Metabolism and chemical composition of zooplankton from 500–5,000 m depth of the western subarctic Pacific Ocean

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Abstract Respiration (=oxygen consumption) rates of 28 zooplankton species belonging to 10 taxa from 500–5,000 m depth of the western subarctic Pacific Ocean were determined as 0.027–0.44 μLO_2 mg dry mass^{-1} h^{-1} at *in situ* temperatures (1.5–3^{o}C), which are 80% lower than the rates of the epipelagic Antarctic zooplankton with similar body mass and at a comparable temperature. In terms of Adjusted Metabolic Rate to 1 mg body N (AMR; μLO_2 mgN$^{-0.8}$h^{-1}) at 1^{o}C, the present results (mean: 1.66) fall well within the range (0.84–3.32) reported for copepods, chaetognaths and mixed crustaceans from 500–7,000 m in the subarctic Pacific Ocean and Antarctic waters. Judging from their body C:N elemental ratios and ash-free dry mass (=organic matter) data, the major component of organic matter is deduced to be protein (C:N = 3.4–8.1, by mass) for 19 out of 28 species and lipids (C:N = 8.6–13.0) for the remaining 9 species.

Keywords Zooplankton·Respiration·Subarctic Pacific·500–5,000 m depth·C:N ratio

1 Introduction

Metabolic rates of zooplankton living in the epipelagic zones have been documented as a function of body mass and habitat temperature (Ivleva 1980; Ikeda 1985). From the viewpoint of the entire earth system, the epipelagic zone (0–200 m) occupies only a modest fraction (5.4%) of the volume ($1{,}350 \times 10^6$ km^3, Menard and Smith 1966) of the world's oceans, which have an average depth of 3,700 m. For deep-living micronektonic fishes, crustaceans and cephalopods, reduced metabolic rates have been reported (Childress 1995; Seibel and Drazen 2007). For zooplankton, the effect of habitat depth on metabolic rates is controversial; Ikeda et al. (2006a, 2007), Ikeda (2011), Ikeda and Takahashi (2012) and Kruse et al. (2010a) reported a significant negative effect of habitat depth on the respiration rates of copepods and chaetognaths while Thuesen and Childress (1993) and Thuesen et al. (1998) noted no effect of habitat depth on the respiration rates of both taxa. High water or low protein content has been observed in deep-sea micronekton (Childress and Nygaard 1973, 1974). For deeper-living copepods, a lower N or a higher C content than in their shallow-living counterparts has been reported (Båmstedt 1986; Ikeda et al. 2006b). Comparable information for zooplankton other than copepods is not available. In order to integrate the global role of zooplankton in biogeochemical cycles of carbon and other elements, and in trophodynamics over the full depth range, there is an urgent need to fill the gap of knowledge on metabolic and chemical compositional features of deep-sea zooplankton (Hernández-León and Ikeda 2005).

In this study, I determined respiration (= oxygen consumption) rates of zooplankton retrieved by shipboard sampling from various depths between 500–5,000 m in the western subarctic Pacific Ocean. The body chemical composition (water content, ash and C and N composition) for zooplankton used for respiration measurements was analyzed. The results are compared with published data on

zooplankton from various bathymetric levels of the world's oceans to explore unique features, if any, of the metabolism and body composition of deep-sea zooplankton in this study.

2 Materials and methods

2.1 Zooplankton:

Twenty two zooplankton species, including two hydromedusae, one polychaete, one nemertean, three ostracods, three mysids, six amphipods, three euphausiids (treating calyptopis larvae of unknown species as one species), two decapods and one leptostracan were collected at stations in the western subarctic Pacific, including Site H (41°30'N 145°50'E) and Station KNOT (44°00'N 155°00'E) during T.S. Oshoro-Maru Cruises 124A (June) in 2002; 133D (March) and 136A (June) in 2003; 143B (February), 144A (March) and 154B (December) in 2004; and 155 (March) in 2005, and 167 (March) in 2006.

The sampling method has been described elsewhere (Ikeda et al. 2006a). Briefly, a vertical closing net [80 cm diameter, 0.3 mm mesh size; modified from Kawamura (1968)] equipped with a large cod-end (2 L capacity) was used to retrieve zooplankton from depth (< 5,000 m). After closing the mouth of the net at the designated depth, the time required to retrieve the net to the surface was at most 17 min when closed at 2,000 m depth. Upon retrieval of the net, undamaged specimens were sorted immediately. Sorted specimens were placed in 1 L glass containers filled with seawater from the mid-depth range of their collection (e.g. 750 m for the specimens collected from 500–1,000 m). The seawater was collected with 20 L Niskin bottles just prior to zooplankton collection for each experiment. Temperature profiles were determined by using a CTD system. Oxygen saturation data at 500–5,000 m depth were taken from

Ikeda et al. (2007). For the identification of zooplankton, keys by Chihara and Murano (1997) were used.

