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Citation	Plankton & benthos research, 4(2), 43-52 https://doi.org/10.3800/pbr.4.43
Issue Date	2009-05
Doc URL	http://hdl.handle.net/2115/52342
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Type	article
File Information	0402_043.pdf

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Plankton Benthos Res 4(2): 43–52, 2009

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Abundance, biomass and life cycle patterns of euphausiids (*Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes*) in the Oyashio region, western subarctic Pacific

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Received 20 August 2008; Accepted 24 December 2008

Abstract: A series of oblique hauls with Bongo nets (0–1000 m) was made during the period of August 2002 through August 2004 in the Oyashio region, western subarctic Pacific, to investigate abundance, biomass and life cycle patterns of the three predominant euphausiids (*Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes*). While the three euphausiids occurred throughout the entire study period, *E. pacifica* was the most abundant (1,120 indiv. m^{-2}, or 832 mg C m^{-2}), followed by *T. inspinata* (163 indiv. m^{-2}, or 144 mg C m^{-2}) and *T. longipes* (73 indiv. m^{-2}, or 75 mg C m^{-2}). Judging from the occurrence of females with spermatophores and furcilia larvae, the spawning was considered to take place twice a year (April–May and August) for *E. pacifica*, year-round (peak season: March–May) for *T. inspinata* and in spring (March–May) for *T. longipes*. The population structure in terms of size (=total length) frequency distributions of the three euphausiids was characterized by the frequent co-occurrence of 2–3 cohorts in the same samples. 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*, 27 mm and 31 mm, respectively, for *T. longipes*. Tracing the sequence of cohorts, 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. These results are compared with reports of the same species in other habitats in the light of regional variations.

Key words: *Euphausia pacifica*, euphausiids, Oyashio region, *Thysanoessa inspinata*, *Thysanoessa longipes*

Introduction

As a component of zooplankton, euphausiids are distributed widely in the world oceans from Arctic through Antarctic waters, and form a vital link between phytoplankton production and production of animals at higher trophic levels, such as fish, seabirds and whales (Mauchline & Fisher 1969, Mauchline 1980). Despite the important roles of euphausiids in biogeochemical cycles and energy flow of marine pelagic ecosystems, our knowledge about their biomass and life cycles is still too scarce to evaluate their roles fully (Siegel 2000).

The euphausiids *Euphausia pacifica* Hansen, *Thysanoessa inspinata* Nemoto and *T. longipes* Brandt are widespread over the entire subarctic Pacific Ocean and its marginal seas including the Bering, Okhotsk and Japan Seas (Brinton et al. 2000). They are considered to be primary grazers and are distributed broadly in the epipelagic zone of the ocean (Brinton 1962, Mauchline & Fisher 1969). Among these three euphausiids, the life cycle patterns and biomass have been studied most extensively on *E. pacifica*; e.g. those in the Japan Sea (Iguchi et al. 1993, Iguchi & Ikeda 2004), off northeastern Japan (Taki 2004, 2006, 2007), off Oregon and southern California (Smiles & Pearcy 1971, Brinton 1976, Feinberg & Peterson 2003) and the southwestern Okhotsk Sea (Ponomareva 1966). Comparable information is much less for *T. longipes* [those in the Japan Sea (Iguchi & 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

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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, is known as a feeding ground of both pelagic and benthic fishes (Yamamura et al. 2002, Sugisaki & Kurita 2004) and euphausiids are an integral diet any component for them (Ikeda et al. 2008). Unfortunately, the biomass and life cycle features of the dominant euphausiids (*E. pacifica*, *T. 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, biomass and life cycle of these species as reported in other regions of the subarctic Pacific and adjacent seas, with notes on the mechanism of coexistence of these euphausiids with similar food habits.

Materials and Methods

Field sampling

Seasonal zooplankton sampling was made at Site H (41°30′N, 145°50′E, Fig. 1) in the Oyashio region during August 2002 through August 2004 (Table 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.

