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**Ecological and physiological studies of euphausiids in
the Oyashio region, western subarctic Pacific**

By

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**A thesis submitted in partial fulfillment of the requirements for
the degree of Doctor of Fisheries Sciences**

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CONTENTS

1. Preface	1
2. Early development of <i>Thysanoessa inspinata</i> and <i>T. longipes</i> observed in the laboratory	4
2-1. Introduction	4
2-2. Materials and methods	5
2-3. Results	6
2-3-1. Laboratory raising	6
2-3-2. Descriptions of eggs, nauplius stage I and II, and metanauplius	6
2-4. Discussion	14
3. Abundance and life cycle patterns	20
3-1. Introduction	20
3-2. Materials and methods	21
3-2-1. Field sampling	21
3-2-2. Identification and enumeration	21
3-2-3. Cohort analysis and growth trajectory	24
3-3. Results	25
3-3-1. Hydrography	25
3-3-2. Body allometry	25
3-3-3. Abundance, biomass and life cycle	25
3-4. Discussion	36
3-4-1. Abundance	36
3-4-2. <i>Euphausia pacifica</i>	37
3-4-3. <i>Thysanoessa inspinata</i> and <i>T. longipes</i>	40
4. Population dynamics of euphausiids during phytoplankton bloom	44

4-1. Introduction	44
4-2. Materials and methods	45
4-2-1. Field sampling	45
4-2-2. Identification and enumeration	48
4-3. Results	49
4-3-1. Hydrography	49
4-3-2. Euphausiid abundance	49
4-3-3. Population structure	51
4-3-4. Gonad maturation	57
4-4. Discussion	60
5. Metabolism and chemical composition	65
5-1. Introduction	65
5-2. Materials and methods	66
5-2-1. Field sampling	66
5-2-2. Metabolic measurements	68
5-2-3. Body composition	68
5-2-4. Regression model, adjusted metabolic rate (<i>AMR</i>) and daily body C and N losses	69
5-3. Results	69
5-3-1. Respiration and ammonia excretion during spring phytoplankton bloom	70
5-3-2. Respiration, ammonia excretion and O:N as influenced by body mass and season	70
5-3-3. Water, ash and elemental composition	75
5-3-4. <i>AMR</i> and daily body C and N losses	75

5-4. Discussion	80
5-4-1. Seasonal metabolic characteristics	80
5-4-2. Metabolic comparison within euphausiids	82
5-4-3. Chemical composition	86
6. General discussion-Synthesis	89
6-1. Impact of euphausiid feeding on spring phytoplankton bloom in the Oyashio region	89
6-2. Regeneration of ammonia through excretion by euphausiids	91
6-3. Life cycle strategies of euphausiids in the Oyashio region	96
7. Summery	102
8. Acknowledgement	106
9. References	108

1. Preface

Eighty-six species of euphausiids (subphylum Crustacea, order Euphausiacea), are known in the world oceans (Baker et al., 1990). Euphausiids are all planktonic, and distributed to the epipelagic through bathypelagic realm of the oceans (Mauchline, 1980). In higher latitude seas, euphausiids are regarded as one of integral components of marine food chains because of their large biomass (Mauchline and Fisher, 1969; Mauchline, 1980). As a good example, the stock size of Antarctic krill (*Euphausia superba*) has been estimated as large as 500 million tons (Nicol and Endo, 1997), and the krill is playing the central role to channel phytoplankton production to the production of fish, squids, penguins, seals and whales in the Southern Ocean ecosystem (Nicol and de La Mare, 1993). Similar features though less pronounced than the Antarctic krill are the case for Norwegian krill (*Meganyctiphanes norvegica*) in the northern North Atlantic (Dalpadado, 2006), Tasmanian krill (*Nyctiphanes australis*) in the waters south of Australia (Hosie and Ritz, 1983) and North Pacific krill (*Euphausia pacifica* Hansen, 1911) in the subarctic Pacific and its marginal seas (Nicol and Endo, 1997).

In addition to trophic importance, euphausiids are known to be playing an important role in the vertical matter flux in the oceans through their extensive diel vertical migration behavior which extends to the order of several hundred meters. In the course of diel vertical migration, euphausiids feed in the epipelagic layer at night and defecate at the mesopelagic zone during daytime (Steinberg et al., 2000). Fecal pellets of euphausiids are large in size, suggesting its faster sinking to depth (González et al., 2000). Active swimming of euphausiids is known to have another function of fragmentation of sinking particle such as marine snow (Goldthwait et al., 2004).

“Swarming” is a behavioral characteristic of many euphausiids distributing in the epipelagic zone of the ocean (Mauchline, 1980). Since the swarm of euphausiids is often so dense (1,000-100,000 individuals m⁻³) and large (5-5,500 m of various shapes, cf. Mauchline, 1980), some euphausiids have been a target of human exploitations. According to Krill fishery statistics, the total global catch amounts to ca. 160,000 metric tons annually, most of this from the Antarctic Ocean (Ichii, 2000). Most of the krill catch is used for aquaculture and aquarium feeds, as bait in sport fishing, or human consumption in Japan (Nicol et al., 2000). In Japan, *Euphausia pacifica* fishery has developed since the Meiji Era (approximately 120 years ago), along with sand lance (*Ammodytes personatus*) fishery by using a bow-mounted trawl in coastal waters of Sanriku district, northeastern Japan (Odate, 1991). The euphausiids *Thysanoessa inermis* Krøyer, 1846 and *E. nana* Brinton, 1962 have also been exploited by local fishermen of the western coast of Hokkaido and Uwajima Bay, Ehime Prefecture, respectively, in Japan (Hanamura et al., 1989; Hirota and Kohno, 1992).

For the conservation of trophic functions of euphausiids in natural marine ecosystem and wise use of this sustainable biological resource, information about ecology and physiology of euphausiids is needed as the basis to establish rational management scheme. From this viewpoint, little has been studied on euphausiids in the world, with a notable exception for *Euphausia superba* in the Southern Ocean.

As part of a research program to evaluate trophodynamics in the pelagic ecosystem of the Oyashio region, western subarctic Pacific, I investigated the early development of *Thysanoessa inspinata* Nemoto, 1963 and *T. longipes* Brandt, 1851 observed in the laboratory (Chapter 2), abundance, biomass, life cycle (Chapter 3), population dynamics during the spring phytoplankton bloom (Chapter 4), metabolism

(oxygen consumption and ammonia excretion), body composition (water and ash contents, carbon and nitrogen) of dominant euphausiids (Chapter 5). These results are combined to estimate grazing impact of euphausiids on primary production and simultaneous nitrogen regeneration via excretion during phytoplankton bloom (Chapter 6).

2. Early development of *Thysanoessa inspinata* and *T. longipes* observed in the laboratory

2-1. Introduction

In the Oyashio region, *Euphausia pacifica* is the most dominant euphausiid, followed by *Thysanoessa inspinata* and *T. longipes* (see Chapter 3). In contrast to a large body of information available about biology and ecology of *Euphausia pacifica*, little has been studied on the two *Thysanoessa* spp. *T. inspinata* and *T. longipes* are morphologically similar species, and adults can be distinguished by the absence (*T. inspinata*) or presence (*T. longipes*) of abdominal spines (Nemoto, 1963).

The egg of euphausiids develops through sequential larval stages; nauplius (2 stages), metanauplius (1 stage), calyptopis (3 stages) and furcilia (6 stages) (cf. Mauchline and Fisher, 1969). Boden (1950) and Suh et al. (1993) analyzed field samples and described detail morphological characteristics of all larval stages of *Euphausia pacifica* in the southern California waters and Yellow Sea, respectively. Endo and Komaki (1979) gave diagnostic features for calyptopis I to juvenile of *Thysanoessa longipes* based on the preserved samples collected in the Japan Sea. To date, the morphological characteristics of eggs and naupliar stage of *T. longipes* are not known. No information is presently available for the morphology of larval stages (except nauplius II) of *T. inspinata* (cf. Gómez-Gutiérrez, 2003).

The aim of this study is to describe morphological characteristics of the early developmental stages (eggs, nauplius and metanauplius) of *Thysanoessa inspinata* and *T. longipes* raised in the laboratory.

2-2. Materials and methods

Euphausiids were collected from 200 m depth to the surface with Bongo nets (70 cm mouth diameter, 330 μm mesh size) aboard the R/V 'Tansei Maru' at Site H (41°30'N, 145°50'E) in the Oyashio region, western subarctic Pacific during 24-25 May 2006. Undamaged females *Thysanoessa inspinata* and *T. longipes* with spermatophores were quickly sorted and transferred individually into 1-L glass bottles filled with surface seawater. To prevent spawned eggs from predation by the females, 2 mm mesh netting was fixed 2-3 cm above the bottom of each bottle (cf. Ross and Quetin, 1983; Harrington and Ikeda, 1986). Glass bottles were placed in a dark plastic bag which was immersed into a water tank on the deck through which the surface seawater (3°C) was overflowing.

Glass bottles were inspected daily for spawned eggs. When eggs were observed, they were transferred individually into wells of multi-well plates filled with chilled seawater with a pasteur pipette. The eggs were examined daily for hatching and seawater in the wells was changed every 3-7 days. After hatching, the development of nauplii was followed up to the metanauplius stage (end of non-feeding stage). During the development, several specimens of nauplii were preserved in 2% borax buffered formalin for detail observations of its morphological characteristics. Naupliar appendages were removed under a dissecting microscope and mounted on slides. Preparations were sealed with transparent nail varnish. Each appendage was drawn under a light microscope equipped with a camera lucida (Olympus BH-2). The total length of nauplii was measured from the anterior tip of carapace to the midpoint of the telson spines (Hirota et al., 1984) with an aid of eye-piece micrometer. Nauplius stage I, nauplius stage II and metanauplius were hereafter abbreviated as NI, NII and MN, respectively, in this study.

2-3. Results

2-3-1. Laboratory raising

The eggs of *Thysanoessa inspinata* and *T. longipes* were slightly heavier than seawater, and tended to settle on the bottom of bottles. The brood size (the number of a batch of eggs released at one spawning event) was 76-142 eggs per female for *T. inspinata*, and 136 eggs per female for *T. longipes* (Table 2-1). Egg hatching success was 81.0-98.7% for *T. inspinata* and 64.7 % for *T. longipes* (Table 2-1). Mortality of both euphausiids during nauplius stages was relatively low, but increased from metanauplius to calytopis I stage from which feeding appendages developed (Fig. 2-1). The laboratory rearing ended in 31 days when all metanauplius specimens died off (Fig. 2-1). The development from one stage to the next stage was largely synchronized. The hatching time, developmental time of NI and NII was 3.0, 4.7 and 7.8 days, respectively, for *T. inspinata* and was 3.0, 4.5 and 8.5 days, respectively, for *T. longipes* (Table 2-2, Fig. 2-1).

2-3-2. Descriptions of eggs, nauplius stage I and II, and metanauplius

Since no apparent morphological differences were observed between *Thysanoessa inspinata* and *T. longipes*, drawing figures are presented only for *T. inspinata* in the present study.

Egg (Figs. 2-2A; 2-4)

Eggs were sphere in shape, and its diameter ranged from 0.33-0.38 mm (mean: 0.36 mm) for *Thysanoessa inspinata*, and 0.35-0.44 mm (mean: 0.39 mm) for *T. longipes*. Perivitelline space of eggs was relatively small.

Nauplius I (Figs. 2-2B, C; 2-3A, D, G; 2-4)

Total length ranged from 0.30-0.42 mm (mean: 0.35 mm) for *Thysanoessa inspinata* and 0.35-0.45 mm (mean: 0.39 mm) for *T. longipes*. Dorsal and lateral view of carapace smooth. Lateral view hood-shaped. Body egg-shaped from the dorsal view, with three pairs of appendages. Antennule uniramous, with one terminal long seta, two terminal spines, and one subterminal seta. Antenna biramous; endopod with two setae and one small seta; exopod with four setae. Mandible biramous; exopod and endopod unsegmented, with three setae.

Nauplius II (Figs. 2-2D, E; 2-3B, E, H; 2-4)

Total length ranged from 0.41-0.48 mm (mean: 0.45 mm) for *Thysanoessa inspinata* and 0.45-0.51 mm (mean: 0.47 mm) for *T. longipes*. Dorsal and lateral views elliptical. Body with one pair of spines on posterior margin. Antennule with two terminal long setae, one terminal spine, and one subterminal seta. Antenna biramous; endopod with two setae and one subterminal seta; exopod four setae and one small seta. Mandible setation and segmentation unchanged from NI, while size larger.

Metanauplius (Figs. 2-2F, G; 2-3C, F, I; 2-4)

Total length ranged from 0.43-0.61 mm (mean: 0.52 mm) for *Thysanoessa inspinata* and 0.51-0.60 mm (mean: 0.55 mm) for *T. longipes*. Carapace fringed with spines on anterior margin and first half of the lateral margin and on both sides of posterior margin. Anterio-median margin slightly indented. Antennule with one aesthete, two long setae, one terminal spine, and one subterminal seta. Antenna biramous; endopod with four setae, one subterminal seta; exopod, six-segmented with

six setae distally. Telson with five pairs of spines on posterior margin, one pair of spines on post-lateral margin.

2-4. Discussion

Brood size of euphausiids has been estimated by (1) the number of eggs in ovary of preserved females, (2) ovary volume and the volume of single eggs, (3) lipid analysis, (4) the number of eggs released in the laboratory (Mauchline and Fisher, 1969; Harrington and Ikeda, 1986). Among these methods, (4) is considered to be superior to the other methods because all eggs in ovaries are not necessarily released at one spawning event (Ross et al., 1982; Harrington and Ikeda, 1986). Brood size of euphausiids based on the counts of released eggs in the laboratory varies from one species to the next: i.e. 600 (second spawning)-2,800 eggs (first spawning) for *Euphausia superba* (Harrington and Ikeda, 1986); 12-296 eggs in Toyama Bay, Japan Sea (Iguchi and Ikeda, 1994), 11-258 eggs in Puget Sound, USA (Ross et al., 1982), 11-599 eggs along the Oregon coast, USA (Gómez-Gutiérrez et al., 2006) and 3-804 eggs in California and Oregon, USA (Feinberg et al., 2007), 6-246 eggs in the Gulf of Alaska (Pinchuk and Hopcroft, 2006) for *E. pacifica*; 5-1,021 eggs for *Thysanoessa inermis* and 46-385 eggs for *T. spinifera* in the Gulf of Alaska (Pinchuk and Hopcroft, 2006). The brood size of *T. inspinata* (76-142 eggs, Table 2-1) and *T. longipes* (136 eggs) observed in this study falls well within the broad range of these previous results on the other euphausiids.

Hatching success of eggs has been reported as 67-69% for *Euphausia superba* (Harrington and Ikeda, 1986), 96-99% for *E. pacifica* within their normal habitat temperature (0-20°C) (Iguchi and Ikeda, 1994), over 90% for *Thysanoessa inermis* and

E. pacifica under 5-12°C (Pinchuk and Hopcroft, 2006), 50-94% for *E. pacifica* off the coast of Newport of their normal habitat (10°C) (Feinberg et al., 2006). The present results on *T. inspinata* (81-99%, Table 2-1) and *T. longipes* (65%) overlap the broad range of previous studies on the other euphausiids.

According to Ikeda (1986), eggs of *Euphausia crystallorophias* and *E. superba* are spherical in shape, but perivitelline space of the former is much wider than that of the latter. Such the species-specific differences in the perivitelline space were not observed on *Thysanoessa inspinata* and *T. longipes* in this study (Fig. 2-2A).

While the general morphology of naupliar stages of euphausiid species are more or less similar each other and often difficult to separate into species, the total length, dorsal and lateral view, the shape of the posterior margin of the body, and the setation pattern of the antennule, antenna and mandible are known as useful species-specific characteristics of nauplius (cf. Mauchline and Fisher, 1969). In the present study, the morphology of NI, NII and MN of *Thysanoessa inspinata* and *T. longipes* were similar each other, and no appreciable morphological differences were recognized, excepting greater sizes of the latter as compared with the former (Fig. 2-4). It is observed that the formation of the abdominal spines (Fig. 2-2) and appendages (Fig. 2-3) from NI to NII were gradual with no obvious moulting, as was reported on *Euphausia superba* by Marschall and Hirche (1984). The moults were only found from NII to MN for both *T. inspinata* and *T. longipes*. While delayed hatching as NII or MN has been reported on *Thysanoessa* spp. (Gómez-Gutiérrez, 2002), this was never observed on *T. inspinata* and *T. longipes* in this study.

It is noted that the morphology of NII *Thysanoessa inspinata* given by Gómez-Gutiérrez (2003) is somewhat different from my results in several points,

including the number of spines in the posterior margin, the terminal margin spine of antennule, the terminal margin spine of endopod of antenna, and the number of setation of endopod of mandible (Table 2-3). The reason for the differences between the two studies is currently not known.

Metanauplii of some euphausiids such as *Euphausia crystallorophias*, *E. triacantha* and *E. frigida* bear characteristic long setae on the frontal margin of carapace, but such the setae are lacking in *E. superba* and *T. macrura* (Mauchline and Fisher, 1969). Frontal and posterior margin of metanauplii of *Thysanoessa inspinata* and *T. longipes* raised in this study was fringed with short spines (Fig. 2-2F). However, metanauplii of *E. pacifica* only fringed with spines on frontal margin (Fig. 2-5, Suh et al., 1993).

Table 2-4 summarizes sizes of adults, eggs, nauplii and metanauplii of various euphausiid species. Based on the summarized data in Table 2-4, I examined the correlation between mean egg diameter and mean adult size (median *TL*), and found there was no correlation between them ($p = 0.3059$). Size of eggs and nauplii of *Thysanoessa inspinata* and *T. longipes* in this study was slightly smaller than those of others euphausiids. For *Euphausia pacifica*, the nauplii derived from the Yellow Sea population (Suh et al., 1993) were larger than those from Toyama Bay population (Kim and Ikeda, unpublished). Regional variation in nauplii size with same species may related with the changes in environmental conditions (temperature, food, etc.). According to Summers (1993), eggs, nauplii and metanauplii of *Thysanoessa spinifera* reared in the laboratory were larger than those of wild populations (Table 2-4). Thus, the size of eggs and early larvae of euphausiids appears to be variable not only habitats but also conditions under which they developed (laboratory raised or wild collected).

3. Abundance and life cycle patterns

3-1. Introduction

The euphausiid *Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes* widespread over the entire subarctic Pacific Ocean and its marginal seas including the Bering, Okhotsk and Japan Seas (Brinton et al., 2000). Among the three euphausiids, the life cycle patterns has studied most extensively on *E. pacifica*; e.g. those in the Japan Sea (Iguchi et al., 1993; Iguchi and Ikeda, 2004), off northeastern Japan (Taki, 2004, 2006, 2007), off Oregon and southern California (Smiles and Percy, 1971; Brinton, 1976) and the southwestern Okhotsk Sea (Ponomareva, 1966). Comparable information is much less for *T. longipes* (those in the Japan Sea [Iguchi and Ikeda, 2004], the northern North Pacific [Nemoto, 1957] and the Okhotsk Sea [Zhuravlev, 1976]), and least for *T. inspinata* (only those off Kuril Islands [Kuznetsova, 1980, 1994]). As is documented well for *E. pacifica*, life cycle parameters (spawning season, growth pattern, life span, etc.) and biomass of euphausiids are highly variable from one region to the next (Siegel, 2000).

The Oyashio region, western subarctic Pacific, has been known as the feeding ground of both pelagic and ground fishes (Yamamura et al., 2002; Sugisaki and Kurita, 2004) and euphausiids are an integral diet component of them (Ikeda et al., 2008). Unfortunately, the biomass and life cycle features of dominant euphausiids (*Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes*) in this region are not well understood as a basis to estimate their trophic roles. The present study aims to fill the gap of knowledge by analyzing time series samples collected in the Oyashio region during 2002-2004. Results are discussed in the light of regional variations in abundance and life cycle of them reported in the other regions of the subarctic Pacific and adjacent

seas.

3-2. Materials and methods

3-2-1. Field sampling

Seasonal zooplankton sampling was made at Site H (41°30'N, 145°50'E, Fig. 3-1) in the Oyashio region during August 2002 through August 2004 (Table 3-1). Bongo nets (70 cm mouth diameter, 350 µm mesh size) were towed obliquely at a speed of 2 knots from 1000 m depth to the surface. The amount of seawater passed through the nets was estimated by the reading of a Rigosha flow-meter mounted in the mouth ring. After collection, all samples were preserved immediately in 5% borax buffered formalin-seawater on board the ship. Temperature and salinity profiles were determined with a CTD system (SBE-9 plus, Sea Bird Electronics) at each zooplankton sampling.

3-2-2. Identification and enumeration

In the land laboratory, *Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes* were sorted from the entire sample and enumerated with the aid of a dissecting microscope. Eggs and nauplii were not found in our samples. Calyptopis larvae occurred in a few number, but were not taken into account in this study because of the lack of morphological characters to separate them into the two *Thysanoessa* spp. in this study. The specimens were separated into furcilia larvae, juveniles, adult males, and adult females based on morphological characteristics described by Suh et al. (1993) for *E. pacifica* and Endo and Komaki (1979) for *T. inspinata* and *T. longipes*. The furcilia larvae and juveniles of *T. inspinata* and *T. longipes* were separated each other based on

the position of carapace lateral denticle: middle margin for *T. inspinata* and posterior margin for *T. longipes*. Adults were separated from juveniles by the development of external secondary sexual characters; petasma for males and thelycum for females (Makarov and Denys, 1981). Adult females with spermatophores attached were considered as an index of recent spawning. Body length (*BL*: mm), from the posterior margin of the eye notch to the terminal end of the sixth abdominal segment, was measured to the nearest 0.1 mm with a dissecting microscope with an eyepiece micrometer. To make comparison possible with the data of previous workers who adopted total length (*TL*; from the tip of rostrum to the distal end of telson), allometric equation of *TL-BL* relationships were established and *BL* data were converted to *TL* in this study. At the same time, preserved specimens of which *BL* was determined were rinsed briefly in distilled water and blotted on a filter paper, then weighed (*WM*: wet mass, mg) with a balance (Mettler Toledo MT 5) to a precision of 1 µg to establish *WM-BL* relationship (allometric model: $WM = aBL^b$, where *a* and *b* are constants). The allometric equation was combined with *BL* frequency distribution data to compute population biomass at a given sampling date of each euphausiid. Population biomass (*WM*) of the three euphausiids thus obtained was converted finally to carbon units by using conversion factors: water content to be 80% of *WM* and carbon content to be 43% of dry mass (*DM*: mg) (cf. Iguchi and Ikeda, 1998).

3-2-3. Cohort analysis and growth trajectory

Prior to the analysis, the data from more than one sampling in the same month (e.g. August in 2002, May and June in 2003, and March in 2004, cf. Table 3-1) were pooled to trace the growth sequence of cohorts on monthly or bi-monthly intervals.

Cohorts were analyzed based on *TL* frequency distribution data of each sampling date fitted to normal distribution curves. Length-frequency data was separated into multiple normal distribution curves by the aid of solver of MS Excel (Aizawa and Takiguchi, 1999).

3-3. Results

3-3-1. Hydrography

Surface temperatures ranged from $\leq 1^{\circ}\text{C}$ (February 2003) to 16°C (August 2002) (Fig. 3-2). The Oyashio Water, characterized by a temperature below 3°C and salinities from 33.0 to 33.3 psu (Ohtani, 1971), was seen in the upper 200 m during December 2002-March 2003, and at 50-200 m during May-December 2003 and May-August 2004. Surface temperatures increased to $>10^{\circ}\text{C}$ and thermoclines developed at 10-50 m during August-October 2002, June-December 2003 and June-August 2004. ‘Modified’ Oyashio water characterized by higher temperature and higher salinity than those of the Oyashio Water (Kono and Sato, personal communication) were observed above 200 m in May 2003 and December 2003 to March 2004, as judged by higher temperatures ($>5^{\circ}\text{C}$) and higher salinities (>33.5 psu) (Fig. 3-2). Below 200 m, temperatures and salinities were nearly constant at $2\text{-}3^{\circ}\text{C}$ and 33.3-34.5, respectively.

3-3-2. Body allometry

The *TL-BL* relationship was $TL = 1.133BL + 1.364$ ($r = 0.998$, $n = 67$, $p < 0.01$) for *Euphausia pacifica*, $TL = 1.262BL + 1.145$ ($r = 0.992$, $n = 90$, $p < 0.01$) for *Thysanoessa inspinata*, $TL = 1.410BL + 0.129$ ($r = 0.998$, $n = 54$, $p < 0.01$) for *T.*

longipes (Fig. 3-3). The *WM-BL* relationship was $WM = 0.0082BL^{3.130}$ ($r = 0.995$, $n = 67$, $p < 0.01$) for *E. pacifica*, $WM = 0.0110BL^{3.190}$ ($r = 0.994$, $n = 53$, $p < 0.01$) for *T. inspinata*, and $WM = 0.0085BL^{3.263}$ ($r = 0.996$, $n = 55$, $p < 0.01$) for *T. longipes* (Fig. 3-4).

3-3-3. Abundance, biomass and life cycle

Euphausia pacifica

This euphausiid was abundant in summer to autumn (October 2002 and August 2004) or spring (May 2003) and less in winter (February-March 2003 and November-March 2004) (Fig. 3-5A). Seasonal changes in biomass paralleled those of numerical abundance, except for August 2003 when adults were the major component of the population, and 2004 when furcilia larvae were the major component of the population (Fig. 3-5A). The mean abundance and biomass over the entire study period were 1,120 individuals m^{-2} and 832 mg C m^{-2} , respectively (Table 3-2).

Furcilia larvae occurred in most of the year with an exception in winter (Fig. 3-5B). Juveniles were observed in all seasons (7-63% of the total, with a mean of 28%). Adult female: male ratios ranged from 1:0.32 to 1:1 throughout the study period (mean 1:0.54). The proportion of adults (females+males) in the total population was large in winter (February-March) and summer (August-September), a pattern opposite to that of furcilia larvae. The adult females with spermatophores were only a small fraction of the total population, with peaks in summer (August 2002 and 2003). This, together with higher proportion of furcilia larvae in the population, the major spawning season is estimated to be in spring (April-May) and summer (August).

The entire range of *TL* (3 to 25 mm) was divided equally into 1 mm

increments (Fig. 3-5C). *TL* ranges were 3.2-8.5 mm for furcilia larvae, 4.8-14.1 mm for juveniles, and 9.1-24.4 mm for adults (minimum maturity size; 12.0 mm for males, 12.3 mm for females). For cohort analysis, no separation of the data into developmental stages or sex was made. One to three cohorts were separated in each sample and were assigned as +0 and +1 or +2 years old (Fig. 3-5C). Sequences of spring and summer cohorts were not necessarily clear. Perhaps, the +0 year-old summer cohort might mixed with the +0 year-old spring cohort of the next year (Fig. 3-5C). If this growth scheme is correct, the cohorts generated in spring and summer reach the minimum maturity size at the age of +0 year-old and +1 year-old, respectively, and complete their lives in 17 months and 26 months, respectively.

Thysanoessa inspinata

This euphausiid was most numerous in August-October 2002 and least in February-March 2003 (Fig. 3-6A), with a mean abundance of 163 individuals m^{-2} (=144 mg C m^{-2}) over the entire study period (Table 3-2). The seasonal patterns of the abundance and population biomass were similar each other, except for August 2003 when the adults prevailed in the population.

Furcilia larvae were found throughout the year, with peaks in May-June 2003 (42-46% of the total population) and May-August 2004 (53-62%) (Fig. 3-6B). Juveniles were the second dominant component of the population throughout the study period (mean: 34%). Adult female: male ratios varied from 1:0.4 to 1:5.4 with a mean of 1:1.8. Females with spermatophores occurred throughout the year, except for December 2003 to February 2004. These results and seasonal sequence in *TL* frequency distribution (mentioned below) suggest that spawning of this euphausiid

continues throughout the year with peaks in March-May.

