# Vertical distribution and diel migration of euphausiids from Oyashio Current to Kuroshio area off northeastern Japan

Kenji Taki\*

National Research Institute of Far Seas Fisheries, 2–12–4, Fukuura, Kanazawa, Yokohama, Kanagawa 236–8648, Japan

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**Abstract:** The vertical distribution of dominant euphausiid species was investigated in the offshore waters of northeastern Japan in April and September 1998 and November 1999 using MOCNESS-I net samples. In total, 32 euphausiid species in eight genera were identified in the study area. Subarctic *Euphausia pacifica* and *Thysanoessa inspinata* occurred over a wide range, although mainly in the Oyashio and cooler transitional areas, and the former made a relative contribution of 78% to the total numerical abundance of euphausiids. At night, these species tended to stay near the surface in the Oyashio area and in deeper layers in warmer areas. During the daytime, they tended to stay in deeper layers in the warmer areas, although *E. pacifica* stayed in deeper layers even in the Oyashio area where the chlorophyll *a* concentration was low. *T. inspinata* did not perform clear diel vertical migration. Except for these subarctic species, five warm-water species of *Euphausia* were abundant among the epipelagic euphausiids. At night, these species tended to stay at a wide range of depths from the surface to subsurface layers in the warmer Kuroshio area, but were concentrated near the surface in the transitional area. During the daytime, they stayed in deeper layers in the Kuroshio area. Diel vertical migration of euphausids seems to be strongly affected by water temperature, but other factors such as phytoplankton abundance may also be important. The possible effects of diel vertical migration of euphausiids on euphausiid fisheries are discussed.

Key words: chlorophyll a, diel vertical migration, Euphausia pacifica, temperature, Thysanoessa inspinata.

#### Introduction

Many euphausiid species perform diel vertical migration, which could play an important role in the downward flux of particulate organic matter (Angel 1985, 1989, Fowler & Knauer 1986). Diel vertical migration of euphausiids is influenced by physical factors such as light intensity, the magnitude of temperature or density discontinuities, and seasonal changes in water mass properties (Mauchline & Fisher 1969) and by biotic factors such as the availability and quality of food organisms, predation pressure, and reproductive strategy (Youngbluth 1975, Bollens et al. 1992, Gibbons 1993, Tarling et al. 1999).

In the North Pacific off northeastern Japan, *Euphausia pacifica* Hansen is the dominant euphausiid (Endo 1981). *E. pacifica* is commercially exploited as bait for recreational and sport fishing and direct human consumption in the coastal waters (36–41°N) off northeastern Japan from

late winter to early summer. The annual catch and annual value on landing was approximately 37,000 ton and 1.2 billion yen, respectively, during the year 2006 (Okazaki & Tadokoro 2007). Several studies have examined the diel vertical migration of E. pacifica in relation to water temperature, molting and reproductive processes, and feeding activity (Terazaki et al. 1986, Nakagawa et al. 2003, Endo & Yamano 2006). This area is characterized by a complex oceanographic structure represented by the Oyashio Current, Kuroshio Extension, Tsugaru Warm Current, and numerous warm-core rings shed by these currents (Kawai 1972, Tomosada 1986). The variability of these oceanographic processes affects the distribution and abundance of euphausiids. However, most previous studies have generally been conducted at a few fixed stations, and the relationship between the vertical distribution of many euphausiid species and different water masses has rarely been examined.

The present study investigated the horizontal and vertical distribution of the dominant euphausiid species in relation

<sup>\*</sup> Corresponding author: Kenji TAKI; E-mail, takisan@fra.affrc.go.jp

to different seasons and water masses in the offshore waters off northeastern Japan using MOCNESS-I net samples. The physical and biotic factors that affect the vertical distribution of euphausiids were examined, and possible effects of the diel vertical migration of euphausiids on euphausiid fisheries are discussed.