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 low numbers, 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 & Komaki (1979) for *T. inspinata* and *T. longipes*. The furcilia larvae of *T. inspinata* and *T. longipes* were separated from each other based on the position of the lateral denticle on the carapace: posterior margin for *T. inspinata* and middle margin for *T. longipes*. Distance between anterior tip and lateral denticle (D) was 70–90% of the total length of the carapace (L: 0.9–1.5 mm) for *T. inspinata* while this was 40–67% of that (0.9–1.8 mm) of the carapace for *T. longipes* (Fig. 2). Adults were separated from juveniles by the development of external secondary sexual characters; petasma for males and thelycum for females (Makarov & Denys 1981). Adult females with spermatophores (attached to thelycum between gills and exopodite of sixth thoracic leg, cf. Mauchline & Fisher 1969) were considered as an index of recent spawning.

Body length (BL: mm), from the posterior margin of the

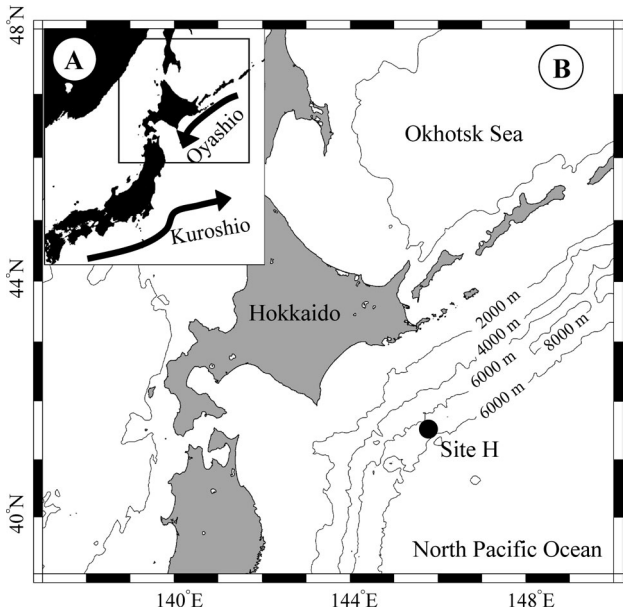


Fig. 1. Oyashio region in the western subarctic Pacific (A) and the sampling site (Site H) in the Oyashio region (B). Depth contours (2000, 4000, 6000 and 8000 m) are superimposed in B.

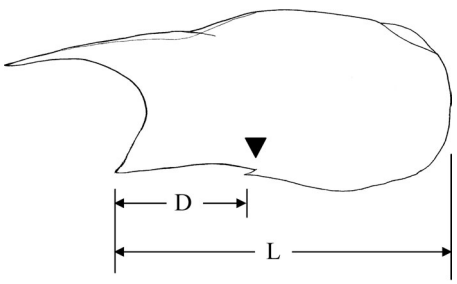
Table 1. Zooplankton sampling data at Site H in the Oyashio region during August 2002–August 2004. Samples were collected by oblique hauls of a Bongo net in the 0–1000 m water column.

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 Jun	16:00–17:15
	7 Jun	06:31–07:49
	15 Jun	08:21–09:47
	28 Jun	14:45–16:15
	23 Aug	23:57–01:17
	5 Oct	06:40–07:50
	17 Dec	12:16–14:00
2004	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 Jun	09:15–10:55
	22 Aug	06:37–08:30

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 equations of TL-BL relationships were established and BL data were converted to TL in this study. At the same time, preserved specimens for 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 the WM-BL relationships (allometric model: $WM = aBL^b$, where a and b are constants). The allometric equations were combined with BL frequency distribution data to compute population biomass at a given sampling date for each euphausiid species. Population biomass (WM) of the three euphausiids thus obtained was converted finally to carbon units by using the following conversion factors: water content to be 80% of WM and carbon content to be 43% of DM (cf. Iguchi & Ikeda 1998).

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 1) were pooled to trace the growth sequence of cohorts on monthly or bimonthly 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 & Takiguchi 1999). Life span of each generation was estimated from assuming that development time of earlier stages (eggs, naupliar and calyptopis larvae) was ca. one month (Ross, 1981).



Thysanoessa inspinata
D:L= 0.70-0.90 (n= 41)

Thysanoessa longipes
D:L= 0.40-0.67 (n= 46)

Fig. 2. Ratios of the distance between anterior tip and lateral denticle (D) to the total length of the carapace (L) in furcilia larvae of *Thysanoessa inspinata* and *T. longipes*. Solid triangle indicates lateral denticle of carapace. Values are ranges for each species.

