Seasonal changes in distribution and abundance of euphausiids in the coastal area of north-eastern Japan

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ABSTRACT: Seasonal changes in distribution and abundance of euphausiids off south-eastern Hokkaido (41°–43°N), Sanriku (38°–41°N), and Joban (36°–38°N) were investigated using cylindrical-conical nets every two months from March 1997 to February 1998. Twenty-six species of seven genera of euphausiids occurred during the survey. Among them, subarctic-transitional *Euphausia pacifica* was the most abundant throughout the year in coastal waters, as their relative contribution to the total abundance of euphausiids was 89–92%. This species occurred in each coastal water throughout the survey and was abundant from winter to early summer (February–June) off Sanriku and Joban and in autumn in south-eastern Hokkaido. *Thysanoessa inspinata* occurred off south-eastern Hokkaido and Sanriku throughout the survey, mainly in spring (April) but rarely occurred off Joban. Three other subarctic *Thysanoessa* species occurred mainly off south-eastern Hokkaido from winter to spring. Conversely, warm- and transitional-water epipelagic species occurred exclusively off Sanriku and Joban in autumn. The characteristics of seasonal distributional patterns of euphausiids are discussed in relation to the spatial and temporal changes of oceanographic conditions and several predators off north-eastern Japan.

KEY WORDS: abundance, distribution, euphausiids, north-eastern Japan, temperature.

INTRODUCTION

Euphausiids are eucarid crustaceans and the order Euphausiacea is divided into two families, the Bentheuphausiidae and the Euphausiidae; there are 86 known species in the order Euphausiacea.¹ They are distributed widely throughout the world oceans and their relative biomass contributes 5–10% to the total zooplankton.² They are considered key species in marine ecosystems because they are food for many endemic and migrant predators,^{3–5} while they ingest a wide variety of food sources such as zooplankton, phytoplankton, and detritus.^{6–8} Off north-eastern Japan, they are consumed by several predators, e.g. pelagic fishes,^{9–12} demersal fishes,^{13–15} myctophids,¹⁶ sea birds,¹⁷ and whales.^{18,19} Especially, *Euphausia pacifica* is considered a predominant zooplankton off the Pacific coast of north-eastern Japan,²⁰ and is commercially exploited in Sanriku and Joban waters from late winter to early summer

(February–June). Thus, the distribution, biomass, and production of *E. pacifica* have been studied extensively off north-eastern Japan.^{21–26} To clarify the distribution and abundance of other euphausiids is important because spatial and temporal changes of species composition may influence the energy flow through the food web. Distribution of euphausiids off north-eastern Japan has been fragmentally investigated,^{22,27} but quantitative studies have not been done until now. In the present study, seasonal changes in the distribution and abundance of euphausiids along the coastal waters off north-eastern Japan were investigated and discussed in relation to the temporal and spatial changes of oceanographic conditions and several predators off north-eastern Japan.

MATERIALS AND METHODS

Analyses of the distribution and abundance of euphausiids were based on samples collected every two months using 5.5-m-long cylindrical-conical nets (diameter 1.3 m, mesh size 0.45 mm)²⁸ in coastal waters off south-eastern Hokkaido

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Received 24 April 2006. Accepted 15 December 2006.

