Seasonal changes in spawning and distribution of *Euphausia pacifica* Hansen along the coastal areas off northeastern Japan

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Spawning and distribution of *Euphausia pacifica* were investigated bimonthly using Norpac and large cylindrical-conical nets along the coastal areas off northeastern Japan [southeastern Hokkaido (41–43°N), Sanriku (38–41°N) and Joban (36–38°N)] from March 1997 to February 1998. Copulated females, eggs and calyptopis stage were abundant off Sanriku in spring and off southeastern Hokkaido in mid fall, but rare throughout the survey areas in late fall. They mainly occurred near the marginal area of the Oyashio Current ($T_{100}=5$°C) throughout the year. Furcilia and immature stages tended to expand their distribution into warmer southern areas compared to younger stages (eggs and calyptopis stage) in each season. Copulated females, eggs, calyptopis, furcilia and immature stages were few or absent throughout the year except in mid fall off southeastern Hokkaido, where cold waters of the Oyashio ($T_{100}<2$°C) dominated. Small adults (≦15 mm) occurred in all survey areas including the area off southeastern Hokkaido throughout the year. Large adults (>15 mm), which are considered to be individuals that have overwintered, however, were few from August to December off Sanriku and Joban where the warmer waters of the transitional area (10°C$<T_{100}\leqq$15°C) dominated. It is suggested that the geographical change in the distribution and spawning activity depend mainly on the seasonal changes of water masses associated with the Oyashio Current.

Key words: *Euphausia pacifica*, distribution, northeastern Japan, Oyashio, spawning

Introduction

Euphausia pacifica is widely distributed and one of the most dominant species within the zooplankton community from the subarctic to the transitional areas of the North Pacific (Brinton, 1962; Ponomareva, 1963; Mauchline and Fisher, 1969). *Euphausia pacifica* has seven developmental stages; egg, nauplius, metanauplius, calyptopis, furcilia, immature and adult stages. According to Ross (1981), 2–2.2, 2.3–6, 13–14 and 27.5–46 days are required for the nauplius, metanauplius, calyptopis and furcilia stages, respectively, at the temperature conditions of 8 and 12°C. Iguchi and Ikeda (1994) showed that egg development times are <1, 2, 4 and 7 days, when ambient temperatures are >15, 10, 5 and 1°C, respectively. Warmer temperatures generally reduce developmental time for each stage (Ross, 1981; Iguchi and Ikeda, 1994). According to field observations at several locations, recruitment time to adult stage (ca. 10 mm BL) is estimated to be ca. 3 months (Brinton, 1976; Endo, 1981; Iguchi *et al*., 1993). Taki (2004) reported that *E. pacifica* off northeastern Japan spawn throughout the year, mainly in spring, and estimated that individuals >15 mm BL had overwintered on the basis of length frequency analysis.

E. pacifica is commercially exploited off the Pacific coast of northeastern Japan. The main fishing period is from March to April, when the first branch of the Oyashio Current extends southward close to the Sanriku (38–41°N) and Joban (36–38°N) coasts (Komaki, 1967). The fishing grounds are formed on the continental shelf near the frontal area between the coastal branch of the Oyashio Current and the coastal waters (Odate, 1991). It is generally considered that dense populations of *E. pacifica* are transported to the Sanriku and Joban coastal areas in spring by the first branch of the Oyashio Current (Odate, 1991). On the other hand, benthopelagic populations of *E. pacifica* exist on the continental slope off Sanriku and Joban during summer and winter, and are an important food resource for benthic fishes (Kodama and Izumi, 1994; Yamamura *et al*., 1998; Endo, 2000). Observations from submersibles confirmed that the benthopelagic *E. pacifica* aggregated in the sea depth range from 160 to 400 m off Sanriku in summer (Endo, 2000). Nakamura (1991) suggested that these benthopelagic populations migrate to the continental shelf off Joban in late spring and become the population targeted by the fishery.

Therefore, studies of the distribution, life history and reproduction have been carried out in the Sanriku and Joban areas (Endo, 1981; Terazaki *et al*., 1986; Taki, 2004). Taki (2004) studied the distribution and life history of this species off northeastern Japan, based on Norpac net samples collected over 10 years. However, the mouth area of Norpac net (0.16 m^2) is too small to collect adult stage euphausiids, and since the sampling area varied with months

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and years, accurate evaluation of the entire life history was not possible.

In this study, the spawning and distribution of *E. pacifica* along the coastal areas off northeastern Japan were investigated using large (mouth area: $1.33\,m^2$) cylindrical-conical nets, bimonthly from March 1997 to February 1998. Observed patterns of spawning and distributions are discussed in light of the relationship between their geographical changes and water masses related to the Oyashio Current.