On the basis of the similar methodologies (sealed chamber method for measuring respiration rates and subsequent determination of C and N elemental composition), the data on 6 deep-sea chaetognaths (*Caecosagitta macrocephala*, *Pseudosagitta scrippsae*, *Solidosagitta zetesio*s, *Eukrohnia hamata, E. bathypelagica* and *E. fowleri*) from 500–3,000 m in the western subarctic Pacific Ocean (Ikeda and Takahashi 2012) were combined with the present results.

2.2 Respiration

A sealed-chamber method (cf. Ikeda et al. 2000) with glass bottles (40–200 mL capacity depending on the size of specimens) was used to determine respiration rates of zooplankton. It is noted that the 1,000–2,000 m depth stratum in the western North Pacific Ocean is characterized by moderately low oxygen concentrations (1.0–2.0 mL O_2 L^{-1}, or 10–30% saturation, Favorite et al. 1976). In order to minimize the change in oxygen concentrations, the seawater from the depth was filtered gently through 10 µm mesh netting to remove large particles and used (oxygen concentration of seawater thus prepared for zooplankton from 1,000-2,000 m was 1.6–2.0 mL O_2 L^{-1}). Experiments started within 1–3 h after the collection of the specimens. Experimental bottles containing specimens (mostly one individual) and control bottles without specimens were prepared simultaneously, and incubated in the dark for 24 h at *in situ* temperatures (1.5–3^{o}C) under 1 atmosphere pressure. The lack of decompression effects on respiration rates of deep-sea zooplankton has been documented by several workers (Childress and Thuesen 1993, and literature therein). At the end of each experiment, the dissolved oxygen concentration was determined by the Winkler titration method on subsamples siphoned from the bottles into two small oxygen vials

(7 or 14 mL capacity). Based on replicate measurements of a homogenous water sample, the precision expressed as the coefficient of variation (CV) was estimated as 0.2%.

2.3 Chemical composition

All specimens used for respiration experiments were rinsed briefly with small amounts of chilled distilled water, blotted on filter paper, and frozen at –60°C on board the ship for later determination of wet mass (WM), dry mass (DM), and carbon (C) and nitrogen (N) compositions. Frozen specimens were weighed (WM) and freeze-dried to obtain DM. Water content was calculated from the difference between WM and DM of the same specimens. A microbalance (MT5; Mettler Toledo International Inc.) was used for weighing to a precision of 1 µg. Specimens of the same species from the same depth stratum were pooled in each cruise and finely ground with a ceramic mortar and pestle. They were used for C and N composition analyses using a CHN elemental analyzer (Elementar vario EL) with acetanilide as a standard. Weighed fractions of the ground samples were incinerated at 480^{o}C for 5 h and reweighed for ash determination. All measurements were made in duplicate, and the general precision (CV) was 3% for C, 7% for N and 10% for ash.

2.4 Parameters affecting respiration rates and chemical composition

Designating the body mass, temperature and sampling depth as independent variables, the attributes of these variables to respiration rates were analyzed by using stepwise multiple regression (Sokal and Rohlf 1995). Linear regression models adopted were; $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 X_3, + a_4 X_4$ where Y is respiration rate (μLO_2 ind.$^{-1}$ h^{-1}), X_1 is body mass (mgDM, C or N ind.$^{-1}$), X_2 is temperature (^{o}C), X_3 is the depth of

sampling (m) and X_4 is ambient oxygen saturation (full saturation = 1.00). The calculation was conducted using SYSTAT J 10.2, designating $p_{in} = p_{out} = 0.05$.

The attributes of the same three variables to the chemical composition (water, ash, C, N and C:N) were also analyzed by calculating Pearson correlation coefficients, and are taken as significant at the $p = 0.05$ level.

3 Results

3.1 Respiration

Across a total of 28 zooplankton species from 500–5,000 m where temperature varied from 1.5 to 3°C, body mass ranged from 0.52 (*Paramollicia dichotoma*) to 239 mgDM (*Chuneola spinifera*). Specific respiration rates ranged from 0.027 (*C. spinifera*) to 0.44 $\mu LO_2\ mgDM^{-1}\ h^{-1}$ (*Tessarabrachion oculatus*) (Table 1).

