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Metabolism and elemental composition of the euphausiids *Euphausia pacifica* and *Thysanoessa inspinata* during the phytoplankton bloom season in the Oyashio region, western subarctic Pacific Ocean

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ABSTRACT

Rates of oxygen consumption (*R*: μl O_2 [individual]$^{-1}$ h^{-1}), and ammonia excretion (*E*: μg NH_4-N [individual]$^{-1}$ h^{-1}), O:N ratios (by atoms) and body water contents (% of wet mass [*WM*], as an index of lipid accumulation) of *Euphausia pacifica* and *Thysanoessa inspinata* were monitored during 9–14 March and 6–30 April 2007, including the onset of the spring phytoplankton bloom in the Oyashio region. Regression analyses revealed that variations in *R* and *E* were generally correlated with dry body mass (*DM*) for both euphausiids. When *R* and *E* were standardized to a body size of 10 mg *DM*, R_{std}, E_{std}, O:N ratios and water contents fluctuated from 6.3 to 10.1, 0.07 to 0.34, 31 to 232 and 73.8 to 78.1, respectively, for *E. pacifica*, and from 8.7 to 11.3, 0.06 to 0.71, 24 to 295 and 75.1 to 82.2, respectively, for *T. inspinata*. None of these variables were significantly correlated with temporal variations in SST (1.7 to 5.7 °C) or chlorophyll *a* standing stock (29.4 to 252.6 mg m^{-2}, 0–100 m) at the study site. However, April *E* and O:N ratio data pooled for both euphausiids were significantly less and greater, respectively, than the pooled values in March, suggesting preferential utilization of dietary protein for body growth or reproduction under conditions of abundant food supply as found in April. No substantial differences were observed in water content, ash, C, N or C:N ratios (by mass) of the two euphausiids collected in either March or April. Water content, C, N, C:N ratio and ash data averaged for *E. pacifica* and *T. inspinata* over the March and April cruises were similar: 76.3 and 78.1% of *WM*, 36.1 and 37.5% of *DW*, 9.4 and 10.1% of *DW*, 3.82 and 3.71 by mass, and 10.6 and 10.8% of *DM*, respectively. Combining the *R-DM* and *E-DM* relationships established with the population structure data of Kim et al. (2010), we estimate that daily ingestion and ammonia-N regeneration by the combined populations of the two euphausiids were 1.5–24.1% (integrated mean: 4.9%) and 0.18–1.32% (0.41%), respectively, of primary production and associated N demand during the bloom.

1. Introduction

In marine pelagic ecosystems, zooplankton play integral roles in trophodynamics and biogeochemical cycles of elements (Corner and Davies, 1971; Banse, 1995). The pelagic ecosystem of the Oyashio region, western subarctic Pacific, is characterized by massive diatom blooms in the spring, and herbivorous zooplankton have unique life cycle patterns to utilize the blooms efficiently (Ikeda et al., 2008). Among herbivorous zooplankton, the most dominant group is large copepods (*Neocalanus*, *Eucalanus*, *Metridia*), followed by euphausiids (*Euphausia*, *Thysanoessa*). In contrast to a large body of information about the trophic role of copepods in the pelagic ecosystem of the Oyashio region (Shinada et al., 2001; Kobari et al., 2003; Ikeda et al., 2008; Takahashi et al., 2008; Kobari et al., 2010), the euphausiids are less well studied (Kim et al., 2009).

As an approach to evaluating the dynamic roles of euphausiids in energy flow and matter cycling, metabolism (oxygen consumption and ammonia excretion rates, O:N ratios) and body chemical composition (water content, ash and carbon and nitrogen composition) provide a wide perspective for understanding energy demand, metabolic balance and nutritional conditions of zooplankton within their environments (cf. Ikeda et al., 2000). To date, such information is available for *Euphausia superba* in the Southern Ocean (Ikeda and Mitchell, 1982; Ikeda and Bruce, 1986; Ikeda and Kirkwood, 1989), *E. lucens* in the Benguela Current (Stuart, 1986), *Nyctiphanes australis* in western Cook Strait, New Zealand (James and Wilkinson, 1988), *E. crystallorophias* in the Southern Ocean (Ikeda and Kirkwood, 1989), *Thysanoessa inermis* in the Barents Sea (Ikeda and Skjoldal, 1989) and *Meganyctiphanes norvegica* in the western North Atlantic (Saborowski et al., 2002). In the Oyashio region, *E. pacifica* and *T. inspinata* have been

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reported as predominant euphausiids (Kim et al., 2009), but no study has been made of their metabolism or chemical composition.

As part of OECOS (Oceanic Ecodynamics COmparison in the Subarctic Pacific) project, which aimed to advance our understanding about lower trophic level pelagic ecology in the subarctic Pacific through a comparison of the east-west regions at a new level of detail (Miller and Ikeda, 2006), we studied sequential changes in oxygen consumption and ammonia excretion rates of *Euphausia pacifica* and *Thysanoessa inspinata* just before (March) and after (April) the initiation of the 2007 phytoplankton bloom in the Oyashio region. For the specimens used in these experiments, the chemical composition (water, ash, carbon and nitrogen) was analyzed. These results were used to elucidate metabolic characteristics and chemical composition of these two euphausiids as they responded to the phytoplankton bloom in the Oyashio region. Further, these results were combined with population structure data for these euphausiids (Kim et al., 2010) to estimate their grazing impact on the spring phytoplankton bloom. The simultaneous nitrogen regeneration as ammonia excretion was also estimated.