Materials and Methods

Seven surveys were carried out using Norpac nets (net mouth diameter: 0.45 m; mesh size: 0.34 mm) and 5.5-m long cylindrical-conical nets (net mouth diameter: 1.3 m; mesh size: 0.45 mm; Watanabe, 1992) on the R/Vs Wakataka-maru (Tohoku National Fisheries Research Institute), Tankai-maru and Hokko-maru (Hokkaido National Fisheries Research Institute) from March 1997 to February 1998. To compare the ecological parameters of *E. pacifica* between geographic areas, the survey area was divided into three areas: 1) off southeastern Hokkaido, 2) Sanriku and 3) Joban (Fig. 1). Two or three transects were set for each coastal area, 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 (Miyashita *et al*., 1998). Off Sanriku and Joban, the survey stations were set at about 100, 200, 300, 500 and 1,000 m isobaths. Off southeastern Hokkaido, the stations were set at about 100, 200, 300, 500, 1,500 and 1,700 m isobaths. Note that the March survey was carried out only off Sanriku, and three offshore stations near the marginal area of the first branch of the Oyashio Current were added in August.

Norpac nets were vertically towed above 150 m at 1 $m\,s^{-1}$. At the stations where the bottom depth was shallower than 150 m, Norpac net was towed from near bottom to the surface. Cylindrical-conical nets were obliquely towed at 2 knots of the ship speed from 15 m above the sea bottom to the surface at the stations where the sea depth was shallower than 300 m, and towed from 150 m to the surface in other stations. A wireless net recorder (CN-2220: FURUNO) was attached on the bridle 2.5 m ahead of the mouth of the cylindrical-conical net to monitor the net depth at the bridge. A flowmeter (Rigosha) was mounted in the mouth of the net to register the volume of water passed through the net. Cylindrical-conical net was towed only at night at all stations because post-calyptopis stages migrate below the 150 m depth in the daytime, but mostly occur at $<$150 m depth at night (Taki, 1998), except at stations along the zigzag acoustic lines in March and April. Samples were preserved with 5% formalin seawater immediately after collection. Water temperature and salinity from 0 to 300 m depth were measured by CTD (SBE 9 Plus), and water samples were collected from 0, 10, 30, 50, 75 m depth to determine chlorophyll *a* concentrations at all stations in March and April, at stations along southeast line from 42°50′N, 144°50′E, and at stations along east lines from 40°N, 38°20′N and 36°50′N.

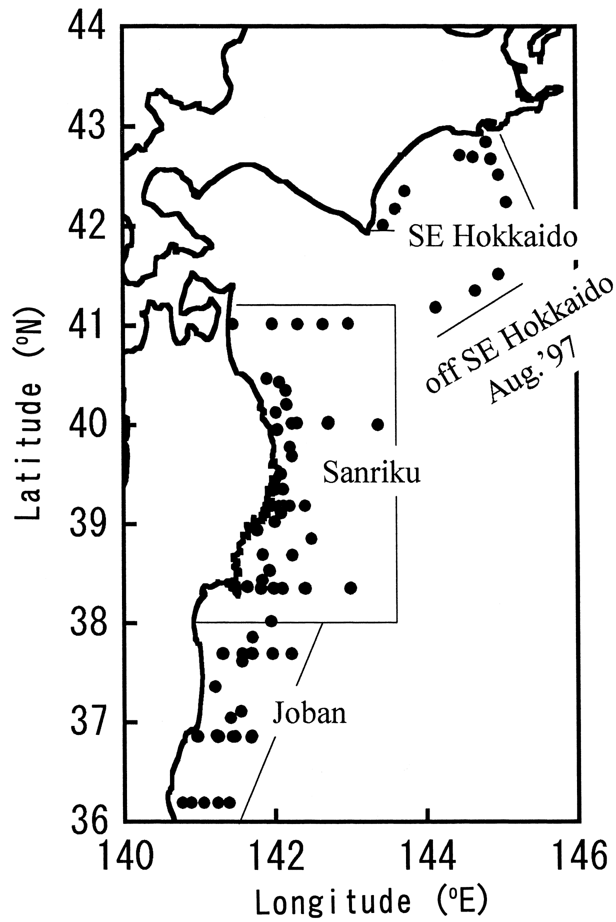

Figure 1. Sampling locations of *Euphausia pacifica* off the northeastern coast of Japan from March 1997 to February 1998.

E. pacifica were sorted and classified into developmental stages except for the nauplius and metanauplius stages, which would pass through both nets. The abundance of eggs and calyptopis stage was determined from the Norpac net collections, those of furcilia, immature and adult stages from the cylindrical-conical net collections. Although the species identification of euphausiid eggs is difficult, I classified *E. pacifica* type eggs as having a capsule diameter of 0.4–0.5 mm and embryo diameter of 0.30–0.38 mm (Taki, 2004). The length for the furcilia, immature and adult stages was measured from the tip of the rostrum to the distal end of the telson to the nearest 0.1 mm. Adults were sexed according to the presence of a thelycum in females or petasma in males. Evidence of copulation, i.e.