(41°–43°N), Sanriku (38°–41°N), and Joban (36°–38°N) from March 1997 to February 1998.²⁵ Either two or three transects were set for each coastal water, and a zigzag line between 100 and 300-m isobaths off Sanriku and Joban was added in March and April, to conduct an acoustic survey.²⁹ Off Sanriku and Joban, the survey stations were set at approximately 100, 200, 300, 500, and 1000-m isobaths. Off south-eastern Hokkaido, the stations were set at approximately 100, 200, 300, 500, 1500, and 1700-m isobaths. The March survey was conducted only off Sanriku. The cylindrical-conical nets were obliquely towed at a ship speed of 2 knots from 15 m above the sea bottom to 0 m where the sea depth was shallower than 300 m, and towed from 150 to 0 m where the sea depth was deeper than 300 m. A flowmeter (Rigisha, Tokyo, Japan) was mounted in the mouth of the net to register the volume of water that passed through the net. The net was towed only at night at all stations except at stations along the zigzag acoustic survey lines between 100 and 300-m isobaths off Sanriku and Joban in March and April. Filtered volume ranged 211–2860 m³ and averaged 888 m³ (± 449 m³ standard deviation, SD). Water temperature and salinity from 0 to 300 m depth or 0 m to the near bottom at stations where the bottom depth was shallower than 300 m were measured by conductivity–temperature–depth (CTD) measurements (Sea-Bird 9 *plus*, Sea-Bird Electronics, Bellevue, WA, USA). Immediately after collection, samples were preserved in 5% formalin on board. Numbers of adult stage individuals for each species of euphausiid was sorted and counted for each sample in the laboratory. More details on methods of sampling and measurements, and the results of seasonal changes in oceanographic features are found in Taki.²⁵

RESULTS

Environment

Oyashio waters, characterized by temperatures less than 5°C at 100 m depth,³⁰ extended south to the Sanriku coastal area from March to June 1997, but gradually receded toward south-eastern Hokkaido from August to December.³¹ Instead, warm waters derived from the Kuroshio Extension expanded off Sanriku and Joban during this period. Then, Oyashio waters strongly extended southward to Joban the following February.³² Extreme cold temperatures <2°C occurred off south-eastern Hokkaido during April and August and the next February.^{31,32} During the survey, the influence of Tsugaru Warm Current water³³ off Shimokita Pen-

Fig. 1 Seasonal changes in average temperature at (a) the surface, and (b) 100 m depth. South-eastern Hokkaido (◆), Sanriku (□), and Joban (▲); vertical bars indicate standard deviation.

insula (~41°N) were strong from June to the next January, but weak from March to May and the next February.^{31,32} The Kuroshio Extension was always located south of the survey area during the survey period.^{31,32} The seasonal pattern of oceanographic conditions closely approximated the average seasonal pattern of this region.³⁴ Throughout the study, the average temperatures at the surface and 100 m depth off Joban were the highest, and those off south-eastern Hokkaido were the lowest (Fig. 1). The surface temperature was the lowest in April or the next February, and the highest in August–October along each coastal area. The temperature at 100-m depth was the lowest in April or the next February, and the highest in October–December along each coastal area.

Euphausiid species identified along each coastal water

Twenty-six species of seven genera of euphausiids occurred during the survey period (Table 1). This number is comparable to that (24 species of 9 genera) found in Sanriku waters from 1976 to 1980 reported by Endo.²² However, one species of epipelagic habitat, i.e. *Thysanopoda tricuspidata* and four species of meso- or bathypelagic habitat, *Nematobrachion boopis*, *Stylocheiron maximum*, *Nematoscelis tenella*, and *Bentheuphausia amblyops* collected by Endo²² were not found in the