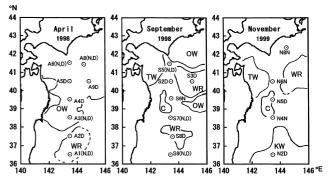
## **Materials and Methods**

Samples were collected at stations mainly from 41°30'N to 36°30'N along the 143°E meridian during 17-21 April and 1-7 September 1998 and during 26-30 November 1999 on the R. V. Wakataka-maru of the Tohoku National Fisheries Research Institute, Fisheries Agency (Fig. 1). A MOCNESS-I net with a mouth opening of  $1.4 \text{ m}^2$  (about  $1 \text{ m}^2$  toward the towing orientation) and a 0.33-mm mesh aperture (Wiebe et al. 1985) was towed obliquely and nets were opened and closed sequentially to sample seven stratified layers (0-25, 25-50, 50-150, 150-250, 250-400, 400-600, and 600-1,000 m). The samples were preserved in 5% buffered formalin seawater immediately after collection. Water temperatures and salinities were determined from conductivity/temperature/depth (CTD) measurements using a Sea-Bird 9 plus (USA) attached to the MOCNESS-I. Salinity data were not used in this study. Seawater samples in nine layers (0, 10, 20, 30, 50, 75, 100, 200, and 300 m) in April and September 1998 and seven layers (0, 10, 20, 30, 50, 75, and 100 m) in November 1999 were collected at each station using a bucket and Niskin sampler to measure the chlorophyll a concentration by a Hitachi 139 spectrofluorometer.

The adult stages of each euphausiid species were sorted from each sample, and the numerical abundance (individuals m<sup>-2</sup>) in each sampling layer was calculated using the volume of water that passed through the net as measured by a flowmeter attached to the MOCNESS-I. The median depth of each species of euphausiid at each station was defined as the depth at which the cumulative percentage of abundance to the total population from the surface corresponded to 50%, with the assumption that an equal density of euphausiids was distributed in each sampling layer. For example, if 20 and 80% of the abundance occurred in the 50–150 and 150–250 m layers, respectively, then the median depth was calculated as follows:  $(50–20\%)/80\% \times$ (250–150 m)+150 m=187.5 m.

The stations used in this study were identified using the sampling month (April [A], September [S] and November [N]), station number, and sampling time (day [D] and night [N]) in order. For example, "Stn. A1D" refers to "Station 1" occupied during the daytime in April. D and N samplings were conducted at seven locations (14 stations); D samplings were conducted at ten stations, and N samplings were conducted at four stations (Fig. 1).

Water masses were classified using the temperature at 100 m in depth as in the Oyashio area ( $\leq$ 5°C), transitional area (>5°C,  $\leq$ 15°C), and Kuroshio area (>15°C). Transi-



**Fig. 1.** Location of sampling stations using MOCNESS-I off northeastern Japan, with monthly average disposition of oceanographic conditions off northeastern Japan (Kato et al. 2000, 2001). OW: Oyashio area, C: Cold waters, WR: warm-core ring, KW: Kuroshio area, TW: Tsugaru Warm Current area.

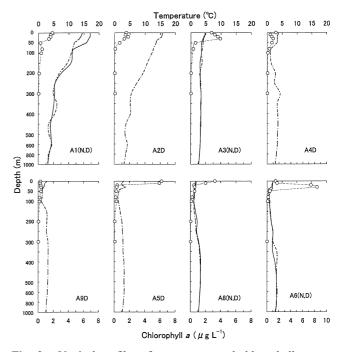


Fig. 2. Vertical profiles of temperature and chlorophyll *a* concentration at each station in April 1998. Temperatures obtained from CTD in MOCNESS-I. Open circles, solid lines and chained lines show the chlorophyll *a* concentration, nighttime temperature, and daytime temperature, respectively.

tional areas were further classified using the temperature at 100 m in depth as cooler transitional ( $\leq 10^{\circ}$ C) and warmer transitional (>10°C) areas.

#### Results

#### Environment

In April 1998, Stns. A1 (N, D) and A2D were located near a warm-core ring (Fig. 1), and the surface temperatures at these stations were 14.5–17.1°C (Fig. 2). The thermal front of the Oyashio Current occurred between Stns.

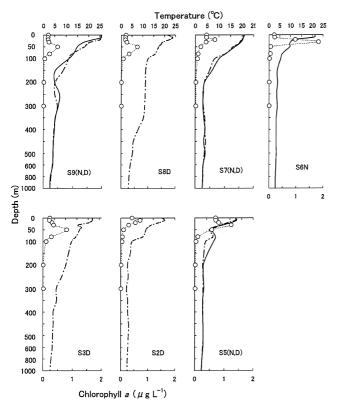


Fig. 3. Vertical profiles of temperature and chlorophyll a concentration at each station in September 1998. Temperatures obtained from CTD in MOCNESS-I. Open circles, solid lines and chained lines show the chlorophyll a concentration, nighttime temperature, and daytime temperature, respectively.

