Deep-Sea Research II 57 (2010) 1733–1741

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

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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ARTICLE INFO

Article history:
Received 15 March 2010
Accepted 15 March 2010
Available online 27 March 2010

Topical issue on "Ecosystem Processes during the Oyashio Spring Bloom." The issue is compiled and guest-edited by the North Pacific Marine Science Organization (PICES).

Keywords:
Metabolism
Body composition
Euphausia pacifica
Thysanoessa inspinata
Phytoplankton bloom

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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doi:10.1016/j.dsr2.2010.03.017

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.

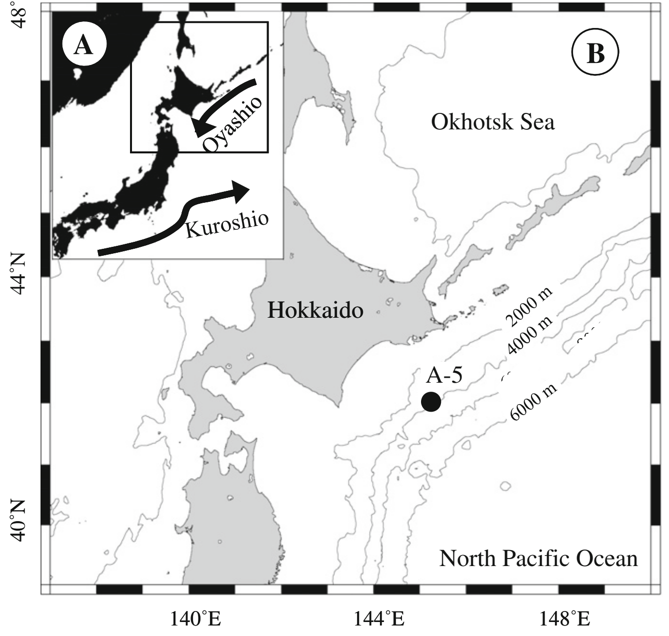

Fig. 1. Location of the Oyashio region in the western subarctic Pacific (A). Sampling station (A-5) in the Oyashio region (B). Depth contours (2000, 4000, 6000 and 8000 m) are superimposed in B.

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,

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

$\sum_{i=1}^{s} Mi$ values for *Euphausia pacifica* and *Thysanoessa inspinata* were calculated from length distribution data (Kim et al., 2010), combined with *BL-DM* relationships ($DM=0.0012BL^{3.3742}$ for *E. pacifica* and $DM=0.0043BL^{3.0574}$ for *T. inspinata*) and with geometric (GM) regression equations for oxygen consumption rate (*R*) as a function of *DM*, based on the data from March-April 2007 (see “Results” section below). Values of $\sum_{i=1}^{s} Mi$ (μl O_2 $m^{-2}\,d^{-1}$) thus obtained are converted to C units by multiplying by $24\times10^{-3}\times0.97\times12/22.4$, where 24 is hours in a day, 10^{-3} is to convert μg to mg, 0.97 is a respiratory quotient (Gnaiger, 1983), and 12/22.4 is the carbon mass (g) in 1 mol of CO_2 (22.4 liters).

The daily growth rates in terms of *BL* ($=\Delta BL$) of *Euphausia pacifica* and *Thysanoessa inspinata* during March–April have been evaluated as 0.082 and 0.022 mm d^{-1}, respectively (Kim et al., 2010). With these data, ΔDM (daily increment in *DM*) of individuals is derived by differentiating equations for *BL-DM* relationships:

$DM=0.0012BL^{3.3742}$, so that
$\Delta DM=0.0012\times\ 3.3742BL^{(3.3742-1)}\times\Delta BL$ for *E. pacifica*
$DM=0.0043BL^{3.0574}$, so that
$\Delta DM=0.0043\times3.0574BL^{(3.0574-1)}\times\Delta BL$ for *T. inspinata.*

A value of $\sum_{i=1}^{s} Gi$ for the population on a given sampling date can be calculated from size distribution data, converted to C units by multiplying C content (% of *DM*) of each species (Table 4). Population ingestion $\sum_{i=1}^{s} Ii$ is calculated from ($\sum_{i=1}^{s} Mi+\sum_{i=1}^{s} Gi$) divided by *A* (taken to be 90%; see Lasker 1966).

2.5. Ammonia regeneration

Primary production expressed in C units (Isada et al., 2010) was converted to N units applying the Redfield ratio for phytoplankton (C: N: P=106: 16: 1 by atoms). Ammonia excretion by the populations of *Euphausia pacifica* and *Thysanoessa inspinata* on a given sampling date was calculated combining size composition data (Kim et al., 2010), *BL-DM* relationships ($DM=0.0012BL^{3.3742}$ for *E. pacifica* and $DM=0.0043BL^{3.0574}$ for *T. inspinata*) and GM regression equations for ammonia excretion rate (*E*) as a function of *DM*, based on the data from March-April 2007; see “Results” section below.