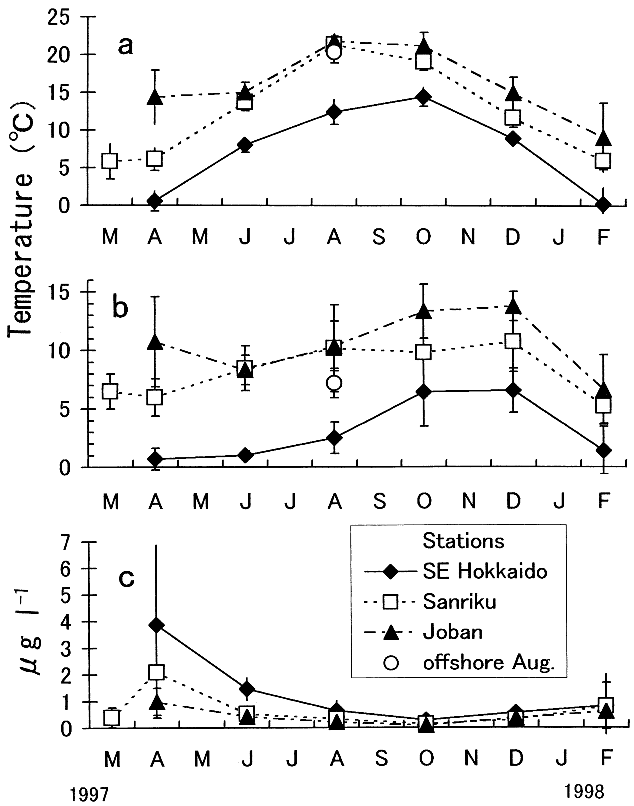

Figure 2. Seasonal changes in the average surface temperature (a), average temperature at 100 m depth (b) and integrated average chlorophyll *a* ($\mu g\,l^{-1}$) in the upper 75 m (c). Vertical bars: ±1 SD.

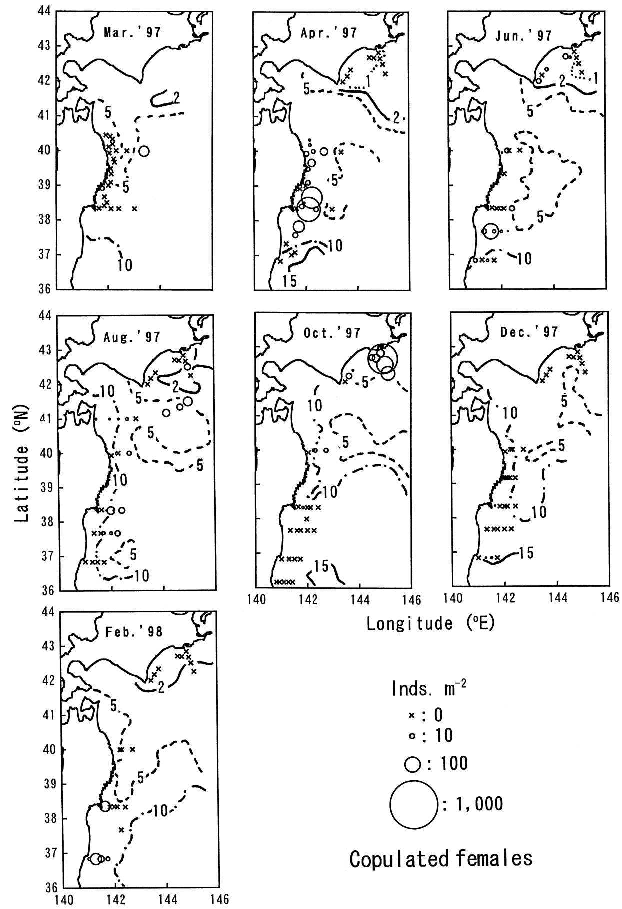

Figure 3. Distribution and abundance of copulated *Euphausia pacifica* females and temperature gradients at 100 m depth from March 1997 to February 1998. Numbers indicate temperatures (°C). Scales as in legend.

the presence or absence of a spermatophore (hereafter referred to as copulated females) was checked in females. Adults were divided into large (>15 mm) and small (≦15 mm) size groups.

Result

Environment

The first branch of the Oyashio Current, characterized by a lower temperature than 5°C at 100 m depth (Murakami, 1994), extended southward to the Sanriku coastal area in March 1997, but it receded and another ≦5°C water related to the second branch of the Oyashio Current occurred off Sanriku and Joban in April and June (Figs. 2–9). Oyashio waters (T_{100}≦5°C) gradually receded toward southeastern Hokkaido from August to December, but the first branch of the Oyashio Current strongly extended southward to Joban in the next February. Extreme cold temperatures <2°C occurred off southeastern Hokkaido during April and August. During the study period, the seasonal pattern of oceanographic condition was as in the average seasonal pattern of this region (Ogawa, 1989).