TL ranges were 3.8-7.5 mm for furcilia larvae, 4.9-13.8 mm for juveniles, and 8.5-23.2 mm for adults (minimum maturity size; 11.6 mm for males, 11.4 mm for females). Growth trajectory of the cohort was analyzed following the same procedure for *Euphausia pacifica* mentioned above (Fig. 3-6C). As a result, clear sequence of growth trajectories was observed only the cohorts generated only in March-May 2002, 2003 and 2004. As life cycle pattern, new cohort generated in March-May grew and overwintered at 11-12 mm *TL*, which matured, reproduced and died off in October in the following year (estimated life span = 17-19 months).

Thysanoessa longipes

Seasonal changes in the abundance and biomass of this species were near in parallel with an exception that in August 2003 when furcilia larvae increased suddenly (Fig. 3-7A, B). The abundance (mean: 72.6 individuals m⁻²) and biomass (mean: 74.6 mg C m⁻²) were the least among the three euphausiids investigated in the present study (Table 3-2).

The population structure (development stage composition) was characterized by the short predominance of furcilia larvae in summer, which was followed by juveniles (Fig. 3-7B). Adult female: male ratios ranged from 1:0.1 to 1:3 throughout the study period (mean 1:0.4). Adult females with spermatophores were found only in March-May 2003 (7-10%) and March 2004 (12%), suggesting that the spawning season is March-May (though the spawning in 2004 did not accompanied with the occurrence of furcilia larvae).

TL ranges were 3.9-7.2 mm for furcilia larvae, 4.5-15.4 mm for juveniles, and

11.5-31.1 mm for adults (minimum maturity size; 14.1 mm for males, 14.1 mm for females). Growth trajectory of the cohort was analyzed following the same procedure for *Euphausia pacifica* mentioned above (Fig. 3-7C). Growth trajectories of the cohort could be traced for those generated in March-May 2001, 2002, 2003 and 2004. Cohorts generated in March-May grew and overwintered at 10-12 mm *TL*. In the following year, the overwintered cohort matured, reproduced and completed their lives in October (estimated life span = 29-31 months).

3-4. Discussion

3-4-1. Abundance

The abundance and biomass of euphausiids *Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes* at Site H were higher during summer 2002 and spring/summer 2003, but low spring (*E. pacifica*) or spring/summer 2004 (*T. inspinata* and *T. longipes*) (Figs. 3-5A, 3-6A and 3-7A). These drastic decreases in the abundance and biomass in 2004 may be related to the changes in water masses in the upper layers. ‘Modified’ Oyashio water characterized by higher temperature (>5°C) and higher salinity (>33.5 psu) than those of the Oyashio water were observed during December 2003 to June 2004 (Fig. 3-2). In the same seasons of 2002 and 2003, cold Oyashio Water was observed instead (Fig. 3-2). Geographical distribution patterns of euphausiid species are governed by temperature regimes of the ocean (cf. Mauchline and Fisher, 1969). While the three euphausiids studied are assigned as all subarctic euphausiids, *E. pacifica* occur from wide temperature ranges (<2-16°C), *T. inspinata* from 0-12°C and *T. longipes* from 0.3-5.1°C (Taki, 2007). From these species-specific temperature preferences, an extremely low abundance of *T. longipes* during December 2003-August

2004 (Fig. 3-7A) may be due to the ‘modified’ Oyashio water observed during that period (Fig. 3-2). The effects of the ‘modified’ Oyashio water to *E. pacifica* and *T. inspinata* might be less since these euphausiids could tolerate against higher temperature regime than *T. longipes* does (Fig. 3-5A and 3-6A).

Mean abundance over the entire study period (August 2002-August 2004) of *Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes* at Site H were the same order of magnitude to those of respective species reported from off southeastern Japan (Taki, 2006, 2007). Among the three euphausiids studied by Taki, biomass data were available only for *E. pacifica*, which is smaller than the half of this study (Table 3-2). Compared with our data derived from Bongo nets (70 cm diameter, 350 μm mesh) towed obliquely from 1000 m, Taki’s (2006, 2007) data were from a combination of Norpac nets (45 cm diameter, 335 μm mesh) towed vertically from 100 m and conical nets (130 cm diameter, 450 μm mesh) towed obliquely from <300 m. This methodological difference may be a reason why our sampling was more efficient to collect larger *E. pacifica* specimens than Taki’s. Iguchi and Ikeda (1999) used Norpac nets (45 cm diameter, 330 μm mesh) to estimate abundance and biomass of *E. pacifica* in Toyama Bay, but such the methodological effects to the results were not evident Table 3-2). As an alternative explanation, higher abundance of *E. pacifica* in Toyama Bay (5,500 individuals m^{-2}) than that in the Oyashio region (1,120 individuals m^{-2}) may be attributed largely by the inclusion of eggs in the abundance of the former. The effect of eggs is masked in biomass comparison (1,090 mg C m^{-2} in Toyama Bay vs. 832 mg C m^{-2} , Table 3-2) because of its smaller biomass. While comparable biomass data are not available for *T. inspinata* and *T. longipes* in the eastern subarctic Pacific, the range of biomass of *E. pacifica* off British Columbia, Baja California and California compiled by

Siegel (2000) (40-1,700 mg C m⁻²) overlaps partially that in the western subarctic Pacific region (381-1,090 mg C m⁻², Table 3-2). The total biomass of the three euphausiids (832 + 144 + 74.6 = 1,051 mg C m⁻², Table 3-2) is 12.8% of the mesozooplankton biomass (annual mean: 8,221 mg C m⁻², Ikeda et al., 2008) at Site H.

3-4-2. *Euphausia pacifica*

The life cycle of *Euphausia pacifica* have been studied at several locations, including off northeastern Japan (Taki, 2004), Toyama Bay, southern Japan Sea (Iguchi et al., 1993), off Oregon (Smiles and Percy, 1971), and off southern California (Brinton, 1976) (Table 3-3). Spawning season and life span of *E. pacifica* off northeastern Japan (Taki, 2004) is in good agreement with the present results in the Oyashio region, largely because both populations are living in neighboring waters. In Toyama Bay, *E. pacifica* spawn during February-April, and offspring overwinter, spawn February-April of the next year and die at the age of <21 months. The life cycles of Toyama Bay population are characterized by “growth stagnation” in summer during which they sink to phytoplankton-poor and cool depth to avoid high surface temperature beyond the tolerance limits of this species (Iguchi et al., 1993).

In the eastern North Pacific (off Oregon and off south California), reproduction of *Euphausia pacifica* continues throughout the year, and cohorts complete their lives in 8-12 months (Smiles and Percy, 1971; Brinton, 1976). The year-round reproduction in the eastern North Pacific regions is considered to be supported by frequent coastal upwelling events throughout the year which lead high phytoplankton production in most seasons (Brinton, 1976). Phytoplankton bloom occurs in spring, but phytoplankton concentrations are low in summer through winter in the Oyashio

region (Kasai et al., 2001). From this view, the first spawning season of *E. pacifica* in the Oyashio region (April-May) coincided the phytoplankton bloom, but the second spawning season (August-September) did not. Recently, Nakagawa et al. (2001) demonstrated that *E. pacifica* off northeast Japan fed phytoplankton, but switched feeding to small copepods during the season when the abundance of phytoplankton was low. This suggests that the second spawning of *E. pacifica* in the Oyashio region (and off northeastern Japan) is supported by small copepods which are numerous in summer (cf. Ikeda et al., 2008).

Growth trajectories of *Euphausia pacifica* has been documented to be highly variable, depending on the extent of seasonal food limitations, and growth rate as high as 0.1 mm *TL* day⁻¹ has been recorded on juveniles in food unlimited seasons (Brinton, 1976; Smiles and Pearcy, 1971; Iguchi et al., 1993). Because of scatter of the cohort data, seasonal growth of *E. pacifica* in the Oyashio region was unable to analyze precisely in the present study (Fig. 3-5C). Recent daily growth monitoring of *E. pacifica* population in the Oyashio region during phytoplankton bloom (March-April 2007) yielded a growth rate of 0.082 mm day⁻¹ (Chapter 4. result 4-3-3), which is still less than 0.1 mm⁻¹ mentioned above. As a possible attribute to slower growth rate of *E. pacifica* in the Oyashio region, lower habitat temperatures may be accounted for. Annual range of surface temperatures are 1-16°C in the Oyashio region (Fig. 3-2), 10-18°C in the southern California (Brinton, 1976), 8-18°C off Oregon (Feinberg and Peterson, 2003). The differences in habitat temperatures of *E. pacifica* within broad subarctic Pacific regions do not affect the minimum maturity size (11-12 mm *TL*) and the maximum adult size (19-21 mm *TL*), but affect the life span of this euphausiid (8-12 months for the eastern inhabitants vs. 17-28 months for the western inhabitants) (Table

3-3).

The sex ratios (female : male) of euphausiids has been reported fairly constant across many species (cf. Siegel, 2000). From this view, the present result on *Euphausia pacifica* (mean 1:0.54) is an exception (Fig. 3-5B). However, such the female-biased ratio has also been observed on the population off California, and is interpreted as a result from net avoidance of larger males, higher mortality of larger males, slower growth rate of females or possibly a shorter life span for males (Brinton, 1976).

3-4-3. *Thysanoessa inspinata* and *T. longipes*

Despite broad distribution across the entire subarctic Pacific (Brinton et al, 2000), study on the life cycle of *Thysanoessa inspinata* is currently limited to that of Kuznetsova (1980, 1994) off Kuril Islands. Off Kuril Islands, *T. inspinata* spawn in spring (May) and its life span is two years (Table 3-3). In the present study, furcilia larvae and adult females with spermatophores occurred in most seasons of the year, suggesting year-round reproduction of *T. inspinata* in the Oyashio region (Fig. 3-6B, C). Nevertheless, the development was traceable only for furcilia larvae emerged in March-May (Fig. 3-6C). The furcilia larvae developed and spawned during spring phytoplankton bloom of the next year. Our estimate of the life span (17-19 months) for *T. inspinata* is less than 2 years for the population off Kuril Islands (Kuznetsova, 1980, 1994) although the minimum maturity size (11-12 mm *TL*) and the maximum size (18-23 mm *TL*) did not differ appreciably between the two studies (Table 3-3).

The sex ratios (female : male) of *Thysanoessa inspinata* was 1:1.8 (mean), which is different markedly from 1:0.54 of *Euphausia pacifica* mentioned above and

1:0.4 of *T. longipes* mentioned below (see Figs. 3-5B, 3-6B, 3-7B). While causative mechanism for this male-biased sex ratio is currently unknown, possible different features between males and females causing biased sex ratios, as suggested by Brinton (1976) for *E. pacifica*, may be the case.

Information about the life cycle of *Thysanoessa longipes* is currently limited to the population around Yamato Rise in the central Japan Sea (Iguchi and Ikeda, 2004). According to Iguchi and Ikeda (2004), *T. longipes* spawn in April-May. Resultant young mature in two years, and complete their lives in three years (Table 3-3). The spawning season (April-May) of *T. longipes* in the Oyashio region observed in this study is similar to that of the population in the central Japan Sea. It is noted that spawning season of this euphausiid overlaps the period of spring phytoplankton bloom both in the central Japan Sea (Chiba and Saino, 2002) and the Oyashio region (Kasai et al., 2001). Co-occurrence of reproduction and spring phytoplankton bloom has also been reported on other subarctic *Thysanoessa* euphausiids (*T. inermis* and *T. raschii*) in the Atlantic Ocean (Falk-Petersen and Hopkins, 1981; Astthorsson, 1990).

Spawning seasons and the maximum size of *Thysanoessa longipes* in the Oyashio region and the central Japan Sea are similar, but the former has shorter life span (2.5 years) than the latter does (3 years) (Table 3-3). As a habitat of euphausiids, the Japan Sea is unique by species-poor (=reduced competition for food resources, cf. Yamada et al., 2002) and the presence of extremely cold water (<1°C) called “Japan Sea Proper Water” (Nishimura, 1969), both of which induce slower growth of euphausiids in the Japan Sea (Iguchi and Ikeda, 2004). Add to a slow growth, delayed maturation have also been documented on such mesopelagic zooplankton species as an amphipod *Primno abyssalis* (Yamada et al., 2002) and an ostracod *Conchoecia pseudodiscophora*

(Kaeriyama and Ikeda, 2002) in the Japan Sea.

Finally, a question may arise; how these primary grazing euphausiids (*Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes*) are co-existing in the epipelagic zone avoiding possible overlap of ecological niches? Like the three euphausiids in the Oyashio region, *T. inermis* and *T. raschii* are known as sympatric euphausiids in a subarctic Norwegian fjord (Falk-Petersen, 1985), the Barents Sea and the Norwegian shelf waters (Dalpadado and Skjoldal, 1996; Dalpadado, 2006). Studies have shown that *T. inermis* spawn during phytoplankton bloom and overwinter without feeding while *T. raschii* spawn late and feed on non-phytoplankton food in winter (Falk-Petersen, 1985) thus avoiding niche competitions. In this study, I was unable to detect possible differences in the timing of the main spawning event of *T. inspinata* and that of *T. longipes* because of long sampling intervals (1-2 months) during phytoplankton bloom season, and no data is presently available on feeding conditions of both species during winter. Recent field observations off northeastern Japan showed that *E. pacifica* underwent a diel vertical migration but *T. inspinata* did not (Taki, 2008). In the Japan Sea where *T. inspinata* do not occur *T. longipes* has shown to have greater energy reserves (higher body C:N ratios) in the body than *E. pacifica* does in the Japan Sea (Iguchi and Ikeda, 2005). While little has been explored on euphausiids as yet, differentiating food preference, feeding time or depth distribution have been known as mechanisms to avoid resources competition among large grazing copepods (*Neocalanus* spp., *Eucalanus bungii*) in the eastern and western subarctic Pacific (Mackas et al., 1993; Sato et al., unpublished).

4. Population dynamics of euphausiids during phytoplankton bloom

4-1. Introduction

In high latitude seas, spring phytoplankton bloom has been documented as a key mechanism to drive biological processes in marine ecosystem. As the major components of secondary producers, many copepods and euphausiids are known to be synchronized their life cycle patterns with spring phytoplankton blooms (cf. Wassmann et al., 2006; Ikeda et al., 2008). Coupling of spawning with the incidence of phytoplankton bloom has been reported on primarily grazing euphausiids, such as *Euphausia superba* in the Southern Ocean (Bargmann, 1945), *Thysanoessa inermis* and *T. longicaudata* in the Barents Sea (Dalpadado and Skjoldal, 1996), *E. pacifica* off southern California (Brinton, 1976) and Toyama Bay (Iguchi et al., 1993), and *E. pacifica* and *T. spinifera* off Oregon (Feinberg and Peterson, 2003). Thus, the magnitude of phytoplankton bloom affects the recruitment size of the euphausiids and subsequent growth of its young, then predators at higher trophic levels through food chains of the pelagic realm.

In the Oyashio region, *Euphausia pacifica* is the most dominant euphausiid, followed by *Thysanoessa inspinata* and *T. longipes* (Chapter 3). The predominance of *E. pacifica* persists over the broad Oyashio-Kuroshio transitional regions off northeastern Japan (Odate, 1994). Since *E. pacifica* is the target species of local krill fishery off northeast Honshu, Japan, intensive studies on this euphausiid have been made including its biomass and distribution (Nishikawa et al., 1995; Taki, 2006, 2008), feeding (Nakagawa et al., 2001, 2003), life cycle (Taki, 2004) and population production (Taki, 2006). Nevertheless, details about population dynamics of this euphausiid during phytoplankton bloom in spring have not been evaluated as yet from

bi-monthly sampling of these previous studies. Compared with *E. pacifica*, almost nothing is known about biology and ecology on *T. inspinata* in the Oyashio region. To fill the gap of knowledge, high frequency sampling in contrast with low frequency sampling (e.g. bi-monthly sampling) in the past is needed to execute during the phytoplankton bloom season.

OECOS (Oceanic Ecodynamics Comparison in the Subarctic Pacific) is a PICES project, aimed at 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). As part of activity of OECOS, the Western Group (OECOS WEST) organized two cruises to the Oyashio region before and during spring phytoplankton blooms in 2007. During the cruises, frequent sampling (every 2-5 days) were undertaken to trace the sequence of population dynamics of *Euphausia pacifica* and *Thysanoessa inspinata*. Results are discussed in the light of the effect of water mass change to the abundance and stability of population structure, and between-species differences in reproduction and growth.

4-2. Materials and methods

4-2-1. Field sampling

A total of ten oblique hauls with Bongo nets (70 cm mouth diameter, 500 μm mesh size) was made at station A-5 (42°00'N, 145°15'E, Fig. 4-1) in the Oyashio region during 9 March to 29 April 2007 (Table 4-1). Bongo nets were towed from 200 m depth to the surface at a speed of 2 knots (= 1.0 m s^{-1}) at night. The speed of the net towing appears to be fast enough to collect euphausiids which swim at 0.02-0.025 m s^{-1} (for *Euphausia pacifica*, Hanamura et al., 1984) with least effect of “net avoidance”, an

artifact known for the quantitative sampling of this group of animals (cf. Brinton, 1967). The volume of seawater passed through the nets was estimated by the reading of a Rigosha flow-meter mounted in the mouth ring. After collection, all samples were preserved immediately in 5% borax buffered formalin-seawater on board the ship. Environmental parameters (temperature, salinity and chlorophyll *a* pigment) were determined with a CTD system (SBE-9 plus or Sea Bird Electronics) at each sampling.

4-2-2. Identification and enumeration

In the land laboratory, euphausiids were sorted from the entire sample and enumerated under a dissecting microscope. The specimens of the two dominant euphausiid *Euphausia pacifica* and *Thysanoessa inspinata* were separated into juveniles and adult males/females based on morphological characters described by Suh et al. (1993) for *E. pacifica* and Endo and Komaki (1979) for *T. inspinata*. For adult females, the presence (an indicator of “recent spawning”) or absence of a spermatophore was noted. Body length (*BL*: mm), from the posterior margin of the eye notch to the distal end of the sixth abdominal segment, was measured to the nearest 0.1 mm under a dissecting microscope with an eyepiece micrometer. To facilitate comparison with the data of previous workers who measured total length (from the tip of rostrum to the distal end of telson, *TL*: mm) (cf. Ross et al., 2000 and references therein), I converted *BL* to *TL* using allometric equations: $TL = 1.292BL + 0.0762$ ($r = 0.998$, $n = 67$, $p < 0.01$) for *E. pacifica*, and $TL = 1.514BL - 0.575$ ($r = 0.995$, $n = 91$, $p < 0.01$) for *T. inspinata*. Note that these regressions were varied with mentioned previously (see Chapter 3). It is partly because of the regressions in Chapter 3 was based on the broader size ranges (*TL*: 14-23 mm), while those in this chapter were based on limited size ranges (*TL*:

13-18 mm, cf. Fig. 4-6).

In order to confirm gonad maturation of *Thysanoessa inspinata* females with spermatophores attached, its cephalothoraxes were detached from the body and immersed in 70% ethanol over night. The cephalothoraxes were dehydrated in a dilution series of ethanol and xylene and embedded in paraffin, which were sliced laterally with microtome, extended on glass slide, then stained with hematoxylin-eosin (e.g. paraffin section technique with HE stain). Glass slides were examined under biological microscope to evaluate gonad maturation histochemically.

4-3. Results

4-3-1. Hydrography

Over the study period, water temperatures of the top 200 m ranged from 1.1°C to 6.1°C (Fig. 4-2A). The Oyashio Water, characterized by temperature below 3°C and salinity from 33.0 to 33.3 psu (Ohtani, 1971), occurred in the upper 300 m during 5-8 April, and in the upper 200 m during 20-25 April. The 'modified' Oyashio water characterized by higher temperature and higher salinity than those of the Oyashio Water were observed above 200 m in 9-14 March and above 100 m in 13-19 April, respectively (Fig. 4-2A, B). The 'modified' Oyashio water is thought to be formed southeast off Hokkaido or carried from the Oyashio Front (Kono and Sato, personal communication). The chlorophyll *a* concentrations were low in March but it increased in April. A peak of chlorophyll *a* concentrations as high as 6.3 mg m⁻³ was seen in the upper 50 m in 7-8 April (Fig. 4-2C). The second peak (4.5 mg m⁻³) was observed in 23 April. The dates of incidences of both chlorophyll *a* peaks coincided with those when the cold, low saline Oyashio Water was observed (Fig. 4-2C).

4-3-2. Euphausiid abundance

Six euphausiid species belonging to the four genera were identified, e.g. *Euphausia pacifica*, *Thysanoessa inspinata*, *T. longipes*, *T. inermis*, *T. raschii*, *Tessarabrachion oculatum* and *Stylocheiron* spp. Among them, *E. pacifica* and *T. inspinata* composed of 63.3% and 33.6% (mean), respectively, of the total euphausiids occurred during the present study period.

The abundance of *Euphausia pacifica* varied greatly in the course of study, ranging from 41 to 1,040 individuals m⁻² (mean: 335) (Fig. 4-3B). The abundance peak was observed in 7-8 April, when the chlorophyll *a* concentration peaked (Fig. 4-3A). The abundance of *Thysanoessa inspinata* ranged from 50 to 186 individuals m⁻² (mean: 111) (Fig. 4-3B). Correlation analysis between the abundance and environmental parameters (temperature and chlorophyll *a*, both integrated over 0-100 m, Fig. 4-4) revealed that temperatures exerted significant negative effects on the abundance of both *E. pacifica* and *T. inspinata*, but chlorophyll *a* concentrations exerted significant positive effects on *E. pacifica* only (Table 4-2).

4-3-3. Population structure

Adult female : male ratios of *Euphausia pacifica* ranged from 1:0.66 to 1:1.14 throughout the study period (mean 1:0.87) (Table 4-3). Adult females with spermatophores occupied about 5% of the total population over the study period (Fig. 4-5A, Table 4-3). The entire range of *TL* (5.2 to 25.4 mm) of *E. pacifica* was divided equally into 1 mm increments (Fig. 4-5A). The range of *TL* was 5.2-11.6 mm for juveniles, 8.7-23.1 mm for adult males, 9.1-25.4 mm for adult females, and 15.5-23.3 mm for females with spermatophores (Fig. 4-5A). *TL* of adult females tended to be

larger than that of adult males throughout all samples. Modal size analyses revealed a consistent occurrence of one large group (mean TL : 13.8-17.6 mm), often accompanied with one discrete small group (mean TL : 6.9-10.5 mm). Plotting mean TL of the large size group against the dates of sampling since 1 March 2007, a mean growth rate of $0.082 \text{ mm } TL \text{ day}^{-1}$ was estimated from the slope of the fitted regression line (Fig. 4-6).

The sex ratios (female : male) of *Thysanoessa inspinata* ranged from 1:0.35 to 1:1.54 throughout the study period (mean 1:0.94) (Table 4-3). Adult females with spermatophores comprised 44% (mean) of the total population over the study period (Fig. 4-5B, Table 4-3). The entire range of TL (3.7 to 26.7 mm) of *T. inspinata* was divided equally into 1 mm increments (Fig. 4-5B). The range of TL was 3.7-11.4 mm for juveniles, 6.8-20.5 mm for adult males, 8.4-22.1 mm for adult females, and 10.3-26.7 mm for females with spermatophores (Fig. 4-5B). Modal size analyses showed a consistent presence of one large size group (mean TL : 16.5-18.1 mm) and one small size group (mean TL : 4.6-9.3 mm). Plot of mean TL s of the large size groups against dates since the first sampling (9 March 2007) yielded a mean growth rate of $0.022 \text{ mm } TL \text{ day}^{-1}$ for *T. inspinata* (Fig. 4-6).

4-3-4. Gonad maturation

Histological observations of *Thysanoessa inspinata* females with spermatophores attached revealed that the ovaries were filled with eggs (Fig. 4-7). Two types of eggs were seen as judged by the color of the cytoplasm; one is pink and the other is purple. In terms of maturity stage of euphausiids established by Kikuno and Kawamura (1983), the eggs with nucleus distinguishable from pink-colored cytoplasm is Stage IX (oocytes of the final maturity stage), and those with nucleus

indistinguishable from purple colored cytoplasm is Stage IV (oocytes of the early peripheral nucleous stage).

4-4. Discussion

As an annual event in the Oyashio region, phytoplankton bloom (chlorophyll *a* concentrations: 2-9 mg m⁻³) has been observed from late March to May (Kasai et al., 2001). In 2007 of this study, chlorophyll *a* concentrations increased from 0.5-1 mg m⁻³ in March to 6 mg m⁻³ in April (Fig. 4-2) thus indicating the incidence of the phytoplankton bloom at the sampling station of this study. The temporal variations in chlorophyll *a* observed during this study were partly due to the change in water mass prevailed in the surface layer; the incidence of high chlorophyll *a* was associated with the occupation of the Oyashio Water and the incidence of low chlorophyll *a* was with 'modified' Oyashio water characterized by higher temperature and higher salinities than those of the Oyashio Water (Fig. 4-2). Despite the change of water mass, both *Euphausia pacifica* and *Thysanoessa inspinata* occurred throughout the entire study period (Fig. 4-3B).

Negative correlation of the abundances of both *Euphausia pacifica* and *Thysanoessa inspinata* with water temperatures (Fig. 4-4A, B, Table 4-2) indicates that the both species occurred numerously during lower temperature periods. As judged by the correlation coefficients, *T. inspinata* ($r = -0.679$, Table 4-2) is more sensitive to the changes in temperature than *E. pacifica* ($r = -0.638$, Table 4-2). According to Taki (2008) who studied horizontal and vertical distribution of euphausiids in the western North Pacific regions under the influence of the Oyashio Current and Kuroshio Extension, both *E. pacifica* and *T. inspinata* were restricted to cold-water region and

their tolerance limits against high temperatures were 15°C for *E. pacifica* and 10°C for *T. inspinata*. Among euphausiids occurring in the subarctic Pacific, temperature preference varies in the following order (low to high temperatures); *Thysanoessa raschii* – *T. inermis* – *Tessarabrachion oculatum* – *T. longipes* – *T. inspinata* – *E. pacifica* (Mauchline and Fisher, 1969). Thus, the present results of higher temperature sensitivity of *T. inspinata* than *E. pacifica* are consistent with those of Mauchline and Fisher (1969) and Taki (2008). The fluctuation of the abundance of *E. pacifica* was positively correlated with chlorophyll *a* concentrations ($r = 0.687$), but this was not case in *T. inspinata* (Table 4-2). *E. pacifica* is documented as a typical grazer when the phytoplankton abundant (Nakagawa et al., 2001). While precise information about food habits of *T. inspinata* is not available, a congener *T. longipes* is known to show their food preference to zooplankton off Sanriku area (Endo, 1981). The differential food preference between *E. pacifica* and *T. inspinata* may be reflected to the dissimilar results of correlation analyses between their abundance and chlorophyll *a* of this study (Fig. 4-4C, D, Table 4-2).

Annual life cycle patterns of *Euphausia pacifica* and *Thysanoessa inspinata* in the Oyashio region have been evaluated based on samples collected every 2-3 months over two years (see Chapter 3). *E. pacifica* spawn twice in the year (March-April and August) in contrast with year-round spawning (peak season: March-May) for *T. inspinata*. New generations of both euphausiids overwinter as juveniles, and reproduce and complete their lives in the following year. Following those life cycle scheme, the large sized groups of *E. pacifica* (14-18 mm, Fig. 4-5A) and for *T. inspinata* (16-18 mm, Fig. 4-5B) found in this study are considered to be those born in the previous year. Despite of a large fluctuation in the abundance during the present study

period, the growth of the large sized-groups was consistent with time yielding the growth rates of $0.082 \text{ mm day}^{-1}$ for *E. pacifica* and $0.022 \text{ mm day}^{-1}$ for *T. inspinata* (Fig. 4-6). Persistence of the large sized groups despite of the change of water mass during this study (Fig. 4-2) suggests strongly that the presence of single populations of each *E. pacifica* and *T. inspinata* in the Oyashio region. According to the life cycle scheme of both euphausiids mentioned above, the single small sized-groups occurred frequently for both of them (Fig. 4-5) is considered to be those born in 2007.