3. Results

3.1. Oxygen consumption and ammonia excretion as a function of body mass

Over both cruises, *DM* varied from 3.87 to 23.80 mg $indiv.^{-1}$, *R* from 3.42 to 18.19 μl O_2 $indiv.^{-1}\,h^{-1}$, and *E* from 0.01 to 0.57 μg NH_4-N $indiv.^{-1}\,h^{-1}$ for *Euphausia pacifica*; and *DM* varied from 3.11 to 23.82 mg $indiv.^{-1}$, *R* from 3.65 to 25.49 μl O_2 $indiv.^{-1}\,h^{-1}$, and *E* from 0.04 to 2.02 μg NH_4-N $indiv.^{-1}\,h^{-1}$ for *Thysanoessa inspinata.* Prior to the analysis, the effects of sex (males and females) on *DW*-specific oxygen consumption and ammonia excretion rates and O:N ratios (by atoms) of *E. pacifica* and *T. inspinata* were tested (data not shown). Since the results of this test showed no significant effects (Mann Whitney U-test, $p=0.364-0.888$), male and female data were pooled in the following analyses.

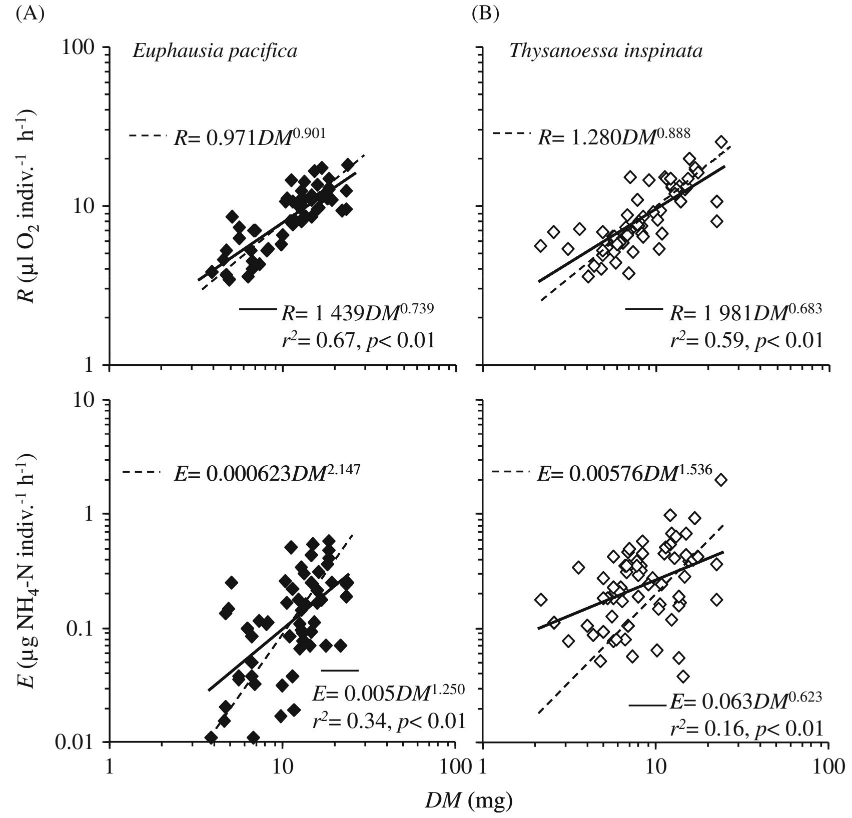

Fig. 2. Relationships between oxygen consumption rate (*R*) and dry mass (*DM*) (upper panel) and between ammonia excretion rate (*E*) and dry mass (*DM*) (bottom panel) of *Euphausia pacifica* (A) and *Thysanoessa inspinata* (B) in the Oyashio region. Arithmetic regression lines (solid lines) and geometric regression lines (dotted lines) are superimposed. See text for details.