Throughout the study period, the average temperatures at the surface and 100 m depth off Joban were highest and those off southeastern Hokkaido were lowest (Fig. 2). The surface temperature was lowest in April or next February and highest in August–October along each coastal area. The temperature at 100 m depth was lowest in April or next February and highest in October–December along each coastal area. Integrated average chlorophyll *a* concentration from 0 to 75 m was highest in April and lowest in October along each coastal area.

Distribution and spawning activity

Copulated females, eggs and calyptopis stage were abundant off Sanriku and Joban in April and off southeastern Hokkaido in October (Figs. 3, 4, 5 and 10). Both areas were near margins of the Oyashio waters (T_{100}=5°C). Off southeastern Hokkaido, however, the abundance was low or nonexistent throughout the year except in October, where cold waters of the Oyashio (T_{100}<2°C) dominated. Eggs were present in June, but larvae were not observed in June and

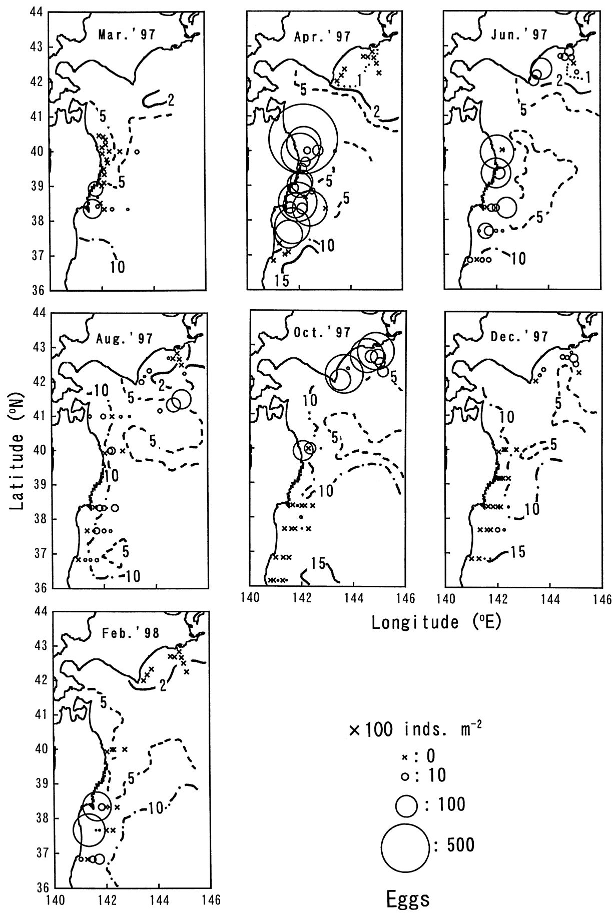

Figure 4. Same as Fig. 3 but for eggs.

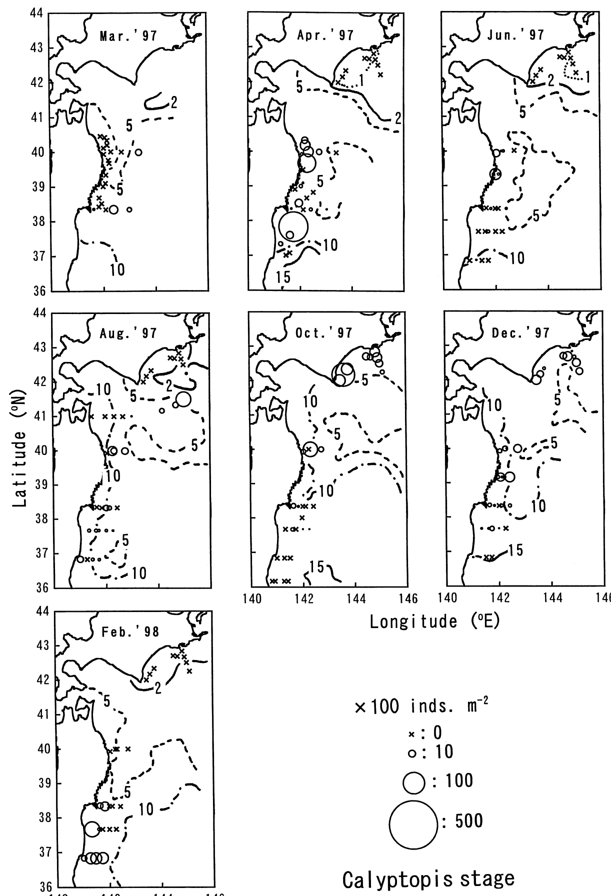

Figure 5. Same as Fig. 3 but for calyptopis stage.

August. Therefore, spawning in June did not contribute to the recruitment to larvae off southeastern Hokkaido. Copulated females, eggs and calyptopis stage were also rare or absent off Sanriku and Joban from August to December, when warmer transitional waters ($10°C<T_{100}\leqq15°C$) dominated. They were present only at the offshore stations near the margins of the first branch of the Oyashio Current in August. Their abundance was also very low throughout the survey area in December. The following February, eggs and calyptopis stage were abundant off southern Sanriku and Joban, where colder transitional waters ($5°C<T_{100}\leqq10°C$) dominated. Seasonal change in the proportion of copulated females to total females was similar to that in abundance of copulated females and eggs (Fig. 10).