Results

Hydrography

Surface temperatures ranged from ≤1°C (February 2003) to 16°C (August 2002) (Fig. 3). The Oyashio Water, characterized by a temperature below 3°C and salinities from 33.0 to 33.3 (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°C and thermoclines developed at 10–50 m during August–October 2002, June-December 2003 and June–August 2004. Effects of a warm-core ring originating from the Kuroshio Extension (cf. Yasuda et al. 1992) were observed above 200 m in May 2003 and December 2003 to March 2004, as judged by high temperatures >5°C and high salinities >33.5 (Fig. 3). Below 200 m, temperatures and salinities were nearly constant at 2–3°C and 33.3–34.5, respectively.

Body allometry

The TL-BL and WM-BL relationships for *Euphausia pacifica*, *Thysanoessa inspinata*, and *T. longipes* obtained in

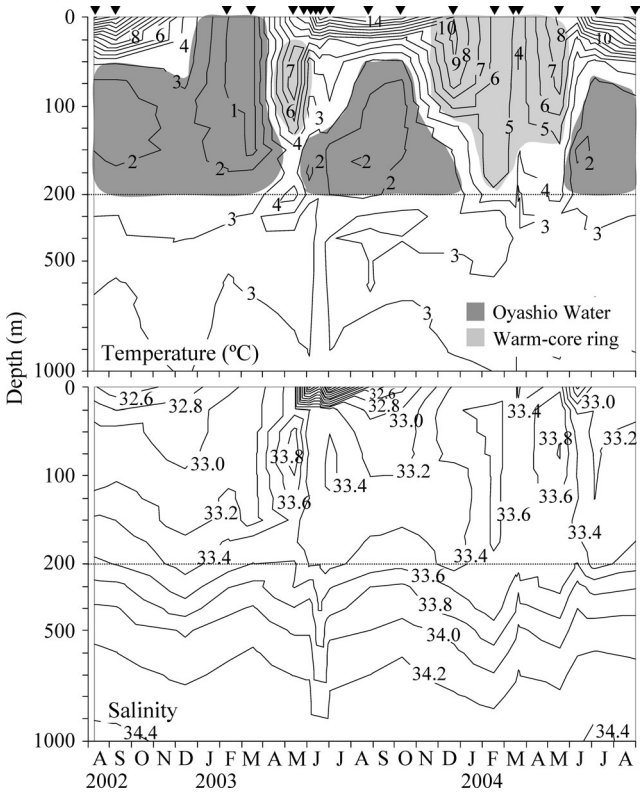


Fig. 3. Temperature (upper panel) and salinity (lower panel) profiles at Site H during the period of August 2002 to August 2004. Incidences of the Oyashio Water and warm-core ring water are shown in the top panel. Sampling dates are indicated by solid triangles on the top abscissa. Note that the depth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

Table 2. Body allometry equations between total length (TL: mm) and body length (BL: mm), and wet mass (WM: mg) and BL for *Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes* in the Oyashio region. **: $p<0.01$.

Species	TL-BL (n, r)	WM-BL (n, r)
Euphausia pacifica	TL=1.133BL+1.364 (67, 0.998**)	WM= $0.0082BL^{3.130}$ (67, 0.995**)
Thysanoessa inspinata	TL=1.262BL+1.145 (90, 0.992**)	WM=$0.0110BL^{3.190}$ (53, 0.994**)
Thysanoessa longipes	TL=1.410BL+0.129 (54, 0.998**)	WM=$0.0085BL^{3.263}$ (55, 0.996**)

this study were summarized in Table 2. All the regressions were highly significant ($p<0.01$).

Abundance, Biomass and Life Cycle

Euphausia pacifica

This euphausiid was abundant in summer to autumn (October 2002 and August 2004) or spring (May 2003) but uncommon in winter (February–March 2003 and November–March 2004) (Fig. 4A). Seasonal changes in biomass paralleled those of numerical abundance, except for August 2003 when adults were the major component of the population, and August 2004 when furcilia larvae were the major component of the population (Fig. 4A). The mean abundance and biomass over the entire study period were 1,120 indiv. m^{-2} and 832 mg C m^{-2}, respectively (Table 3).