Since the growth of euphausiids is known to be highly seasonal, depending on food availability and temperature conditions (cf. Mauchline and Fisher, 1969), our results are compared with those of other workers on the bases of the data of the same or similar species and from growing seasons (mostly phytoplankton bloom seasons in spring or summer) (Table 4-4). Our results ($0.082 \text{ mm day}^{-1}$) of *Euphausia pacifica* in the Oyashio region fall within the range of $0.056 \text{ mm day}^{-1}$ off northeastern Japan population (Taki and Ogishima, 1997) and 0.11 mm day^{-1} off Oregon coast population (Smiles and Pearcy, 1971). Our results ($0.022 \text{ mm day}^{-1}$) of *T. inspinata* are much less than $0.070\text{-}0.123 \text{ mm day}^{-1}$ of other *Thysanoessa* spp. from various locations in the subarctic waters (Table 4-4). Taking into account of the fact that the present study was conducted during phytoplankton blooms, observed slow growth rates of *T. inspinata* may be due to allocation of energy ingested to reproduction rather than somatic growth. To support this, the occurrence of females with spermatophores is much greater for *T. inspinata* (mean: 43.6% of the total population) than that of *E. pacifica* (only 4.9%) (Table 4-3) though the female: male ratios of the adults of two euphausiids were identical (1:0.9). While the observed number is limited, the gonad maturation of females with spermatophores was much advanced (Fig. 4-7). The same line of

explanation may also be applicable to somewhat low growth rates of *E. pacifica* of this study mentioned above. Indeed, the growth rates of juveniles of *E. pacifica* (Iguchi et al., 1993) and *T. inermis* (Astthorsson and Gislason, 1997) are greater than those of adults (allocating ingested energy more or less to gonad development) of each euphausiid (Table 4-4).

One might argue whether or not the incidence of females with spermatophores (= mating) is indicative of “in spawning” in euphausiids (Mauchline and Fisher, 1969). Mating and spawning of *Thysanoessa inermis* and *T. raschii* in the Barents Sea occur in the same period (April) (Drobysheva, 1957), whereas mating of Antarctic krill *Euphausia superba* occurs several weeks before spawning (Bargmann, 1945). In Clyde Sea (UK), *Meganyctiphanes norvegica* with spermatophore attached occurs in February but spawning does not occur until the beginning of April, in contrast to co-occurrence of mating and spawning in *T. raschii* in the same region (Mauchline, 1968). Perhaps, there are many variations in the timing of mating and actual egg release not only between-species but also within-species of euphausiids depending on the environmental conditions of the habitats (Mauchline and Fisher, 1969). Histological examination of female *T. inspinata* with spermatophore attached of this study showed that the ovaries were filled with mature eggs (Fig. 4-7). Furthermore, females of both *E. pacifica* and *T. inspinata* were observed to lay eggs during incubation for metabolic measurements of this study (Chapter 5). All these results suggest that the incidence of females with spermatophores attached is a good indicator of recent spawning of both euphausiids I studied.

5. Metabolism and chemical composition

5-1. Introduction

The pelagic ecosystem of the Oyashio region, western subarctic Pacific, is characterized by the incidence of massive diatom blooms in the spring and unique life cycle patterns of herbivorous zooplankton to utilize the bloom 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), little has been studied on euphausiids (Kim et al., in press).

As an approach to evaluate dynamic roles of euphausiids in energy flow and matter cycling, metabolic measurement (oxygen consumption, ammonia excretion) and body chemical composition (water content, ash and C and N composition) provide a wider perspective for energy demand, metabolic balance and nutritional conditions of zooplankton within their environments (Ikeda et al., 2000). To date, such the information is available on *Euphausia superba* in the Southern Ocean (Ikeda and Mitchell, 1982; 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 western North Atlantic (Saborowski et al., 2002). In the Oyashio region, *E. pacifica* and *T. inspinata* have been reported as predominant euphausiids (Kim et al., in press), but no study has been made on their metabolism and chemical composition.

As part of OECOS (Oceanic Ecodynamics Comparison in the Subarctic Pacific) project which aimed at 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), I studied oxygen consumption and ammonia excretion of *Euphausia pacifica* and *Thysanoessa inspinata* during cruises in March, April and December 2007 to the Oyashio region. For the specimens used in these experiments, the chemical composition (water, ash, carbon and nitrogen) was analyzed. The results are compared with those of other euphausiids to elucidate unique metabolic and body structural features of these euphausiids in the Oyashio region, if any.

5-2. Materials and methods

5-2-1. Field sampling

Field studies were made at A-5 (42°00'N, 145°15'E) or Site H (41°30'N, 145°50'E) in the Oyashio region, western subarctic Pacific (Fig. 5-1) during the three periods: 9-14 March, 6-30 April, and 11-13 December 2007. 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 cod end 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 until the experiments commenced. Prior to each experiment, seawater was collected from 10 m depth with 10 liter Niskin bottles and filtered through GF/F filters and well oxygenated for the use of metabolic experiments

below.

5-2-2. Metabolic measurements

Oxygen consumption and ammonia excretion 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 in the beaker 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 10.6°C). At the end of experiments, duplicate 15 (or 40) and 10 ml water samples were siphoned out for the measurements of dissolved oxygen and ammonia, respectively. Dissolved oxygen and ammonia were determined by the Winkler titration method (Strickland and Parsons, 1972) and the phenol-hypochlorite method (Solórzano, 1969), respectively. Euphausiids used for 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.

5-2-3. Body composition

In the land laboratory, frozen samples were weighed (*WM*: wet mass) and freeze-dried for 5h then dried at 60°C for 1h, 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 species in each field season, then finely ground with a ceramic mortar and pestle. Powdered samples were used for elemental composition analyses (carbon [C] and nitrogen [N]) with a CHN elemental analyzer (Micro CHN

order JM-10). Weighed fraction 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. General precisions (coefficient of variations) 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*).

5-2-4. Regression model, adjusted metabolic rate (*AMR*) and daily body C and N losses

The relationship between body dry mass (*DM*: mg indiv.⁻¹) and oxygen consumption (*R*: µl O₂ indiv.⁻¹ h⁻¹) or ammonia excretion rate (*E*: NH₄-N indiv.⁻¹ h⁻¹) of animals is described as R (or E) = aDM^b (or $\log_{10}R$ [or E] = $\log_{10}a + b\log_{10}DM$), where a and b are proportional constants (Prosser, 1961). For rigorous metabolic comparison between individuals with different body masses and living in dissimilar temperatures, R or E was adjusted to the rate of a body size of 1 mg *DM* (*AMR*-O₂ or *AMR*-NH₄-N) and at 10°C, assuming a body mass exponent (= constant b) of 0.8 (Ikeda, 1988) and Q_{10} value of 2 (Ikeda et al., 2001).

For the calculation of daily losses in body C, R was converted first to daily CO₂-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 C mass in 1 mol of CO₂ (22.4 liters), 24 is number of hours per day, and 10⁻³ is to convert µg to mg. An $RQ = 0.97$ (protein metabolism; cf. Gnaiger, 1983) was assumed. For the estimation of metabolic body N loss, ammonia was assumed to be only form of nitrogen excreta. The daily body C or N losses due to metabolism thus obtained was expressed as a fraction of body C or N (% of body C or N loss d⁻¹).

5-3. Results

5-3-1. Respiration and ammonia excretion during spring phytoplankton bloom

During the spring phytoplankton bloom period (9 March-30 April), sea surface temperatures and chlorophyll *a* concentrations (0-100 m) in the Oyashio region varied from 1.7 to 5.7°C and from 29.4 to 252.6 mg m⁻², respectively. During the same period, *AMR-O₂* and *AMR-NH₄-N* of ranged from 1.345 to 2.226 µl O₂ (mg *DM*)^{-0.8} h⁻¹ and from 0.0109 to 0.0503 µg NH₄-N (mg *DM*)^{-0.8} h⁻¹, respectively, for *Euphausia pacifica*, and from 1.866 to 2.508 µl O₂ (mg *DM*)^{-0.8} h⁻¹ and from 0.0154 to 0.1004 µg NH₄-N (mg *DM*)^{-0.8} h⁻¹, respectively, for *Thysanoessa inspinata* (Fig. 5-2). Correlation analyses between *AMRs* and environmental parameters (sea surface temperatures and chlorophyll *a* standing stocks) revealed that neither temperature nor chlorophyll *a* related with the changes in *AMRs* (Table 5-1).

5-3-2. Respiration, ammonia excretion and O:N as influenced by body mass and season

The data collected from March, April and December were pooled in the following analyses. Seasonally, mean *DM* ranged from 6.60 to 13.15 mg indiv.⁻¹, mean *R* from 4.32 to 9.99 µl O₂ indiv.⁻¹ h⁻¹, and mean *E* from 0.11 to 0.61 µg NH₄-N indiv.⁻¹ h⁻¹ for *Euphausia pacifica* (adult males and females) (Table 5-2). For *Thysanoessa inspinata* (adult males and females), mean *DM* varied from 8.32 to 13.08 mg indiv.⁻¹, mean *R* from 8.30 to 15.00 µl O₂ indiv.⁻¹ h⁻¹, and mean *E* from 0.28 to 0.98 µg NH₄-N indiv.⁻¹ h⁻¹ (Table 5-2).

The relationships between *DM* and *R* and *E* were highly significant for both *Euphausia pacifica* and *Thysanoessa inspinata* ($p < 0.01$, Fig. 5-3). Resultant

regression equations by the least-square fitting were $R = 1.440DM^{0.788}$ and $E = 0.006DM^{1.273}$ for *E. pacifica*, and $R = 1.852DM^{0.729}$ and $E = 0.046DM^{0.829}$ for *T. inspinata*. As an alternative regression method, the body mass exponent was fixed to 0.8, and regression lines were re-calculated and superimposed in Fig. 5-3. From the elevations of the alternative regression lines of which slopes were in parallel, it became clear that R and E of *T. inspinata* were 1.1 time and 2.6 times, respectively, those of *E. pacifica* with equivalent DM (Fig. 5-3).

The ratios of R to E (O : N ratios by atoms) varied significantly with season (one-way ANOVA, $p < 0.01$), ranging from 18.6 to 87.5 for *Euphausia pacifica* and from 19.8 to 46.0 for *Thysanoessa inspinata* (Table 5-3). Subsequent analysis showed that the O : N ratios in April were significantly higher than those in March and December for both euphausiids (Fisher's PLSD, $p < 0.01$) (Table 5-3).

5-3-3. Water, ash and elemental composition

Seasonally, water contents, ash, C and N varied from 76.05-77.74% of WM , 9.46-12.82% of DM , 32.81-36.25% of DM and 9.19-9.52% of DM , respectively, for *Euphausia pacifica*, and 75.35-78.19% of WM , 9.74-11.48% of DM , 35.15-37.10% of DM and 9.54-10.00% of DM , respectively, for *Thysanoessa inspinata* (Table 5-4). The range of C:N ratios was 3.58-3.91 for *E. pacifica* and 3.69-3.71 for *T. inspinata*. The effects of seasonal and sex on the chemical composition were not significant (two-way ANOVA, $p > 0.05$). Between-species differences in the chemical composition were also not significant (Mann Whitney U -test, $p > 0.05$).

5-3-4. AMR and daily body C and N losses

Some female euphausiids spawned during experiments but the differences in R or E between spawned female and non-spawned females were not significant as judged by $AMR-O_2$ and $AMR-NH_4-N$ (Mann Whitney U -test, $p = 0.72-0.96$). No sexual differences within species were also evident in $AMR-O_2$ and $AMR-NH_4-N$ of both euphausiids ($p = 0.13-0.88$). From these results, all data were pooled into each season in the following analyses.

The ranges of $AMR-O_2$ and $AMR-NH_4-N$ were $1.17-1.87 \mu l O_2 (mg DM)^{-0.8} h^{-1}$ and $0.030-0.082 \mu g NH_4-N (mg DM)^{-0.8} h^{-1}$, respectively, for *Euphausia pacifica*, and $1.90-2.28 \mu l O_2 (mg DM)^{-0.8} h^{-1}$ and $0.067-0.125 \mu g NH_4-N (mg DM)^{-0.8} h^{-1}$, respectively, for *Thysanoessa inspinata* (Table 5-5). While seasonal differences were not seen in $AMR-O_2$ of *T. inspinata* ($p > 0.05$), $AMR-O_2$ of *E. pacifica* and $AMR-NH_4-N$ of both *E. pacifica* and *T. inspinata* differed significantly with season (one-way ANOVA, $p < 0.01$). Post hoc test by Fisher's PLSD showed that compared with those of other seasons, the $AMR-O_2$ in April was significantly higher in *E. pacifica*, and $AMR-NH_4-N$ in December was significantly higher in *E. pacifica* and *T. inspinata* (Table 5-5).

Daily C and N losses were 2.4-3.0% and 0.26-1.04%, respectively, for *Euphausia pacifica*, and 3.7-4.3% and 0.65-1.56%, respectively, for *Thysanoessa inspinata* (Table 5-5). No seasonal differences were detected in daily C losses in each species (one-way ANOVA, $p > 0.05$), but *T. inspinata* exhibited significantly higher value than *E. pacifica* (Mann Whitney U -test, $p < 0.01$). Common to both species, daily N losses varied significantly with season (one-way ANOVA, $p < 0.01$) and was due to higher values in December (Fisher's PLSD, $p < 0.01$) (Table 5-5). Daily N losses were significantly greater in *T. inspinata* than *E. pacifica* (Mann Whitney U -test, $p < 0.01$).

5-4. Discussion

5-4-1. Seasonal metabolic characteristics

Respiration to ammonia excretion ratios (O:N ratios) have been used as an index of the proportion of protein in total metabolic substrates, and the ratios range from 7-8 (by atoms, protein-oriented metabolism) to several hundred or more (lipid-oriented metabolism) (Ikeda et al., 2000). As metabolic substrates, carbohydrate is considered to be not important, since its content is too small to support the energy demand of one day for zooplankton. When protein and lipid are metabolized in equal amounts, the O:N ratio was predicted as 24 (Ikeda et al., 2000) or 50-60 (Mayzaud and Conover, 1988), depending on the make-up of protein and lipid of zooplankton assumed.

Metabolic response of herbivorous zooplankton to spring phytoplankton blooms has been studied most extensively on copepods in northern North Atlantic (Marshall and Orr, 1958; Conover and Corner, 1968; Butler et al., 1970; Båmstedt, 1985; Mayzaud and Conover, 1988). According to their results, incidence of phytoplankton bloom accelerate both respiration and excretion, but the magnitude of acceleration of the former is greater than that of the latter, since most of ingested food is utilized to somatic growth or reproduction preferentially to the metabolism. In fact, lowered O:N ratios are typical for herbivorous copepods during the phytoplankton bloom (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 respiration rates, but depressed ammonia excretion, resulting in the increase of O:N ratios in contrast to the decrease of O:N ratios for copepods. Ikeda and Kirkwood

(1989) interpreted the decline in ammonia excretion to be due to preferential use of ingested N to replenish body protein which had been utilized heavily as an energy source during preceded winter. Different from copepods mentioned above, *E. superba* do not store large amounts of lipids in the body therefore body protein is the major energy source during food deprived winter.

Seasonal patterns of respiration and ammonia excretion rates of *Euphausia pacifica* and *Thysanoessa inspinata* determined during non-phytoplankton bloom season (March, December) and phytoplankton bloom season (April) (Table 5-5) are in general agreement with those of *E. superba* of Ikeda and Kirkwood (1989). While higher respiration rates during phytoplankton bloom (April) were seen only for *E. pacifica*, both euphausiids exhibited higher O:N ratios (Table 5-3) during the same season. Higher ammonia excretion coupled with lower O:N ratios of both euphausiids during winter (December) are indicative of relative importance of protein as a metabolic substrate. Relevant here, *E. pacifica* off northeast Japan are reported to shift their diet to zooplankton when phytoplankton abundance is low (Nakagawa et al., 2001). Compared to *E. pacifica*, *T. inspinata* are known to exhibit food preference to zooplankton off Sanriku waters (Endo, 1981).

Nevertheless, the present correlation analyses between metabolic rates (respiration and ammonia excretion) and environmental parameters (chlorophyll *a* and temperature) failed to find significant relationship between the two (Table 5-1). Perhaps, the correlations between metabolic rates (respiration and ammonia excretion) and food abundance may emerge with seasonal data, but not with the data of short time scales like days of this study. In the review of O:N ratios as a tool to analyze zooplankton metabolism, Mayzaud and Conover (1988) emphasized the complexity of

the processes which determine the ratios; not only by external parameters (temperature, food quantity and quality) and internal parameters (life stage, nutritional condition, food habits).

5-4-2. Metabolic comparison within euphausiids

To date, a number of studies on the respiration rates have been made on euphausiids inhabiting various regions of the world oceans (cf. Mauchline and Fisher, 1969; Mauchline, 1980). Among them, the studies of Ikeda and Mitchell (1982) on *Euphausia superba* in the Southern Ocean, Ross (1982) on *E. pacifica* raised in the laboratory, Stuart (1986) on *E. lucens* in the southern Benguela current are of special interest in terms of simultaneous determination of respiration and ammonia excretion as a function of body mass and temperature. The respiration and ammonia excretion experiments of these previous workers were run at -1.1°C (Ikeda and Mitchell, 1982), 8°C (Ross, 1982) and 12.5°C (Stuart, 1986). To make meaningful comparison among the data, all data were standardized to the rates at 10°C assuming $Q_{10} = 2$ (Fig. 5-4).

The R - DM relationships at 10°C of *Euphausia superba* in the Southern Ocean, *E. pacifica* raised in the laboratory, Stuart (1986) on *E. lucens* in the southern Benguela current thus re-calculated are in line with those of *E. pacifica* and *Thysanoessa inspinata*. On the other hand, the E - DM relationships of *E. pacifica* and *T. inspinata* of this study diverged from those of *E. superba*, *E. pacifica* and *E. lucens* of previous workers (Fig. 5-4). In theory, R represents total metabolism but E protein metabolism, then E may not be detected for zooplankton metabolizing lipids or carbohydrates (Ikeda et al., 2000). As is evident in Fig. 5-3, E is highly variable as compared with R even in the same experiments. While statistical tests for the E - DM relationships in Fig. 5-4 are

not amenable since raw data of the previous workers are not available, lower *E* of *E. pacifica* and *T. inspinata* of this study may be a result from complex interactions of regional/seasonal characteristics of quality and quantity of diet and life cycle patterns of these euphausiids (see discussion on O:N ratios below).

The O:N ratios varied greatly from one euphausiid to the next: 18.6 (December)-87.5 (April) for *Euphausia pacifica* and 19.8 (December)-46.0 (April) for *Thysanoessa inspinata* (this study), 30.3-34.6 (November, pre-bloom season; Ikeda and Kirkwood, 1989), 59-103 (December, bloom season; Ikeda and Bruce, 1986) and 15.9-17.5 (January, post-bloom season; Ikeda and Mitchell, 1982) for *E. superba*, 10.3 for *E. lucens* (Stuart, 1986), 27.1 for *Nyctiphanes australis* (James and Wilkinson, 1988), 4.8-12.1 for *Meganyctiphanes norvegica* (Mayzaud, 1973) and 12-45 for *M. norvegica* (Saborowski et al., 2002) (Table 5-6). Among them, *M. norvegica* is known as a carnivore (Sargent and Falk-Petersen, 1981) but such the difference in food habits is not reflected the O:N ratios. Overall, the metabolic substrates of these euphausiids as judged by the O:N ratios are protein based on the criterion (<50-60 for protein-oriented metabolism) of Mayzaud and Conover (1988) or a mixture of protein and lipids based on the criterion (<24 for protein-oriented metabolism) of Ikeda (1974).

Information about metabolic rates expressed by daily body C or N losses for euphausiids is currently limited to those on *Thysanoessa inermis* in the Barents Sea (0.9-1.89% of body C loss, 0.34-0.80% of body N loss, cf. Ikeda and Skjoldal, 1989) and *Euphausia superba* in the Southern Ocean (0.8-1.3% of body C loss, 0.7-1.1% of body N loss, cf. Ikeda and Mitchell, 1982). Taking into account lower habitat temperature of these polar euphausiids living much colder environments throughout the year than the Oyashio region, daily C and N losses of *E. pacifica* (2.4-3.0% and

0.3-1.0%, respectively) and *T. inspinata* (3.7-4.3% and 0.6-1.6%, respectively) may be reasonable (Table 5-5).

5-4-3. Chemical composition

The chemical composition of marine zooplankton varies markedly between and within taxonomic groups of animals, depending on not only internal factors (development stage, sex, trophic conditions) but also extrinsic factors (season, geographical distribution, depth of occurrence) (Omori, 1969; Ikeda, 1974; Båmstedt, 1986). For *Euphausia superba* in the Southern Ocean, their body chemical composition (water, ash, C and N) and C : N ratio have been evaluated to change drastically through phytoplankton rich summer; C composition and C : N ratios increase appreciably from 40-41% to 46-48% of *DM* and from 3.5 to 4.5, respectively, during November to January (Ikeda and Mitchell, 1982). At the same time, N composition decreased progressively from 12% to 10% of *DM*. In the present study, the chemical composition of both *E. pacifica* and *Thysanoessa inspinata* determined during phytoplankton bloom season (April) and non-bloom season (March, December) fell into a narrow range (C = 33-36% of *DM*, N = 9.2-9.5, C : N = 3.6-3.9 for *E. pacifica*, and C = 35-37% of *DM*, N = 9.5-10% of *DM*, C : N = 3.7 for *T. inspinata*), showing no appreciable differences (Table 5-4). Despite the fact that *E. superba*, *E. pacifica* and *T. inspinata* are all primary herbivores, the different features in body chemical composition in response to phytoplankton bloom may be interpreted by the magnitude of food shortage they encountered during preceded winter season; e.g. food shortage for *E. pacifica* and *T. inspinata* in the Oyashio region is less severe than *E. superba* in the Southern Ocean.

The present results of the chemical composition of *Euphausia pacifica* and *Thysanoessa inspinata* can be put into a wider perspective if compared with those for euphausiids from various regions of the world oceans (Table 5-7). Among 16 euphausiids compared, the entire ranges of variations were 70-81% of *WM* for water, 8-18% of *DM* for ash, 31-52% of *DM* for C, 9-12% for N and 3.1-5.9 for C : N ratios. For copepods, Båmstedt (1986) compiled a voluminous data from world oceans, and noted a progressive increase in C composition (from 37.2% to 54.4% of *DM*) and C:N ratios (from 3.7 to 9.4) but a progressive decrease in N composition with the increase of latitude (12.6% to 7.8% of *DM*). For euphausiids summarized in Table 5-7, no such the latitudinal trend in the chemical composition is apparent. According to Ikeda (1974), C composition greater than 45% of *DM* accompanied with C:N ratios greater than 5 is an indication of accumulation of lipids in the body. From this viewpoint, accumulation of lipids in the body is unlikely in the most euphausiids including *E. pacifica* and *T. inspinata*, with exceptions of *T. longipes* (C = 50.9% of *DM*, C : N = 5.9) from the Japan Sea and *T. inermis* (C = 51.9% of *DM*, C : N = 5.9) from the Barents Sea. As euphausiids, possible lipid accumulation in *T. longipes* and *T. inermis* may not species-specific characteristics nor related to their cold habitats, since the same *T. inermis* but from Balsfjorden and *E. superba*, *E. crystallorophias* and *E. triacantha* from the coldest habitat in the world oceans did not show any sign of large accumulation of lipids (Table 5-7). Regional variations in the chemical composition are most prevailed in *E. pacifica* from the Oyashio region, North Pacific and Japan Sea.

6. General discussion

6-1. Impact of euphausiid feeding on spring phytoplankton bloom in the Oyashio region

In marine pelagic ecosystems, zooplankton has been known to play integral roles in trophodynamics and biogeochemical cycles of elements (Corner and Davies, 1971). Zooplankton consume phytoplankton directly or indirectly, and regenerate nutrients needed for phytoplankton growth at the same time. Grazing impact of zooplankton on phytoplankton production has been reported as 18-72% in the Kuroshio region (Ikeda and Motoda, 1978), 1-12% at the equator in the central Pacific (Dam et al., 1995), 23-50% in oligotrophic waters (Lenz et al., 1993; Dam et al., 1995; Hernández-León et al., 1999, 2001), and 34-63% in the world oceans (Hernández-León and Ikeda, 2005). Such the estimation for euphausiids only is currently limited to those of Sameoto (1976) and Lasker (1966). According to Sameoto (1976), ingestion of the three euphausiids (*Meganyctiphanes norvegica*, *Thysanoessa inermis*, *T. raschii*) accounted to 1.5% in June-July, 29% in September and 60% in December of primary production in the Gulf of St. Lawrence. Lasker (1966) estimated that ingestion by *Euphausia pacifica* attributed 3% of primary production over the area of North Pacific Ocean.

OECOS cruise to the Oyashio region during phytoplankton bloom season in 2007 (Chapter 4) provided an opportunity to estimate grazing impact of euphausiids on primary production by combining the data of the size-distribution, biomass (Chapter 4) and oxygen consumption (Chapter 5) of euphausiids all collected on short time scales.

Ingestion (I) can be estimated from metabolism (M), growth (G) and assimilation efficiency (A) using a carbon budget equation for a zooplankter (Ikeda and

Motoda, 1978):

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

For a population composed of i individuals of a given sampling date,

$$\sum_{i=1}^s I_i \times A = \sum_{i=1}^s M_i + \sum_{i=1}^s G_i$$

$\sum_{i=1}^s M_i$ for *Euphausia pacifica* and *Thysanoessa inspinata* is calculated from size distribution data (Chapter 4, Fig. 4-5), combined with *BL-DM* relationship ($DM = 0.0012BL^{3.3742}$ for *E. pacifica* and $DM = 0.0043BL^{3.0574}$ for *T. inspinata*) and oxygen consumption-*DM* relationship based on the data during March-April 2007 ($R = 1.281DM^{0.8}$ for *E. pacifica*, and $R = 1.612DM^{0.8}$ for *T. inspinata*). $\sum_{i=1}^s M_i$ ($\mu\text{l O}_2 \text{ m}^{-2} \text{ d}^{-1}$) thus obtained is converted to C unit by multiplying $24 \times 10^{-3} \times 0.97 \times 12/22.4$, 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 litres).

As a basis to estimate $\sum_{i=1}^s G_i$, ΔDM (daily increment in *DM*) of individuals is computed for both euphausiids from differential equations of *BL-DM* relationships as; $DM = 0.0012BL^{3.3742}$, then $\Delta DM = 0.0012 \times 3.3742BL^{(3.3742-1)} \times \Delta BL$ for *Euphausia pacifica*, and $DM = 0.0043BL^{3.0574}$, then $\Delta DM = 0.0043 \times 3.0574BL^{(3.0574-1)} \times \Delta BL$ for *Thysanoessa inspinata*, where $\Delta BL = 0.082$ (mm BL d^{-1} , cf. Fig. 4-6) for the former and $\Delta BL = 0.022$ (mm d^{-1} , cf. Fig. 4-6) for the latter. $\sum_{i=1}^s G_i$ for the population of a given sampling date can be calculated from size distribution data, converted to C unit by multiplying C content (% of *DM*) of each euphausiid (Table 5-4). Population ingestion $\sum_{i=1}^s I_i$ is calculated from $(\sum_{i=1}^s M_i + \sum_{i=1}^s G_i)$ divided by *A* (90%; cf. Lasker 1966).