Distributional patterns of furcilia stage were similar to that of the younger stages (Figs. 6 and 10). However, furcilia stage was rare off Sanriku and Joban in April, but abundant off Sanriku in December, where 10°C isotherm at 100 m depth occurred.

Immature stage was abundant off Sanriku and Joban from June to December and off southeastern Hokkaido in October, where temperatures at 100 m depth were mainly between the 5 and 10°C (Figs. 7 and 10). Immature stage tended to expand its distribution toward southern warmer areas as opposed to the younger stages. Immature stage was less abundant throughout the rest of the year than October off southeastern Hokkaido, although this stage was always present there.

Small adults occurred in all survey areas throughout the year. They were abundant in the survey area, especially off Sanriku in February, when the first branch of the Oyashio Current strongly moved southward (Figs. 8 and 10).

Large adults were abundant off Sanriku in March, April and the following February, while off Joban they were abundant in June and the following February. During these months, the 5°C isotherm shifted southward. Large adults were few from August to December, when the warmer transitional waters dominated (Figs. 9 and 10). Off southeastern Hokkaido, they were not abundant in April, but increased after April and peaked in abundance in October. In December, they were rare throughout the survey area.

Discussion

Taki (2004) suggested that the occurrence of copulated fe-

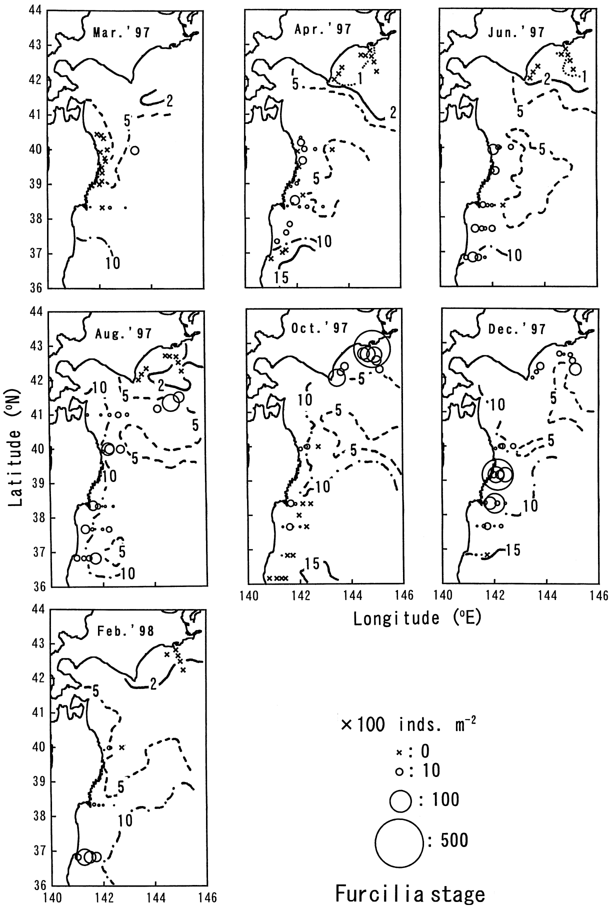

Figure 6. Same as Fig. 3 but for furcilia stage.

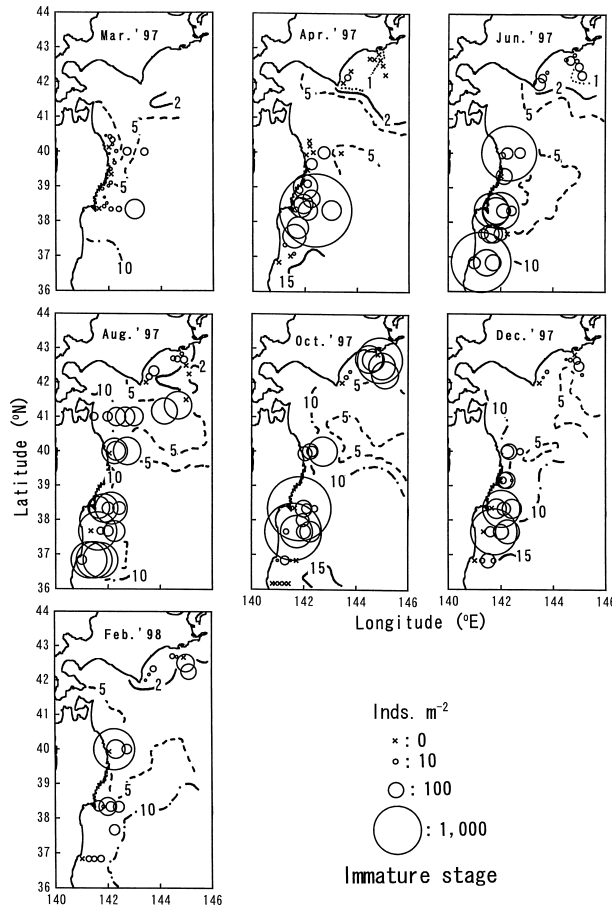

Figure 7. Same as Fig. 3 but for immature stage.

