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メタデータ	言語: English 出版者: 水産総合研究センター 公開日: 2024-10-02 キーワード (Ja): キーワード (En): distribution; Euphausia pacifica; fishery; life history; northeastern Japan 作成者: 瀧, 憲司 メールアドレス: 所属:
URL	https://fra.repo.nii.ac.jp/records/2010837

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水研センター研報，第18号，41－165，平成18年
Bull. Fish. Res. Agen. No. 18, 41-165, 2006

博士号論文

Studies on fisheries and life history of *Euphausia pacifica* HANSEN off northeastern Japan[*1]

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Abstract *Euphausia pacifica* is the dominant euphausiid in the North Pacific Ocean. In the Japanese waters of the Pacific Ocean, it occurs as far south as Suruga Bay, 34° 50'N and extends northwards as far as the southwestern area of the Okhotsk Sea. *E. pacifica* is commercially exploited in Sanriku (38°－41° N) and Joban (36°－38° N) waters off northeastern Japan from late winter to early summer. The average annual catch and average annual value on landing is 66,000 ton and 3.1 billion yen, respectively, during the years 1992 and 2001. Because the annual catch, fishing period and landing value of *E. pacifica* varies between regions and years, accurate assessment of the fishery resource and prediction of fishing conditions for the next season have been demanded to maintain the stability of this fishery. On the other hand, *E. pacifica* is considered a key species because many endemic and migrant predators depend on this species as prey. In addition, the feeding impact by *E. pacifica* on the lower trophic levels in the ecosystem are significantly high considering its high biomass. Considering the important role of *E. pacifica* to transport organic matter from the lower trophic levels to higher trophic levels in the North Pacific, qualitative and quantitative analyses of distribution, life history and carbon budgets of *E. pacifica* have great importance for understanding the structure of marine ecosystems in this area. From the above mentioned reasons, the fishery, horizontal and vertical distribution, life history, biomass, carbon budgets (production and metabolism) and feeding of *E. pacifica* off northeastern Japan were examined in this study.

To examine how oceanographic conditions have affected fishing conditions, annual variations of fishing conditions such as the strength of catch and CPUE (catch per unit effort) were investigated in relation to the oceanographic conditions such as the first branch of the Oyashio Current as well as the history of development of fishing methods and regulations in *E. pacifica* fishery. The relationship between the fishing conditions and oceanographic conditions is as follows. When the first branch of the Oyashio Current is weak, fishing conditions in northernmost Iwate Prefecture are rather stable but fishing condition in Miyagi Prefecture and southernmost Joban area is unstable, showing low CPUE and delayed formation of the fishing ground. On the other hand, when the first branch of the Oyashio Current is strong, fishing conditions in Miyagi Prefecture and Joban area are favorable as well as in Iwate Prefecture, showing high CPUE and early formation of the fishing ground.

To examine the distribution and life history of *E. pacifica*, seasonal changes in spawning, distribution and growth patterns and life span of this species were investigated over a broad geographical area (mainly 36°－43° 00' N and west of 145° E) using Norpac net and cylindrical-conical net samples. Mating and spawning occurred throughout the year in the Oyashio area ($T_{100} \leqq 5$℃) and colder waters of the transitional area (5℃ $<T_{100} \leqq 10$℃ , with a peak in spring but less in late fall-winter. Apparent growth was recognized from March to June for

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2006年６月23日受理（Received: June 23, 2006）

[*1] 東京大学審査学位論文（Ph.D. Thesis, Tokyo University）（掲載に際し投稿規程に沿って一部修正した）

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the small-sized group of adults. The life span of male and female *E. pacifica* off northeastern Japan was estimated to be 24 months and 28 months, respectively. *E. pacifica* gradually adapts to colder areas as the developmental stage progresses from furcilia to adults, and advanced-age adults (large-sized group of adult) rarely occur in warmer areas. Geographical distributional pattern of spawning and each stage was generally closely related to the distribution of the water masses.

To examine physical and biological factors which determine the vertical distribution of *E. pacifica*, seasonal variations of vertical distribution of *E. pacifica* were investigated in the coastal and offshore waters (36°-42° 00' N and west of 145° E), using ORI, beam-trawl and MOCNESS-I net samples. In the Sanriku coastal waters, benthopelagic *E. pacifica* occurred on the upper slope from early summer to fall where strong thermocline occurred in the middle layer above colder temperatures under 8℃ in the low layer. In spring, adult *E. pacifica* forms dense pelagic aggregations throughout the day on the continental shelf where water with 7-8℃ dominates in the total water column. In the offshore area, annual average median depth of each developmental stage of *E. pacifica* at night tended to increase with the developmental stages from middle-furcilia to large adults, while the median depth in the daytime tended to increase with developmental stages from first calyptopis to sixth furcilia. Median depth at night of immature and adult stages tended to be deeper in the warmer areas in summer and fall, especially large adults hardly reached beyond the thermocline in the mid layer. In spring, the median depth during daytime of immature and adult stages was significantly shallower than that in other months and thus the distance of diurnal vertical migration tended to be shorter.

To examine the characteristics of carbon budgets of *E. pacifica,* biomass, production and metabolism of *E. pacifica* were investigated along the coastal waters (36° 50'-42° 50'N). High biomass was found in summer-fall off southeastern Hokkaido, and in the late winter-early summer off Sanriku and Joban. Annual mean biomass was 381, 314 and 258mg C m^{-2} off southeastern Hokkaido, Sanriku and Joban, respectively. The total production (sum of growth, moults and eggs) during the survey period off southeastern Hokkaido (3,829mg C m^{-2}) was comparable with that off Sanriku (3,872mg C m^{-2}); both were much higher than that off Joban (2,243mg C m^{-2}). The somatic production during the survey period contributed to the highest proportion (51.5-70.9 %) of the total production in the respective coastal areas. The total metabolism (routine and diurnal vertical migration) during the survey period ranged from 3,846mg C m^{-2} off southeastern Hokkaido to 3,062mg C m^{-2} off Joban, accounting for 50.1-57.7% of the assimilation (production and metabolism). The routine metabolism during the survey period ranged from 2,783mg C m^{-2} off Sanriku to 2,257mg C m^{-2} off Joban, contributing the highest proportion (32.8-42.5 %) to the assimilation in each coastal area.

To examine how diets and feeding behavior change according to ambient food conditions, seasonal change in stomach contents of *E. pacifica* was surveyed in the coastal waters off southeastern Hokkaido and Joban. *E. pacifica* tended to consume many diatoms when high chlorophyll *a* concentrations occurred but tended to consume large numbers of copepods when the chlorophyll *a* concentration was low in each of the coastal areas surveyed. Both the numerical number and carbon content of copepods in the stomach of *E. pacifica* off Joban were generally higher than those off southeastern Hokkaido throughout the year. The copepod contribution to the total food ingestion for adult size of *E. pacifica* is estimated to be 7.3% and 30.0% off southeastern Hokkaido and Joban, respectively. The contribution of copepods as food of *E. pacifica* is thought to be higher in the southern warmer waters.

Finally, three key points are discussed from the results obtained in this study, in comparison with the cases of *Euphausia superba* and *Neocalanus species*, i.e. (1) significances of seasonal migration of *E. pacifica,* (2) mechanism of formation of fishing ground in *E. pacifica* in the Sanriku and Joban coastal waters, and (3) impact of feeding by *E. pacifica* on the primary and secondary production.

Key Words: distribution, *Euphausia pacifica*, fishery, life history, northeastern Japan

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Contents

Chapter 1. Introduction

Euphausiids are eucarid crustaceans and the order Euphausiacea is divided into two families, the Bentheuphausiidae containing the single genus and species *Bentheuphausia amblyops*, and the Euphausiidae containing all the other species and there are 86 known species in the order Euphausiacea (Baker *et al.,* 1990). There are currently at least six commercial fisheries harvesting six different species of euphausiids; Antarctic krill (*Euphausia superba*) which is fished off Antarctic, *Euphausia pacifica* fished off Sanriku and Joban (northeastern Japan), western Canada, *Euphausia nana* fished in Uwajima-Bay in Ehime Prefecture (southwestern Japan), *Thysanoessa inermis* fished off western Hokkaido and off eastern Canada, and *Thysanoessa raschi* and *Meganyctiphanes norvegica* fished off eastern Canada. Most of these fisheries have been in operation for over 30 years. The current world catch of all species of krill is approximately 160,000 tonnes (Nicol and Endo, 1997).

Euphausia pacifica is the dominant euphausiid in the North Pacific Ocean (Brinton, 1962; Mauchline and Fisher, 1969). In the Japanese waters of the Pacific Ocean, it occurs as far south as Suruga Bay, 34° 50'N (Sawamoto, 1992) and extends northwards as far as the southwestern area of the Okhotsk Sea (Ponomareva, 1963; Ohtsuki, 1975). It is present over almost the entire Sea of Japan extending northwards as far as the southern part of the Gulf of Tartary (Komaki and Matsue, 1958; Ponomareva, 1963). *E. pacifica* is considered a key species in the marine ecosystem off northeastern Japan because many endemic and migrant predators, including pelagic and demersal fishes, marine mammals, seabirds and benthic organisms, depend on this species for food (Nemoto, 1957, 1962; Takeuchi, 1975; Ogi and Tanaka, 1984; Odate, 1991; Nicol and Endo, 1997; Yamamura *et al.,* 1998).

Euphausia pacifica is commercially exploited in Sanriku and Joban waters from late winter to early summer. 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). Generally, the southern tip of the first branch of the Oyashio Current reaches its southernmost latitude in April and recedes to its northernmost latitude in December (Ogawa, 1989). The fishing grounds are formed near the frontal area between the coastal branch of the Oyashio Current and the coastal waters (Odate, 1991). It is generally considered that the dense population of *E. pacifica* is transported to the Sanriku and Joban coastal areas in spring by the first branch of the Oyashio Current (Odate, 1991).

So, several studies on the mechanism of formation of fishing ground and condition have been conducted (Terazaki, 1981; Odate, 1991; Kotani, 1992; Kodama, 1995a; Ebisawa, 1995). The average annual catch and landing value is 66,000 tonnes and 3.1 billion yen, respectively, during the years 1992 and 2001. But, fishery of *E. pacifca* has drastically changed historically, i.e. fishing effort and catch increased remarkable from the late 1960s; fishing methods changed drastically in the late 1980s; and several self-regulation restrictions by fishermen have been set from the early 1990s. Therefore, annual variations of fishing conditions have been closely related to social and economical reasons other than the natural variations of oceanographic conditions and the resources. Because annual catch, fishing period and landing value of *E. pacifica* varies between regions and years, fishermen and the processing industry have been demanding accurate assessment of fishery resource and prediction of fishing condition to maintain stability of this fishery.

Euphausia pacifica has seven developmental stages; egg, nauplius, metanauplius, calyptopis, furcilia, immature and adult stages. Iguchi and Ikeda (1994) showed that the egg (capsule diameter: ca. 0.4-0.5mm) development time is <1, 2, 4 and 7 days, when the ambient temperatures is >15, 10, 5 and 1 ℃, respectively. According to Ross (1981), 2.0–2.2, 2.3–6.0, 13–14 and 27.5–46 days are required for the nauplius (ca. 0.3–0.5mm body length), metanauplius (ca. 0.4–0.6mm BL), calyptopis (ca. 0.8–2.2mm BL) and furcilia (ca. 1.8–6.0mm BL) stages, respectively, at the temperature conditions of 8 and 12℃. 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. 10mm BL) via larval and immature (ca. 6.0–10.0mm) stages is estimated to be ca. 3 months (Brinton, 1976; Endo, 1981; Iguchi *et al.,* 1993).

Several studies on the life history of *E. pacifica* have been conducted and have elucidated that the life history varies between regions (Nemoto, 1957; Ponomareva, 1963; Smiles and Pearcy, 1971; Brinton, 1976; Heath, 1977; Endo, 1981; Ross *et al.,* 1982; Fulton and LeBrasseur, 1984; Odate, 1991; Pogodin, 1990; Bollens *et al.*, 1992; Iguchi *et al.,* 1993; Tanasichuk, 1998a). For example, spawning occurs throughout the year and life span is estimated to be 8-12 months off warmer southern California (Brinton, 1976). While, spawning was limited in early summer and life span is estimated to be 2 years in colder Okhotsk Sea (Ponomareva, 1963). Endo (1981) reported that eggs and larvae of this species occur throughout the year in Sanriku waters, but are most abundant in April-June. He estimated the life span of females to be more than 2 years and males to be less than 2 years on the basis of length-frequency distributions. However, the distributional area of *E. pacifica* is characterized by a complex oceanographic structure represented by the Oyashio Current, Kuroshio Current Extension, Tsugaru Warm Current, and numerous warm-core rings shed by these currents (Uda, 1938; Kawai, 1972; Tomosada, 1986). The variabilities of these oceanographic processes combine to affect the distribution and abundance of euphausiids. Given the wide distributional range of *E. pacifica* as well as probable horizontal advection, large areas need to be surveyed using the same gear and methods to effectively investigate the life history of this species. To date, however, population dynamics studies of *E. pacifica* in the northwestern Pacific have been conducted at a few fixed stations (Endo, 1981; Terazaki *et al.,* 1986) or based on catches by commercial fishing boats (Komaki, 1967; Odate, 1991).

Diurnal vertical migration performs an important role to transport organic matter vertically. Several studies on diurnal vertical migration of *E. paciifca* has been conducted (Boden, 1950; Ponomareva, 1963; Brinton, 1967; Alton and Blackburn, 1972; Frost and McCrone, 1974; Marlowe and Miller, 1975; Youngbluth, 1976; Endo, 1981; Terazaki *et al.,* 1986; Bollens *et al.,* 1992; Iguchi *et al.,* 1993; Iguchi, 1995; DeRobertis *et al.,* 2000). Eggs of *E. pacifca* are usually released in the surface layers as other species of euphausiid which live in the surface layer. These eggs are thought to sink and hatch at the first nauplius in the middle layer which develops through the second nauplius into metanauplius. The mouthparts of the nauplius and matanauplius are not functional and so they presumably do not feed in the middle layer. The first calyptopis following metanauplius begins to feed using functional mouthparts in the surface euphotic layer. After calyptopis, *E. pacifica* gradually extends its vertical migration range with developmental stages (Brinton, 1967; Endo, 1981; Bollens *et al.,* 1992; Iguchi *et al.,* 1993; Iguchi, 1995). Due to their weak swimming ability, larval stages of euphausiids generally undergo diurnal vertical migration in the shallower layer in order to effectively utilize phytoplankton in the surface layer (Mauchline and Fisher, 1969; Iguchi, 1995). On the other hand, Bollens *et al.* (1992) showed that vertical distribution during daytime of furcilia stage in *E. pacifica* depended on the abundance of visual fish predators which varied between years and months in the Dabob Bay, off western USA. Endo (1981) assumed that the difference of diurnal vertical migration pattern of adult *E. pacifica* between off eastern Hokkaido, Sanriku, Yamato-tai (Japan Sea) was attributable to the development of the thermocline. On the other hand, Terazaki *et al.* (1986) showed that diurnal vertical migration of copulated females of *E. pacifica* was different from that of other individuals in Sanriku waters in spring. However, studies on the vertical distribution of *E. pacifica* off northeastern Japan has been conducted only at a few fixed stations during limited seasons.

Euphausia pacifica is important not only as the target species of fishery but also as the food for commercial fishes in the ecosystem in the northeastern Pacific Ocean and several studies on the biomass and production of this species has been conducted there (Lasker, 1966; Heath, 1977; Mauchline, 1977; Brinton and Reid, 1986; Gomez-Gutierrez and Robinson, 1997; Tanasichuk, 1998a). The annual mean biomass of *E. pacifica* in the coastal water in the upstream California Current (Heath, 1977; Mauchline, 1977) tends to be higher than that in downstream California Current (Brinton, 1976; Gomez-Gutierrez and Robinson, 1997). The annual $P_g : B$ ratio is high (6.4-16.7) for *E. pacifica* off Barkley Sound (Tanasichuk, 1998a) that shows continuous occurrence of larvae throughout the year and high growth rates, but is low (2.6; recalculated value by Iguchi and Ikeda (1999)) for *E. pacifica* in Saanich Island (Heath, 1977). The annual production due to growth and moults of larval and immature specimens (＜9mm) showed a high proportion to the total (25-72% for growth and 7-46% for moults), although their annual mean biomass showed a low proportion to the total (14-24%) from 1991 to 1997 in *E. pacifica* off Barkley Sound (Tanasichuk, 1998a). In the northwestern Pacific Ocean, however, such a study has been conducted only in Toyama Bay, Japan Sea by Iguchi and Ikeda (1999).

Considering the important role of *E. pacifica,* to transport organisms from lower trophic level to higher trophic level studies on the feeding ecology of *E. pacifica* have great importance for understanding the structure of marine ecosystems off northeastern Japan. Several studies on the feeding ecology of euphausiids have been conducted and these are generally divided into three categories; morphological studies (Ponomareva, 1963; Nemoto, 1967), laboratory experiments on ingestion (Lasker, 1966; Parsons *et al.,* 1967; Ross, 1982; Ohman, 1984; Williason and Cox, 1987; Dilling *et al.,* 1998) and stomach content analysis (Ponomareva, 1963; Endo, 1981; Nakagawa *et al.,* 2001). Nakagawa *et al.* (2001) analyzed the stomach contents of *E. pacifica* in Sanriku waters and showed that ingestion of copepods was most important to effectively acquire energy while the stomachs contained largest number of diatoms in spring when diatoms were most abundant in the ambient water. However, feeding studies of *E. pacifica* have been conducted only in Sanriku waters (Endo *et al.,* 1985; Nakagawa *et al.,* 2001) and comparison of diet and feeding behavior between different areas showing various productivities has not yet been conducted off northeastern Japan.

In **Chapter 2,** annual variations of several fishing condition indices such as catch per unit effort, first fishing day and location of fishing ground were investigated in relation to the oceanographic condition indices such as surface water temperatures and southward shift of the first branch of the Oyashio Current. In addition, the history of development of fishing methods and regulations in *E. pacifica* fishery was investigated. From these results, how annual variations of the oceanographic conditions have affected those of fishing conditions and development of *E. pacifica* fishery in Sanriku (Iwate and Miyagi prefectures) and Joban (Fukushima and Ibaraki prefectures) coastal waters was examined.

In **Chapter 3,** seasonal changes in spawning, distribution and growth pattern and life span of *E. pacifica* off northeastern Japan were investigated using Norpac net samples collected widely (mainly 36°-43°00' N and west of 145°E) from several monthly multi-vessel line transect surveys during 10 years, and the average pattern of the distribution and life history of *E. pacifica* off northeastern Japan was examined. In addition, seasonal changes in spawning and distribution of *E. pacifica* in several fixed stations from off southeastern Hokkaido to Joban (36° 50'-42°50'N) were investigated bimonthly using cylindrical-conical nets with large mouth opening, and geographical changes of spawning and distribution of *E. pacifica* were examined in relation to water masses.

In **Chapter 4,** seasonal variations of vertical distribution of *E. pacifica* were investigated in the coastal and offshore waters off northeastern Japan. At first, seasonal variations of distribution of pelagic and benthopelagic *E. pacifica* were investigated along the coastal waters off Sanriku using ORI and beam-trawl net samples, and their trophic significance in the coastal waters ecosystem off Sanriku is discussed in light of predator-prey relationships. Secondly, seasonal variations of vertical distribution of each developmental stage of *E. pacifica* were investigated in the offshore waters off northeastern Japan using

MOCNESS-I net samples, and physical and biological factors which determine their vertical distribution of *E. pacifica* were examined.

In **Chapter 5,** biomass, production (somatic, eggs, moults) and metabolism (routine and diurnal vertical migration) of *E. pacifica* were investigated along the coastal waters off northeastern Japan, and characteristics of carbon budgets of *E. pacifica* off northeastern Japan are discussed comparing with the same species from other regions as well as other euphausiid species.

In **Chapter 6,** seasonal change in stomach contents of *E. pacifica* was surveyed in the coastal waters off southeastern Hokkaido and Joban. From the results, how diets and feeding behavior change according to ambient food conditions was examined. In addition, the significance of ingestion of copepods by *E. pacifica* was compared between the coastal waters off northeastern Japan.

In **Chapter 7 (General discussion)**, three key points are discussed from the results obtained in each chapter. At first, significances of seasonal migration of *E. pacifica* off northeastern Japan is discussed from the point of view of feeding, reproductive maturation and segregation between developmental stages, comparing with the cases in *E. superba.* Secondly, the mechanism of formation of fishing ground for *E. pacifica* in the Sanriku and Joban coastal waters is discussed in relation to its seasonal horizontal and vertical distribution pattern and physical environments. Finally, impact on the primary and secondary production by ingestion of *E. pacifica* off northeastern Japan was estimated and is discussed comparing with *Neocalanus* species.

Chapter 2. Fishery of *Euphausia pacifica*

Several studies on the *Euphausia pacifica* fishery in relation to the oceanographic conditions have been conducted (Odate, 1979; Kotani, 1992; Kodama, 1995a; Ebisawa, 1995). Odate (1979) found an inverse relationship between the southernmost latitude of the 5℃ sea surface temperature isotherms and the annual *E. pacifica* catch. Kodama (1995a) classified oceanographic patterns into three types according to the fishing conditions for *E. pacifica* in the vicinity of Kinkazan Island. However, the annual variations in fishing conditions have been affected not only by the natural environmental conditions but also by several social and economic background effects.

In this chapter, annual variations of several fishing condition indices such as catch per unit effort, first fishing day and location of fishing ground were investigated in relation to the oceanographic condition indices such as surface water temperature and southward shift of the first branch of the Oyashio Current. In addition, history of development of fishing methods and regulations in *E. pacifica* fishery was investigated. From these results, how annual variations of the oceanographic conditions have affected those of fishing conditions and development of *E. pacifica* fishery in Sanriku (Iwate and Miyagi prefectures) and Joban (Fukushima and Ibaraki prefectures) coastal waters was examined.

Materials and Methods

Landing price, number of fishing vessels and catch in each fishery port (Fig. 2-1) from 1984 to 2001 were referred to daily reports from National Federation of Fisheries Co-operative Associations, Tohoku Branch (FCA). Landing price in the total area from 1975 to 1983 were also referred to data from FCA. Landing price, number of fishing vessels and catch in each prefecture from 1984 to 2001 were referred to data from each prefectural Fisheries Experimental station (Table 2-1).

Characteristics in conditions of *Euphausia pacifica* fishery in each year were referred to 'Quick reports on fishing and oceanographic conditions' from Japan Fisheries Information Service Center. History of development in the *E. pacifica* fishery was investigated by questioning several fishermen and owners of processing industries for the fished *E. pacifica* and by referring to Odate's monograph on the fisheries biology of *E. pacifica* (Odate, 1991).

Surface temperatures for 10 day intervals in the Sanriku (38°-41°N, 142°-143°E and 38°-38.5°N, the west of 142°E) and Joban (36°-38°N, 141°-142°E) coastal areas from 1981 to 2001 were referred to the data from Japan Fisheries Information Service Center. The southernmost latitude in each month of the first branch of the Oyashio Current from 1971 to

2001 were referred to the reports on the fishing and oceanographic conditions in Tohoku area from Tohoku National Fisheries Research Institute, National Fisheries Agency (Fig. 2-2). The weekly location of fishing ground with surface temperature isotherms from 1995 to 2001 were referred to the 'Quick reports on fishing and oceanographic conditions' from Japan Fisheries Information Service Center.

Results

History and present status of the *E. pacifica* fishery

About 100 years ago, dip net fishing, which later developed into the use of bow-mounted trawl, was operated in Sanriku coastal waters for sand lance (*Ammodytes personatus*). The same method was used to harvest *Euphausia pacifica* in the mid-1940s by the fishermen of the Oshika Peninsula in Miyagi Prefecture (Odate, 1991). Fishery statistics for *E. pacifica* have been available since 1953 from the Onagawa Fish Market. The fishery had been re-

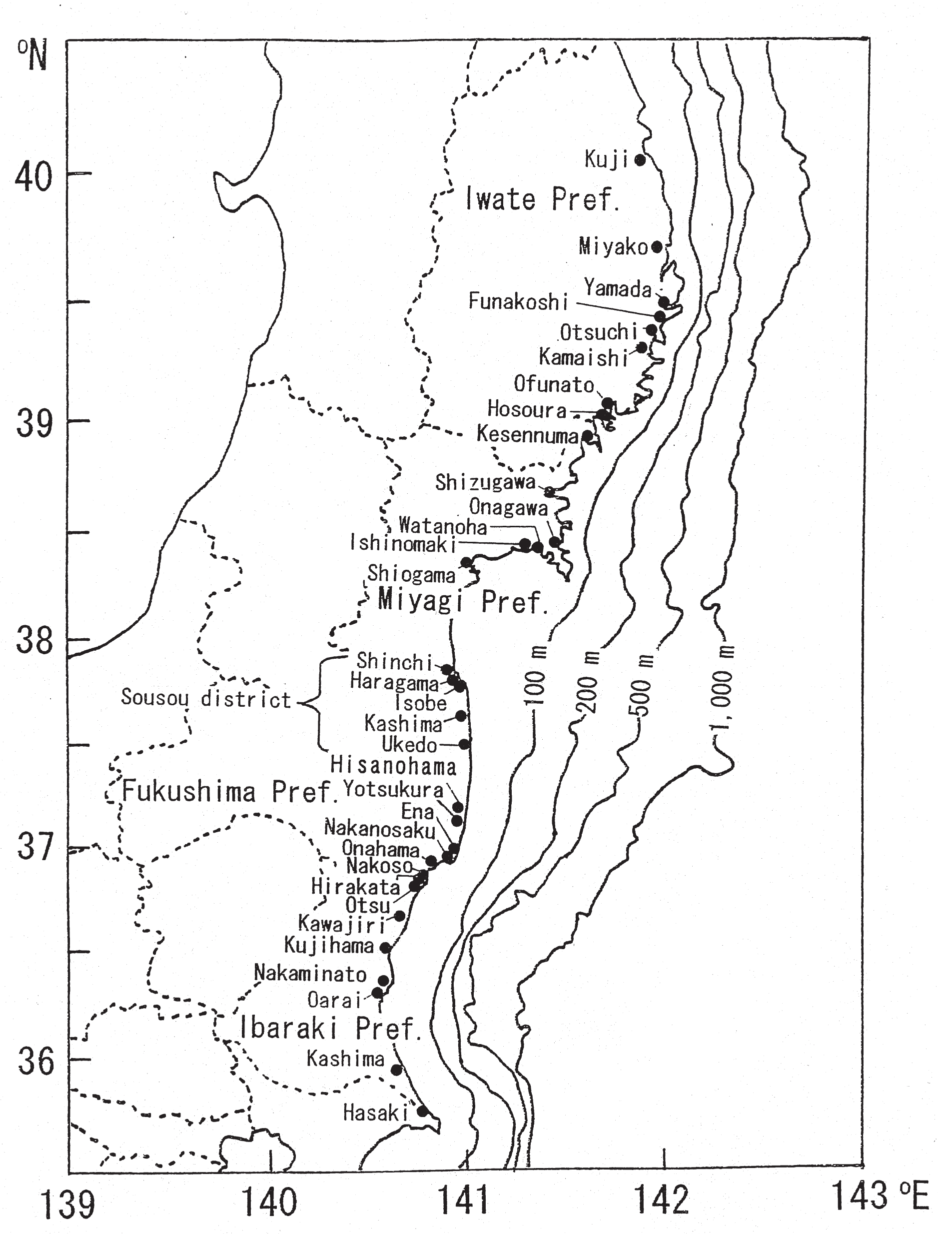

Fig. 2-1. Map of northeastern Japan indicating landing ports for *Euphausia pacifica*.

Table 2-1. References and estimation methods of fishery data

	Data	Period	Reference and method of estimation
Port	Catch	'84〜'01	From FCA[*1] except '96 and '00 of Ibaraki & a part of '97 of Iwate from PRF[*2].
	Fishing days	'84〜'01	Same as above.
	No. of boats	'84〜'01	(*Fishing days*)/(*Fishing days no. of boats available*[*3]) × (*Available no. of boats*)
	No. of boats per day	'84〜'01	(*Available no. of boats*)/(*Fishing days no. of boats available*)
	CPUE	'84〜'01	(*Total catch over the days no. of boats available*)/(*Available no. of boats*)
Prefecture	Price	'84〜'01	Iwate: From PRF except '84–'91 from FCA. Miyagi: From PRF except '84 from FCA. Fukushima: From PRF. Ibaraki: From PRF except '84–'91 from FCA.
	Catch	'71〜'01	Iwate: From PRF except '75〜'88 from Odate (1991). Miyagi: From PRF except '71〜'84 from Odate (1991). Fukushima: From PRF. Ibaraki: From PRF except '72〜'76 from Odate (1991).
	Fishing days	'84〜'01	From FCA except '96 & '00 of Ibaraki and a part of '97 for Iwate from PRF.
	No. of boats	'84〜'01	Iwate: From PRF except '84–'91 and '99 estimated by summing no. of port boats (est. from 3rd raw of table) over pref. from FCA. Miyagi: From PRF except '84 estimated by summing no. of port boats over pref. from FCA. Fukushima: From PRF except '84–'86 estimated by summing no. of port boats over pref. from FCA. Ibaraki: From PRF except '84–'91 estimated by summing no. of port boats over pref. from FCA.
	No. of boats per day	'84〜'01	(*No. of boats*)/(*Fishing days*)
	CPUE	'84〜'01	(*Catch*)/(*No. of boats*) but, if (*No. of boats*) was estimated from FCA as shown on the 9th raw of table, any (*catch*) is estimated by summing no. of port boats over each pref. from FCA.

[*1] Daily reports on fishery data for each port from National Federation of Fisheries Co-operative Associations, Tohoku Branch from 1984 to 2001 (except for Ofunato). Fishery data for Ofunato from 1984 to 1991 referred to from the daily reports of the Ofunato Fishery Market.

