



# Population dynamics of the euphausiids *Euphausia pacifica* and *Thysanoessa inspinata* in the Oyashio region during the 2007 spring phytoplankton bloom

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## ARTICLE INFO

### Article history:

Received 15 March 2010

Accepted 15 March 2010

Available online 27 March 2010

Topical issue on "Ecosystem Processes during the Oyashio Spring Bloom."

The issue is compiled and guest-edited by the North Pacific Marine Science Organization (PICES).

### Keywords:

*Euphausia pacifica*  
*Thysanoessa inspinata*  
 Oyashio region  
 Euphausiids  
 Population structure  
 Phytoplankton bloom

## ABSTRACT

The abundance and population structure of *Euphausia pacifica* and *Thysanoessa inspinata* were investigated during the period 9 March–29 April 2007 at a single station in the Oyashio region. Water temperature and chlorophyll *a* concentration varied from 1.1 to 6.1 °C and from 0.02 to 6.3 mg m<sup>-3</sup>, respectively, primarily reflecting the effects of varying mixtures of the water masses prevailing in this region. The abundance of euphausiids, collected by oblique hauls with Bongo nets (0–200 m) at night, fluctuated from 41 to 1040 individuals m<sup>-2</sup> for *E. pacifica* and from 50 to 186 individuals m<sup>-2</sup> for *T. inspinata*. Correlation analyses revealed that the variations in the abundance of *E. pacifica* were related to water temperature and chlorophyll *a*, while abundance of *T. inspinata* only varied with temperature. Adult males and females (with and without spermatophores) were the major components of both euphausiid stocks (> 90% of the total). Modal size (= total length or TL) analysis revealed that one group with large sizes (14–18 mm TL for *E. pacifica*, 16–18 mm TL for *T. inspinata*) occurred throughout the study period, often accompanied by one discrete group of smaller individuals (< 11 mm TL for both euphausiids), suggesting the distribution of the same euphausiid populations across the heterogeneous water masses. Adult males were significantly smaller than adult females in *T. inspinata*, but this was not the case in *E. pacifica*. Tracing the progressive increase in the mean sizes of the larger size groups, growth rates were estimated to be 0.082 mm day<sup>-1</sup> for *E. pacifica* and 0.022 mm day<sup>-1</sup> for *T. inspinata*. The difference in the growth rates of the two euphausiids is discussed in light of species-specific differences in the allocation of energy to reproduction and somatic growth during the present study period.

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## 1. Introduction

In high latitude seas, the spring phytoplankton bloom has been documented as a key mechanism driving biological processes in marine ecosystems. As major taxonomic groups among secondary producers, many copepod and euphausiid species are known to have life cycle patterns synchronized with the spring phytoplankton bloom (cf. Wassmann et al., 2006; Ikeda et al., 2008). Coupling of spawning with the incidence of the bloom has been reported primarily for particle-grazing euphausiids, such as *Euphausia superba* in the Southern Ocean (Bargmann, 1945), *Thysanoessa inermis* and *Thysanoessa longicaudata* in the Barents Sea (Dalpadado and Skjoldal, 1996), *Euphausia pacifica* off southern California (Brinton, 1976) and in Toyama Bay (Iguchi et al., 1993) and *E. pacifica* and *Thysanoessa spinifera* off Oregon (Feinberg and

Peterson, 2003). Thus, the magnitude of the phytoplankton bloom affects the recruitment rates of the euphausiids and the subsequent growth of their young. Their predators and higher trophic levels along the food chains of the pelagic realm are affected in turn.

In the Oyashio region, *E. pacifica* is the dominant euphausiid, followed by *Thysanoessa inspinata* and *Thysanoessa longipes* (Kim et al., 2009). The predominance of *E. pacifica* persists over all of the broad Oyashio-Kuroshio transitional regions off northeastern Japan (Odate, 1994). Since *E. pacifica* is the target species of a 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 the population dynamics of this euphausiid during the spring phytoplankton bloom have not been evaluated as yet because of the bi-monthly sampling of these previous studies. Compared with *E. pacifica*, almost nothing is known about the biology and ecology of *T. inspinata* in the Oyashio region. To fill these gaps in knowledge,

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high-frequency sampling is needed, more resolved than the typically bi-monthly sampling done in the past, especially during the phytoplankton bloom season.