A2D and A3 (N, D), and cold water of about 1°C occurred at approximately 100 m depth at stations north of Stn. A4D. The chlorophyll *a* concentration in the surface layer at each station exceeded  $1 \,\mu g \, L^{-1}$ , and was as high as  $8.4 \,\mu g \, L^{-1}$  at 30 m at Stn. A6 (N, D), except at Stn. A9D (Fig. 2).

In September 1998, Stns. S3D and S8D were located near the center of warm-core rings, and Stns. S7 (N, D) and S9 (N, D) were located near the margins of a warm-core ring (Fig. 1). Stn. S6N was located on the east side of the cold area. Stn. S5 (N, D) was located between the first branch of the Oyashio Current and the Tsugaru Warm Current. At Stns. S2D, S6N and S5 (N, D), temperatures  $<5^{\circ}$ C dominated (Fig. 3). The maximum chlorophyll *a* concentration generally occurred at 30 to 50 m at each station but was lower than  $1 \mu g L^{-1}$  except at 30 m at Stns. S5 (N, D) and S6N (Fig. 3).

In November 1999, Stn. N2D was strongly influenced by the Kuroshio Extension (Figs. 1, 4). Stn. N4N also appeared to be under the influence of the Kuroshio Extension based on the temperature profile (Fig. 4), although this station was located near the cold area (Fig. 1). Stn. N5D was located along the margin of the cold area. Stn. N6N was located near the margin of the Tsugaru Warm Current, and no thermocline was apparent at this station. Stn. N8N was influenced by the Oyashio Current and had temperatures  $<4^{\circ}C$ 

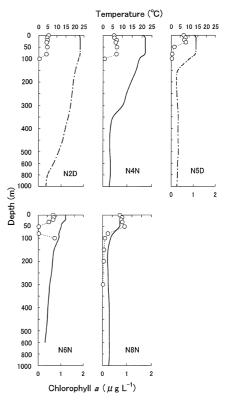


Fig. 4. Vertical profiles of temperature and chlorophyll a concentration at each station in November 1999. Temperatures obtained from CTD in MOCNESS-I. Open circles, solid lines and chained lines show the chlorophyll a concentration, nighttime temperature, and daytime temperature, respectively.

below 100 m. The chlorophyll *a* concentration tended to be higher at the northern stations, and was 0.7 to  $0.9 \,\mu g \, L^{-1}$ between the surface and 50 m at Stn. N8N (Fig. 4).

#### Euphausiids identified in the survey area

Thirty-two euphausiid species in eight genera were identified (Table 1). Subarctic-transitional epipelagic *Euphausia pacifica* had the highest cumulative abundance in all of the layers sampled in the survey area, with a relative contribution to the total euphausiid abundance of 78.1%. Subarctic epipelagic *Thysanoessa inspinata* Nemoto and subarctic mesopelagic *Tessarabrachion oculatum* Hansen were the second and third most abundant, with relative contributions to the total abundance of 5.6 and 4.1%, respectively. Five warm-water species of *Euphausia* followed, with relative contributions to the total abundance of 1.2 to 2.0%.

#### Horizontal distribution of euphausiids

*Euphausia pacifica* and *T. oculatum* were widely distributed in the survey area but rare in the warmer transitional area (Stns. S3D and S8D) and in the Kuroshio area (Stns. N2D and N4N; Fig. 5). The distribution pattern of *T. inspinata* was similar to that of these two species, but *T. inspinata* tended to be more abundant in the cooler Oyashio

**Table 1.** Mean abundance of euphausiid species (individuals  $m^{-2}\pm SE$ ) pcr station in the survey area. Relative contribution (%) to the total abundance of euphausiids is shown in parentheses.

