Metabolism and chemical composition of four pelagic amphipods in the Oyashio region, western subarctic Pacific Ocean

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ABSTRACT: As a basis for estimating trophic functions of amphipods in the pelagic ecosystem, oxygen consumption and ammonia excretion rates were determined for 4 amphipods, *Themisto pacifica*, *T. japonica*, *Primno abyssalis* and *Cyphocaris challengeri* in the Oyashio region in the western subarctic Pacific Ocean. Water, ash and elemental composition (carbon, C; nitrogen, N) were also determined. For the 4 amphipod species, water content ranged from 67.8 to 89.7 % of wet weight, ash from 15.2 to 46.5 % of dry weight, C from 27.4 to 67.1 % of dry weight, and N from 5.3 to 11.8 % of dry weight. Comparisons of weight-adjusted metabolic rate (AMR) among amphipods showed *T. pacifica* to be the most active species (15.2 µl O_2 body $N^{-0.90}$ h^{-1}), followed by *T. japonica* (10.3), *P. abyssalis* (10.2) and *C. challengeri* (5.9). The first 2 species changed order when the AMR for ammonia excretion was determined (*T. japonica*, *T. pacifica*, *P. abyssalis* and *C. challengeri*). The atomic ratio of O:N derived from oxygen consumption and ammonia excretion data varied by species, ranging from 18.7 (*T. japonica*) to 85.2 (*C. challengeri*). An alternate method of assessing metabolic activity using daily metabolic losses in body C (from oxygen consumption data) and N (from ammonia excretion data) was also computed. The results led to a similar conclusion to that reached from AMR results. The interspecific differences in metabolism and body composition among these 4 sympatric amphipods are discussed in terms of species-specific vertical distribution patterns and differing food habits. The present results are compared with published data on congeneric amphipods in other regions.

KEY WORDS: Pelagic amphipods · Metabolism · Chemical composition · Vertical distribution · Food habits

INTRODUCTION

Pelagic amphipods are primarily considered to be carnivores, and are a common component of zooplankton communities throughout the oceans of the world (Raymont 1983). Their importance, however, has long been overlooked in the study of energy flow and matter cycling in pelagic marine ecosystems. This is partly due to their low contribution to the total zooplankton biomass; usually less than 0.5 % (cf. Longhurst 1985). However, recent studies suggest that amphipod populations (mostly *Themisto* spp.) exert significant predation pressure (30 to 70 %) on secondary production in the waters around South Georgia in the Southern Ocean (Pakhomov & Perrissinotto 1996) and in the southern Japan Sea (Ikeda & Shiga 1999). In the pelagic zone of the Kerguelen waters, in the southern Indian Ocean, *Themisto gaudichaudii* have been reported to have an integral role in zooplankton–sea bird couplings (Bocher et al. 2001).

In the western subarctic Pacific Ocean and its neighboring seas, a total of 67 pelagic amphipod species are known to occur (Yoo 1970). The 4 most abundant amphipods include 3 hyperiids (*Themisto pacifica*,

T. japonica and *Primno abyssalis*) and 1 gammarid (*Cyphocaris challengeri*). In terms of bathymetric distribution, *T. pacifica* and *T. japonica* are epipelagic, and *P. abyssalis* and *C. challengeri* are mesopelagic species (Yoo 1970, Wing 1976, Bowman 1978). These 4 amphipods have been reported as dietary components of salmon (Fukataki 1967, 1969, Tadokoro et al. 1996), walleye pollock (Fujita et al. 1995, Kooka et al. 1997, Yamamura et al. 2002), squid (Okiyama 1965) and mesopelagic fishes (Beamish et al. 1999, Moku et al. 2000, Uchikawa et al. 2001), suggesting that they may have trophic importance in the pelagic ecosystems of this region. However, solid data for estimating the trophic functions, e.g. production and predation pressure to other zooplankton of these amphipods in the western subarctic Pacific, are currently lacking.

As part of a research program to evaluate energy flow and matter cycling in the pelagic ecosystem of the Oyashio region of the western subarctic Pacific Ocean, we investigated metabolism (oxygen consumption and ammonia excretion) and body composition (water, ash, carbon and nitrogen) of the 4 dominant amphipods, as bases for estimating the magnitude of carbon and nitrogen demands, metabolic substrates and nutritional conditions. Inter-specific differences in these parameters are discussed in relation to the bathymetric distribution, swimming abilities, food habits and feeding patterns of these amphipods. The present results are compared with published data on congeneric amphipods in other regions.