From C budgets thus calculated (Table 6-1), it becomes clear that over the study period *Euphausia pacifica* allocated 59% of assimilated C into metabolism and 41% into somatic growth, while *Thysanoessa inspinata* allocated 86% assimilated C into metabolism and 14% into somatic growth (Fig. 6-1). Ingestion varied from 5.9 to 131.9 mg C m⁻² d⁻¹ for *E. pacifica*, and from 7.7 to 25.1 mg C m⁻² d⁻¹ for *T. inspinata* (Table 6-1). Primary production during the study period varied from 541 to 2,586 mg C m⁻² d⁻¹ (mean ± 1SD: 1,138 ± 617, Isada et al., unpublished data) (Table 6-1). Ingestion by the two euphausiids [18.4-155.8 mg C m⁻² d⁻¹ (mean ± 1SD: 65.8 ± 51.9), Fig. 6-2] corresponds 1.5-25.2% (mean: ca. 5.8%) (Table 6-1) of primary production, which is near similar to 3% of grazing impact of *E. pacifica* distributing in broad North Pacific estimated by Lasker (1966) and fall within the range of 1.5-60% of the three euphausiids by Sameoto (1976). As is evident in Sameoto (1976), the grazing impact of euphausiids on primary production would vary with season. From this view, the present results would represent seasonal minimum since primary production in the Oyashio region during non-bloom seasons is low (Kasai, 2000) while euphausiids biomass is maintained throughout the year in the Oyashio region (Figs. 3-5 and 6).

6-2. Regeneration of ammonia through excretion by euphausiids

Ammonia is the major form in dissolved nitrogenous excreta by marine zooplankton (Corner and Davies, 1971; Ikeda et al., 2000) and 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 confirmed the importance of zooplankton excretion in nutrient regeneration in the sea; 40-50% in

nutrient-depleted subtropical gyre in the North Pacific (Eppley et al., 1973), 11-44% in the Kuroshio region (Ikeda and Motoda, 1978), 1.5-51% in the upwelling region of N.W. Africa (Fernández, 1981), 36% in the oligotrophic waters off N.W. USA (Jawed, 1973), 43% in the N.W. Mediterranean (Alcaraz et al., 1994), 15-82% in the south Georgia (Southern Ocean) (Atkinson and Whitehouse, 2000, 2001), and 31-36% in the equatorial Pacific (Gaudy et al., 2003). However, information about contribution of ammonia excretion by euphausiids to nitrogen requirements for phytoplankton growth is scarce. As a notable exception, Atkinson and Whitehouse (2001) calculated that ammonia excretion by *Euphausia superba* attributed to 16-50% of nitrogen demand by phytoplankton growth in the eastern area, but only 3-4% in the western area (3-4%) of S. Georgia in summer.

OECOS cruise to the Oyashio region during phytoplankton bloom season in 2007 (Chapter 4) provided an opportunity to estimate possible contribution of ammonia excretion by euphausiids to nitrogen requirements for phytoplankton growth by combining the data of size distribution, biomass (Chapter 4), ammonia excretion consumption (Chapter 5) of euphausiids and primary production (Isada et al., unpublished) all collected on short time scales.

Primary production expressed by C units (Isada et al., unpublished) was converted to N units applying Redfield ratio for phytoplankton (C : N : P = 106 : 16 : 1 by atoms) (Table 6-2). Ammonia excretion by the populations of *Euphausia pacifica* and *Thysanoessa inspinata* at given sampling date was calculated combining the data of size composition (Fig. 4-5) and *BL-DM* relationships ($DM = 0.0012BL^{3.3742}$ for *E. pacifica* and $DM = 0.0043BL^{3.0574}$ for *T. inspinata*) and ammonia excretion rate-*DM* relationships based on the data during March-April 2007 ($E = 0.0221DM^{0.8}$ for *E.*

pacifica, and $E = 0.0533DM^{0.8}$ for *T. inspinata*).

Ammonia excretion thus calculated varied from 0.10 to 2.32 mg N m⁻² d⁻¹ for *Euphausia pacifica* populations, and from 0.38 to 1.24 mg N m⁻² d⁻¹ for *Thysanoessa inspinata* populations (Table 6-2). During the same period, N-demand for primary production was 95-453 mg N m⁻² d⁻¹ (mean ± 1SD: 199 ± 108), of which 0.33-2.94% (mean: 0.84%) was supported by the ammonia-N excreted by the two euphausiids (Fig. 6-2). During the period of this study, nutrient conditions in surface layers were characterized by high NO₃ and low NH₄ concentrations. The range of NO₃ was 10-15 μmol L⁻¹ in March and decreased 3-10 μmol L⁻¹ throughout the incidence of spring phytoplankton bloom in April, while NH₄ remained near stable at 0.5-1.0 μmol L⁻¹ throughout this study (Kuma et al., unpublished). Low contribution of ammonia excretion by the two euphausiids to the need of phytoplankton growth during phytoplankton bloom is expected, since the Oyashio region is known to be nutrient-rich before the onset of the spring phytoplankton bloom (Saito et al., 2002). Considering persistence of the biomass of euphausiids throughout the year in the Oyashio region (Figs. 3-5, 6 and 7), their ammonia excretion would be more important in summer through winter when most nutrients are depleted in the upper layer.

6-3. Life cycle strategies of euphausiids in the Oyashio region

For herbivorous copepods living in the extreme environments such as Arctic and Antarctic waters, three broad life cycle strategies were defined; (1) herbivorous in summer, a short reproductive period and winter diapauses at depth; (2) predominantly omnivorous/detritivorous diet, and extended period of feeding, growth and reproduction and less reliance on diapauses at depth, and (3) overwintering and feeding within sea ice

as early nauplii (Atkinson, 1998). While environmental conditions in the Oyashio region are somewhat mild as compared with Arctic and Antarctic waters, seasonal amplitude of temperatures were from near zero to 16°C (Fig. 3-2) and phytoplankton abundance from 0.4 to >9 mg chlorophyll *a* m⁻³ (cf. Ikeda et al., 2008). Because of the lack of sea ice life cycle strategy (3) is not applicable to the primary herbivorous zooplankton in the Oyashio region. For herbivorous zooplankton in the Oyashio region, life cycle strategies (1) and (2) appear to fit for *Neocalanus* copepods (Kobari and Ikeda, 2000; Kobari et al., 2003) and euphausiids (*Euphausia pacifica*, *Thysanoessa inspinata*, *T. longipes* of this study), respectively.

Neocalanus copepods have annual life cycle and accumulate a large amount of lipids in the body through spring phytoplankton bloom (C : N ratios as high as 7-11, Ikeda et al., 2004; Ikeda, unpublished) (Table 6-3), and sink to depth to enter diapauses then molt to adults for reproduction. Adults cease feeding and entire energy needed for reproduction at depth is supplied from stored lipids in the body. In contrast to *Neocalanus* copepods, *Euphausia pacifica* and *Thysanoessa inspinata* do not store lipids in the body (C : N ratios = 3.5-3.9, Table 5-4) and adults continue to feed even during reproduction season. Metabolic rates in terms of AMR at 10°C determined during the phytoplankton bloom was 1.5-2.0 $\mu\text{l O}_2 (\text{mg DM})^{-0.8} \text{ h}^{-1}$ for *E. pacifica* and *T. inspinata*, which are near 2 times higher than 0.76-0.91 $\mu\text{l O}_2 (\text{mg DM})^{-0.8} \text{ h}^{-1}$ for *Neocalanus cristatus* (C5) and *N. flemingeri* (C5) of the same season (Table 6-3). While chemical composition data of *T. longipes* in the Oyashio region were unable to collect in this study, near stable C : N ratios (5.9-6.9) over the year have been reported on the specimens (>10 mm BL) in the central Japan Sea (Iguchi and Ikeda, 2005), suggesting the similar life cycle strategy to that of *E. pacifica* and *T. inspinata* in the

Oyashio region. Since these euphausiids remain in the surface layer and maintain active swimming instead of entering in diapause at depth during phytoplankton-poor winter season, they have to switch to non-phytoplankton diet such as microzooplankton or zooplankton as has been postulated for *T. raschii* in Balsfjorden, northern Norway (Falk-Petersen, 1981). For *E. superba* inhabiting in Antarctic waters, body shrinkage (utilization of body proteins instead of lipids as an energy source) has been proposed as a new strategy (Ikeda and Dixon, 1982). Falk-Petersen (1981) traced seasonal sequences of body mass (*DM*, protein, lipids) of cohorts of *Meganycitiphanes norvegica*, *T. raschii* and *T. inermis* in Balsfjorden, northern Norway, and observed a significant weight loss of specimens throughout food-limited winter season.

Thus, life cycle strategies of herbivorous euphausiids in cope with winter food shortage are quite different from those of herbivorous copepods (Fig. 6-3). Between herbivorous euphausiids *Euphausia pacifica* and *Thysanoessa inspinata*, the present results also showed clearly that the mode of utilization of spring phytoplankton bloom was species-specific: *E. pacifica* invested largely into growth and *T. inspinata* into reproduction (Table 4-3, Fig. 4-6). While the present study revealed gross features of population biomass, life cycle patterns and metabolism of the dominant euphausiids in the Oyashio region, more studies on the population production and the mechanism of co-existence of multispecies are required in the future for full evaluation of the trophic functions of the euphausiids in the pelagic ecosystem of the Oyashio region.

7. Summery

(1) The present study was made to fill the gap of our knowledge about biological (early larval morphology), ecological (abundance, biomass, life cycle) and physiological characteristics (oxygen consumption, ammonia excretion, chemical composition of the body) of dominant euphausiids (*Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes*) in the Oyashio region as a basis to evaluate their trophic importance in the pelagic ecosystem of this region.

(2) Brood size and egg hatchability of *Thysanoessa inspinata* and *T. longipes* were 76-142 eggs and 81-99%, and 136 eggs and 65%, respectively. In terms of morphology, eggs, Nauplius I, II and Metanauplius larvae of *T. inspinata* and *T. longipes* raised in the laboratory showed no marked differences between the two, excepting for the general sizes (*T. inspinata* < *T. longipes*).

(3) Analysis of time series Bongo net samples (0-1000 m) over 2 years (August 2002 through August 2004) revealed that *Euphausia pacifica* was the most abundant (1,120 individuals m⁻², or 832 mg C m⁻²), followed by *Thysanoessa inspinata* (163 individuals m⁻², or 144 mg C m⁻²) and *T. longipes* (73 individuals m⁻², or 75 mg C m⁻²). *E. pacifica* spawn twice in a year (April – May and August), *T. inspinata* year-round (peak season: March – May), and *T. longipes* in spring (March – May). The maximum size of males and females found were 21 mm and 24 mm, respectively, for *E. pacifica*, 18 mm and 23 mm, respectively, for *T. inspinata*, and 27 mm and 31 mm, respectively, for *T. longipes*. The life spans of *E. pacifica*, *T. inspinata* and *T. longipes* were estimated to be 17-26 months, 17-19 months and 29-31 months, respectively.

(4) During phytoplankton bloom season (9 March – 29 April 2007) where water temperatures ranged from 1.1 to 6.1°C and chlorophyll *a* from 0.02 to 6.3 mg m⁻³, the abundance fluctuated from 41 to 1,040 individuals m⁻² for *Euphausia pacifica* and from 50 to 186 individuals m⁻² for *Thysanoessa inspinata*. Population of both species was composed of one large modal group (14-18 mm *TL* for *E. pacifica*, 17-18 mm *TL* for *T. inspinata*) often accompanied with one small modal group (<11 mm *TL* for both euphausiids). Tracing the progressive increase in the mean sizes of the large modal group, growth rates were estimated to be 0.082 mm day⁻¹ for *E. pacifica* and 0.022 mm day⁻¹ for *T. inspinata*. The difference in the growth rates between the two euphausiids is interpreted as species-specific differences in the allocation of energy ingested into reproduction and somatic growth.

(5) Respiration and ammonia excretion rates were determined on *Euphausia pacifica* and *Thysanoessa inspinata* in March, April and December 2007 at *in situ* temperature (3.8-10.6°C). Respiration rate (*R*: µl O₂ indiv.⁻¹ h⁻¹) and excretion rate (*E*: µg NH₄-N indiv.⁻¹ h⁻¹) were expressed as a function of body dry mass (*DM*: mg): $R = 1.440DM^{0.788}$ and $E = 0.006DM^{1.273}$ for *E. pacifica*; $R = 1.852DM^{0.729}$ and $E = 0.046DM^{0.829}$ for *T. inspinata* (all in $p < 0.01$). The rates standardized to a body size of 1 mg *DM* (*AMR*) and at 10°C, the differences due to sex and season were not significant. In terms of respiration to ammonia excretion ratio (O : N ratio, by atoms), *E. pacifica* exhibited higher ratio (88) than *T. inspinata* (46), suggesting that the proportion of protein in metabolites was relatively less in the former than the latter.

(6) Body chemical composition (water, ash, C, N) of *Euphausia pacifica* and

Thysanoessa inspinata were analyzed in March, April and December 2007. The ranges of water content (% of *WM*), ash (% of *DM*), C (% of *DM*) and N (% of *DM*) were 76.0-77.7, 9.5-12.8, 32.8-36.3 and 9.2-9.5, respectively, for *E. pacifica*, and 75.4-78.2, 9.7-11.5, 35.2-37.1 and 9.5-10.0, respectively, for *T. inspinata*. C : N ratios were 3.6-3.9 for *E. pacifica* and 3.7 for *T. inspinata*. Differences in the composition due to species, sampling season and sex were not significant ($p > 0.05$).

(7) Daily ingestion (*I*) by *Euphausia pacifica* and *Thysanoessa inspinata* populations in the Oyashio region during phytoplankton bloom (7-29 April 2007) was estimated as the sum of daily metabolism (*R*) and daily growth (*G*) assuming an assimilation efficiency to be 0.9 [$I = (R + G) / 0.9$]. *R* was calculated by combining data of size (*BL*) structure, *BL-DM* relationship and *R-DM* relationship and *G* was tracing the increment in modal *BL* and *BL-DM* relationship. Resultant *R* and *G* were expressed by C unit. Over the 22 days, daily *I* thus estimated ranged from 5.9 to 131.9 mg C m⁻² day⁻¹ for *E. pacifica* and from 7.7 to 25.1 mg C m⁻² day⁻¹ for *T. inspinata*, total of which attributed to 1.5-25.2% of primary production (mean 5.8%).

(8) Daily ammonia-N regeneration by *Euphausia pacifica* and *Thysanoessa inspinata* populations was calculated during phytoplankton bloom (7-29 April 2007) by combining data of size (*BL*) structure, *BL-DM* relationship and *E-DM* relationship. Over the 22 days, daily N regeneration ranged from 0.10 to 2.32 mg N m⁻² day⁻¹ for *E. pacifica* and from 0.38 to 1.24 mg N m⁻² day⁻¹ for *T. inspinata*, total of which attributed to 0.33-2.94% of primary production (mean 0.84%).

(9) Physiological and ecological characteristics of the euphausiids (*Euphausia pacifica* and *Thysanoessa inspinata*) in the Oyashio region are highlighted from the comparison with *Neocalanus* copepods in the same Oyashio region. Both euphausiids and *Neocalanus* copepods are similar in terms of primary herbivores, euphausiids are different from *Neocalanus* in that higher metabolic rates enabling active forage, less depending energy reserve and utilizing phytoplankton bloom for rapid somatic growth/reproduction (not lipid accumulation). In contrast, *Neocalanus* copepods are characterized by less active swimming (lower metabolic rates), large capacity of energy storage in the form of lipids, energy saving life history trait (diapauses) yet strong dependence on phytoplankton bloom for large accumulation of lipids in the body.

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Table 2-1. Brood size and hatching success of eggs of *Thysanoessa inspinata* and *T. longipes* from the Oyashio region observed at 3°C.

Experimental no.	Species	Brood size	Hatching success (%)
1	<i>Thysanoessa inspinata</i>	112	85.7
2	<i>T. inspinata</i>	76	98.7
3	<i>T. inspinata</i>	142	81.0
4	<i>T. longipes</i>	136	64.7

Table 2-2. Stage duration (days) of eggs, nauplius I and nauplius II of *Thysanoessa inspinata* and *T. longipes* observed at 3°C. Values are mean \pm 1SD. The number of observations is in parentheses.

Stage	<i>Thysanoessa inspinata</i>	<i>Thysanoessa longipes</i>
Egg	3.0 \pm 0.0 (330)	3.0 \pm 0.0 (136)
Nauplius I	4.7 \pm 0.3 (286)	4.5 \pm 0.5 (88)
Nauplius II	7.8 \pm 0.6 (265)	8.5 \pm 0.5 (71)

Table 2-3. Differences in the morphology of NII of *Thysanoessa inspinata* between Gómez-Gutiérrez (2003) and this study.

Body part	Gómez-Gutiérrez (2003)	This study
Posterior body margin	Two broad spines and four small spine	Only two broad spines
Antennule	Two long setae and one subterminal seta	Two long setae and one terminal spine, and one subterminal seta
Antenna	Endopod: two setae and one small spine, and one subterminal seta Exopod: five setae	Endopod: two setae and one subterminal seta Exopod: four setae and one small seta (five setae)
Mandible	Endopod: two setae and one terminal spine Exopod: three setae and one terminal spine	Endopod: three setae Exopod: three setae

Table 2-4. Egg diameter and total length of adults, nauplius I, II and metanauplius of euphausiids from wild samples or laboratory-raised. Values are mean \pm 1SD (mm) with its range and replicate number are in parentheses. *Nauplius I and II were combined. Data on total length range of adults are from Brinton et al. (2000).

Species	Habitat	Adults	Eggs	Nauplius I	Nauplius II	Metanauplius	References
<i>Thysanoessa inspinata</i>	Site H (laboratory-raised)	12-18	0.36 \pm 0.01 (0.33-0.38, 88)	0.35 \pm 0.02 (0.30-0.42, 52)	0.45 \pm 0.02 (0.41-0.48, 24)	0.52 \pm 0.03 (0.43-0.61, 43)	This study
<i>Thysanoessa longipes</i>	Site H (laboratory-raised)	18-30	0.39 \pm 0.02 (0.35-0.44, 34)	0.39 \pm 0.02 (0.35-0.45, 22)	0.47 \pm 0.02 (0.45-0.51, 9)	0.55 \pm 0.03 (0.51-0.60, 14)	This study
<i>Euphausia pacifica</i>	Toyama Bay (wild)	11-25	-	0.45 \pm 0.02 (0.43-0.48, 6)	0.46 \pm 0.02 (0.42-0.50, 35)	0.48 \pm 0.03 (0.42-0.52, 54)	Kim and Ikeda (unpublished)
<i>Euphausia pacifica</i>	Yellow Sea (wild)	11-25	0.58 \pm 0.03 (0.50-0.68, 326)	0.38 \pm 0.03 (0.35-0.45, 13)	0.52 \pm 0.01 (0.50-0.53, 7)	0.58 \pm 0.05 (0.45-0.70, 239)	Suh et al. (1993)
<i>Euphausia nana</i>	Suruga Bay Sagami Bay (wild)	7-8.5	0.47 \pm 0.04 (0.40-0.54, 281)	0.44 \pm 0.02 (0.42-0.48, 6)	0.44 \pm 0.02 (0.40-0.47, 34)	0.46 \pm 0.01 (0.43-0.48, 14)	Hirota et al. (1984)
<i>Euphausia superba</i>	Prydz Bay (laboratory-raised)	42-65	0.57 \pm 0.01 (10)	0.70 \pm 0.02 (5)	0.78 \pm 0.04 (4)	0.91 \pm 0.02 (5)	Ikeda (1984)
<i>Euphausia crystallorophias</i>	Prydz Bay (laboratory-raised)	23-35	0.60 \pm 0.02 (6)	0.58 \pm 0.02* (6)	0.58 \pm 0.02* (6)	0.69 \pm 0.05 (7)	Ikeda (1986)
<i>Thysanoessa spinifera</i>	Barkley Sound (wild)	16-25	0.41 \pm 0.003 (185)	0.46 \pm 0.005 (142)	0.49 \pm 0.004 (196)	0.54 \pm 0.003 (161)	Summers (1993)
	Barkley Sound (laboratory-raised)		0.42 (10)	0.49 (0.38-0.56)	0.54 (0.38-0.54)	0.56 (0.49-0.59)	Summers (1993)

Table 3-1. Zooplankton sampling data at Site H in the Oyashio region during August 2002-August 2004. Samples were collected by oblique hauls of Bongo nets from 0-1000 m water column.

Year	Date	Time of day
2002	9 Aug.	08:30-09:30
	10 Aug.	00:56-02:06
	9 Oct.	03:10-04:35, 12:46-14:10
2003	11 Feb.	17:22-19:05
	13 Mar.	02:06-03:48
	11 May	11:12-12:40
	12 May	00:30-02:10
	21 May	15:30-16:50, 21:28-23:00
	4 June	16:00-17:15
	7 June	06:31-07:49
	15 June	08:21-09:47
	28 June	14:45-16:15
	23 Aug.	23:57-01:17
	5 Oct.	06:40-07:50
2004	17 Dec.	12:16-14:00
	8 Feb.	12:45-14:15
	10 Mar.	14:18-16:00
	15 Mar.	00:35-02:02
	9 May	10:44-11:17
	26 June	09:15-10:55
	22 Aug.	06:37-08:30

Table 3-2. Regional comparison of the abundance (indiv. m⁻²) and biomass (mg C m⁻²) of the euphausiid *Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes* from waters around Japan. Values are annual or biannual means.

Species	Region	Abundance (indiv. m ⁻²)	Biomass (mg C m ⁻²)	References
<i>Euphausia pacifica</i>	Oyashio region	1120	832	This study
	southeastern Hokkaido	1570	381	Taki (2006, 2007)
	Toyama Bay, Japan Sea	5500	1090	Iguchi <i>et al.</i> (1993) Iguchi and Ikeda (1999)
<i>Thysanoessa inspinata</i>	Oyashio region	163	144	This study
	southeastern Hokkaido	146		Taki (2007)
<i>Thysanoessa longipes</i>	Oyashio region	72.6	74.6	This study
	southeastern Hokkaido	24.0		Taki (2007)

Table 3-3. Regional comparison of maximum body size, spawning seasons and life span of the euphausiid *Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes* in the North Pacific regions.

Species	Location	Maximum size (<i>TL</i> : mm)	Spawning season	Life span	References
<i>Euphausia pacifica</i>	Oyashio region	♂: 21 ♀: 24	Apr.-May, Aug.-Sep.	17-26 months	This study
	Toyama Bay (Japan Sea)	♂: 22 ♀: 23	Feb. - Apr.	< 21 months	Iguchi <i>et al.</i> (1993)
	off Oregon	♂,♀: 22-24	All season	12 months	Smiles and Pearcy (1971)
	off southern California	♂,♀ : 21	All season	8-12 months	Brinton (1976)
	off northeastern Japan	♂,♀ : 19-20	Apr.-May, Aug.-Oct.	24-28 months	Taki (2004)
<i>Thysanoessa inspinata</i>	Oyashio region	♂: 18 ♀: 23	All season (Mar.-Apr.)	17-19 months	This study
	off Kuril Islands	♂: 23 ♀: 23	May	2 years	Kuznetsova (1980, 1994)
<i>Thysanoessa longipes</i>	Oyashio region	♂: 27 ♀: 31	Mar.-May	29-31 months	This study
	Yamato Rise (Japan Sea)	♂: 25 ♀: 32	Apr.-May	3 years	Iguchi and Ikeda (2004)

Table 4-1. Euphausiid sampling data in the Oyashio region during 9 March to 29 April 2007. Samples were collected by oblique hauls of Bongo nets from 0-200 m water column at night.

Date	Time of day	Volume of water filtered (m ³)
9 Mar. 2007	21:05-21:27	435.2
14 Mar. 2007	03:43-04:07	580.4
7 Apr. 2007	21:55-22:20	632.4
8 Apr. 2007	21:15-21:42	673.0
10 Apr. 2007	20:43-21:17	773.2
12 Apr. 2007	21:51-22:17	643.8
17 Apr. 2007	19:53-20:24	801.3
20 Apr. 2007	21:24-21:51	699.1
25 Apr. 2007	21:40-22:07	723.5
29 Apr. 2007	23:41-00:09	628.7

Table 4-2. Relationships between the abundance (indiv. m⁻²: 0-200 m) and environmental parameters (temperature [Temp.: °C] and chlorophyll *a* [Chl. *a*: mg m⁻²], both integrated mean over 0-100 m) of the two euphausiids dominated in the Oyashio region during 9 March to 29 April 2007. *n* = 10. *: *p* < 0.05. NS: not significant.

Euphausiids	Correlation coefficient (<i>r</i>)	
	Abundance vs. Temp.	Abundance vs. Chl. <i>a</i>
<i>Euphausia pacifica</i>	-0.638*	0.687*
<i>Thysanoessa inspinata</i>	-0.679*	0.257 ^{NS}

Table 4-3. Mean abundance (indiv. m⁻²) of juveniles, adult males and adult females (with and without spermatophores) of the two euphausiids dominated in the Oyashio region during 9 March to 29 April 2007. Values are mean \pm 1SD. Percentages to the total are in parentheses.

Euphausiids	Juveniles	Males	Females without spermatophores	Females with spermatophores
<i>Euphausia pacifica</i>	12.1 \pm 7.7 (8.3)	150.6 \pm 172.1 (41.9)	162.1 \pm 196.5 (44.8)	10.4 \pm 17.0 (4.9)
<i>Thysanoessa inspinata</i>	4.8 \pm 3.7 (5.3)	51.1 \pm 28.1 (44.6)	6.3 \pm 4.2 (6.5)	48.3 \pm 27.7 (43.6)

Table 4-4. Growth rates (mm *TL* day⁻¹) of *Euphausia pacifica* and *Thysanoessa* spp. being observed at various subarctic regions during their growing seasons of the year.

Euphausiids	Location	Period	Age	Temp. (°C)	Growth rate (mm <i>TL</i> day ⁻¹)	Reference
<i>Euphausia pacifica</i>	Oyashio region	Mar. - Apr.	1+	1-6	0.082	This study
<i>Thysanoessa inspinata</i>			1+		0.022	
<i>Thysanoessa inermis</i>	North of Iceland	Apr. - July	0+	2-4	0.08	Astthorsson and Gislason (1997)
			1+		0.07	
<i>Euphausia pacifica</i>	Toyama Bay (Japan Sea)	Apr. - June	0+	1-18	0.102	Iguchi et al. (1993)
		Feb. - Apr.	1+	1-10	0.076	
<i>Euphausia pacifica</i>	Northeastern Japan	Mar. - May	1+	<5	0.056	Taki and Ogishima (1997)
<i>Euphausia pacifica</i>	off Oregon coast	Jan. - Mar.	1+	-	0.107	Smiles and Percy (1971)
		Mar. - June	1+		0.067	
<i>Thysanoessa inermis</i>	northern Gulf of Alaska	May	1+	~5	0.123	Pinchuk and Hopcroft (2007)
<i>Thysanoessa spinifera</i>			1+		0.091	
<i>Euphausia pacifica</i>			1+		< 0.07	

Table 5-1. Correlation between $AMR-O_2$ ($\mu\text{l O}_2 [\text{mg DM}]^{-0.8} \text{h}^{-1}$) or $AMR-NH_4-N$ ($\mu\text{g NH}_4-N [\text{mg DM}]^{-0.8} \text{h}^{-1}$) and the environmental parameters (sea surface temperature [SST] 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. 5-2.

Euphausiids	AMRs	Correlation coefficient (<i>r</i>)	
		SST (°C)	Chl. <i>a</i>
<i>Euphausia pacifica</i>	$AMR-O_2$	-0.173 ^{NS}	0.454 ^{NS}
	$AMR-NH_4-N$	0.648 ^{NS}	-0.273 ^{NS}
<i>Thysanoessa inspinata</i>	$AMR-O_2$	0.460 ^{NS}	-0.097 ^{NS}
	$AMR-NH_4-N$	-0.073 ^{NS}	0.440 ^{NS}

Table 5-2. Dry mass (*DM*), oxygen consumption rate (*R*) and ammonia excretion rate (*E*) of *Euphausia pacifica* and *Thysanoessa inspinata* as determined at near *in situ* temperature in the Oyashio region in March, April and December 2007. *n* = number of replicates. Values are mean \pm 1SD. Ranges are in the parentheses.