[*2] Data of Iwate Prefectural Fisheries Technical Center, Miyagi Prefecture Fisheries Research and Development Center, Fukushima Prefectural Fisheries Experimental Station and Ibaraki Prefectural Fisheries Experimental Station.

[*3] The port catch was always recorded on the fishing day, but no. of boats at ports was sometimes not recorded on the same day by FCA or PRF ('96 of Iwate).

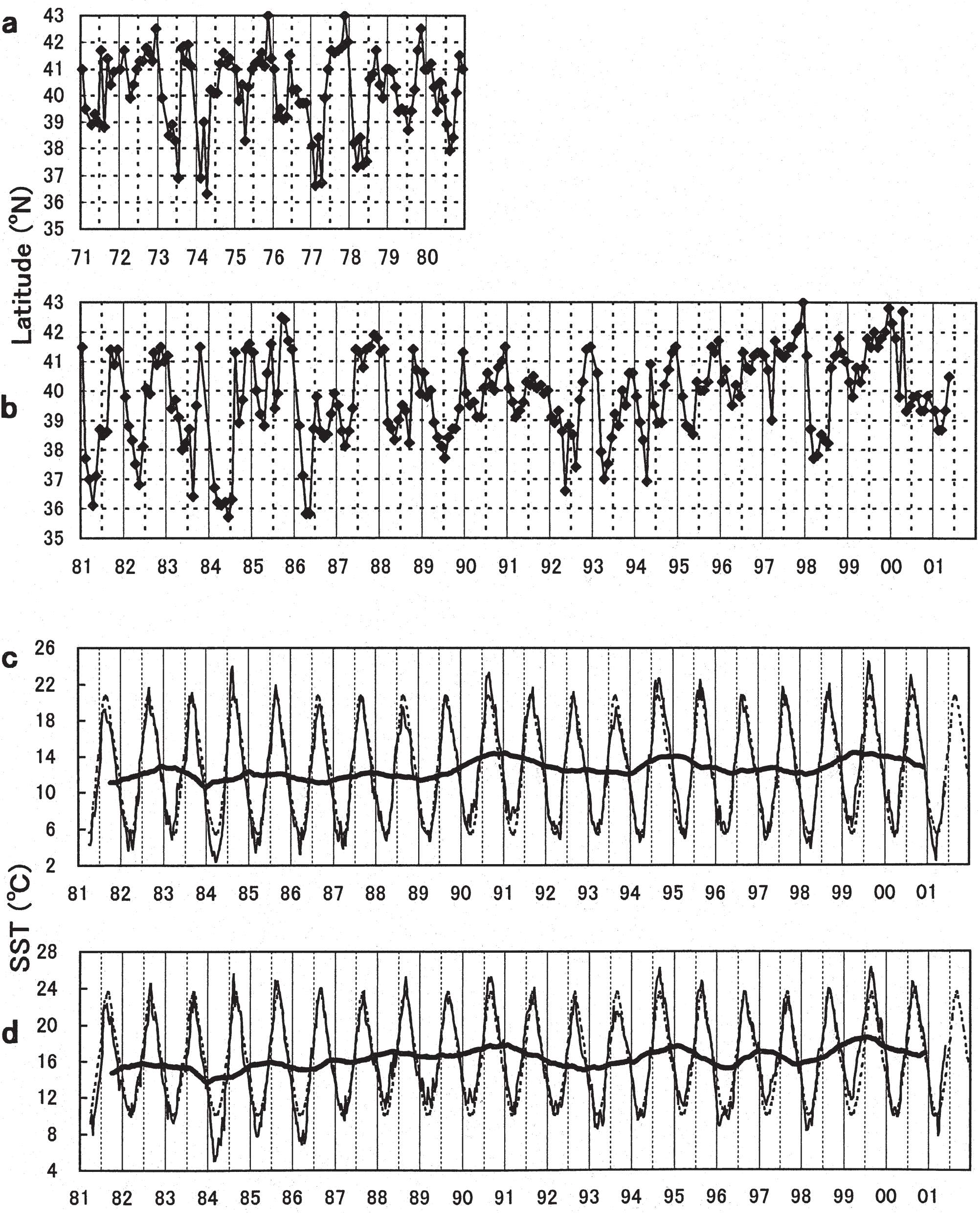

Fig. 2-2. The southern limits in each month of the first branch of the Oyashio Current from 1971 to 1980 (a) and from 1981 to 2001 (b), and the surface water temperature (SST) in the Sanriku (c) and Joban (d) waters. The southern limits of the first branch of the Oyashio Current are based on the data from the Tohoku National Fisheries Research Institute. SST is based on data from the Japan Fisheries Information Service Center. The solid thin lines, broken thin ones and solid thick ones in (c) and (d) show the raw data, mean values of the last 21 years and the 12-month running mean, respectively.

quired for a small demand for direct human consumption and for culture baits only from the local area until the 1960s.

The increased requirement for sea bream culture and bait for sport fishing in the late-1960s caused an expansion in the fishery to the north as well as along the southern coasts of Miyagi Prefecture. In Ibaraki Prefecture, fishing for *E. pacifica* began in 1972. Shortly thereafter in 1974, Fukushima Prefecture began an *E. pacifica* fishery to be followed by Iwate Prefecture in 1975 (Table 2-2).

Fished *E. pacifica* were stored in the fish hold in bulk and held in bamboo baskets until 1975. However, since 1975 plastic container which holds about 30kg of *E. pacifica* was introduced and helped reduce the rate of deterioration (Odate, 1991). Furthermore, high-speed fishing boats and effective fishing gear, such as fish pumps, echo-sounders, sonar and larger net haulers were introduced from the late 1970s to 1980s.

In Joban coastal waters, bow-mounted trawls which target the surface swarms of *E. pacifica* were adopted as well as in Sanriku coastal waters in the 1970s, but seine boats were introduced to detect benthopelagic swarms since the 1980s. The fishery to target benthopelagic swarms was established in 1985 in Joban coastal waters (Ishikawa, 1990). In Iwate Prefecture, bow-mounted trawls were adopted initially but the fishery efficiency was less efficient than in Miyagi Prefecture because the vessels were used alongside for squid fishing and were not specially designed for krill fishing as designed in Miyagi Prefecture (Minato, pers. comm.). In Miyagi Prefecture, bow-mounted trawls have been conventionally used, but seine boats were introduced in 1991 and became the main fishing method since 1992.

Therefore, seine boats are currently used in all prefectures, including Miyagi Prefecture, where they have been used alongside bow-mounted trawls since 1991. Only small boats of less than 20 tonnes GRT are engaged in the fishery. Bow-mounted trawls, which have a net opening of approximately 75m^2, only catch aggregations within 8m of the surface. In this method, when an aggregation is sighted, the boat approaches and two poles slide forward like probing antennae. The booms tilt and plunge, causing the net to spread open beneath the bow. The boat pushes the net slowly through the aggregation, engulfing the krill (Kodama, 1995b). Seine boats, the other fishing method, can catch aggregations as deep as 150m. When an aggregation is detected, a buoy fixed to the free end of a rope is thrown overboard, and the wing net, 100m long by 50m high, pocket net and second wing net are streamed out to surround the krill aggregation. After the buoy has been retrieved, both ropes are hauled whilst ensuring that the vessel orientates downwind and down current (Kodama, 1995a).

The fishing grounds lie usually over the continental shelf (<200m) within 10-20 nautical miles of the shore. Fishing operations are restricted to the daytime for two reasons. Firstly, because ports are only open during the daytime, and secondly, because fishing vessels are not equipped with freezing facilities and so they must return within a day for onshore processing and freezing of their catch (Odate, 1991). The fishing season lasts generally from February to July, but varies from area to area and from year to year. The main fishing season in Sanriku waters is from March to April. That of Joban waters is from May to June (Odate, 1991).

The *E. pacifica* fishery is categorized as a licensed fishery, licenses being issued by the prefectural governor. Fishery regulations are set separately for each prefecture. The license of the prefectural governor defines the fishing period, the time allowed at sea before the vessel must return to port (also referred to as the operational time), fishing area, boat size and other factors (Table 2-3). Other regulations which are decided by the fishermen themselves include total catch limit for the season and the maximum number of plastic containers permitted for each boat. In 1993, the total catch decreased remarkably to 60,881 tonnes as compared to the highest one (107,566 tonnes) in the previous year. That was the result of the introduction of catch regulations which were imposed in Miyagi and Iwate prefectures in order to control the market and obviate a decline in value of the catch. In 1994, catch regulations were introduced in Fukushima and Ibaraki prefectures in concert with those of Sanriku.

Annual change in the oceanographic conditions in the Sarniku and Joban coastal waters

The oceanographic conditions can be divided into

Table 2-2. Development and regulation of the *Euphausia pacifica* fishery

	Sanriku coastal waters (Iwate & Miyagi)	Joban coastal waters (Fukushima & Ibaraki)
1970		
	Fishery ground expanded from north to south along the coastal waters of Miyagi.	
		Fishery with seine boats commenced along Ibraki coast (1972).
1975	Fishery commenced using bow-mounted trawls in Iwate (1975). Fish-pumps were introduced in Miyagi.	Fishery with seine boats commenced along Fukushima coast (1974). Plastic catch containers were introduced in Ibraraki.
	Hydroacoustics were introduced.	Hydroacoustics were introduced.
1980	Seine boats were introduced along the southern coast of Iwate.	Benthopelagic swarms targeted for first time along coastal waters of Ibaraki.
1985		Benthopelagic swarms were commonly targeted.
	Seine boats commonly adopted along entire coast of Iwate.	Fishermen set self-regulation restrictions on landing time and max. no. of containers per boat (1989).
1990	Fishermen in Iwate set self-regulation on the max. no. of containers per boat (1990). Seine boats were permitted and adopted in Miyagi Pref. (1991). Fishermen in Miyagi set self-regulation restrictions (1991). Fishermen set self-regulation restrictions on total catch for each pref. (1993).	
		Fishermen set self-regulation restrictions in concert with those of Sanriku on the total catch for each pref. (1994).
1995		

Table 2-3. Regulatory measures of the *Euphausia pacifica* fishery from 1993 to 2001

	Iwate	Miyagi	Fukushima	Ibaraki
1993	①25,000 t ②12 t for boat > 9 t 9 t for boat <9 t ③1 Feb.–30 Apr.	①Sb^{*1}: 21,000 t, Bmt^{*2}: 4,000 t ②10.5 t for boat > 15 t 9.6 t for boat =10–15 t, 9 t for boat < 9 t ③Sb: 22 Feb.–30 Apr., Bmt: 1 Feb.–31 May	①No regulation ②6 t ③*1 Feb.–31 Jul.*	①No regulation ②6 t ③*11 Feb.–31 Jul.*
1994	①28,500 t ②15 t for boat > 9 t 11.4 t for boat < 9 t ③*Year round*	①28,500 t Minimum reserved^{*3} for Bmt: 2,000 t ②10.5 t for boat > 15 t 9.6 t for boat =10–15 t, 9 t for boat < 9 t ③Sb: 20 Feb.–30 Apr., Bmt: 1 Feb.–30 Apr.	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
1995	①28,500 t ②15 t for boat > 9 t 11.4 t for boat < 9 t ③*Year round*	①31,000 t Minimum reserved for Bmt: 4,000 t ②9 t for boat > 10 t, 8.4 t for boat < 10 t ③Sb: 1 Mar.–30 Apr., Bmt: 1 Mar.–13 May	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
1996	①28,500 t ②15 t for boat > 9 t 11.4 t for boat < 9 t ③*Year round*	①32,500 t Minimum reserved for Bmt: 4,000 t ②9.6 t for boat >10 t, 9 t for boat < 10 t ③Sb: 15 Feb.–13 May, Bmt: 1 Mar.–11 May	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
1997	①28,500 t ②12 t for boat > 9 t 9 t for boat <9 t ③*Year round*	①32,500 t Minimum reserved for Bmt: 4,000 t ②10.5 t for boat > 10 t, 9.9 t for boat < 10 t ③Sb: 75 days from the first fishing day Bmt: 1 Feb.–30 Jun.	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
1998	①30,000 t ②12 t for boat > 9 t 9 t for boat <9 t ③*Year round*	①32,500 t Minimum reserved for Bmt: 4,000 t ②10.5 t for boat > 10 t, 9.9 t for boat < 10 t ③Sb: 75 days from the first fishing day Bmt: 25 Feb.–31 May	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
1999	①29,000 t ②10.5 t for boat > 9 t 8.25 t for boat < 9 t ③*Year round*	①29,000 t Minimum reserved for Bmt: 200 t ②10.5 t for boat > 10 t, 9.9 t for boat < 10 t ③Sb: 75 days from the first fishing day Bmt: 1 Mar.–31 May	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
2000	①29,000 t ②7.5 t for boat > 9 t 6 t for boat < 9 t ③*Year round*	①29,000 t Minimum reserved for Bmt: 200 t ②10.5 t for boat > 10 t, 9.9 t for boat <10 t ③Sb: 1 Mar.–13 May, Bmt: 21 Feb.–23 May	①9,000 t ②6 t ③*1 Feb.–31 Jul.*	①9,000 t ②6 t ③*11 Feb.–31 Jul.*
2001	①22,500 t ②7.5 t for boat > 9 t 6 t for boat < 9 t ③*Year round*	①22,500 t ②9 t for boat >10 t, 7.8 t for boat < 10 t ③Sb: 1 Mar.–14 May, Bmt: 1 Mar.–14 May	①7,000 t ②6 t ③*1 Feb.–31 Jul.*	①7,000 t ②6 t ③*11 Feb.–31 Jul.*

①: Total catch, ②: Max. no. of landings per boat, ③: Fishing period

② & ③ were alternated according to fishery and market conditions during the fishing period.

Italics: licenses issued by prefectural govenors

^{*1}Seine boats, ^{*2}Bow-mounted trawls

^{*3}Minimum reserved for dip net catch was transferred to seine boats when surface swarm disappeared in Miyagi Prefecture.

three groups according to the southernmost latitude of the first branch of the Oyashio Current (shortened hereafter as SFO) during February and July (fishing period) of *E. pacifica* as follows. The years 1973, 1974, 1977, 1978, 1981, 1982, 1984, 1986, 1989, 1992–1994 and 1998 were southward anomaly years with SFO during February and July being south of 37.7°N. The years 1975, 1979, 1983, 1987, 1988, 1995 and 2001 were intermediate years with SFO during February and July being 37.8° ~ 38.7°N. The years 1971, 1972, 1976, 1980, 1985, 1990, 1991, 1996, 1997, 1999 and 2000 were northward anomaly years with SFO during February and July

On the other hand, the oceanographic conditions in the Sanriku coastal waters can be divided into three groups according to the trend of surface water temperatures during February and July as colder years (1981, 1982, 1984–1987, 1998 and 2001), intermediate years (1983, 1988, 1989, 1992–1997 and 2000) and warmer years (1990, 1991 and 1999) (Fig. 2–2). The oceanographic conditions in the Joban coastal waters can be divided into three groups according to the trend of surface water temperatures during February and July as colder years (1981, 1983-1986, 1993, 1996, 1998 and 2001), intermediate years (1982, 1987, 1991, 1992, 1994 and 2000) and warmer years (1988-1990, 1995, 1997 and 1999).

Annual landing values and unit price

Annual total landing of the *E. pacifica* fishery in the total area fluctuated largely from 1975 to 2001 (Fig. 2-3). It tended to increase from 1975 to 1983 and attained the maximum (4,859 million yen) in 1983. It was also higher than 4,000 million yen in 1985, 1989, 1996, 1997 and 2000, but much lower than 2,000 million yen in 1984, 1993 and 2001.

Annual landing in Iwate Prefecture increased significantly from 1987 to 1989 and attained 1,282 million yen in 1989. Since then, it has been generally higher than 1,000 million yen and attained the maximum (2,160 million yen) in 1997. Annual landing of bow-mounted trawls in Miyagi Prefecture attained the maximum (1,745 million yen) in 1987 but decreased rapidly after that and has been lower than 300 million yen since 1991. On the other hand, annual landing of the seine boats in Miyagi Prefecture has been generally higher than the average value of bow-mounted trawls from 1984 to 1990 and attained the maximum (2,239 million yen) in 1997. Annual landing in Fukushima and Ibaraki prefectures attained the maximum (1,040 and 2,177 million yen, respectively) but has been lower than 500 million yen since 1990. Therefore, the annual landing of bow-mounted trawls in Miyagi Prefecture and seine boats in Fukushima and Ibaraki prefectures had been dominant to the total form 1984 to 1988, but the annual landing of seine boats in Iwate and Miyagi prefectures had been dominant to the total since 1991.

Annual unit price fluctuated largely in each prefecture, especially in Fukushima and Ibaraki prefectures from 1984 to 1988. For example, it was 21 yen per kg in 1984 but 138 yen in 1988 in Ibaraki Prefecture. The annual unit price in Iwate Prefecture (35 yen per kg) was about 100 yen cheaper than that in Ibaraki Prefecture in 1988. This was due to strong demands for the fished *E. pacifica* in mid-June when the fishing ground in the Joban coastal waters had formed for the first time in this year after the end of fishing operation in the Sanriku coastal waters in late April (Odate, 1991). Since 1989, the annual unit price in Fukushima and Ibaraki prefectures was lower than that in Iwate and Miyagi prefectures but the annual change of unit price in the former prefectures synchronized well with that in the latter prefectures. This was because that the unit price in the Joban coastal waters had depended largely on the unit price in the Sanriku coastal waters since 1989 when the major part of fishing ground shifted to the Sanriku coastal waters as detailed below. Average annual price during 1991 and 2001 was 49 yen per kg in Iwate Prefecture, 51 yen per kg in Miyagi Prefecture, 40 yen per kg in Fukushima Prefecture and 36 yen per kg in Ibaraki Prefecture, thus being about 10 yen cheaper in the latter two prefectures than in the former two prefectures.

Number of krill fishing vessels

Annual number of fishing vessels in Iwate Prefecture increased remarkably from 1986 (859 vessels) to 1992 (5,807 vessels) (Fig. 2-4). After that, it decreased until 1994 (3,831 vessels) but increased again from 1994 to 1998 (6,177 vessels), and then decreased again after 1998. Annual number of ves-

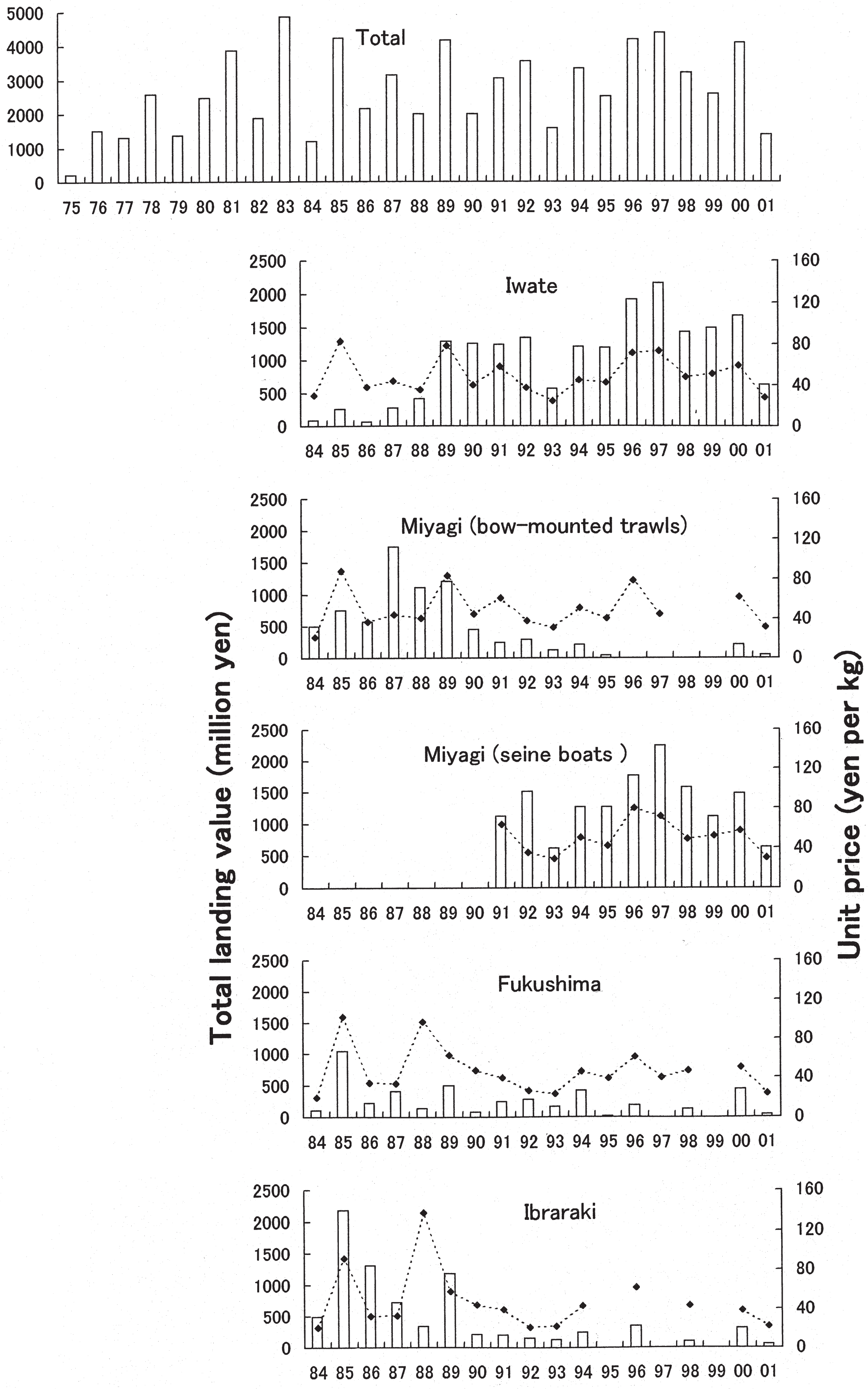

Fig. 2-3. Annual variations in the total value (bars) and unit price (broken lines) of *Euphausia pacifica* fishery by prefecture.

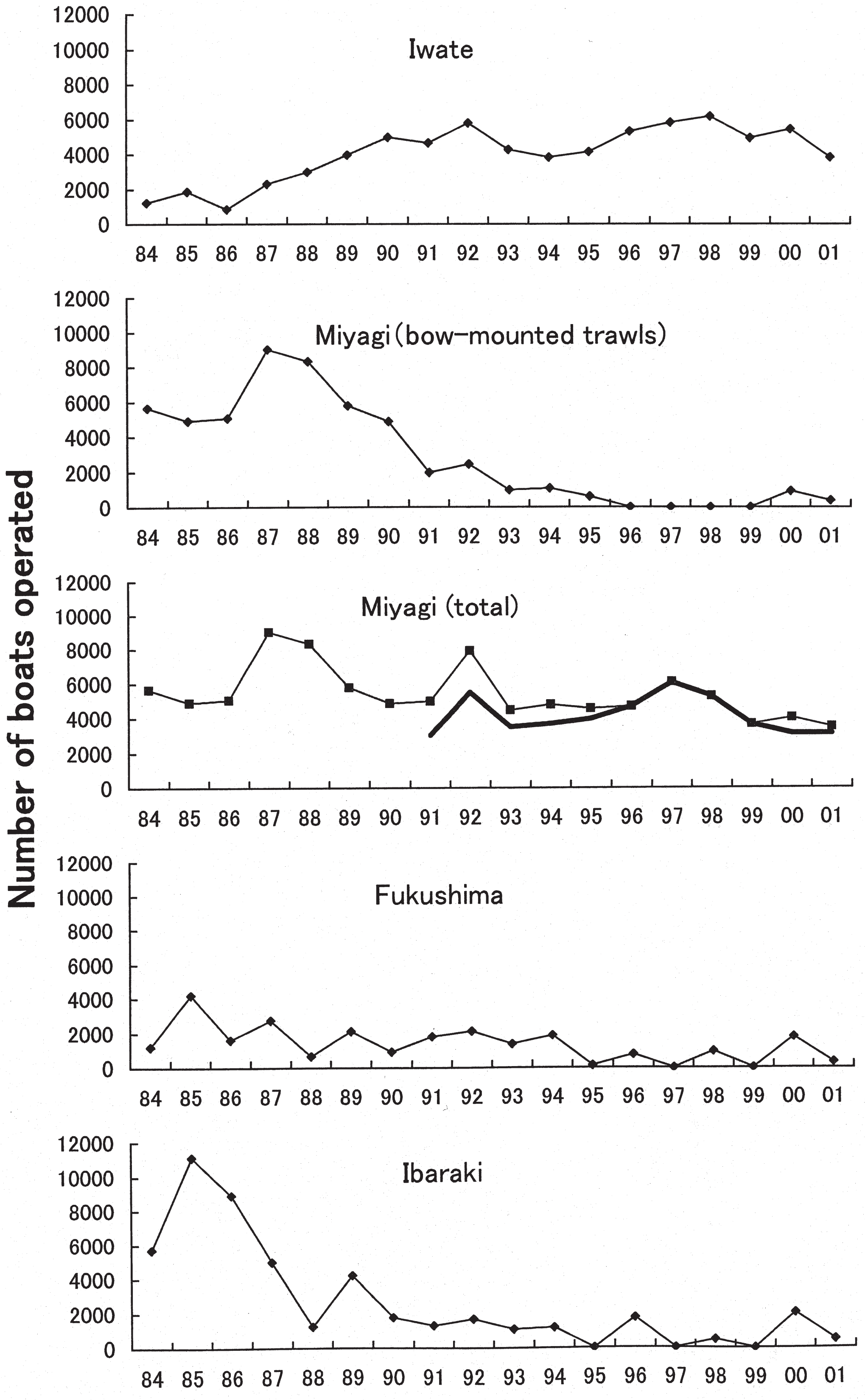

Fig. 2-4. Annual variations in the number of boats in each prefecture. Thick line shown in the panel of Miyagi (total) indicates the number of seine boats.

sels by bow-mounted trawls in Miyagi Prefecture attained the maximum (9,006 vessels) in 1987 but decreased after that and has been generally lower than 1,000 vessels since 1993. Annual number of seine boats in Miyagi Prefecture ranged from 3,019 to 6,060 vessels after 1991 when this fishing method was adopted for the first time. The relative contribution in number of seine boats to the total vessels in Miyagi Prefecture was 61% in 1991, 69% in 1992 and 77-100% after 1993. Annual number of seine boats in Fukushima Prefecture attained the maximum (4,202 vessels) in 1985 but decreased since then and has been generally lower than 2,000 vessels after 1990. Annual number of seine boats in Ibaraki Prefecture attained the maximum (11,119 vessels) in 1985 but decreased since then and has been generally lower than 2,000 vessels after 1991.

Catch

The total annual catch of *E. pacifica* varied between years but tended to increase steadily from mid-1970 to 1992 exceeding 40,000 tonnes in 1978, 80,000 tonnes in 1989 and 100,000 tonnes in 1992 (Fig. 2-5). In 1993, the total catch decreased to 60,881 tonnes, following the introduction of catch regulations which were imposed in Miyagi and Iwate prefectures in order to control the market and obviate a decline in price of the catch. Since then, the total annual catch had been around 60,000 tonnes.

Most of the catch in the 1970s was landed in Mi-

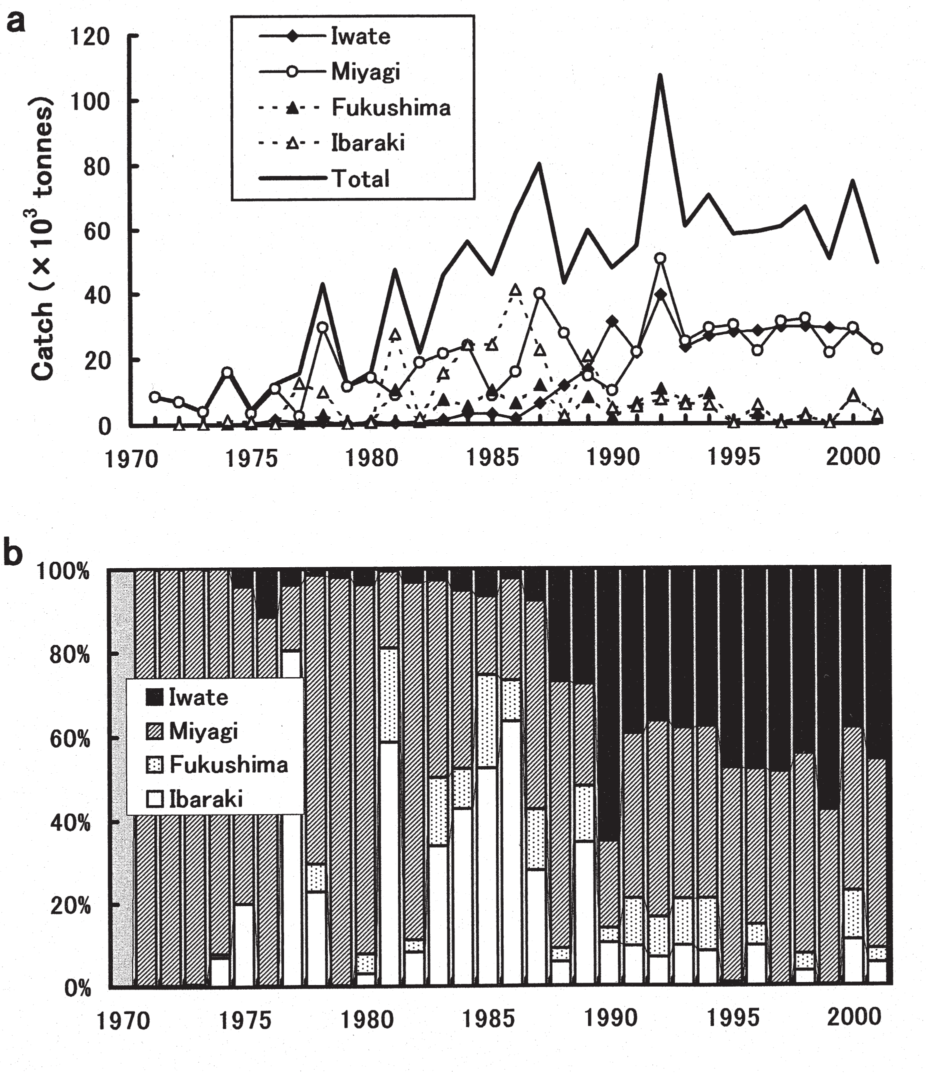

Fig. 2-5. Annual variations in the catch (a) and the percentage composition by prefecture (b) from 1971 to 2001.

yagi Prefecture (Fig. 2-5). In the early to mid-1980s, Ibaraki Prefecture expanded its catch taking more than 60% of the total catch in 1986. Since 1990, Iwate and Miyagi prefectures have shown similar catch levels and the sum of their catch showed a high percentage (79-100%) to the total. There were no catch or nearly no catch in Fukushima Prefecture in 1999 and Ibaraki Prefecture in 1995, 1997 and 1999.