MATERIALS AND METHODS

Sampling. Live amphipods were collected from several sites in the western subarctic Pacific Ocean between May 2000 and April 2001, while aboard the

Table 1. Summary of sampling data of amphipods in the western subarctic Pacific

Species	Site	Position	Date
Themisto pacifica	1	44° N, 155° E	31 July 2000
	2	42° 30' N, 155° E	1 August 2000
	3	41° N, 155° E	2 August 2000
T. japonica	4	42° N, 141° 30' E	10 May 2000
			31 May 2000
			26 June 2000
			13 December 2000
Primno abyssalis	5	41° 30' N, 145° 47' E	29 July 2000
	6	43° 01' N, 151° 21' E	30 July 2000
Cyphocaris challengeri	4	42° N, 141° 30' E	20 October 2000
			17 March 2001
			6 April 2001

TS 'Hokusei Maru', TS 'Oshoro Maru' and RV 'Ushio Maru' (Table 1, Fig. 1). At each sampling site, oblique tows were made with a bongo net (mouth opening 70 cm, mesh size 333 µm) from about 500 m depth. Each time the net was retrieved, all contents were gently transferred to 10 l plastic buckets filled with chilled surface seawater. Undamaged amphipods were quickly sorted and placed into 500 or 1000 ml glass containers filled with seawater, and kept at 5°C until the experiments commenced.

At each amphipod sampling site, seawater was collected from 100 m depth with Niskin bottles, filtered through GF/F filters and well oxygenated for use in the experiments. In order to obtain metabolic rates at near natural oxygen concentrations for the experiments on mesopelagic *Primno abyssalis* and *Cyphocaris challengeri*, seawater was collected from 300 m depth with Niskin bottles, and passed gently through a siphon system with 20 µm mesh netting covering the outlet
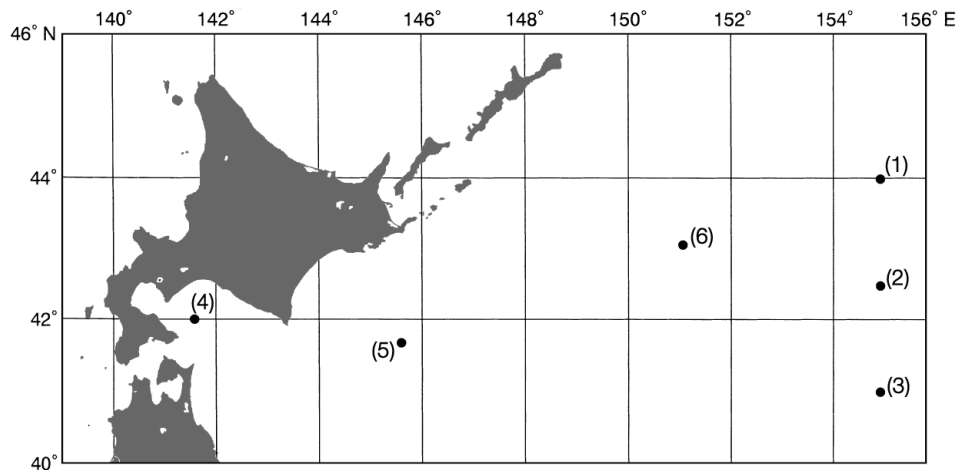

Fig. 1. Sampling locations in the western subarctic Pacific Ocean

to remove large particles. Mean dissolved oxygen concentrations were 6.8 µl O_2 ml^{-1} at 100 m depth and 5.5 µl O_2 ml^{-1} at 300 m depth.

Metabolic measurements. Experiments were started within 12 to 16 h after the collection of specimens. A water bottle method (Omori & Ikeda 1984) was used to simultaneously determine the oxygen consumption and ammonia excretion rates of amphipods, i.e. bottles with and without experimental animals inside were prepared simultaneously, and the differences in dissolved oxygen and NH_4^+-N concentrations after a certain period of incubation were assumed to be attributed to respiration and excretion of the animals, respectively. The bottles used to incubate specimens were 100, 200 or 300 ml, depending on the size of the specimens. Bottles containing specimens (1 to 6 ind. bottle^{-1}) and control bottles without specimens were prepared concurrently, and incubated at 5°C for 24 h in the dark. The experimental temperature (5°C) represented the temperature typically encountered by the 4 amphipods in the Oyashio Region (Yamada et al. 2002). At the end of each experiment, dissolved oxygen was determined by the Winkler method (Strickland & Parsons 1972) in subsamples of water siphoned from the bottles. Further subsamples of water were removed to 60 ml polyethylene bottles, which were frozen (–30°C) for later ammonia analysis. Ammonia was determined by the phenolhypochlorite method (Solórzano 1969). Specimens recovered from experimental bottles at the end of experiments were rinsed briefly in distilled water, blotted on filter paper, and frozen (–30°C) for determination of their weight and elemental composition.