Furcilia larvae occurred throughout the year with the exception of February–March and August 2003 and February 2004, with peaks in August 2002 (30% of the total population), June and October–December 2003 (37–47% of the total population) and May and August 2004 (62–73% of the total population) (Fig. 4B). 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 the higher proportion of furcilia larvae in the population at that time, suggests that the major spawning season is spring (April–May) and summer (August).

The entire range of TL (3 to 25 mm) was divided equally into 1 mm increments (Fig. 4C). 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. 4C).

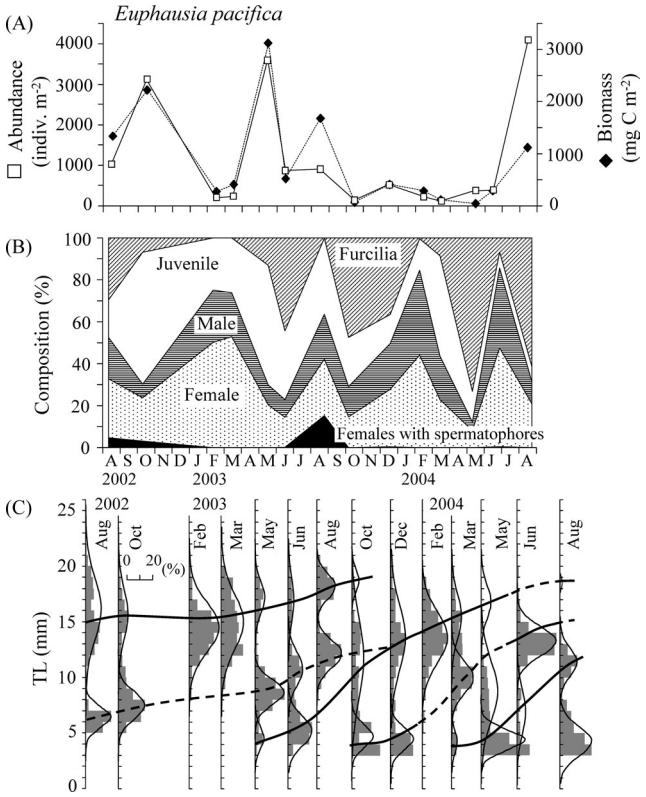


Fig. 4. *Euphausia pacifica*. Seasonal changes in numerical abundance and biomass (A), developmental stage composition (B) and length-frequency histograms (C) at Site H in the Oyashio region from August 2002 through August 2004. Hypothetical TL distribution curve of each cohort and clear (solid lines) and unclear (dotted lines) growth sequences of cohorts are superimposed in (C).

Sequences of spring (April–May) and summer (August) cohorts were not necessarily clear. For example the +0 year-old summer cohort might have mixed with the +0 year-old spring cohort of the next year (Fig. 4C). If this growth scheme is correct, the cohort generated in May reached 12–13 mm TL and matured in October–December of the same year. They overwintered and reproduced, and completed their lives at 18–19 mm TL, for 17 months since birth. On the other hand, the cohort generated in August grew and overwintered at 7–8 mm TL. In the following

Table 3. Regional comparison of the abundance (indiv. m^{-2}) and biomass (mg C m^{-2}) of the euphausiids *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
Euphausia pacifica	Oyashio region	1120	832	This study
	southeastern Hokkaido	1570	381	Taki (2006, 2007)
	Toyama Bay, Japan Sea	5500	1090	Iguchi et al. (1993)
				Iguchi & Ikeda (1999)
Thysanoessa inspinata	Oyashio region	163	144	This study
	southeastern Hokkaido	146		Taki (2007)
Thysanoessa longipes	Oyashio region	72.6	74.6	This study
	southeastern Hokkaido	24.0		Taki (2007)

year, the overwintered cohort matured, reproduced and completed their lives at 19–20 mm TL in 26 months since birth.