OECOS (Oceanic Ecodynamics Comparison in the Subarctic Pacific) is a PICES project, aimed at advancing our understanding of 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 OECOS activity, the Western Group (OECOS WEST) organized two cruises to the Oyashio region before and during the spring phytoplankton blooms in 2007. During the cruises, we undertook frequent sampling (every 2–5 days) to trace the sequence of population dynamics of *Euphausia pacifica* and *Thysanoessa inspinata*. Results are discussed, with particular attention to the effects of water mass exchange on the abundance and stability of population structure. The species are compared in respect to differences in reproductive activities and growth.

## 2. Materials and methods

### 2.1. Field sampling

A total of ten oblique hauls with Bongo nets (70 cm mouth diameter, 500  $\mu\text{m}$  mesh size) were made at site St. A-5 (42°00'N, 145°15'E, Fig. 1) in the Oyashio region during 9–14 March (Oshoro-Mar cruise 177) and 6–30 April 2007 (Hakuho-Mar cruise KH-07-1) (Table 1). Bongo nets were towed from 200 m depth to the surface at a speed of 2 knots ( $=1.0 \text{ m s}^{-1}$ ) at night. The speed of the net towing appears to be sufficient to collect euphausiids, which swim at  $0.02\text{--}0.03 \text{ m s}^{-1}$  (for *E. pacifica*, Hanamura et al., 1984), with minimal effects from “net avoidance”, a known artifact in the quantitative sampling of this group of animals (cf. Brinton, 1967). The volume of seawater passed through the nets was estimated with a Rigosha flow-meter mounted in the mouth ring. After collection, all samples were preserved immediately in 5% borax-buffered formalin-seawater. Environmental parameters (temperature, salinity and chlorophyll

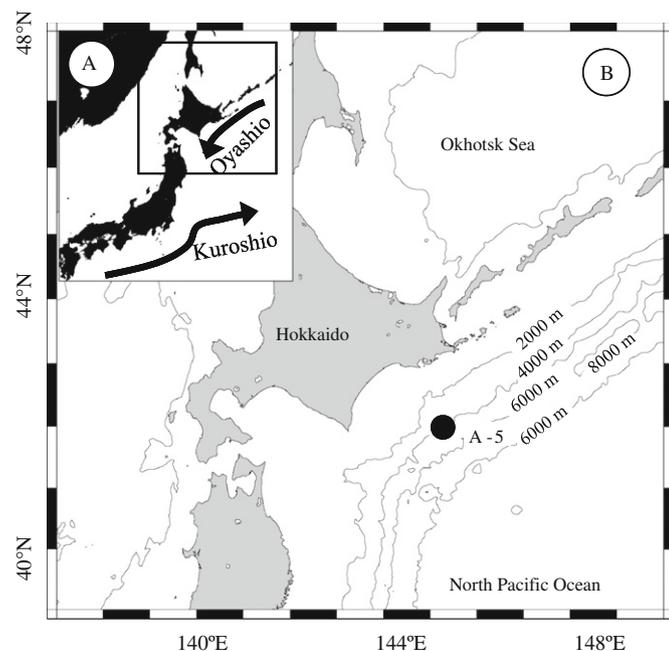


Fig. 1. Location of the Oyashio region in the western subarctic Pacific (A). Sampling station (A-5) in the Oyashio region (B). Depth contours (2000, 4000, 6000 and 8000 m) are superimposed in B.

Table 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 ( $\text{m}^3$ )
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

*a* pigment) were determined with a CTD system (SBE-9 plus, Sea Bird Electronics) at each sampling. For details about chlorophyll *a* measurement, see Isada et al. (2010).