CPUE

Catch per unit effort (CPUE) is defined as catch per boat per day in this study. Annual CPUE in Iwate Prefecture increased remarkably from 1986 (1.9 tonnes) to 1990 (6.3 tonnes) (Fig. 2-6). It fluctuated between 4.6 and 7.0 tonnes from 1991 to 1995, but leveled off at 4.8-5.9 tonnes since 1996. Annual CPUE of bow-mounted trawls in Miyagi Prefecture was high (about 4 tonnes) in 1987, 1993, 1994, 2000 and 2001, but was low (about 2 tonnes) in 1990, 1991, 1995 and 1997. It was 0 or nearly 0 tonnes in 1996, 1998 and 1999. Annual CPUE of seine boats in Miyagi Prefecture was high in 1992 (7.8 tonnes) and 2000 (8.3 tonnes), but was low from 1996 to 1999, especially in 1996 (4.1 tonnes) and 1997 (5.1 tonnes). Annual CPUE of seine boats averaged 6.1 tonnes from 1991 to 2001, but annual CPUE of bow-mounted trawls averaged 2.7 tonnes during the same period in Miyagi Prefecture. Therefore, fishing efficiency of seine boats was suggested to be more than two times higher than that of bow-mounted trawls. Annual CPUE in Fukushima and Ibaraki prefectures showed the similar change, being higher than 4 tonnes in 1987, 1992-1994, 2000 and 2001, but about 2 tonnes in 1985, 1988 and 1990. Annual CPUE in 1995, 1997 and 1999 was 0 or nearly 0 tonnes in both prefectures, except for in 1995 in Fukushima Prefecture. Krill abundance in the Fukushima coastal waters in 1995 was perhaps low because the fishing period was very short (only 8 days), although annual CPUE was intermediate (3.2 tonnes).

Annual catch in Iwate and Miyagi prefectures has generally fulfilled the regulated catch since 1993, but annual catch in Fukushima and Ibaraki prefectures has been lower than the regulated catch since 1994 (Fig. 2-6). Total catch limit was set as the sum of bow-mounted trawls and seine boats in Miyagi Prefecture (Table 2-3) but the total catch substantially depended on the catch by seine boats since 1994 (Fig. 2-3). Therefore, it is suggested that the regulation on total catch limit did not strongly affect the annual CPUE of bow-mounted trawls in Miyagi Prefecture and seine boats in Fukushima and Ibaraki prefectures. Accordingly, these CPUEs are suggested to reflect the real abundance of krill resources. Annual CPUE of bow-mounted trawls in Miyagi Prefecture from 1984 to 2001 has a significant negative correlation ($P < 0.05$) with SFO during February and July but does not have a significant negative correlation with the lowest surface temperature in the Sanriku coastal waters (Fig. 2-7). Annual CPUE of seine boats in Ibaraki Prefecture from 1984 to 2001 has a significant negative correlation ($P < 0.05$) with both SFO during February and July and the lowest surface temperature in the Joban coastal waters (Fig. 2-7).

Fishing period

First fishing day was generally in early-or mid-February in the Sanriku coastal waters (Fig. 2-8). However, it should be noted that the limit of first fishing day in the Sanriku coastal waters has been regulated since 1993 (Table 2-3), so the first fishing day did not always reflect to the natural environmental conditions. On the other hand, the first fishing day has occurred after mid February, thus the regulation on the first fishing day (1 February; Table 2-3) had not been substantial in the Joban coastal waters (Fig. 2-8).

The first fishing day in the Joban coastal waters from 1984 to 2001 has a significant positive correlation ($P < 0.05$) with both SFO during February and July and the lowest surface temperature in the Joban coastal waters (Fig. 2-9). The first fishing day in the Joban coastal waters from 1984 to 2001 has a significant negative correlation ($P < 0.05$) with annual CPUE in Ibaraki Prefecture during the same period (Fig. 2-10).

The last fishing day was determined not only by the rising of temperatures concurrently with the northward shift of the warmer Kuroshio waters but also by social and economic reasons. For example, the sudden plunge of unit price of *E. pacifica* fishery triggered the conversion to the sand lance fishery in

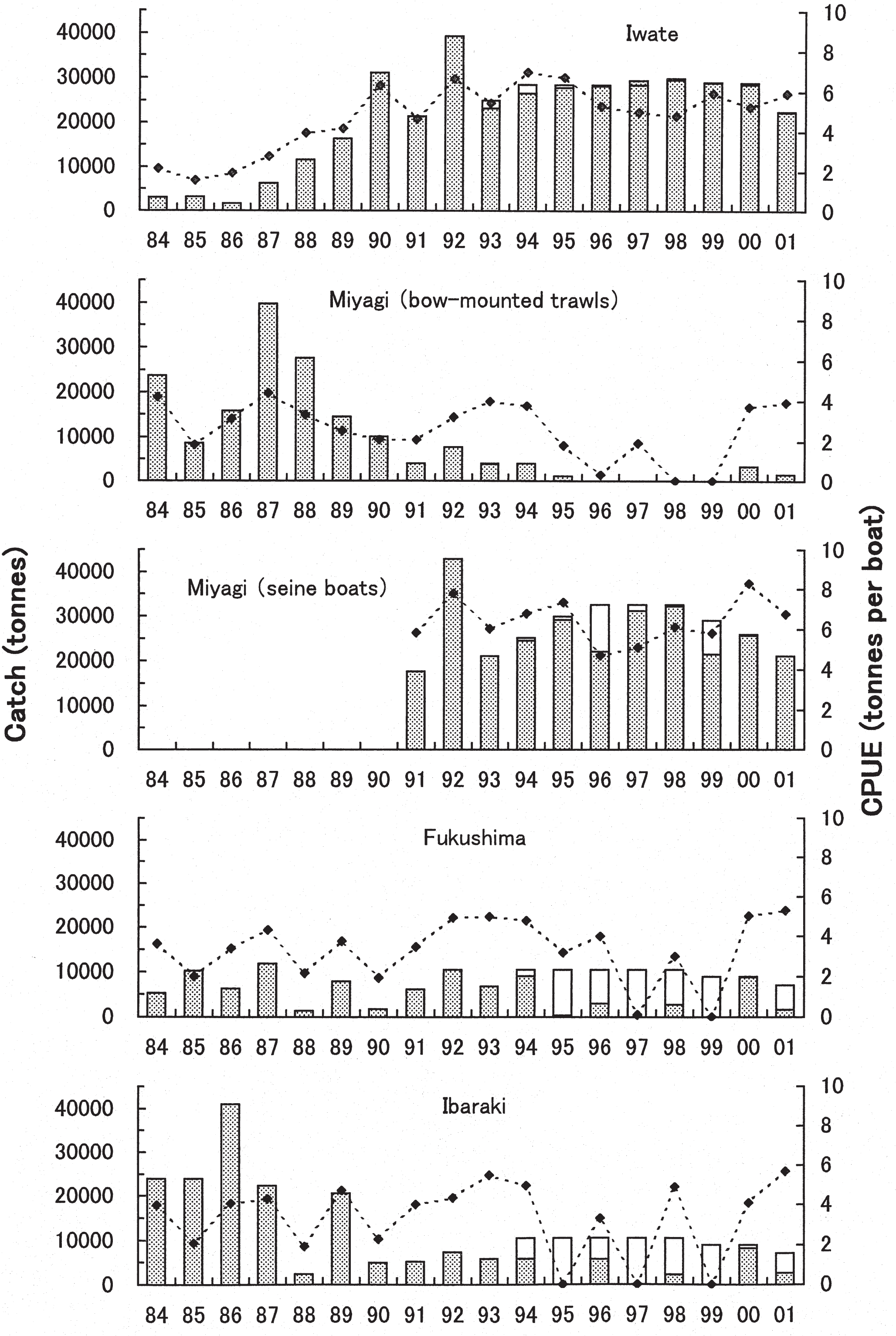

Fig. 2-6. Annual variations in the catch (dotted bars) and CPUE (line). Open bars represent the remainder of the total regulated catch after accounting for actual landings. The regulated value shown for seine boats in Miyagi Prefecture from 1994 to 2001 is calculated as the total regulated value over the prefecture value minus the actual catch of bow-mounted trawls fishing.

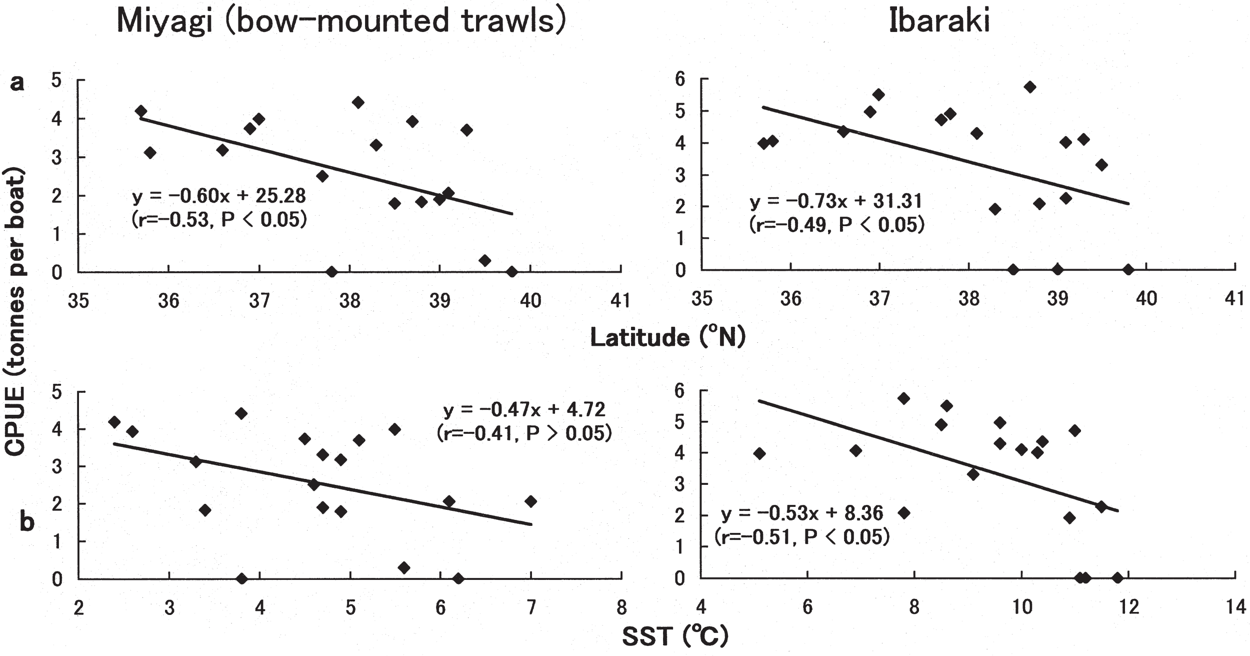

Fig. 2-7. Relationship between the annual CPUE in Miyagi (bow-mounted trawls) and Ibaraki prefectures and the southernmost latitude of the first branch of the Oyashio Current (SFO) during February and July (a), and between the CPUE and the lowest SST along the Sanriku and Joban coastal waters (b).

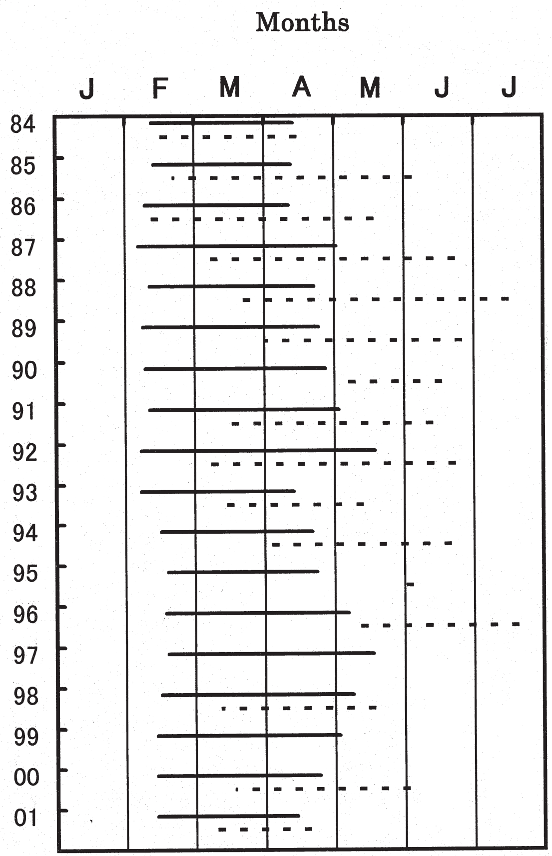

Fig. 2-8. Fishing period in Sanriku (solid lines) and Joban (broken lines) waters from 1984 to 2001. The first fishing day is defined as the first day when the catch was larger than 5 tonnes and fishing continued for the next 3 days. The last fishing is defined as the last day when the catch was larger than 5 tonnes and fishing had been conducted within the previous 3 days.

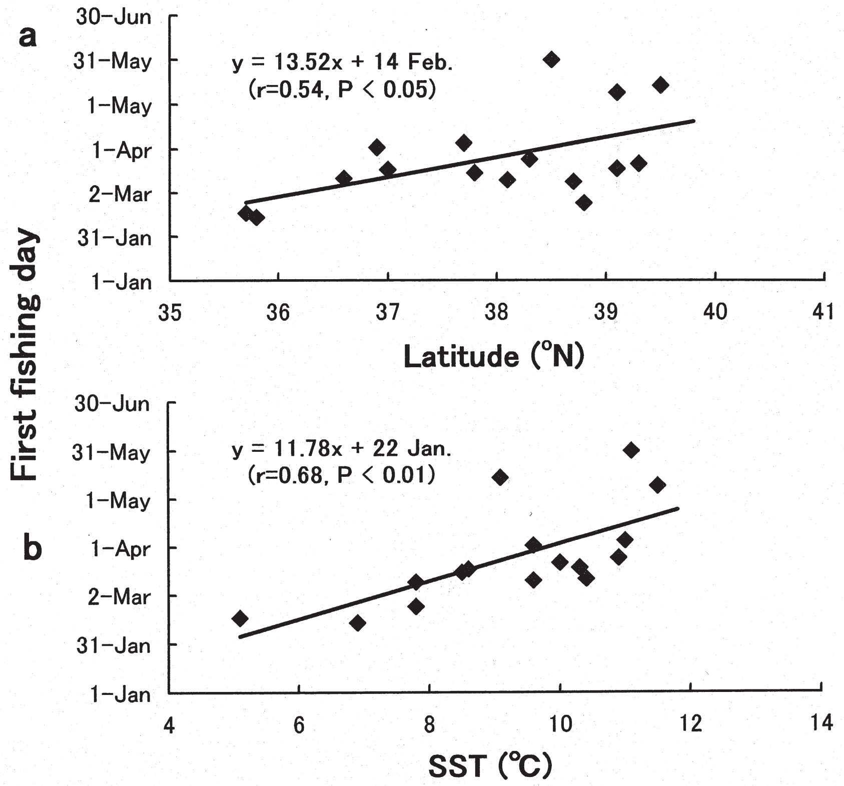

Fig. 2-9. Relationship between the first fishing days along Joban coastal waters and SFO during February and July (a) and between the first fishing days and the lowest SST along Joban coastal waters (b).

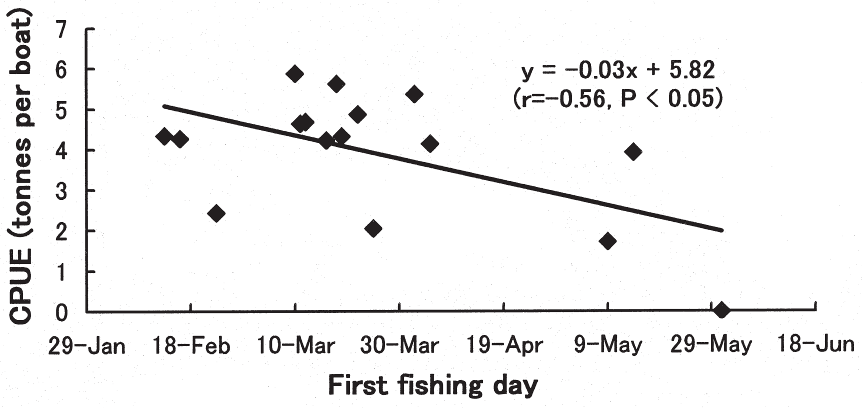

Fig. 2-10. Relationship between the first fishing day along Joban coastal waters and the annual CPUE of Ibaraki Prefecture.

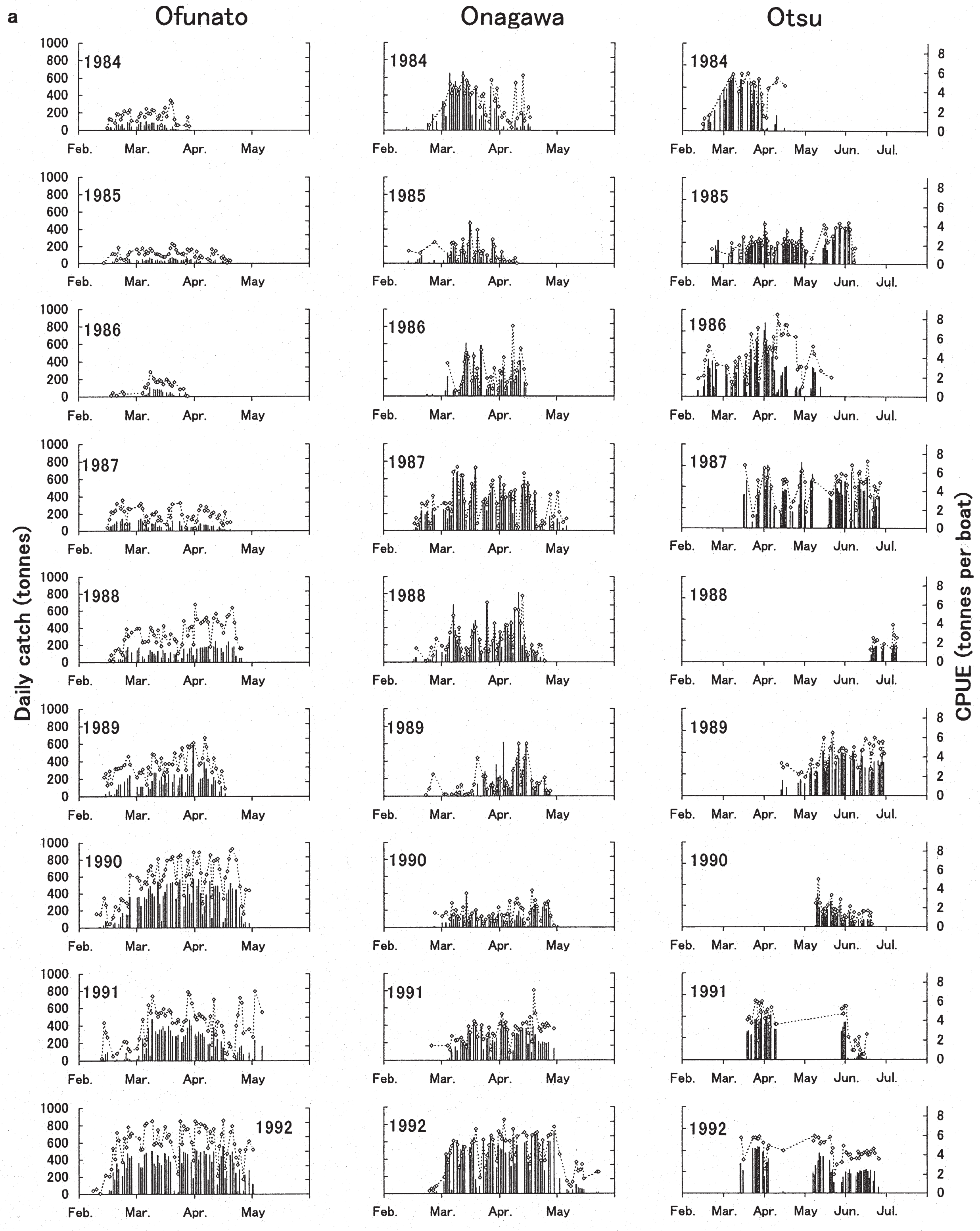

Fig. 2-11. Daily catch (bars) and CPUE (line) at the three principal ports; Ofunato (Iwate Pref.), Onagawa (Miyagi Pref.) and Otsu (Ibaraki Pref.). a: 1984-1992, b: 1993-2001.

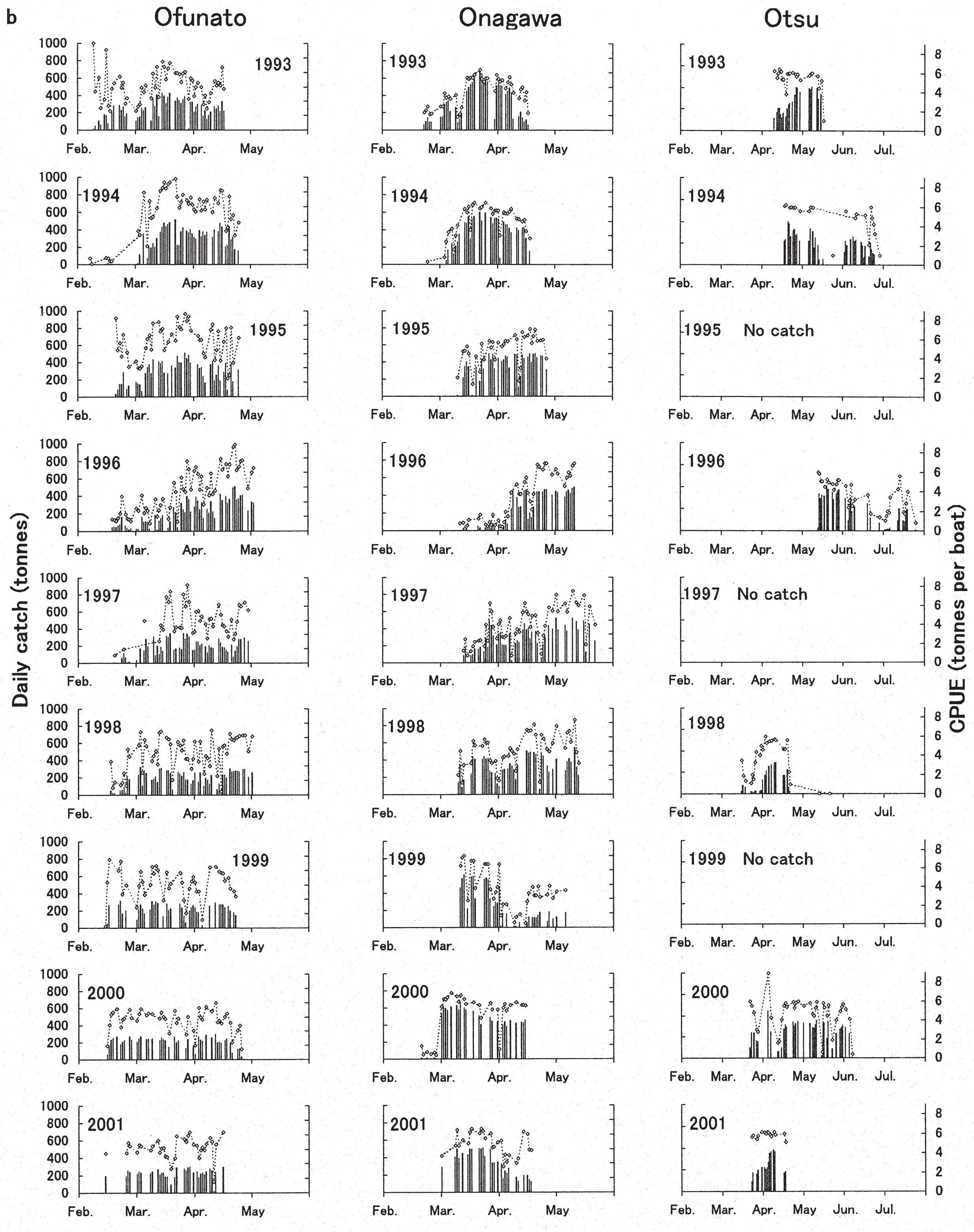

Fig. 2-11. Continued (1993-2001).

1984 and 1986 in the Joban coastal waters. On the other hand, the fishing had been generally finished due to fulfillment of the regulated catch since 1993 in Iwate and Miyagi prefectures. CPUE tended to remain high level in the last fishing day in Ofunato and Onagawa ports (Fig. 2-11).

Location of fishing ground from 1995 to 2001

The weekly change in location of fishing ground with surface temperature isotherms was examined from 1995 to 2001 as follows.

[1995] The fishing ground was formed in the coastal waters off the middle part of Iwate Prefecture, located on the coastal side of the 7℃ isotherm related to the first branch of the Oyashio Current, in late February (Fig. 2-12). It tended to shift southward with the southward shift of 7℃ isotherm from early March to late March. However, it was limitedly formed on the north side of Oshika Peninsula (ca. 38°20'N) and not formed on the warmer side than 10 ℃ isotherm from late March to late April.

[1996] The fishing ground was formed in the coastal waters off northern or middle part of Iwate Prefecture, located on the coastal side of the 7℃ isotherm related to the first branch of the Oyashio Current, during mid- and late February (Fig. 2–13). It expanded southward along the 7℃ isotherm to the upper continental slope off Oshika Peninsula from late March to late April. It was formed in the coastal waters off northern part of Ibaraki Prefecture near the 10℃ isotherm in mid-May. It was formed in the upper continental slope off Fukushima and Ibaraki prefectures near the 15℃ isotherm in mid June. The *E. pacifica* fishery in the Joban coastal waters lasted until late July in this year.

[1997] The fishing ground was formed in the coastal waters off the middle part of Iwate Prefecture, located on the coastal side of the 7℃ isotherm related to the first branch of the Oyashio Current, in mid-February (Fig. 2-14). It expanded southward along the 7℃ isotherm to the coastal waters off northern part of Miyagi Prefecture from early March to late March. However it was formed in the upper continental slope off Iwate and Miyagi prefectures near the 5–7℃ isotherms related to the second branch of the Oyashio Current which intruded southward instead of the northward retreat of the first branch of the Oyashio Current during mid- and late April. In mid-May, it was formed in the coastal waters off northern part of Miyagi Prefecture, located on the warmer side than 10℃ isotherm. In this year, the fishing ground had been rarely formed in the Joban coastal waters.

[1998] The fishing ground was formed in the coastal waters off Iwate Prefecture, located on the coastal side of 5℃ isotherm related to the first branch of the Oyashio Current, in mid-February (Fig. 2-15). It expanded southward along the 7℃ isotherm to the coastal waters off Ibaraki Prefecture from late February to late March. It was formed in the upper continental slope off Iwate and Miyagi prefectures near the 5-7℃ isotherms in early March and mid-April.

[1999] Warm-core ring cut off from the Kuroshio Extension occurred off Iwate Prefecture had been blocking the southward shift of the first branch of the Oyashio Current (Fig. 2-16). The fishing ground was formed in the upper continental slope off the middle part of Iwate Prefecture near the 7℃ isotherm related to the first branch of the Oyashio Current in mid-February, but it expanded southward to the coastal waters off northern Miyagi Prefecture along with the southward shift of the 7℃ isotherm from late February to late March. However, warm-core ring was close to the coastal waters off Iwate Prefecture and then the fishing ground was divided into two areas off northern Iwate Prefecture and northern Miyagi Prefecture in early April. The latter area located near the 7℃ isotherm related to the second branch of the Oyashio Current. The fishing ground had not been formed south of the Oshika Peninsula in this year.

[2000] The fishing ground was formed in the coastal waters off middle part of Iwate Prefecture, and was located on the southwest side of the 7℃ isotherm related to the first branch of the Oyashio Current, in mid-February (Fig. 2-17). It expanded southward along with the southward shift of the 7℃ isotherm to the coastal waters off northern part of Ibaraki

Prefecture from mid February to late March. Since then, it had been formed in the Joban coastal waters until mid-May. It was formed on the warmer side than 10℃ isotherm from late April to early May.

[2001] The fishing ground was formed in the coastal waters off the middle part of Iwate Prefecture in mid-February (Fig. 2-18). It shifted to the coastal waters off southern part of Iwate Prefecture and Miyagi Prefecture from late February to mid-March, when the 0℃ isotherm was close to the coastal waters off northern-middle Iwate Prefecture. However, it expanded from north to south of the coastal waters off Iwate Prefecture in early April, when the 5℃ isotherm was close to the coastal waters off middle part of Iwate Prefecture instead of the northward retreat of 0℃ isotherm. The fishing ground was formed in the coastal waters off the boundary area between Fukushima and Ibaraki prefectures near the 7℃ isotherm from mid-March to early April.

Discussion

Development of *Euphausia pacifica* fishery

The history of the *E. pacifica* fishery was classified into four time periods as follows.