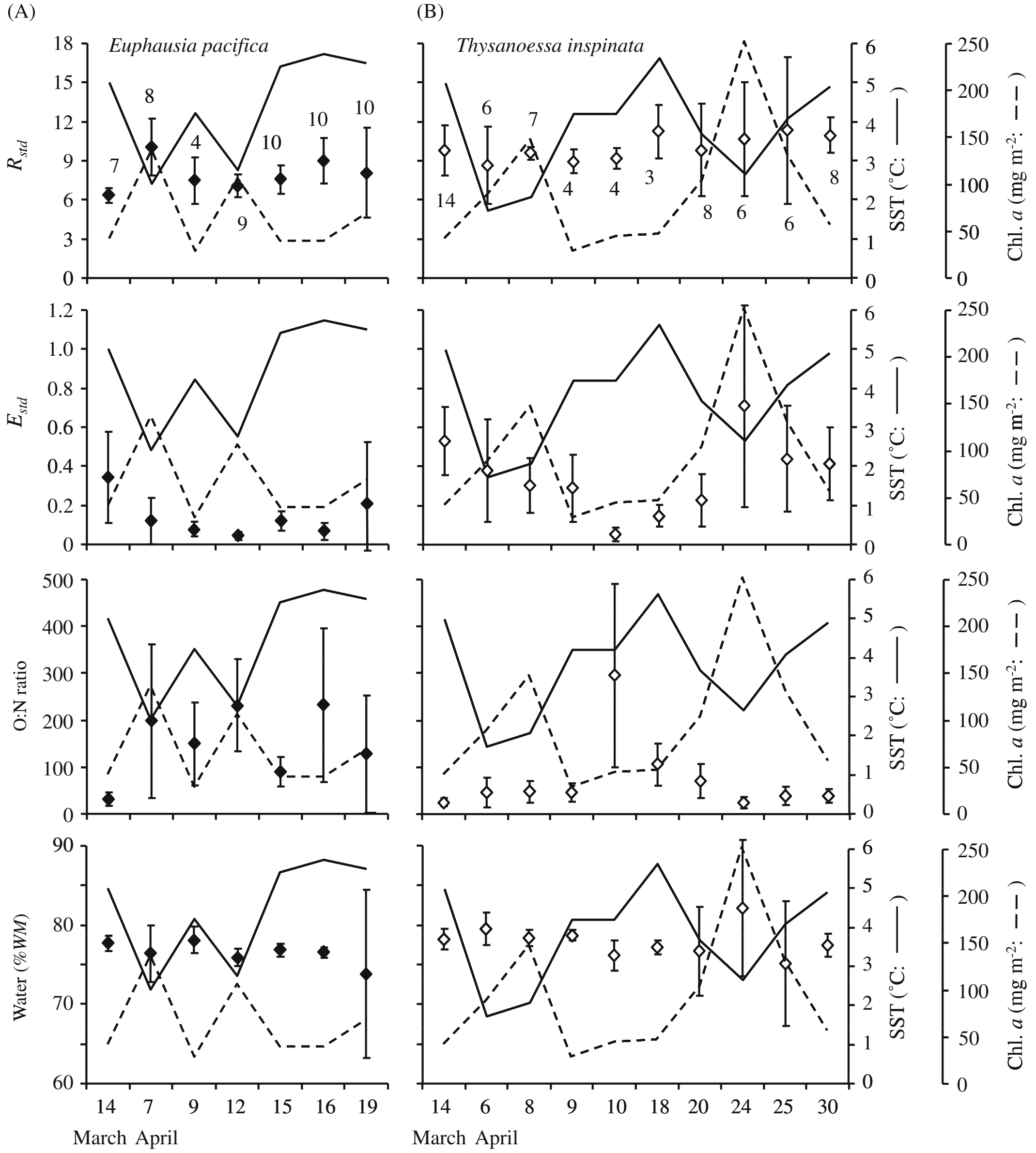

Fig. 3. Temporal changes in standardized oxygen consumption (R_{std}), standardized ammonia excretion (E_{std}), O:N ratio and water content of *Euphausia pacifica* (A) and *Thysanoessa inspinata* (B) during March and April 2007. Sea surface temperature (SST; solid line) and chlorophyll *a* standing stock (Chl. *a*, 0–100 m; dotted line) are superimposed. Vertical bars indicate standard deviations. The number of replicate determinations on each sampling date is shown on the top panel.

Log-log plots of *R* and *E* data against *DM* data for each euphausiid showed significant relationships (Fig. 2). Arithmetic (AM) regression (least square fitting) equations calculated for *Euphausia pacifica* and *Thysanoessa inspinata* are significant ($p<0.01$), and the effect of *DM* on the variance of *E* ($r^2=0.16-0.34$) was relatively less than on *R* ($r^2=0.59-0.67$). According to Ricker (1973), GM regression is generally superior to AM regression for purposes of prediction, particularly in situations where the distribution of variables is non-normal and open-ended, as in this study. The difference between AM regression and GM regression is small when the correlation coefficients (r) are close to 1.00, but the slope of the latter becomes greater when $r<1.00$, as is the present case for *E-DM* relationships (Fig. 2). GM regressions were calculated as $R=0.971DM^{0\ .901}$ and $E=0.000623DM^{2.147}$ for *E. pacifica*, and $R=1.280DM^{0.888}$ and $E=0.00576DM^{1.536}$ for *T. inspinata*.

3.2. Temporal changes in respiration, ammonia excretion and O:N ratios

In order to remove the effect of body mass, *R* and *E* data were standardized to the rates (R_{std} and E_{std}, respectively) of a body size of 10 mg *DW* (near the mid-range of *DW*s of both euphausiids, cf. Fig. 2) based on the GM regression equations shown in Fig. 2; $R_{std}=(R/DM^{0.901})\times10^{0.901}$ and $E_{std}=(E/DM^{2.147})\times10^{2.147}$ for *Euphausia pacifica*, and $R_{std}=(R/DM^{0.888})\times10^{0.888}$ and $E_{std}=(E/DM^{1.536})\times10^{1.536}$ for *Thysanoessa inspinata*. O:N ratios were calculated from R_{std} and E_{std}.

