plankton biology & ecology © The Plankton Society of Japan 1998

Metabolism and body composition of zooplankton in the cold mesopelagic zone of the southern Japan Sea

Tsutomu Ikeda¹ & Kazumasa Hirakawa²

¹Biological Oceanography Laboratory, Faculty of Fisheries, Hokkaido University, Minato-machi, Hakodate 041, Japan ²Japan Sea National Fisheries Research Institute, 1 Suido-cho, Niigata 951, Japan

Received 5 March 1997; accepted 27 May 1997

Abstract: Metabolic activity (=oxygen consumption) and body composition (water, ash, C, H, N) were determined for 1 ctenophore, 7 copepods, 2 amphipods, 1 ostracod and 1 chaetognath species from the mesopelagic zone of the Japan Sea, a sea which is characterized by near-zero temperature (<1°C) and an abundant oxygen $(ca. 5 m | O_2|^{-1})$. Using these results, combined with data on a mysid reported previously, metabolic activity in terms of "Adjusted Metabolic Rate (AMR)" at 0.5°C was computed at 3.48 (±1.32, SD) µIO₂ (mg bodyN)^{-0.85} h⁻¹ for crustacean species. As another expression of metabolic activity, body C loss due to metabolism at 0.5°C was calculated at 1.10 (\pm 0.54)% d⁻¹ for all species. Neither of these expressions of the metabolic activity of crustaceans differs significantly from those of zooplankton living at similar depths and/or thermal regimes in polar seas. Body composition was highly species-specific; water content ranged from 63.9 to 96.2% of wet weight, and ash from 6.1 to 65.3%, C from 11.2 to 61.3%, H from 2.7 to 9.8%, and N from 3.0 to 12.7% of dry weight. The C:N ratio varied from 3.0 to 9.1. All of this data on body composition are within the ranges reported for zooplankton inhabiting similar cold habitats. Interspecific differences in metabolic activity and body composition of zooplankton species are noted in relation to dissimilar life history patterns and feeding habits of some species.

Key words: metabolism, body composition, mesopelagic, Japan Sea

Introduction

The Japan Sea is located in the subarctic and is a marginal sea, being connected with the Pacific Ocean through shallow straits. The upper waters of the southern part of the Japan Sea exhibit subtropical characters due to the intrusion of the Tsushima Warm Current (a branch of the Kuroshio). Below 300 m, "The Japan Sea Proper Water" (Uda 1934), which is characterized by "near-zero" temperatures (<1°C), rather low salinity (ca. 34.1 psu), and abundant oxygen (>5 ml $O_2 l^{-1}$) is widespread over the entire Japan Sea, and occupies more than 80% of the total water volume of the Japan Sea (Yasui et al. 1967). Compared with the adjacent Okhotsk Sea and Bering Sea, the pelagic fauna in the Japan Sea is species-poor with only a few predominant species, and lacks true bathypelagic communities (Vinogradov 1968). De-

spite its near-zero temperature, zooplankton biomass maxima have often been recorded in the mesopelagic zone (Vinogradov & Sazhin 1978; Hirakawa et al. 1990).

The zooplankton community occurring in the cold mesopelagic zone of the Japan Sea has two components, mesopelagic and "eurybathy" (cf. Zenkevitch 1963, hereforth referred to as eurybathic) species. The mesopelagic species are those which complete entire life cycles largely within the mesopelagic zone (>300 m). Eurybathic species include ontogenetic migrators (such as *Neocalanus plumchrus*, *N. cristatus*; cf. Heinrich 1962; Miller & Terazaki 1989), diel vertical migrators (*Themisto japonica*, *Euphausia pacifica*, *Metridia pacifica*; cf. Ikeda et al. 1992; Iguchi et al. 1993; Hirakawa & Imamura 1993), and species exhibiting a broad vertical distribution range (*Sagitta elegans*, *Pseudocalanus minutus*, *Oithona atlantica*; cf. Terazaki 1993; Hirakawa et al. 1990).

Metabolic activity of zooplankton is known to be a function of animal size and habitat temperature for those species living in the epipelagic zone (Ikeda 1974, 1985). In addition to size and temperature, the depth of occurrence is considered to be another parameter that affects the metabolic activity of pelagic animals, i.e. the deeper the habitat, the lower the metabolism (Childress 1971, 1975; Torres et al. 1979; Quetin et al. 1980; Ikeda 1988; Torres & Somero 1988). This progressive decrease of metabolic activity with depth in deeper-living animals has been explained by the reduction of locomotory activity with increasing depth (Childress & Mickel 1985; Cowles & Childress 1988), which reflects body structure (=body composition) of animals (Childress & Nygaard 1973, 1974; Stickney & Torres 1989). With this in mind it should be interesting to examine whether or not metabolic activity and body composition of mesopelagic and eurybathic zooplankters in the Japan Sea fit the general trend established for zooplankton in other seas. Data presently available for the metabolic activity (=oxygen consumption) and body composition of zooplankton from the mesopelagic zone of the Japan Sea are limited to a mysid *Meterythrops microphthalma* by Ikeda (1991) and an ostracod *Conchoecia pseudodiscophora* by Ikeda (1990).

As part of a research project to evaluate the mechanism of matter cycling in the Japan Sea, the present study investigates metabolic activity and body composition of various zooplankton species occurring in the mesopelagic zone of the Japan Sea. The results are combined with those of Ikeda (1990, 1991) and compared with those of zooplankton living in similar thermal regimes in polar seas.