Table 1 Mean abundance (individuals/m²) per month by area of euphausiid species

Species	SE Hokkaido	Sanriku	Joban	Total
<i>Euphausia pacifica</i> [†]	130.8 (89.4)	146.5 (92.2)	112.3 (90.1)	126.6 (90.4)
<i>Thysanoessa inspinata</i> [†]	12.2 (8.3)	7.3 (4.6)	1.8 (1.4)	7.2 (5.1)
<i>Euphausia recurva</i> [§]	0.1 (0.1)	1.4 (0.9)	3.4 (2.7)	1.8 (1.3)
<i>Euphausia mutica</i> [§]	0.02 (0.02)	1.7 (1.1)	1.9 (1.5)	1.2 (0.8)
<i>Euphausia tenera</i> [¶]	0	0.1 (0.1)	2.8 (2.3)	1.0 (0.7)
<i>Thysanoessa longipes</i> [†]	2.0 (1.4)	0.3 (0.2)	0.01 (0.004)	0.7 (0.4)
<i>Euphausia hemigibba</i> [§]	0	0.5 (0.3)	0.5 (0.4)	0.3 (0.2)
<i>Euphausia gibboides</i> ^{††}	0.02 (0.02)	0.1 (0.1)	0.6 (0.5)	0.3 (0.2)
<i>Thysanoessa inermis</i> [†]	1.0 (0.7)	0	0	0.3 (0.2)
<i>Euphausia similis</i> ^{††}	0	0.4 (0.3)	0.1 (0.1)	0.2 (0.1)
<i>Nematoscelis microps</i> [§]	0.02 (0.01)	0.1 (0.1)	0.3 (0.2)	0.1 (0.1)
<i>Euphausia nana</i> ^{††}	0	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)
<i>Tessarabrachion oculatum</i> ^{§§}	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)
<i>Stylocheiron affine</i> [§]	0	0.1 (0.1)	0.1 (0.05)	0.1 (0.04)
<i>Nematoscelis difficilis</i> ^{††}	0	0.1 (0.1)	0.1 (0.1)	0.1 (0.04)
<i>Nematoscelis gracilis</i> [¶]	0	0.03 (0.02)	0.1 (0.1)	0.05 (0.03)
<i>Euphausia diomedae</i> [¶]	0	0	0.1 (0.1)	0.04 (0.03)
<i>Thysanoessa gregaria</i> ^{††}	0	0.04 (0.03)	0.04 (0.04)	0.04 (0.03)
<i>Pseudeuphausia latifrons</i> ^{††}	0	0	0.1 (0.1)	0.03 (0.02)
<i>Nematoscelis atlantica</i> [§]	0	0	0.1 (0.1)	0.03 (0.02)
<i>Euphausia pseudogibba</i> ^{††}	0	0	0.1 (0.1)	0.03 (0.02)
<i>Stylocheiron carinatum</i> [¶]	0	0	0.04 (0.04)	0.01 (0.01)
<i>Stylocheiron longicorne</i> ^{¶¶}	0	0	0.02 (0.02)	0.01 (0.01)
<i>Thysanoessa raschi</i> [†]	0.02 (0.02)	0	0	0.01 (0.005)
<i>Stylocheiron suhmi</i> [§]	0	0.01 (0.01)	0	0.01 (0.004)
<i>Thysanopoda aequalis</i> [§]	0	0	0.01 (0.01)	0.002 (0.002)
Total	146.3	158.9	124.6	140.0

Highest values among areas for each species are in bold type. Species are ranked according to mean abundance in the total survey area. Relative contribution (%) to the total abundance of euphausiids is shown in parentheses. Groups are as follows:

[†]Subarctic-transitional.

[‡]Subarctic.

[§]West North Pacific.

[¶]Equatorial water.

^{††}Boundary.

^{‡‡}West Pacific coastal.

^{§§}Subarctic mesopelagic.

^{¶¶}Central-Equatorial mesopelagic.

present study. Endo²² investigated the distribution of euphausiids using mainly MTD nets (diameter 0.56 m, mesh size 0.33 mm)³⁵ towed down to 1000 m depth. However, tows from 0–150 m where the sea was deeper than 300 m perhaps failed to collect these meso- and bathypelagic species in the present study. It should be noted that the abundance of other mesopelagic species *Stylocheiron longicorne* and *Tessarabrachion oculatum* found in the present study might be apparently underestimated.

Euphausia pacifica was the most abundant throughout the year off each coastal water, and their relative contribution to the total abundance of euphausiids was 89–92% (Table 1). *Thysanoessa inspinata* was the second highest in abundance off south-eastern Hokkaido and Sanriku, and their relative contribution to the total abundance of

euphausiids was 5–8%. Warm- and transitional-water epipelagic species (corresponding to the Equatorial water group, the West North Pacific group excluding *Stylocheiron suhmi*, the West Pacific coastal group excluding *Euphausia similis*, and the Boundary group of Nemoto³⁶) showed higher abundances off Joban than off the other two areas, and especially, *Euphausia recurva*, *E. mutica*, and *E. tenera* showed higher abundance among them.