During March through April, R_{std}, E_{std} and O:N ratios fluctuated from 6.34 to 10.07, 0.068 to 0.342 and 30.9 to 232, respectively, for *Euphausia pacifica*, and from 8.69 to 11.32, 0.055 to 0.708 and 24.2 to 295, respectively, for *Thysanoessa inspinata* (Fig. 3). None of the variations were correlated with the simultaneous variations in SST (1.7 to 5.7 °C) or of chlorophyll *a* standing stock (29.4 to 252.6 mg m^{-2}, 0–100 m) in the water column, as judged by the correlation coefficients (all $p > 0.05$, Table 1).

The R_{std}, E_{std} and O:N ratio data pooled for March and April for both euphausiids, and the effects of presence (April) or absence (March) of bloom-level phytoplankton were analyzed (Table 2). Little or no difference was seen in R_{std} between March and April; E_{std} and O:N ratio data in April were significantly less and greater, respectively, than those of March for *E. pacifica* and *T. inspinata*. *Euphausia pacifica* was characterized by lower R_{std}, and E_{std} and higher O:N ratios, as compared with *T. inspinata*.

Table 1
Correlation coefficient (*r*) between physiological parameters (standardized oxygen consumption rates [R_{std}: µl O$_2$ indiv.$^{-1}$ h^{-1}], standardized ammonia excretion rates [E_{std}: µg NH$_4$-N indiv.$^{-1}$ h^{-1}] , O:N ratios [by atoms] calculated from R_{std} and E_{std} or water contents of the body [% of *WM*]) and environmental parameters (sea surface temperature [SST: °C] or chlorophyll *a* standing stock [Chl. *a*: mg m^{-2}, 0–100 m]) of *Euphausia pacifica* and *Thysanoessa inspinata* in the Oyashio region during March to April 2007. *NS*: not significant. For details, see Fig. 3.

Euphausiids	Physiological parameters	*df*	Correlation coefficient (*r*)	
			SST	Chl. *a*
Euphausia pacifica	R_{std}	5	-0.249^{NS}	0.511^{NS}
	E_{std}	5	0.346^{NS}	-0.204^{NS}
	O:N ratio	5	-0.453^{NS}	0.481^{NS}
	Water content	5	-0.083^{NS}	-0.409^{NS}
Thysanoessa inspinata	R_{std}	8	0.484^{NS}	0.276^{NS}
	E_{std}	8	-0.261^{NS}	0.617^{NS}
	O:N ratio	8	0.198^{NS}	-0.343^{NS}
	Water content	8	-0.504^{NS}	0.532^{NS}

3.3. Water, ash and elemental composition

Water was the only body component monitored throughout March and April; water as percent of *WM* fluctuated from 73.8 to 78.1 for *Euphausia pacifica* and from 75.1 to 82.2 for *Thysanoessa inspinata* (Fig. 3). Correlation analysis indicated that the variations in the water contents of these euphausiids were not related to the 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) during the same period. Male-female differences in C, N, C:N ratio (by mass) and ash data were not significant for *E. pacifica* (Mann Whitney U-test, $p=0.08-0.858$) or for *T. inspinata* (Mann Whitney U-test, $p=0.10-0.66$), with only the exception that N was significantly higher in males (10.6% of *DM*) than in females (9.8% of *DM*) ($p=0.025$). Since the difference in N between males and females observed in *T. inspinata* was small (albeit statistically significant), all male and female data were combined, and the differences between March and April were tested (Table 3). The between-month differences were not significant for any of the body composition components for *E. pacifica* (Mann Whitney U-test, $p=0.051-0.699$) or *T. inspinata* (Mann Whitney U-test, $p=0.101-0.881$). Extending the analysis to between-species differences on March-April composite data showed that both euphausiids are the same in C, C:N and ash but not in N (Table 3). *Euphausia pacifica* showed significantly less N than *T. inspinata* (Mann Whitney U-test, $p=0.021$).

Table 2
Between-month and between-species differences in standardized oxygen consumption rates (R_{std}), standardized ammonia excretion rates (E_{std}), O:N ratios calculated from R_{std} and E_{std} and water contents of *Euphausia pacifica* and *Thysanoessa inspinata* in the Oyashio region in March and April 2007. Italic figures of O:N ratios were those calculated from *R* and *E*. Values are mean ± 1SD and the number of replicates (*n*). *WM*=wet mass. *DM*=dry mass. *NS*: not significant.