During the first period (from the mid-1940s to the late 1960s), a small-scale fishery was conducted limitedly in the vicinity of the Oshika Peninsula in Miyagi Prefecture for local consumption and culture baits.

During the second period (from the late 1960s to the late 1980s), the fishing grounds were extended throughout the Sanriku and Joban waters and the annual total catch increased substantially, because strong demands for the fished *E. pacifica* for aquaculture and sport fishing increased remarkably, and fishing and storage techniques developed. The southward shift of SFO also contributed to expand fishing grounds into Joban during this period (Fig. 2-2).

During the third period (from the late 1980s to the early 1990s), the main fishing grounds shifted to the Sanriku coastal waters. This shift was thought to be triggered by the northward retreat of SFO during this period (Fig. 2-2). Especially, fishing efforts and catches increased concurrently with the establishment of the seine boat method in Iwate Prefecture. On the other hand, both fishing efforts and catches decreased in the Jonan coastal waters, and the unit price of landing in this waters has strongly depended on that in the Sanriku coastal waters since this period.

During the fourth period (from the early 1990s to 2001), annual and daily total catch has been regulated due to control the unit price of the fished *E. pacifica*. *E. pacifica* fishery has been exclusively conducted from February to April in the Sanriku coastal waters, nevertheless other fisheries such as seine boats for sand lance and squid jiggling are run together by the same vessels (Minato, pers. comm.). Iwate and Miyagi prefectures have dominated the *E. pacifica* fishery and maintaining the stable unit price (approximately 40 yen per kg) by setting several regulations. The *E. pacifica* fishery in the Joban coastal waters has been easily replaced by other fisheries such as sand lance and Shirasu (larval Japanese anchovy) when fishing condition of *E. pacifica* is not favorable in the Joban coastal waters. The fishing ground of Shirasu is formed when the Kuroshio warmer waters prevailed. The unit price of Shirasu is much higher than that of *E. pacifica* and the workload onboard of Shirasu fishery is lighter than that of *E. pacifica* fishery (Ando, pers. comm.).

It is suggested that the regime shift in the Pacific Ocean had occurred in the mid-1970 and late 1980 (Minobe, 1997; Yasunaka and Hanawa, 2002). Watanabe *et al.* (2003) suggested that the strength in southward shift of the Oyashio Current is closely related to the decadal change of the Pacific Ocean. Annual catch of *E. pacifica* increased mainly along the coastal waters off Miyagi Prefecture and Joban from mid-1970 to 1987, but increased mainly along the coastal waters off Iwate Prefecture instead of decrease in Joban after 1988. Therefore, the history of *E. pacifica* fishery has been closely related to the regime shift in the Pacific Ocean. Kodama *et al.* (1995) showed that colder fish species such as walleye pollack, Pacific cod, herring and sand lance increased from mid-1970 to 1987 but decreased after 1988 with the shift of oceanographic condition in the vicinity of Kinkazan Island. Abundant *E. pacifica* transported by the first branch of the Oyashio Current may af-

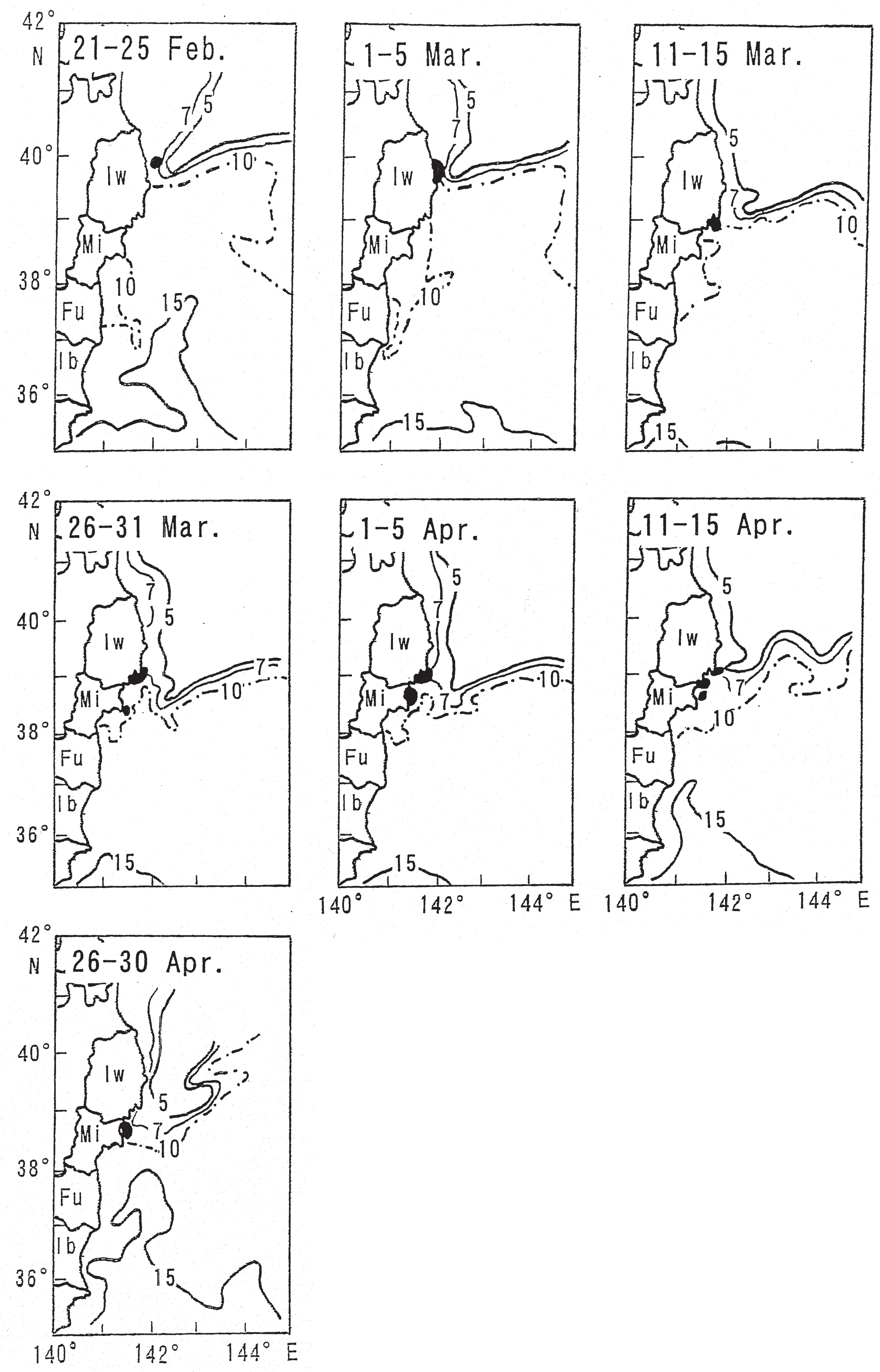

Fig. 2-12. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 1995 off northeastern Japan. Iw: Iwate ; Mi: Miyagi; Fu: Fukushima; Ib: Ibaraki. Figures indicate SST (℃). Modified from 'Quick reports on fishing and oceanographic conditions' from Japan Fisheries Information Service Center.

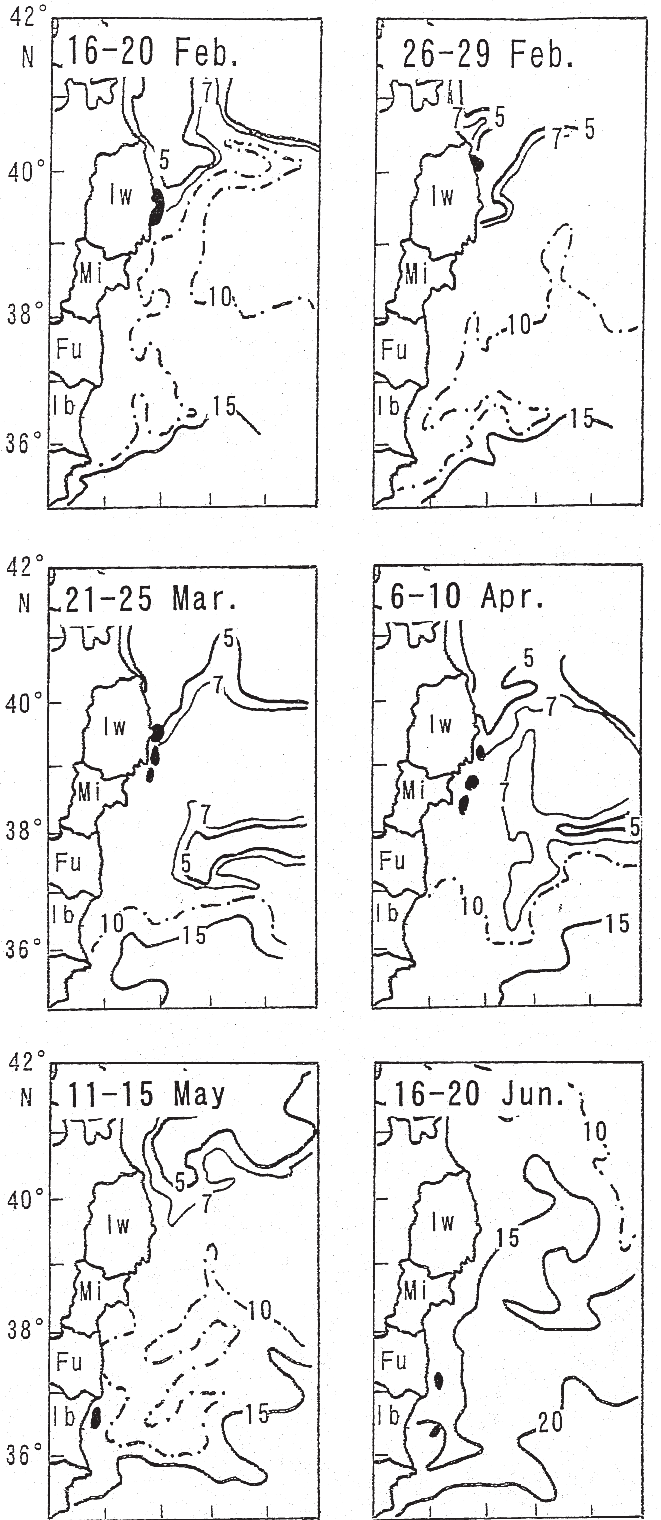

Fig. 2-13. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 1996 off northeastern Japan. Details are as shown in Fig. 2-12.

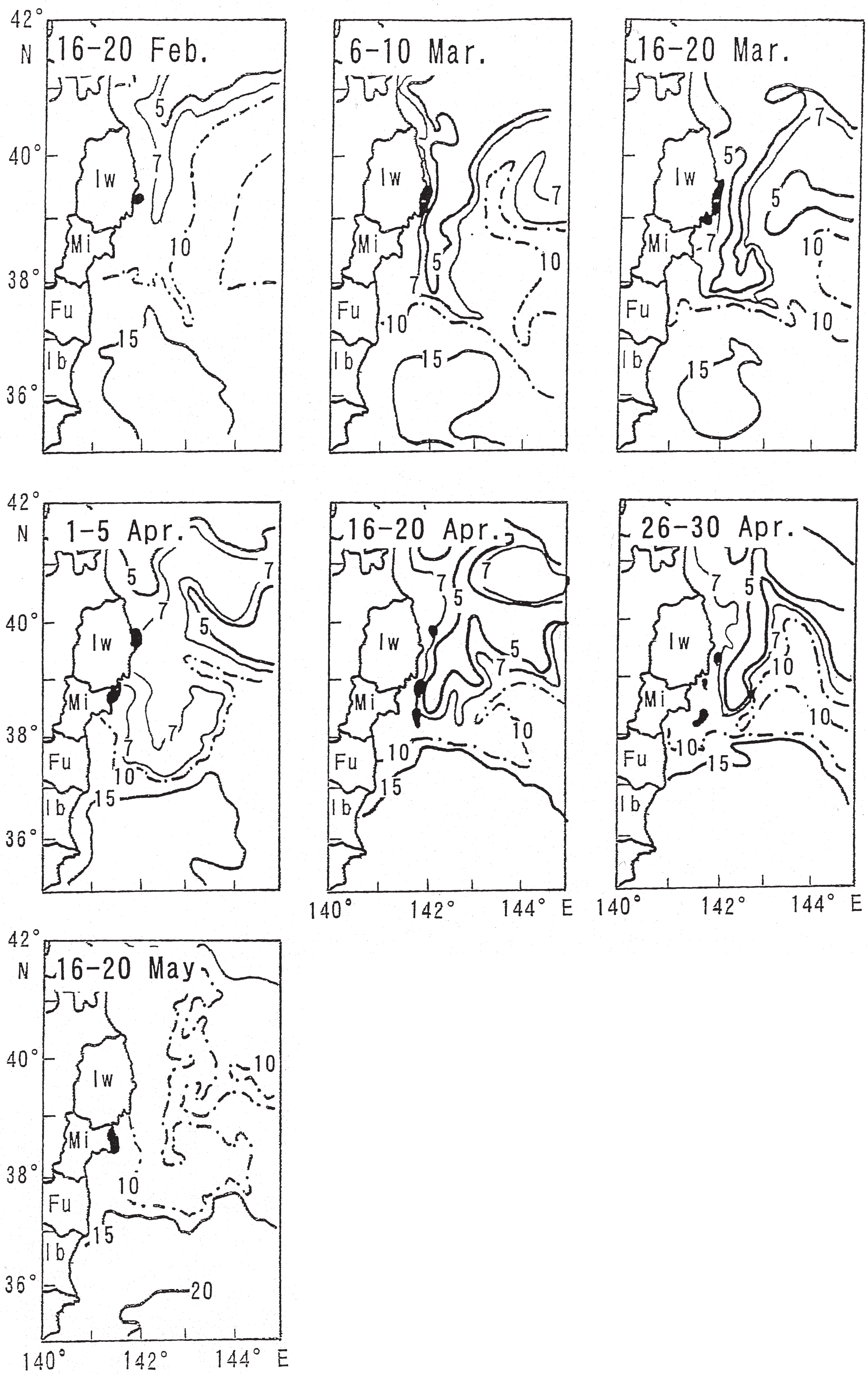

Fig. 2-14. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 1997 off northeastern Japan. Details are as shown in Fig. 2-12.

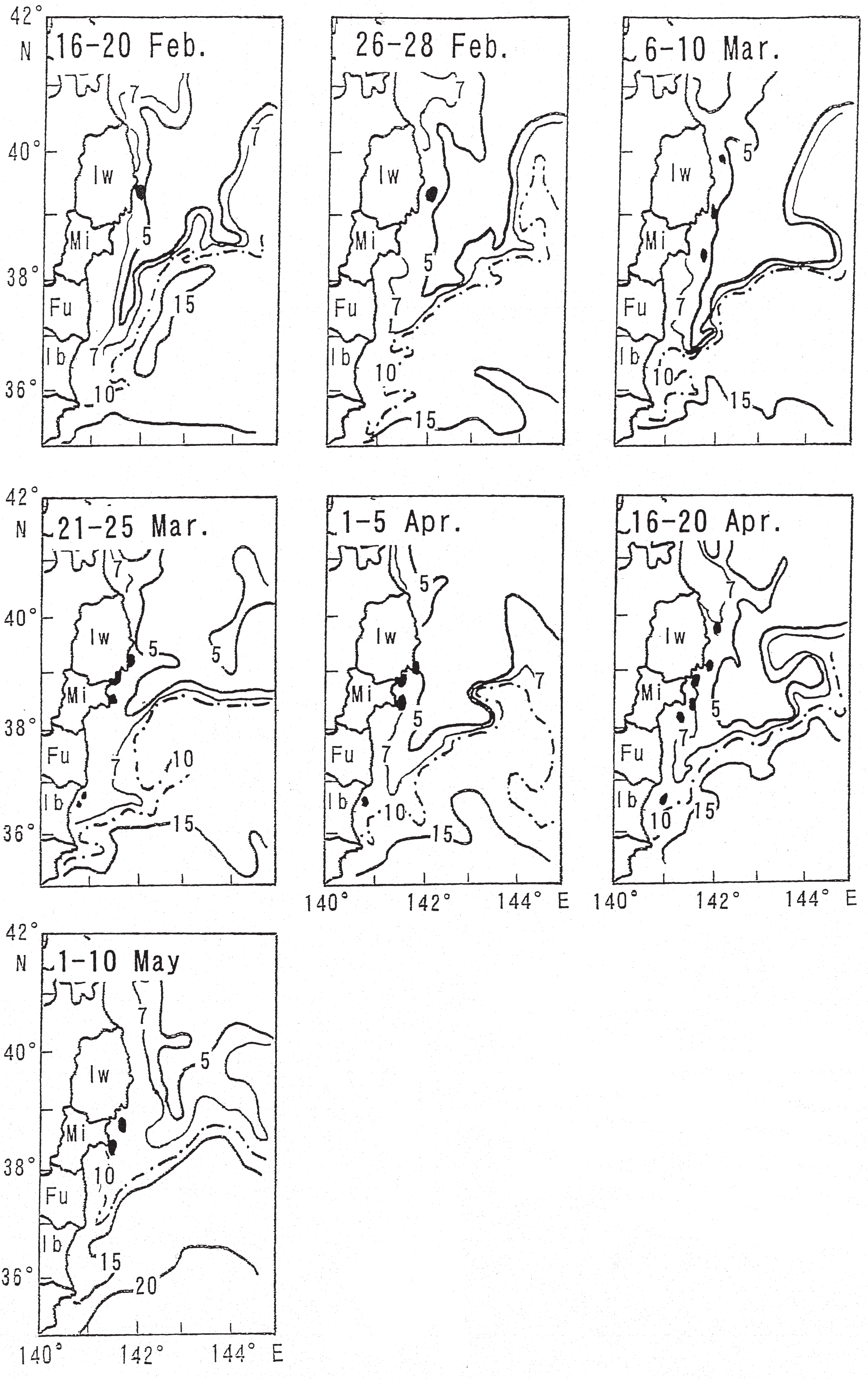

Fig. 2-15. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 1998 off northeastern Japan. Details are as shown in Fig. 2-12.

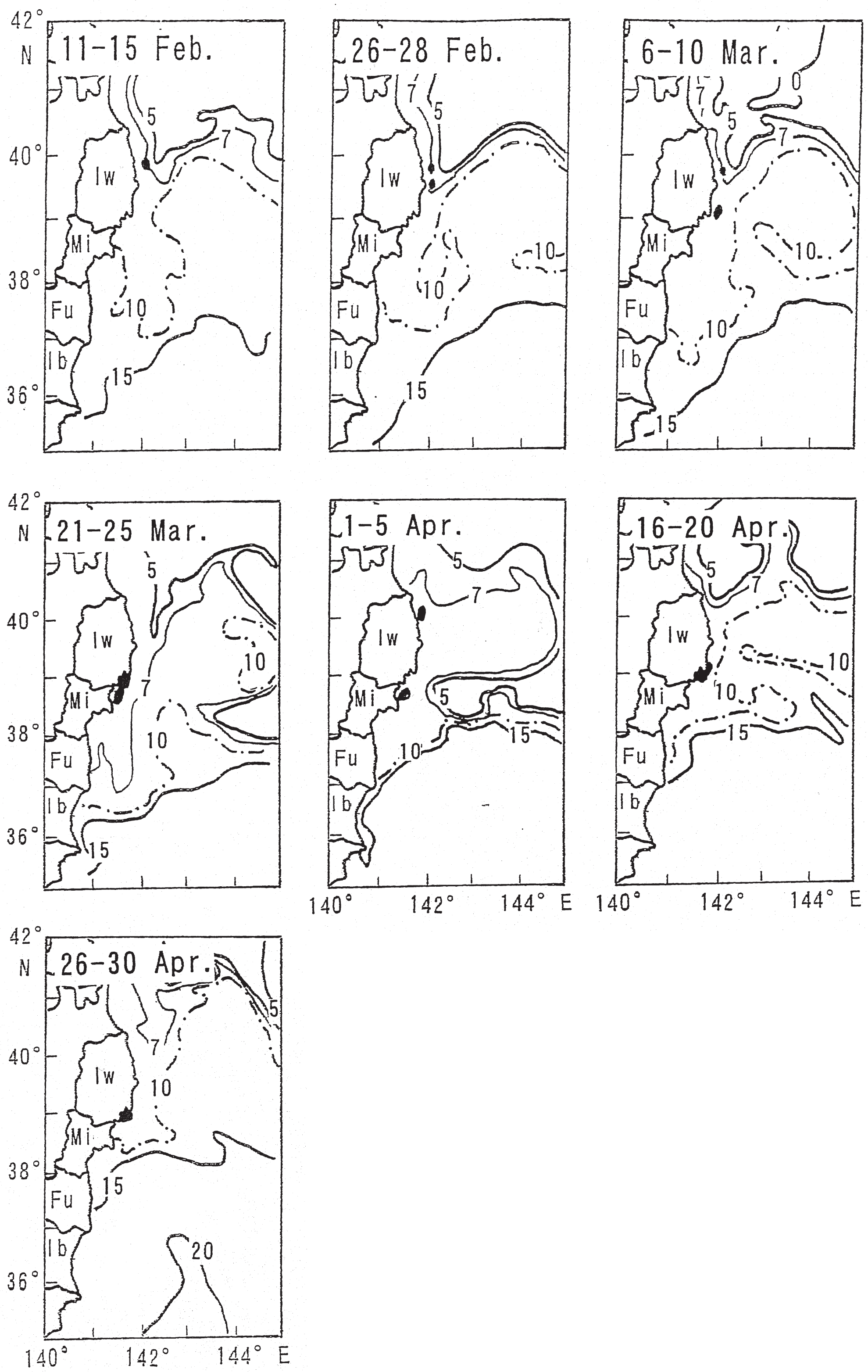

Fig. 2-16. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 1999 off northeastern Japan. Details are as shown in Fig. 2-12.

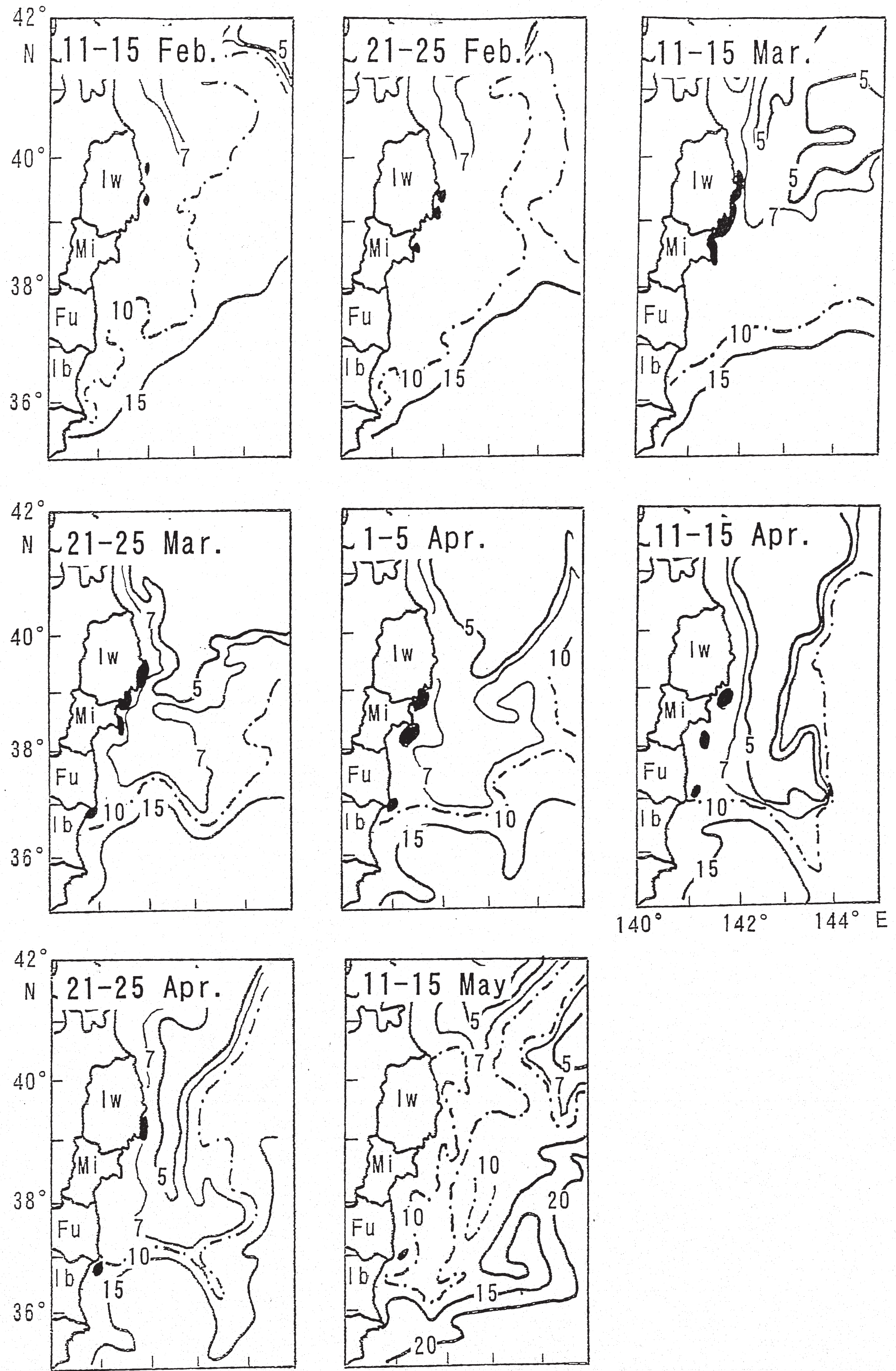

Fig. 2-17. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 2000 off northeastern Japan. Details are as shown in Fig. 2-12.

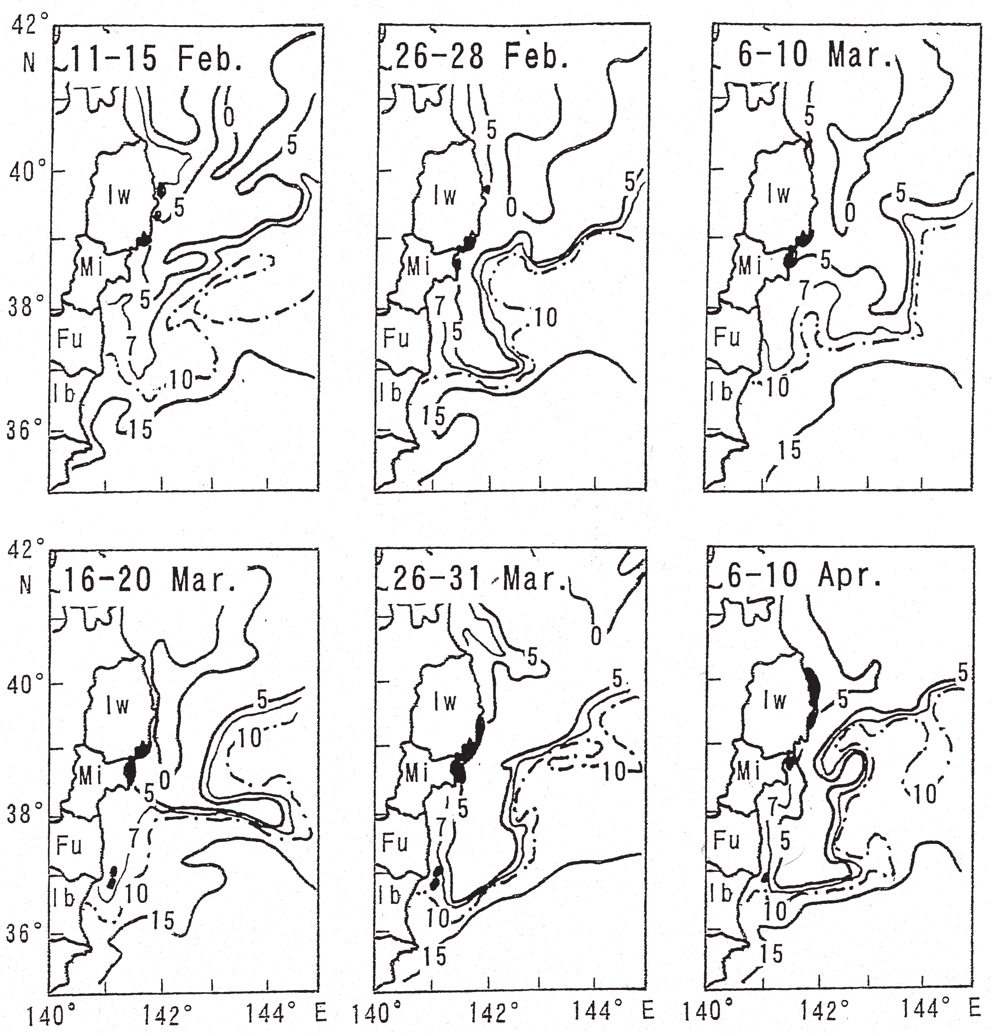

Fig. 2-18. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 2001 off northeastern Japan. Details are as shown in Fig. 2-12.

fect the good condition for growth and reproduction of these fishes in the colder years.

Relationship between oceanographic conditions and fishing conditions

Several studies have examined the mechanisms of formation of fishing grounds since 1960s (Komaki, 1967; Endo, 1981; Odate, 1991; Kodama, 1995a). Kodama (1995a) classified oceanographic patterns in the vicinity of Kinkazan Island, Miyagi Prefecture into three types based on the *E. pacifica* fishing conditions as follows. (1) When the Oyashio Current is moderately strong narrowing the area with suitable temperatures (5-7℃) in the Sanriku coastal waters, *E. pacifica* is concentrated there and good catches are expected. (2) When the Oyashio Current is weak and only present in the northern part of Sanriku waters, poor catches are expected. (3) When the Oyashio Current is very strong and comes close to the shore, suitable temperatures are restricted to the Joban area, a larger catch is landed in the Joban area compared to the Sanriku area.