Materials and Methods

Zooplankton

An unidentified deep-purple ctenophore (Beroe sp.), seven copepods (Neocalanus cristatus, N. plumchrus, Pseudocalanus minutus, Gaidius variabilis, Paraeuchaeta elongata, Metridia pacifica, Oithona atlantica), two amphipods (Themisto japonica, Primno abyssalis), an ostracod (Conchoecia pseudodiscophora), and a chaetognath (Sagitta elegans) were studied. Of these 12 species, the mesopelagic species are G. variabilis (Brodskii 1963; Hirakawa et al. 1990), P. elongata (Brodskii 1963; Morioka 1975; Ikeda & Hirakawa 1996), P. abyssalis (Ikeda 1995), and C. pseudodiscophora (Ikeda 1990). The occurrence of deep-purple ctenophore Beroe sp. in the mesopelagic zone is our own observation. The other 7 species are eurybathic species. These zooplankton, plus a mesopelagic mysid Meterythrops microphthalma studied by Ikeda (1991), constitute the major species occurring in the mesopelagic zone of the Japan Sea. Of these 13 species, the copepods N. cristatus, N. plumchrus, P. minu-

Fig. 1. A. Location of Toyama Bay in the southern Japan Sea. B. The sampling station (*circled star*) in Toyama Bay, where depth contours (1000, 500 and 200 m) are superimposed.

tus and M. pacifica are primarily herbivores, and the rest are primarily detritivores/carnivores.

Samplings were made aboard the R.V. *Mizuho-Maru* at an offshore station in Toyama Bay (Fig. 1), southern Japan Sea, during the period from September 1990 to March 1992. A closing Norpac net (45-cm diameter, 0.33-mm mesh) designed by Kawamura (1989) was used to retrieve live specimens from 700-m to 400-m depths. To avoid "thermal-shock" of specimens at the surface, a coolant (a small plastic bag containing ice and iron bolts) was placed in the bottom of the cod-end (a removable 500-ml plastic bottle with fine-mesh-covered drain windows at the top). The time required for the recovery of the net after closing at 400-m depth was 3 to 4 min (towing speed of the closed net: 2 m s^{-1}). A fish-larva net (1.5-m diameter, 0.5-mm mesh) was also used to collect some of the specimens of *P. abyssalis*. After the net was retrieved, the contents of the cod end were immediately transferred to a large container filled with chilled seawater (0.5°C), and undamaged specimens were sorted out for the following experiments. All samples were taken at night.

Prior to the collection of zooplankton, profiles of temperature and salinity were determined using a Neil Brown CTD. The oxygen profile was determined by the Winkler titration method on water samples from rosette samplers attached to the CTD unit.

Oxygen consumption

A water-bottle method (cf. Omori & Ikeda 1984) with glass bottles (5, 10, 25, 30, 60, 100 or 200-ml capacity, depending on the size of specimens) was used to determine oxygen consumption rates of individual specimens or batches of specimens of the same species. In order to obtain oxygen consumption rates under near natural oxygen concentrations (i.e. mesopelagic zone ca. 61 to 64% saturation, see Fig. 2), seawater was collected from 500-m depth with 10-liter Niskin bottles, filtered gently through $20-\mu m$ mesh netting to remove large particles and used. A slight increase in oxygen concentration (70 to 80% saturation) by this procedure was unavoidable. Fresh seawater was collected prior to the start of each experiment. Experiments started within 24 h of the collection for most species. For some species (*Beroe* sp., *Neocalanus plumchrus, Pseudocalanus minutus* and *Sagitta elegans*), specimens were

brought back to the land laboratory, and oxygen consumption rates were measured using GF/F filtered, oxygenated seawater (near 100% saturation) within 4 to 5 d of the collection. The effect of the use of oxygen saturated water on the results is considered to be minimal, at least for crustaceans, since oxygen consumption rates of midwater crustaceans are largely independent of the oxygen concentration of ambient water (cf. Childress 1975).

General experimental parameters are summarized in Table 1. Bottles containing specimens and control bottles without specimens were prepared simultaneously and incubated at 0.5° C for 8 to 48 h in the dark. A temperature of 0.5° C correspond to the average mesopelagic temperature at the sampling site ($0.2-0.8^{\circ}$ C, cf. Fig. 2). At the end of each experiment, dissolved oxygen concentration was determined by the Winkler method directly on the entire bottle (capacity of bottle: <30 ml), or on subsamples siphoned out from the bottles (capacity of bottle: >60 ml). The amounts of manganous chloride and alkaline iodide solutions were varied proportionally according to the size of bottle. The bottles (<30-ml capacity) were first rinsed with concentrated hydrochloric acid and then distilled water before re-use. A batch of specimen subsamples collected prior to the experiment or those recovered at the end of each experiment were frozen (-20° C) for later measurement of wet and dry weights and chemical compositions.

Based on replicate measurements on a homogeneous water sample, the precision of the Winkler procedure expressed as the coefficient of variation (CV) was estimated to be 0.46% for 5-ml bottles, 0.16% for 10-ml bottles, and 0.13% for 30-ml bottles. Using the lowest values of the precision of the determination of oxygen concentration using 5-ml bottles (CV: 0.46%) and the oxygen concentration of natural mesopelagic water (5 ml $O_2 l^{-1}$), the limit of detection (95% confidence limits: CL) is estimated as: $5 \times 0.0046 \times 1.96/\sqrt{1} = 0.045$ (ml $O_2 l^{-1}$), or $0.225 \,\mu l O_2 (0.045 \times 5 \times 1000/1000)$. Oxygen concentration in the bottles at the end of each experiment was 90% or more of the initial value.

Chemical composition

Frozen specimens were weighed (WW: wet weight) and then freeze-dried to obtain dry weight (DW). Water contents of the specimens were calculated from the differences between WW and DW. Dried specimens were pooled according to species and ground into a fine powder with a ceramic mortar and pestle. Powdered samples were used for elemental composition analyses (carbon: C, hydrogen: H, nitrogen: N) with an elemental analyser (Yanaco CHN Corder MT-5) using antipyrine as a standard. Weighed fractions of powdered samples were incinerated in a muffle furnace at 480°C for 4 h and reweighed for ash determination. All measurements were done in duplicate. Precision (CV) of these measurements was 1% for C, 3% for H, 10% for N and 7% for ash.

Metabolic comparison

"Adjusted metabolic rate (AMR)" and "daily body C loss" were used for metabolic comparisons.