Stepwise multiple regression analyses found that the body mass was the only significant variable ($p < 0.002$) among the four variables tested. The choice of body mass unit (DM, C or N) had little effect on the results of this analysis, attributing 76–78% of the variance of Y (Table 2).

3.2 Chemical composition

Water content varied from 65.1 (euphausiid caliptopis larvae) to 95.2% of WM (*Crossota* sp.), ash from 4.3 (*Nebaliopsis typica*) to 53.8% of DM (*Crossota* sp.), N from 3.6 (*Crossota* sp.) to 10.5% of DM (*Solidosagitta zetesios*), C from 19.7 (*Crossota* sp.) to 60.6% of DM (*Hymenodora frontalis*), and C:N ratios from 3.4 (*Lanceola loveni*) to 13.0 (*Cyphocaris* sp.) (Table 1).

None of the between-species variations in water content, ash, C, N and C:N ratio of the 28 species was correlated with the depth of sampling, temperature or ambient oxygen saturation (Pearson correlation matrix, $p > 0.05$).

4 Discussion

4.1 Respiration

Combining respiration data of epipelagic copepods from the world oceans with those of mesopelagic, bathypelagic and abyssopelagic copepods of the western subarctic Pacific Ocean, Ikeda et al. (2007) demonstrated the habitat depth and ambient oxygen saturation to be significant determinants, in addition to body mass and habitat temperatures. In contrast, the present analysis of 28 zooplankton species from the mesopelagic through abyssopelagic zones showed neither the depth of habitat nor temperature to be significant; but body mass alone was significant (Table 2). Narrow ranges of habitat temperature [1.5–3^{o}C cf. –1.7 to 28.5^{o}C in Ikeda et al. (2007)], habitat depth (750–4,000 m cf. 2–4,000 m) and ambient oxygen saturation (13–45% cf. 13–100%) in the present study may have contributed to the dissimilar results of the two studies.

Since the reduction in zooplankton respiration rates with increasing depth of occurrence is most rapid in the transition from the epipelagic zone to the mesopelagic zone (Ikeda et al. 2007; Kruse et al. 2010a), the analysis of the effect of habitat depth based on the respiration data from 500–4,000 m above may not be sensitive enough to detect an effect. For this reason, the respiration data sets of Antarctic zooplankton from < 210 m depth [1 ctenophore, 3 pteropods, 1 polychaete (2 size categories for *Tomopteris carpenteri*), 2 copepods, 3 amphipods [2 size categories for *Themisto* (formerly *Parathemisto*) *gaudichaudii*], 2 euphausiids (4 size categories for *Euphausia superba*), and 2 salps] determined at *in situ* temperature (–1.4 to –0.8^{o}C) (Ikeda and Mitchell 1982) were selected and compared with the present results (Fig. 1). Specific respiration rates were standardized to the rates at 1^{o}C by using a Q_{10} value of 2 (Ikeda 1985). As body mass units, DM and N were selected since preliminary tests indicated

that C body mass yielded the results somewhere between those of DM and N. For both, DM specific respiration rates-DM and N specific respiration rates-N relationships, the difference in the slope of the deep-living zooplankton and that of the shallow-living Antarctic zooplankton was not significant (*F*-test, $p > 0.25$), but the intercept of the former was significantly less than that of the latter (*F*-test, $p < 0.005$). From the intercepts of the regression lines adjusted to the common slope, the DM or N specific respiration rates of the deep-living zooplankton were low and 0.21 times the rates of shallow-living Antarctic zooplankton. Thus, the present results of reduced respiration rates of deeper-living zooplankton are consistent with those of Ikeda et al. (2007) and Ikeda (2011) on copepods and Kruse et al. (2010a) and Ikeda and Takahashi (in press) on chaetognaths, but not with those of Thuesen et al. (1998) and Thuesen and Childress (1993) . According to the "predation-mediated selection hypothesis" (Ikeda et al. 2006a), reduced respiration rates of deep-living zooplankton is explained as a result of lowered selective pressure for high activity at depth because of the decrease in visual predators in the dark.