Chemical composition. Frozen specimens were weighed for wet weight (WW) and then freeze-dried to obtain a dry weight (DW). Amphipod water content was then calculated. Freeze-dried samples were ground into a powder using a 1.5 ml polypropylene Micro-Tube (Iwaki Glass). Powdered samples were used for carbon (C) and nitrogen (N) composition analysis, which was done with an elemental analyzer (Yanaco CHN Coder MT-5), using p-nitroaniline as a standard. Precisions of analyses (coefficient of variation) were 0.8% for C and 0.3% for N.

Statistical analysis. In order to analyze the relationship between oxygen consumption rates (R) or ammonia excretion rates (E) and body weight, a GM regression model $\ln M = a + b \ln DW$ was used, where M is µl O_2 ind.$^{-1}$ h^{-1} or µg NH_4^+-N ind.$^{-1}$ h^{-1}, DW is body dry mass (mg ind.$^{-1}$), and a and b are proportional constants (cf. Ricker 1973).

RESULTS

Metabolic rates

Preliminary analyses indicated that R or E versus DW relationships from different locations and dates for each amphipod (Table 1, Fig. 1) did not differ significantly (analysis of covariance, ANCOVA: p = 0.13 to 0.84). On this basis, these data were pooled together for each amphipod. DW among the amphipods ranged from 1.1 (*Themisto pacifica*) to 6.5 mg (*Primno abyssalis*); for R from 1.2 (*T. pacifica*) to 5.4 µl O_2 ind.$^{-1}$ h^{-1} (*P. abyssalis*); and for E from 0.07 (*Cyphocaris challengeri*) to 0.24 µg NH_4^+-N ind.$^{-1}$ h^{-1} (*T. japonica*) (Table 2). Scatter diagrams of R or E for each amphipod species plotted against DW on a log-log (base e) graph showed that the variations in DW, R and E were

Table 2. Regression statistics of oxygen consumption rates (R: µl O_2 ind.$^{-1}$ h^{-1}, upper panel) and ammonia excretion rates (E: µg NH_4^+-N ind.$^{-1}$ h^{-1}, lower panel) on dry weight (DW: mg) of 4 amphipod species at 5°C (see Fig. 1). The GM regression model adopted is $\ln R$ (or E) = $a + b \ln DW$. Since the differences in slope (b) between the 4 species are insignificant, common b was computed as 0.90 for R, and 1.18 for E. Intercepts (a) are for regression lines adjusted to these common slopes

| Species	n	Body DW (mg)	O_2 consumption (µg O_2 ind.$^{-1}$ h^{-1})	b (95% CI)	a for b = 0.90	r
Themisto pacifica	22	1.17 ± 0.77	1.19 ± 1.11	0.947 (0.794–1.099)	0.451	0.939
T. japonica	47	3.01 ± 3.28	2.51 ± 1.98	0.771 (0.694–0.848)	0.102	0.942
Primno abyssalis	17	6.49 ± 4.33	5.38 ± 3.84	1.003 (0.815–1.190)	−0.035	0.941
Cyphocaris challengeri	38	5.73 ± 3.63	2.45 ± 1.73	0.880 (0.795–0.965)	−0.675	0.958
Species	n	Body DW (mg)	Ammonia excretion (µg NH_4^+-N ind.$^{-1}$ h^{-1})	b (95% CI)	a for b = 1.18	r
Themisto pacifica	23	1.06 ± 0.76	0.090 ± 0.09	1.366 (1.059–1.674)	−2.653	0.868
T. japonica	45	2.03 ± 1.92	0.220 ± 0.19	1.005 (0.902–1.108)	−2.266	0.940
Primno abyssalis	17	6.49 ± 4.33	0.210 ± 0.17	1.045 (0.787–1.303)	−3.751	0.894
Cyphocaris challengeri	37	5.75 ± 3.68	0.072 ± 0.08	1.292 (1.080–1.503)	−4.912	0.878
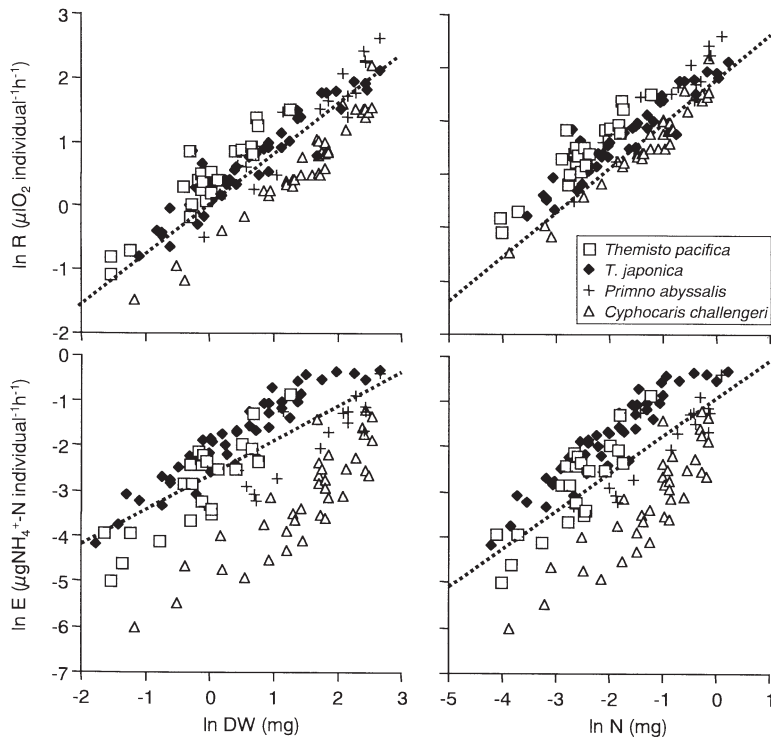
Fig. 2. Relationships between metabolism (oxygen consumption rate (R; μl O$_2$ ind.$^{-1}$ h^{-1}, upper panels), ammonia excretion rate (E; μg NH$_4{}^+$-N ind.$^{-1}$ h^{-1}, lower panels) and dry weight (DW; mg, left panels) or nitrogen (N; mg, right panels) of 4 amphipods at 5°C. Dashed lines: regression equation of 'general zooplankton' (Ikeda 1985) at 5°C. See Table 2 for regression statistics