Species	Date	Temp. (°C)	<i>n</i>	<i>DM</i> (mg indiv. ⁻¹)	<i>R</i> (μ l O ₂ indiv. ⁻¹ h ⁻¹)	<i>E</i> (μ g NH ₄ -N indiv. ⁻¹ h ⁻¹)
<i>Euphausia pacifica</i>	Mar.	4.0-6.0	7	6.60 \pm 1.40 (4.69-8.24)	4.32 \pm 0.80 (3.42-5.42)	0.11 \pm 0.02 (0.08-0.15)
	Apr.	3.8-6.2	51	13.15 \pm 5.02 (3.87-23.80)	9.99 \pm 3.29 (3.83-18.19)	0.18 \pm 0.15 (0.01-0.57)
	Dec.	10.3-10.6	5	11.77 \pm 1.21 (10.69-13.64)	8.60 \pm 1.18 (7.12-10.42)	0.61 \pm 0.18 (0.42-0.90)
<i>Thysanoessa inspinata</i>	Mar.	4.0-7.0	14	8.32 \pm 4.99 (3.11-23.82)	8.30 \pm 5.38 (3.65-25.49)	0.45 \pm 0.48 (0.08-2.02)
	Apr.	3.8-7.8	54	9.79 \pm 4.76 (2.16-22.49)	9.65 \pm 4.25 (3.77-19.74)	0.28 \pm 0.21 (0.04-0.98)
	Dec.	10.3-10.4	10	13.08 \pm 3.49 (7.60-17.94)	15.00 \pm 3.30 (8.70-21.05)	0.98 \pm 0.27 (0.63-1.50)

Table 5-3. O:N ratio of *Euphausia pacifica* and *Thysanoessa inspinata* in the Oyashio region in March, April and December 2007. n = number of replicates. Values are mean \pm 1SD. Ranges are shown in the parentheses. Results of one-way ANOVA and post-hoc test are also shown. Any season not connected by the same underline are significantly different ($p < 0.01$).

Date	<i>Euphausia pacifica</i>		<i>Thysanoessa inspinata</i>	
	n	O:N ratio (by atoms)	n	O:N ratio (by atoms)
Mar.	7	49.0 \pm 14.3 (28.8-67.0)	14	27.6 \pm 11.2 (13.8-52.2)
Apr.	39	87.5 \pm 48.5 (26.1-192.3)	46	46.0 \pm 21.3 (10.2-96.4)
Dec.	5	18.6 \pm 4.4 (14.4-25.6)	10	19.8 \pm 4.1 (15.2-26.6)
Grand mean	3	51.7 \pm 34.5	3	31.1 \pm 13.5
one-way ANOVA	df	2		2
	F	7.07		8.76
	p	< 0.01		< 0.01
	Fisher's PLSD	<u>Dec.</u> <u>Mar.</u> <u>Apr.</u>		<u>Dec.</u> <u>Mar.</u> <u>Apr.</u>

Table 5-4. Water content, ash, carbon (C) and nitrogen (N), and C:N ratio (by mass) of *Euphausia pacifica* and *Thysanoessa inspinata* in the Oyashio region in March, April and December 2007. Water contents are mean \pm 1SD, the number of replicates (*n*) and ranges in parentheses. *WM* = wet mass, *DM* = dry mass.

Species	Date	<i>n</i>	Water (% <i>WM</i>)	Ash (% <i>DM</i>)	C (% <i>DM</i>)	N (% <i>DM</i>)	C:N ratio
<i>Euphausia pacifica</i>	Mar.	7	77.74 \pm 0.92 (77.00-79.52)	12.82	34.40	9.52	3.62
	Apr.	51	76.05 \pm 4.92 (53.59-88.74)	9.68	36.25	9.27	3.91
	Dec.	5	76.73 \pm 0.59 (75.98-77.46)	9.46	32.81	9.19	3.58
	Grand mean	3	76.84 \pm 0.85	10.65 \pm 1.88	34.49 \pm 1.72	9.33 \pm 0.17	3.70 \pm 0.18
<i>Thysanoessa inspinata</i>	Mar.	14	78.19 \pm 1.31 (75.91-79.94)	11.48	36.59	9.93	3.69
	Apr.	54	78.10 \pm 5.03 (60.22-90.44)	10.29	37.10	10.00	3.71
	Dec.	10	75.35 \pm 1.27 (73.20-76.90)	9.74	35.15	9.54	3.69
	Grand mean	3	77.21 \pm 1.61	10.50 \pm 0.89	36.28 \pm 1.01	9.82 \pm 0.25	3.70 \pm 0.01

Table 5-5. Respiration and ammonia excretion rates at 10°C expressed as Adjusted Metabolic Rates (AMR), and daily body C and N losses of *Euphausia pacifica* and *Thysanoessa inspinata* in the Oyashio region during March, April and December 2007. n = number of replicates. Values are mean \pm 1SD. Ranges are shown in the parentheses. Results of one-way ANOVA and post-hoc test are also shown. Any season not connected by the same underline are significantly different ($p < 0.01$). *NS*: not significant.

Species	Date	n	AMR at 10°C		Metabolic loss	
			$\mu\text{l O}_2$ (mg DM) ^{-0.8} h ⁻¹	$\mu\text{g NH}_4\text{-N}$ (mg DM) ^{-0.8} h ⁻¹	% body C d ⁻¹	% body N d ⁻¹
<i>Euphausia pacifica</i>	Mar.	7	1.34 \pm 0.12 (1.17-1.52)	0.037 \pm 0.014 (0.026-0.059)	2.39 \pm 0.26 (2.07-2.86)	0.373 \pm 0.150 (0.2515-0.604)
	Apr.	51	1.87 \pm 0.47 (1.04-3.18)	0.030 \pm 0.026 (0.003-0.112)	2.95 \pm 0.88 (1.48-6.10)	0.259 \pm 0.222 (0.032-0.997)
	Dec.	5	1.17 \pm 0.15 (1.01-1.39)	0.082 \pm 0.024 (0.058-0.120)	2.65 \pm 0.35 (2.21-3.10)	1.040 \pm 0.308 (0.731-1.491)
	Grand mean	3	1.46 \pm 0.37	0.050 \pm 0.028	2.66 \pm 0.28	0.557 \pm 0.422
one-way ANOVA	<i>df</i>		2	2	2	2
	<i>F</i>		9.55	9.99	1.59	28.03
	<i>p</i>		<0.01	<0.01	0.21 (<i>NS</i>)	<0.01
	Fisher's PLSD		<u>Dec.</u> <u>Mar.</u> <u>Apr.</u>	<u>Apr.</u> <u>Mar.</u> <u>Dec.</u>		<u>Apr.</u> <u>Mar.</u> <u>Dec.</u>
<i>Thysanoessa inspinata</i>	Mar.	14	1.95 \pm 0.40 (1.53-3.08)	0.091 \pm 0.043 (0.044-0.197)	3.67 \pm 0.82 (2.75-6.27)	0.937 \pm 0.382 (0.484-1.704)
	Apr.	54	2.28 \pm 0.76 (0.90-4.70)	0.067 \pm 0.042 (0.007-0.178)	3.91 \pm 1.60 (1.30-9.74)	0.645 \pm 0.426 (0.052-1.914)
	Dec.	10	1.90 \pm 0.30 (1.38-2.32)	0.125 \pm 0.028 (0.082-0.168)	4.26 \pm 0.77 (2.92-5.34)	1.558 \pm 0.385 (1.022-2.243)
	Grand mean	3	2.04 \pm 0.21	0.094 \pm 0.029	3.95 \pm 0.30	1.047 \pm 0.466
one-way ANOVA	<i>df</i>		2	2	2	2
	<i>F</i>		2.38	9.39	0.51	21.24
	<i>p</i>		0.10 (<i>NS</i>)	< 0.01	0.60 (<i>NS</i>)	< 0.01
	Fisher's PLSD			<u>Apr.</u> <u>Mar.</u> <u>Dec.</u>		<u>Apr.</u> <u>Mar.</u> <u>Dec.</u>

Table 5-6. Comparison on the metabolic O:N ratios of euphausiids.

Species	Region	O:N ratio (by atoms)	References
<i>Euphausia pacifica</i>	Oyashio region	18.6-87.5	This study
<i>Thysanoessa inspinata</i>		19.8-46.0	
<i>Euphausia lucens</i>	Southern Benguela current	10.3 ± 2.2	Stuart (1986)
<i>E. superba</i>	Southern Ocean	30.3-34.6 (November) 58.7-103.0 (December) 15.9-17.5 (January)	Ikeda and Kirkwood (1989) Ikeda and Bruce (1986) Ikeda and Mitchell (1982)
<i>Nyctiphanes australis</i>	Western Cook Strait, New Zealand	27.1 ± 12.7	James and Wilkinson (1988)
<i>Meganyctiphanes norvegica</i>	Mediterranean Sea	4.8 (winter)-12.1 (spring)	Mayzaud (1973)
	Ligurian Sea, Clyde Sea, and Kattegat	12-45	Saborowski et al. (2002)

Table 5-7. Comparison on contents of water, ash, carbon (C) and nitrogen (N) and C : N ratio of euphausiids from various regions. WM= wet mass, DM= dry mass.

Species	Region	Water (% WM)	Ash (% DM)	C (% DM)	N (% DM)	C:N ratio (by mass)	References
<i>Euphausia pacifica</i>	Oyashio region	76.84 ± 0.85	10.65 ± 1.88	34.49 ± 1.72	9.33 ± 0.17	3.70 ± 0.18	This study
	North Pacific	-	8.25 ± 0.35	39.15 ± 0.64	10.4 ± 0.42	3.76	Omori (1969)
	Japan Sea	78.45 ± 1.78	12.8 ± 0.60	43.57 ± 1.81	11.07 ± 0.74	3.94	Iguchi and Ikeda (1998)
<i>E. superba</i>	Antarctic waters	81.23 ± 0.57	17.37 ± 0.60	40.51 ± 0.32	11.89 ± 0.08	3.41	Ikeda and Kirkwood (1989)
<i>E. crystallorophias</i>	Antarctic waters	76.65 ± 1.63	14.0 ± 0.85	42.92 ± 2.91	11.89 ± 0.66	3.61	
<i>E. tricantha</i>	Antarctic waters	74.1 ± 1.5	10.7	47.3	10.7	4.42	Ikeda (1988)
<i>E. krohnii</i>	Northern Mediterranean Sea	-	-	31.1	10.0	3.1	Gorsky et al. (1988)
<i>Thysanoessa inspinata</i>	Oyashio region	77.21 ± 1.61	10.50 ± 0.89	36.28 ± 1.01	9.82 ± 0.25	3.70±0.01	This study
<i>T. longipes</i>	Japan Sea	69.8	9.4	50.9	8.6	5.92	Iguchi and Ikeda (2005)
<i>T. inermis</i>	Balsfjorden Norway	78.5 ± 5.0	17.9 ± 0.62	43.92 ± 2.81	9.59 ± 1.75	4.58	Hopkins et al. (1978)
	Barents Sea	70.95 ± 4.45	9.25 ± 1.48	51.89 ± 4.99	8.74 ± 1.84	5.94	Ikeda and Skjoldal (1989)
<i>Tessarabrachion oculatum</i>	North Pacific	-	8.1	47.2	10.0	4.72	Omori (1969)
<i>Meganyctiphanes norvegica</i>	Northern Mediterranean Sea	-	-	36.8	11	3.4	Gorsky et al. (1988)
<i>Nematoscelis difficilis</i>	North Pacific	-	-	40.68	10.69	3.81	Nemoto et al. (1972)
<i>N. atlantica</i>	(41°00'N,	-	-	42.89 ± 1.39	11.34 ± 0.41	3.78	
<i>N. Microps</i>	165°07'E)	-	-	43.66 ± 2.61	10.59 ± 0.65	4.12	

Table 6-1. 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 are mg C m⁻² d⁻¹.

Date in 2007	(1) Primary production	(2) Metabolism		(3) Growth		(4) Ingestion ([2]+[3])/ 0.9		(5) Ingestion
		<i>E. pacifica</i>	<i>T. inspinata</i>	<i>E. pacifica</i>	<i>T. inspinata</i>	<i>E. pacifica</i>	<i>T. inspinata</i>	<i>E. pacifica</i> + <i>T. inspinata</i> % of (1)
7 Apr.	2,586	69.9	18.5	48.8	3.0	131.9	23.9	6.0
8 Apr.	541	66.0	9.4	45.9	1.5	124.3	12.1	25.2
10 Apr.	1,067	3.1	19.5	2.1	3.1	5.9	25.1	2.9
12 Apr.	808	21.7	14.3	15.0	2.3	40.7	18.4	7.3
17 Apr.	988	16.5	6.0	11.3	0.9	30.9	7.7	3.9
20 Apr.	924	21.9	14.7	15.0	2.3	40.9	18.9	6.5
25 Apr.	980	8.9	8.5	6.1	1.4	16.7	10.9	2.8
29 Apr.	1,214	3.4	9.3	2.4	1.5	6.5	11.9	1.5
Total (7-29 Apr.)	21,553	416.5	251.6	287.2	39.9	781.9	323.9	5.1

Table 6-2. 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., unpublished) expressed by C unit were converted to N unit based on Redfield ratio (C:N:P=106:16:1 by atoms). All values are mg N m⁻² d⁻¹.

Date in 2007	(1) Primary production	(2) Ammonium excretion		(3) Ammonium excretion
		<i>E. pacifica</i>	<i>T. inspinata</i>	<i>E. pacifica</i> + <i>T. inspinata</i> % of (1)
7 Apr.	453	2.32	1.18	0.77
8 Apr.	95	2.19	0.60	2.94
10 Apr.	187	0.10	1.24	0.72
12 Apr.	142	0.72	0.91	1.15
17 Apr.	173	0.55	0.38	0.54
20 Apr.	162	0.73	0.93	1.03
25 Apr.	172	0.30	0.54	0.49
29 Apr.	213	0.11	0.59	0.33
Total (7-29 Apr.)	3,780	13.8	16.0	0.79

Table 6-3. Comparison of adjusted metabolic rates *AMR* at 10°C and body chemical composition between herbivorous zooplankton (euphausiids and *Neocalanus* copepods) during spring phytoplankton bloom in the Oyashio region in 2007.

Species		<i>AMR</i> at 10°C	Body chemical composition			References
			$\mu\text{l O}_2 (\text{mg DM})^{-0.8} \text{ h}^{-1}$	C (% <i>DM</i>)	N (% <i>DM</i>)	
Euphausiids	<i>Euphausia pacifica</i>	1.46 ± 0.37	34.5 ± 1.7	9.3 ± 0.2	3.7 ± 0.2	This study
	<i>Thysanoessa inspinata</i>	2.04 ± 0.21	36.3 ± 1.0	9.8 ± 0.3	3.7 ± 0.01	
Copepods	<i>Neocalanus cristatus</i> (C5)	0.76 ± 0.10	62.6 ± 0.4	6.7 ± 0.1	9.6 ± 0.3	Ikeda unpublished
	<i>N. flemingeri</i> (C5)	0.91 ± 0.10	62.7 ± 1.8	6.3 ± 0.4	10.1 ± 1.1	

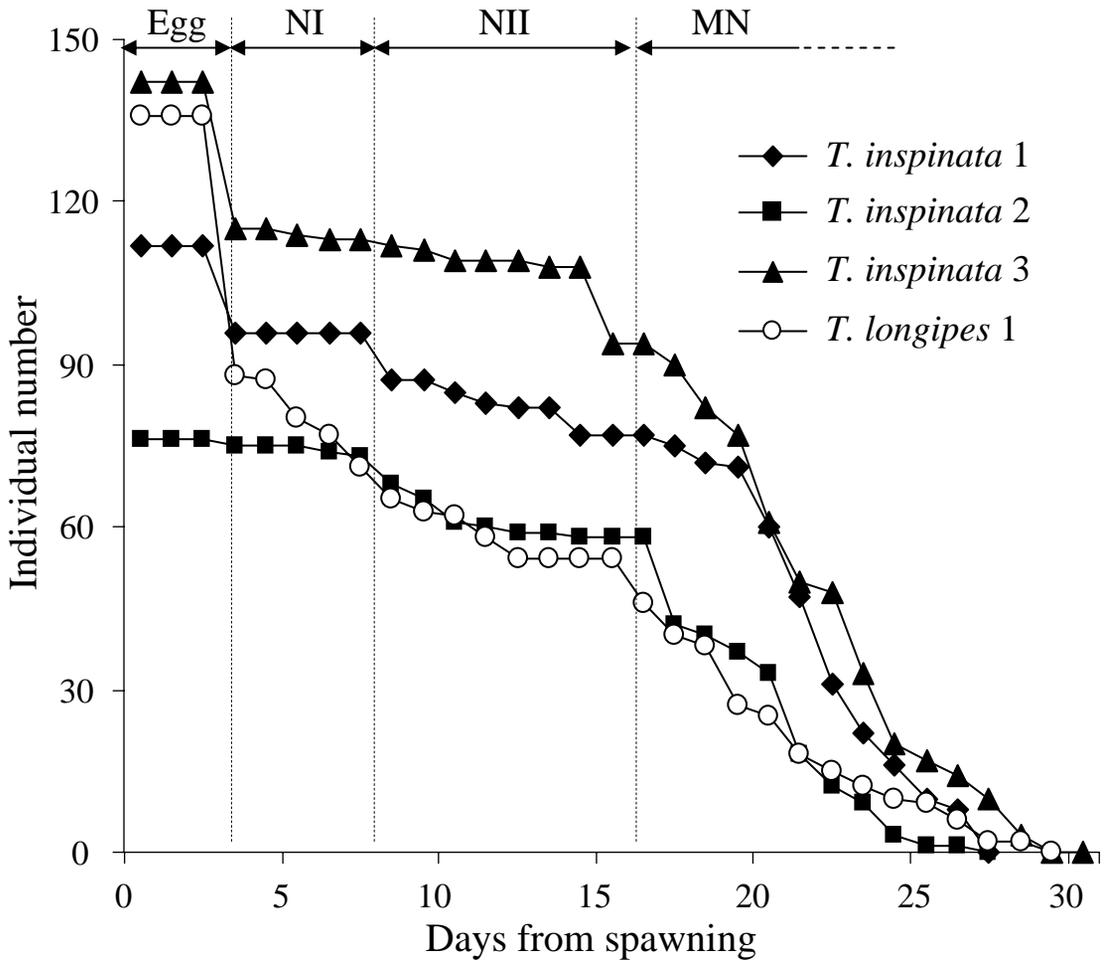


Fig. 2-1. Survivals of *Thysanoessa inspinata* ($n=3$) and *T. longipes* ($n=1$) reared in the laboratory. Approximate duration of eggs, nauplius I (NI), nauplius II (NII) and metanauplius (MN) are superimposed (hatched vertical line).

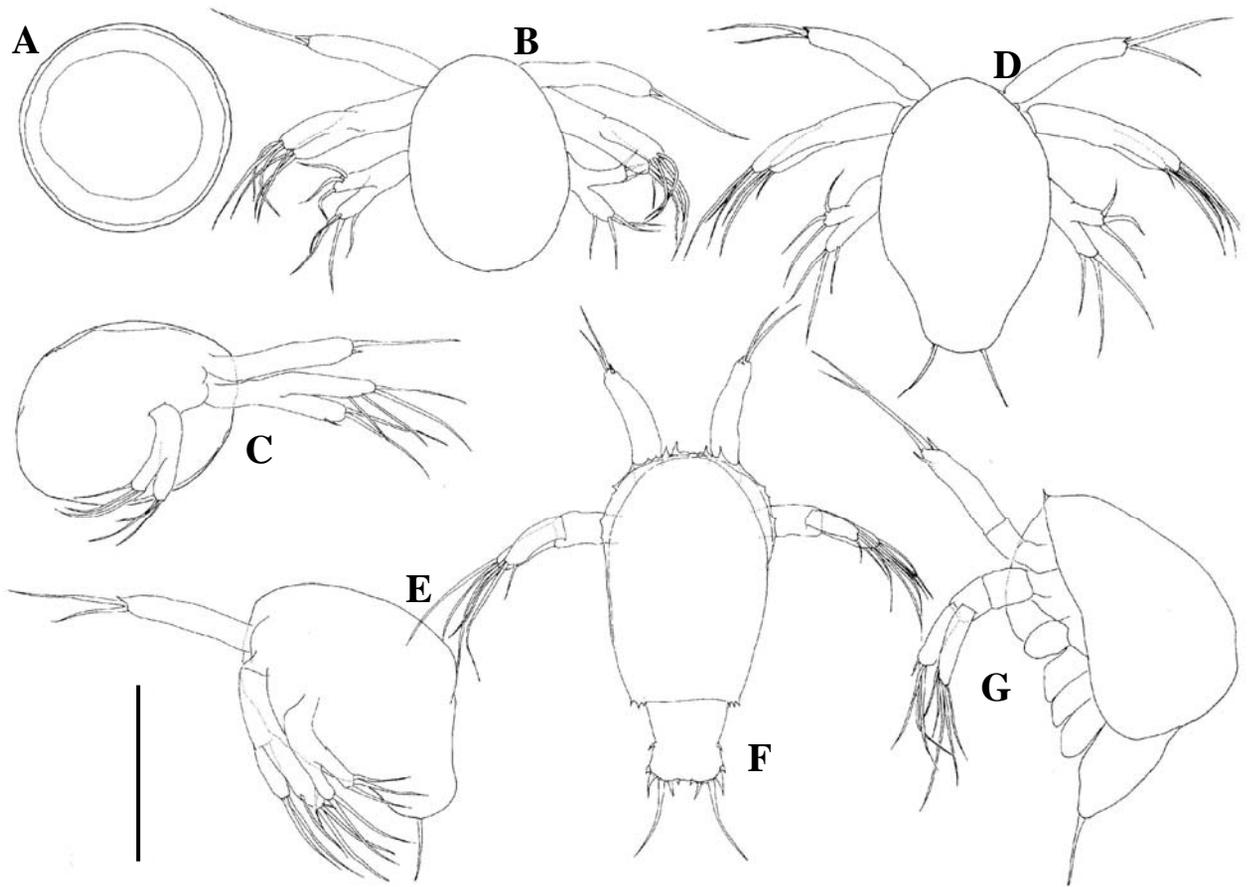


Fig 2-2. *Thysanoessa inspinata*. Egg (A); NI in dorsal (B), lateral (C); NII in dorsal (D), lateral (E); MN in dorsal (F), lateral (G). Scale bar: 0.3 mm.

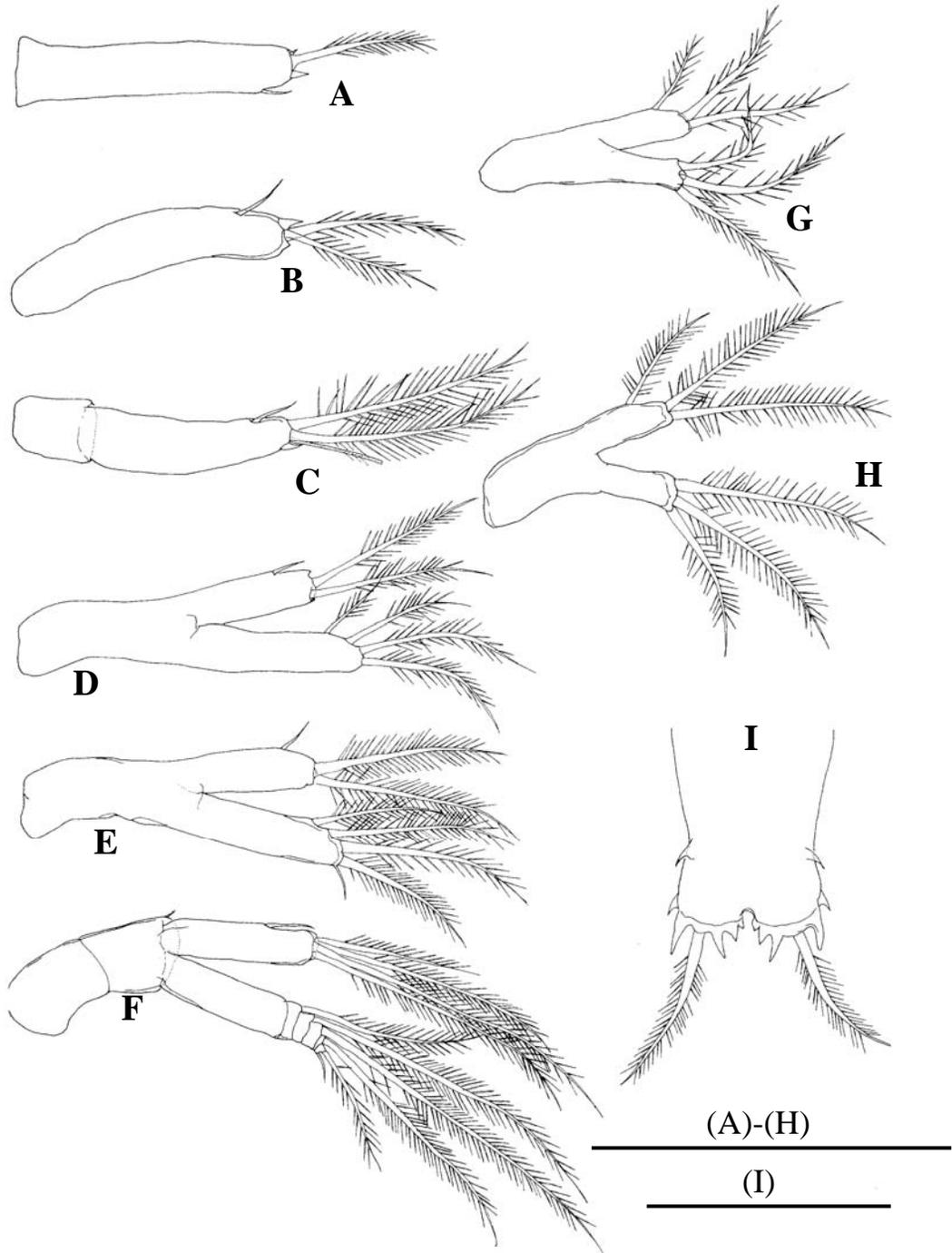


Fig. 2-3. *Thysanoessa inspinata*. Antennule of NI (A), NII (B) and MN (C). Antenna of NI (D), NII (E) and MN (F). Mandible of NI (G) and NII (H). Telson of MN (I). Scale bars: 0.1 mm

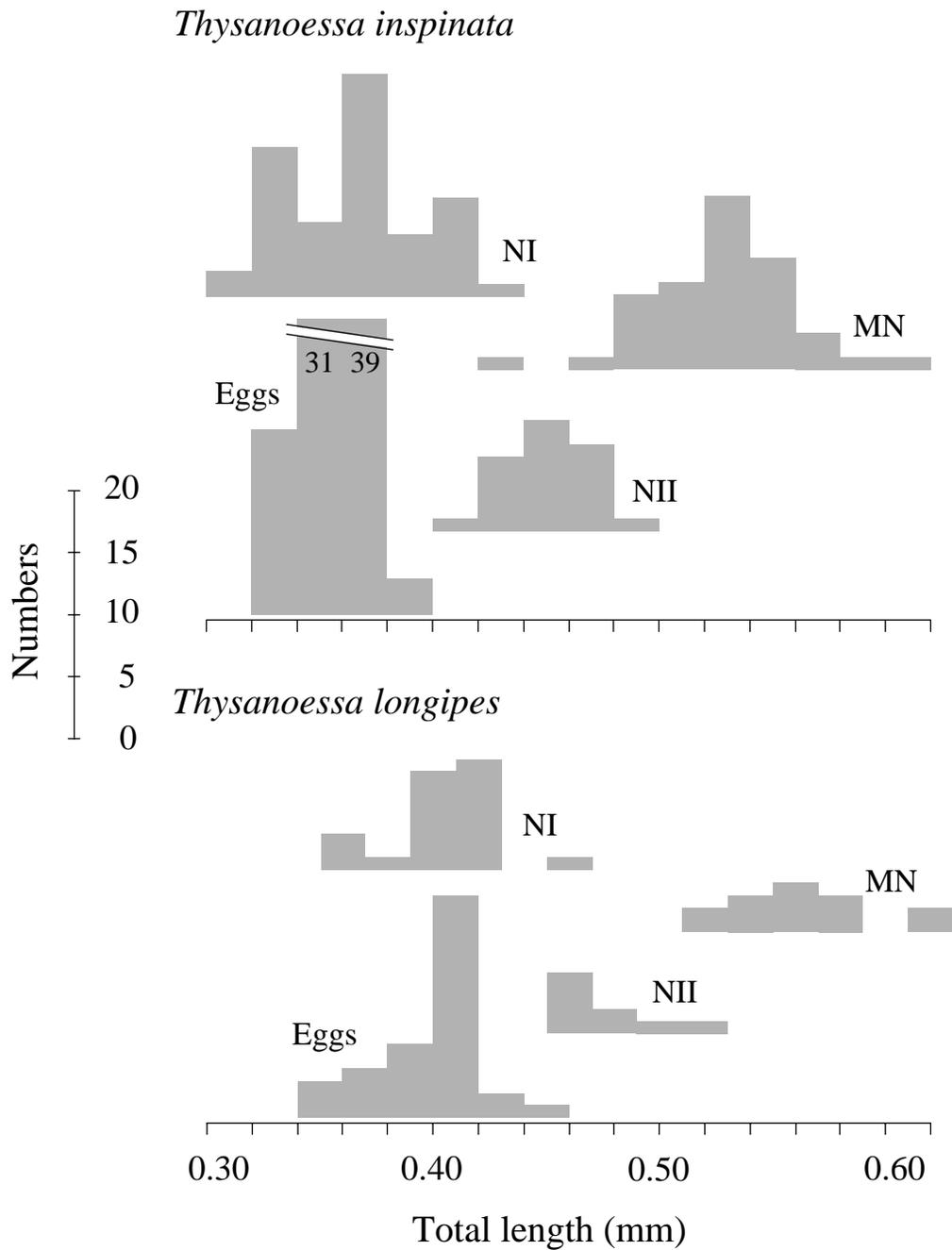


Fig. 2-4. Length-frequency data of eggs, nauplius I (NI) and II (NII), and metanauplius (MN) of *Thysanoessa inspinata* and *T. longipes* observed at 3°C.