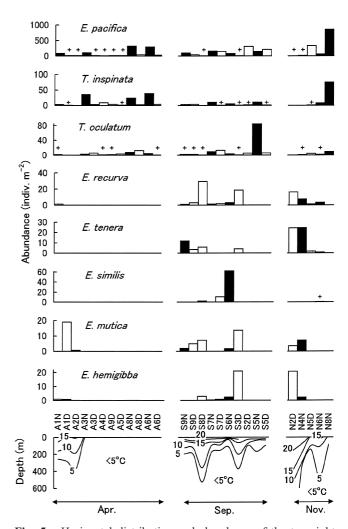
Species	Abundance
Euphausia pacifica Hansen, 1911	125.8±34.7 (78.1)
Thysanoessa inspinata Nemoto, 1963	9.0±3.2 (5.6)
Tessarabrachion oculatum Hansen, 1991	6.7±3.1 (4.1)
Euphausia recurva Hansen, 1905	3.2±1.4 (2.0)
Euphausia tenara Hansen, 1905	2.8±1.3 (1.7)
Euphausia similis G. O. Sars, 1883	2.8±2.3 (1.7)
Euphausia mutica Hansen, 1905	2.2±0.9 (1.4)
Euphausia hemigibba Hansen 1910	1.9±1.1 (1.2)
Nematoscelis microps G. O. Sars, 1883	1.5±0.5 (0.9)
Thysanoessa longipes Brandt, 1851	0.9±0.4 (0.6)
Nematobrachion boopis (Calman, 1905)	0.5±0.3 (0.3)
Nematoscelis gracilis Hansen, 1910	0.5±0.3 (0.3)
Stylocheiron longicorne G. O. Sars, 1883	0.4±0.2 (0.3)
Nematoscelis difficilis Hansen, 1911	0.4±0.2 (0.2)
Stylocheiron carinatum G. O. Sars, 1883	0.3±0.2 (0.2)
Thysanoessa gregaria G. O. Sars, 1883	0.3±0.2 (0.2)
Thysanopoda aequalis Hansen, 1905	0.2±0.2 (0.1)
Euphausia gibboides Ortmann, 1893	0.2±0.1 (0.1)
Stylocheiron affine Hansen, 1910	0.2±0.1 (0.1)
Euphausia nana Brinton, 1962	0.2±0.1 (0.1)
Euphausia diomedeae Ortmann, 1894	0.2±0.1 (0.1)
Stylocheiron abbreviatum G. O. Sars, 1883	$0.1\pm0.1~(0.1)$
Stylocheiron suhmi G. O. Sars, 1883	$0.1\pm0.1$ (0.1)
Stylocheiron elogatum G. O. Sars, 1883	0.1±0.05 (0.1)
Euphausia pseudogibba Ortmann, 1893	$0.1\pm0.1~(0.1)$
Stylocheiron maximum Hansen, 1908	0.1±0.05 (0.1)
Stylocheiron microphthalma Hansen, 1910	0.1±0.05 (0.05)
Nematoscelis tenella G. O. Sars, 1883	0.1±0.1 (0.05)
Pseudeuphausia latifrons (G. O. Sars, 1883)	0.1±0.04 (0.04)
Thysanopoda orientalis Hansen, 1910	0.1±0.1 (0.04)
Nematobrachion flexipes (Ortmann, 1893)	0.04±0.03 (0.02)
<i>Thysanopoda tricuspidata</i> H. Milne Edwards, 1837	0.02±0.02 (0.01)

stations. The number of individuals of *T. inspinata* and *E. pacifica* collected at night was generally higher than that collected during the daytime at the same locations, which may have resulted mainly from net avoidance during the day.

Five warm-water species of *Euphausia* generally occurred in the transitional and Kuroshio areas (Fig. 5), but *Euphausia similis* G. O. Sars was found only in the transitional area and did not occur in the Kuroshio area. This species had a high mean abundance in the whole survey area (Table 1), but was not widely distributed; its high mean abundance was attributed to its very high abundance at Stn. S6N.