Thysanoessa inspinata

This euphausiid was most numerous in August–October 2002 and least in February–March 2003 and February and June 2004 (Fig. 5A) with a mean abundance of 163 indiv. m^{-2} (=144 mg C m^{-2}) over the entire study period (Table 3). The seasonal patterns of the abundance and population biomass were similar to each other, except for August 2003 when 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. 5B). Juveniles were the second most 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 *E. pacifica* mentioned above (Fig. 4C). New cohorts generated in March–May grew and overwintered at 11–13 mm TL, then matured, reproduced and died off in June–October in the following year (estimated life span = 17–19 months, Fig. 5C).

Thysanoessa longipes

Seasonal changes in the abundance and biomass of this species were nearly in parallel with the other species with the exception that in August furcilia larvae increased suddenly (Fig. 6A, B). The abundance (mean: 72.6 indiv. m^{-2}) and biomass (mean: 75 mg C m^{-2}) were the least among the three euphausiids investigated in the present study (Table 3).

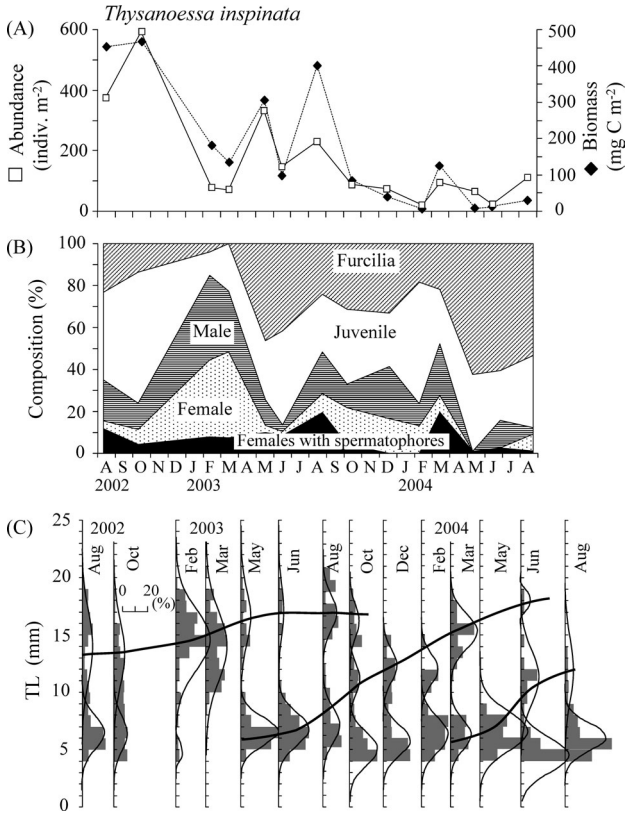


Fig. 5. *Thysanoessa inspinata*. Seasonal changes in numerical abundance and biomass (A), developmental stage composition (B) and length-frequency histograms (C) at Site H in the Oyashio region from August 2002 through August 2004. Hypothetical TL distribution curve of each cohort and clear (solid lines)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

The population structure was characterized by the short predominance of furcilia larvae in summer, which was followed by juveniles (Fig. 6B). Adult female: male ratios ranged from 1 : 0.1 to 1 : 3 throughout the study period