In addition to the epipelagic Antarctic zooplankton data (Ikeda and Mitchell 1982) in Fig. 1, published respiration data on deep-sea copepods (Ikeda 2011, Ikeda et al. 2006a; Thuesen et al. 1998), chaetognaths (Thuesen and Childress 1993; Kruse et al. 2010b) and various crustaceans (Childress 1975; Ikeda 1988) from diverse bathymetric levels (500–7,000 m) of the world's oceans are compared with the present results in terms of AMR (adjusted metabolic rate to 1 mg body N; $\mu LO_2\ mgN^{-0.8}h^{-1}$) at 1^oC, by adopting a body mass exponent (0.8) and a Q_{10} (2), both derived from a comprehensive analysis of respiration rate-body mass data sets of epipelagic zooplankton (Ikeda 1985). In calculating AMR for the copepods studied by Thuesen et al. (1998) and Ikeda (2011), body N was estimated from protein (WM × % protein) by multiplying 0.2 (Ikeda unpublished data). For the chaetognaths studied by Thuesen and Childress

(1993) in which the body mass was expressed as WM unit only, body N was computed by using general conversion factors of this taxon (cf. Ikeda and Takahashi 2012). It is noted that the habitat depth of zooplankton has been defined as (a) "minimum depth of occurrence" below which 80% or 90% of the population is found (Childress 1975; Thuesen and Childress 1993), (b) "minimum capture depth" (Thuesen et al. 1998) or (c) "mid-sampling depth" (Ikeda 2011; Ikeda et al. 2006a; Kruse et al. 2010a; this study), and the actual sampling depth of 500 m defined by (a) and (b) would be > 500 m. Among various body mass units (DM, C or N), N has been shown to be superior for comparison of respiration rates of diverse marine zooplankton taxa in general (Ikeda 1985). The temperature of 1^{o}C was chosen as an approximate mid-range of the extreme experimental temperatures of these studies compared (–1.4 to 5^{o}C).

From Table 3, it is apparent that the mean AMRs at 1^{o}C for zooplankton inhabiting > 500 m vary from 0.84 for chaetognaths (Thuesen and Childress 1993) to 3.32 for crustaceans (Ikeda 1988), and the mean of 10 zooplankton taxa (1.66) from this study falls favorably within the range. The variations in AMR at 1^{o}C data between zooplankton from > 500 m may be attributed to dissimilarities in actual habitat depths defined as > 500 m, ambient oxygen saturations of the habitats that vary regionally or taxon-specific AMRs. Notwithstanding this, it is clear from Table 3 that all AMRs at 1^{o}C of zooplankton living in > 500 m are much less than that (6.64) of the epipelagic Antarctic zooplankton (Ikeda and Mitchell 1982) by a factor of 0.3–0.50.

4.2 Chemical composition

With the increase of habitat depth, the water content of the body has been documented to increase for micronektonic fishes (Childress and Nygaard 1973) while the N content declines for micronektonic crustaceans (Childress and Nygaard 1974). For zooplankton, Båmstedt (1986) noted high C and low N (thus leading to high C:N) for deep-sea

copepods as compared with shallow-living counterparts in low latitude seas but the phenomenon was less marked in high latitude seas. A recent study on copepods living in the epipelagic through abyssopelagic zones of the western subarctic Pacific Ocean revealed a gradual decline in the N content and an increase in C:N ratios downward (Ikeda et al. 2006b). In contrast to these results by previous workers, no significant effects of the habitat depth was detected on water content, ash, C and N composition, and C:N ratios of deep-sea zooplankton in the present study (see "Results" section). The lack of depth-related patterns in the chemical composition components in the present study may be partly due to the mixture of 10 different taxa in which both gelatinous and non-gelatinous groups are included. In general, the chemical composition of gelatinous zooplankton is characterized by high water and ash contents, but low C and N contents (cf. Bailey et al. 1995).

Analyzing chemical composition data on 182 zooplankton species (mostly crustaceans), Ventura (2006) calculated an average C and N composition of 52.8% and 16.0% for protein, and 81.0% and 0% for lipids (represented by wax esters). 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. On this basis, the predominance of protein or lipids was examined by plotting C:N ratios against "organic matter" or "ash-free DM (100% – Ash)" of the present data (Fig. 2). Since ash data are not available for the epipelagic zooplankton from Antarctic waters (Ikeda and Mitchell 1982), the mean C:N ratio (4.4, range 3.5–6.6) and its 95% confidence interval (2.8–6.0) were plotted for comparison. From Fig. 2, it is evident that all the epipelagic Antarctic zooplankton data, and 19 out of 28 of deep-sea zooplankton data (including the 3 data on which ash was not determined, cf. Table 1) from this study fall within the range of 3.3–8.4, suggesting the