AMR: The relationship between oxygen consumption rate $(R: \mu I O_2 \text{ individual}^{-1} h^{-1})$ and body mass (W: mg N) of zooplankton can be expressed as $R=aW^b$, where a and b are constants. AMR is defined as RW^{-b} , or the rate adjusted to 1 mg body N (cf. Ikeda 1988). Body N was chosen as the body mass unit since this reduces inter-specific variations in the relationship between metabolic rates and body mass (Ikeda 1988). A weight exponent (b) of 0.85 was used. This value was derived from statistical analyses of the oxygen consumption rates and

Table 1. Zooplankton species and vertical distribution patterns (mesopelagic or eurybathic), sampling dates, experimental parameters (container size, individual number of specimens per container, incubation time), dry weight (DW), and oxygen consumption rates. Mean \pm 1SD with the number of replicates in parentheses. DW of some species is derived from a batch of specimens.

Animal group	Species	E: Eurybathic M: Mesopelagic	Date	Container volume (ml)	Nos. of indiv.	Incubation time (h)	DW (mg)	Oxygen consumption (μ l O ₂ indiv. ⁻¹ h ⁻¹)
Ctenophora	Beroe sp.	М	Nov. 1991	200	1	48	63.55±31.32 (2)	2.28±0.92 (2)
Copepoda	Neocalanus cristatus V	Е	Sept. 1991	30	1	24	3.74	0.60±0.27(6)
	Neocalanus plumchrus V, VI 🤉	Е	Nov. 1991	10	1	26	0.428	0.13±0.03 (7)
	Pseudocalanus minutus V, VI ♀	Е	Dec. 1991	5	5	48	0.0342	0.0072±0.0014 (7)
	Gaidius variabilis VI ♀	Μ	Sept. 1990	10	I	12	0.424	0.25±0.02 (7)
	Gaidius variabilis V ර	М	Sept. 1990	5	1	12	0.242	0.17±0.02 (4)
	Paraeuchaeta elongata VI 9	М	Sept. 1990	30	1	12	2.52	1.02±0.17(7)
	Paraeuchaeta elongata V	М	Sept. 1990	30	1	12	1.34	0.61±0.01 (4)
	Metridia pacifica VI ♀	E	Sept. 1990	5	1	36	0.163	0.074±0.012 (14)
	Oithona atlantica VI ♀	E	Sept. 1990	10	15	48	0.0027	0.0020±0.0001 (11)
Amphipoda	Themisto japonica \Im	Е	Sept. 1990	60	1	12	3.14±0.64 (8)	2.04±0.50 (8)
	Primno abyssalis 9	М	Nov. 1991	100	1	8	12.98±2.75 (7)	$4.84 \pm 1.75(7)$
	Primno abyssalis 9 ovigeous	М	Nov. 1991	100	i	8	16.67±2.75 (7)	6.57±1.33 (7)
Mysidacea*	Meterythrops microphthalma \Im	М	May 1989	60	1	8	18.35±4.38 (7)	6.41±1.67(7)
	Meterythrops microphthalma ඊ	М	May 1989	60	1	8	19.71±3.06 (9)	8.37±3.13 (9)
	Meterythrops microphthalma juv.	Μ	May 1989	25	1	8	7.54±4.72 (17)	3.08±1.41 (17)
Ostracoda	Conchoecia pseudodiscophora VIII 9	М	May 1990	5	1	36	0.0423**	0.018±0.005 (8)
	Conchoecia pseudodiscophora VII	М	May 1990	5	1	36	0.0275**	0.010±0.001 (6)
Chactognatha	Sagitta elegans	Е	Mar. 1992	60	1	24	3.56±0.74 (10)	0.98±0.32 (10)

* Data from Ikeda (1991). ** Data from Ikeda (1990).

body N of epipelagic zooplankton (Ikeda 1985).

Daily body C loss: Oxygen consumption rate (*R*) was converted first to CO_2 -C production rate, $R \times RQ \times 12/22.4 \times 24 \times 10^{-3}$, where RQ is a respiratory quotient, 12/22.4 is carbon mass in 1 mol of CO_2 (22.4 liter), 24 is the number of hours per day, and 10^{-3} is to convert μg to mg. An RQ=0.71 (lipid metabolism, cf. Gnaiger 1983) was assumed for herbivores, and an RQ=0.97 (protein metabolism, Gnaiger 1983) for detritivores/carnivores. The daily body C loss due to metabolism thus obtained was expressed as a fraction of body C (% of body carbon loss d⁻¹) in each species.

Results

Mesopelagic environments

Temperature, salinity and oxygen profiles determined in November 1991, and May, April and July 1992 at the sampling station in Toyama Bay are shown in Fig. 2. Temperature in the top 400 m varied with season. Below 400 m the temperature was 0.2 to 0.8°C throughout the year. Salinity of >34.0 psu occurred in the top 200 m in November 1991 and July 1992 and was due to the effect of the Tsushima Warm Current. As with temperature, the salinity of water below 400 m showed little seasonal variation (34.05 to 34.07 psu). Oxygen content ranged from 5.2 to 6.8 ml O₂ l⁻¹ at the surface, and from 4.9 to 5.0 ml O₂ l⁻¹ below 400 m.

Oxygen consumption/body composition

The size expressed as dry weight of the 12 zooplankton species investigated in the present study varied by four orders of magnitude, ranging from 0.0027 mg DW (*Oithona atlantica*) to 63.55 mg DW (*Beroe* sp.), and oxygen consumption rates varied by three orders of magnitude, from 0.0020 (*O. atlantica*) to $6.57 \,\mu$ I O₂ indiv.⁻¹ h⁻¹ (*Primno abyssalis*) (Table 1). With re-



Fig. 2. Vertical profiles of temperature (T), salinity (S) and dissolved oxygen (DO) at the station in Toyama Bay, investigated in November 1991, and March, April and July 1992.

gard to chemical composition, the lowest water content was found in *Pseudocalanus minutus* (63.9% of WW) and the greatest water content in *Beroe* sp. (96.2% of WW). Ash varied from 6.1% of DW in *Metridia pacifica* to 65.3% of DW in *Beroe* sp. The lowest C, H and N contents were consistently recorded in *Beroe* sp. For the rest of the 11 species, C varied from 37.1 to 61.3% of DW; H, from 5.8 to 9.8% of DW; and N, from 6.7 to 12.7% of DW (Table 2). In both Tables 1 and 2 metabolic and body composition data for the mesopelagic mysid *Metery-throps microphthalma* collected from the same station in Toyama Bay and determined using the same procedures as Ikeda (1991) were included and combined with the present data for the following analyses.