the R versus DW and 1.18 for the E versus DW regression, and were used to re-compute intercept values (a) of the regression lines for each species (Table 2). Thus re-computed intercepts of the R versus DW and E versus DW regression lines ranged from –0.675 (*C. challengeri*) to 0.451 (*T. pacifica*), and from –4.912 (*C. challengeri*) to –2.266 (*T. japonica*), respectively.

O:N ratio

The mean atomic ratio of R to E (O:N ratio, by atoms) ranged from 18.7 (*Themisto japonica*) to 85.2 (*Cyphocaris challengeri*; see Table 4), and differed significantly among the 4 species (analysis of variance, ANOVA: $F = 34.2$, df = 3,114, p < 0.0001). Subsequent interspecific analysis revealed that the mean O:N ratio of *C. challengeri* was highest and that of *T. japonica* was lowest, with the ratios of *T. pacifica* and *Primno abyssalis* being intermediate (Fisher's PLSD: p < 0.02).

Chemical composition

The chemical composition, including water, ash, C, N and C:N ratio, of each amphipod species was plotted against DW (Fig. 3). Water content was expressed as a percentage of WW, and the ash, C and N as percentages of DW. In the scatter diagrams, chemical compositions varied widely between inter- and intraspecific. None of the chemical components correlated significantly with DW for any amphipod (correlation coefficients: –0.08 to 0.27 for water, –0.22 to –0.09 for ash, –0.33 to 0.14 for C, –0.25 to 0.20 for N, and –0.40 to 0.16 for C:N, all p > 0.05). Using these results, the mean composition of each component was computed for each species in order to make interspecific comparisons (Table 4).

There were significant between-species differences for all the body composition components analyzed

of 1 to 2 orders of magnitude (Fig. 2), and both R and E increased with an increase of DW. The correlation coefficients (r) for R versus DW and E versus DW relationships fitted to the regression model were significant for all 4 species (0.868 to 0.958, p < 0.001; Table 2). The slope of the R versus DW regression line ranged from 0.771 (*T. japonica*) to 1.003 (*P. abyssalis*), while for E versus DW the slope ranged from 1.005 (*T. japonica*) to 1.366 (*T. pacifica*). Between-species differences were not significant in either the R versus DW or the E versus DW relationship (the 95% confidence interval (CI) ranges overlapped, Table 2). On this basis, common slopes (mean b-values) were computed as 0.90 for

Table 3. Summary of body composition analyses of water, ash, C and N and resultant C:N ratios of 4 amphipods in the Oyashio region. Means ± 1 SD. Superscript numbers show rank of between-species differences examined by Fisher's PLSD test