#### Vertical distribution of euphausiid species

*Euphausia pacifica* underwent clear diel vertical migration (Fig. 6a). This species tended to stay near the surface in the Oyashio area but in the deeper layers down to 450 m

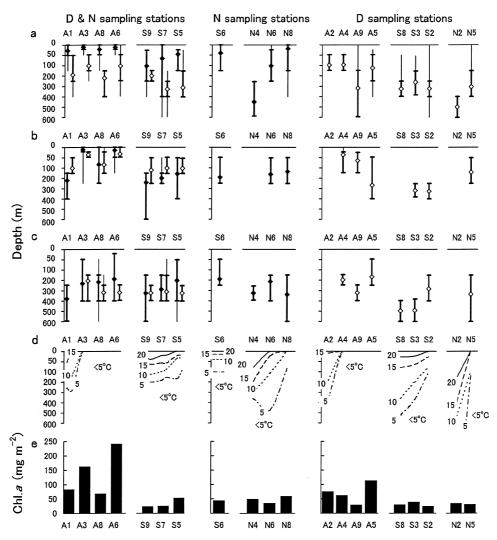


**Fig. 5.** Horizontal distribution and abundance of the top eight most abundant species of euphausiids within the 0-1,000 m depth range for each station with vertical temperature gradients. +denotes relatively low abundance. Solid and open bars indicate stations at nighttime and daytime, respectively.

in median depth (at Stn. N4N) in the transitional and Kuroshio areas. This species tended to be rare in the warmer layers (>15°C contour) at night, except at Stn. A1N, where the median depths remained at approximately 17°C (Fig. 6a, d). The median depth during daytime tended to be shallower than 100 m at several stations in the Oya shio area in April, but deeper than 300 m in the transitional and Kuroshio areas in September and November, especially the deepest median depth of 500 m at Stn. N2D. This species tended to stay in layers cooler than 10°C during the daytime. However, the median depth during the daytime was shallower (97–189 m) at the warmer Stns. A1D and A2D, but deeper (317 m) at the cooler Stn. A9D. The concentration of chlorophyll *a* at Stn. A9D was lower than that at Stns. A1D and A2D (Fig. 6e).

*Thysanoessa inspinata* tended to stay near the surface at several stations in the Oyashio area in April, but in the deeper layers in the transitional area down to 240 m at night

#### Vertical distribution of euphausiids



**Fig. 6.** Vertical distribution of three subarctic euphausiid species with vertical temperature gradients and integrated chlorophyll *a* concentration from 0 to 100 m. a: *Euphausia pacifica*, b: *Thysanoessa inspinata*, c: *Tessarabrachion oculatum*, d: temperature gradients, e: chlorophyll *a* concentration. Solid and open diamonds indicate the median distribution depths at nighttime and day-time, respectively. Vertical bars with and without both end bars show the range of layers where >80% and 100% of abundance occurred, respectively. Note that the latter vertical bars are hidden by the former in cases where both ranges overlap.

at Stn. S9N and 330 m during the day at Stn. S2D as its median depth (Fig. 6b). This species tended to stay in layers cooler than  $10^{\circ}$ C (Fig. 6b, d). The daytime depths were shallower than the nighttime depths at several locations.

*Tessarabrachion oculatum* generally stayed in deeper layers than did *E. pacifica* and *T. inspinata* both day and night (Fig. 6c). This species tended to make short diel migrations (<133 m of the distance based on median depth between nighttime and daytime), and rarely occurred in the warmer layers (>5°C contour; Fig. 6c, d). *Tessarabrachion oculatum* tended to stay in the deeper layers in the warmer area down to 499 m in median depth during the daytime (at Stns. S3D and S8D).

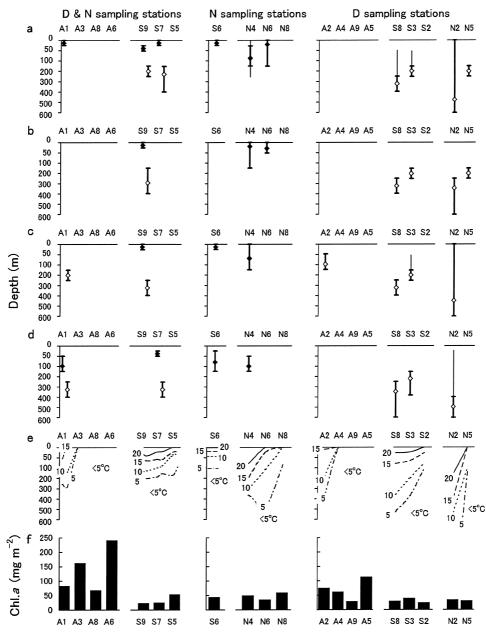
The nighttime depths of *Euphausia recurva* Hansen, *Euphausia mutica* Hansen, and *Euphauisa tenera* Hansen were generally concentrated near the surface, except at Stn. N4N (Fig. 7a–c). At Stn. N4N, the vertical distribution