males, spawning and recruitment to larvae of *E. pacifica* continue throughout the year in the Oyashio waters (T_{100}≦5°C) and the colder waters of the transitional area (5°C<T_{100}≦10°C) off northeastern Japan, with a larger peak in spring and a smaller peak in fall, and to a lesser extent in winter, based on widely collected Norpac net samples. These results agreed well with those of the present study conducted along the coastal area. However, eggs and larvae were rare or absent throughout the year except in mid fall off southeastern Hokkaido, where cold waters of the Oyashio (T_{100}<2°C) dominated (cf. Figs. 4–6). Spawning in such cold waters may be unfavorable for the development of eggs and early larvae as shown in laboratory experiments (Ross, 1981; Iguchi and Ikeda, 1994). *E. pacifica* seems to copulate and spawn mainly near the marginal area of the Oyashio Current (T_{100}=5°C) throughout the year (cf. Figs. 3 and 4).

The active spawning of *E. pacifica* is reported to correspond to the phytoplankton bloom period in several locations (Brinton, 1976; Iguchi *et al*., 1993). In the present study, however, the biomass of phytoplankton shown as the concentration of chlorophyll *a* was lowest off southeastern Hokkaido in fall, where eggs and larvae were most abundant like off Sanriku in spring (cf. Figs. 2, 4–6). Nakagawa *et al*. (2001) suggested that *E. pacifica* can ingest a wide variety of organisms (diatoms, dinoflagellates, tintinnids, invertebrate eggs and copepods) by switching feeding behavior according to the ambient food conditions. Therefore, the variety of food sources of *E. pacifica* may affect the timing of food induced copulation and spawning season of this species. On the other hand, the present study showed that active copulation and spawning of *E. pacifica* was largely limited to the marginal area of the Oyashio Current (T_{100}=5°C) throughout the year (cf. Figs. 3 and 4). Accordingly, the temperature conditions may be important triggers of copulation and spawning regardless of season off northeastern Japan.

Taki (2004) suggests that *E. pacifica* off northeastern Japan gradually adapts to colder areas as the developmental stage progresses from furcilia to adults, and advanced-age adults (large size adult) rarely occur in warmer areas. These results agree well with the results of the present study (cf. Figs. 6–9). On the other hand, immature stage and small adults existed in all survey areas throughout the year, even

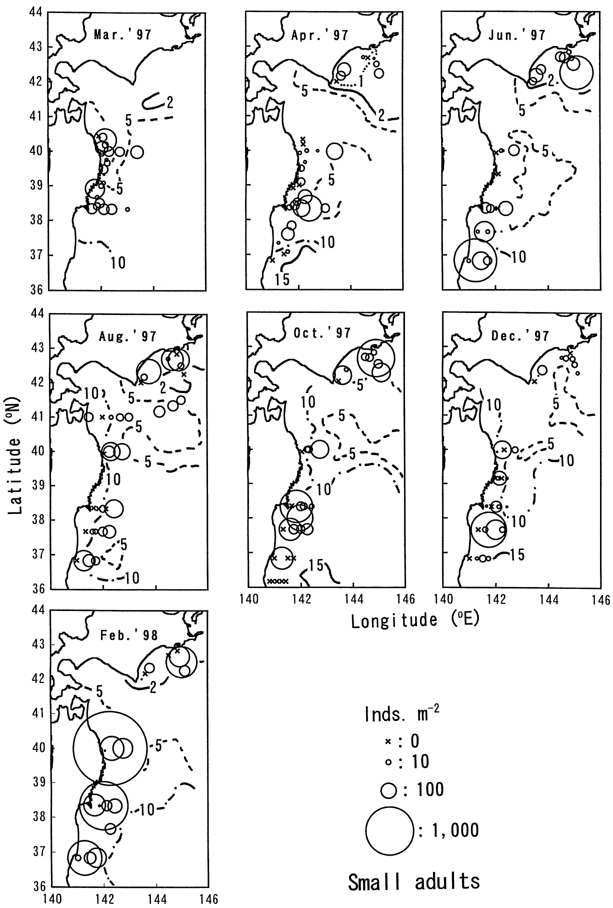

Figure 8. Same as Fig. 3 but for small adults.