Seasonal change in abundance of euphausiid species in each area

Thysanoessa inermis mainly occurred off south-eastern Hokkaido in February and April (Fig. 2), while it occurred at only one station off south-

Fig. 2 Seasonal changes in the average abundance of the top 10 abundant species (*Thysanoessa* and *Euphausia*) in the total survey area (Table 1) by area from March 1997 to February 1998. South-eastern Hokkaido (◆), Sanriku (□), and Joban (▲).

eastern Hokkaido in August and October (Fig. 3). *Thysanoessa longipes* mainly occurred off south-eastern Hokkaido during spring (Fig. 2) as did *T. inermis*, but *T. longipes* also occurred there in summer–autumn (August–October) and off Sanriku in spring–early summer (April–June) (Fig. 3). *Thysanoessa inspinata* occurred off south-eastern Hokkaido and Sanriku throughout the survey period, mainly in spring but also occurred off Joban throughout the year in small numbers (Fig. 2). Its distributional range extended to near the 10°C contour at 100 m during April–August and up to the south of 10°C contour in October (Fig. 3). *Thysanoessa raschi* occurred in small numbers only at one station (42°10'N, 143°38'E) off south-eastern Hokkaido in April (not figured), when temperatures at 0 and 100 m were the lowest (Fig. 1).

Euphausia pacifica occurred off each coastal water throughout the survey period (Figs 2 and 3). *Euphausia pacifica* was abundant off Sanriku in March, April, October, and the following February, while off Joban it was abundant in June and the following February. During these months except October, Oyashio waters shifted south and temperatures at 0 and 100 m were lower (Fig. 1). Off south-eastern Hokkaido, *E. pacifica* was not abundant in April, but increased after April and peaked in abundance in October. In December, *E. pacifica* was scarce throughout the survey area. The distributional range of *E. pacifica* always extended

further south than that of *T. inspinata* during the survey period (Fig. 3). *Euphausia pacifica* showed the highest abundance among euphausiids off each coastal water in each month and their relative abundance contributed generally higher than 80% (up to 99% off Joban in April) to the total euphausiids during the survey period, except for off Joban in October and off south-eastern Hokkaido in April, where their relative abundance contributed 44–51%. More detailed analyses of the distributional pattern by body length were given in Taki.²⁵

The top six abundant species among warm- and transitional-water euphausiids, *Euphausia recurva*, *E. mutica*, *E. hemigibba*, *E. gibboides*, *E. similis*, and *E. tenera* (Table 1) mainly occurred off Sanriku or Joban in autumn (Fig. 2), when temperatures at 0 and 100 m were higher (Fig. 1). Other epipelagic warm- and transitional-water species also occurred mainly off Sanriku or Joban in autumn (not figured in Fig. 2), but *N. gracilis*, *E. diomedae*, and *S. carinatum*, which belong to the Equatorial water group,³⁶ occurred more abundantly in Joban than in Sanriku as well as *E. tenera*.

In October, six warm- and transitional-water species mainly occurred up to south of the 10°C contour (Fig. 4). However, *E. gibboides* and *E. similis* occurred mainly near the 10°C contour but were scarce in the southern two transect lines near the 15°C contour. In December, *E. recurva* and *E. mutica* occurred between the 10° and 15°C contours but *E. hemigibba*, *E. similis*, and *E. tenera* occurred only in the south transect line near the 15°C contour. However, *E. gibboides* occurred in the offshore stations near the 10°C contour and was scarce near the 15°C contour as in October. *Euphausia recurva*, *E. mutica*, and *E. gibboides* occurred in small numbers near the 5°C contour off south-eastern Hokkaido.