predominance of protein. For the rest of the 9 deep-sea zooplankton data that exhibited C:N ratios of 8.6–13.0, lipids are considered to predominate the organic matter. According to Ikeda (1974), typical C:N ratios for diverse zooplankton phyla from the epipelagic zones of the world's oceans are in the range between 3 and 5, which is consistent with the epipelagic Antarctic zooplankton data in Fig. 2. As exceptions, C:N ratios as high as 11–13 have been recorded on mesopelagic/bathypelagic copepods such as *Paraeuchaeta sarsi*, *Scaphocalanus affinis* and *Pseudochirella spinifera* (Omori 1969; Ikeda et al. 2006b) and a mesopelagic gammarid amphipod *Paracallisoma coecus* (Childress and Nygaard 1974). All these results suggest that extremely high C:N ratios (or a large lipid deposition in the body) may be a unique feature of some, but not all, deep-living zooplankton species. The function of large lipid deposits (mostly as wax esters) in deep-sea zooplankton is considered as an energy reserve for coping with temporal food scarcity and reproduction, as is the case for large grazing zooplankton living in high latitude seas, or energy saving for swimming by achieving neutral buoyancy as is seen in deep diapausing copepods (Lee et al. 2006).

In conclusion, respiration rates of 28 zooplankton species from 500–5,000 m in the western subarctic Pacific Ocean were shown to be 80% lower than the rates of those from 0–210 m in Antarctic waters, but were similar to the rates of those from 500–7,000 m of various regions of the world's oceans when the differences in body mass and temperature were taken into account. As judged by high body C:N ratios and AFDM, the predominance of lipids in the organic matter appears to be a unique feature of some zooplankton species from 500–5,000 m in the present study, but protein predominated in the rest of the species as was the case for epipelagic zooplankton.

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Figure captions

Fig. 1. The relationships of (A) DM specific respiration rate at 1^{o}C and body mass (DM), and (B) N specific respiration rate at 1^{o}C and body mass (N) of zooplankton from 500–5,000 m in the western subarctic Pacific Ocean (this

study) and that of zooplankton from 0–210 m in Antarctic waters (Ikeda and Mitchell 1982). Data points represent means of each species. Parallel regression lines were derived from the results of ANCOVA. See text for details.

Fig. 2. The relationship between body C:N ratios and ash-free dry mass (AFDM; % of DM) of zooplankton from 500–5,000 m in the western subarctic Pacific Ocean (this study). The mean C:N ratio (4.4) and its 95% confidence interval (CI = 2.8–6.0) of zooplankton from 0–210 m in Antarctic waters (Ikeda and Mitchell 1982) are superimposed for comparison.

Table 1. Summary of sampling data, body mass and specific respiration rates, and chemical composition (water content, ash, C and N composition and C:N ratio) of various zooplankton species from 500–5,000 m depth in the western subarcic Pacific Ocean. Data on six chaetognaths by Ikeda and Takahashi (in press) are also included in this table. ND = no data.