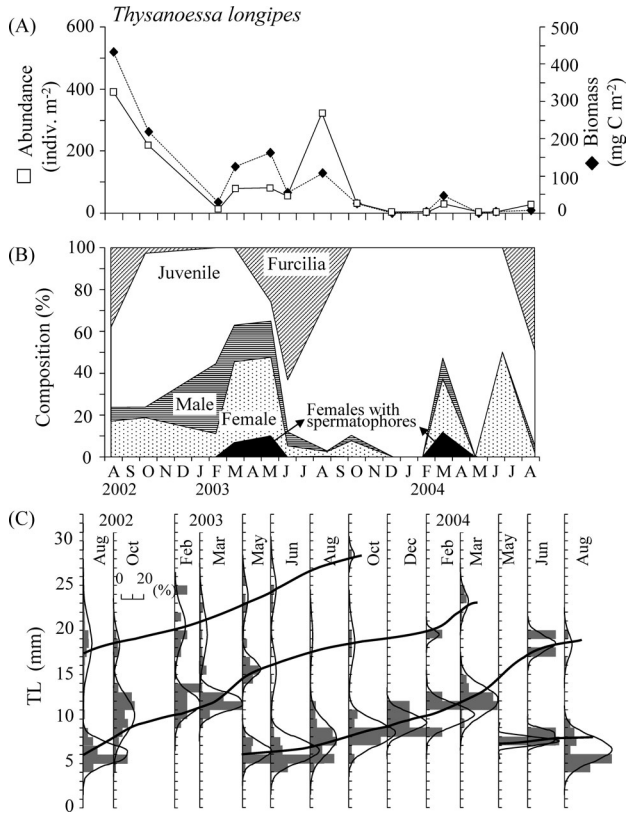


Fig. 6. *Thysanoessa longipes*. Seasonal changes in numerical abundance and biomass (A), developmental stage composition (B) and length-frequency histograms (C) at Site H in the Oyashio region from August 2002 through August 2004. Hypothetical TL distribution curve of each cohort and clear (solid lines) and unclear (dotted lines) growth sequences of cohorts are superimposed in (C).

(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 was 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 *E. pacifica* mentioned above (Fig. 6C). 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).

Discussion

Abundance and biomass

The abundance and biomass of the euphausiids *Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes* at Site H were higher during summer 2002 and spring/summer 2003, but low in spring (*E. pacifica*) or spring/summer 2004 (*T. inspinata* and *T. longipes*) (Figs. 4A, 5A, 6A). These decreases in the abundance and biomass in 2004 may be related to the changes in water masses in the upper layers. The effects of a warm-core ring (named as "2003C", Ito et al. 2006) defined by high temperature >5°C and high salinity >33.5, originating from the Kuroshio Extension Water (Yasuda et al. 1992) were observed during December 2003 to June 2004 (Fig. 3). In the same seasons of 2002 and 2003, cold Oyashio Water was observed instead (Fig. 3). Geographical distribution patterns of euphausiid species are governed by water mass properties of the ocean (cf. Mauchline & Fisher 1969). While the three euphausiids are all subarctic euphausiids, *E. pacifica* occur over a wide temperature range (<2–16°C), as compared to *T. inspinata* from 0–12°C and *T. longipes* from 0.3–5.1°C at 100 m depth (Taki 2007). From these species-specific temperature preferences, an extremely low abundance of *T. longipes* during December 2003–August 2004 (Fig. 6A) may be due to the effect of the warm-core ring observed during that period (Fig. 3). The effects of the warm-core ring on *E. pacifica* and *T. inspinata* might be less since these euphausiids could tolerate a higher temperature regime than *T. longipes* (Figs. 4A, 5A).

Mean abundance over the entire study period (August 2002–August 2004) of *E. pacifica*, *T. inspinata* and *T. longipes* at Site H were of the same order of magnitude to those of respective species reported from off northeastern Japan (Taki 2006, 2007). Among the three euphausiids studied by Taki, biomass data were available only for *E. pacifica*, with a reported value of less than half that found in our study (Table 3). 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 150 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 & Ikeda (1999) used Norpac nets (45 cm diameter, 330 μm mesh) to estimate abundance and biomass of *E. pacifica* in Toyama Bay, but such methodological effects on the results were not evident (Table 3). As an alternative explanation, a higher abundance of *E. pacifica* in Toyama Bay (5,500 indiv. m^{-2}) than that in the Oyashio region (1,120 indiv. m^{-2}) may be attributed largely to the inclusion of eggs in the abundance of the former. The effect of eggs is masked in the biomass comparison (1,090 mg C m^{-2} in Toyama Bay vs. 832 mg C m^{-2}, Table 3) because of their 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). The total

biomass of the three euphausiids (832+144+74.6= 1,051 mg C m^{-2}, Table 3) is 12.8% of the mesozooplankton biomass (annual mean: 8,221 mg C m^{-2}, Ikeda et al. 2008) at Site H.