range was deeper and wider in the former two species and wider in the latter species. On the other hand, the nighttime median distribution depth of *Euphausia hemigibba* Hansen was not near the surface (Fig. 7d). The daytime depth for these four species was deepest at Stn. N2D, with a median depth of 347–498 m, and a little shallower at Stn. S8D. The nighttime median distribution depth of *E. similis* was concentrated near the surface with a median depth of 16 m at Stn. S6N, where this species was very abundant (not shown in Fig. 7). The daytime depth range of this species was 150–250 m and 250–400 m at Stns. S7D and S8D, respectively.

## Discussion

For *Euphausia pacifica*, the nighttime ascent was restricted by higher temperatures (>15°C), except at Stn.

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**Fig. 7.** Vertical distribution of four warm-water species of *Euphausia* with vertical temperature gradients and integrated chlorophyll *a* concentration from 0 to 100 m. a: *Euphausia recurva*, b: *Euphausia tenera*, c: *Euphausia mutica*, d: *Euphausia hemigibba*, e: temperature gradients, f: chlorophyll *a* concentration. Solid and open diamonds indicate the median distribution depths at night-time and daytime, respectively. Vertical bars with and without both end bars show the range of layers where >80 % and 100% of abundance occurred, respectively. Note that the latter vertical bars are hidden by the former in cases where both ranges overlap.

A1N (Fig. 6a, d). This result is comparable with the vertical distribution pattern of *E. pacifica* in Toyama Bay, Japan Sea, where its upper migration was restricted by warmer water with temperatures of approximately 20°C (Iguchi et al. 1993). However, according to them, the greatest population density always occurred at depths where the temperature was 15–16°C at night from June to December in Toyama Bay. Thus, *E. pacifica* seems to be adapted to warmer water in this bay compared to off northeastern Japan.

The concentrated distribution in the warm surface waters

at Stn. A1N, where the chlorophyll a was higher above 50 m (Fig. 2), is probably related to feeding activity or acceleration of reproductive processes. *Euphausia pacifica* tends to shift its food preference to phytoplankton when phytoplankton abundance is high (Nakagawa et al. 2001), therefore this species possibly was feeding on the abundant phytoplankton in the surface layer at Stn. A1N. On the other hand, a high percentage (72%) of mating females occurred mainly above 50 m at Stn. A1N (Taki unpubl.), suggesting that the warmer temperatures in the surface layer

could accelerate their reproductive processes as observed in spawning females of *Meganyctiphanes norvegica* (M. Sars) (Tarling et al. 1999).

During the daytime, the median distribution depths of *E. pacifica* were shallower in the Oyashio area in April but deeper in the transitional and Kuroshio areas (Fig. 6a, d). This result seems to be consistent with the suggestion of Endo (1981) that *E. pacifica* does not need to descend to deeper layers during daytime in the colder regions because it can reduce its metabolic expenditure in the shallow cold layers, whereas it must descend to the deeper layers below the thermocline in the warmer regions, referring to the hypothesis of the adaptive value of vertical migration by McLaren (1963).

Among the daytime stations in April, the median distribution depth of the species at Stn. A9D in the Oyashio area was deepest, whereas that at Stns. A1D and A2D in the warmer transitional area was shallower. The chlorophyll *a* concentration from the surface to 100 m depth was lower  $(27 \text{ mg m}^{-2})$  at the former station, but higher  $(75-83 \text{ mg m}^{-2})$  at the latter staface layers probably caused the apparently deeper distribution, although *E. pacifica* feeds mainly at night (Nakagawa et al. 2003).

In a survey conducted at three stations in the Oyashio area off northeastern Japan (Nakagawa et al. 2003), *E. pacifica* stayed mainly in the 50–150 m layer at one station but below the 150–300 m layer at two stations during daytime in September. The integrated chlorophyll *a* concentration from the surface to 100 m was about 75–120 mg m<sup>-2</sup> at the former station, but approximately 30–40 mg m<sup>-2</sup> at the latter two stations. Therefore, the daytime distribution depths of *E. pacifica* seem to be affected by the chlorophyll concentration in the shallow layers regardless of seasonality.