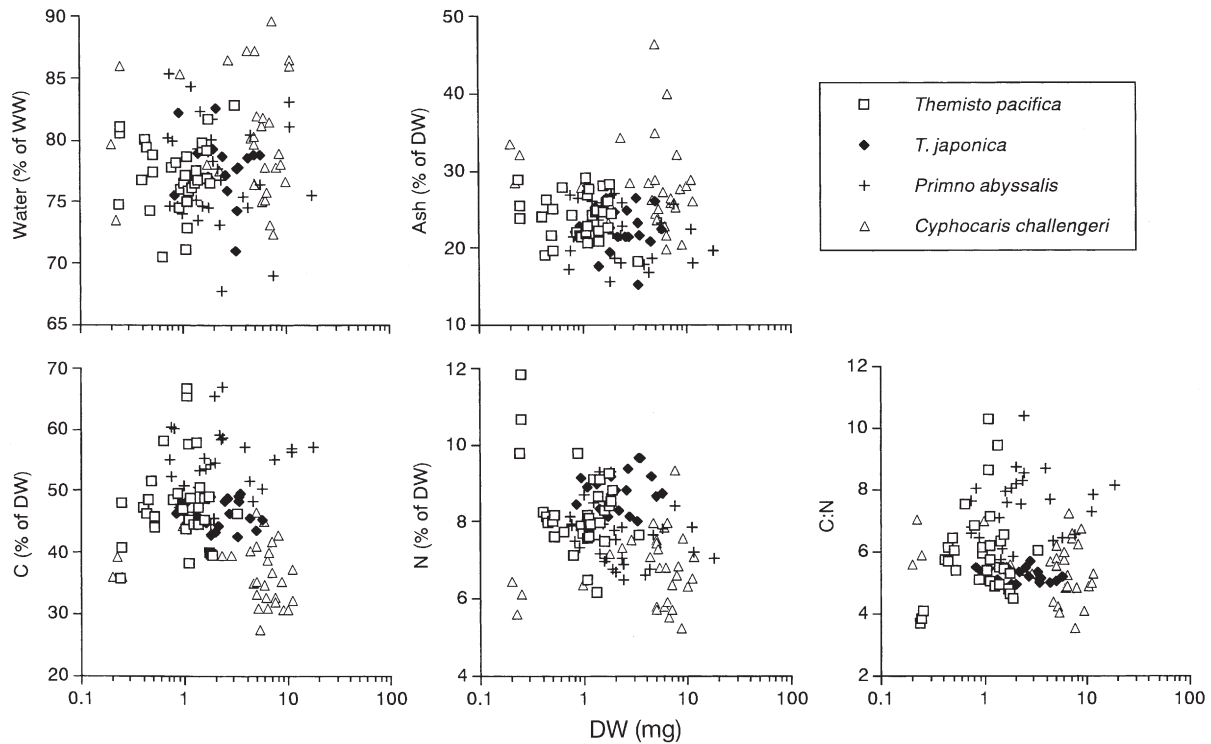| Species	n	Water (% of WW)	Ash (% of DW)	C (% of DW)	N (% of DW)	C:N (by weight)
Themisto pacifica	33	77.2 ± 2.8[2]	24.0 ± 2.9[2]	47.9 ± 7.0[2]	8.3 ± 1.1[2]	5.9 ± 1.5[2]
T. japonica	20	77.7 ± 2.6[2]	22.8 ± 3.2[2]	46.3 ± 2.3[2]	8.8 ± 0.5[1]	5.2 ± 0.2[4]
Primno abyssalis	30	77.4 ± 4.2[2]	22.0 ± 3.4[2]	54.3 ± 5.4[1]	7.6 ± 0.7[3]	7.2 ± 1.2[1]
Cyphocaris challengeri	31	80.1 ± 4.7[2]	28.0 ± 5.6[1]	36.8 ± 4.8[2]	6.8 ± 0.9[4]	5.5 ± 0.9[3]

Fig. 3. Relationships between body composition (water, ash, C and N), C:N ratios and body dry weight (DW) of 4 amphipods

(ANOVA: p < 0.05). Further analysis using Fisher's PLSD tests revealed species-specific features in body composition. For example, *Cyphocaris challengeri* was characterized by high water (80.1% of WW) and ash (28.0% of DW) contents, and low C (36.8% of DW) and N (6.8% of DW) values. *Primno abyssalis* contained the highest C content (54.3% of DW) and exhibited the highest C:N ratio (7.2), while *Themisto japonica* contained the highest N (8.8% of DW). The body composition of *T. pacifica* was similar to that of *T. japonica*.