Relationship between temperatures and relative abundance of euphausiids

Thysanoessa inermis occurred in the area with a temperature range −0.3°–1.3°C at 100 m, mainly in the −0.1°–1.1°C area in April (Fig. 5). It occurred only at 2.1° and 3.3°C at August and October, respectively. *Thysanoessa longipes* occurred in the 0.3°–5.1°C area, mainly in the 0.3°–2.4°C area in April. It occurred mainly in the 0.9°–1.2°C area but up to 9.4°C in June. It occurred in the 1.5°–2.7° and 3.3°C areas in August and October, respectively. *Thysanoessa inspinata* occurred in a warmer range than other *Thysanoessa* species. Its temperature range extended to near 8°C in April, near 10°C in June, and near 12°C in August and October. *Thysanoessa raschi* occurred only at 1.1°C in April (not figured in Fig. 5).

Fig. 3 Distribution and abundance of four species of subarctic euphausiids (genus *Thysanoessa* and *Euphausia*) and temperature gradients at 100 m depth from April to October 1997 adapted from Tohoku National Fisheries Research Institute.³⁷ Numbers indicate temperature (°C) contours; abundances given as open circles.

Fig. 4 Distribution and abundance of six species of warm- and transitional-water euphausiids (genus *Euphausia*) and temperature gradients at 100-m depth in October and December 1997 adapted from Tohoku National Fisheries Research Institute.³⁷ Numbers indicate temperature (°C) contours; abundances given as open circles.

Euphausia pacifica occurred most widely as compared with other species (Fig. 5). It occurred up to near 15°C at 100 m in April (not figured) and October, and up to 16°C in August. Conversely, it was relatively scarce at <2°C compared to *Thysanoessa* species. The relationship between temperatures and the relative abundance for each subarctic species closely reflected the seasonal variations of geographic distribution (Figs 2 and 3). *Euphausia recurva* occurred in the widest temperature range among warm-water species but showed higher abundance at high temperatures (15.2° and 16.2°C at 100 m) in October and December, respectively (Fig. 6). *Euphausia mutica* also occurred in the wider temperature range and was relatively abundant at 11.4° and 13.3°C in October and December, respectively. *Euphausia hemigibba* occurred in a warmer range than these two species, and showed higher abundance at high temperatures (15.2° and 16.2°C in October and December, respectively), as *E. recurva* did. *Euphausia gibboides* was relatively abundant at 11.1°C in October but occurred down

to approximately 4°C in December, equal to *E. recurva* and *E. mutica*. *Euphausia similis* occurred in the 8.5°–14.6°C area in October and occurred only at 14.1°C in December. *Euphausia tenera* occurred in the highest temperature range among these six species. It occurred in the 11.1°–15.1°C and 14.1°–16.2°C areas in October and December, respectively. The West North Pacific group (including 8 species shown in Table 1) occurred in the widest temperature range among warm- and transitional-water species (Fig. 7). This group occurred in the 5.4°–15.2°C and 4.0°–16.2°C areas at 100 m in October and December, respectively, but was relatively abundant at high temperatures (15.2° and 16.2°C, respectively) in both months. It should be noted that occurrences at cooler temperatures mainly comprised *E. recurva* (Fig. 6). The Boundary group (3 species) also occurred in the wide temperature range. This group was relatively abundant at 11.1°C in October. The West Pacific coastal group (4 species) occurred in 8.5°–14.6°C and 12.5°–14.1°C areas in October and December,

Fig. 5 Relationship between relative abundance of (a) *Thysanoessa inspinata* (◆), *Thysanoessa longipes* (○), *Thysanoessa inermis* (△), and (b) *Euphausia pacifica* (◇), and temperature (°C) at 100 m from April to October 1997. Relative abundance is the ratio of abundance at a station to the total sum of abundance at all stations. No catch data are omitted.

respectively. The Equatorial water group (4 species) occurred in the highest temperature range among warm- and transitional-water species. This group occurred in the 11.1–15.1°C and 14.1–16.2°C areas in October and December, respectively.