Species	Date	*n*	R_{std} (µl O$_2$ indiv.$^{-1}$ h^{-1})	E_{std} (µg NH$_4$-N indiv.$^{-1}$ h^{-1})	O:N ratio (by atoms)	Water content (% of *WM*)
Euphausia pacifica	Mar.	7	6.34 ± 0.60	0.342 ± 0.232	30.9 ± 14.7 *49.0 ± 14.3*	77.7 ± 0.9
	Apr.	51	8.24 ± 2.22	0.111 ± 0.155	172.1 ± 129.8 *152.6 ± 148.9 (median: 105.6)*	76.1 ± 4.9
Mann Whitney *U*-test	*p*		0.01	< 0.01	< 0.01	< 0.05
Thysanoessa inspinata	Mar.	14	9.79 ± 1.92	0.531 ± 0.175	25.2 ± 9.0 *32.6 ± 19.6*	78.2 ± 1.3
	Apr.	52	10.07 ± 2.99	0.351 ± 0.175	68.1 ± 86.7 *66.0 ± 68.3 (median: 41.4)*	78.1 ± 5.0
Mann Whitney *U*-test	*p*		0.71^{NS}	< 0.01	< 0.01	0.534^{NS}
Euphausia pacifica	Mar.+Apr.	58	8.01 ± 2.18	0.139 ± 0.180	155.0 ± 130.2	76.3 ± 4.7
Thysanoessa inspinata	Mar.+Apr.	66	10.01 ± 2.79	0.388 ± 0.273	59.0 ± 78.9	78.1 ± 4.5
Mann Whitney *U*-test	*p*		< 0.01	< 0.01	< 0.01	< 0.01

Table 3
Carbon (C), nitrogen (N), C:N ratio, and ash of *Euphausia pacifica* and *Thysanoessa inspinata* in the Oyashio region in March and April 2007. Values are mean ± 1SD and the number of replicates (*n*). *DM*=dry mass. *NS*: not significant.

Species	Date	*n*	C (% of *DM*)	N (% of *DM*)	C:N ratio (by mass)	Ash (% of *DM*)
Euphausia pacifica	Mar.	2	34.41 ± 1.05	9.52 ± 0.06	3.61 ± 0.08	12.82 ± 2.62
	Apr.	5	36.73 ± 2.19	9.39 ± 0.56	3.91 ± 0.06	9.74 ± 0.58
Mann Whitney *U*-test	*p*		0.25^{NS}	0.70^{NS}	0.051^{NS}	0.053^{NS}
Thysanoessa inspinata	Mar.	3	36.46 ± 0.46	9.87 ± 0.37	3.69 ± 0.11	11.79 ± 1.11
	Apr.	5	38.08 ± 1.66	10.25 ± 0.62	3.72 ± 0.07	10.17 ± 0.60
Mann Whitney *U*-test	*p*		0.18^{NS}	0.65^{NS}	0.88^{NS}	0.10^{NS}
Euphausia pacifica	Mar.+Apr.	7	36.06 ± 2.16	9.43 ± 0.46	3.82 ± 0.16	10.62 ± 1.90
Thysanoessa inspinata	Mar.+Apr.	8	37.48 ± 1.53	10.11 ± 0.54	3.71 ± 0.08	10.78 ± 1.12
Mann Whitney *U*-test	*p*		0.20^{NS}	< 0.05	0.06^{NS}	0.49^{NS}

Table 4
Daily metabolism, growth and ingestion of *Eupahusia pacifica* and *Thysanoessa inspinata* and primary production during spring phytoplankton bloom in the Oyashio region in 2007. All values of (1) to (4) are in mg C m^{-2} d^{-1}.

Date in 2007	(1) Primary production	(2) Metabolism		(3) Growth		(4) Ingestion ([2]+[3])/ 0.9		(5) Ingestion
		E. pacifica	*T. inspinata*	*E. pacifica*	*T. inspinata*	*E. pacifica*	*T. inspinata*	*E. pacifica+T. inspinata* % of (1)
7 Apr.	2,586	63.9	17.6	49.2	3.0	125.7	22.9	5.7
8 Apr.	541	60.6	9.0	46.3	1.5	118.8	11.6	24.1
10 Apr.	1,067	3.0	18.8	2.2	3.1	5.7	24.3	2.8
12 Apr.	808	20.1	13.6	15.1	2.3	39.1	17.6	7.0
17 Apr.	988	15.3	5.8	11.4	0.9	29.7	7.5	3.8
20 Apr.	924	20.5	14.0	15.1	2.3	39.5	18.1	6.2
25 Apr.	980	8.3	8.1	6.2	1.3	16.1	10.5	2.7
29 Apr.	1,214	3.2	8.9	2.4	1.5	6.2	11.5	1.5
Total (7–29 Apr.)	21,553	385.8	240.8	290.0	39.9	750.5	311.9	4.9

Table 5
Daily ammonia-N excretion by *Euphausia pacifica* and *Thysanoessa inspinata* and N demand for primary production during spring phytoplankton bloom in the Oyashio region in 2007. Primary production data (Isada et al., 2010) expressed by C unit were converted to N unit based on Redfield ratio (C:N:P = 106:16:1 by atoms). All values of (1) and (2) are in mg N m^{-2} d^{-1}.