Annual CPUE of the bow-mounted trawls in Miyagi Prefecture has a significant negative correlation with SFO during February and July, which is consistent well with Kodama's (1) and (2) pattern (Fig.

2-7). On the other hand, the fishing conditions of seine boats in Miyagi Prefecture are difficult to examine because total catch limits has been set since 1993. However, annual CPUE was significantly low from 1996 to 1999 when SFO during February and July showed the northward shift except in 1998 (Fig. 2-2). Therefore, it is suggested that fishing conditions are generally unfavorable when the Oyashio Current is weak in Miyagi Prefecture.

The catch of bow-mounted trawls in Miyagi Prefecture was low but the catch in Joban coastal waters was high in 1977 and 1981 when SFO during February and July showed a large southward shift (Figs. 2-2 and 5). Odate (1991) suggested that most of the target populations in these years migrated toward the Joban coastal waters according to the strong southward current of the first branch as Kodama's (3) pattern. Both Odate (1991) and Kodama (1995a) suggested that the water <5℃ is not suitable for *E. pacifica*. Because the fishing ground was formed off southern Iwate Prefecture when the 0℃ isotherm was close to the coastal waters off northern-middle Iwate Prefecture during late February and mid-March 2001 (Fig. 2-18), it is suggested that *E. pacifica* avoids at least such extreme cold temperatures.

The remarkable increase of catch and CPUE in Iwate Prefecture was mainly due to the increase in number of seine boats and active introduction of hydro-acoustic. The reason why annual CPUE after 1996 was slightly lower than that before 1996 was partly due to the strengthening of the regulation on the total landing limits per boat for the purpose of the maintenance of appropriate unit prices against the increase of fishing vessels in 1996 and 1997 in Iwate Prefecture (Minato, pers. comm.). Therefore, it is difficult to examine how oceanographic condition affects the fishing condition in this Prefecture. However, annual CPUE did not decrease when SFO was northward anomaly. Thus, the reason why the fishing condition in Iwate Prefecture was rather stable is suggested to be due to regular occurrence of suitable temperatures (5-7℃) for *E. pacifica* near the coastal waters off Iwate Prefecture in spring even in the northward anomaly years (Figs. 2-13, 14 and 16).

Annual CPUE in Ibaraki Prefecture has a significant negative correlation with SFO during February and July and the lowest temperature in the Joban coastal waters (Fig. 2-7). The first fishing day in the Joban coastal waters has significant positive correlation with both SFO during February and July and the lowest temperature in the Joban coastal waters (Fig. 2-9). Thus the fishing conditions in the Joban coastal waters are thought to be affected significantly by the southward shift of the first branch of the Oyashio Current and surface colder waters.

The relationship between fishing conditions and oceanographic conditions is concluded as follows. When the first branch of the Oyashio Current is weak, fishing condition in Iwate Prefecture is rather stable but not in Miyagi Prefecture and Joban, showing low CPUE and delayed formation of fishing ground. On the other hand, when the first branch of the Oyashio Current is strong, fishing condition in Miyagi Prefecture and Joban area is favorable as well as in Iwate Prefecture, showing high CPUE and early formation of fishing ground.

When comparing these results there are two key points that need to be born in mind. The first is that only catch per boat per day is used as the relative abundance density (CPUE) and the absolute density of each target population can not be analyzed in this approach. Therefore, the fishery data on catch per tow and towing time for each boat should be collected together to elucidate a more appropriate abundance index and to allow comparison of the density of swarms between different fishing grounds in the future. The second point is that the fishing grounds gradually extended to the area with the high thermal isotherms after May up to 15℃ isotherm in June (Figs. 2-13, 14 and 17), although they were usually formed along the 5-7℃ isotherms at the surface and their southward distributional limits rarely reached at 10℃ isotherm during February and April. This phenomenon is thought to be related to the seasonal change of vertical distribution pattern of *E. pacifica* and of physical condition in the mid-layer off Joban as discussed in the **Chapter 7 'General discussion'**.

Chapter 3. Distribution and life history of *Euphausia pacifica*

Given the wide distributional range of *Euphau-*

sia pacifica as well as probable horizontal advection, large areas need to be surveyed using the same gear and methods to effectively investigate the life history of this species. To date, however, population dynamics studies of *E. pacifica* in the northwestern Pacific have been conducted at a few fixed stations (Endo, 1981; Terazaki *et al.,* 1986).

In this chapter, seasonal changes in spawning, distribution and growth pattern and life span of *E. pacifica* off northeastern Japan were investigated using Norpac net samples collected widely (mainly 36°-43°00' N and west of 145°E) from several monthly multi-vessel line transect surveys during 10 years, and the average pictures of the distribution and life history of *E. pacifica* off northeastern Japan were examined. In addition, seasonal changes in spawning and distribution of *E. pacifica* in several fixed stations from off southeastern Hokkaido to Joban (36°50'-42°50'N) were investigated bimonthly using cylindrical-conical nets with large mouth opening, and geographical changes of spawning and distribution of *E. pacifica* were examined in relation to water masses.

Materials and Methods

Norpac net survey

A total of 3,073 discrete Norpac net samples was collected during 206 cruises in the northwestern Pacific between the years 1992 and 2001 (Table 3-1). These collections were from 13 oceanographic and fishery research institutions conducting monthly multi-vessel line transect surveys to examine oceanographic conditions or Pacific saury and squid resources. The sampling area was between 35°30'-48°00'N and west of 158°E, however about 70% of the Norpac net samples were carried out between 36°-43°00' N and west of 145°E (Fig. 3-1). Nets (mouth opening 45 cm and mesh opening throughout 335 μm; no closing mechanism) were lowered to 150m depth, and hauled vertically to the surface at 1 m s^{-1} while the vessel was stationary for all stations. Samples were preserved in 5% buffered formalin seawater immediately after collection.

E. pacifica were sorted into its developmental stages except for the nauplius and metanauplius stages, most of which would pass through nets. Although the identification of euphausiid eggs is difficult, *E. pacifica* type eggs were classified as having a capsule diameter of 0.4-0.5mm and embryo diameter of 0.30-0.38mm based on the size of eggs in Sanriku waters in April 1992, when *E. pacifica* dominated (Taki and Kotani, 1994). The length for the post-calyptopis stages was measured from the tip of the rostrum to the distal end of the telson to the nearest 0.1mm. Adults were sexed according to the presence of a thelycum in females or petasmas in males. Mature male euphausiids have one pair of ejaculatory ducts on the ventral side of cephalothorax which contains developed spermatophores, and males attach the spermatophores to the thelycum of females during mating. However, no female *E. pacifica* specimens were observed with more than two spermatophores in this study. So, it is thought that a male *E. pacifica* attaches its spermatophore to the thelycum during mating, and the female with a spermatophore avoids mating until it casts with the exuviae the spermatophore at the subsequent moult. Evidence of mating, i.e. the presence or absence of a spermatophore (hereafter as copulated females) was checked for females. The abundance of each developmental stage and each 1 mm length class was calculated on the assumption that the filtering rate was 100% for all samples. Only night samples were used for the calculation of average abundance (1,406 hauls) and length measurements (1,151 hauls) of post-calyptopis stages, because they migrate below 150 m depth in daytime, but mostly are at <150 m depth at night (**see Chapter 4**).

Water masses were classified on the basis of the temperature at 100m depth as the Oyashio area (OW; ≦5℃), cold waters of the transitional area (CW; >5℃, ≦10℃), warm waters of the transitional area (WW; >10℃, ≦15℃), and Kuroshio area (KW; >15℃), based on the water mass classifications of Odate (1994) and Yokouchi *et al.* (1997).

Average surface temperature was highest in August-September, and lowest in February-April (January in KW), when water mixing between the surface and deeper layer actively occurs in each water mass (Fig. 3-2). The order of higher temperature was KW > WW > CW > OW in every month.

Growth and age structure were analyzed from length-frequency distributions, using a computer program devised by Tsutsumi and Tanaka (1988), which is modified from the graphic methods of Cassie (1954) and Taylor (1965).

Cylindrical-conical net survey

Seven surveys were carried out using Norpac nets and 5.5-m long cylindrical-conical nets (net mouth diameter: 1.3m; mesh size: 0.45mm; Watanabe, 1992) on the R. V. *Wakataka-maru* (Tohoku National Fisheries Research Institute, Fisheries Research Agency), *Tankai-maru* and *Hokko-maru* (Hokkaido National Fisheries Research Institute, Fisheries Research Agency) 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. 3-3). Two or three transects were set for each coastal area, and a zigzag line between 100 and 300m isobaths off Sanriku and Joban was added in March and April in order 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 1,700m 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 150m at 1 m s^{-1}. At the stations where the bottom depth was shallower than 150m, Norpac net was towed from the near bottom to the surface. Cylindrical-conical nets were obliquely towed at 2 knots of the ship speed from 15m above the sea bottom to the surface at the stations where the sea depth was shallower than 300m, and towed from 150m to the surface in other stations. A wireless net recorder (CN-24: FURUNO) was attached on the bridle 2.5m ahead of the mouth of the cylindrical-conical net to monitor the net depth at the bridge. Cylindrical-conical net was towed only at night at all stations because post-calyptopis stages migrate below the 150m depth in the daytime, but mostly occur at < 150m depth at night (see Chapter IV), except at stations along the zigzag acoustic lines in March and April. A flowmeter (Rigosha) was mounted in the mouth of both nets to register the volume of water passed through the net. Samples were preserved with 5% formalin seawater immediately after collection. Water temperature and salinity from 0 to 300m depth were measured by CTD (Sea-Bird), and water samples were collected from 0, 10, 30, 50, 75m depth to determine chlorophyll *a* concentrations at all stations in March and April, at stations along the southeast line from 42° 50'N, 144° 50'E, and at stations along the east lines from 40° N, 38° 20'N and 36° 50'N.

E. pacifica were sorted and classified into developmental stages except for the nauplius and metanauplius stages, most of 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. Identification of developmental stages, sex and reproductive condition and measurements of body length for post calyptopis stages were conducted according to the same methods as done in the Norpac net survey.

Results

Seasonal changes in the developmental stage composition in water masses

In OW, copulated females and eggs showed high abundances in April and May, and showed another peak during August-October (Fig. 3-4). Calyptopis, furcilia and immature stages were most abundant in May, and these stages showed a second peak during August-December. Copulated females and pre-adult stages rarely occurred in January and February. Seasonal changes in abundance of small (≦15mm) and large (>15mm) adults were more stable than those of the pre-adult stages, but both showed higher abundance during August-October.

In CW, copulated females and eggs showed the highest abundance in April, and showed a second small peak during August-November (Fig. 3-4). In April, eggs in this water mass were remarkably more abundant than in the other water masses. Calyptopis, furcilia and immature stages were most abundant in May, and those stages showed a second peak during August-December in OW. The abundances of calyptopis and furcilia stages in this water mass were comparable to their abundances in OW in

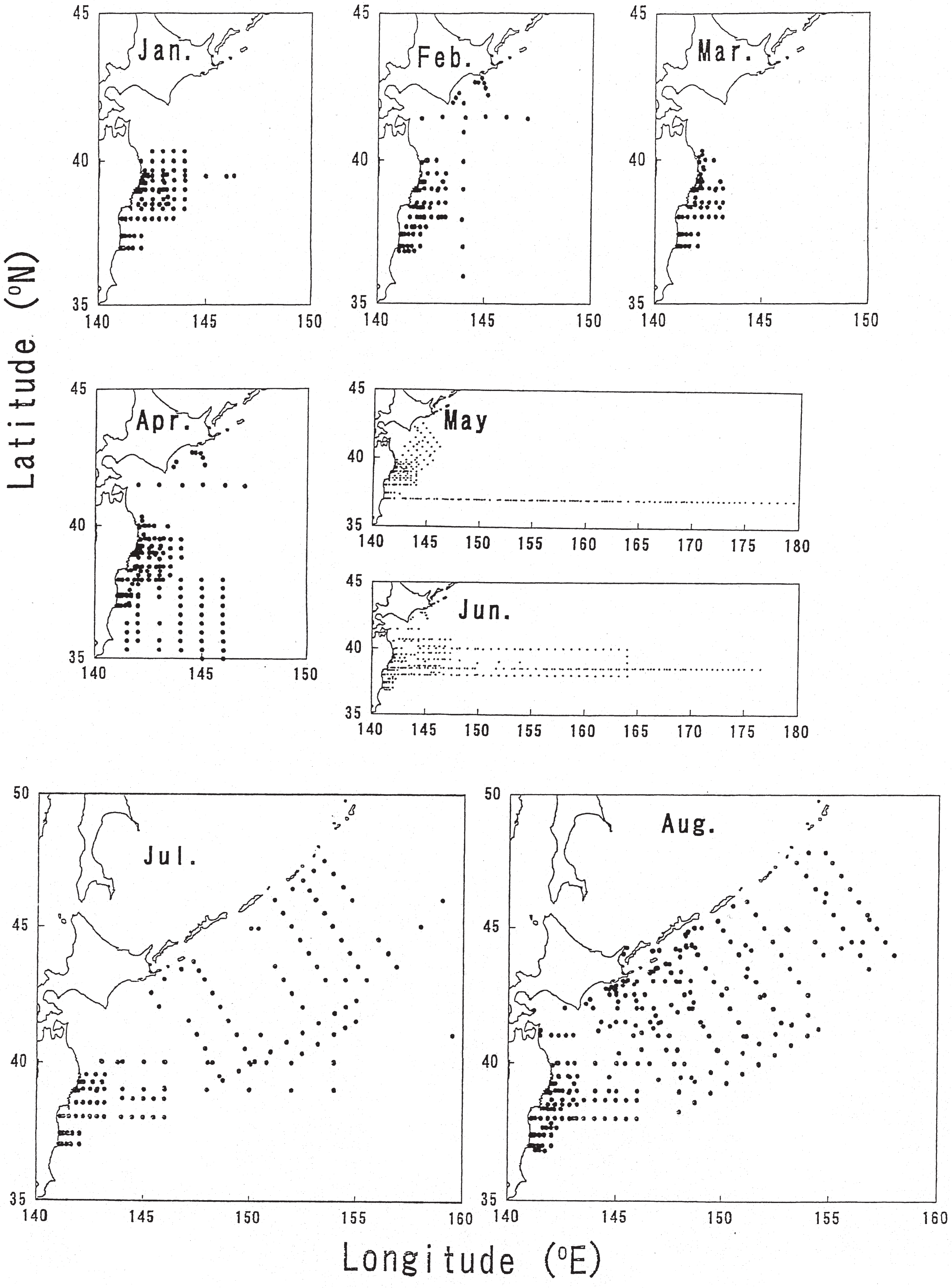

Fig. 3-1. Sampling locations of zooplankton using Norpac net in the northwestern Pacific for each month from 1992 to 2001.

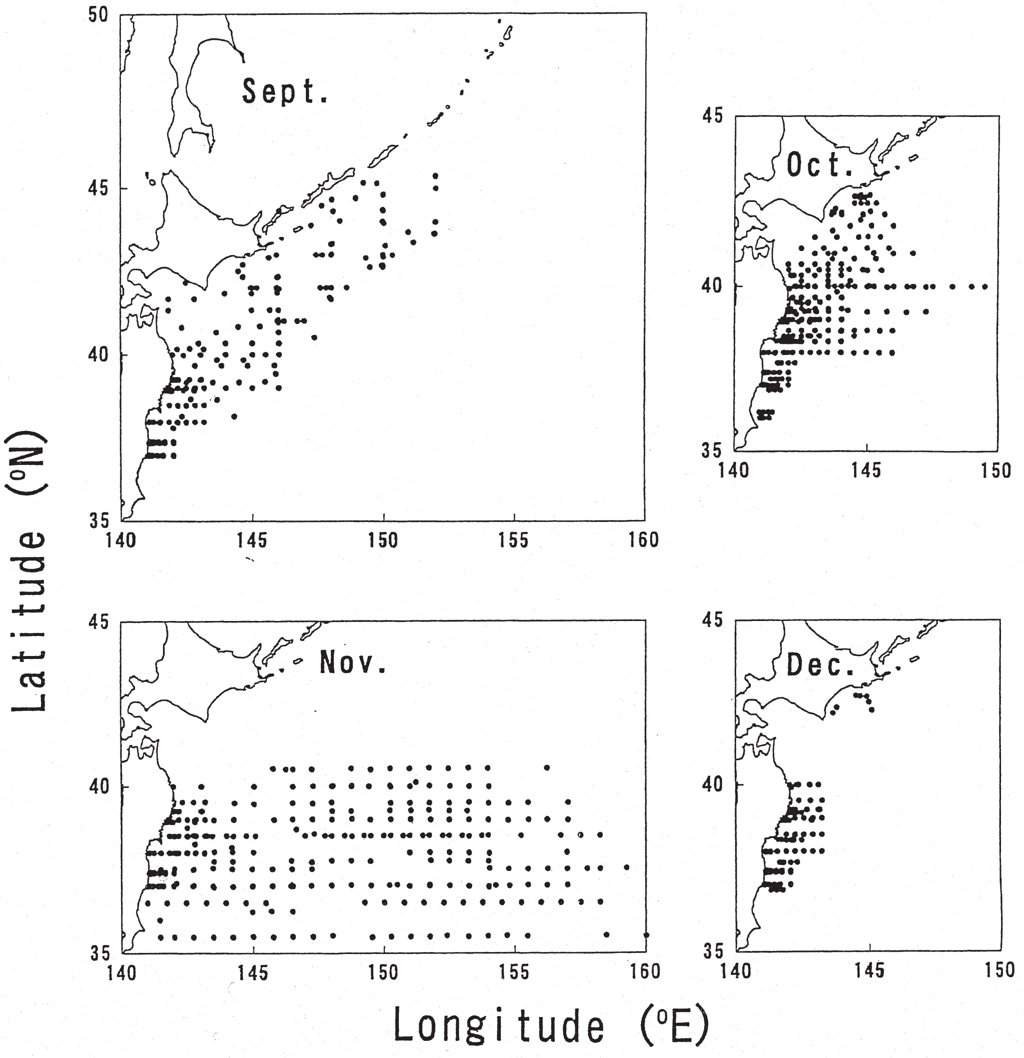

Fig. 3-1. Continued.

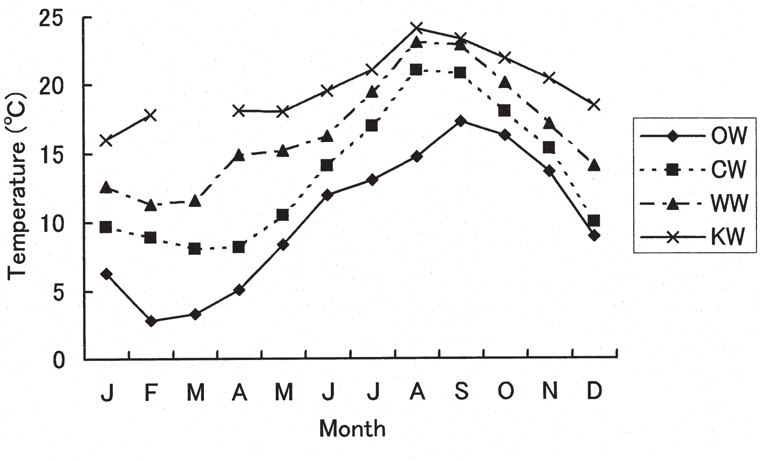

Fig. 3-2. Seasonal changes in the average surface temperature in OW, CW, WW and KW.

Table 3-1. Number of Norpac net samples per month during 1992-2001

month	area	number of samples			years	month	area	number of samples			years
		Day	Night[*1]	Total				Day	Night	Total	
Jan.	OW[*2]	2	3 (0)	5	’95,’96	Jul.	OW	53	30 (29)	83	’93～’99
	CW[*3]	37	42 (32)	79	’94～’00		CW	54	23 (15)	77	’93～’99
	WW[*4]	32	33 (28)	65	’94～’00		WW	59	34 (18)	93	’93～’95
	KW[*5]	0	2 (1)	2	’97		KW	0	1 (1)	1	’98
	Total	71	80 (61)	151			Total	166	88 (63)	254	
Feb.	OW	14	15 (13)	29	’94,’96,’98	Aug.	OW	143	117 (117)	260	’93～’99
	CW	33	27 (16)	60	’94,’96～’00		CW	61	46 (38)	107	’93～’99
	WW	12	14 (12)	26	’94,’96～’99		WW	85	36 (29)	121	’93～’99
	KW	0	1 (1)	1	’94		KW	7	6 (6)	13	’93,’94,’96’98
	Total	59	57 (42)	116			Total	296	205 (190)	501	
Mar.	OW	6	12 (10)	18	’94,’97,’98	Sept.	OW	20	61 (61)	81	’93～’99
	CW	44	25 (12)	69	’94,’96～’99		CW	28	31 (20)	59	’93～’99
	WW	6	9 (8)	15	’94,’96～’99		WW	68	29 (20)	97	’93～’99
	KW	0	0	0			KW	6	7 (7)	13	’93,’94,’96～’98
	Total	56	46 (30)	102			Total	122	128 (108)	250	
Apr.	OW	34	45 (41)	79	’93～’99	Oct.	OW	21	30 (28)	51	’94～’00
	CW	50	59 (46)	109	’93～’99		CW	36	46 (29)	82	’93～’00
	WW	6	15 (12)	21	’95～’97,’99		WW	63	88 (72)	151	’93～’00
	KW	1	13 (13)	14	’96,’97		KW	6	11 (8)	17	’94.’95,’97,’99
	Total	91	132 (112)	223			Total	126	175 (137)	301	
May	OW	35	23 (21)	58	’93～’95,’97～’99,’01	Nov.	OW	8	14 (12)	22	’93～’96
	CW	82	44 (31)	126	’93～’99,’01		CW	9	18 (13)	27	’93～’97
	WW	74	30 (25)	104	’93～’95,’98,’99,’01		WW	55	70 (57)	125	’93～’98
	KW	21	6 (6)	27	’93,’94,’99,’01		KW	85	93 (93)	178	’93～’98
	Total	212	103 (83)	315			Total	157	195 (175)	352	
Jun.	OW	35	23 (20)	58	’93～’98	Dec.	OW	0	4 (4)	4	’97
	CW	109	51 (36)	160	’93～’98		CW	1	12 (11)	13	’95,’97
	WW	118	29 (19)	147	’93～’98		WW	20	38 (21)	58	’93～’98
	KW	4	3 (3)	7	’93～’95		KW	11	7 (6)	18	’94.’96～’98
	Total	266	106 (78)	372			Total	32	61 (42)	93	

[*1] Night data in perentheses indicate samples for which body length, sex and presence of a spermatophore were examined.

[*2] Oyashio waters

[*3] Colder waters of transitionl area

[*4] Warmer waters of transitional area

[*5] Kuroshio waters

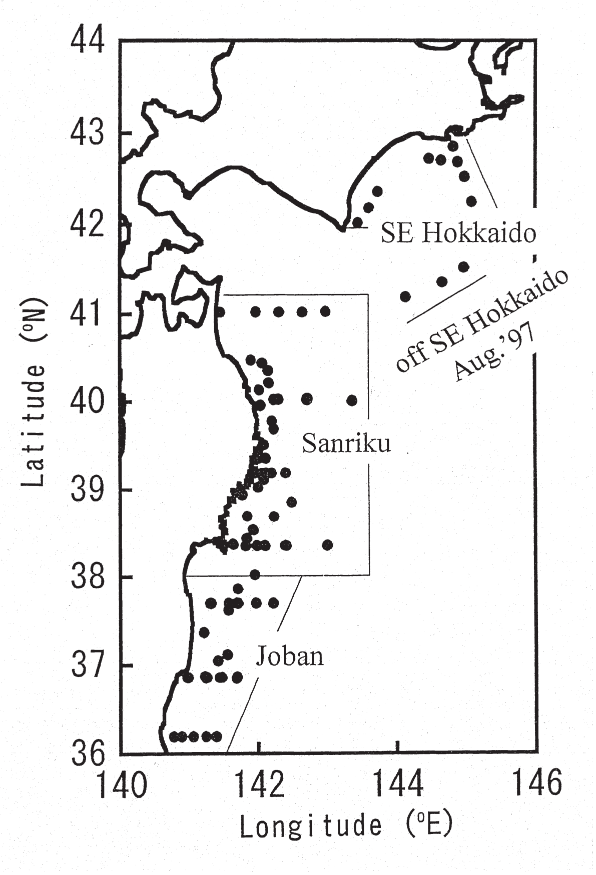

Fig. 3-3. Sampling locations of *Euphausia pacifica* off the northeastern coast of Japan from March 1997 to February 1998.

May. Copulated females and pre-adult stages rarely occurred in January and February as also observed in OW. Seasonal changes in abundance of small and large adults were more stable than those of pre-adult stages, but large adults rarely occurred in January and February. Both size adults in CW tended to be less abundant than those in OW throughout the year, but large adults in CW were more abundant than those in OW during March-June.

In WW, all stages of *E. pacifica* were less abundant than in the colder water masses except for large adults in July, when high abundance occurred at one station (Fig. 3-4). Seasonal variations of each stage were similar to those of CW, although the peak of calyptopis was observed a month earlier than in CW.

All of the stages rarely occurred in KW throughout the year (Fig. 3-4).

The average abundances of eggs, calyptopis and furcilia in CW were significantly higher (t-test, $P < 0.01$) than those in the other areas throughout the year (Table 3-2). The abundances of copulated females and immature stage in OW were as high as those in CW, and significantly higher (t-test, $P < 0.01$) than those in WW and KW. The abundances of small and large adults in OW were significantly higher (t-test, $P<0.001$) than those in the other areas, and the occurrence of large adults was mostly limited to OW and CW. This suggests that *E. pacifica* gradually adapts to colder areas with the developmental stage from furcilia to adults, and advanced-age adults rarely occur in warmer areas.

In OW and CW, copulated females mainly occurred in the 16-21mm size classes and the relative percentage of copulated females to the total abundance of females was 67-100% for >20mm size classes in April and May (Fig. 3-5). Copulated females mainly occurred > 16mm size classes in June, August and September. However, they also occurred among small size classes of 11-14mm from April to November.

Seasonal growth pattern and life span

In the monthly average length-frequency distributions in OW and CW, two modal size groups were generally recognized for male *E. pacifica*: both small and large adults occurred throughout the year (Fig. 3-6). It was difficult to rationally divide the size groups in April based only on the length-frequency data alone. By considering the sequence of modal groups from March to May, the groups were divided into three modal groups based.

Also two modal size groups were generally recognized for female *E. pacifica* in the monthly average length-frequency distributions in OW and CW, except for April, August and September when three groups were recognized (Fig. 3-7). Although it was difficult to rationally divide the modal size groups into two and three groups in March and April, respectively, these were considered to be composed of two and three groups, on account of the sequence of modal groups from February to May.

Based on the modal growth pattern, the average growth of males follows this pattern: The newly-appearing cohort of ca. 10mm in April shows slow, steady growth until the following March, but grows rapidly to ca. 17mm from March to June (Fig. 3-8).

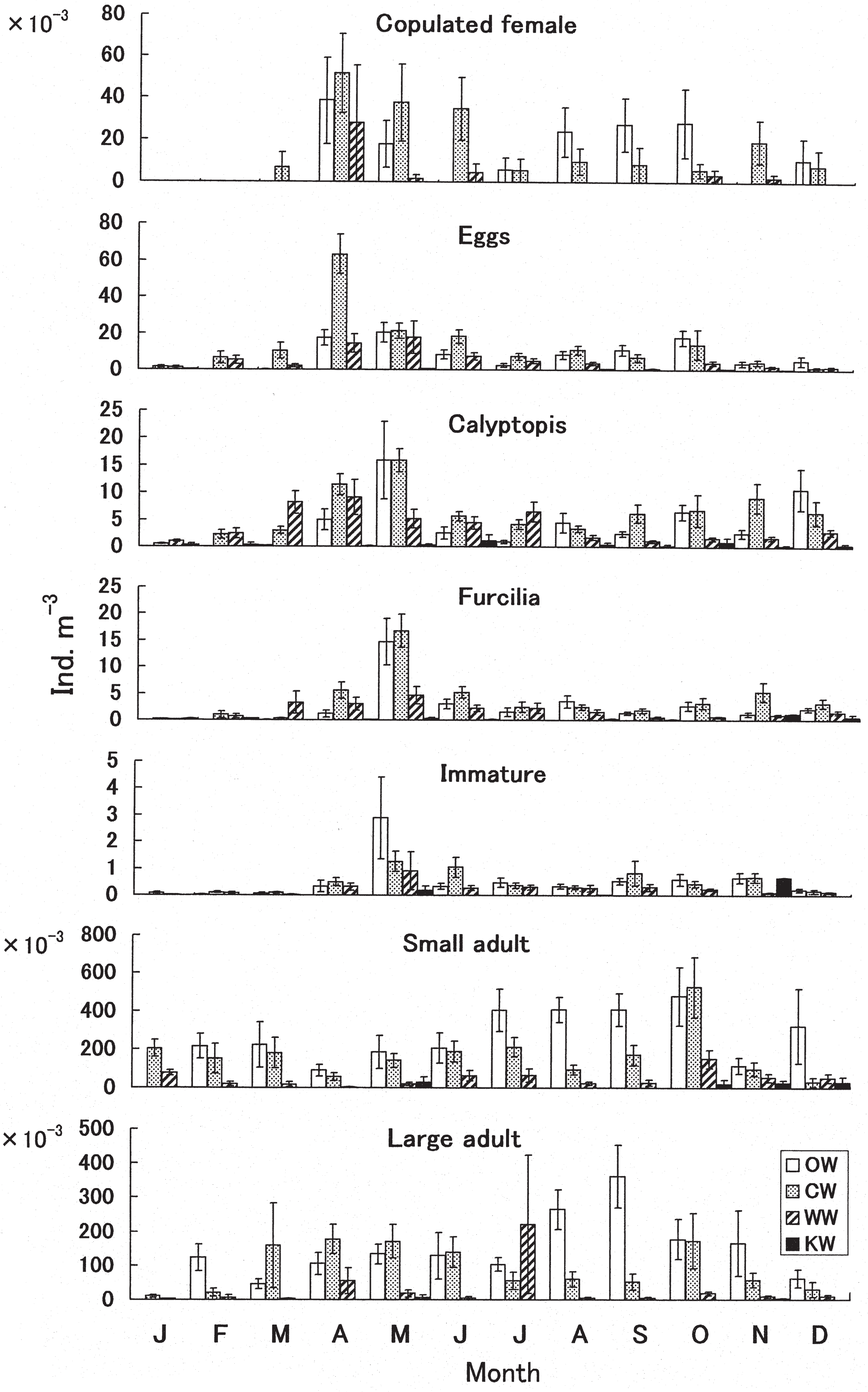

Fig. 3-4. Seasonal changes in the average abundance of each developmental stage of *Euphausia pacifica* by water mass from the Norpac net samples. Vertical bars: SE. No data from OW in January and KW in March. Details of theNorpac net samples are shown in Table 3-1.