### 2.2. Identification and enumeration

In the land laboratory, euphausiids were sorted from the entire sample and enumerated under a dissecting microscope. Specimens of the two dominant euphausiids, *Euphausia pacifica* and *Thysanoessa inspinata*, were separated into juveniles, adult males and 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 “active spawning”) or absence of a spermatophore was noted. 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 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 telson, *TL*: mm) (cf. Ross et al., 2000 and references therein), we converted *BL* data to *TL* using allometric equations:  $TL = 1.292BL + 0.0762$  ( $r = 0.998$ ,  $n = 67$ ) for *E. pacifica*, and  $TL = 1.514BL - 0.575$  ( $r = 0.995$ ,  $n = 91$ ) for *T. inspinata* (Kim et al., unpublished).

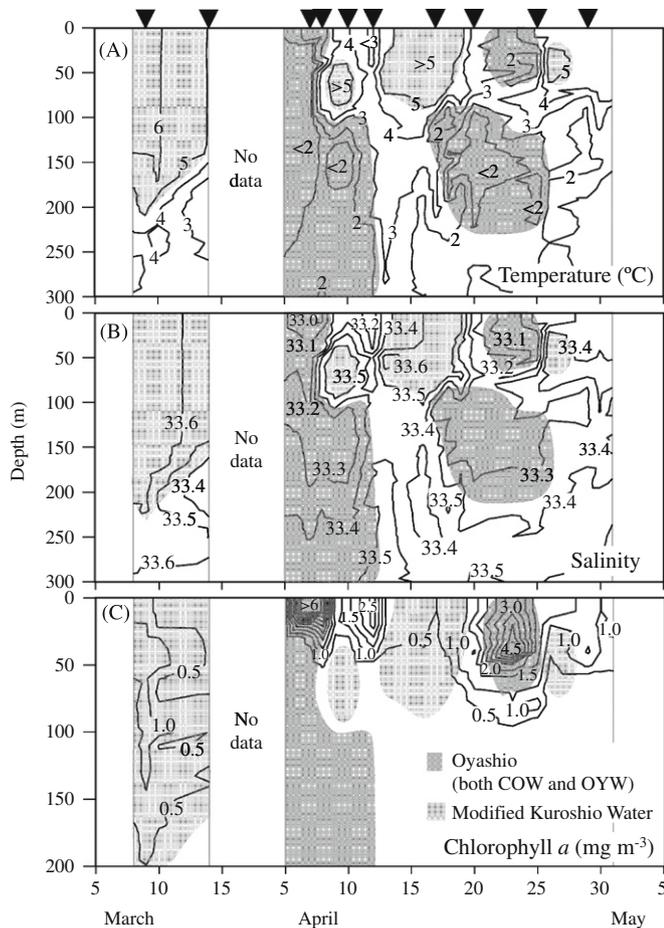
### 2.3. Statistical treatment of data

The effects of environmental parameters (temperature, chlorophyll *a*) on the abundance of euphausiids were analyzed by calculating correlation coefficients. Comparison of slope and elevation of regression lines (abundance of euphausiids vs. temperature or chlorophyll *a*, and mean *TLs* vs. time elapsed) was made by analysis of covariance (ANCOVA). Significance was tested at the  $p = 0.05$  level, unless otherwise specified.

## 3. Results

### 3.1. Hydrography

Over the study period, water temperatures of the top 200 m ranged from 1.1 to 6.1 °C (Fig. 2A). Three water masses coastal Oyashio water (COW), Oyashio water (OYW), and modified Kuroshio water (MKW) were present during the study period (Kono and Sato, 2010). Oyashio Water (both COW and OYW), characterized by temperatures 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. Modified