Date in 2007	(1) Primary production	(2) Ammonia-N excretion		(3) Ammonia-N excretion
		E. pacifica	*T. inspinata*	*E. pacifica+T. inspinata* % of (1)
7 Apr.	453	0.87	0.60	0.32
8 Apr.	95	0.93	0.33	1.32
10 Apr.	187	0.06	0.71	0.41
12 Apr.	142	0.37	0.46	0.59
17 Apr.	173	0.27	0.22	0.28
20 Apr.	162	0.41	0.48	0.55
25 Apr.	172	0.16	0.29	0.26
29 Apr.	213	0.06	0.32	0.18
Total (7–29 Apr.)	3,780	6.82	8.54	0.41

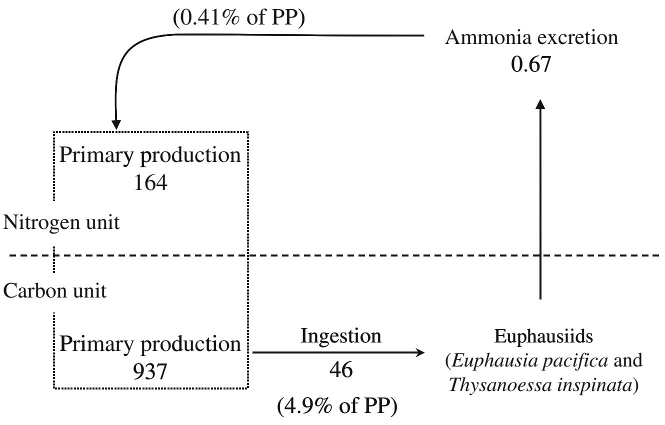

Fig. 4. Schematic presentation of daily grazing impact and simultaneous daily ammonia-N regeneration by euphausiids (*Euphausia pacifica* and *Thysanoessa inspinata*) on phytoplankton during spring phytoplankton bloom in April 2007 in the Oyashio region. Note that calculation of grazing impact is based on carbon units (lower section), while ammonia regeneration is based on nitrogen units (upper section). Values are integrated means in mg C m^{-2} d^{-1} or mg N m^{-2} d^{-1}, and the percentage contributions to primary production are in parentheses. See Tables 4 and 5 for details.

3.4. Ingestion and ammonia excretion by euphausiids during phytoplankton bloom

During the period 7–29 April, daily primary production fluctuated from 541 to 2,586 mg C m^{-2} d^{-1} (Isada et al., 2010). During the same period, estimated daily ingestion varied from 5.7 to 125.7 mg C m^{-2} d^{-1} for *Euphausia pacifica*, and from 7.5 to 24.3 mg C m^{-2} d^{-1} for *Thysanoessa inspinata* (Table 4). The total daily ingestion of the two euphausiids was 17.7–148.6 mg C m^{-2} d^{-1} or 1.5–24.1% (integrated mean: 4.9%) of the daily primary production (Table 4). The cumulative carbon-budget calculation over 23 days (7–29 April) suggests that *E. pacifica* allocated 59% of assimilated C to metabolism and 41% to somatic growth, while *T. inspinata* allocated 86% assimilated C to metabolism and 14% to somatic growth.

Daily ammonia excretion varied from 0.06 to 0.93 mg N m^{-2} d^{-1} for *Euphausia pacifica* populations, and from 0.22 to 0.71 mg N m^{-2} d^{-1} for *Thysanoessa inspinata* populations (Table 5). During the same period, N-demand for primary production was 95–453 mg N m^{-2} d^{-1} (Table 5), of which 0.18–1.32% (mean: 0.41%) could be supplied by the ammonia-N excreted by the two euphausiid species (Fig. 4).

4. Discussion

4.1. Metabolic response to phytoplankton bloom

Metabolic responses of herbivorous zooplankton to spring phytoplankton blooms have been studied most extensively for large copepods (e.g. *Calanus hyperboreus*, *C. finmarchicus* or *C. glacialis*) in the northern North Atlantic (Marshall and Orr, 1958; Conover and Corner, 1968; Butler et al., 1970; Båmstedt, 1985a; Mayzaud and Conover, 1988). These studies have shown that phytoplankton blooms accelerate both oxygen consumption and nitrogen/phosphorus excretion, but the acceleration of the latter is greater than that of the former, since most ingested food is utilized for lipid synthesis (high deamination activity, with a high nitrogen excretion level). In fact, lowered O:N ratios are typical for herbivorous copepods during phytoplankton blooms (Conover and Corner, 1968; Mayzaud and Conover, 1988). For euphausiids, comparable information is currently limited to that of Ikeda and Kirkwood (1989) on *Euphausia superba* in the Southern Ocean; the metabolism of *E. superba* during early summer (phytoplankton bloom season) is characterized by moderate increase in oxygen consumption rates, but depressed ammonia excretion, resulting in the increase of O:N ratios in euphausiids in contrast to the decrease of O:N ratios for copepods. Ikeda and Kirkwood (1989) interpreted the decline in ammonia excretion to preferential use of ingested N to replenish body protein utilized during the preceding winter as an energy source. Unlike copepods mentioned above, *E. superba* does not store large amounts of lipids in the body; therefore; body protein is the major energy source during winter when phytoplankton stocks are low.