Adjusted metabolic rates

R and *E* were standardized to adjusted metabolic rates (AMR), as proposed by Ikeda (1988), in order to compare the 4 amphipods, which had dissimilar body masses. Since the metabolic rate (*M*) is a function of body mass (*W*) (i.e. $M = aW^b$; *a* and *b* are constants), AMR is calculated as M/W^b. In our calculation of AMR, *W* is expressed as N units to reduce interspecific variations (cf. Ikeda 1988) by using the data shown in Table 3, and using the common *b* values mentioned above (0.90 for *R*–DW relationships, and 1.18 for *E*–DW relationships; Table 4). The resultant AMR_{O_2} at 5°C for the 4 amphipods was greatest for *Themisto pacifica* (mean: 15.18), followed by *T. japonica* (10.33),

Primno abyssalis (10.22), and *Cyphocaris challengeri* (5.88). These 4 mean AMR_{O_2} values were significantly different from each other (Table 4). Similarly, the mean $AMR_{NH_4^+}$ values differed significantly from one amphipod to the next (ANOVA: $F = 86.4$, df = 3,120, p < 0.0001), with *T. japonica* (mean: 1.93) being highest, followed by *T. pacifica* (1.38), *Primno abyssalis* (0.60) and *C. challengeri* (0.20) (Fisher's PLSD: p < 0.01).

Metabolic losses in body C and N

An alternate method of assessing metabolic activity using daily metabolic losses in body C (from oxygen consumption data) and body N (from ammonia excretion data) was also calculated (cf. Ikeda & Hirakawa 1998). For daily body C loss, *R* was converted first to CO_2-C production rates $R \times RQ \times 12/22.4 \times 24 \times 10^{-3}$, where RQ is a respiratory quotient, 12/22.4 is the C mass in 1 mol of CO_2 (22.4 l), 24 is the number of h d^{-1}, and 10^{-3} is to convert µg to mg. An RQ of 0.97 was used (protein metabolism; Gnaiger 1983). The daily body C and N losses due to metabolism were expressed as a function of body C and N. Among the 4 amphipods, mean daily C and N losses thus calculated ranged from 1.6% (*Cyphocaris challengeri*) to 4.2% (*Themisto pacifica*), and from 0.4% (*C. challengeri*) to 3.1% (*T. japon-*

Table 4. O:N ratios, adjusted metabolic rates in terms of oxygen consumption (AMR_{O_2}) and ammonia excretion rates ($AMR_{NH_4^+}$), and daily metabolic losses in body C and N at 5°C of 4 amphipods in the Oyashio region. Superscript numbers show rank of between-species differences examined by Fisher's PLSD test

Species	O:N	n	Adjusted metabolic rate				Metabolic loss	
			AMR_{O_2} (μl O_2 mg body $N^{-0.90}\,h^{-1}$)	n	$AMR_{NH_4^+}$ (μg NH_4^+-N mg body $N^{-1.18}\,h^{-1}$)	n	(% body C d^{-1})	(% body N d^{-1})
Themisto pacifica	38.5 ± 20.2[3]	20	15.18 ± 4.03[1]	22	1.38 ± 0.65[2]	23	4.24 ± 1.19[1]	2.23 ± 1.08[1]
T. japonica	18.7 ± 8.4[4]	44	10.33 ± 3.50[2]	47	1.93 ± 0.66[1]	45	2.99 ± 1.19[2]	3.06 ± 0.94[2]
Primno abyssalis	45.5 ± 22.0[2]	17	10.22 ± 2.86[2]	17	0.60 ± 0.35[3]	17	1.97 ± 0.58[2]	1.07 ± 0.40[2]
Cyphocaris challengeri	85.2 ± 47.8[1]	37	5.88 ± 1.54[3]	38	0.20 ± 0.14[1]	370	1.55 ± 0.47[3]	0.40 ± 0.28[3]

ica), respectively. Between-species differences were highly significant for both C and N loss expressions (ANOVA: $F = 42.0$, df = 3,120, $p < 0.0001$ for C loss; $F = 87.3$, df = 3,120, $p < 0.0001$ for N loss; Table 4). Subsequent analysis revealed that the significant interspecific variations in daily body C losses were composed of a high group (*T. pacifica* and *T. japonica*) and a low group (*Primno abyssalis* and *C. challengeri*) (Fisher's PLSD: $p < 0.001$). *T. japonica* had the greatest daily body N losses, followed by *T. pacifica*, *P. abyssalis* and *C. challengeri* (Fisher's PLSD: $p < 0.001$).

DISCUSSION

The comparison of *R* or *E* among *Themisto pacifica*, *T. japonica*, *Primno abyssalis* and *Cyphocaris challengeri* is of particular interest when elucidating possible species-specific features of these co-occurring pelagic amphipods from the Oyashio Region. Both *R* and *E* as functions of DW were similar for *T. pacifica*, *T. japonica* and *P. abyssalis*, but the data for *C. challengeri* were distributed below the data of the other 3 species (Fig. 2). While metabolic comparisons between zooplankton species are often sensitive to the body mass chosen (cf. Ikeda 1985), the markedly reduced metabolic rates of *C. challengeri* remained the same, regardless of using N as the body mass unit (Fig. 2).