DISCUSSION

Euphausia pacifica was widely distributed and dominant in abundance in each coastal water (Table 1). As off north-eastern Japan, the relative abundance of *E. pacifica* always contributed the

highest proportion among euphausiids off western USA in the wide latitudinal range from off Vancouver (49°N),³⁸ through off Oregon (44°39'N),³⁹ to off southern California (32°N),⁴⁰ although their biomass changes greatly between years in each region. The tolerance to the wide temperature range (Fig. 5) is suggested to make the species the predominant zooplankton off north-eastern Japan, which is characterized by a complex oceanographic structure represented by the Oyashio Current, Kuroshio Extension, Tsugaru Warm Current, and several warm-core rings shed by these currents.^{41–43} The distributional pattern of *E. pacifica* is comparable to that of *Metridia pacifica*, a

Fig. 6 Relationship between the relative abundance of six species of warm- and transitional-water euphausiids and temperature (°C) at 100 m in (a,b) October and (c,d) December 1997; *Euphausia recurva* (◇), *Euphausia mutica* (□), *Euphausia hemigibba* (×), *Euphausia gibboides* (◆), *Euphausia similis* (○), and *Euphausia tenera* (△). Relative abundance is the ratio of abundance at a station to the total sum of abundance at all stations. No catch data are omitted.

Fig. 7 Relationship between the relative abundance of four distributional groups of warm- and transitional-water euphausiids and temperature (°C) at 100 m in (a,b) October and (c,d) December 1997; West North Pacific (◇), Boundary (◆), Coastal (○), and Equatorial (△) groups. Relative abundance is the ratio of abundance at a station to the total sum of abundance at all stations. No catch data are omitted.

cold-water species of copepod, which has tolerance to the wide temperature range^{44,45} and is reported to occur in the transitional Sanriku waters throughout the year.⁴⁶

However, it should be noted that *E. pacifica* controls its diel vertical migration according to the vertical distribution of temperatures and avoids high surface temperatures (~>20°C) during the night.^{47,48} Conversely, Nakagawa *et al.*⁸ suggested that *E. pacifica* can ingest a wide variety of organisms by switching feeding behavior according to the ambient food condition. Therefore, such flexibility in feeding behavior might overcome the disadvantage of limitation in food intake in the

surface layer and help extend their distribution toward warmer waters.

In the present study, the order of cold water preference among the subarctic species is thought to be *Thysanoessa raschi* > *T. inermis* > *T. longipes* > *T. inspinata* > *E. pacifica* from their seasonal distributional patterns and relationships between temperature and relative abundance (Figs 2,3 and 5). This tendency is consistent with the latitudinal zonation pattern of subarctic euphausiid associations in the wide area of North Pacific reported previously.^{6,49,50}

Thysanoessa inspinata had the second widest distributional range in geography and temperature

regime (Figs 2, 3 and 5). Itoh and Kubota⁵¹ and Sawamoto⁵² reported that among subarctic epipelagic euphausiids, only this species and *E. pacifica* occurred in Suruga Bay, central Japan, that is strongly affected by Kuroshio warm waters. This result is consistent with present results. Brinton⁴⁹ reported that four *Thysanoessa* species were found mainly above 140 m at night in the Oyashio area. However, *T. inspinata* avoids high surface temperatures as well as *E. pacifica*, and a substantial portion stays below 150 m depth throughout the day around a warm-core ring off Sanriku.⁴⁸ Therefore, the abundance of *T. inspinata* in the warmer area might be underestimated in the present study.