AMR and daily body C loss

AMR ranged from 1.26 in *Pseudocalanus minutus* to 6.03 in *Themisto japonica* (Table 2), with a mean of 3.84 (\pm 0.78, SD) for the 5 mesopelagic species, and 2.65 (\pm 1.60) for the 7 eurybathic species. The mean AMR for mesopelagic and eurybathic crustaceans was 3.84 (\pm 0.78) and 2.78 (\pm 1.72), respectively. Differences between mean AMRs of mesopelagic and eurybathy crustaceans were not significant (t=1.63, df=17, p>0.1), so a grand mean of 3.48 (\pm 1.22) was calculated.

Daily body C loss ranged from 1.26% (*Pseudocalanus minutus*) to 6.03% (*Themisto japonica*) (Table 2). The relationship between body C loss d^{-1} and body C is shown in Fig. 3. Regression analysis of \log_{10} metabolic loss (% body C d^{-1}) on \log_{10} body C (mg) revealed that the relationship was not significant for both mesopelagic (r=-0.276, df=10, $p \ge 0.05$) and eurybathic species (r=-0.225, df=5, $p \ge 0.05$). Using these results, the mean daily body C loss for mesopelagic species was computed as 1.17% (± 0.35) and for eurybathic species as 0.99% (± 0.78). Since these two means did not differ significantly each other (t=0.294, df=17, p>0.5) a grand mean of 1.10% (± 0.54) was computed.

Discussion

Metabolism

Oxygen consumption rates of zooplankton collected from 400 to 700-m depth (hydrostatic pressure: 40–70 atm) were determined at 1 atm in this study. Therefore the effect of the rapid change in hydrostatic pressure may be a source of error in the present study. However, this "decompression" effect is unlikely to have been a major source of error, since hydrostatic pressure is found to have little effect on the metabolic activity of a variety of deep-living pelagic animals including a ctenophore (Youngbluth et al. 1988), hydromedusae (Childress & Thuesen 1993), crustaceans (Pearcy & Small 1968; Teal & Carey 1967; Teal 1971), a polychaete (Childress & Thuesen 1993), and a chaetognath (Thuesen & Childress 1993). As an only exception, Baily et al. (1994) observed a loss of activity and reduced oxygen consumption rates in several deep-sea gelatinous zooplankton recovered to the surface.

Considering the thermal regime of the mesopelagic zone of the Japan Sea (0.2 to 0.8°C, cf. Fig. 2), we believe metabolic data on mesopelagic zooplankton from polar seas to be appropriate to compare with the present data because environmental temperature and oxygen concentrations are similar. Ikeda (1988) determined oxygen consumption rates for 7 mesopelagic crustaceans (an ostracod *Gigantocypris muelleri*, an amphipod *Cyphocaris* sp., a mysid *Gnathophausia gigas*, three decapods *Pasiphaea scotiae*, *Gennadas kempi*, *Petalidium foliaceum*, and a euphausiid *Euphausia triacantha*) from 200–1000-m depths in Prydz Bay

Snecies	Water (%WW)	Ash (%DW)	Elemental composition (%DW)			Body	Metabolic loss	AMR at 0.5°C
Species			С	Н	N	C:N	(% body C d ^{-1})	$(\mu I O_2 [body N]^{-0.85} h^{-1})$
Beroe sp.	96.2	65.3	11.2	2.7	3.0	3.7	0.41±0.04 (2)	1.34±0.04(2)
Neocalanus cristatus V	82.0	7.3	50.5	8.2	8.7	5.8	0.29±0.13 (6)	1.56±0.69(6)
Neocalanus plumchrus V, VI 🎗	82.2	ND	56.6	9.4	6.9	8.2	$0.48 \pm 0.10(7)$	2.55 ± 0.52 (7)
Pseudocalanus minutus V, VI 🎗	63.9	ND	61.3	9.8	6.7	9.1	0.31 ± 0.06 (7)	1.26±0.24(7)
Gaidius variabilis VI 🎗	78.9	9.4	49.3	7.4	10.0	4.9	1.48±0.10(7)	3.64 ± 0.26 (7)
Gaidius variabilis V 👌	77.7	ND	49.2	7.5	9.6	5.1	1.80±0.25 (4)	4.21 ± 0.58 (4)
Paraeuchaeta elongata VI 🎗	77.3	8.0	52.9	8.6	8.5	6.2	0.96±0.16(7)	3.98±0.69(7)
Paraeuchaeta elongata V	74.5	ND	56.3	9.1	8.4	6.7	1.01±0.13 (4)	3.89±0.51 (4)
Metridia pacifica VI 🎗	81.2	6.1	53.9	8.2	7.6	7.1	0.77±0.12 (14)	3.07±0.50 (14)
Oithona atiantica VI 9	ND	ND	46.6	6.9	9.8	4.8	1.98±0.55 (11)	2.19±0.61 (11)
Themisto japonica \Im	78.1	25.6	37.1	5.9	8.9	4.2	2.19±0.35 (8)	6.03 ± 0.97 (8)
Primno abyssalis 🖇	82.2±2.6 (7)	23.6	40.2	6.3	9.3	4.3	1.16±0.41 (7)	$4.12 \pm 1.42(7)$
Primno abyssalis 9 ovigeous	82.9±2.5 (7)	26.9	37.8	6.0	9.4	4.0	1.30±0.12 (7)	4.46±0.45 (7)
Meterythrops microphthalma \Im	77.2±3.5 (7)*	13.1*	46.1*	7.3*	9.3*	5.0	0.95±0.15 (7)*	4.06±0.71 (7)*
Meterythrops microphthalma 8	80.9±2.1 (9)*	17.6*	41.2*	6.7*	9.8*	4.2	1.29±0.39 (9)*	4.74±1.35 (9)*
Meterythrops microphthalma juv.	80.2±1.4 (17)*	17.3*	41.6*	6.7*	9.9*	4.2	1.43±0.63 (17)*	4.37±1.64 (17)*
Conchoecia pseudodiscophora VIII 9	75.9±2.9 (8)**	25.2**	39.9**	5.8**	7.3**	5.5	1.32±0.37 (8)	2.43±0.67 (8)
Conchoecia pseudodiscophora VII			47.5**	7.3**	5.7**	8.3	0.92±0.13 (6)	2.32 ± 0.32 (6)
Sagitta elegans	91.1±0.6 (10)	13.4	38.3	7.0	12.7	3.0	0.89±0.23 (10)	1.91±0.50 (10)