2. Materials and methods

2.1. Field sampling

Field studies were made at station A-5 (42°00′N, 145°15′E) in the Oyashio region, western subarctic Pacific (Fig. 1) during 9–14 March (Oshoro-Maru Cruise 177), and 6–30 April 2007 (Hakuho-Maru Cruise KH-07-1). Oblique tows with Bongo nets (70 cm mouth diameter, 500 μm mesh size) were made from 200 m depth to the surface at night to collect live euphausiids. All contents of the cod ends were gently transferred to 10 liter plastic buckets filled with chilled surface seawater. Undamaged adult females and males of *Euphausia pacifica* and *Thysanoessa inspinata* were quickly sorted and placed into 500 ml glass containers filled with chilled seawater, and kept at *in situ* (sea surface) temperature for 1–2 h until the experiments commenced. Prior to each experiment, seawater was collected from 10 m depth with 10-L Niskin bottles and filtered through GF/F filters and well oxygenated for use in metabolic experiments.

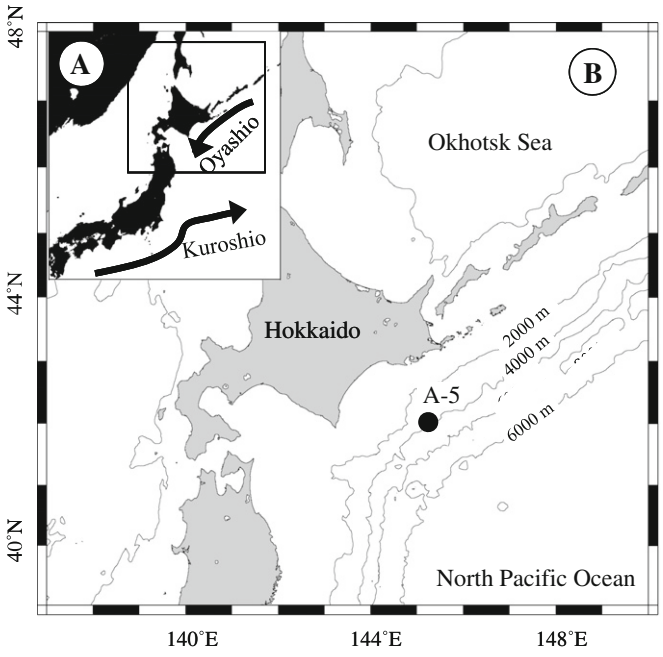

Fig. 1. Location of the Oyashio region in the western subarctic Pacific (A). Sampling station (A-5) in the Oyashio region (B). Depth contours (2000, 4000, 6000 and 8000 m) are superimposed in B.

2.2. Metabolic measurements

Oxygen consumption and ammonia excretion rates were measured simultaneously by a sealed-chamber method (cf. Ikeda et al., 2000). The specimens were rinsed briefly 3–4 times with well-oxygenated filtered seawater and transferred individually to glass bottles (100 or 200 ml capacity) filled with well-oxygenated filtered seawater. Control bottles without euphausiids were prepared concurrently. Experiments were run for 24 h in the dark at near *in situ* temperature (3.8 to 6.2 °C). At the ends of experiments, duplicate 15 (or 40) and 10-ml water samples were siphoned out for the measurements of dissolved oxygen and ammonia by the Winkler titration (Strickland and Parsons, 1972) and the phenol-hypochlorite method (Solórzano, 1969), respectively. Euphausiids from these experiments were rinsed briefly with a small amount of distilled water, blotted on a filter paper to remove water adhering to the body and stored at −60 °C for later weighing and elemental composition analyses in the laboratory.

Oxygen consumption to ammonia excretion ratios (O:N ratios, by atoms) have been used as an index of the proportion of protein in total metabolic substrates, and the ratios range from 7-8 (protein-oriented metabolism) to several hundred (lipid-oriented metabolism) or more (carbohydrate-oriented metabolism) (Ikeda et al., 2000).

2.3. Chemical composition

In the land laboratory, frozen samples were weighed (*WM*: wet mass) and freeze-dried for 5 h then dried at 60 °C for 1 h, and weighed on a microbalance (Mettler Toledo MT5) to a precision of 1 μg to obtain dry mass (*DM*). The dried samples were pooled by sex and body size of each species, then finely ground with a ceramic mortar and pestle. Powdered samples were used for analysis with a CHN elemental analyzer (Micro CHN corder JM-10). Weighed fractions of powdered samples were incinerated in a muffle furnace at 480 °C for 5 h and reweighed for ash determination. All measurements were made in duplicate. Coefficients of variation of these measurements were 3% for C, 7% for N and 10% for ash. Water content was expressed as percent of wet mass (*WM*), whereas the contents of ash, carbon and nitrogen were expressed as percent of dry mass (*DM*). Among these compositional components, water content is of special interest in this study as an index sensitive to lipid accumulation in the bodies of crustacean zooplankton; the higher the water content the less the lipid or C content, as has been verified in *Euphausia superba* (Ikeda and Kirkwood, 1989) and *Neocalanus cristatus* (Ikeda et al., 2004).

2.4. Grazing impact

Ingestion (I) can be estimated by knowing metabolism (M), growth (G) and assimilation efficiency (A) to apply in a carbon budget equation for zooplankters (Ikeda and Motoda, 1978):

$$I \times A = M + G$$

For a population composed of S individuals on a given sampling date,

$$\sum_{i=1}^{s} Ii \times A = \sum_{i=1}^{s} Mi + \sum_{i=1}^{s} Gi.$$