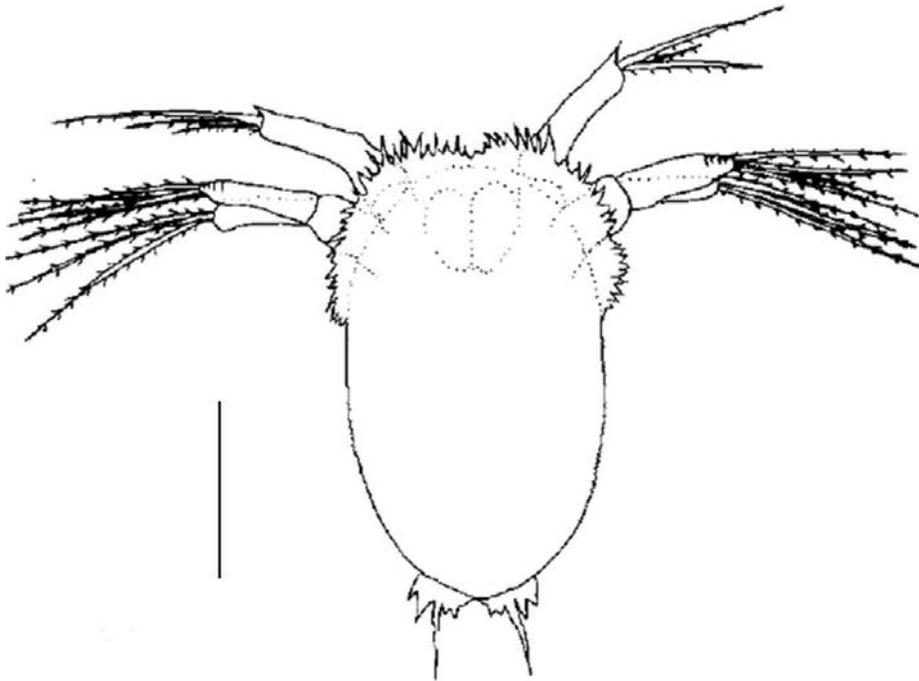


Fig 2-5. Metanauplius dorsal view of *Euphausia pacifica* (after Suh et al., 1993).
Scale bar: 0.2 mm.

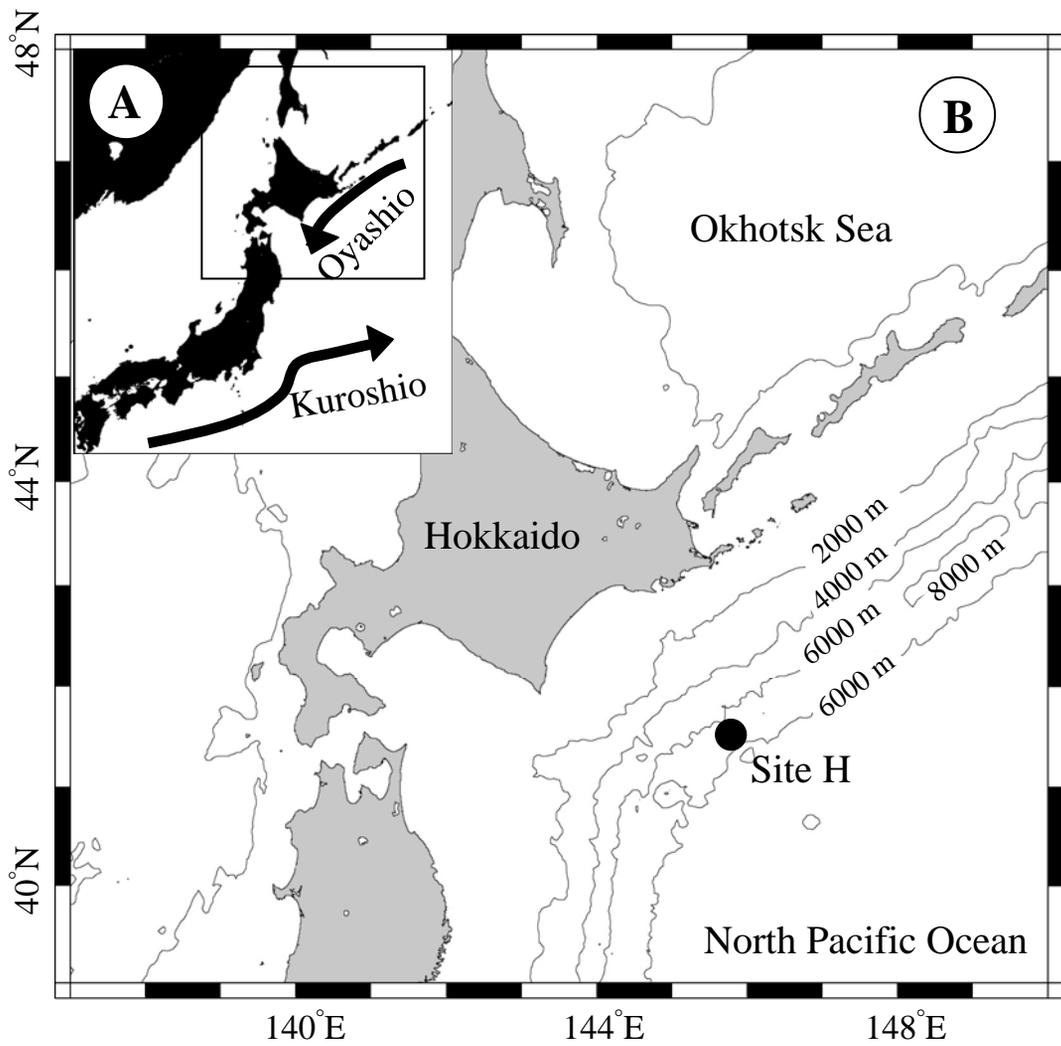


Fig. 3-1. Oyashio region in the western subarctic Pacific (A) and the sampling Site H in the Oyashio region (B). Depth contours (2000, 4000, 6000 and 8000 m) are superimposed in B.

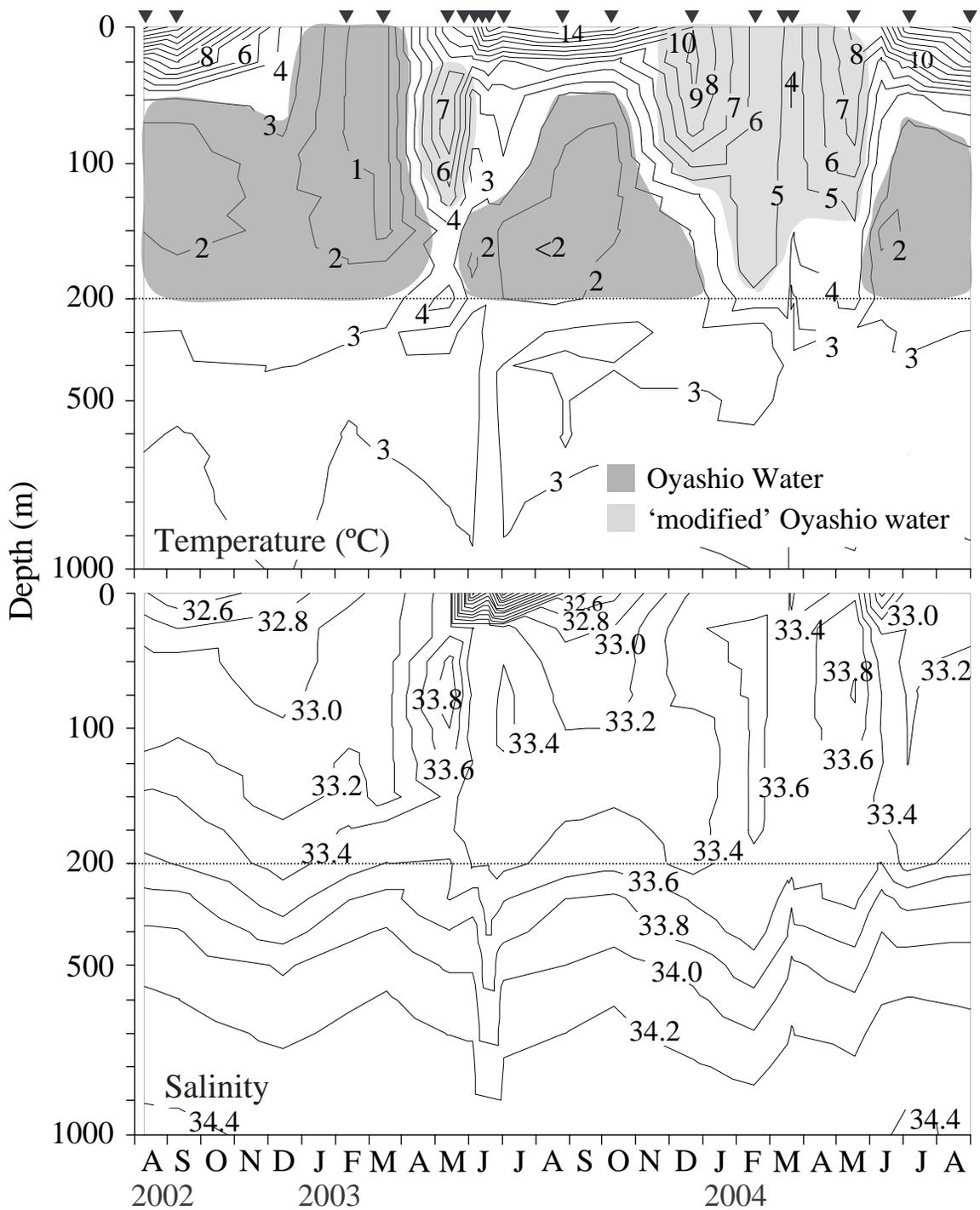


Fig. 3-2. Temperature (upper panel) and salinity (lower panel) profiles at Site H during the period of August 2002 to August 2004. Incidences of the Oyashio Water and 'modified' Oyashio water are shown in the top panel. Sampling dates are indicated by solid triangles on the top abscissa. Note that the depth scale changed at 200 m.

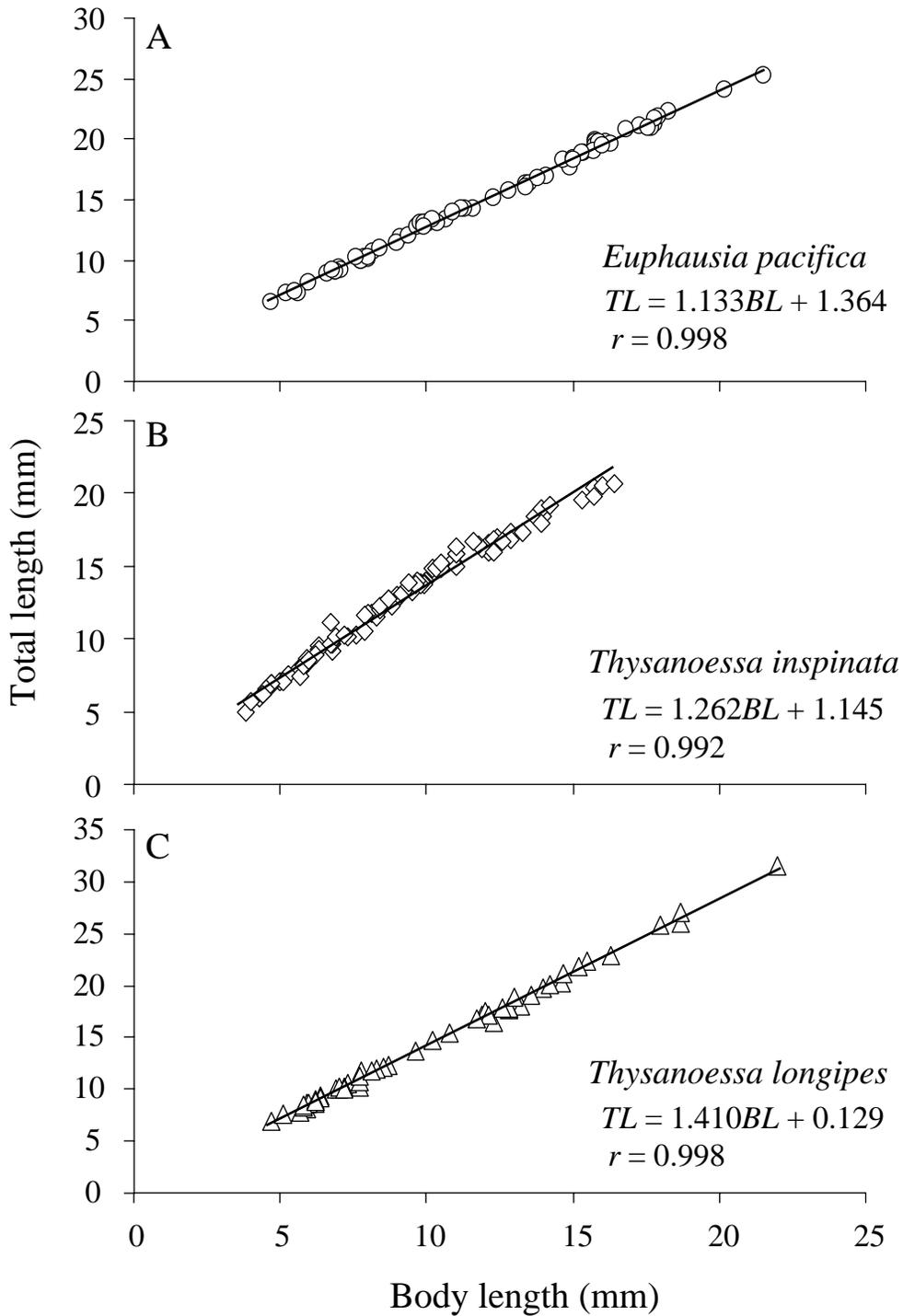


Fig. 3-3. Relationship between total length (TL) and body length (BL) of *Euphausia pacifica* (A), *Thysanoessa inspinata* (B) and *T. longipes* (C) at Site H in the Oyashio region.

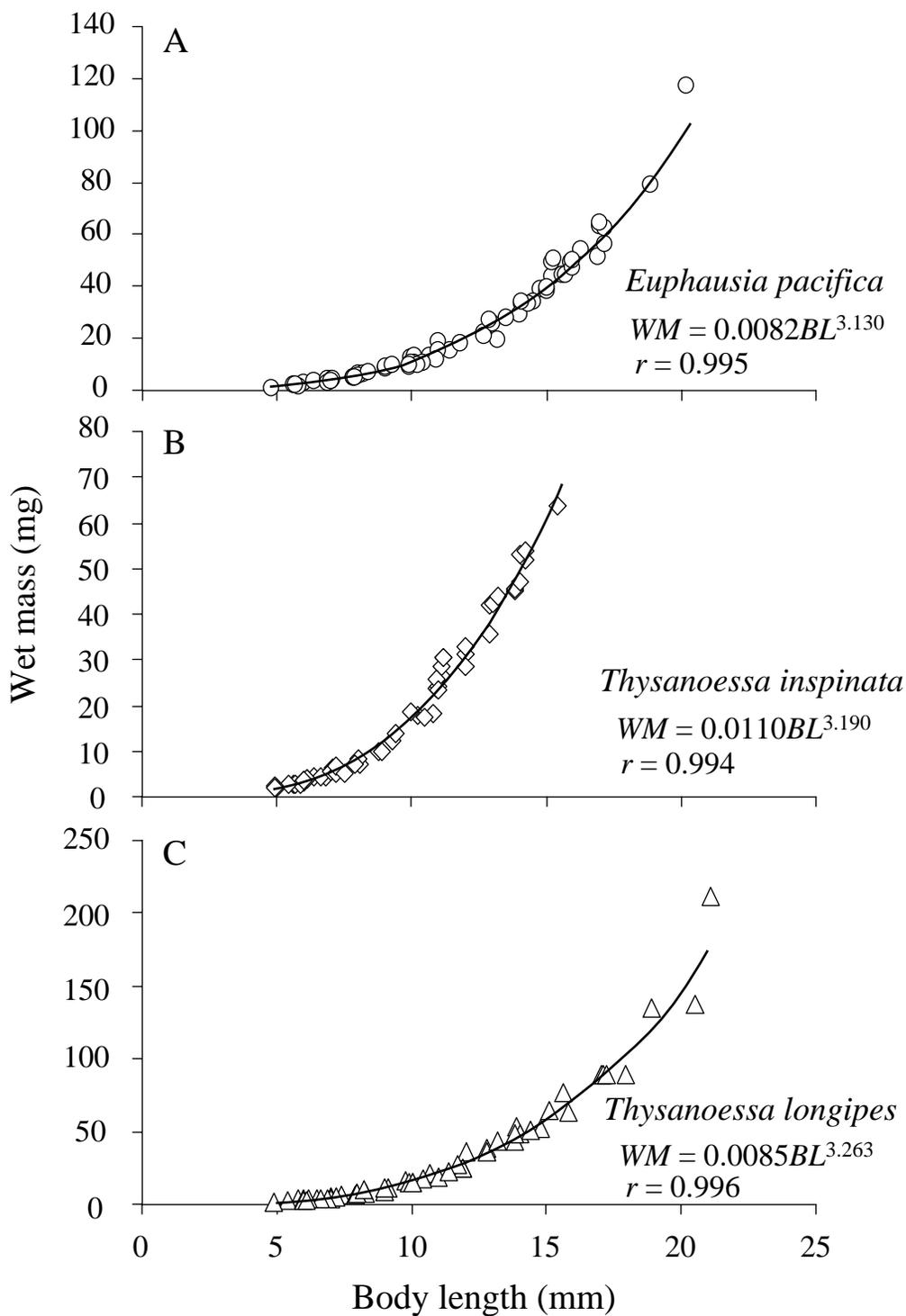


Fig. 3-4. Relationship between wet mass (*WM*) and body length (*BL*) of *Euphausia pacifica* (A), *Thysanoessa inspinata* (B) and *T. longipes* (C) at Site H in the Oyashio region.

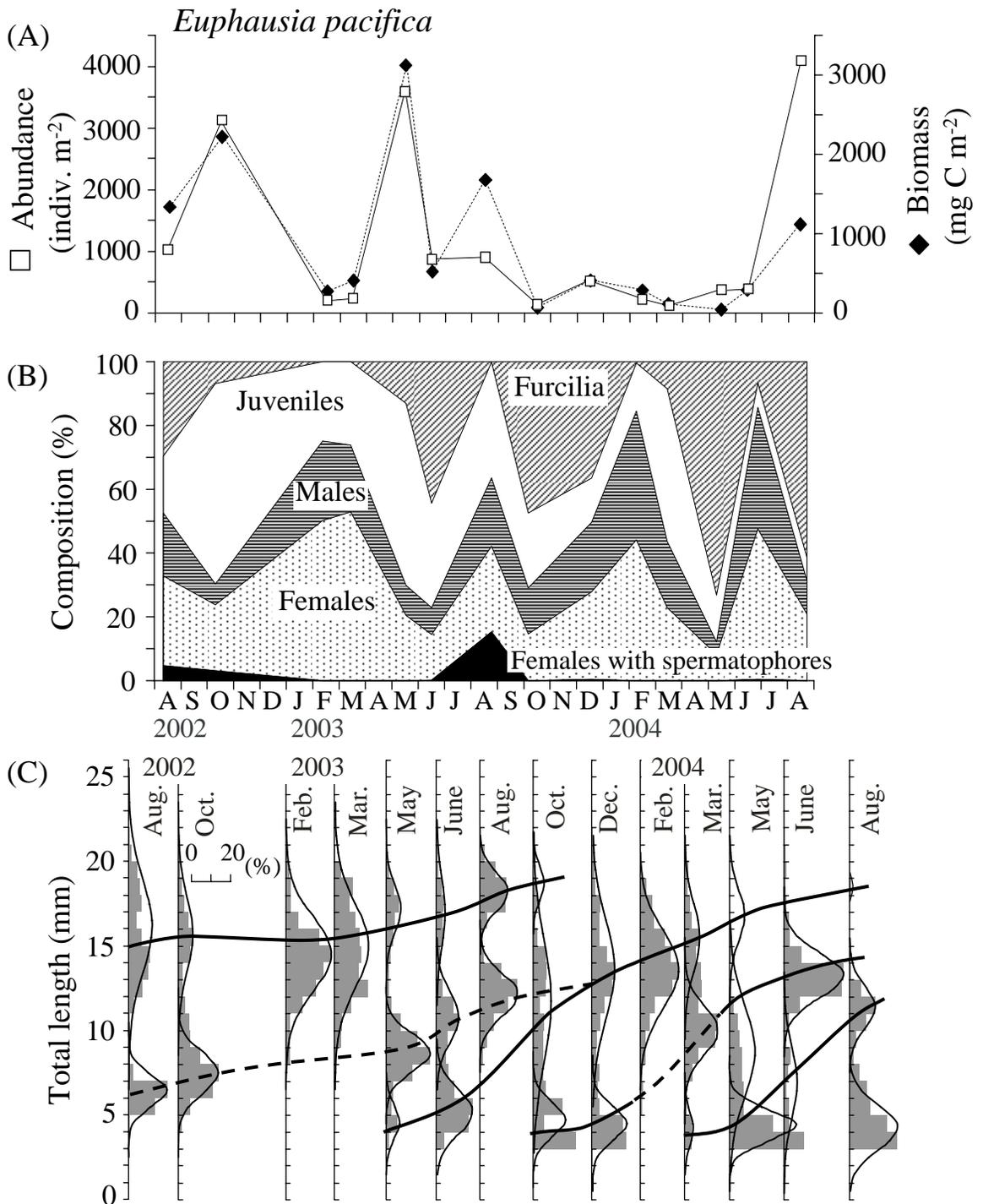


Fig. 3-5. Seasonal changes in numerical abundance and biomass (A), developmental stage composition (B) and length-frequency histograms (C) of *Euphausia pacifica* at Site H in the Oyashio region from August 2002 through August 2004. Hypothetical *TL* distribution curve of each cohort and clear (solid lines) and unclear (dotted lines) growth sequences of cohorts are superimposed in (C).

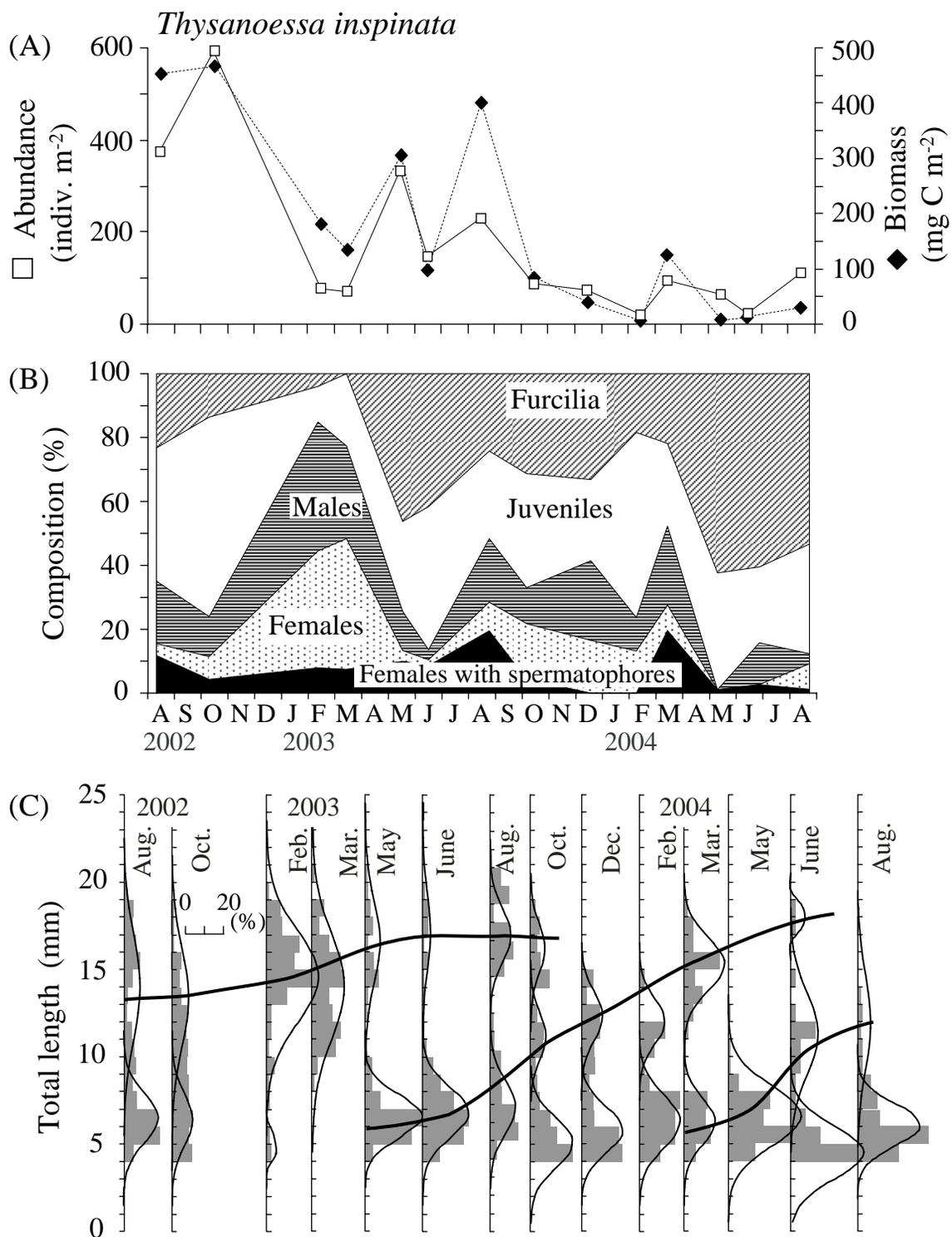


Fig. 3-6. As in Fig. 3-5, for *Thysanoessa inspinata*.