Animal group	Scientific name	Sampling depth (m) Median	Sampling depth (m) Range	O2 saturation (1.00=100%)	Expt T (^oC)	N	Body mass (mgDM ind.$^{-1}$) Mean	Body mass (mgDM ind.$^{-1}$) Range	Specific respiration rate (μLO_2 mgDM^{-1}h^{-1}) Mean ± SD	Water (% of WM)	Ash (% of DM)	N (% of DM)	C (% of DM)	C:N (by mass)	Reference
Hydromedusae	*Crossota* sp.	750	(500–1,000)	0.13	3	9	3.05	(1.05–22.63)	0.13 ± 0.06	95.2	53.8	3.6	19.7	5.4	This study
	Pantachogon haeckeli	1,000	(500–1,500)	0.15	2.5	3	33.76	(26.1–44.3)	0.10 ± 0.05	92.9	31.5	7.1	36.7	5.2	This study
Polychaetes	*Tomopteris* sp.	4,000	(3,000–5,000)	0.45	1.5	1	3.51		0.11	88.8	18.5	9.5	39.0	4.1	This study
Nemerteans	*Nectonemertes mirabilis*	2,500	(2,000–3,000)	0.32	1.5	1	15.85		0.045	91.0	20.9	8.3	38.5	4.6	This study
Ostracods	*Conchoecia haddoni*	1,500	(1,000–2,000)	0.20	2	2	0.86	(0.79–0.92)	0.34 ± 0.03	72.3	ND	8.3	35.7	4.4	This study
	Concoesissa ametera	2,500	(2,000–3,000)	0.32	1.5	9	2.66	(1.75–3.31)	0.23 ± 0.09	83.7	14.8	7.9	47.1	5.9	This study
	Paramollicia dichotoma	4,000	(3,000–5,000)	0.45	1.5	1	0.52		0.25	73.1	ND	5.8	53.7	9.3	This study
Mysids	*Longithorax fuscus*	750	(500–1,000)	0.13	3	1	24.63		0.079	82.9	9.9	6.5	55.6	8.6	This study
	Acanthomysis sp.	750	(500–1,000)	0.13	3	1	12.90		0.10	72.3	8.9	7.2	55.1	7.7	This study
	Eucopia grimaldii	1,000	(500–1,500)	0.15	2.5	18	30.53	(6.63–183)	0.080 ± 0.032	77.9	9.9	6.5	58.0	8.9	This study
Amphipods	*Chuneola spinifera*	4,000	(3,000–5,000)	0.45	1.5	1	239.00		0.027	84.3	20.1	4.6	49.4	10.9	This study
	Lanceola loveni	1,500	(1,000–2,000)	0.20	2	4	4.40	(2.13–9.32)	0.12 ± 0.05	93.0	28.6	9.3	31.4	3.4	This study
	Phronima sedentaria	750	(500–1,000)	0.13	3	3	4.06	(1.04–18.12)	0.23 ± 0.08	93.1	47.5	5.6	23.0	4.1	This study
	Scina borealis	1,500	(1,000–2,000)	0.20	2	1	8.74		0.18	89.2	29.6	7.8	35.6	4.6	This study
	Cyphocaris sp.	750	(500–1,000)	0.13	3	1	1.23		0.30	78.9	ND	4.3	56.1	13.0	This study
	Gammaridea sp.	750	(500–1,000)	0.13	3	1	4.01		0.20	67.6	9.1	4.7	59.8	12.7	This study
Euphausiids	Calyptopis larvae	4,000	(3,000–5,000)	0.45	1.5	2	3.88	(3.84–3.91)	0.084 ± 0.002	65.1	4.8	6.7	58.3	8.9	This study
	Tessarabrachion oculatus	750	(500–1,000)	0.13	3	2	9.17	(9.01–9.34)	0.44 ± 0.08	78.1	11.6	10.3	43.8	4.2	This study
	Bentheuphausia amblyosis	4,000	(3,000–5,000)	0.45	1.5	1	41.65		0.21	74.8	9.9	9.0	52.1	5.8	This study
Decapods	*Hymenodora frontalis*	750	(500–1,000)	0.13	3	3	22.77	12.31–34.97)	0.10 ± 0.03	70.4	6.7	6.2	60.6	10.1	This study
	Acanthophyla quadrispinosa	1,000	(500–1,500)	0.15	2.5	2	8.29	(1.60–43.0)	0.23 ± 0.15	74.3	4.8	8.0	51.2	6.4	This study
Leptostracans	*Nebaliopsis typica*	2,500	(2,000–3,000)	0.32	2	2	2.79	(1.01–7.66)	0.18 ± 0.1	65.9	4.3	6.6	58.5	8.9	This study
Chaetognaths	*Caecosagitta macrocephala*	1,500	(1,000–2,000)	0.2	2	3	5.50	(3.54 – 11.56)	0.10 ± 0.03	86.7	17.4	9.9	44.9	4.5	Ikeda & Takahashi (2012)
	Pseudosagitta scrippsae	750	(500–1,000)	0.13	3	7	13.65	(11.48 – 18.74)	0.083 ± 0.016	94.4	50.4	5.9	22.8	3.9	Ikeda & Takahashi (2012)
	Solidosagitta zetesios	1,500	(1,000–2,000)	0.20	2	7	8.57	(5.28 – 12.05)	0.14 ± 0.06	89.8	14.0	10.5	41.1	3.9	Ikeda & Takahashi (2012)
	Eukrohnia bathypelagica	750	(500–1,000)	0.13	3	16	1.58	(1.25 – 2.12)	0.095 ± 0.030	92.2	27.1	8	37.7	4.7	Ikeda & Takahashi (2012)
	Eukrohnia fowleri	2,500	(2,000–3,000)	0.32	1.5	32	7.12	(2.04 – 14.28)	0.066 ± 0.020	90.3	21.4	8.5	43.2	5.1	Ikeda & Takahashi (2012)
	Eukrohnia hamata	750	(500–1,000)	0.13	3	5	1.24	(1.09 – 1.42)	0.11 ± 0.02	92.9	31.7	7.8	32.6	4.2	Ikeda & Takahashi (2012)

Table 2. Stepwise multiple regression analyses of metabolic rate (Y: µL O_2 ind.$^{-1}$h^{-1}) on body mass (X_1: mg DM, C or N ind.$^{-1}$), temperature (X_2: ^{o}C), mid-sampling depth (X_3: m) and ambient oxygen saturation (X_4: 1 = 100%).