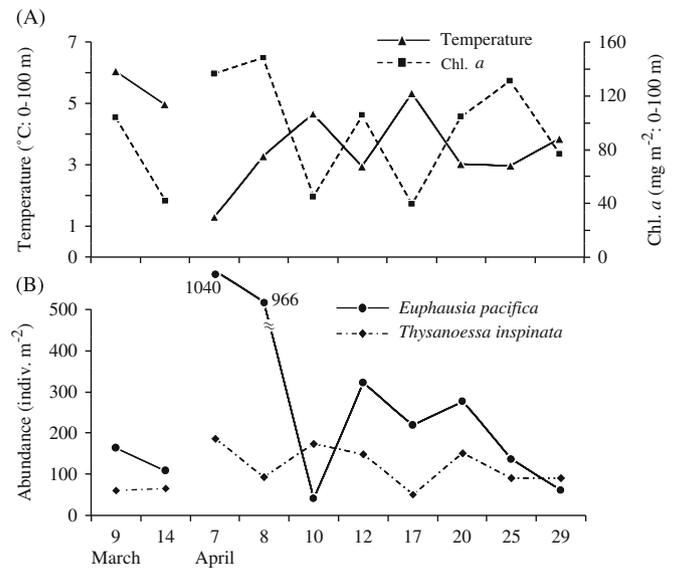
**Fig. 2.** Temporal changes in temperature (A), salinity (B) and chlorophyll *a* (C) profiles at St. A-5 in the Oyashio region during March to April 2007. Solid triangles along the top abscissa indicate sampling dates. Note that depth scale of (C) is not the same as that of (A) and (B). Dominant water masses (Oyashio [includes Coastal Oyashio Water and Oyashio Water] and Modified Kuroshio Water) are shown in the panels (cf. Kono and Sato, 2010).

Kuroshio Water, characterized by higher temperature and higher salinity than in the Oyashio Water, was observed above 200 m during 9–14 March and above 100 m during 13–19 April (Fig. 2A, B). Chlorophyll *a* concentrations were low in March then increased in April. A peak of chlorophyll *a* concentrations as high as  $6.3 \text{ mg m}^{-3}$  was seen in the upper 50 m on 7–8 April (Fig. 2C). A second peak ( $4.5 \text{ mg m}^{-3}$ ) was observed on 23 April. The incidence of both chlorophyll *a* peaks coincided with presence at St. A-5 of cold, low-salinity Oyashio Water (Fig. 2C).

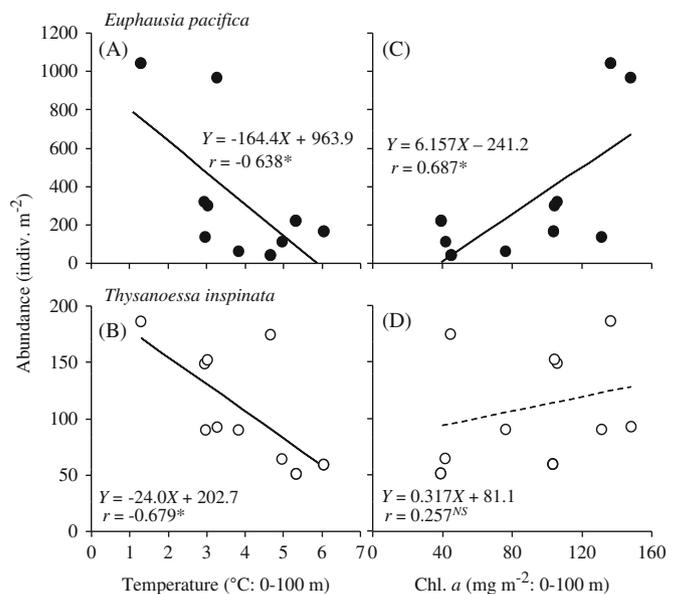
### 3.2. Euphausiid abundance

Six euphausiids belonging to three genera were identified to species level: *Euphausia pacifica*, *Thysanoessa inspinata*, *Thysanoessa longipes*, *Thysanoessa inermis*, *Thysanoessa raschii*, and *Tessarabrachion oculatum*, there were also a few specimens of *Stylocheiron* spp. Among these, *E. pacifica* and *T. inspinata* composed 63.3% (mean) and 33.6% (mean), respectively, of the total euphausiids occurring during the present study period.