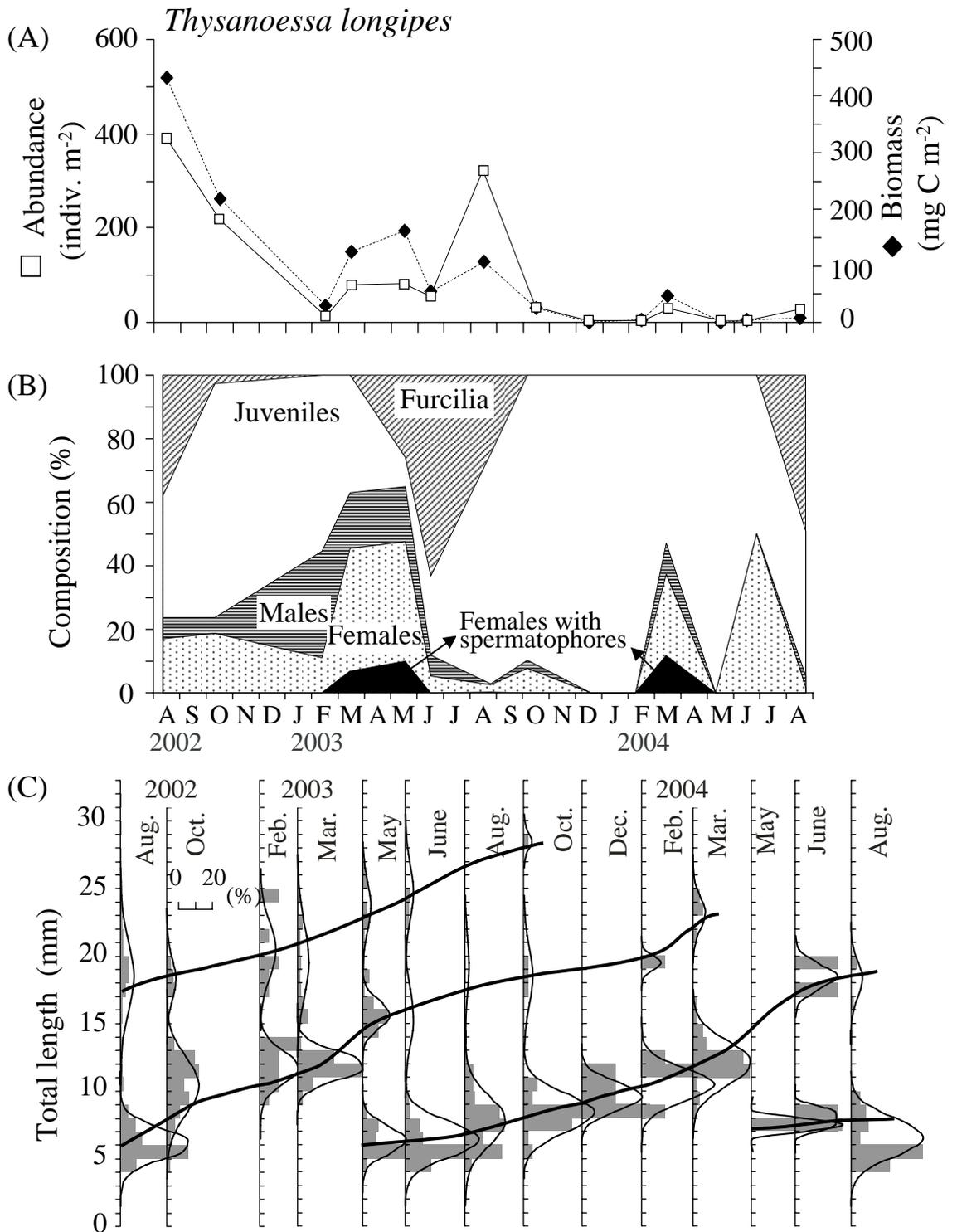


Fig. 3-7. As in Fig. 3-5, for *Thysanoessa longipes*.

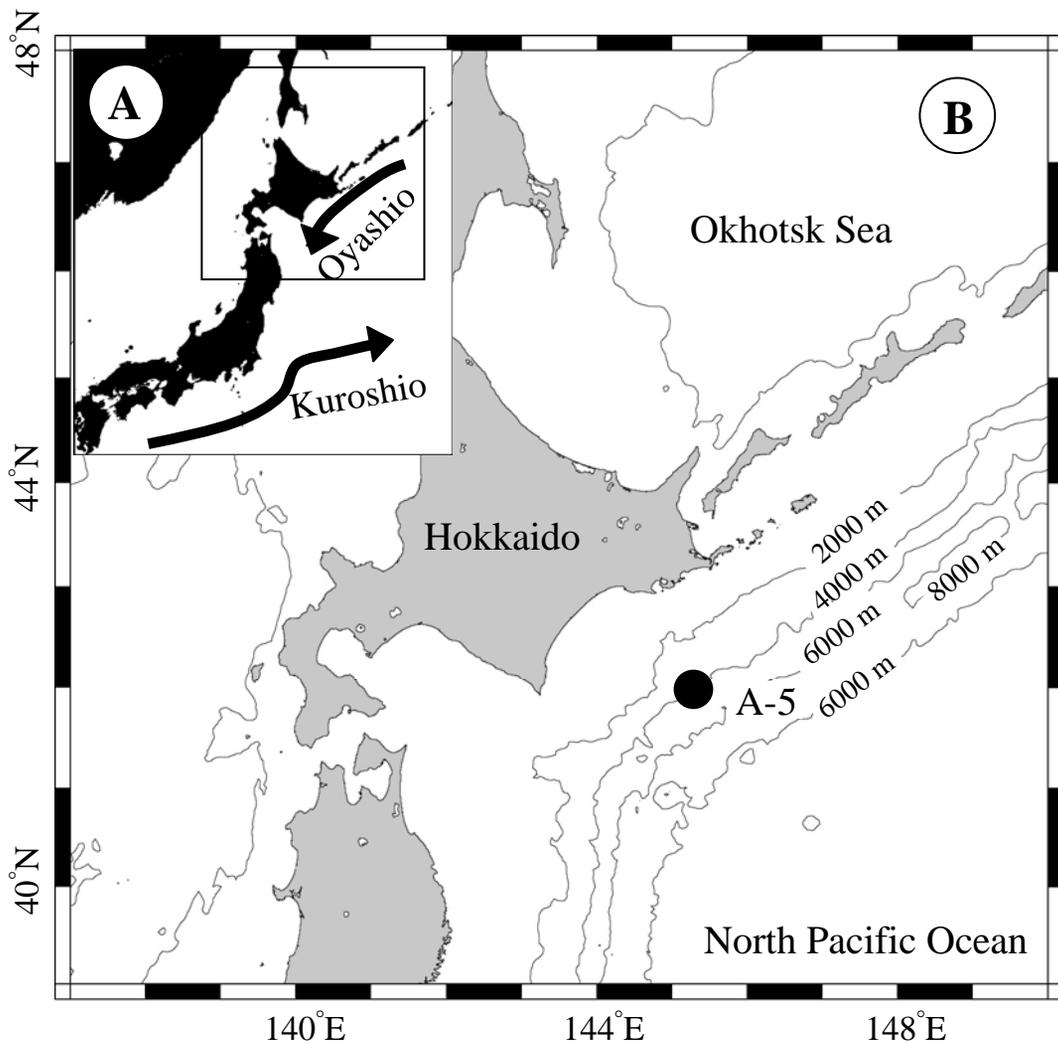


Fig. 4-1. Location of the Oyashio region in the western subarctic Pacific (A). Sampling station (A-5) in the Oyashio region (B). Depth contours (2000, 4000, 6000 and 8000 m) are superimposed in B.

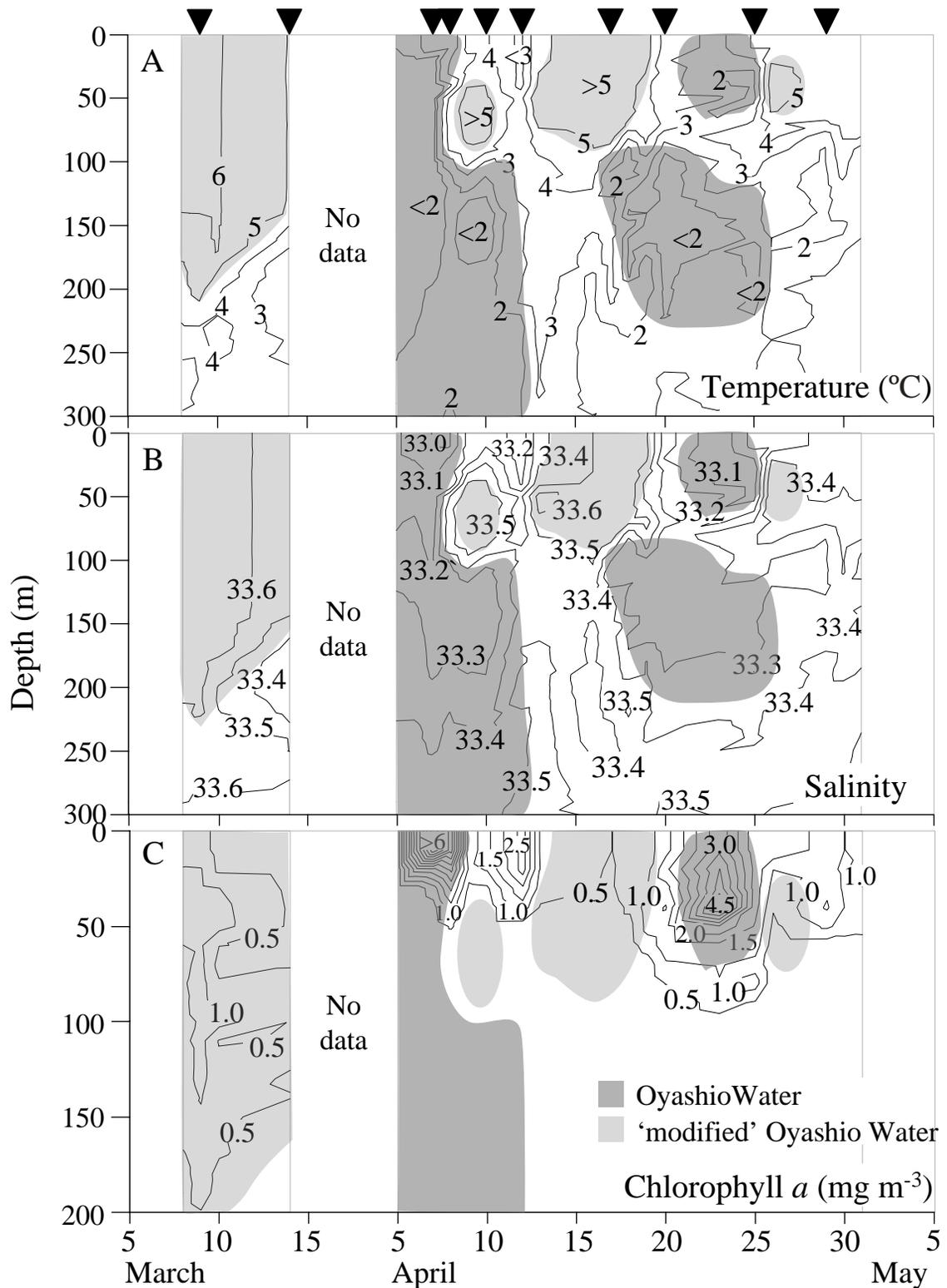


Fig. 4-2. Temporal changes in temperature (A), salinity (B) and chlorophyll *a* (C) profiles at the station A-5 in the Oyashio region during March to April 2007. Solid triangles in the top abscissa indicate sampling dates. Note that depth scale of (C) is not the same to those of (A) and (B).

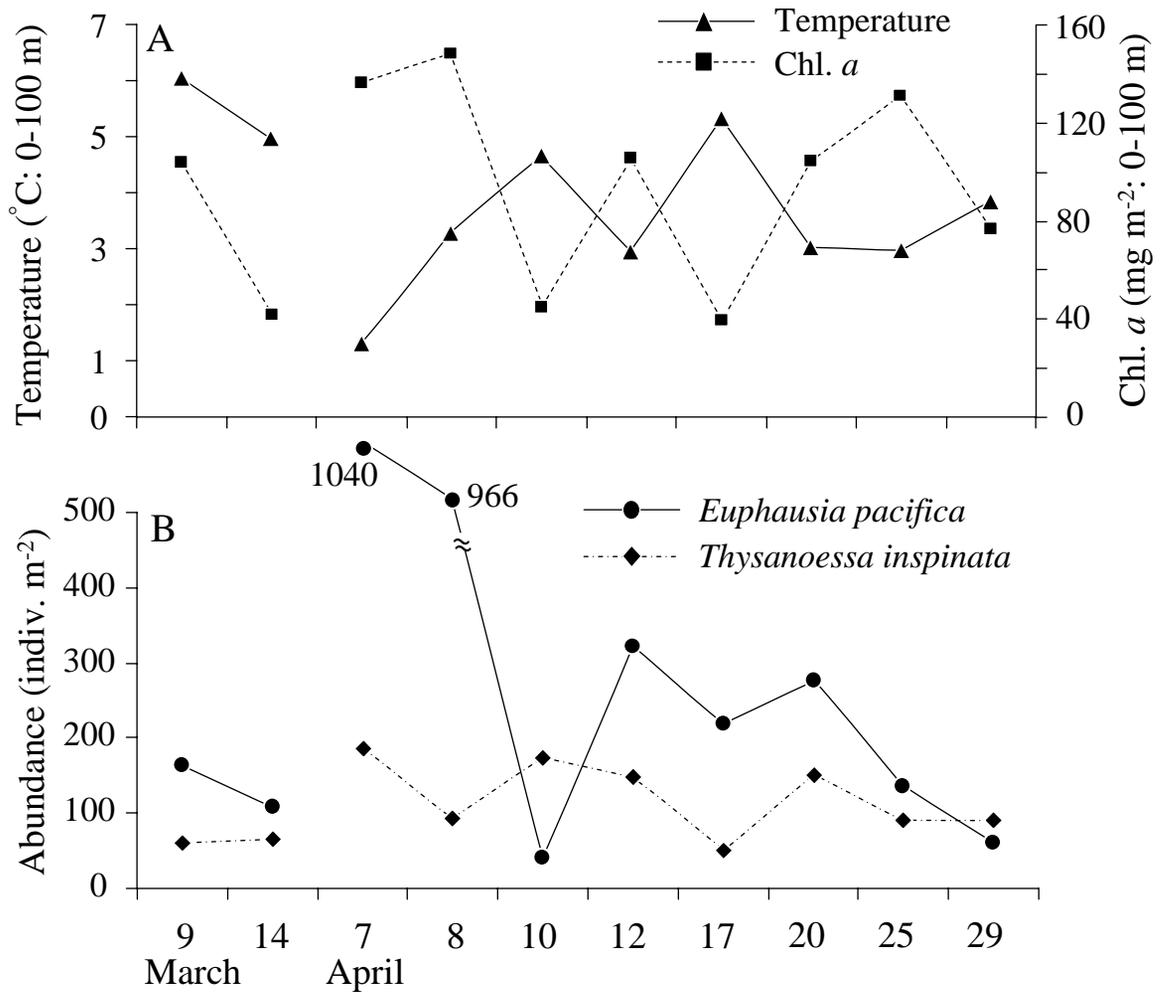


Fig. 4-3. Temporal changes in mean temperature and standing stock of chlorophyll *a* integrated over 0-100 m depth (A) and abundance of *Euphausia pacifica* and *Thysanoessa inspinata* (B) at the station A-5 in the Oyashio region during 9 March to 29 April 2007.

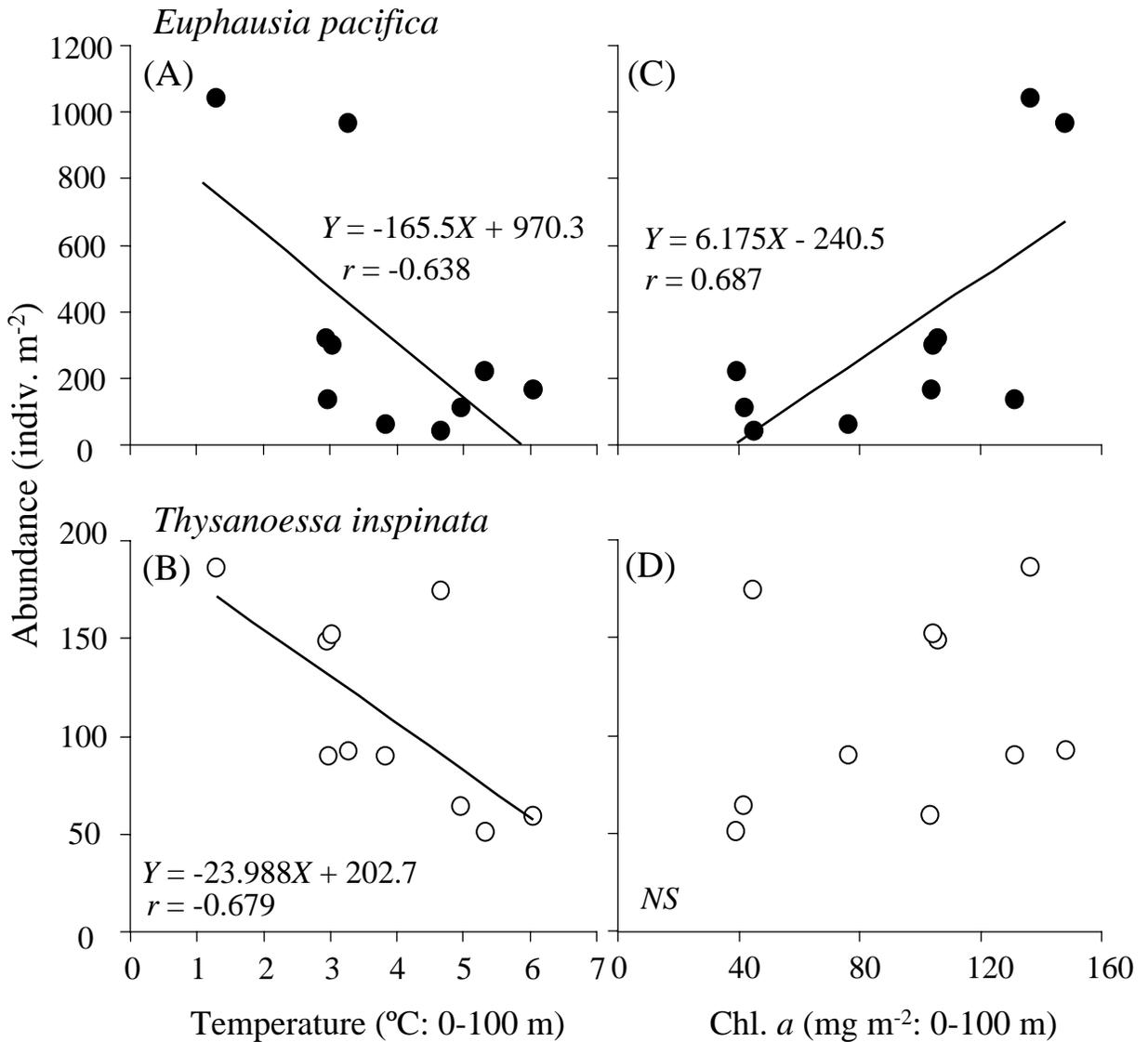


Fig. 4-4. Relationship between abundance and integrated mean temperature for *Euphausia pacifica* (A) and *Thysanoessa inspinata* (B), and that between abundance and chlorophyll *a* for *E. pacifica* (C) and *T. inspinata* (D) at station A-5 in the Oyashio region during 9 March to 29 April 2007. The regression line is superimposed for the significant relationship only. NS: not significant.

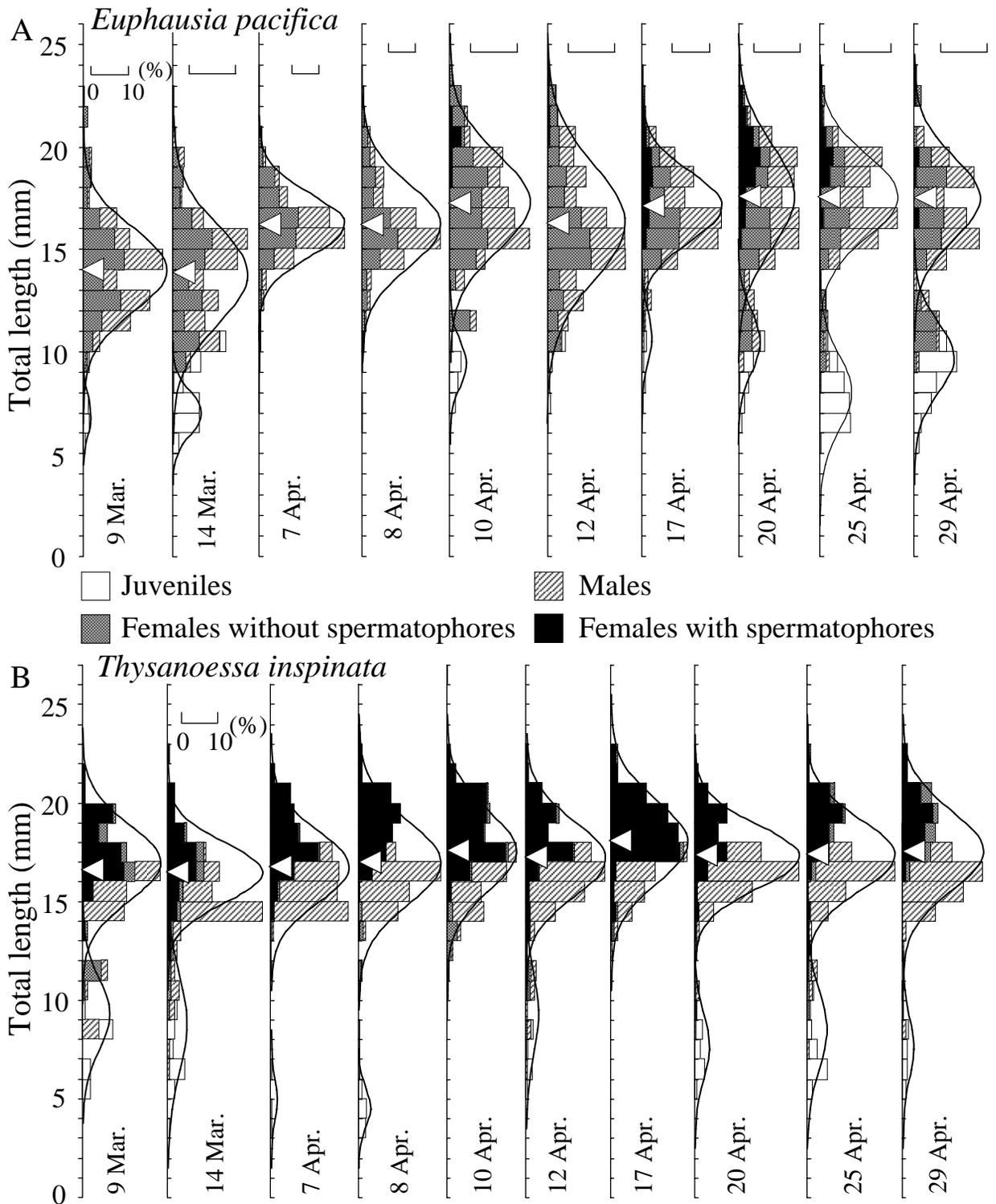


Fig. 4-5. Population structure (juveniles, adult males and females, and females with spermatophores) and total length frequency distributions of *Euphausia pacifica* (A) and *Thysanoessa inspinata* (B) collected at the station A-5 in the Oyashio region during 9 March to 29 April 2007. Hypothetical normal distribution curves and mean TLs (open triangles; major mode only) are superimposed.

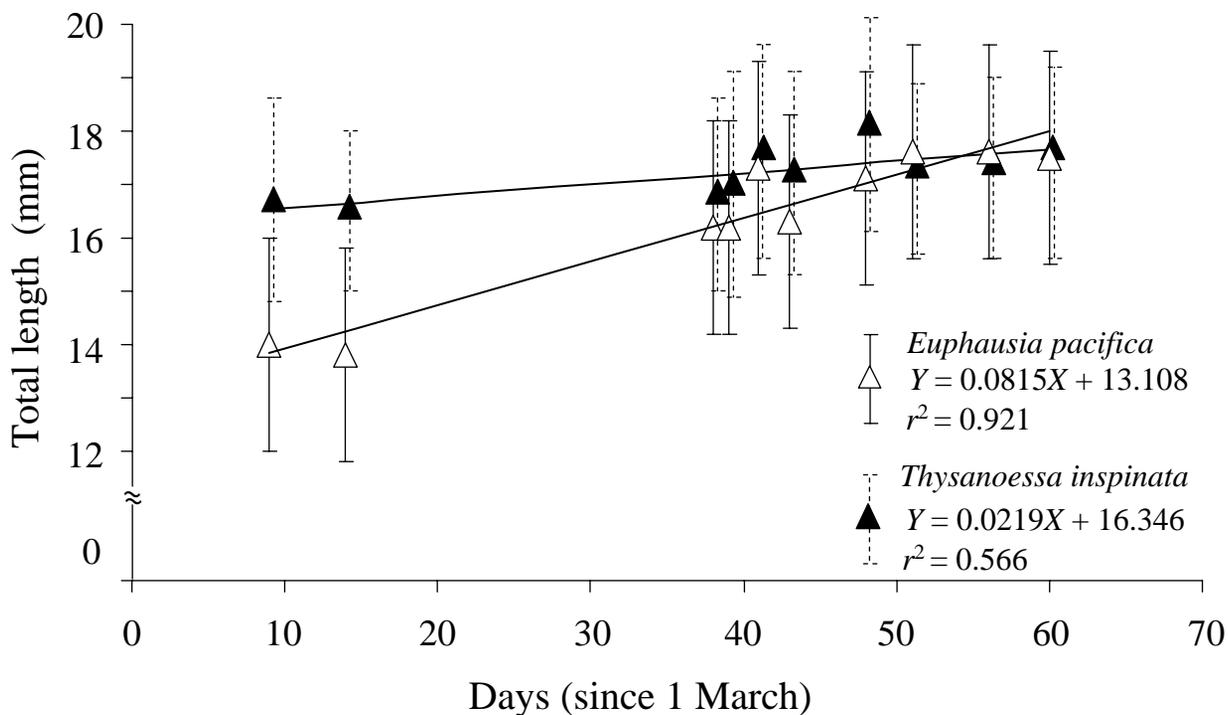


Fig. 4-6. Linear growth of *Euphausia pacifica* and *Thysanoessa inspinata* based on the progressive increase in mean TLs of the large sized-groups from 9 March to 29 April 2007 (see Fig. 4-5). Vertical bars through the means denote \pm SD.

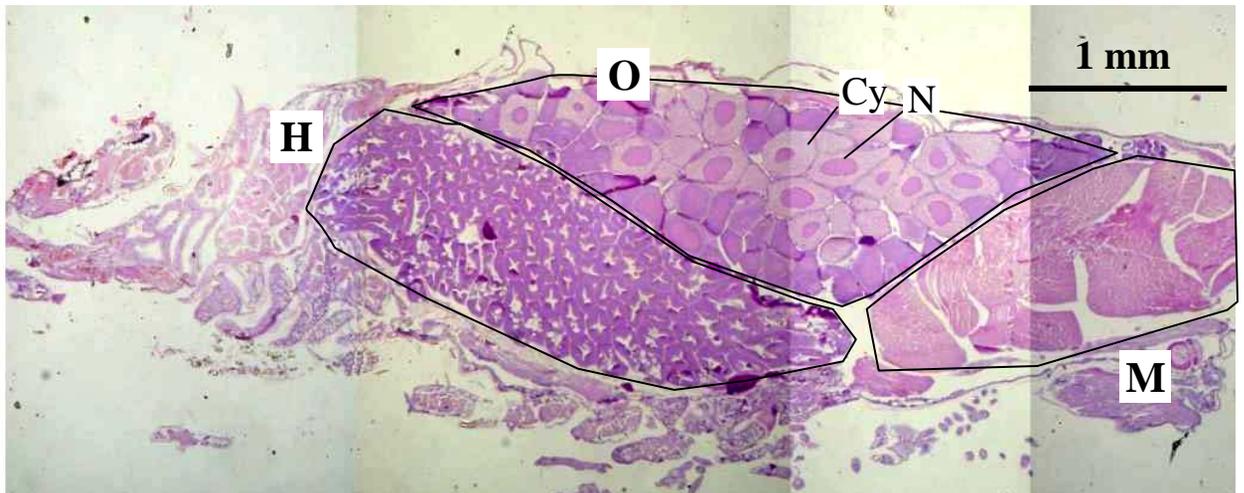


Fig. 4-7. Medial sagittal section of *Thysanoessa inspinata* female with spermatophore attached (hematoxylin-eosin stained). H: hepatopancreas, O: ovary, M: muscle, Cy: cytoplasm, N: nucleus.