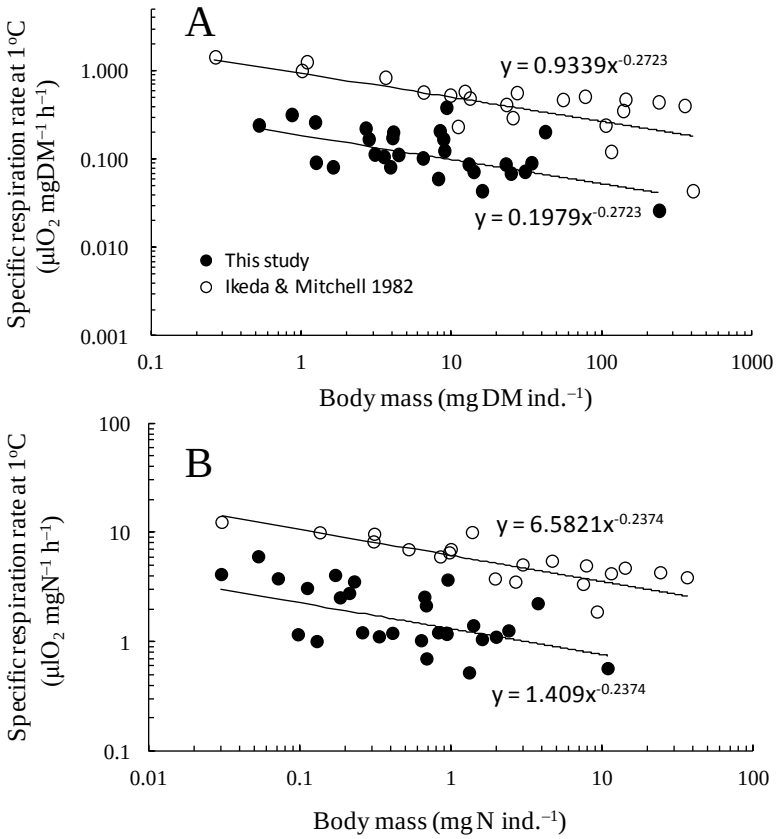
			Regression model $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 X_3 + a_4 X_4$					
Body mass unit	N	Step No.	a_0	a_1	a_2	a_3	a_4	R^2 (Adjusted R^2)
DM	28	0		0.748	1.088	2.397	–8.263	0.803
	28	1		0.739	0.048		–0.628	0.796
	28	2		0.739			–0.852	0.796
	28	3	–1.535	0.733				0.787 (0.779)
C	28	0		0.703	0.661	1.573	–6.419	0.797
	28	1		0.700		0.193	–2.210	0.794
	28	2		0.699			–1.308	0.794
	28	3	–0.858	0.684				0.773 (0.765)
N	28	0		0.738	1.342	2.131	–5.917	0.803
	28	1		0.732	0.610	0.350		0.799
	28	2		0.729	0.268			0.796
	28	3	0.395	0.712				0.772 (0.763)

Table 3. Metabolic comparison of zooplankton from various bathymetric levels of the world's oceans. Respiration rates are standardized to AMR at 1°C, assuming common body mass exponent and Q_{10} to be 0.8 and 2, respectively. Habitat depth is defined as mid-sampling depth, but those of Childress (1975), Thuesen and Childress (1993) and Thuesen et al. (1998) are different. See text for details.