Table 2. Water content, ash, elemental composition (C, H, N) and the C: N ratio of zooplankton from the mesopelagic zone of the Japan Sea. Daily metabolic loss of body C and adjusted metabolic rate (AMR) at 0.5° C were calculated by combining oxygen consumption data in Table 1 with the body composition data. Mean±1SD whenever applicable, with the number of replicates in parentheses. ND=Not determined.

* Data from Ikeda (1991). ** Data from Ikeda (1990).

(60–64°S, 58–88°E), Antarctica, where the water temperature varied from 0 to 1.5°C, and oxygen was ca. 4.6 ml O₂1⁻¹. The size of the 7 crustaceans studied by Ikeda (1988) (47.97 to 494.3 mg DW) is much larger than those animal groups investigated in this study (0.0020 to 19.71 mg DW, see Table 1). Consequently, the AMR at 0.5°C was adopted as an appropriate basis for metabolic comparison. The AMR at 0.5°C of the 5 Antarctic mesopelagic crustaceans ranged from 1.03 to $4.18 \,\mu$ I O₂ (mg body N)^{-0.85} h⁻¹ with a mean of 3.20 (±1.14, SD) (original data expressed at 0.2°C was re-calculated using Q₁₀=1.89; cf. Ikeda 1985). The mean AMR at 0.5°C of crustaceans from the mesopelagic zone of the Japan Sea was 3.84 (±0.74) for the 5 mesopelagic species, 2.78 (±1.72) for the 6 eurybathic species, and 3.48 (±1.22) for all these species combined. None of these three mean AMRs differ significantly from that for the Antarctic mesopelagic crustaceans (*t*=1.38, df=15, *p*>0.1 for mesopelagic species; *t*=0.70, df=11, *p*>0.5 for eurybathic species; and *t*=0.49, df=21, *p*>0.5 for all species combined). Thus, oxygen consumption rates, expressed as AMR, of crustaceans from the mesopelagic realm of the Japan Sea are comparable to those of the mesopelagic crustaceans from the mesopelagic realm of the Japan Sea are comparable to those of the mesopelagic crustaceans from the mesopelagic realm of the Japan Sea are comparable to those of the mesopelagic crustaceans from the mesopelagic realm of the Japan Sea are comparable to those of the mesopelagic crustaceans from the mesopelagic crustaceans from the mesopelagic crustaceans from the mesopelagic realm of the Japan Sea are comparable to those of the mesopelagic crustaceans from the mesopelagic realm of the Japan Sea are comparable to those of the mesopelagic crustaceans from the mesopelagic realm of the Japan Sea are comparable to those of the mesopelagic crustaceans from the mesopelagic realm of the Japan Sea are comparable to those of the mesopelagic crustaceans from th

Species-specific differences in oxygen consumption rates of zooplankton inhabiting the mesopelagic zone of the Japan Sea were examined in terms of daily body C loss (Fig. 3). In Fig. 3, the predicted relationship (limits at the 95% CL above and below the regression line) derived from oxygen consumption data in the Arctic (Ikeda & Skjoldal 1989) and Antarctic (Ikeda & Mitchell 1982) epipelagic zooplankton, combined with a factor of 0.48 (to convert



Fig. 3. The relationship between daily metabolic loss (% body C d⁻¹) and body C (mg) of zooplankton from the mesopelagic zone of the Japan Sea. Broken lines represent the upper and lower 95% confidence limits derived from epipelagic polar zooplankton (Y=1.99X-0.21, calculated from the data of Ikeda & Mitchell, 1982, and Ikeda & Skjoldal, 1989) when multiplied by the mesopelagic/epipelagic metabolism factor for crustaceans (0.48, from Ikeda, 1988). Mesopelagic species (closed circles): B=*Beroe* sp., GvJM=*Gaidius variabilis* stage V and adult male, GvF=*G. variabilis* adult female, PeJ=*Paraeuchaeta elongata* stage V, PeF=*P. elongata* adult female, PaF=*Primno abyssalis* female, PaO=*P. abyssalis* ovigerous female, MmJ=*Meterythrops microphthalma* juvenile, MmM=*M. microphthalma* adult male, MmF=*M. microphthalma* adult female, CpJ=*Conchoecia pseudodiscophora* juvenile, CpF=*C. pseudodiscophora* adult female. Eurybathic species (open circles): Nc=*Neocalanus cristatus* stage V, Np=*N. plumchrus* stage V and adult female, Pm=*Pseudocalanus minutus* stage V and adult female, Mp=*Metridia pacifica* adult female, Oa=*Oithona atlantica* adult female, Tj=*Themisto japonica* female, Se=*Sagitta elegans*.

from epipelagic to mesopelagic AMRs in Antarctic pelagic crustaceans, cf. Ikeda 1988) was superimposed for comparison. Both the data sets of Ikeda & Skjoldal (1989) and Ikeda & Mitchell (1982) include various zooplankton groups, containing a ctenophore, a hydromedusa, pteropods, copepods, euphausiids, amphipods, a chaetognath and salps. It is evident that all 12 mesopelagic and 3 out of the 7 eurybathic data points from the Japan Sea fall within this predicted 95% CL range, confirming the conclusion reached from the comparison of mean AMRs above.