The dominance in abundance of *E. pacifica* among euphausiids in each water (Table 1) is well reflected by the diet of several fishes previously reported.^{9–16} For example, demersal fishes such as walleye pollock *Theragra chalcogramma* exclusively feed on *E. pacifica* among euphausiids throughout the year in the Sanriku area.^{13,14} Yamamura *et al.*¹⁵ found that *E. pacifica* is the most important food item for walleye pollock throughout the year off south-eastern Hokkaido, but their relative importance as food declined in spring because of the superabundance of *Neocalanus cristatus*. From the present study, the low biomass of *E. pacifica* off south-eastern Hokkaido in spring (Figs 2 and 3), probably caused by unfavorable temperature conditions (Fig. 5), is suggested to be a reason for the relative importance as food declined. Conversely, Pacific saury *Cololabis saira* actively feeds on *E. pacifica* during their north migration, i.e. the transitional area (off Sanriku and Joban) in spring and Oyashio area (off south-eastern Hokkaido) in summer.¹² The north migration route of Pacific saury is well synchronized with the seasonal change in geographic distribution of *E. pacifica* (Figs 2 and 3), and therefore, the migration of Pacific saury might be closely related to the distribution of *E. pacifica*.

It is suggested from the results obtained in the present study (Figs 2 and 3) that only *E. pacifica* is considered as the resident species in the total survey area. In addition, *T. inspinata* is considered as the resident species off south-eastern Hokkaido and Sanriku (Figs 2 and 3). However, Endo²² showed that in addition to these two epipelagic species, *T. raschi*, *T. inermis*, and *T. longipes* are also considered as resident species off Sanriku. These species rarely occurred during summer and autumn in the total survey area in the present study (Figs 2 and 3). In 1976–1980, Endo²² showed a south anomaly in the first branch of the Oyashio Current,⁵³ while the present survey period (1997–1998) corresponded to the north anomaly of the

first branch of the Oyashio Current. Therefore, the difference in annual distributional pattern of subarctic euphausiids might reflect that of cold water mass distribution. However, the abundance of these *Thysanoessa* species in warmer areas could be underestimated because the high temperatures in the shallow layer may limit the upward movement to the upper 150 m shown by *T. inspinata*.⁴⁸

Odate⁵⁴ and Kodama and Izumi⁵⁵ suggested that fishery conditions of *E. pacifica* is not favorable in the Sanriku area when the first branch of Oyashio Current is extremely strong and extreme cold temperatures are prevailing over Sanriku waters, because fishable populations are distributed in the southern Joban area. That *E. pacifica* contributed low biomass off south-eastern Hokkaido in spring, i.e. in the coldest temperature regime (Figs 1 and 2), supports this hypothesis. Odate⁵⁴ reported that *T. inermis* was contaminated in the fished *E. pacifica* in the Sanriku waters in the year of extremely strong Oyashio. The distribution of *Thysanoessa* species is suggested to be spread further south in spring in such cold years.

Warm- and transitional-water epipelagic species which exclusively occurred off southern part of survey area in the warmer season are considered southerly or offshore guests off the north-eastern Japan, as suggested by Endo²² from seasonal distribution patterns (Figs 2 and 4).

The Equatorial water group, the West Pacific coastal group and the West North Pacific group species are thought to be advected from their respective southern original distributional areas through the Kuroshio region.³⁶ However, the Boundary group species are mainly distributed in the boundary region between the Kuroshio Extension and the subarctic waters,³⁶ and therefore, may be advected from offshore to the Sanriku and Joban areas in autumn when the Oyashio waters recede. According to Brinton,⁴⁹ *Thysanoessa gregaria* belonging to this group was limited to the cold patch off southern Japan during October 1953, but it was more widespread and abundant in the area during April when the Kuroshio waters recede. These transitional characteristics are consistent with the geographic distributional patterns of *E. gibboides* (Fig. 4) and the relationship between the abundance of this group and temperatures (Figs 6 and 7).