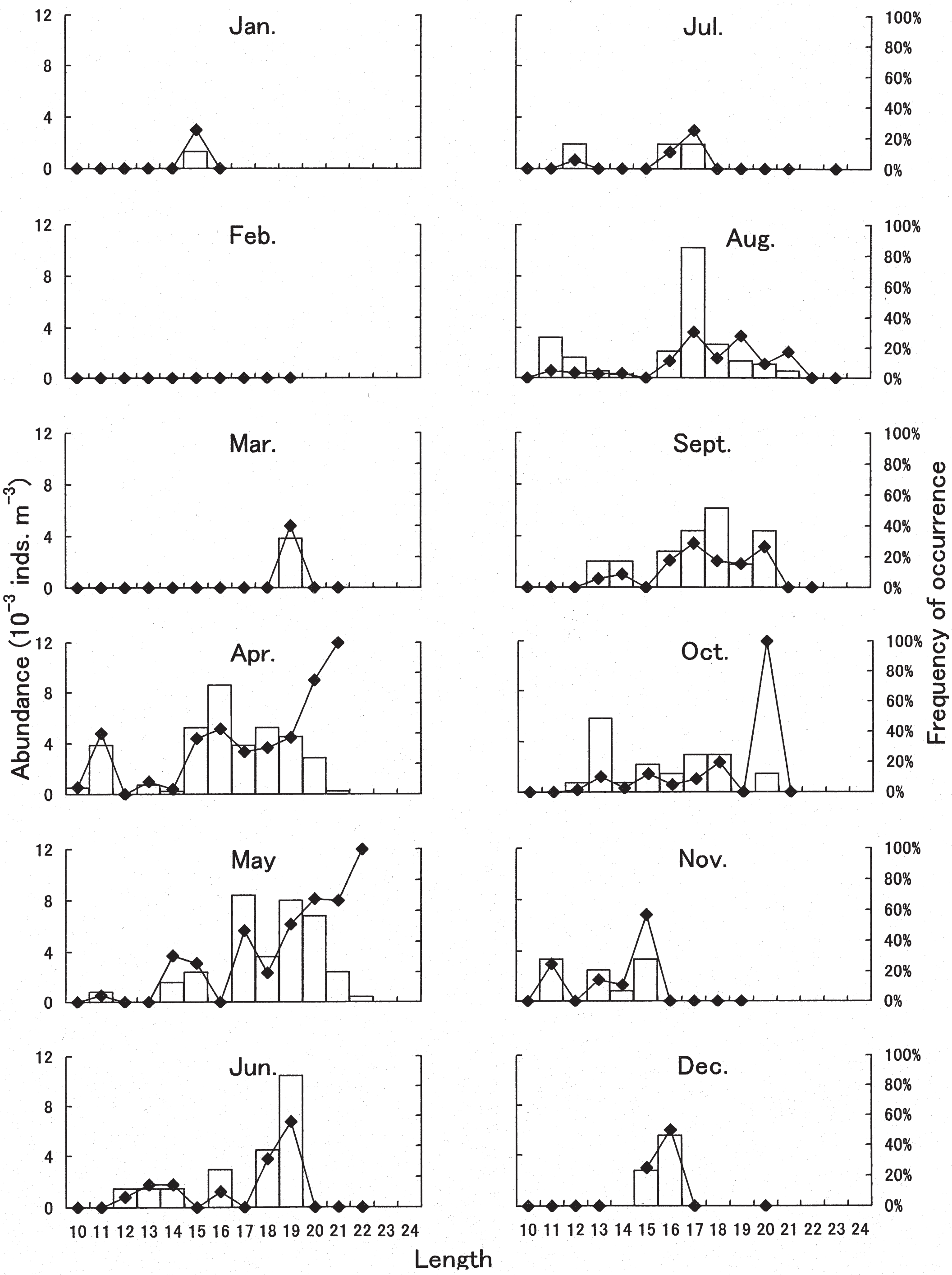

Fig. 3-5. Length-frequency distribution for *Euphausia pacifica* females with a spermatophore (bars) and their frequency (%) to the total abundance of females (solid diamonds) in OW and CW from the 10-year Norpac net samples.

Table 3-2. Average abundance (± SE; 10^{-3} inds. m^{-3}) of each developmental stage of *Euphausia pacifica* by water mass from the 10 year Norpac net samples*

stage	average abundance (±SE; 10^{-3} inds. m^{-3})			
area	OW	CW	WW	KW
Copulated female	21±5.2 (48)	20±4.1 (46)	2.6±1.3 (6)	0
Eggs	9,700±1,100 (30)	17,700±1,800 (54)	5,200±1,000 (16)	235±56 (0.7)
Calyptopis	4,430±880 (31)	6,660±510 (46)	3,090±320 (21)	279±76 (1.9)
Furcilia	2,910±490 (33)	4,420±490 (50)	1,440±180 (16)	128±58 (1.4)
Immature	540±110 (40)	536±76 (40)	238±54 (18)	34±11 (2.5)
Small adult	328±32 (56)	173±21 (29)	67±12 (11)	20±9.8 (3.4)
Large adult	213±26 (62)	105±15 (31)	24±12 (6.9)	2.0±1.3 (0.6)

*Data in parentheses indicate percentage of abundance to the total for each developmental stage.

This cohort then seems to grow negatively after the summer to fall and attains a maximum of ca. 19mm by the following April. The seasonal growth pattern of females is similar to that of males except that the cohort of larger individuals (ca. 18mm) in April grew to ca. 20mm by August and existed until September (Fig. 3-8). Average length of males tended to be larger than that of females in winter but vice versa for the cohort of ca. 17mm during spring and fall.

Seasonal change in developmental stage composition among areas

Throughout the study period, the average temperatures at the surface and 100m depth off Joban were highest and those off southeastern Hokkaido were lowest (Fig. 3-9). The surface temperature was lowest in April or next February and highest in August-October along each coastal area. The temperature at 100m 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 75m was highest in April and lowest in October along each coastal area.

The first branch of the Oyashio Current, characterized by a lower temperature than 5℃ at 100m depth (Murakami, 1994), extended southward to the Sanriku coastal area in March 1997, but it receded and another ≦5℃ water related to the second branch of the Oyashio Current occurred off Sanriku and Joban in April and June (Figs. 3-10-16). Oyashio waters (T_{100}≦5℃) 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℃ occurred off southeastern Hokkaido during April and August. During the study period, the seasonal pattern of oceanographic conditions closely approximated the average seasonal pattern of this region (Ogawa, 1989).

Copulated females, eggs and calyptopis stage were abundant off Sanriku and Joban in April and off southeastern Hokkaido in October (Figs. 3-10, 11, 12 and 17). Both areas were near margins of the Oyashio waters (T_{100} = 5℃). Off southeastern Hokkaido, however, these abundances were low or non-existent throughout the year except in October, where cold waters of the Oyashio (T_{100} < 2℃) dominated. Eggs were present in June, but larvae were not observed in June and August. Therefore, spawning in June might 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℃ < T_{100}≦15℃) 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. In the following February, eggs and calyptopis stage were abundant off southern Sanriku and Joban, where colder transitional waters (5℃ < T_{100} ≦10℃) dominated. Seasonal change in the proportion of copulated females to total females was similar to that in abundance of copulated females and eggs (Fig. 3-17).

Distributional patterns of furcilia stage were similar to that of the younger stages (Figs. 3-13 and 17).

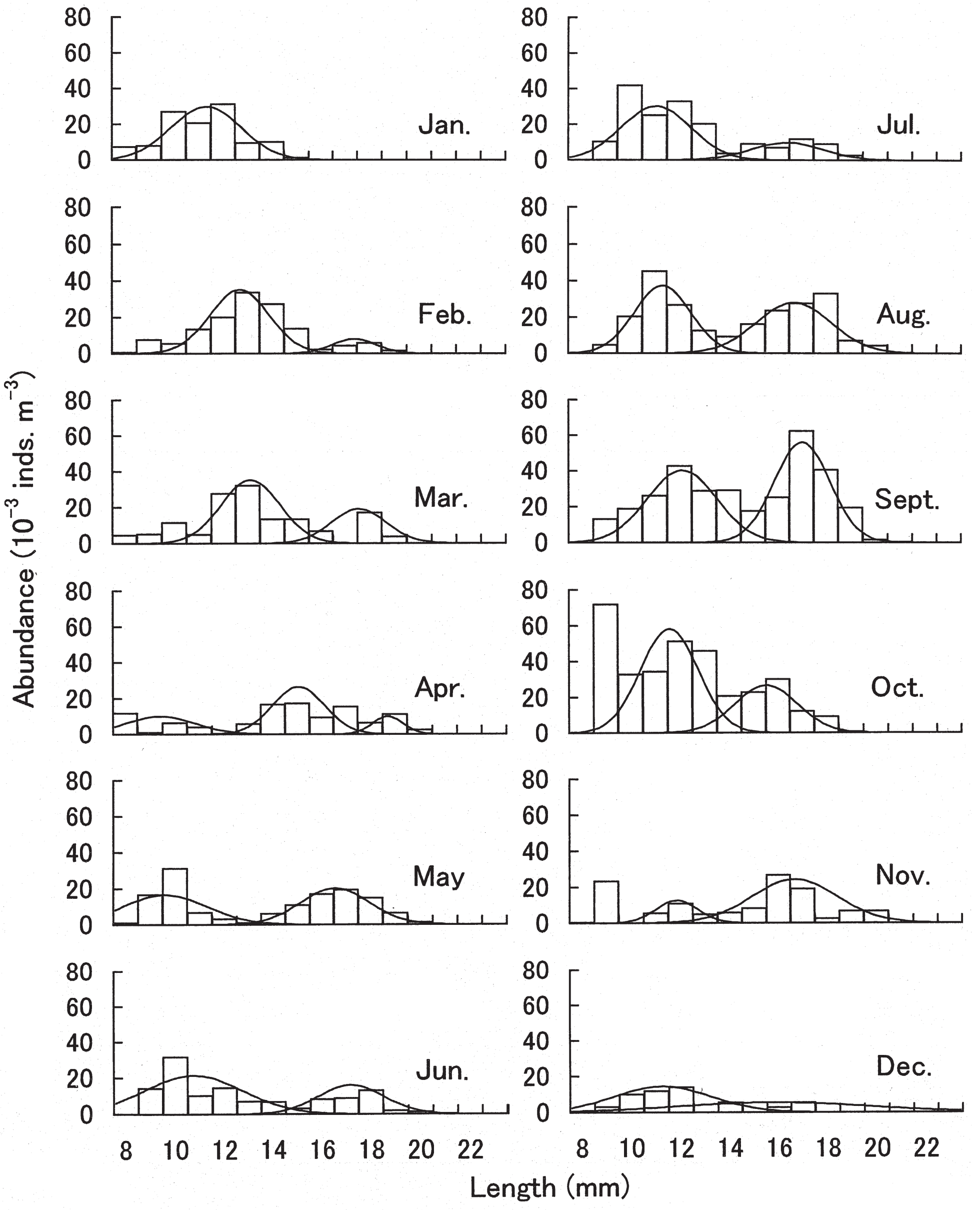

Fig. 3-6. Length-frequency distributions of male *Euphausia pacifica* in OW and CW from the Norpac net samples. Hypothetical distribution curve of each cohort is superimposed using a computer program devised by Tsutsumi & Tanaka (1988).

However, furcilia stage was rare off Sanriku and Joban in April, but abundant off Sanriku in December, where 10℃ isotherm at 100m depth occurred.

Immature stage was abundant off Sanriku and Joban from June to December and off southeastern Hokkaido in October, where temperatures at 100m depth were mainly between the 5 and 10℃ (Figs. 3-14 and 7). 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. 3-15 and 17).

Large adults were abundant off Sanriku in March, April and the following February, while off Joban

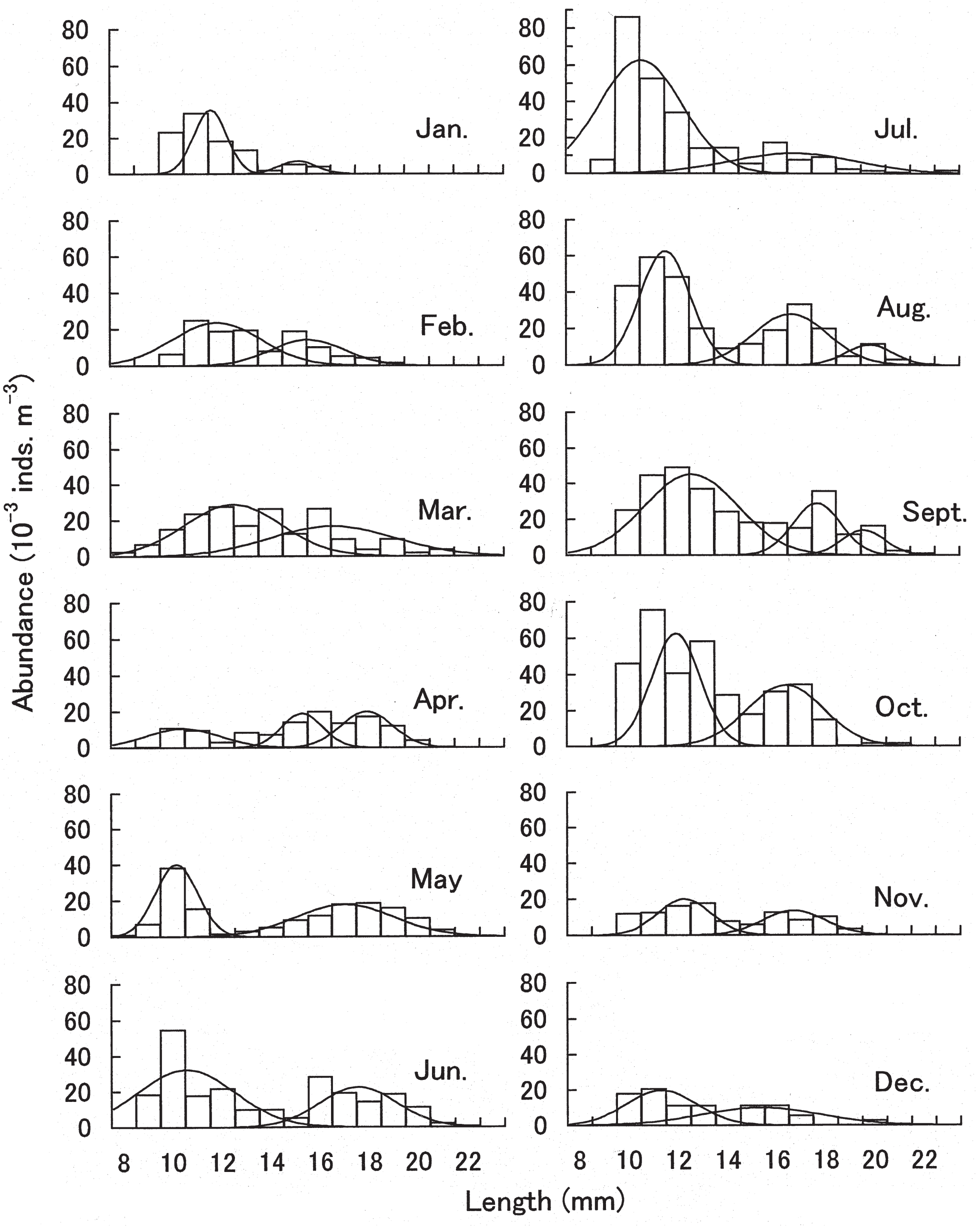

Fig. 3-7. Length-frequency distributions of female *Euphausia pacifica* in OW and CW from the Norpac net samples. Hypothetical distribution curve of each cohort is superimposed using a computer program devised by Tsutsumi & Tanaka (1988).

they were abundant in June and the following February. During these months, the 5℃ isotherm shifted southward. Large adults were few from August to December, when the warmer transitional waters dominated (Figs. 3-16 and 17). 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.

In April, copulated females mainly occurred among 17-21mm and 16-18mm size classes off Sanriku and Joban, respectively (Fig. 3-18). In June, they mainly occurred among 16-22mm size classes off Joban. In August, they mainly occurred among 11-12mm and 15-18mm size classes near the margins of the first branch of the Oyashio Current. In October, they mainly occurred among 12-14mm and 16-19mm size classes off southeastern Hokkaido. In February, they occurred across a wide size range of 10-19mm and mainly occurred among 16-18mm size

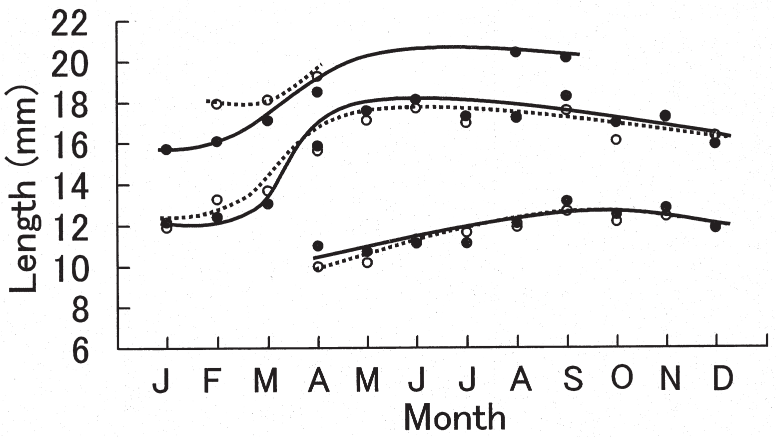

Fig. 3-8. Seasonal changes in the average length of each cohort of male (open circles) and female (solid circles) *Euphausia pacifica* estimated by the length-frequency distributions in OW and CW (Figs. 3-6 and 7). Lines: Hypothetical growth (males: dashed lines; females: solid lines).

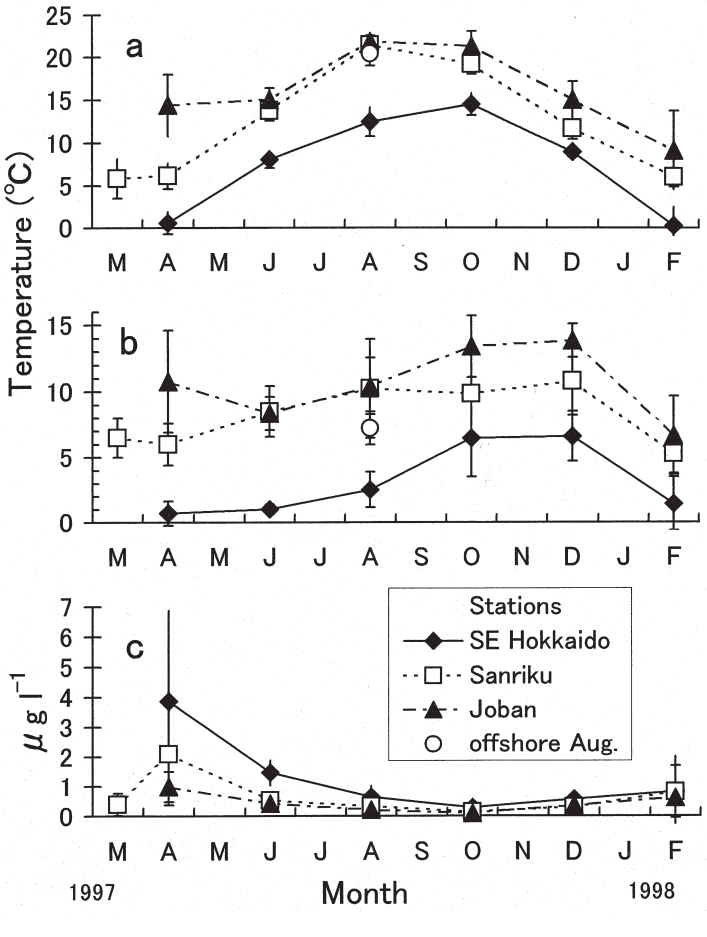

Fig. 3-9. Seasonal changes in the average surface temperature (a), average temperature at 100m depth (b) and integrated average chlorophyll *a* (μg l^{-1}) in the upper 75m (c). Vertical bars: ±1 SD.

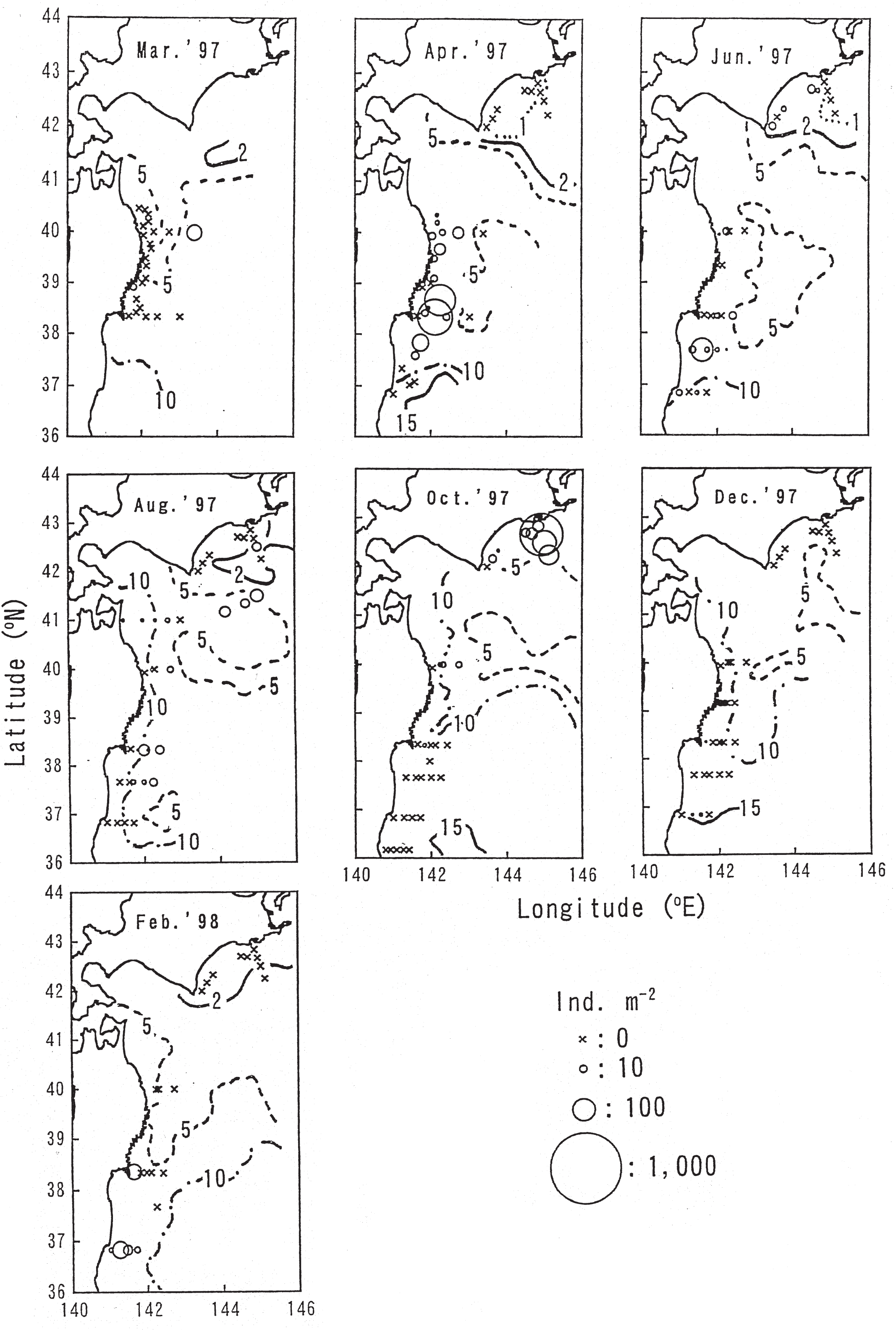

Fig. 3-10. Distribution and abundance of copulated *Euphausia pacifica* females and temperature gradients at 100m depth from March 1997 to February 1998. Numbers indicate temperatures (℃). Scales as in legend.

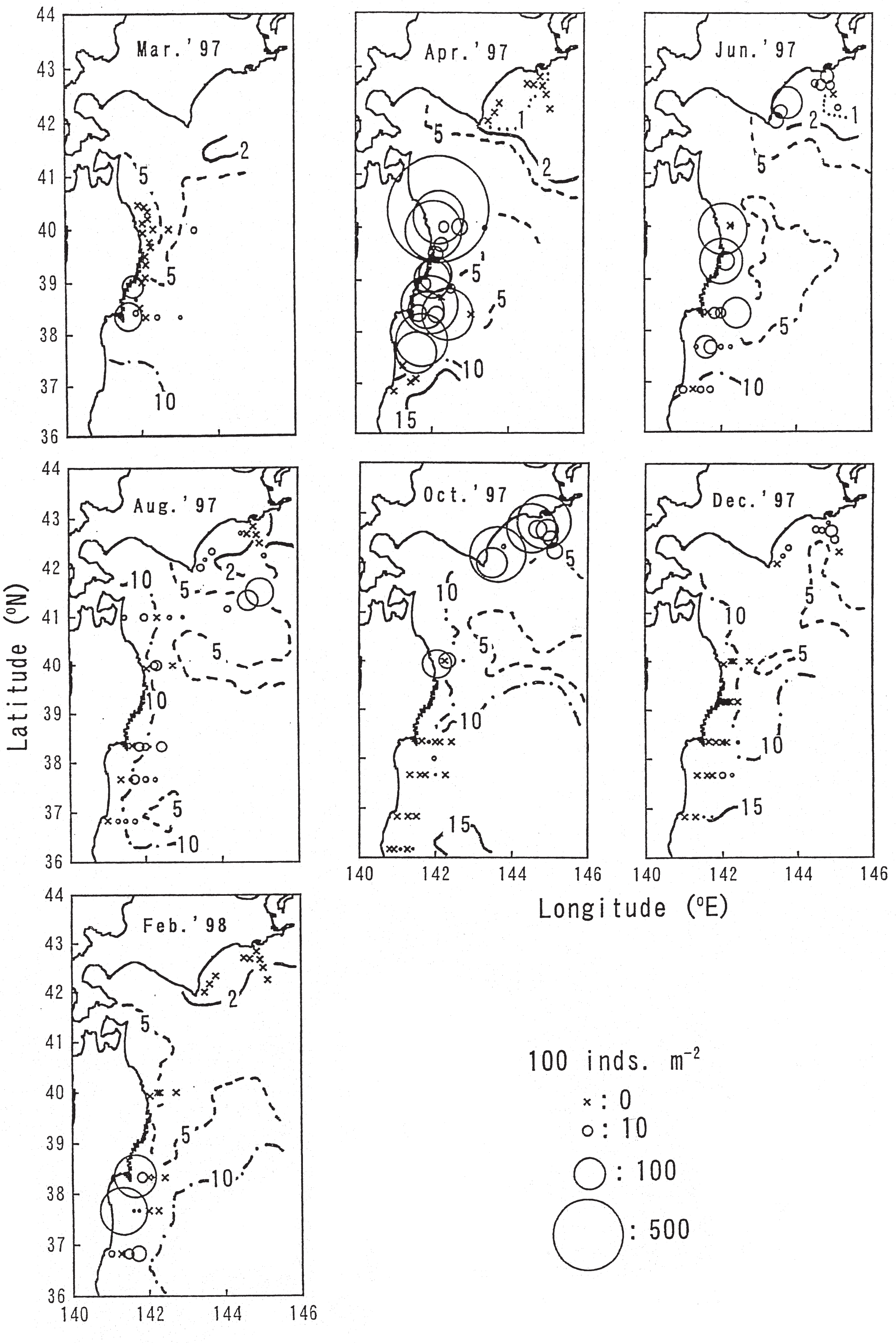

Fig. 3-11. Same as Fig. 3-10 but for eggs.