The abundance of *E. pacifica* varied greatly in the course of the sampling, ranging from 41 to 1,040 individuals  $\text{m}^{-2}$  (mean: 335 individuals  $\text{m}^{-2}$ ) (Fig. 3B). The abundance peak was on 7–8 April, when the chlorophyll *a* concentration also peaked. The abundance of *T. inspinata* ranged from 50 to 186 individuals  $\text{m}^{-2}$  (mean: 111 individuals  $\text{m}^{-2}$ ) (Fig. 3B). Correlation between the abundance and environmental parameters (integrated over 0–100 m, Fig. 4)



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



**Fig. 4.** Relationships between the abundance and mean water temperature and standing stock of chlorophyll *a* integrated over 0–100 m depth for *Euphausia pacifica* [(A), (C)] and *Thysanoessa inspinata* [(B), (D)] at St. A-5 in the Oyashio region during 9 March to 29 April 2007. \*:  $p < 0.05$ , NS: not significant.

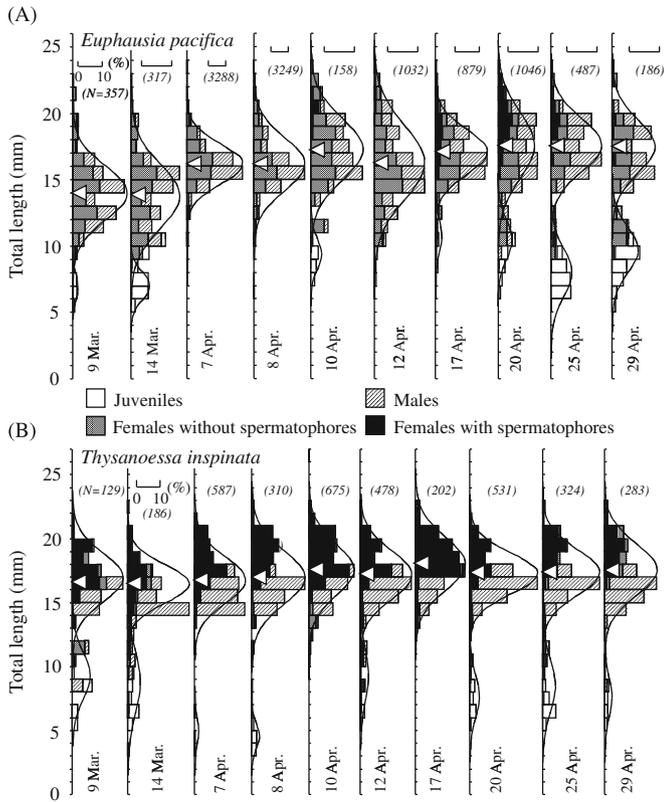
was significantly negative with temperature for both *E. pacifica* and *T. inspinata* stocks (Fig. 4A, B), but chlorophyll *a* concentrations had a significantly positive relationship only for *E. pacifica* (Fig. 4C). As an index of temperature sensitivity, the slope of the regression line of the abundance of *E. pacifica* ( $-164.4$ ) on temperature did not differ significantly from that ( $-24.0$ ) of *T. inspinata* (ANCOVA, *F*-test,  $p > 0.05$ ).

### 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 2). Adult females with spermatophores occupied about 5%

**Table 2**  
Mean abundance (indiv.  $m^{-2}$ ) of juveniles, adult males and adult females (with and without spermatophores) of the two dominant euphausiids in the Oyashio region during 9 March to 29 April 2007. Values are mean  $\pm$  1sd. Percentages of the total are in the parentheses.