Three eurybathic data points which occurred below the lower limits of this 95% CL range are the copepods Neocalanus cristatus, N. plumchrus and Pseudocalanus minutus. Of these three copepods, N. cristatus and N. plumchrus are known to be typical ontogenetic migrators with an annual life cycle. Their development is achieved in the phytoplankton-rich epipelagic zone from spring through summer. These species accumulate large amounts of food reserves (lipids) in the body, then sink to depth prior to reproduction in the winter to early spring of the following year (Heinrich 1962; Miller et al. 1984; Miller & Terazaki 1989). In addition to their lack of feeding and large lipid accumulations in the body, reduced metabolic rate is a common characteristic of copepods in diapause (Hirche 1983; Arashkevich & Kosobokova 1988; Arashkevich et al. 1996). The present results with lower metabolic rates in conjunction with high C contents (as discussed below) from these two chiefly herbivorous copepods are consistent with this life history scenario. While the life cycle of P. minutus occurring in the mesopelagic zone of the Japan Sea is not known, its very low level of metabolic activity and high body C content suggest that the specimens were in diapause. Metridia pacifica is also primarily a herbivore and is likely to not feed in the mesopelagic zone of the Japan Sea. Nevertheless, M. pacifica exhibited a higher metabolic rate than the three eurybathic copepods discussed above, and this may reflect greater swimming activity. In this study, M. pacifica was observed to swim continuously, while N. cristatus, N. plumchrus and P. minutus were motionless and suspended in the water column at most times. Unlike these herbivores, feeding in the carnivorous eurybathic species, Oithona atlantica, Themisto japonica and Sagitta elegans may not be restricted to the epipelagic zone, thereby allowing the maintenance of their metabolic rates at similar levels to those of endemic mesopelagic species (cf. Fig. 3). These results suggest that all oxygen consumption data for zooplankton from mesopelagic habitats in the Japan Sea fall within the range predicted from polar values with the exception of eurybathic copepods in diapause.

Recently, Thuesen & Childress (1993) proposed a new view that the decrease in metabolic activity with increasing depth of occurrence is not the case for non-visual predators such as chaetognaths. In this light, the present use of the mesopelagic/epipelagic metabolic factor ($\times 0.48$, derived by Ikeda, 1988, from Antarctic pelagic crustaceans) for predicting "general" mesopelagic rates from epipelagic rates, may be regarded as provisional, and requires further characterization when metabolic data from mesopelagic non-crustacean species accumulate in future studies.

Body composition

The body composition of marine zooplankton is known to be highly variable between and within taxonomic groups of animals (Omori 1969; Ikeda 1974; Båmstedt 1986). In a given taxonomic group, body composition is in part under the influence of habitat temperature (Ikeda 1974). Analyzing elemental composition data for various zooplankton species collected from tropical, subtropical, temperate and boreal waters, Ikeda (1974) noted that the

body C: N ratio of most species varied from 3 to 5. However, body C: N ratios greater than 5 coupled with higher C content (>45% of DW) were the case for species from cold waters (boreal and deep-sea) due to a large deposition of lipids in the body. Such large depositions of lipid in the body have also been observed for some zooplankton inhabiting Arctic and Antarctic waters (Ikeda & Mitchell 1982; Ikeda & Skjoldal 1989). Considering the near-zero temperature of the mesopelagic zone in the Japan Sea, body C: N ratios greater than 5, combined with body C levels higher than 45% of DW as seen in all eurybathic species (excepting Themisto japonica) and 3 mesopelagic species (Gaidius variabilis stage V males, Paraeuchaeta elongata stages V, VI females, Conchoecia pseudodiscophora instar VI) in this study (Table 2), suggest a large deposition of lipids in the bodies of these species. For some copepods, Neocalanus cristatus, N. plumchrus and Pseudocalanus minutus, conspicuous oil droplets were observed in this study. The C: N ratios of 3 to 5 for the other species (both eurybathic and mesopelagic) are most commonly seen in zooplankton inhabiting epipelagic zones over wide geographical ranges including polar seas (Ikeda 1974; Båmstedt 1986; Ikeda & Bruce 1986; Ikeda & Mitchell 1982; Ikeda & Skjoldal 1989). The present body composition data for zooplankton from the cold mesopelagic realm of the Japan Sea fall within the

range of values reported by previous workers on zooplankton living in cold thermal regimes. Apart from temperature, depth of occurrence may also affect the body composition of zooplankton, although depth and temperature usually covary. This depth-related body composition change has been well demonstrated in pelagic fishes; e.g. higher water content and lower protein content of deeper living fishes as a result of reduced muscles and skeletal structure (cf. Childress & Nygaard 1973). Similar depth-related changes in body composition are less clear for pelagic crustaceans, excepting a trend towards lower protein content in deeper-living species (Childress & Nygaard 1974; Stickney & Torres 1989). However, Ikeda (1988) found no general depth-related patterns in the elemental (C, H, N, P) composition of epipelagic and mesopelagic crustaceans in Antarctic waters. Perhaps, depth-related body protein (or N) changes in pelagic crustaceans will emerge from comparisons of crustaceans from broad bathymetric ranges, and are masked by species-specific variations when comparing narrow bathymetric ranges (epipelagic vs. mesopelagic). Apart from fishes and crustaceans, no information on depth-related patterns in body composition is presently available for other groups of pelagic animals.

Terazaki (1993) compared C and N composition of the chaetognath Sagitta elegans collected from the meso- and bathypelagic zones of the Japan Sea with those collected from the epipelagic zone in the North Pacific. His results showed that specimens from the Japan Sea were characterized by a higher C: N ratio (4.7) compared to that of the specimens from the North Pacific (3.5), due to the accumulation of small oil droplets in the intestinal tissue of the former. While the *S. elegans* individuals analysed in this study were from the mesopelagic zone and did not include specimens from bathypelagic zone of the Japan Sea, the C: N ratio was 3.0, which is much less than the 4.7 reported by Terazaki (1993) but close to the range of 3.1 to 3.5 obtained on specimens from various locations in the western North Pacific by Ikeda (1974). It is noted that Omori (1969) found a higher C: N ratio (4.4) for *S. elegans* from 0 to 550 m in the western North Pacific.