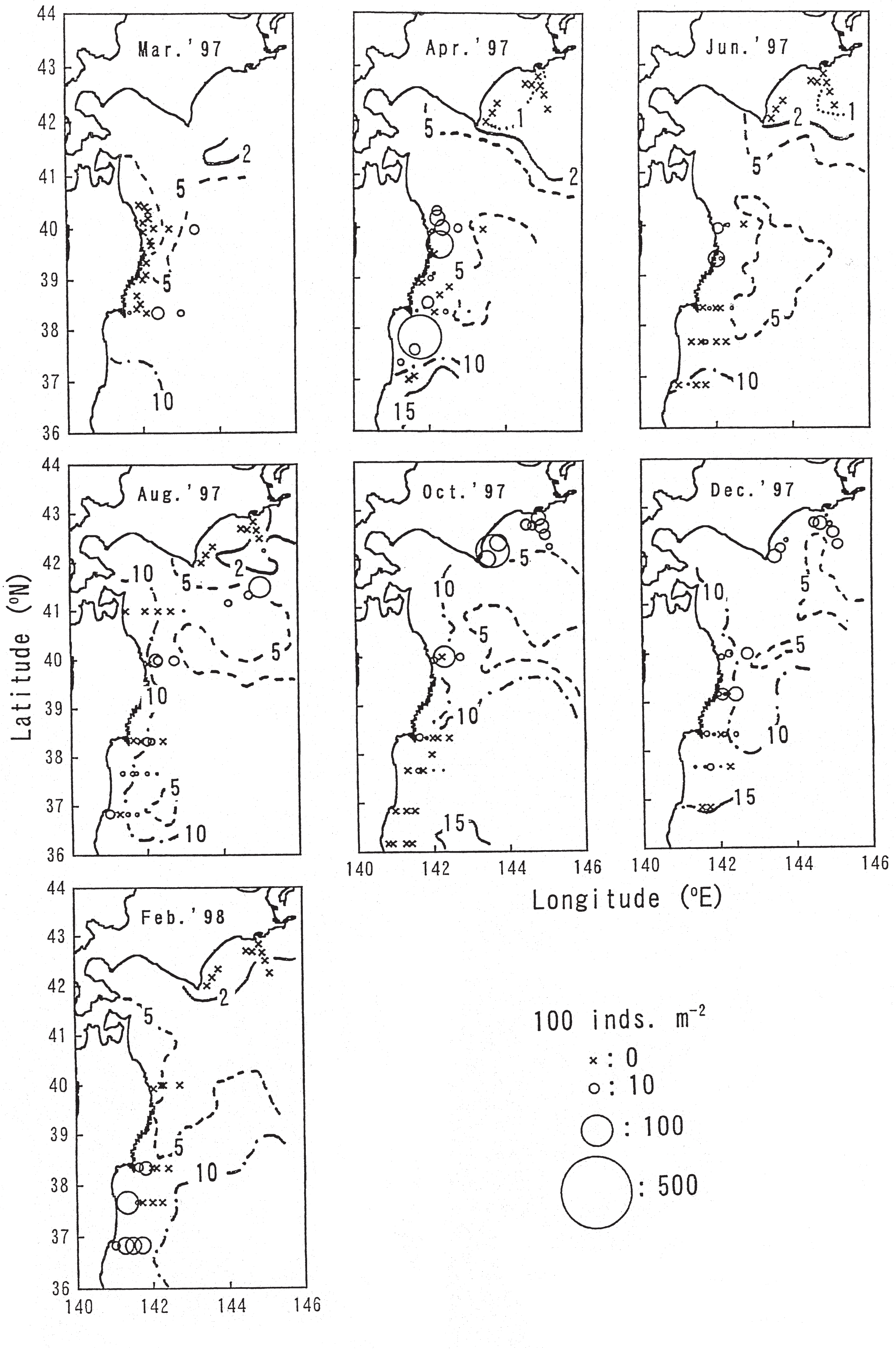

Fig. 3-12. Same as Fig. 3-10 but for calyptopis stage.

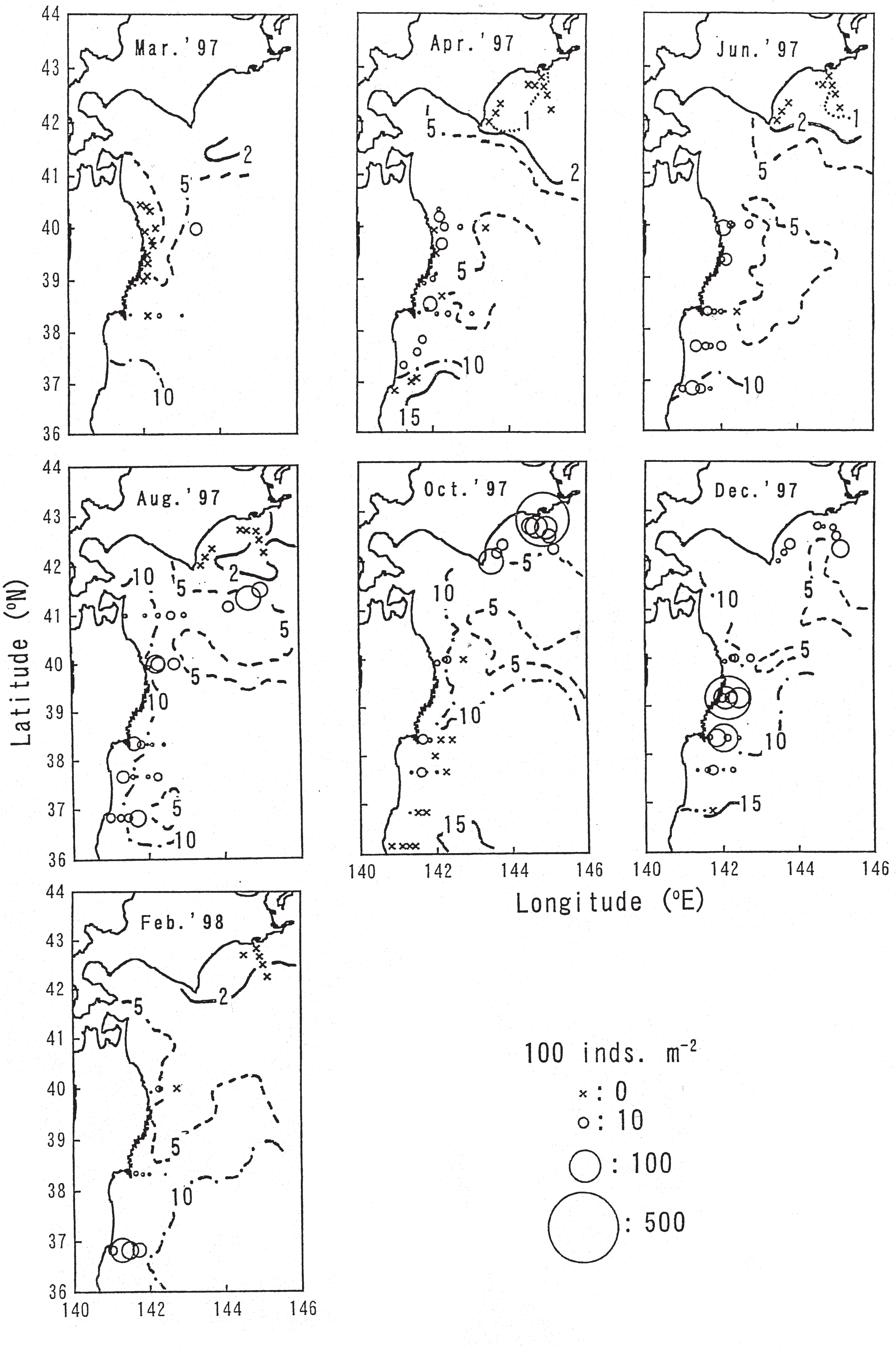

Fig. 3-13. Same as Fig. 3-10 but for furcilia stage.

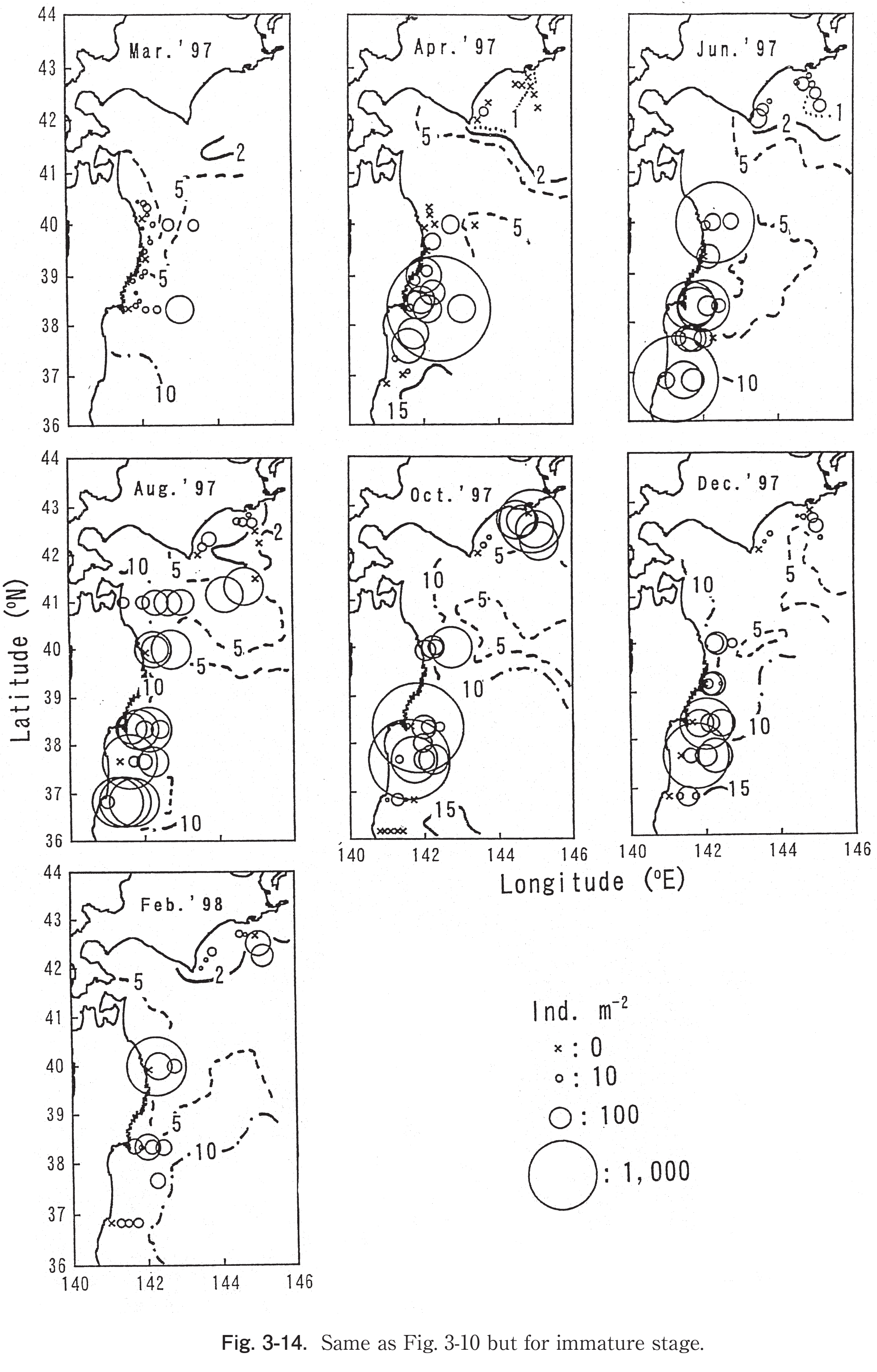

Fig. 3-14. Same as Fig. 3-10 but for immature stage.

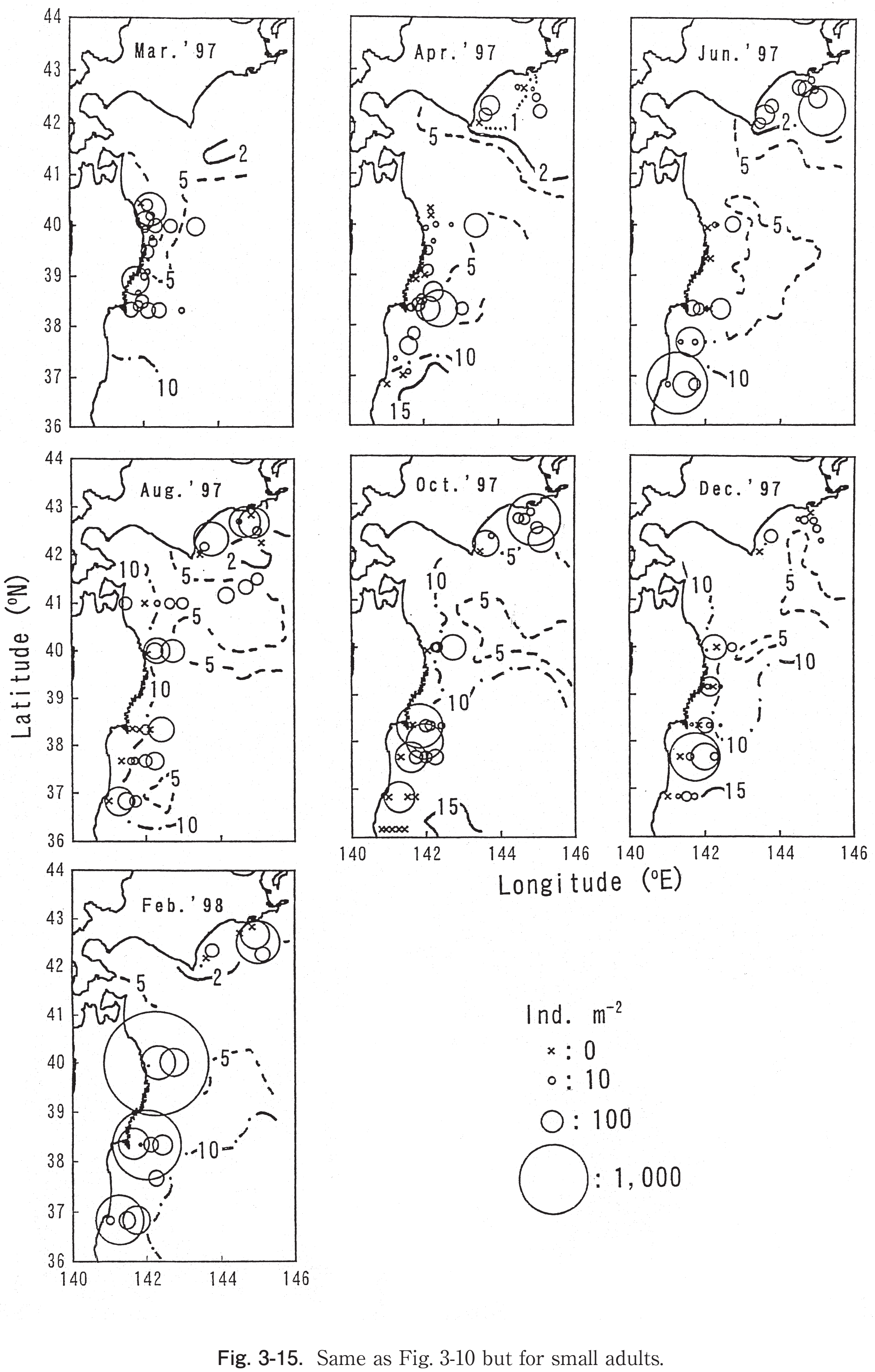

Fig. 3-15. Same as Fig. 3-10 but for small adults.

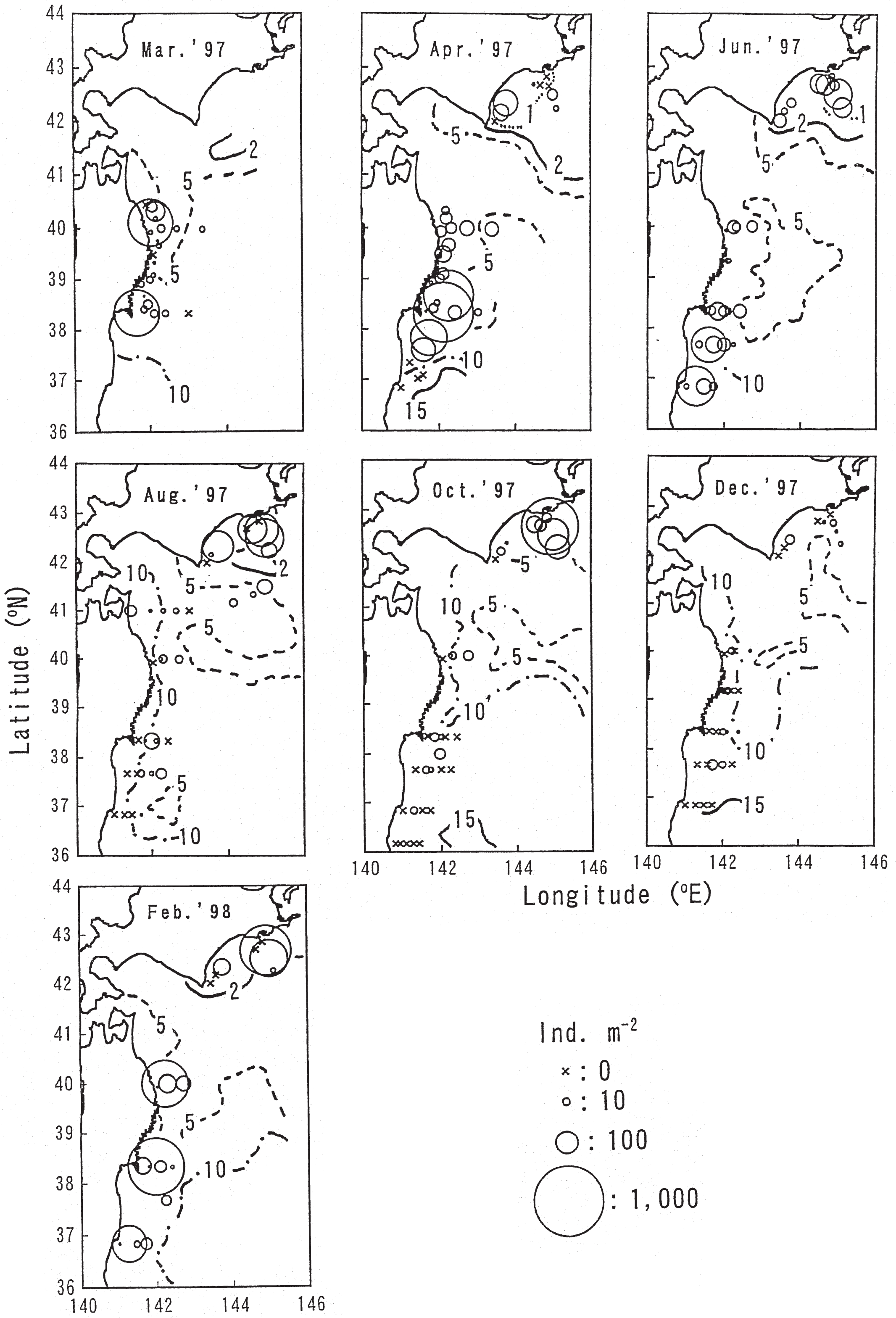

Fig. 3-16. Same as Fig. 3-10 but for large adults.

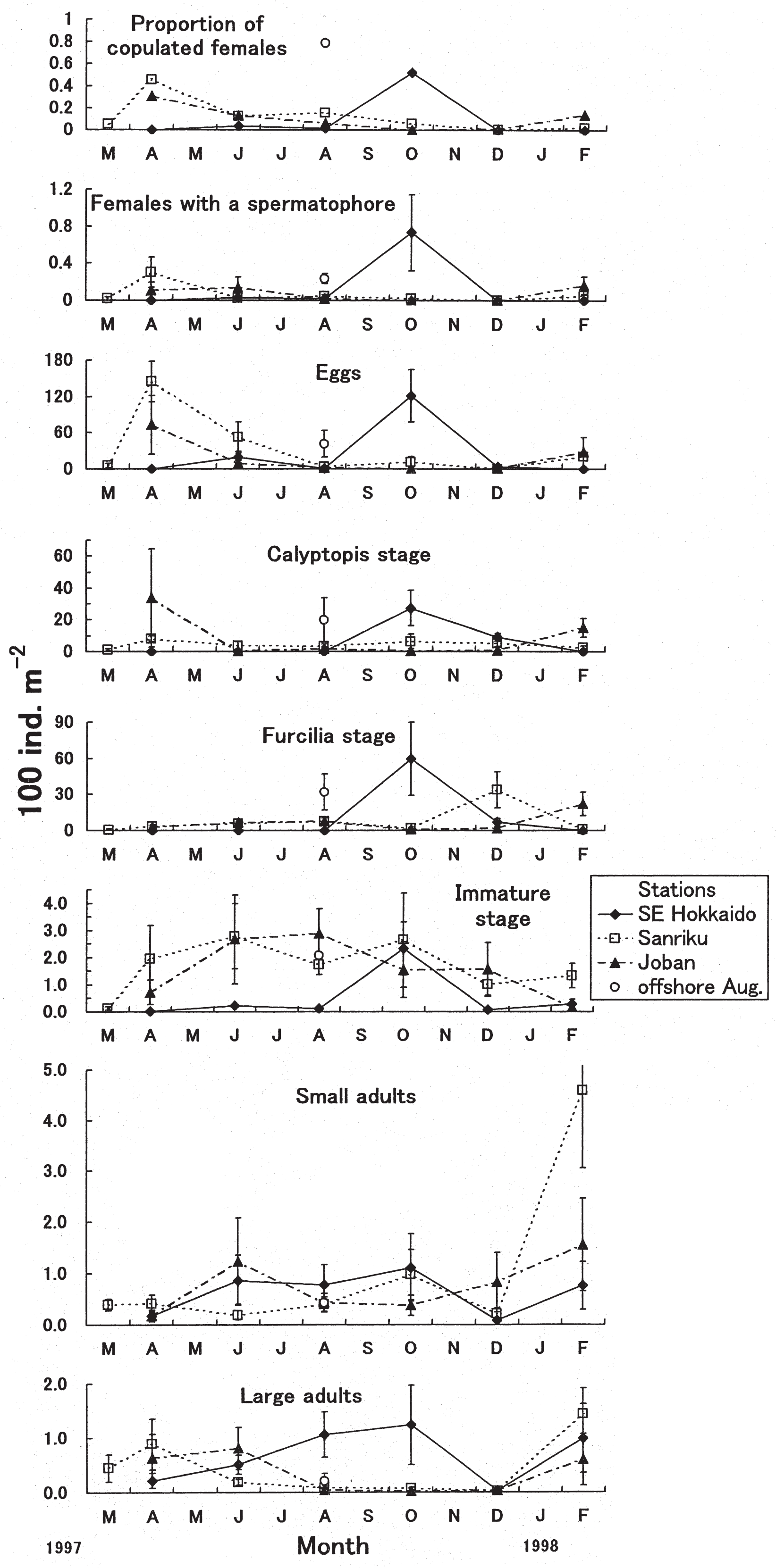

Fig. 3-17. Seasonal changes in the proportion of copulated females and average abundance of each developmental stage of *Euphausia pacifica* by area from March 1997 to February 1998. Vertical bars: ±1 SE.

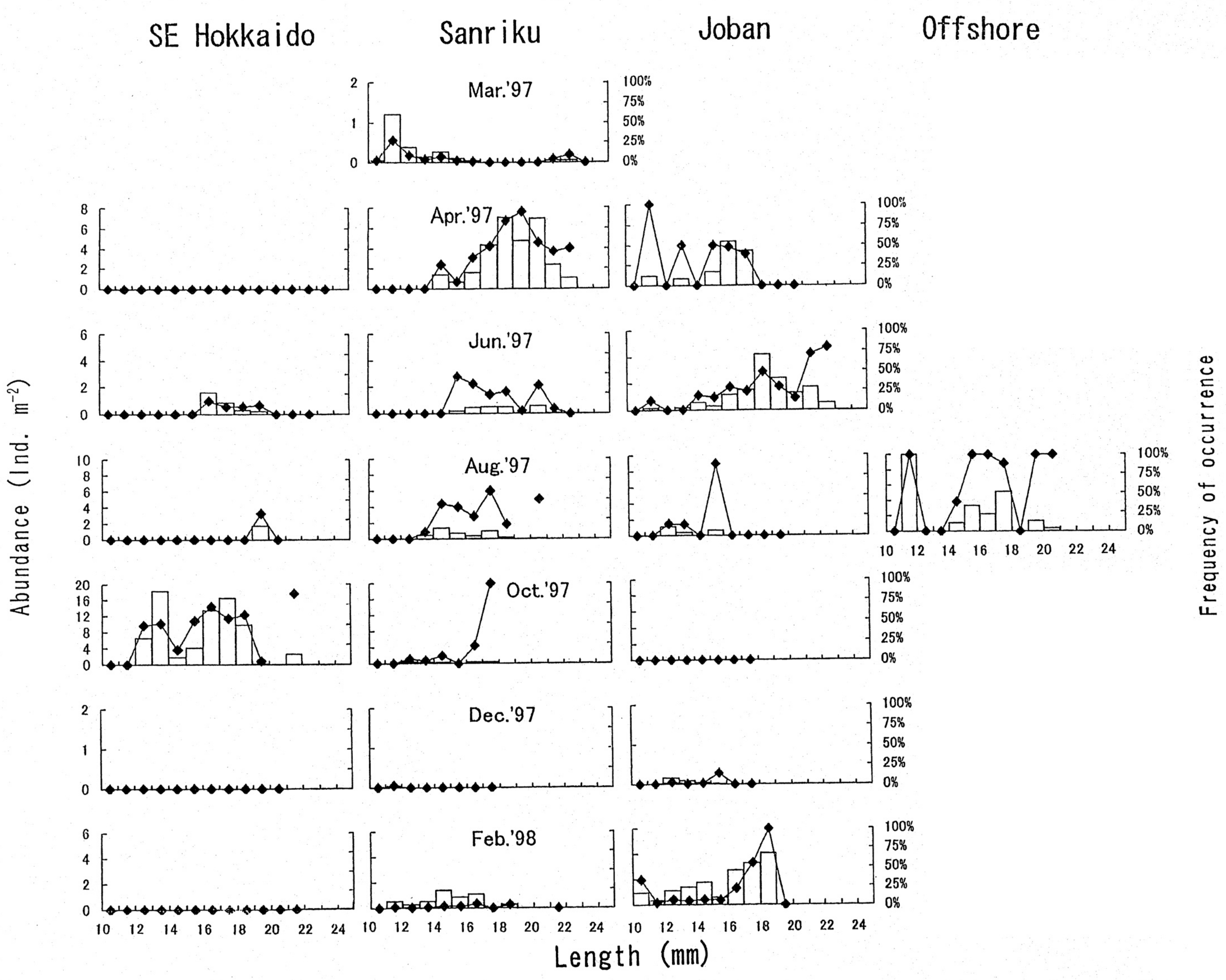

Fig. 3-18. Length-frequency distribution for *Euphausia pacifica* females with a spermatophore (bars) and their frequency (%) to the total abundance of females (solid diamonds) in each region on the basis of cylindrical-conical net samples.

classes off Joban.

Discussion

Seasonal change in spawning and distribution in water masses and life history

Mating and spawning occurred throughout the year in OW and CW, with the main peak occurring in spring and to a lesser extent in late fall-winter on the basis of the Norpac net samples (Fig. 3-4). The main spawning area, which occurred in CW in spring and in OW and CW in summer-fall, agrees closely with to the distributional pattern of large adults. Seasonal changes in abundance of larval and immature stages, which were most abundant in spring-early summer and least abundant in winter, were well synchronized with those of copulated females and eggs. It is therefore suggested that the seasonal activity of spawning depends on the feeding conditions as shown by the high abundances of phytoplankton, microzooplankton and mesozooplankton in spring and low abundances in winter, which are widely recognized patterns in the northern part of the northwest Pacific (Odate, 1994; Kotani *et al.,* 1996; Kasai *et al.,* 2001). This also explains observations in northeastern Pacific waters, where *E. pacifica* reaches its highest spawning intensity during upwelling periods (Smiles and Pearcy, 1971; Brinton, 1976; Heath, 1977; Ross *et al.,* 1982).

Iguchi *et al.* (1993) showed that the modal size (ca. 10mm) of *E. pacifica* hatched in spring indicated no growth from summer to the following winter, but then rapid growth through the following spring in Toyama Bay, southern part of the Japan Sea. Apparent growth in OW and CW, where both larger and smaller adults occurred throughout the year, was recognized from March to June for the smaller group of adults, identical to the growth patterns in Toyama Bay (Fig. 3-8). Such apparent growth was perhaps supported by the favorable food conditions in the region off northeastern Japan as shown by previous reports on seasonal changes in the abundance of phytoplankton, microzooplankton and mesozooplankton (Odate, 1994; Kotani *et al.,* 1996; Kasai *et al.,* 2001).

The negative growth of adult *E. pacifica* during summer and winter was observed both in Toyama Bay (Iguchi *et al.,* 1993) and off northeastern Japan (Fig. 3-8). Iguchi *et al.* (1993) suggested that the negative growth in Toyama Bay was due to the result of the selective death for larger sized individuals. On the other hand, Marinovic and Mangel (1999) documented the shrinkage of *E. pacifica* experimentally. They showed that individuals shrank at temperatures higher than 16.5℃ despite access to excess food. Whether negative growth in *E. pacifica* really occurs in the same conditions (temperatures and food) as experienced during daily vertical migration needs to be examined in the future.

Because spawning and recruitment of larval stages of *E. pacifica* occur throughout the year except for the winter season off northeastern Japan (Fig. 3-4), it is difficult to estimate the age/length relationships from length-frequency distributions precisely. However, the most dense occurrence in abundance of eggs and early developmental stages was observed in April and May, respectively (Fig. 3-4) and two modal cohorts of males and females were consistently recognized in OW and CW (Figs. 3-6 and 7). Endo (1981) estimated that the recruitment time from hatching to adult in *E. pacifica* in Sanriku waters was 2-3 months on the basis of both laboratory experiments and field sampling. Therefore spring hatching and summer recruitment to the adult stage is considered to be the origin of the main cohort off northeastern Japan.

If we connect the April-hatched to the smaller adult cohort in June-July, we can estimate the life span of male and female *E. pacifica* off northeastern Japan to be 24 months and 28 months, respectively. That the life span of females was longer than that of males is identical with that of the Sanriku population estimated by Endo (1981).

On the other hand, a second smaller peak in copulated females and spawning was recognized in summer-fall (Fig. 3-4). It is speculated that hatching in these seasons may greatly contribute to maintaining the population, although this group could not be clearly defined. That is to say, this group hatching compensates for the decrease of the spring hatching by recruiting adults by the next spring, and also spawns during two springs, together with the spring hatching group.