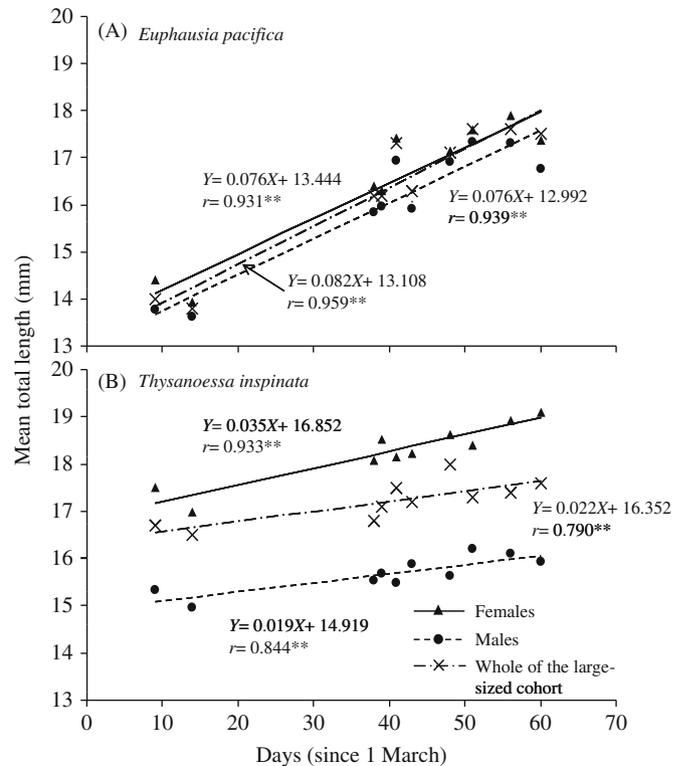
Euphausiids	Juveniles	Males	Females without spermatophores	Females with spermatophores
<i>Euphausia pacifica</i>	12.1 $\pm$ 7.7 (8.3)	150.6 $\pm$ 172.1 (41.9)	162.1 $\pm$ 196.5 (44.8)	10.4 $\pm$ 17.0 (4.9)
<i>Thysanoessa inspinata</i>	4.8 $\pm$ 3.7 (5.3)	51.1 $\pm$ 28.1 (44.6)	6.3 $\pm$ 4.2 (6.5)	48.3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



**Fig. 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 St. A-5 in the Oyashio region during 9 March to 29 April 2007. Hypothetical normal distribution curves, mean TLs (open triangles; major mode only) and the numbers (N) of individuals measured are superimposed.

of the total population over the study period (Fig. 5A, Table 2). The entire range of TL (5.2 to 25.4 mm) of *E. pacifica* was binned by 1 mm increments (Fig. 5A) to show the size-frequency distribution. The ranges of TL were 5.2–11.6 mm for juveniles, 8.7–23.1 mm for adult males, 9.1–25.4 mm for adult females without spermatophores and 15.5–23.3 mm for females with spermatophores (Fig. 5A). Modal size analyses revealed consistent occurrence of one large group (13.8–17.6 mm TL), often accompanied by one discrete group of smaller individuals (6.9–10.5 mm TL). Plotting the mean TL of the larger size group against dates since the first sampling (9 March 2007), a mean growth rate of 0.082 mm TL day<sup>-1</sup> was estimated from the slope of the regression line (Fig. 6A). Adult males and females were exclusive components of the large size group, and plotting their mean TL data against sampling dates yielded two parallel regression lines with the same slope (0.076 mm day<sup>-1</sup>). The elevation of the two regression lines did not differ significantly (ANCOVA, *F*-test,  $p > 0.05$ ).

The sex ratio (female:male) of *Thysanoessa inspinata* ranged from 1:0.35 to 1:1.54 over the study period (mean 1:0.94). Adult females with spermatophores comprised 44% (mean) of the total population over the study period (Fig. 5B, Table 2). The entire



**Fig. 6.** Linear growth of *Euphausia pacifica* (A) and *Thysanoessa inspinata* (B) based on the progressive increase in mean total length of males, females and whole of the large-sized cohort from 9 March to 29 April 2007 in Fig. 5. \*\*:  $p < 0.01$ .