The Equatorial water group is mainly distributed in the equatorial water mass, the most southern region among warm-water species.³⁶ This group occurred exclusively off Joban in the warm season (Table 1, Fig. 2), and is suggested to have the most preference for warmer temperatures among warm- and transitional-water species from the geographic

distributional pattern of *E. tenera* (Fig. 4) and the relationship between the abundance of this group and temperatures (Figs 6 and 7). According to Nemoto,³⁶ the West Pacific coastal group is mainly distributed in the neritic waters off western Pacific and, with the Equatorial water group, it is suggested to be subject to transportation by the Kuroshio Current. However, Nemoto³⁶ also pointed out that *E. similis* and *E. nana* belonging to this group are forced to move to the coastal area off southern Japan by the strong Kuroshio Current in summer. Hirota *et al.*⁵⁶ found that these two species are the most abundant among euphausiids in Sagami Bay, central Japan, but are scarce in the warmer offshore region where other euphausiids belonging to the Equatorial group and the West North Pacific group are abundant. The characteristic distributional pattern of the West Pacific coastal group was obscure in the present study, but this group is not likely to prefer the high temperature regime as compared to the Equatorial water group (Figs 4, 6 and 7).

Like the Equatorial water group, the West North Pacific group is generally thought to prefer warmer temperatures as compared to the Boundary group from the geographic distributional patterns of *E. recurva*, *E. mutica*, and *E. hemigibba* (Fig. 4), and the relationship between the abundance of this group and temperatures (Figs 6 and 7). However, *E. recurva* showed apparent tolerance to lower temperatures compared to the Equatorial water group and other species of the West North Pacific group (Figs 4 and 6). According to Brinton,⁴⁹ *E. recurva* occur abundantly in the northern cooler margin of the West North Pacific water mass where other species of the same group scarcely occur, except for *E. mutica*. Hirota⁵⁷ reported that the distributional pattern of *E. recurva* is different from that of other species of the West North Pacific group and the Equatorial water group in Sagami Bay because it occurs mainly on the warmer outside of the Bay in spring, but occurs in the cooler Bay in autumn in large numbers. Therefore, these reports are consistent with the present results.

Six warm-and transitional-water species, *Euphausia nana*, *Stylocheiron affine*, *Nematoscelis gracilis*, *Euphausia diomedae*, *Pseudeuphausia latifrons*, and *Thysanoessa gregaria* collected in this study are found in the Sea of Japan.^{58–60} None of them occurred off northern Sanriku (40°–41°N) influenced by the Tsugaru Warm Current during the survey period except *S. affine*, which occurred in 6.0 inds./m² at one station (40°N, 142°19'E) in December. Therefore, few *S. affine* were advected through the Tsugaru Warm Current from the Sea of Japan.

CONCLUSION

The latitudinal zonation pattern of epipelagic euphausiid associations reflected the temperature regime off north-eastern Japan, which is consistent with that in the wide area of the North Pacific reported previously.^{6,49,50} *Euphausia pacifica* is thought to be the most dominant among euphausiids widely off north-eastern Japan, which may make it a staple food for several demersal and migrant predators such as walleye pollock and Pacific saury.^{12,14,15} Conversely, the species composition identified in the present study and their distributional pattern are slightly different from those in the same waters investigated previously.²² This result is perhaps caused by the sampling failure for meso- and bathypelagic species in the present study, and also by the interannual change of distributional pattern of euphausiids with oceanographic conditions. The underestimation of abundance should be considered also for epipelagic species which change the diel vertical distributional pattern according to the change of several environmental factors such as light intensity, density, temperature, and food abundance,^{61,62} and stay below 150 m depth at night. Therefore, the distribution and biomass of euphausiids using effective sampling methods to cover their whole vertical distributional range need to be surveyed interannually in relation to the interannual or decadal changes of oceanographic conditions in the North Pacific.^{63,64}

ACKNOWLEDGMENTS

I thank the captain and crew of the R/V Wakataka Maru, Hokko Maru, and Tankai Maru of the Fisheries Research Agency.

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