The characteristics of diel vertical migration for *E. pacifica* in the offshore area observed in the present study may be closely related to the formation of the fishing grounds during daytime in the Sanriku and Joban coastal waters  $(36-40^{\circ}N)$ . Both lower temperatures and high density of phytoplankton during spring likely cause the distribution depths of *E. pacifica* to be shallower and allow seine boats to target epipelagic populations shallower than 50 m. However, the higher temperatures and lower density of phytoplankton during early summer are likely to deepen the distribution and necessitate the switch from boat seine to trawl net fishing, which targets the benthopelagic populations (Nicol & Endo 1997).

Thysanoessa inspinata did not perform an obvious diel vertical migration (Fig. 6b). The range of the vertical distribution was limited by a temperature barrier of  $>10^{\circ}$ C (Fig. 6b, d), which indicates that this species is adapted to colder water than is *E. pacifica* (>15°C). The median depth during daytime was somewhat shallower and in warmer water than that of *E. pacifica*, and at several stations daytime ascent was observed. Brinton (1962) also indicated that *T. inspinata* stays mainly above 280 m both day and night and undergoes no vertical migration in the North Pacific. Con-

versely, Taniguchi (1969) observed vertical migration of *T. inspinata* off southeast Hokkaido, northeastern Japan, although one-third of the population stays in the shallower layer (50–65 m) during daytime. Ascending during the daytime increases the vulnerability of this species to predation, whereas *T. inspinata* itself could benefit if it is a visual predator. Endo (1981) suggested that *T. inspinata* and its allied species, *Thysanoessa longipes* Brandt, show their food preference to zooplankton compared to *E. pacifica* in Sanriku waters.

A restricted vertical migration was observed for *T. oculatum* (Fig. 6c). The nighttime ascent of this species has also been reported in the North Pacific (Brinton 1962) and off southeast Hokkaido (Taniguchi 1969). Brinton (1962) mentioned that this species does not stay in the upper layers <150 m near the southern limit of its horizontal distribution range. From the present results, its vertical distribution may be restricted in deeper layers by warmer water with temperatures of approximately 5°C in such area (Fig. 6c, d).

Three warm-water euphausiids, i.e., E. recurva, E. tenera and E. mutica that originated from the Kuroshio region were narrowly concentrated near the surface at night in transitional areas where the lower temperatures in the shallow layer were  $<15^{\circ}$ C (Fig. 7). In the Kuroshio area, these species had a wider vertical range from the surface to the subsurface at night. In other warmer regions (the central waters of the eastern South Pacific, Sagami Bay, western Pacific Ocean, and eastern Indian Ocean), the temperatures at nighttime distribution depths of these species range from 15 to >25°C, whereas the depths varied according to region (Youngbluth 1975, Hirota et al. 1983, Hirota 1987). Avoiding unsuitable cold temperatures in the middle layers (perhaps <15°C) might cause this surface concentration, and such a distribution pattern might provide good feeding opportunities for zooplanktivores with weak tolerance of cooler temperatures such as immature skipjack tuna (Nihira 1996).

Four warm-water euphausiids (*E. recurva, E. tenera, E. mutica* and *E. hemigibba*) tended to stay in layers cooler than  $15^{\circ}$ C during the daytime, and in deeper layers in some warmer areas (at Stns. N2D and S8D) (Fig. 7). According to Hirota and Nemoto (1989), in the western Pacific Ocean these species show clear nocturnal feeding habits but rest in the cooler middle layers during the daytime. It seems that the daytime depths of these species are somewhat related to low temperatures which can reduce their metabolic expenditures as suggested for *E. pacifica* by Endo (1981), whereas Hirota (1987) considered light intensity as a possible factor affecting the vertical distribution of these species.

In conclusion, the diel vertical migration of euphausiids off northeastern Japan was strongly affected by water temperature, and the effects of temperature differed among species and among seasons for the same species. Generally, subarctic euphausiids have deeper vertical distributions both day and night in the transitional and Kuroshio areas compared to in the Oyashio area, whereas warm-water species have shallower vertical distributions both day and night in the transitional area compared to in the Kuroshio area. However, several exceptions were observed. To clarify the mechanism of the diel vertical migrations in more detail, a synthetic survey covering molting, reproduction, and feeding activity (e.g., Endo & Yamano 2006) and of predator behaviors (e.g., Sugisaki & Kurita 2004) is needed in the future.

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