range of TL (3.7 to 26.7 mm) of *T. inspinata* was binned by 1 mm increments to show the size-frequency distribution (Fig. 5B). The ranges of TL were 3.7–11.4 mm for juveniles, 6.8–20.5 mm for adult males, 8.4–22.1 mm for adult females without spermatophores, and 10.3–26.7 mm for females with spermatophores (Fig. 5B). Modal size analyses showed the consistent presence of one group of large individuals (16.5–18.1 mm TL) and one group of small individuals (4.6–9.3 mm TL). A plot of the mean TLs of the larger groups against dates since the first sampling (9 March 2007) yielded a mean growth rate of 0.022 mm TL day<sup>-1</sup> for *T. inspinata* (Fig. 6B). Mean growth rates of adult males and females estimated separately were 0.019 and 0.035 mm day<sup>-1</sup>, respectively. The growth rate of adult females was significantly greater than that of adult males (ANCOVA, *F*-test,  $p < 0.025$ ). Comparison of adjusted mean TLs revealed that adult females were significantly larger than adult males (ANCOVA, *F*-test,  $p < 0.01$ ).

## 4. Discussion

### 4.1. Abundance

As an annual event in the Oyashio region, the phytoplankton bloom (chlorophyll *a* concentrations: 2–9 mg  $m^{-3}$ ) has been observed from late March to May (Kasai et al., 2001). During this

**Table 3**Growth rates (mm TL day<sup>-1</sup>) of *Euphausia pacifica* and *Thysanoessa* spp. observed at various subarctic regions during their growing seasons of the year.

Euphausiids	Location	Period	Age	Temp (°C)	Growth rate (mm TL day <sup>-1</sup> )	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 Pearcy (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	

2007 study, chlorophyll *a* concentrations increased from 0.5–1 mg m<sup>-3</sup> in March to 6 mg m<sup>-3</sup> in April (Fig. 2), at the peak of the phytoplankton bloom at the sampling station. The temporal variations in chlorophyll *a* were partly due to the exchange in water masses in the surface layer at St. A-5. The incidence of higher chlorophyll *a* was associated with occupation by Coastal Oyashio Water, and the incidence of lower chlorophyll *a* accompanied the presence of Modified Kuroshio Water with higher temperature and higher salinity than the Oyashio Water (Kono and Sato, 2010). Despite the shifting of water masses, both *Euphausia pacifica* and *Thysanoessa inspinata* occurred in samples throughout the entire study period (Fig. 3A). Negative correlation of the abundances of both *Euphausia pacifica* and *Thysanoessa inspinata* with water temperatures (Fig. 3A, B) indicates that both occurred more numerously during lower temperature periods. According to Taki (2008) who studied horizontal and vertical distributions 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 areas, and their tolerance limits for high temperatures were 15 °C for *E. pacifica* and 10 °C for *T. inspinata*. Among subarctic euphausiids, temperature preferences vary in the following order (low to high temperatures); *Thysanoessa raschii* – *T. inermis* – *Tessarabrachion oculatum* – *T. longipes* – *T. inspinata* – *E. pacifica* (Mauchline and Fisher, 1969). Therefore, it is anticipated that the slope of a regression line of the abundance vs. temperature for *T. inspinata* would be steeper than that for *E. pacifica* (Fig. 4). However, our significance tests for the difference in the slopes failed to confirm that (ANOVA, *F*-test, *p* > 0.05). That is probably due to a temperature range too narrow (1.3–6.1 °C) to detect the significant difference between these two euphausiid species. Fluctuation of *E. pacifica* abundance was positively correlated with chlorophyll *a* concentration (*r*=0.687), but this was not the case for *T. inspinata* (Fig. 4C, D). *Euphausia pacifica* preferentially consumes phytoplankton when they are available at relatively high concentrations (Nakagawa et al., 2001). While precise information about food habits of *T. inspinata* is not available, a congener, *T. longipes*, is known to prefer a zooplankton diet off Sanriku (Endo, 1981). The differential in food preferences between *E. pacifica* and *T. inspinata* may be reflected in the dissimilar results of correlation analyses in this study (Fig. 4C, D).

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 (Kim et al., 2009). According to those results, *E. pacifica* spawns 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, then mature, reproduce and complete their lives in the following year.