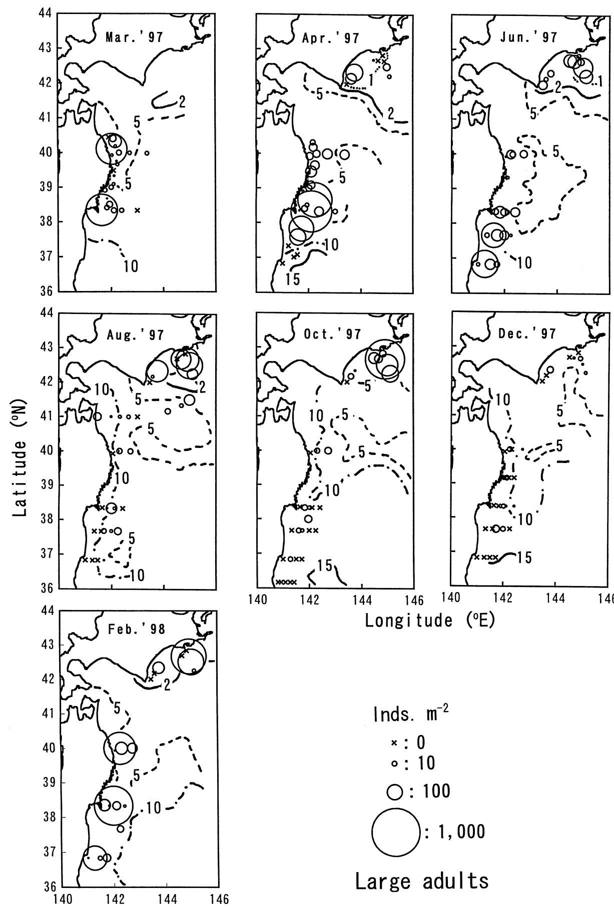

Figure 9. Same as Fig. 3 but for large adults.

off Joban in summer-fall, where the surface water temperatures were relatively high. Immature stage and smaller adults may not ascend toward the surface to avoid the high temperature at night (Iguchi *et al*., 1993; Taki, 1998) and may form benthopelagic aggregations during the day (Nakamura, 1991; Endo, 2000) off Sanriku and Joban in summer-fall. One of the reasons why over-wintered individuals (larger adults) could not exist in such areas is due to the migration toward the colder regions. Migration ability (=swimming speed) of *E. pacifica* is reported to be up to and potentially in excess of 112 m h^{-1} from laboratory observations (Torres and Childress, 1983). This implies that over-wintered population of *E. pacifica* could migrate horizontally 350 km corresponding to the distance between off Sanriku and off southeastern Hokkaido in 130 days. Besides the horizontal migration to the north, the deeper distribution of adults to avoid high temperature of the surface layer (Iguchi *et al*., 1993; Taki, 1998) should be considered. Around the warm-core ring off Sanriku (SST=23°C), the proportion of abundance below 150 m depth at night was 10% for small adults and 29% for large adults (Taki, unpubl.). However, a deeper distribution of large adults implies diminish of population size, because 1) forage limitation and 2) predation by mesopelagic and benthic predators. These two factors (horizontal migration to the north and deeper distribution) are considered as possible causes of absence of large adults (=over-wintered individuals) in the warmer waters off Sanriku and Joban in summer to fall.

Nakamura (1991) suggested that the fishing resources of *E. pacifica* off Joban was supplied from the benthopelagic population formed on the continental slope during summer and winter. However, most of fishery-targeted population may be transported by the Oyashio Current, because the abundance of adults abruptly increased both on the continental shelf and slope in February 1998, when the first branch of the Oyashio Current shifted southward to the southern Sanriku area (cf. Figs. 8 and 9).

Adults were rare off southeastern Hokkaido in spring (cf. Figs. 8–10). Taki (2003) showed that the average depth of adult stage was about 150 m in spring during the day, which was shallower than in summer. The relationship between the abundance of adult stage and average temperature from 0 to 150 m showed that the abundance higher than 500 inds. m^{-2} occurred in the waters with temperatures be-