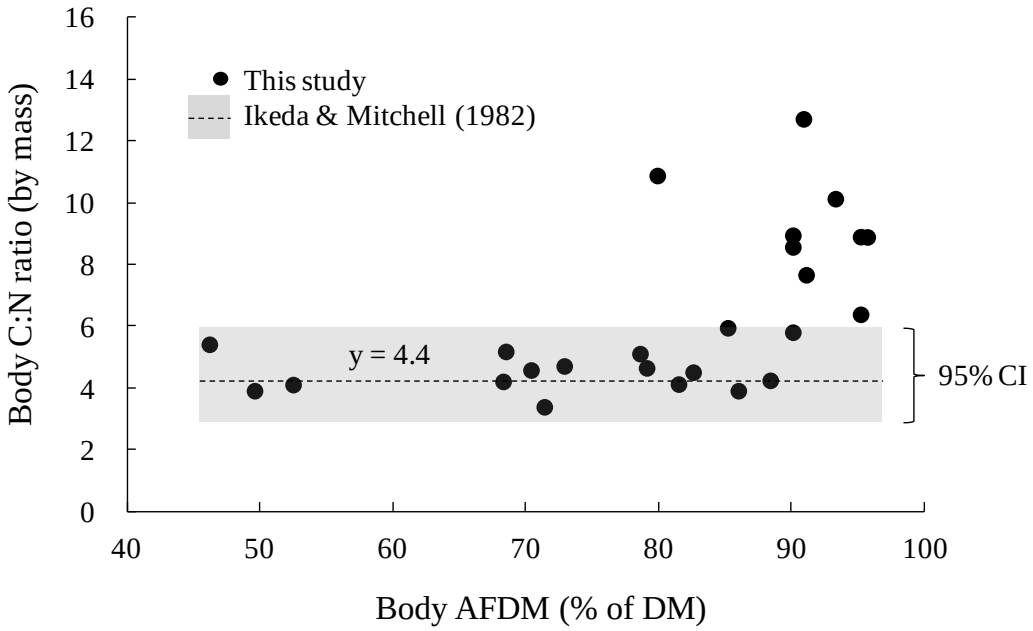
Zooplankton	Study site	Habitat depth (m)	Expt. Temp (°C)	No. of species	Original units		AMR at 1°C (μLO_2 $mgN^{-0.8}h^{-1}$)	Reference
					Body mass	Respiration rate		
7 taxa	Antarctic waters	100	–1.4 to –0.8	14	0.21–402 mgDM	0.32–124 μLO_2 $ind.^{-1}h^{-1}$	6.64 ± 1.69	Ikeda & Mitchell (1982)
10 taxa (see Table 1)	W. subarctic Pacific	500–5,000	1.5 to 3	28	0.52–239 mgDM	0.027–0.44μLO_2 $mgWM^{-1}h^{-1}$	1.66 ± 0.87	This study
Copepods	W. subarctic Pacific	500–3,000	2 to 3	59	0.025–2.38 mgN	0.05–4.16 μLO_2 $ind.^{-1}h^{-1}$	2.03 ± 0.77	Ikeda et al. (2006b)
Copepods	Off south California	540–1,350	5	10	0.007–0.061gWM	0.67–2.05$\mu molO_2$ $gWM^{-1}h^{-1}$	2.72 ± 1.56	Thuesen et al. (1998)
Copepods	W. subarctic Pacific	5,000–7,000	1.5	mixed	0.33 mgWM	0.052 μLO_2 $mgWM^{-1}h^{-1*}$	1.13 ± 0.46	Ikeda (2011)
Chaetognaths	Off south California	700–1,900	5	3	0.015–0.204 gWM	0.35–0.78 $\mu molO_2$ $gWM^{-1}h^{-1}$	0.84 ± 0.21	Thuesen & Childress (1993)
Chaetognaths	Weddell Sea	500–1,500	0	2	2.2–2.8 mgDM	0.15 μLO_2 $mgDM^{-1}h^{-1}$	1.65 ± 0.88	Kruse et al. (2010b)
Crustaceans**	Off South California	500–1,200	5	10	0.07–48.2 gWM	0.0015–0.036 μLO_2 $mgWM^{-1}h^{-1}$	1.97 ± 0.64	Childress (1975)
Crustaceans**	Antarctic waters	600	–1 to 0.3	7	49–494 mgDM	2.8–63.3 μLO_2 $ind.^{-1}h^{-1}$	3.32 ± 1.08	Ikeda (1988)

*estimated from ETS activity

**some micronektonic species included


A
Specific respiration rate at 1°C
(µlO2 mgDM−1 h−1)
1.000
0.100
0.010
0.001
y = 0.9339x-0.2723
y = 0.1979x-0.2723
This study
Ikeda & Mitchell 1982
0.1
1
10
100
1000
Body mass (mg DM ind.−1)
B
Specific respiration rate at 1°C
(µlO2 mgN−1 h−1)
100
10
1
0.1
y = 6.5821x-0.2374
y = 1.409x-0.2374
0.01
0.1
1
10
100
Body mass (mg N ind.−1)

Ikeda Fig. 1


16
14
12
10
8
6
4
2
0
Body C:N ratio (by mass)
This study
Ikeda & Mitchell (1982)
y = 4.4
95% CI
40
50
60
70
80
90
100
Body AFDM (% of DM)

Ikeda Fig. 2