The present results show that the changes in metabolic rates (oxygen consumption, ammonia excretion, O:N ratios) of *Euphausia pacifica* and *Thysanoessa inspinata* between before (March) and after (April) the onset of the spring phytoplankton bloom in the Oyashio region were not related to environmental parameters (SST or chlorophyll *a* standing stock) (Table 1). Perhaps the effects of SST changes (1.7–5.7 °C) were masked within general variations in the metabolic rates. Correlations between metabolic rates and phytoplankton abundance may emerge only on a seasonal timescale, but not with data from short time scales like the days to weeks of this study. Nevertheless, an effect of the phytoplankton bloom was detected in the comparison of ammonia excretion rates and O:N ratios pooled for March and for April (Table 2). Compared with March, lowered ammonia excretion rates and elevated O:N ratios of *E. pacifica* and *T. inspinata* in April indicate reduced importance of protein as a metabolic substrate during the phytoplankton bloom, which is in agreement with *E. superba* results from the Southern Ocean (Ikeda and Kirkwood, 1989). At the same time, low ammonia excretion in association with high O:N ratios of the euphausiids during the phytoplankton bloom suggests preferential utilization of dietary protein for somatic growth and/or reproduction rather than metabolism.

Metabolic responses of *Euphausia pacifica* and *Thysanoessa inspinata* to the onset of the bloom were more or less the same, but *E. pacifica* was characterized by lower oxygen consumption and ammonia excretion rates and higher O:N ratios, as compared with *T. inspinata* (Table 2). Populations of *E. pacifica* and *T. inspinata* in the Oyashio region during the present study were characterized by fast growth and less active spawning of the former and slow growth and active spawning of the latter (Kim et al., 2010). Species-specific differences in metabolism between the two euphausiids may be partially related to their life cycle phases.

Euphausiid O:N ratios have been reported as 16–103 for *Euphausia superba* in the Southern Ocean (Ikeda and Mitchell, 1982; Ikeda and Bruce, 1986; Ikeda and Kirkwood, 1989), 10.3 for *E. lucens* in the Benguela Current (Stuart, 1986), 27 for *Nyctiphanes australis* in western Cook Strait, New Zealand (James and Wilkinson, 1988), 37–41 for *E. crystallorophias* in the Southern Ocean (Ikeda and Kirkwood, 1989), 21–78 for *Thysanoessa inermis* in the Barents Sea (Ikeda and Skjoldal, 1989) and 12–45 for *Meganyctiphanes norvegica* in western North Atlantic (Saborowski et al., 2002). In this study, the O:N ratios (calculated from R and E) observed in April were characterized by large standard deviations near or exceeding means for both *E. pacifica* and *T. inspinata* (Table 2), implying non-normality of the data distribution. Medians instead of means re-calculated for April O:N ratio data were 106 for *E. pacifica* and 41 for *T. inspinata*. Thus, the O:N ratios of *E. pacifica* and *T. inspinata* observed in March-April were 33–106, which fall almost within the range (10.3–103).

4.2. Chemical composition

The chemical composition of marine zooplankton varies markedly between and within taxonomic groups, depending not only on internal factors (development stage, sex, trophic conditions) but also on extrinsic factors (season, geographical distribution, depth of occurrence) (Omori, 1969; Ikeda, 1974; Båmstedt, 1986). For *Euphausia superba* in the Southern Ocean, the composition (water, ash, C and N) and C:N ratio have been shown to change drastically through the phytoplankton-rich Antarctic summer; C content increases appreciably from 40-41% to 46-48% of *DM*, and C:N ratios increase from 3.5 to 4.5 by mass from November to January (Ikeda and Mitchell, 1982). At the same time, N composition decreases progressively from 12% to 10% of *DM*.

As indicators of lipid accumulation in the body, water contents of *Euphausia pacifica* and *Thysanoessa inspinata* were rather stable from March through April (Fig. 3), despite the changes in SST and chlorophyll *a* standing stock during the same period (Table 1). Comparison of C and N composition, C:N and ash data pooled for March and April showed no between-month differences in these chemical components (Table 3). While no comparable information about chemical composition of *T. inspinata* is presently available, a seasonal study of *E. pacifica* in Toyama Bay, southern Japan Sea, showed rather stable C and N composition, C:N ratios and ash contents throughout the year (Iguchi and Ikeda, 1998). C and N composition, C:N and ash data of *E. pacifica* and *T. inspinata* pooled for March-April show no appreciable between-species differences (Table 3). Clearly, *E. pacifica* and *T. inspinata* in the Oyashio region are different from *E. superba* in the Southern Ocean in terms of body compositional response to phytoplankton blooms. Despite the fact that all three species are considered to be primarily herbivores, the lower C contents of *E. pacifica* and *T. inspinata* (36–37% of *DM*, Table 3) as compared with that of *E. superba* (40–48% of *DM*, Ikeda and Mitchell, 1982) implies less reserve energy in the body and possibly less tolerance against food deprivation. They may, therefore, need to seek other food resources whenever phytoplankton becomes scarce. Relevant here is that *E. pacifica* off northeast Japan are reported to shift their diet to zooplankton when phytoplankton abundance is low (Nakagawa et al., 2001), and *T. inspinata,* as compared with *E. pacifica*, are known to exhibit a preference for zooplankton as food in waters off Sanriku (Endo, 1981).