Life cycles of *Euphausia pacifica*

The life cycle of *E. pacifica* has been studied at several locations, including off northeastern Japan (Taki 2004), Toyama Bay, southern Japan Sea (Iguchi et al. 1993), off Oregon (Smiles & Pearcy 1971, Feinberg & Peterson 2003), and off southern California (Brinton 1976) (Table 4). 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 in February–April of the next year and die at the age of <21 months. The life cycles of the Toyama Bay population are characterized by "growth stagnation" in summer during which they sink to phytoplankton-poor, cooler depths to avoid high surface temperatures beyond the tolerance limits of this species (Iguchi et al. 1993).

In the eastern North Pacific (off south California), reproduction of *E. pacifica* continues throughout the year, and cohorts complete their lives in 8–12 months (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 to high phytoplankton production in most seasons (Brinton 1976). In the Oregon upwelling zone, reproduction of euphausiids can take place in spring (March–May) and summer (July–September) with close association with phytoplankton bloom events (Feinberg & Peterson 2003). Phytoplankton blooming occurs in spring, but phytoplankton concentrations are low in summer through winter in the Oyashio region (Kasai et al. 2001). In this respect, the first spawning season of *E. pacifica* in the Oyashio region (April–May) coincided with the phytoplankton bloom, while the second spawning season (August–September) did not. Recently, Nakagawa et al. (2001) demonstrated that *E. pacifica* off northeast Japan fed on phytoplankton, but switched to feeding on 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 *E. pacifica* have been documented to be highly variable, depending on the extent of seasonal food limitations, and growth rates as high as 0.1 mm TL day^{-1} have been recorded for juveniles during food unlimited seasons (Smiles & Pearcy 1971, Brinton 1976, Iguchi et al. 1993). Because of scatter of the cohort data, seasonal growth of *E. pacifica* in the Oyashio region could not be analyzed precisely in the present study (Fig. 4C). Our recent daily growth monitoring of the *E. pacifica* population in the Oyashio region during a phytoplankton bloom (March–April 2007) yielded a growth rate of 0.061 mm day^{-1} (Kim, unpublished), which is still less than the 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 need to be accounted for. The annual range of sea surface temperatures in the Oyashio region is 1–16°C (Fig. 3), 10–18°C in southern California

Table 4. Regional comparison of maximum body size, spawning seasons and life span of the euphausiids *Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes* in the North Pacific region.

Species	Location	Maximum size (TL: mm)	Spawning season	Life span	References
Euphausia pacifica	Oyashio region	♂: 21 ♀: 24	Apr–May, Aug–Sep	17–26 months	This study
	Toyama Bay (Japan Sea)	♂: 22 ♀: 23	Feb–Apr	<21 months	Iguchi et al (1993)
	off Oregon	♂, ♀: 22–24	All seasons	12 months	Smiles & Pearcy (1971)
	off Oregon		Jul–Aug	—	Feinberg & Petersen (2003)
	off southern California	♂, ♀: 21	All seasons	8–12 months	Brinton (1976)
	off northeastern Japan	♂, ♀: 19–20	Apr–May, Aug–Oct	24–28 months	Taki (2004)
Thysanoessa inspinata	Oyashio region	♂: 18 ♀: 23	All seasons (Mar–May)	17–19 months	This study
	off Kuril Islands	♂: 23 ♀: 23	May	2 years	Kuznetsova (1980, 1994)
Thysanoessa longipes	Oyashio region	♂: 27 ♀: 31	Mar–May	29–31 months	This study
	Yamato Rise (Japan Sea)	♂: 25 ♀: 32	Apr–May	3 years	Iguchi & Ikeda (2004)

(Brinton 1976), and 8–18°C off Oregon (Feinberg & Peterson 2003). The differences in habitat temperatures of *E. pacifica* within the broad subarctic Pacific regions probably do not affect the minimum maturity size (11–12 mm TL) or the maximum adult size (19–21 mm TL), but may affect the life span of this euphausiid (8–12 months for the eastern inhabitants vs. 17–28 months for the western inhabitants) (Table 4).

The sex ratio (female : male) of euphausiids has been reported to be fairly constant across many species (cf. Siegel 2000). In this respect, the present result (mean 1 : 0.54) is an exception. However, such a female-biased ratio has also been observed in the population off California, and is interpreted as a result of net avoidance by larger males, higher mortality of larger males, slower growth rate of females or possibly a shorter life span for males (Brinton 1976).

