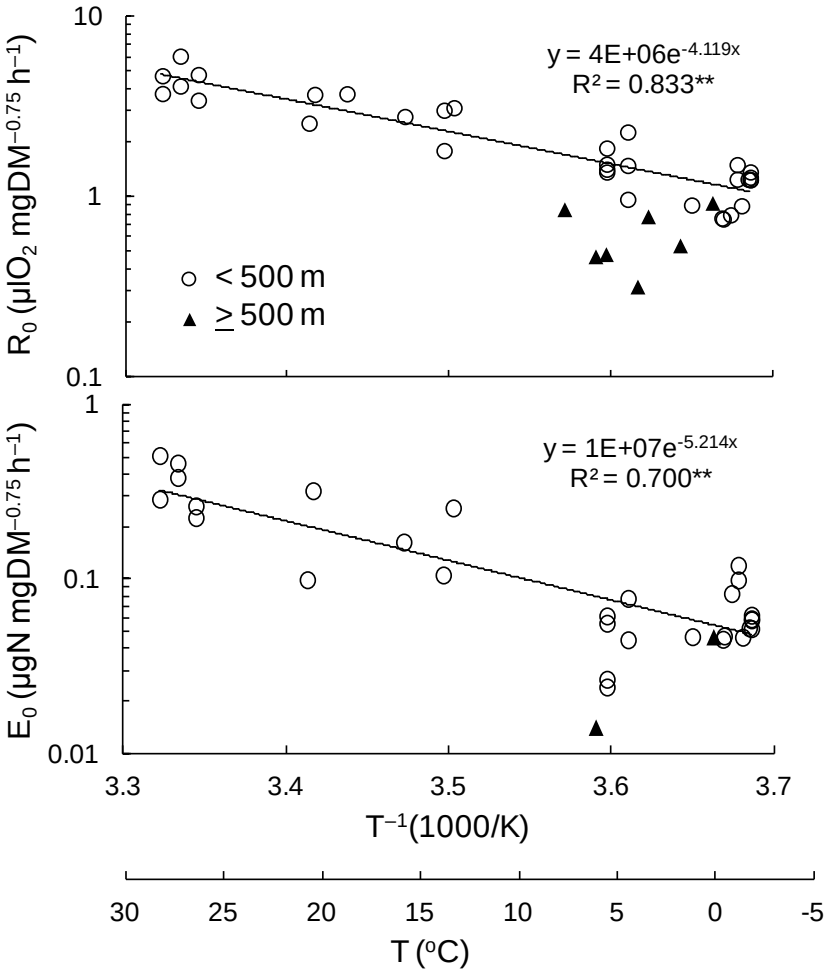
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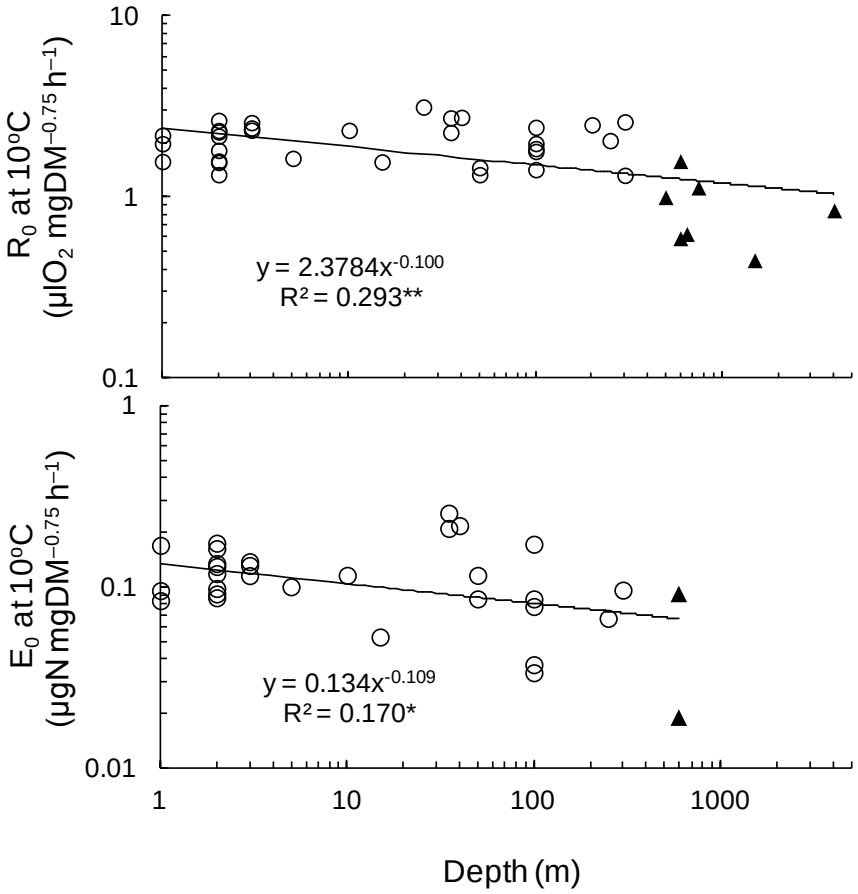


Ikeda Fig. 1

608


y = 4E+06e-4.119x
R² = 0.833**
< 500 m
≥ 500 m
R0 (μlO2 mgDM−0.75 h−1)
10
1
0.1
y = 1E+07e-5.214x
R² = 0.700**
E0 (μgN mgDM−0.75 h−1)
1
0.1
0.01
3.3
3.4
3.5
3.6
3.7
T−1(1000/K)
30
25
20
15
10
5
0
-5
T (°C)

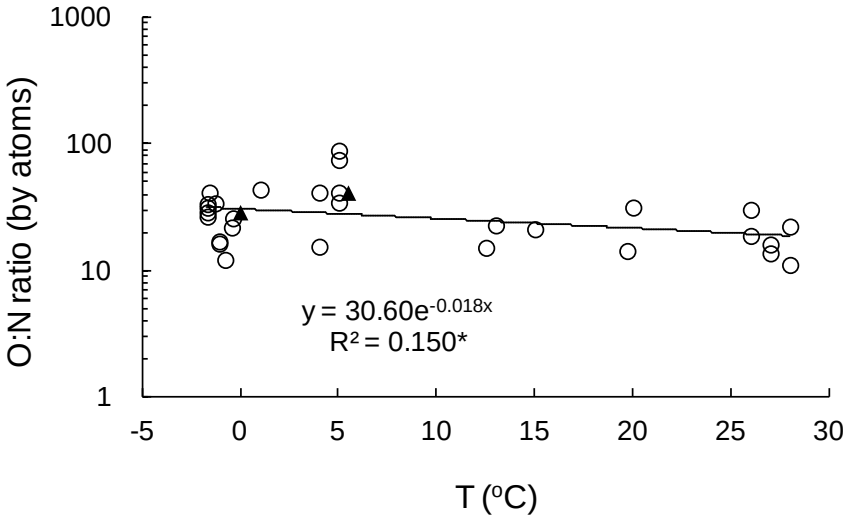
Ikeda Fig. 2


10
1
0.1
R_0 at 10°C
(µlO_2 mgDM$^{-0.75}$ h^{-1})
y = 2.3784x$^{-0.100}$
R² = 0.293**
1
0.1
0.01
E_0 at 10°C
(µgN mgDM$^{-0.75}$ h^{-1})
y = 0.134x$^{-0.109}$
R² = 0.170*
1
10
100
1000
Depth (m)

Ikeda Fig. 3

638

639



Ikeda Fig. 4

640

641

642

643

644