4.3. Grazing impact and ammonia regeneration of euphausiids during the spring phytoplankton bloom in the Oyashio region

The grazing impact of mesozooplankton during the spring phytoplankton bloom has been estimated as 16–59% of daily primary production in the middle shelf-oceanic regions of the southeastern Bering Sea (Dagg et al., 1982), and 13–26% in the Oyashio region (Takahashi et al., 2008; Kobari et al., 2010). Mesozooplankton components considered in these previous studies have been mostly or entirely copepods, because of their extreme predominance in mesozooplankton communities. Currently, studies on grazing impacts by euphausiids are limited to those of Sameoto (1976) for three euphausiids (*Meganyctiphanes norvegica*, *Thysanoessa inermis*, *T. raschii*) in the Gulf of St. Lawrence and of Lasker (1966) on *Euphausia pacifica* in the broad North Pacific Ocean.

The present results showed that daily ingestion by *Euphausia pacifica* and *Thysanoessa inspinata* accounted for 1.5–24.1%

(integrated mean: 4.9%, Table 4) of primary production in April (Fig. 4), which is similar to the 3% grazing impact of *E. pacifica* across the subarctic North Pacific as a whole (Lasker, 1966) and which falls within the range of 1.5–60% for the three euphausiids mentioned previously (Sameoto, 1976). According to Sameoto (1976), ingestion by *Meganyctiphanes norvegica*, *T. inermis* and *T. raschii*) accounted for 1.5% of primary production in June–July, 29% in September and 60% in December in the Gulf of St. Lawrence. The present results would represent the seasonal minimum, since primary production is low in the Oyashio region during non-bloom seasons (Kasai, 2000), while euphausiid biomass is maintained throughout the year (Kim et al., 2009).

Ammonia is the major form of dissolved nitrogenous excretion by marine zooplankton (Corner and Davies, 1971; Ikeda et al., 2000), and it is utilized preferentially as a nitrogen source by phytoplankton (cf. Dugdale, 1976). Since the study of Harris (1959), who postulated significant contribution (77–90%) of zooplankton excretion to nitrogen demand by phytoplankton in Long Island Sound, many studies have confirmed the importance of mesozooplankton excretion in nutrient regeneration in the sea. Estimates have included 40–50% in the nutrient-depleted subtropical gyre in the North Pacific (Eppley et al., 1973), 11–44% in the Kuroshio region (Ikeda and Motoda, 1978), 4–50% off the Swedish coast (Båmstedt, 1985b), 43% in the N.W. Mediterranean (Alcaraz et al., 1994), 15–82% near south Georgia (Southern Ocean) (Atkinson and Whitehouse, 2000, 2001), and 31–36% in the equatorial Pacific (Gaudy et al., 2003). Dagg et al. (1982) estimated that ammonia excretion by mesozooplankton was equivalent to 6–22% of the N demand for daily primary production during the spring phytoplankton bloom in the middle-shelf-oceanic regions of the southeastern Bering Sea. In contrast with a wealth of information about the importance of bulk mesozooplankton excretion, little is known about the role of ammonia excretion by solely euphausiids relative to the nitrogen requirements for phytoplankton growth. As a notable exception, Atkinson and Whitehouse (2001) calculated that ammonia excretion by just *E. superba* contributed 16–50% of nitrogen demand by phytoplankton growth in the eastern area, but only 3–4% in the western area off South Georgia in summer.

Our calculation indicated that daily N regeneration by *Euphausia pacifica* and *Thysanoessa inspinata* accounted for 0.18–1.32% (Table 5) of the N demand for primary production (mean 0.41%) (Fig. 4). Phytoplankton would not be N-limited during the period we studied, since NO_3 concentrations in the surface layer were as high as 10–15 $\mu mol\,L^{-1}$ in March and decreased to 3–10 $\mu mol\,L^{-1}$ by the end of April, while NH_4 remained nearly stable at 0.5–1.0 $\mu mol\,L^{-1}$ throughout (Kuma et al., unpublished). Considering the persistence of the biomass of euphausiids throughout the year in the Oyashio region (Kim et al., 2009), their ammonia excretion would be more important from summer through early winter when most nutrients are depleted in the upper layer (Saito et al., 2002). That pattern was also observed during a seasonal study off the Swedish coast by Båmstedt (1985b).

Acknowledgments

We are grateful to the comments of two anonymous reviewers which improved the text. We thank the captain, officers and crews of the T/S '*Oshoro-Maru*' (Hokkaido University) and R/V '*Hakuho-Maru*' (Japan Agency for Marine-Earth Science and Technology) for their help in field sampling. This study was part of OECOS WEST project sponsored by PICES.

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