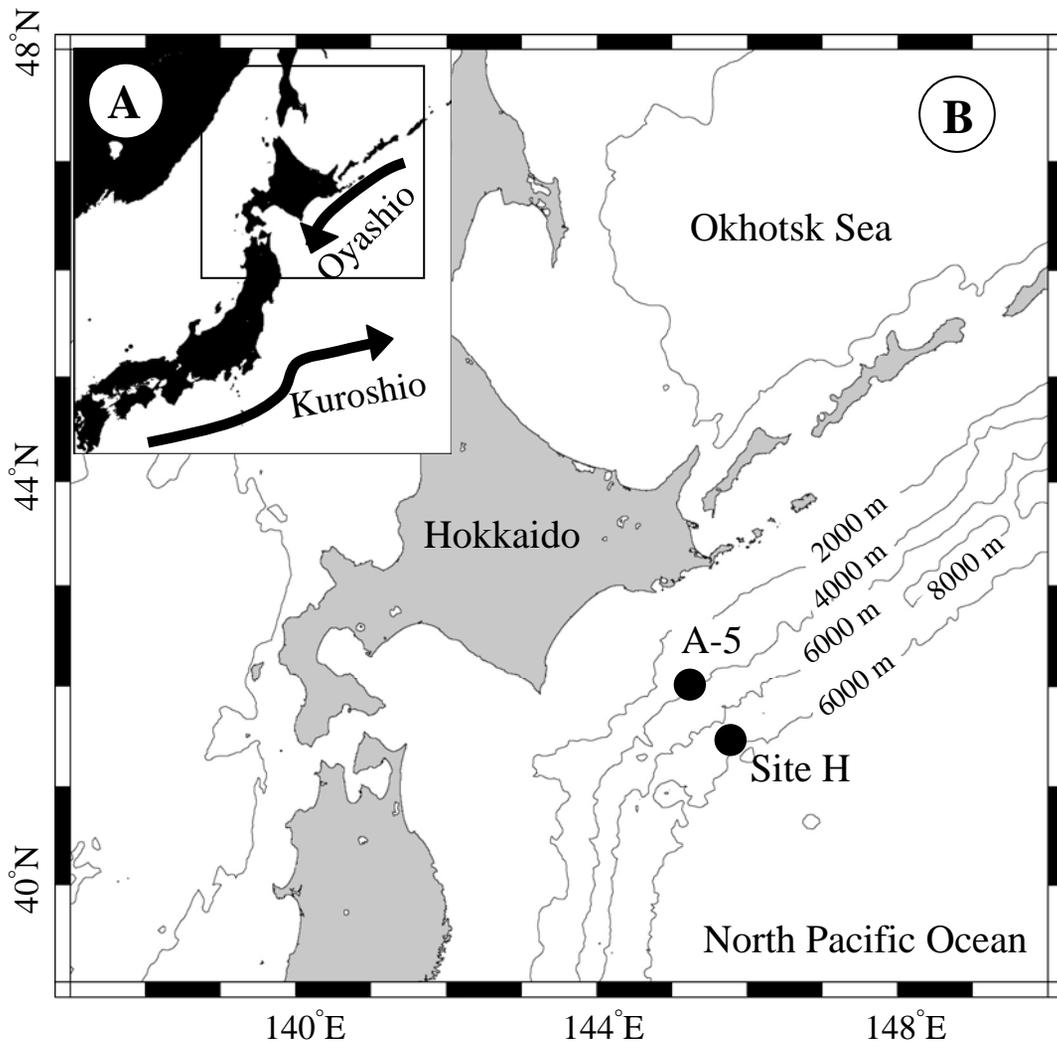


Fig. 5-1. Location of the Oyashio region in the western subarctic Pacific (A). Sampling station (A-5 and Site H) in the Oyashio region (B). Depth contours (2000, 4000, 6000 and 8000 m) are superimposed in B.

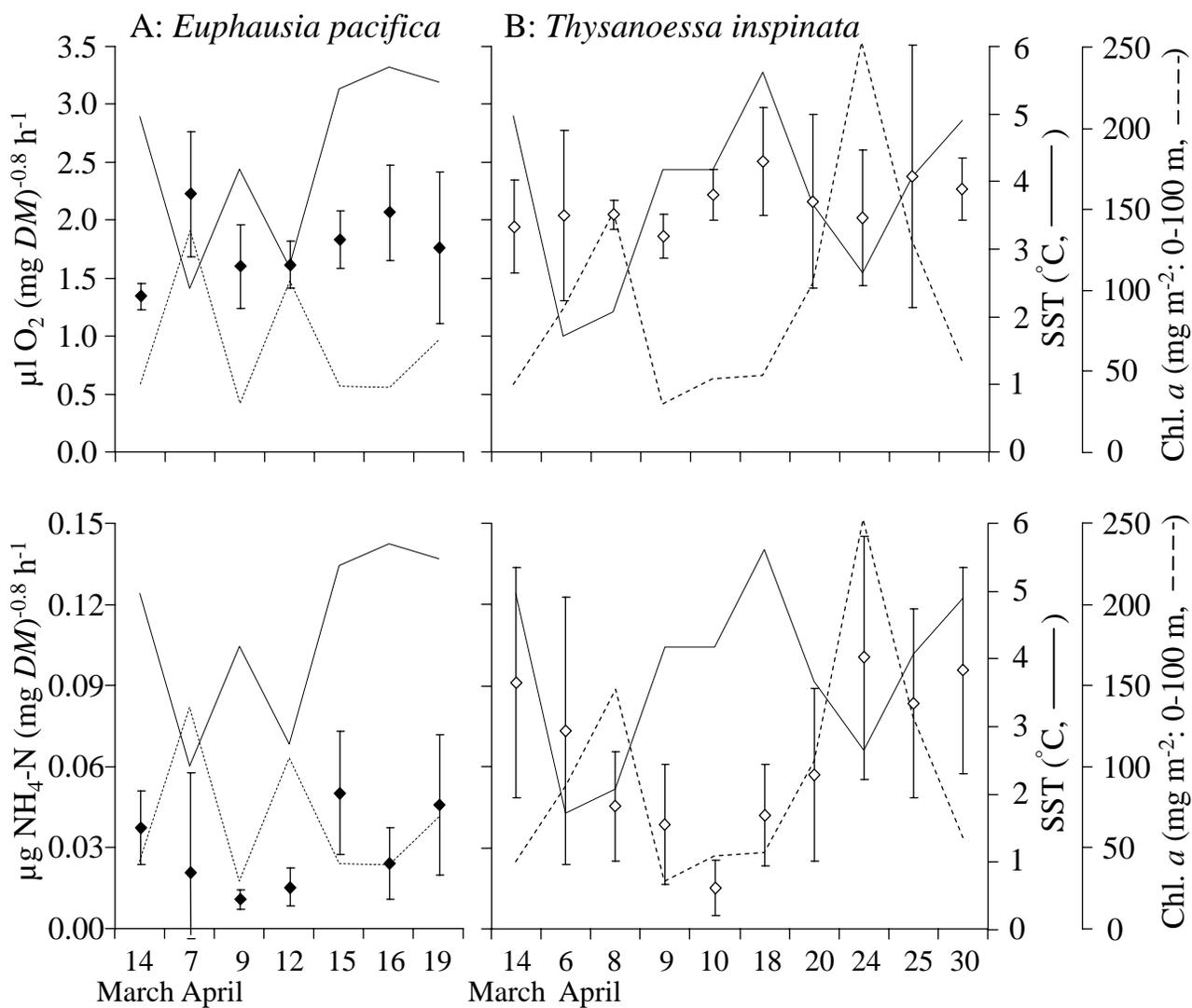


Fig. 5-2. Temporal changes in *AMR-O₂* (upper panels) and *AMR-NH₄-N* (lower panels) at 10°C of *Euphausia pacifica* (A) and *Thysanoessa inspinata* (B) during March and April 2007. As the environmental parameters, sea surface temperature (SST) and chlorophyll *a* standing stock (Chl. *a*, 0-100 m) are superimposed. Vertical bars indicate standard deviations.

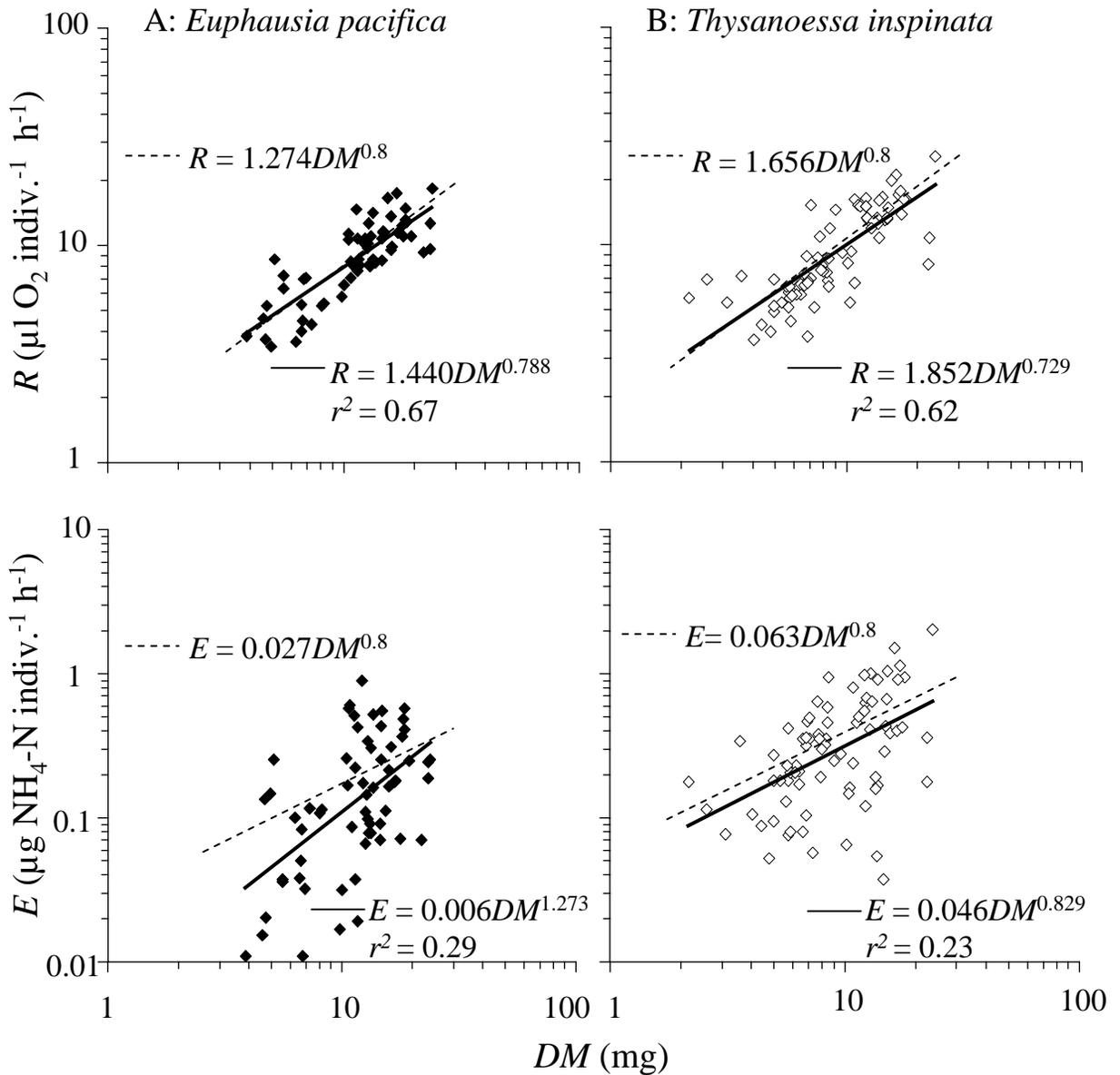
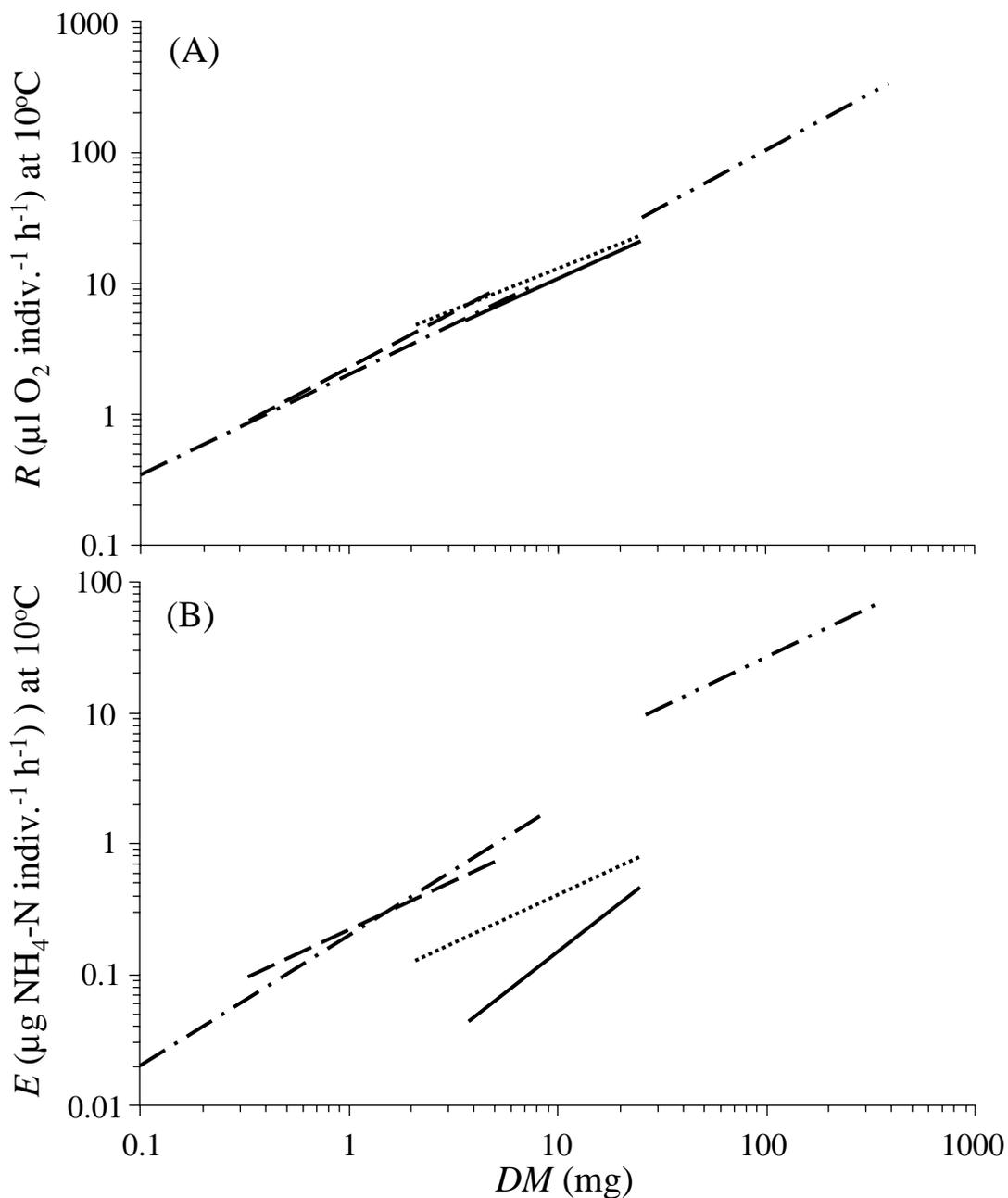


Fig. 5-3. Relationships between oxygen consumption rate (R) and dry mass (DM) (upper panel) and ammonia excretion rate (E) and dry mass (DM : mg) (bottom panel) of *Euphausia pacifica* (A) and *Thysanoessa inspinata* (B) in the Oyashio region. Regression lines are calculated based on directly (solid lines) or on standardized body size of 1 mg DM with exponent of 0.8 (broken lines).



— *E. pacifica* (this study) *T. inspinata* (this study) --- *E. lucens* (Stuart, 1986)
 -·-·-· *E. superba* (Ikeda and Mitchell, 1982) -·-·-· *E. pacifica* (8°C: Ross, 1982)

Fig. 5-4. Comparison of the relationships between dry mass (DM) and oxygen consumption rate (R) (A) or ammonia excretion rate (E) (B) of *Euphausia pacifica* and *Thysanoessa inspinata* of this study with those of *Euphausia lucens* (Stuart, 1986), *E. superba* (Ikeda and Mitchell, 1982), and *E. pacifica* (Ross, 1982). All data were standardized to the rates at 10°C assuming $Q_{10} = 2$.

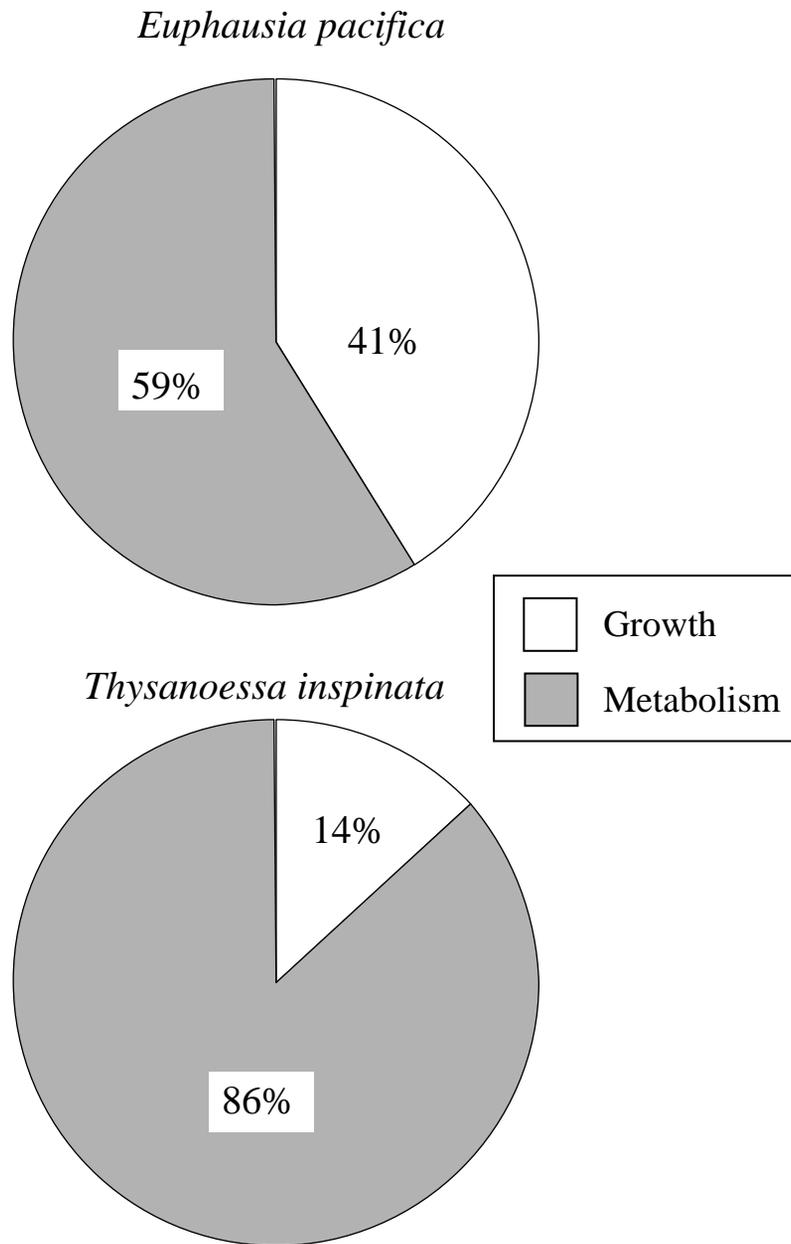


Fig 6-1. Partition of assimilated carbon to somatic production and metabolism in *Euphausia pacifica* and *Thysanoessa inspinata* in the Oyashio region during spring phytoplankton bloom in 2007.

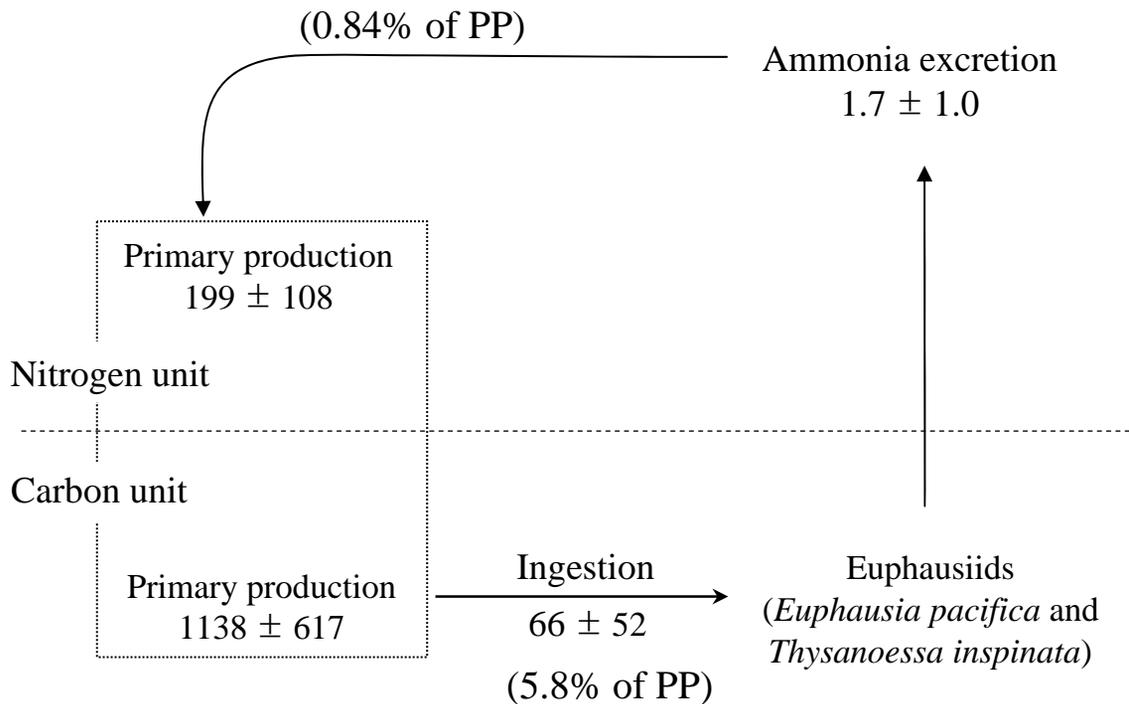


Fig. 6-2. Daily grazing impact and simultaneous daily ammonia-N regeneration by *Euphausia pacifica* and *Thysanoessa inspinata* on phytoplankton during spring phytoplankton bloom in the Oyashio region (April 2007). Note that calculation of grazing impact is based on carbon unit (lower panel) that of ammonia regeneration nitrogen unit (upper panel). Values are mean \pm 1SD in mg C m⁻² d⁻¹ or mg N m⁻² d⁻¹, and its percentages to primary production are in parentheses. For detailed data see Table 6-1 and 6-2.

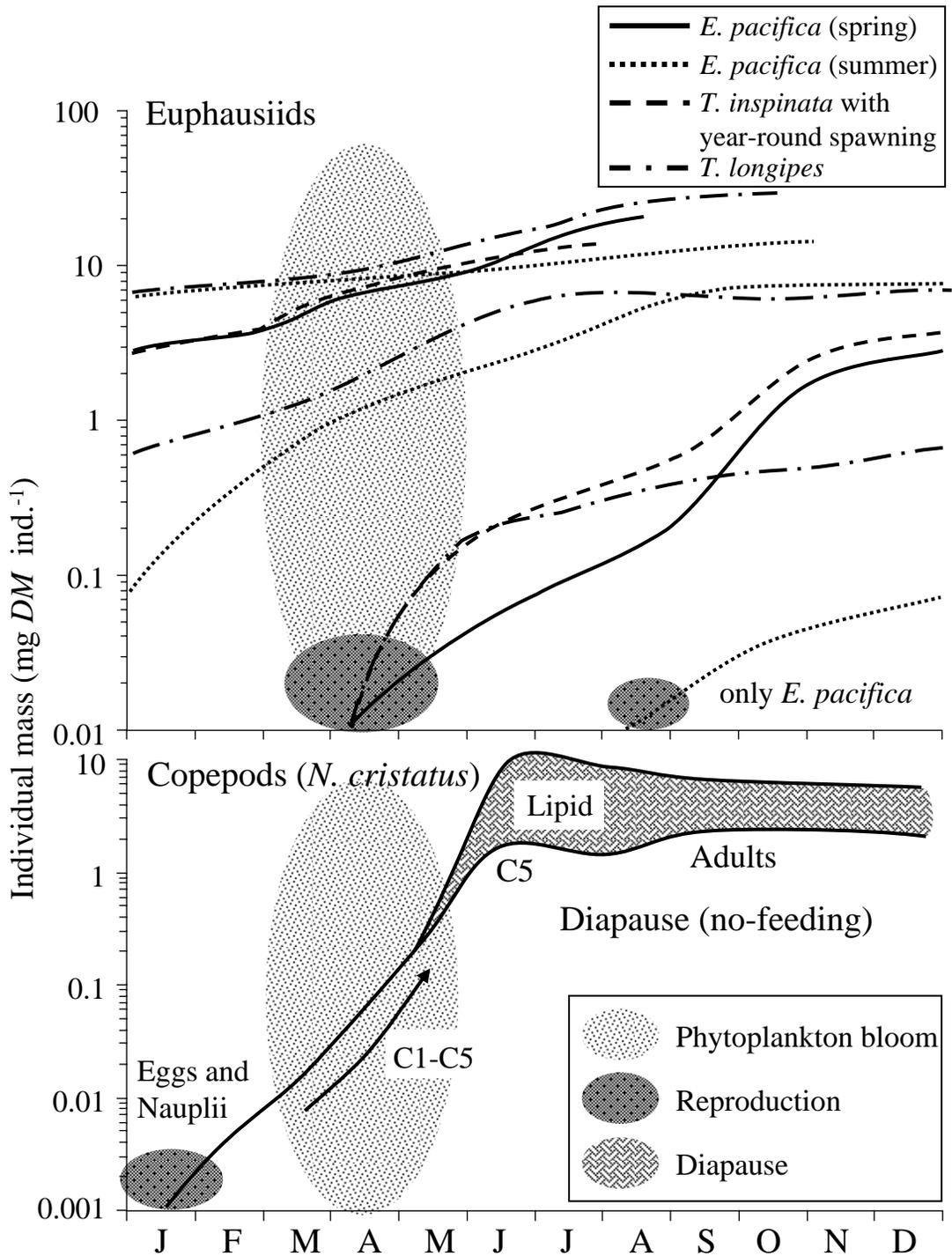


Fig. 6-3. Schematic representation of life cycle trajectories in relation with annual phytoplankton bloom of euphausiids (*Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes*) and copepods (*Neocalanus cristatus*) in the Oyashio region. Seasonal development and mass data on *N. cristatus* are from Kobari et al. (2003) and Ikeda et al. (2004). Note that mass data on C5 and adults *N. cristatus* had range of lipid accumulation.