Following those life cycle schemes, the larger sized individuals of *E. pacifica* (14–18 mm, Fig. 5A) and *T. inspinata* (16–18 mm, Fig. 5B) found in this study are considered to be those born in the previous year. Despite large fluctuations in abundance during the present study period, the large size-groups of both species were growing: 0.082 mm day<sup>-1</sup> for *E. pacifica* and 0.022 mm day<sup>-1</sup> for *T. inspinata* (Fig. 6). Persistence of the large individuals, despite the exchange of water masses during this study (Fig. 2) strongly suggests the presence of single populations of *E. pacifica* and *T. inspinata* throughout the Oyashio region. According to the life cycle scenario for both euphausiids, as mentioned above, groups of smaller individuals occurred frequently for both species (Fig. 5), young very likely developed from eggs spawned in 2007. While no appreciable differences in TLs between adult males and females were detected for *E. pacifica*, adult males of *T. inspinata* were significantly smaller than adult females (Fig. 6). A growth curve with males achieving a smaller size than females, despite both sexes exhibiting the same longevity, has been reported for *Thysanoessa longipes* (Iguchi and Ikeda, 2004) and *Thysanopoda acutifrons* (Mauchline, 1985). The incidence of adult males but not adult females in the small size group of *T. inspinata* suggests that males mature earlier than females in this species (Fig. 5).

Since the growth of euphausiids is 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 basis of data for the same or similar species and mostly from phytoplankton bloom seasons in spring or summer (Table 3). Our result (0.076 mm day<sup>-1</sup> for adult males and females or 0.082 mm day<sup>-1</sup> for the whole large sized populations [includes adult male, female and juveniles], Fig. 6A) for *Euphausia pacifica* in the Oyashio region falls between the estimates of 0.056 mm day<sup>-1</sup> for the population off northeastern Japan (Taki and Ogishima, 1997) and of 0.11 mm day<sup>-1</sup> for a stock off the Oregon coast (Smiles and Pearcy, 1971). Our results (0.019 mm day<sup>-1</sup> for adult males, 0.035 mm day<sup>-1</sup> for adult females or 0.022 mm day<sup>-1</sup> for the mixed adult male and female populations, Fig. 6B) for *T. inspinata* are much less than the range of 0.070–0.123 mm day<sup>-1</sup> for other *Thysanoessa* spp. from various locations in subarctic and arctic waters (Table 3). Taking into account that the present study was conducted during a phytoplankton bloom, the observed slow growth of *T. inspinata* may be due to allocation of ingested nutrient to reproduction rather than somatic growth. To support this, the occurrence of females with spermatophores was much greater for *T. inspinata* (mean: 43.6% of the total population) than for *E. pacifica* (only 4.9%) (Table 3), although the adult female:male ratios of the two euphausiids were identical (1:0.9). The same cause may explain the somewhat low growth rates of *E. pacifica* in our study. One might argue whether or not the incidence of females with spermatophores (=mating) is indicative of active spawning in

euphausiids (Mauchline and Fisher, 1969). As examples, April mating and spawning of *Thysanoessa inermis* and *T. raschii* in the Barents Sea occur in the same brief period (Drobysheva, 1957), whereas mating of Antarctic krill *Euphausia superba* occurs several weeks before spawning (Bargmann, 1945). In the Clyde Sea (UK), *Meganyctiphanes norvegica* with spermatophores attached occur in February, but spawning is delayed until the beginning of April. That is 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 depending on the environmental conditions (Mauchline and Fisher, 1969). In the course of metabolic measurements on *E. pacifica* and *T. inspinata*, which were run in parallel with the Bongo net sampling of this study, the females of both euphausiids were often observed to spawn during incubations (Kim et al., 2010), confirming that the incidence of females with spermatophores attached is a good indicator of current spawning activity for both euphausiids.

### Acknowledgments

We thank the captain, officers and crews of the T/S 'Oshoro-Marui' (Hokkaido University) and R/V 'Hakuho-Marui' (Japan Agency for Marine-Earth Science and Technology) for their help in field sampling. This study was part of OECOS WEST project sponsored by PICES.

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