Extremely high water content (96.2% of WW) and ash (65.3% of DW), in association with extremely low elemental composition (11.2% of DW for C, 3.0% for N), were recorded for the mesopelagic ctenophore *Beroe* sp. in this study. While difficulty in identifying the species makes meaningful comparison not possible, similarly high water content (96% of WW) and ash (73% of DW), but low C (5–6% of DW) and N (1–2% of DW) have been reported on an-

other *Beroe* sp. from Antarctic waters (Ikeda & Bruce 1986). *Beroe gracilis* from the North Sea contained water at 96.1% of WW (Hoeger 1983), and *B. ovata* from a tropical sea, 3.7% of DW for C and 1.0% of DW for N (Kremer 1986). Regional differences in body composition of *Beroe* spp. cannot be determined from these data, since Reeve et al. (1989) found that the C content of the ctenophore *Mnemiopsis mccradyi* could vary from 10% to 1% of DW depending on the size and on recent feeding history.

Acknowledgments

We are grateful to M. J. Youngbluth and J. J. Torres for their critical reading of the manuscript. Thanks are extended to T. Nagasawa for elemental analysis, and the captain, officers and crew members of the R.V. *Mizuho-Maru* for their cooperation in the sampling at sea.

Literature Cited

- Arashkevich, E. G., A. V. Drits & A. G. Timonin 1996. Diapause in the life cycle of *Calanoides carinatus* (Krøyer) (Copepoda, Calanoida). *Hydrobiologia* 320: 197–208.
- Arashkevich, Ye. G. & K. N. Kosobokova 1988. Life strategy of plant-eating copepods: Physiology and biochemistry of overwintering *Calanus glacialis* under starvation conditions. *Oceanology* 28: 513–517.
- Bailey, T. G., J. J. Torres, M. J. Youngbluth & G. P. Owen 1994. Effect of decompression on mesopelagic gelatinous zooplankton: a comparison of *in situ* and shipboard measurements of metabolism. *Mar. Ecol. Prog. Ser.* 113: 13–27.
- Båmstedt, U. 1986. Chemical composition and energy content, p. 1–57, In *The Biological Chemistry of Marine Copepods* (eds. Corner, E. D. S. & S. C. M. O'Hara). Clarendon Press, Oxford.
- Brodskii, K. A. 1950. Calanoida of the Far-Eastern Seas and Polar Basin of the USSR. Israel Program for Scientific Translations. Jerusalem, 440 pp.
- Childress, J. J. 1971. Respiratory rate and depth of occurrence of midwater animals. *Limnol. Oceanogr.* 16: 104–106.
- Childress, J. J. 1975. The respiratory rates of midwater crustaceans as a function of depth of occurrence and relation to the oxygen minimum layer off southern California. *Comp. Biochem. Physiol.* **50A**: 787–799.
- Childress, J. J. & T. J. Mickel 1985. Metabolic rates of animals from the hydrothermal vents and other deepsea habitats. *Biol. Soc. Wash. Bull.* 6: 249–260.
- Childress, J. J. & M. Nygaard 1973. The chemical composition of midwater fishes as a function of occurrence off southern California. *Deep-Sea Res.* 20: 1093–1109.
- Childress, J. J. & M. Nygaard 1974. Chemical composition and buoyancy of midwater crustaceans as a function of occurrence off southern California. *Mar. Biol.* 27: 225–238.
- Childress, J. J. & E. V. Thuesen 1992. Effects of hydrostatic pressure on metabolic rates of six species of deep-sea gelatinous zooplankton. *Limnol. Oceanogr.* 38: 665-670.
- Cowles, D. L. & J. J. Childress 1988. Swimming speed and oxygen consumption in the bathypelagic mysid *Gnathophausia ingens. Biol. Bull.* **175**: 111–121.
- Gnaiger, E. 1983. Calculation of energetic and biochemical equivalents of respiratory oxygen consumption, p. 337–345. In *Polarographic Oxygen Sensors* (eds. Gnaiger, E. & H. Horstner). Springer-Verlag, Berlin.
- Heinrich, A. K. 1962. The life history of plankton animals and seasonal cycles of plankton communities in the oceans. J. Cons. perm. int. Explor. Mer. 27: 15-24.
- Hirakawa, K., T. Ikeda & N. Kajihara 1990. Vertical distribution of zooplankton in Toyama Bay, southern Japan Sea, with special reference to Copepoda. *Bull. Plankton Soc. Jpn* 37: 111-126.
- Hirakawa, K. & A. Imamura 1993. Seasonal abundance and life history of *Metridia pacifica* (Copepoda: Calanoida) in Toyama Bay, southern Japan Sea. *Bull. Plankton Soc. Jpn* **40**: 41-54.
- Hirche, H.-J. 1983. Overwintering of Calanus finmarchicus and Calanus helgolandicus. Mar. Ecol. Prog. Ser. 11: 281–190.
- Hoeger, U. 1983. Biochemical composition of ctenophores. J. Exp. Mar. Biol. Ecol. 72: 251-261.