Several studies have shown that water column depth affects the metabolic rates of pelagic fishes and crustaceans, and that rates decrease rapidly with increasing depth (Childress 1975, Quetin et al. 1980, Donnelly & Torres 1988, Ikeda 1988, Cowles et al. 1991, Torres et al. 1994a). In antarctic waters, where the temperature is fairly homogenous from the surface to the deeper layers, pelagic crustaceans living in the mesopelagic zone have been reported to have *R* of 50%, and *E* of 30%, of epipelagic crustacean rates (Ikeda 1988). This depth-related decline in metabolic rates of pelagic animals has been interpreted as reduced locomotive activity of deeper-living animals (see Childress 1995 for a review).

The 4 amphipods used in this study are classified as either epipelagic (*Themisto pacifica*, *T. japonica*) or mesopelagic species (*Primno abyssalis*, *Cyphocaris challengeri*) (Yoo 1970, Wing 1976, Bowman 1978). The reduction in AMR_{O_2} with increasing depth occurred as expected for *C. challengeri*, but *P. abyssalis* exhibited AMR identical to that of the epipelagic *T. japonica*. In our laboratory observations, *P. abyssalis* was found to be a very active swimmer which readily preyed on other zooplankton, e.g. copepods and euphausiids. In contrast, *C. challengeri* was a less active swimmer, and may be a necrophagous feeder in nature. Successful maintenance of *C. challengeri* by providing whelk or shrimp as prey may support this (Yamada & Ikeda 2000). The depths where the 4 amphipods in this study were found spanned only 0 to 500 m, compared with 0 to 2000 m in Ikeda's study (1988) and 0 to 4000 m in Childress' study (1975). Nonetheless, the reduced metabolism and the body composition features (high water and ash, low C and N, cf. Table 3) displayed by *C. challengeri* were considered to reflect the lower locomotive activity occurring in the mesopelagic.

It may be questioned how typical the metabolic rates of the 4 amphipods in this study are of marine zooplankton. Ikeda (1985) analyzed metabolic data of marine epipelagic zooplankton (crustaceans and non-crustaceans) living in oceans around the world, and expressed metabolic rates as a function of body mass and habitat temperature. His data are superimposed on our data in Fig. 2 and are labeled as 'general zooplankton'. For comparisons of metabolic rates for marine zooplankton with differing body chemical composition, C or N, rather than DW, has been postulated to be a valid basis for body mass (Ikeda 1985). The *R* and *E* of the 4 amphipods were therefore re-plotted against their body N (Fig. 2). Overall, the scatter diagram of rates against body N is similar to that of rates against body DW. Clearly, the *R* of the 4 amphipods in this study does not deviate appreciably from the 'general zooplankton' line. While *E* of *Cyphocaris challen-*

geri is less, the rates of the other 3 amphipods are close to the 'general zooplankton' line. These results imply that the metabolic rates of the 4 dominant amphipods from the Oyashio region are in general agreement with those of zooplankton from other oceans around the world.

The O:N atomic ratio has been used as an index of metabolic substrate in zooplankton (Ikeda 1977). When zooplankton use protein as their sole substrate, this ratio is expected to be around 8, and when lipid alone is used, the ratio is an infinite number (i.e. lipid contains extremely low nitrogen). An O:N ratio of 24 is seen when equal amounts of protein and lipid are metabolized (Ikeda 1974). From simultaneous measurements of R and E in antarctic amphipods (*Themisto gaudichaudii*, *Vibilia antarctica* and *Hyperia gaudichaudii*), Ikeda & Mitchell (1982) calculated O:N ratios to be in the range of 10.9 to 18.4, indicating a largely protein-oriented metabolism for these amphipods. The amphipods used in this study (*T. pacifica*, *T. japonica*, *Primno abyssalis* and *Cyphocaris challengeri*) are hypothesized to be primarily carnivores, but an O:N ratio < 24 was only seen in *T. pacifica*. The ratios obtained for the other 3 amphipods were considerably > 24 (38.5 to 85.2, Table 4). Such a high O:N ratio has been reported previously for *T. libellula*, an amphipod in the Barents Sea (69.4, Ikeda & Skjoldal 1989), and for some deep-living crustaceans (Quetin et al. 1980, Hiller-Adams & Childress 1983, Ikeda 1988).