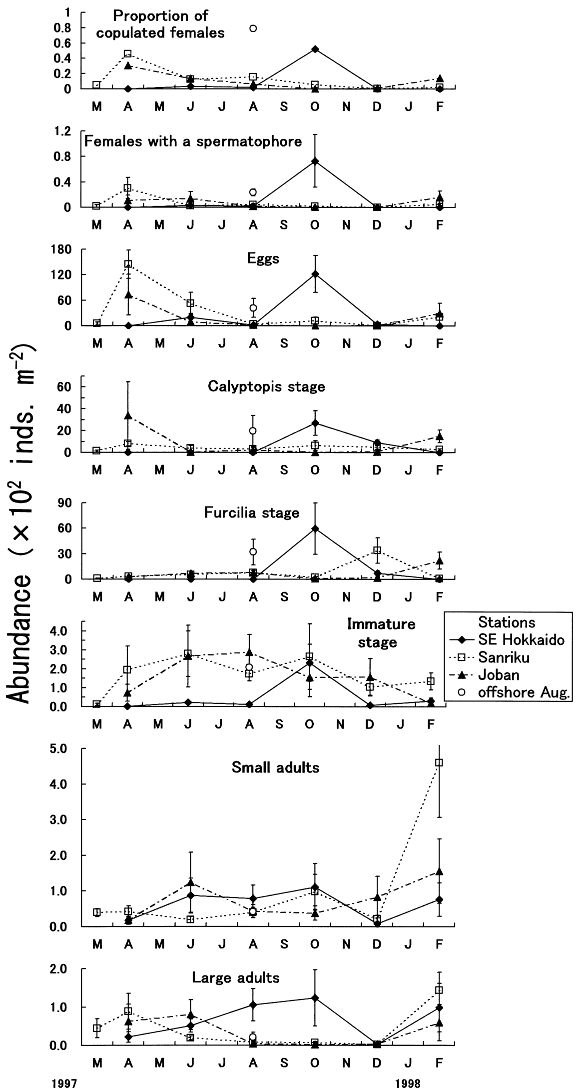

Figure 10. Seasonal changes in the proportion of copulated females and average abundance of each developmental stage of *Euphausia pacifica* by area from March 1997 to February 1998. Vertical bars: ±1 SE.

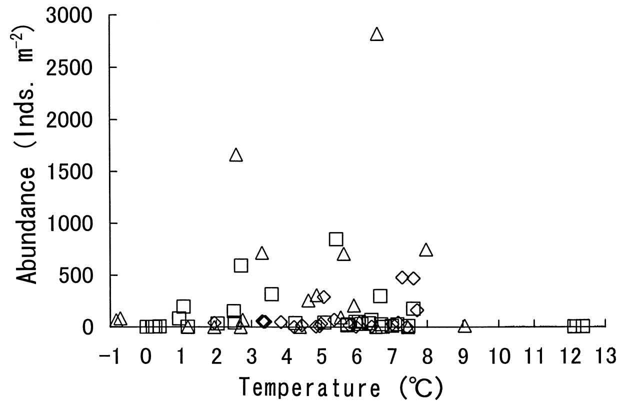

Figure 11. Relationship between the average temperature from 0 to 150 m and abundance of adult *Euphausia pacifica* in March (◇) and April (□) 1997 and February 1998 (△).

tween 2.6 and 8.0°C, but the abundance was low at <1°C and >9°C (Fig. 11). The environment off southeastern Hokkaido may be suboptimal for *E. pacifica* where temperatures lower than 1°C dominated throughout the water column, and therefore they may migrate horizontally toward more southern, warmer areas. Kodama and Izumi (1994) classified the oceanographic patterns off Sanriku into 3 types according to the fishing conditions for *E. pacifica*. They suggested that the fishery-targeted population migrate from the Sanriku area to the Joban area, when the Oyashio coastal branch is very strong and comes close to the shore off Sanriku and the suitable temperature area (>5°C) for *E. pacifica* is restricted to the Joban area. The present study corroborates the hypothesis by Kodama and Izumi (1994) except that the lower limit for suitable temperatures (5°C) suggested by them is higher than the lower limit of temperatures (about 3°C) at which high abundances of adults were observed in this study. As mentioned before, it is implied that the *E. pacifica* population could migrate 50 km within 19 days, which nearly corresponds to the distance between the isobaths $T_{100}=1$°C and $T_{100}=5$°C off south Hokkaido in April (cf. Figs. 8 and 9). Seasonal horizontal migrations of *Euphausia superba* are also reported and the migration is suggested to be induced by spawning (Kanda *et al*., 1982) and the reduction of intraspecific food competition (Siegel, 1988).

Therefore, it is suggested that the *E. pacifica* fishery ground in Sanriku and Joban waters is at its highest abundance in spring. On the other hand, high abundances were also observed off southeastern Hokkaido during summer and fall. It is important to clarify the density of fishery-targeted populations off Sanriku and Joban in spring compared to off southeastern Hokkaido, using the acoustic method, to examine whether a fishery is feasible or not off southeastern Hokkaido.

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本州東方沿岸域におけるツノナシオキアミの産卵，分布の季節変化について

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1997年3月～翌2月にノルパックネットと新型稚魚ネットを用いて道東～常磐沿岸域におけるツノナシオキアミの産卵，分布の季節変化を調べた．交尾雌，卵，カリプトピス期は，春季の三陸沿岸域および秋季の道東沿岸域で多く出現したが，晩秋には全域で少なかった．これらは周年主に親潮縁辺域（T_{100}=5°C）で出現したが，ファーシリア期と未成体はより南の暖海域に出現域を拡げる傾向を示した．交尾雌および成体より若い発育段階は親潮系の冷水（T_{100}<2°C）が優占する道東沿岸域では秋季を除き殆ど出現しなかったが，小型成体（≦15 mm）は道東沿岸域を含め周年全域に出現した．しかし、越冬個体と考えられる大型成体（＞15 mm）は，黒潮系暖水（10°C<T_{100}≦15°C）が優占する8～12月の三陸，常磐沿岸域で殆ど出現しなかった．本種の分布，産卵活動の地理的変化は，主に親潮に関連する水塊の季節変化に依存すると考えられる．

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