- Iguchi, N., T. Ikeda & A. Imamura 1993. Growth and life cycle of a euphausiid crustacean (*Euphausia pacifica* Hansen) in Toyama Bay, southern Japan Sea. *Bull. Jpn Sea Natl Fish. Res. Inst.* 43: 69–81. (In Japanese with English abstract.)
- Ikeda, T. 1974. Nutritional ecology of marine zooplankton. Mem. Fac. Fish. Hokkaido Univ. 22: 1-97.
- Ikeda, T. 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Mar. Biol. 85: 1–11.
- Ikeda, T. 1988. Metabolism and chemical composition of crustaceans from the Antarctic mesopelagic zone. Deep-Sea Res. 35: 1991-2002.
- Ikeda, T. 1990. Ecological and biological features of a mesopelagic ostracod Conchoecia pseudodiscophora in the Japan Sea. Mar. Biol. 107: 453–461.
- Ikeda, T. 1991. Ecological and physiological features of the mesopelagic mysid *Meterythrops microphthalma* in the Japan Sea. J. Oceanogr. Soc. Jpn 47: 94–103.
- Ikeda, T. 1995. Distribution, growth and life cycle of the mesopelagic amphipod Primno abyssalis (Hyperiidae: Phrosinidae) in the southern Japan Sea. Mar. Biol. 123: 789-798.
- Ikeda, T. & B. Bruce 1986. Metabolic activity and elemental composition of krill and other zooplankton from Prydz Bay, Antarctica, during early summer (November–December). *Mar. Biol.* 92: 545–555.
- Ikeda, T. & K. Hirakawa 1996. Early development and estimated life cycle of the mesopelagic copepod *Pareuchaeta elongata* in the southern Japan Sea. *Mar. Biol.* **126**: 261–270.
- Ikeda, T., K. Hirakawa & A. Imamura 1992. Abundance, population structure and life cycle of a hyperiid amphipod *Themisto japonica* (Bovallius) in Toyama Bay, southern Japan Sea. *Bull. Plankton Soc. Jpn* 39: 1–16.
- Ikeda, T. & A. W. Mitchell 1982. Oxygen uptake, ammonia excretion and phosphate excretion by krill and other Antarctic zooplankton in relation to their body size and chemical composition. *Mar. Biol.* 71: 283–298.
- Ikeda, T. & H. R. Skjoldal 1989. Metabolism and elemental composition of zooplankton from the Barents Sea during early Arctic summer. *Mar. Biol.* 100: 173–183.
- Kawamura, A. 1989. Fast sinking mouth ring for closing Norpac net. Nippon Suisan Gakkaishi 55: 1121.
- Kremer, P., M. F. Canino & R. W. Gilmer 1986. Metabolism of epipelagic tropical ctenophores. *Mar. Biol.* 90: 403-412.
- Miller, C. B., B. Frost, H. P. Batchelder, M. J. Clemons & R. E. Conwey 1984. Life history of large, grazing copepeds in the subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the Northeast Pacific. *Prog. Oceanogr.* 13: 201–243.
- Miller, C. B. & M. Terazaki 1989. The life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* in the Sea of Japan. *Bull. Plankton Soc. Jpn* **36**: 27–41.
- Morioka, Y. 1975. A preliminary report on the distribution and life history of a copepod Pareuchaeta elongata in the vicinity of Sado Island, the Japan Sea. Bull. Jpn Sea Reg. Fish. Res. Lab. 26: 41-56.
- Omori, M. 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. *Mar. Biol.* **3**: 4–10.
- Omori, M. & T. Ikeda 1984. *Methods in Marine Zooplankton Ecology*. John Wiley & Sons, New York, 332 pp.
- Pearcy, W. G. & L. F. Small 1968. Effects of pressure on the respiration of vertically migrating crustaceans. J. Fish. Res. Bd. Canada 25: 1311–1316.
- Quetin, L. B., R. M. Ross & K. Uchio 1980. Metabolic characters of midwater zooplankton: Ammonia excretion, O: N ratio and the effects of starvation. *Mar. Biol.* 59: 201–209.
- Reeve, M.R., M.A. Syms & P. Kremer 1989. Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply. I. Carbon biomass, feeding, egg production, growth and assimilation efficiency. J. *Plankton Res.* 11: 535–552.
- Stickney, D. G. & J. J. Torres 1989. Proximate composition and energy content of mesopelagic fishes from the eastern Gulf of Mexico. *Mar. Biol.* 103: 13-24.
- Teal, J. M. 1971. Pressure effects on the respiration of vertically migrating decapod Crustacea. Am. Zool. 11: 571–576.
- Teal, J. M. & F. G. Carey 1967. Respiration of a euphausiid from the oxygen minimum layer. *Limnol.* Oceanogr. 12: 548-550.

- Terazaki, M. 1993. Deep-sea adaptation of the epipelagic chaetognath Sagitta elegans in the Japan Sea. Mar. Ecol. Prog. Ser. 98: 79-88.
- Thuesen, E. V. & J. J. Childress 1993. Enzymatic activities and metabolic rates of pelagic chaetognaths: Lack of depth-related declines. *Limnol. Oceanogr.* **38**: 935–948.
- Torres, J. J., B. W. Belman & J. J. Childress 1979. Oxygen consumption rates of midwater fishes as a function of depth of occurrence. *Deep-Sea Res.* 26: 185-197.
- Torres, J. J. & G. N. Somero 1988. Metabolism, enzymic activities and cold adaptation in antarctic mesopelagic fishes. *Mar. Biol.* 98: 169–180.
- Uda, M. 1934. The results of simultaneous oceanographical investigations in the Japan Sea and its adjacent waters in May and June, 1932. J. Imp. Fish. Exp. Sta. 5: 57–190. (In Japanese with English abstract.)
- Vinogradov, M. E. 1968. Vertical Distribution of the Oceanic Zooplankton. Israel Program for Scientific Translations, Jerusalem, 339 pp.
- Vinogradov, M. E. & A. F. Sazhin 1978. Vertical distribution of the major groups of zooplankton in the northern part of the Sea of Japan. *Oceanology*, *Wash.* 18: 205–209.
- Yasui, M., T. Yasuoka, K. Tanioka & O. Shiota 1967. Oceanographic studies of the Japan Sea–Water characteristics. Oceanogr. Mag. 19: 177–192.
- Youngbluth, M. J., P. Kremer, T. G. Bailey & C. A. Jacoby 1988. Chemical composition, metabolic rates and feeding behavior of the midwater ctenophore *Bathocyroe fosteri*. *Mar. Biol.* **98**: 87–94.
- Zenkevitch, L. 1963. *Biology of the Seas of the U.S.S.R.* (English translation by S. Botcharkaya). George Allen and Unwin Ltd., London, 955 pp.