O:N ratios vary considerably from 1 individual to the next, even in the same species collected at the same time (Ikeda 1988). Quetin et al. (1980) postulated that the O:N ratios of a deep-living mysid, *Gnathophausia ingens*, increased as starvation progressed (i.e. an increased use of body lipid as a metabolic substrate). Thus, the feeding history of individuals prior to sampling and the amount of lipids and protein deposited in the body all affect the measured O:N ratio. Of the 3 amphipods exhibiting O:N ratios > 24, *Themisto pacifica* and *Primno abyssalis*, both of which contained a large amount of C (= lipids) (cf. Table 4), might use their stored lipid for metabolism. *Cyphocaris challengeri* also showed O:N ratios > 24, but this species contained less C, although it had more water and ash (Table 4). *C. challengeri* may be an opportunistic feeder that periodically encounters starvation conditions in nature. Only *T. japonica* had an O:N ratio < 24. This species exhibited greater losses of body C and N for metabolism (Table 4), suggesting that their low O:N ratio reflects continuous feeding on high-protein foods.

Table 5 compares the present results for C and N composition and the C:N ratios of the 4 dominant amphipods in the Oyashio region with similar species living in other regions. Clearly, the C composition and C:N ratios of *Themisto pacifica*, *T. japonica* and *Primno abyssalis* in the Oyashio region are greater than those of *Themisto* spp. and *Primno* spp. analyzed by other studies. A high C composition, in association with high C:N ratios, is indicative of a relative abundance of lipids in the body (Ikeda 1974). The body composition of marine zooplankton is highly variable and depends on both intrinsic factors (development, maturity and sex) and extrinsic factors (temperature, food supply and depth of occurrence) (Omori 1969, Ikeda 1974, Båmstedt 1986). The most likely cause of the lipid-rich bodies of 3 of the amphipods studied is their feeding on large lipid-rich zooplankton, such as *Neocalanus* copepods, which are abundant in the Oyashio region (Kobari & Ikeda 1999). In fact, the body of *Neocalanus* spp. is often filled with oil-droplets, and its body C exceeds 60% of DW (T.I. unpubl. data). A close coupling of body lipid with dietary lipid has been demonstrated through seasonal investigations on a benthic amphipod, *Monoporeia affinis* (Lehtonen 1996).

Table 5. Body C and N compositions and C:N ratio of pelagic amphipods from various regions

Genus	Species	Region	C (% of DW)	N (% of DW)	C:N ratio	Reference
Themisto	*gaudichaudii*	Southern Ocean	35.9–41.5	7.4–8.6	4.2	Ikeda & Mitchell (1982)
	compressa	Northeastern Atlantic	36.8	7.8	4.7	Williams & Robins (1979)
	libellula	Barents Sea	38.2	8.1	4.7	Ikeda & Skjoldal (1989)
	japonica	Japan Sea (Toyama Bay)	37.1	8.9	4.2	Ikeda & Hirakawa (1998)
	japonica	Oyashio region	45.2–46.7	8.2–9.6	4.8–5.6	This study
	pacifica	Oyashio region	45.3–59.5	7.9–12.1	3.9–7.7	This study
Primno	*macropa*	Southern Ocean	47.3	9.2	4.9	Torres el al. (1994b)
	abyssalis	Japan Sea (Toyama Bay)	37.8–40.2	9.3–9.4	4.0–4.3	Ikeda & Hirakawa (1998)
	abyssalis	Oyashio region	50.5–59.2	7.2–8.0	6.4–8.0	This study
Cyphocaris	*faueeri*	Southern Ocean	50.0	6.5	7.7	Torres el al. (1994b)
	richardi	Southern Ocean	50.1–56.6	7.1–7.7	6.5–8.0	Torres el al. (1994b)
	challengeri	Oyashio region	34.4–40.0	6.3–7.2	5.2–6.2	This study

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Among the 4 amphipods studied from the Oyashio region, *Cyphocaris challengeri* differed markedly from the other 3 species by having a lower metabolism, as discussed above, and a different body composition (lower values for C composition and C:N ratios, Table 3). Living in the mesopelagic zone does not appear to be responsible for these lower values, since no clear effect of depth of occurrence on body composition has been observed for pelagic crustaceans (cf. Childress & Nygaard 1974). *C. challengeri* is a relatively slow swimmer, and possibly a necrophagous feeder. Its daily metabolic losses of body C and N were the lowest among the 4 amphipods in the Oyashio region (Table 4). Recently, Yamaguchi et al. (2002) found abundant dead zooplankton (carcasses) in the mesopelagic zone of the western subarctic Pacific Ocean. Thus, combined with their reduced metabolism, the need for lipid energy reserves may be less for *C. challengeri* in comparison to the other 3 amphipods in the Oyashio region.

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