Life cycles of *Thysanoessa inspinata* and *T. longipes*

Despite a broad distribution across the entire subarctic Pacific (Brinton 2000), studies of the life cycle of *T. inspinata* are currently limited to those of Kuznetsova (1980, 1994) off Kuril Islands. Off the Kuril Islands, *T. inspinata* spawns in spring (May) and its life span is two years (Table 4). 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. 5B, C). Nevertheless, cohort development was traceable only for the furcilia larvae that emerged in March–May (Fig. 5C). The furcilia larvae grew, overwintered, and spawned during the spring phytoplankton bloom of the next year. Our estimate of the life span (17–19 months) for *T. inspinata* is less than the 2 years estimated for the population off the 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 4).

The sex ratio (female : male) of *T. inspinata* was 1 : 1.8 (mean), which is different markedly from 1 : 0.5 of *E. pacifica* mentioned above and 1 : 0.4 of *T. longipes* mentioned below (see Figs. 4B, 5B, 6B). The causative mechanism for this male-biased sex ratio is currently unknown, but it may be related to the year-round occurrence of females with spermatophores in *T. inspinata* (Fig. 5B). In contrast limited seasonal occurrence of spermatophore-bearing females was found in *E. pacifica* and *T. longipes* (Figs. 4B, 6B). Some possible differences leading to male- or female-biased sex ratios are discussed by Brinton (1976) for *E. pacifica*.

Information about the life cycle of *T. longipes* is currently limited to the population around Yamato Rise in the central Japan Sea (Iguchi & Ikeda 2004). According to Iguchi & Ikeda (2004), *T. longipes* spawns in April–May. Resultant young mature in two years, and complete their lives in three years (Table 4). The spawning season (March–May) of *T. longipes* in the Oyashio region observed in this study is similar to that reported for the population in the central Japan Sea. It is noted that the spawning season of this euphausiid overlaps the period of the spring phytoplankton bloom both in the central Japan Sea (Chiba & Saino 2002) and in the Oyashio region (Kasai et al. 2001). Coincidence of reproduction and the spring phytoplankton bloom has also been reported for other subarctic *Thysanoessa* euphausiids (*T. inermis* Krøyer and *T. raschii* M. Sars) in the Atlantic Ocean (Falk-Petersen & Hopkins 1981, Astthorsson 1990).

Spawning seasons and the maximum size of *T. longipes* in the Oyashio region and the central Japan Sea are similar, but the former has a shorter life span (2.5 years) than the latter (3 years) (Table 4). As a habitat for euphausiids, the Japan Sea is unique by being 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 & Ikeda 2004). In addition to slow growth, delayed maturation has also been documented for mesopelagic zooplankton species such as the amphipod *Primno abyssalis* Bowman (Yamada et al. 2002) and the ostracod *Discoconchoecia pseudodiscophora* Rudjakov (Kaeriyama & Ikeda 2002) in the Japan Sea.

Finally, a question may arise: how do these herbivorous euphausiids (*E. pacifica*, *T. inspinata* and *T. longipes*) coexist in the epipelagic zone and avoid possible overlap of reproduction and growth? 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), in the Barents Sea and in Norwegian shelf waters (Dalpadado & Skjoldal 1996, Dalpadado 2006). Studies have shown that *T. inermis* spawn during the phytoplankton bloom and overwinter without feeding while *T. raschii* spawn late and feed on non-phytoplankton food in winter (Falk-Petersen 1985) thus avoiding between-species competition. In this study, we were 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 the 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 been shown to have greater energy reserves (higher body C : N ratios) than *E. pacifica* does (Iguchi & Ikeda 2005). While little has been explored on euphausiids as yet, differentiating food preference, feeding time or depth distribution are known to be mechanisms for avoidance of resource competition among large grazing copepods (*Neocalanus, Eucalanus*) in the eastern and western subarctic Pacific (Mackas et al. 1993, Sato et al. unpublished).

Acknowledgements

We thank the captains, officers and crews of the R.V. '*Ushio-Maru*' and T.S. '*Oshoro-Maru*' (Hokkaido University) for their help in the field sampling.

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