The life span of *E. pacifica* tends to be longer

(2 years old) in colder regions, such as in the sea of Okhotsk (Ponomareva, 1963) and off Kamchatka / south of the Aleutians (Nemoto, 1957) than in warmer regions (at most 1 year), such as off south California (Brinton, 1976). Larger adults, which are thought to over-winter, occurred mainly in OW and CW but rarely in WW throughout the year. So, it appears to be difficult for *E. pacifica* to prolong their life span in warmer water masses off Japan, as has been observed in other warmer regions (Brinton, 1976).

The average abundance of large adults in OW was significantly higher (*t*-test, $P < 0.001$) than those in CW during August and September, but the latter was significantly higher (*t*-test, $P < 0.001$) than the former during March and April (Fig. 3-3). So, they seem to control their distribution according to the seasonal change of the surface temperature. That is to say, they migrate toward OW in summer to avoid high surface temperatures (> ca. 20℃), which would limit their night ascent and reduce both feeding in the euphotic zone and avoidance from mesopelagic predators (see **Chapter 4**); on the contrary, they migrate toward CW in spring to avoid low temperatures throughout the total water column.

Geographical change in spawning and distribution

Geographical distributional pattern of copulation, spawning and recruitment to larval stage in relation to the water masses in the cylindrical-conical net survey generally agrees with those in the Norpac net survey, because they occurred mainly near the marginal area of the Oyashio Current ($T_{100} = 5$ ℃) throughout the year (Figs. 3-10 and 11). However, copulated females, eggs and larvae were rare or absent throughout the year except in mid fall off southeastern Hokkaido, where extreme cold waters of the Oyashio ($T_{100}<2$℃) dominated (Figs. 3-10-13). Spawning in such extreme cold waters may be unfavorable for the development of eggs and early larvae as shown in laboratory experiments (Ross, 1981; Iguchi and Ikeda, 1994).

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 cylindrical-conical net survey, however, the biomass of phytoplankton shown as the concentration of chlorophyll *a* was lowest off southeastern Hokkaido in fall, where copulated females, eggs and larvae were most abundant like off Sanriku in spring (Figs. 3-9-13). This appears to reflect the second smaller peak in spawning in summer-fall in the wide area of northwestern Pacific by Norpac net survey (Fig. 3-4). 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 used by *E. pacifica* may affect the timing of copulation and spawning season that are closely related to the trophic conditions experienced by this species. On the other hand, active copulation and spawning of *E. pacifica* occurred in OW and CW (Fig. 3-4) or near the marginal area of the Oyashio Current ($T_{100} = 5$℃) throughout the year (Figs. 3-10 and 11). Accordingly, the temperature conditions may be important triggers of copulation and spawning regardless of the season off northeastern Japan.

Results of cylindrical-conical net survey suggest 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 as well as results of Norpac net survey (Figs. 3-13-16). On the other hand, immature stage and small adults existed in all survey areas throughout the year, even 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; see **Chapter 4**) 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, as suggested in the results of Norpac net survey. Migration ability (= swimming speed) of *E. pacifica* is reported to be up to and potentially in excess of 112m h^{-1} from laboratory observations (Torres and Childress, 1983). This implies that the over-wintered population of *E. pacifica* could migrate horizontally 350km 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 the high temperature of the surface layer (Iguchi *et al.,* 1993; see **Chapter 4**) should be considered. For example, around the warm-core ring off Sanriku in July 1995 (SST=23℃ ; St. 10; see **Chapter 4**), the proportion of abundance below 150m depth at night was 10% for small adults and 29% for large adults. However, a deeper distribution of large adults implies the potential for a reduction in the population size, because of forage limitation and predation by mesopelagic and benthic predators as mentioned in the Norpac net survey. 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 fishery-targeted population of *E. pacifica* off Joban in early summer was supplied from the benthopelagic population formed on the continental slope during previous summer and winter. However, most of the 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 (Figs. 3-15 and 16).

Adults were rare off southeastern Hokkaido in spring (Figs. 3-15-17). The average depth of adult stage was about 150 m in spring during the day, which was shallower than in summer (see **Chapter 4**). The relationship between the abundance of adult stage and average temperature from 0 to 150m showed that the abundance higher than 500 inds. m^{-2} occurred in the waters with temperatures between 2.6 and 8.0℃ , but the abundance was low at <1℃ and >9℃ (Fig. 3-19). The environment off southeastern Hokkaido may be suboptimal for *E. pacifica* where temperatures lower than 1℃ dominated throughout the water column, and therefore they may migrate horizontally toward more southern, warmer areas, which is well consistent with the result in the Norpac net survey. Kodama and Izumi (1994) classified the oceanographic patterns off Sanriku into three 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℃) for *E. pacifica* is restricted to the Joban area. The present study corroborates the conclusions by Kodama and Izumi (1994) except that the lower limit for suitable temperatures (5℃) suggested by them is higher than the lower limit of temperatures (about 3℃) 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℃ and T_{100}=5℃ off south Hokkaido in April (Figs 3-15 and 16). 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).

While the *E. pacifica* fishery ground in Sanriku and Joban waters is at its highest abundance in spring, high abundances were also observed off southeastern Hokkaido during summer and fall. It is important to clarify the density and scale of the 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.

Spawning period during the life span

It is suggested that some female *E. pacifica* attain reproductive maturity when they recruit to adult because copulated females occurred among smaller size classes throughout the year off northeastern Japan (Figs. 3-5 and 18), as has been reported in the other warmer areas (Brinton, 1976). If the first spawning age is supposed to be four months after hatching and the non-spawning season is supposed to be during December and March, the spawning period during the life span (28 months) can be estimated to be 18 months, which is considerably longer than that in the other areas (at most 12 months for warmer regions such as off Oregon and southern California).

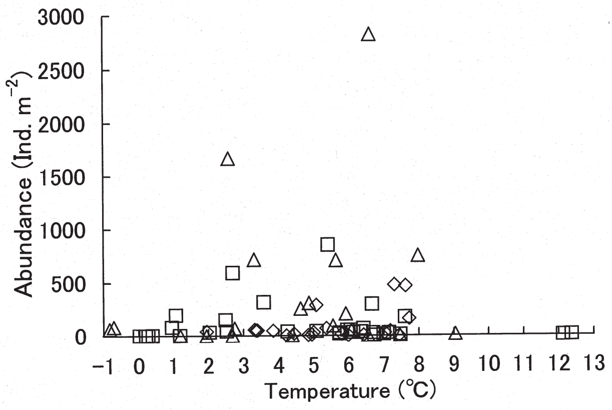

Fig. 3-19. Relationship between the average temperature from 0 to 150m and abundance of adult *Euphausia pacifica* in March (◇) and April (□) 1997 and February 1998 (△).

Chapter 4. Vertical distribution of *Euphausia pacifica*

In northeastern Japan, several studies on the vertical distribution of *Euphausia pacifica* had been carried out (Taniguchi, 1969; Endo, 1981; and Terazaki *et al.,* 1986), but these have been done only at a few fixed stations and the samples are limited seasonally from spring to early summer. Furthermore, the relationship between the vertical distribution and water masses has not been examined until now.

In this chapter, seasonal variations of the vertical distribution of *E. pacifica* were investigated in the coastal and offshore waters off northeastern Japan. At first, seasonal variations of the distribution of pelagic and benthopelagic *E. pacifica* were investigated along the coastal waters off Sanriku using ORI and beam-trawl net samples, and their trophic significance in the coastal water ecosystem off Sanriku is discussed in light of the predator-prey relationships. Secondly, seasonal variations of the vertical distribution of each developmental stage of *E. pacifica* were investigated in the offshore waters off northeastern Japan using MOCNESS-I net samples, and physical and biological factors which determine their vertical distribution of *E. pacifica* were examined.

Materials and Methods

Distribution of pelagic and benthopelagic *E. pacifica* in the Sanriku waters

Six surveys were carried out on the transect line at 50m (St. 1, 10), 100m (St. 2, 9), 150m (St. 3, 8), 200m (St. 4, 7) and 300m (St. 5, 6) isobaths in the vicinity of Kinkazan Island in Miyagi Prefecture (38° 22' N, 141° 32.5' -141° 58'E) from April 1993 to February 1994 on R. V. *Wakataka-maru,* Tohoku National Fisheries Research Institute, Fisheries Research Agency (Fig. 4-1). Sts. 1-5 were surveyed during daytime and Sts. 6-10 were surveyed at night. Water temperatures and salinities were measured by CTD (Neil-Brown) and sea water samples in 6-13 layers were collected at each station using a bucket for the surface sample, and Niskin sampler to measure the concentration of chlorophyll *a*.

ORI net (net mouth diameter: 1.6m; mesh size: 0.33mm; Omori, 1965) was double-obliquely towed from 5m above the sea bed to the surface at 2 knot of the ship speed to collect the pelagic *E. pacifica.* A wireless net recorder (CN-24: FURUNO) was attached on the bridle 2.5m ahead of the mouth of ORI net to monitor the net depth at the bridge. Bongo net (net mouth diameter: 0.7m; mesh size: 0.34mm; McGowan and Brown, 1966) was substituted at Sts. 3-10 in December because of breakage of the ORI net. Beam-trawl net (height: 1m; width: 2m; cod end mesh size: 3mm; no closing mechanism; Nakamura, 1991) was trawled on the sea bed during 10minutes at 1.7 knot of the ship speed to collect the benthopelagic *E. pacifica.*

Samples were preserved with 5% formalin seawater immediately after collection. *E. pacifica* were sorted into immature and adult stages and the lengths (from the tip of the rostrum to the distal end of the telson) were measured to the nearest 0.1mm. The abundance of immature and adult stages for the ORI net samples was calculated using the volume of water passed through the net by a flowmeter (Rigosha) mounted in the mouth of net. On the other hand, the abundance of immature and adult stages for the beam-trawl net samples was calculated using the trawled area on the assumption that all the animals on the area were caught.

Distribution in the offshore waters of northeastern Japan

Samples were collected at stations from 41°30' N to 36°30' N along the 143°E line in late July 1995, mid-April and early September 1998 and late November 1999 on the R. V. *Wakataka-maru*, Tohoku National Fisheries Research Institute, Fisheries Research Agency (Fig. 4-2; Tables 4-1-4). Other samples were collected at about 200m isobath in mid-April and early September 1998. A MOCNESS-I with nets having a mouth opening of 1.4m^2 (about 1m^2 toward the towing orientation) and 0.33mm mesh aperture (Wiebe *et al.*, 1985) was obliquely towed and nets were sequentially opened and closed to sample five stratified layers (0-50, 50-150, 150-250, 250-500, 500-1,000m) in late July 1995 and seven stratified layers (0-25, 25-50, 50-150, 150-250, 250-400, 400-600, 600-1,000m) in mid-April and early September 1998 and late November 1999. Five stratified layers (0-25, 25-50, 50-100, 100-150, 150-170 [or 150-220] m) were sampled for the coastal stations in mid-April and early September 1998. The samples were preserved in 5% buffered formalin seawater immediately after collection. Water temperatures and salinities were measured by CTD (SBE) attached to MOCNESS-I and seawater samples in 6 layers (0, 10, 20, 30, 50, 75m) were collected in each station using a bucket and Niskin sampler to measure the concentration of chlorophyll *a* at each station except late July 1995.

E. pacifica were sorted into its developmental stages except for the nauplius and metanauplius stages, which would pass through nets. 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 0.1mm. The abundance of each stage was calculated using the volume of water that passed through the net by a flowmeter attached to MOCNESS-I.

The median depth and 80% range of abundance from the median depth ($D_{80\%}$) for each developmental stage were calculated according to Pennak (1943).

Results

Distribution of pelagic and benthopelagic *E. pacifica* in the Sanriku coastal waters

The coastal branch of the Oyashio Current with low temperatures and salinities came close to the shore and water with 7-8℃ dominated in the total water column at 50-150m isobaths in April (Fig. 4-3). Surface temperature rose after April and attained 18-22℃ in August, but decreased gradually after August. Water with 8℃ dominated in the surface layer at all stations in February. A ther-

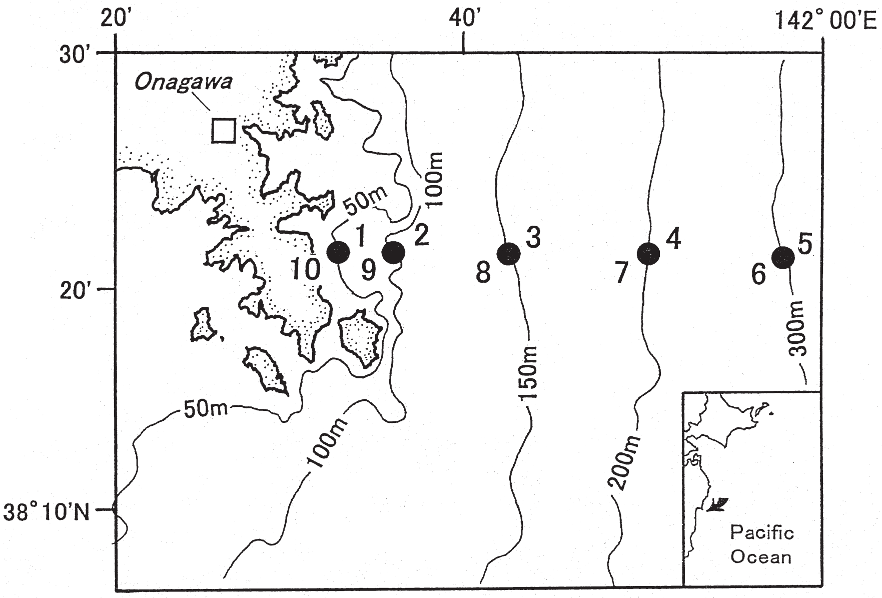

Fig. 4-1. Sampling stations off Onagawa, Miyagi Prefecture from April 1993 to February 1994. Stations. 1-5 were sampled during the day and stations. 6-10 at night.

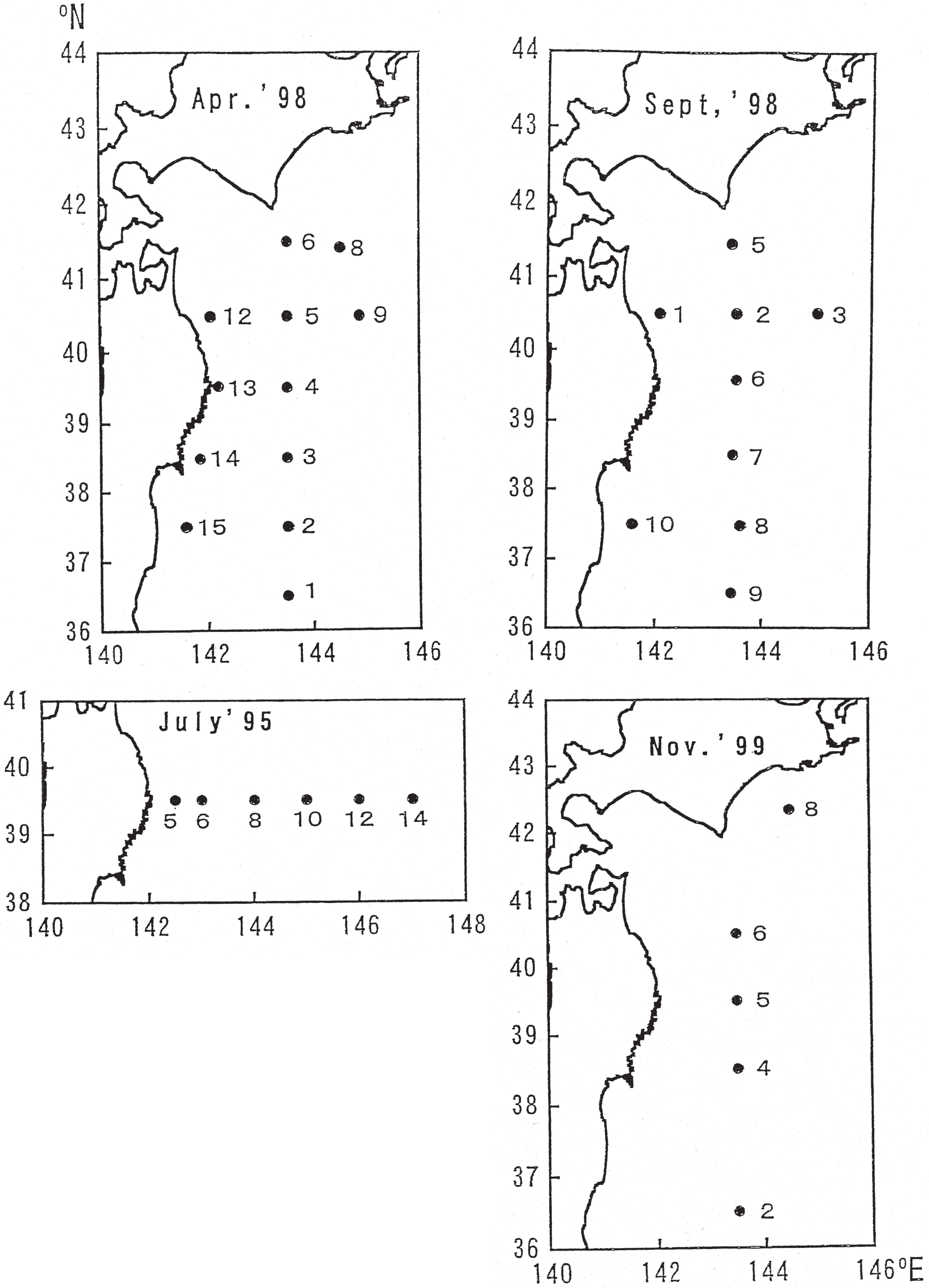

Fig. 4-2. Location of sampling stations using MOCNESS-I in Tohoku waters. Stations are numbered.

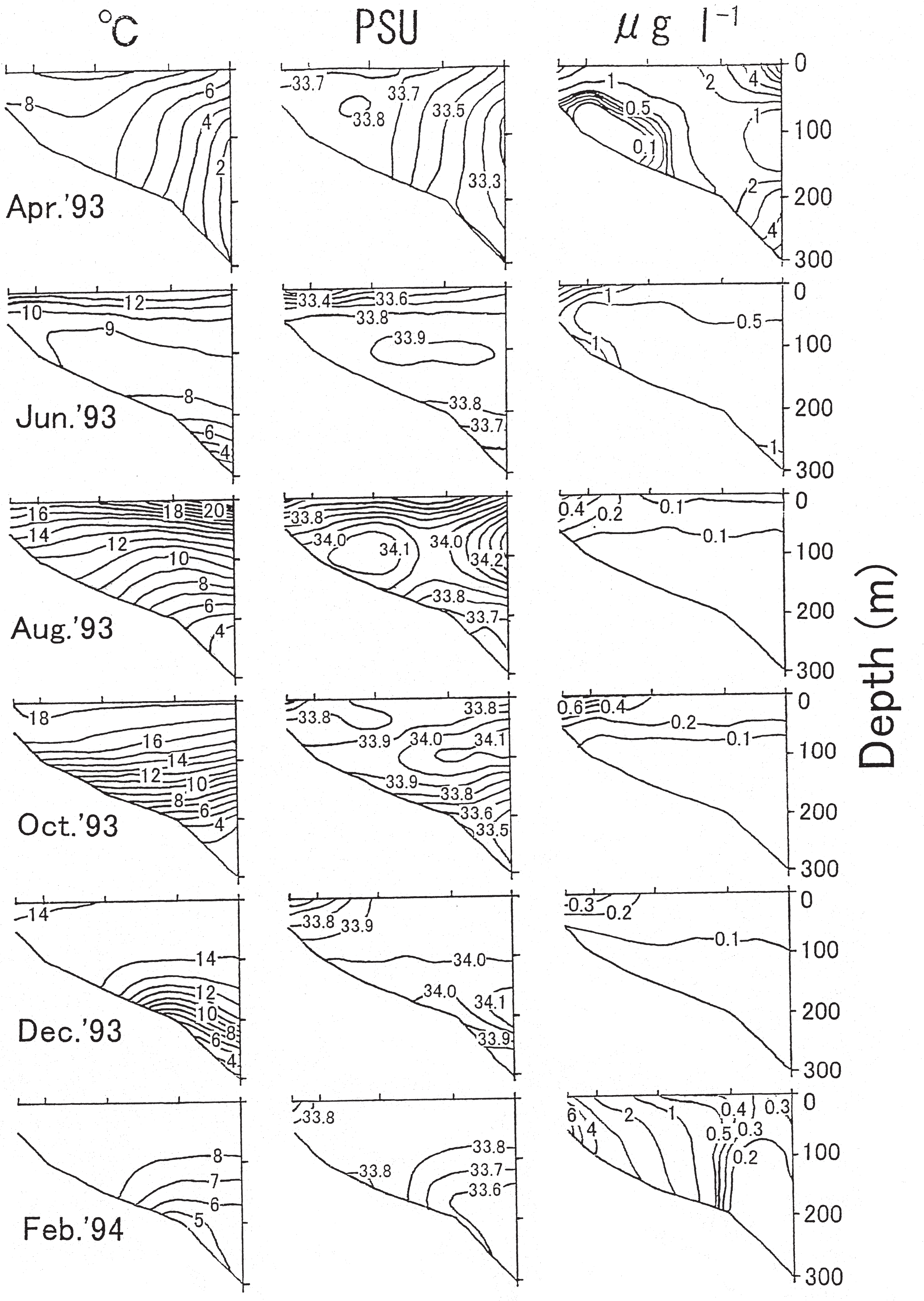

Fig. 4-3. Vertical profiles of temperature (℃), salinity (PSU) and chlorophyll *a* (μ g l^{-1}) off Onagawa from April 1993 to February 1994.

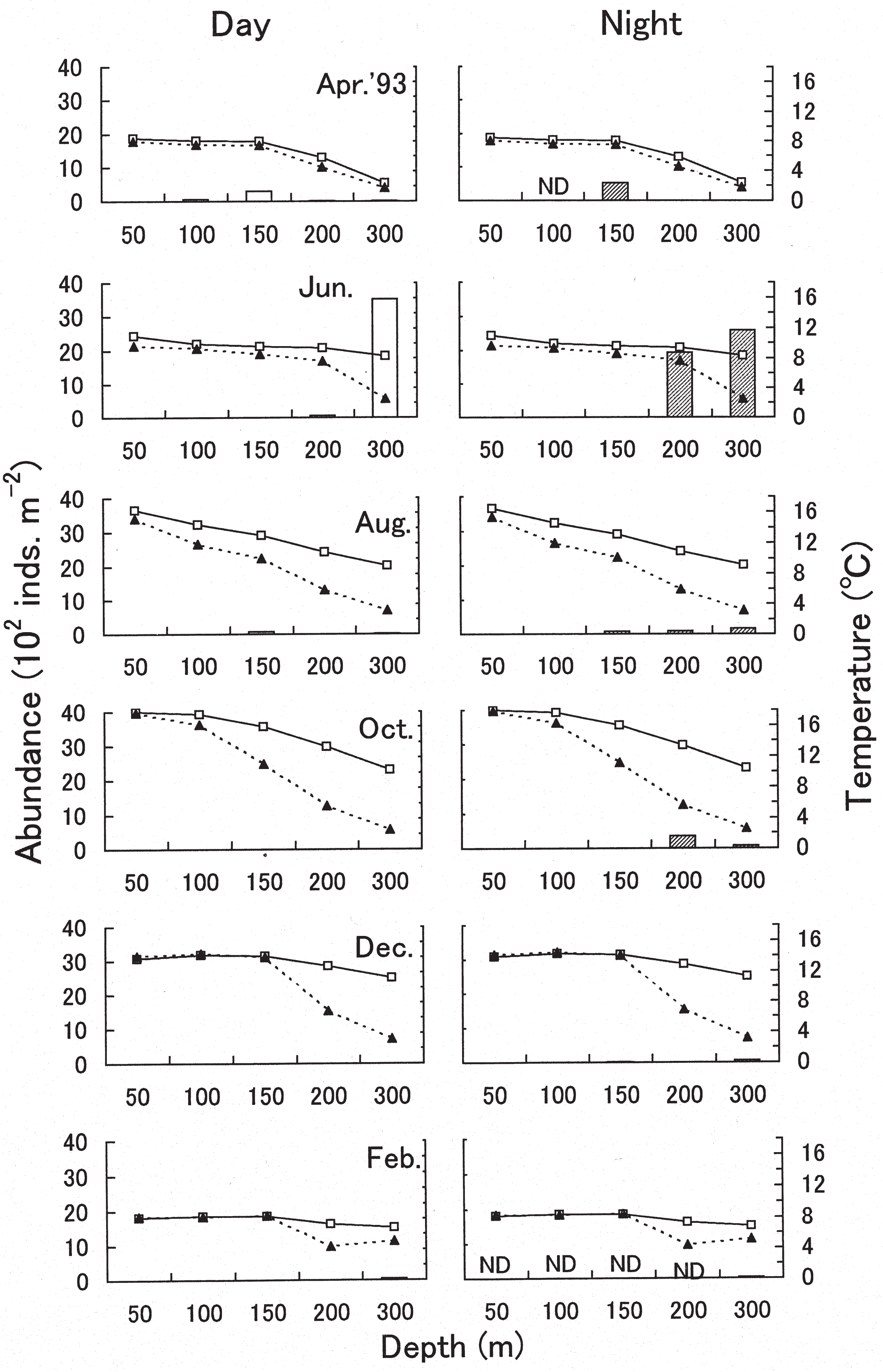

Fig. 4-4. Seasonal changes in the abundance of immature *Euphausia pacifica* sampled by ORI net. Solid and broken lines show the average temperature over the water column from the sea surface to about 5 m above the sea bed and temperature of about 5 m above the sea bed, respectively. ND = no data.

Table 4-1. Locations of stations, times of samplings and sampling depth using MOCNESS-I in Tohoku waters during 17-23 April 1998

St.	Approx. tow location	Date	Depth (m), when towing commenced	Tow time	Tow range (m)
1	36°33'N/143°32'E	17	6,504	7:29–8:58(D^{*1})	0–23, 23–50, 50–152, 152–252, 252–401, 401–599, 599–961
1	36°35'N/143°30'E	17	6,535	1:13–2:36(N^{*2})	0–25, 25–50, 50–148, 148–247, 247–401, 401–596, 596–973
2	37°37'N/143°30'E	17	4,201	16:20–17:51(D)	0–17, 17–47, 47–147, 147–246, 246–396, 396–599, 599–987
3	38°33'N/143°25'E	18	2,136	7:31–9:07(D)	0–23, 23–48, 48–148, 148–248, 248–400, 400–599, 599–984
3	38°34'N/143°32'E	18	2,791	1:06–2:16(N)	0–21, 21–49, 49–147, 147–248, 248–401, 401–600, 600–1,000
4	39°35'N/143°27'E	18	2,624	16:05–17:31(D)	0–22, 22–47, 47–146, 146–247, 247–399, 399–600, 600–994
5	40°28'N/143°29'E	19	2,217	7:09–8:26(D)	0–22, 22–47, 47–146, 146–249, 249–400, 400–600, 600–992
5	40°25'N/143°29'E	19	2,226	1:25–3:43(N–DWN^{*3})	0–22, 22–47, 47–146, 146–248, 248–399, 399–601, 601–980
6	41°26'N/143°30'E	19	1,804	15:31–16:46(D)	0–21, 21–47, 47–149, 149–247, 247–395, 395–596, 596–1,000
6	41°27'N/143°31'E	19	1,717	20:30–22:13(N)	0–21, 21–49, 49–149, 149–248, 248–400, 400–600, 600–993
8	41°25'N/144°37'E	20	4,182	10:58–12:41(D)	0–22, 22–48, 48–151, 151–249, 249–401, 401–597, 597–992
8	41°26'N/144°35'E	20	4,383	21:15–22:52(N)	0–25, 25–48, 48–149, 149–249, 249–400, 400–599, 599–993
9	40°30'N/144°55'E	21	5,997	6:52–8:11(D)	0–25, 25–45, 45–146, 146–247, 247–399, 399–596, 596–991
12	40°30'N/142°03'E	21	214	20:24–20:35(N)	0–24, 24–50, 50–97, 97–147, 147–169
13	39°32'N/142°12'E	22	221	2:07–2:18(N)	0–24, 24–50, 50–95, 95–146, 146–166
14	38°31'N/141°51'E	22	207	9:07–9:20(D)	0–25, 25–50, 50–97, 97–148, 148–165
14	38°31'N/141°51'E	22	204	19:50–20:05(N)	0–25, 25–51, 51–98, 98–149, 149–167
15	37°30'N/141°34'E	23	203	6:20–6:34(D)	0–25, 25–51, 51–99, 99–148, 148–172
15	37°30'N/141°35'E	23	204	1:58–2:10(N)	0–23, 23–48, 48–97, 97–146, 146–172

^{*1}Day, ^{*2}Night, ^{*3}Dawn

Table 4-2. Locations of stations, times of samplings and sampling depth using MOCNESS-I in Tohoku waters during 22-26 July 1995

St.	Approx. tow location	Date	Depth (m), when towing commenced	Tow time	Tow range (m)
5	39°31'N/142°34'E	22	1,002	7:28–8:14(D^{*1})	0–47, 47–133, 133–236, 236–499, 499–902
5	39°31'N/142°34'E	23	1,020	0:42–1:24(N^{*2})	0–47, 47–147, 147–248, 248–499, 499–899
6	39°33'N/143°03'E	22	1,718	17:07–17:53(D)	0–47, 47–146, 146–245, 245–498, 498–995
6	39°29'N/143°02'E	25	1,733	1:59–2:40(N–DWN^{*3})	0–48, 48–149, 149–248, 248–494, 494–1,000
8	39°30'N/144°08'E	23	5,626	21:44–22:39(N)	0–47, 47–150, 150–250, 250–502, 502–965
10	39°29'N/145°06'E	25	5,508	10:43–11:42(D)	0–52, 52–153, 153–253, 253–502, 502–994
10	39°26'N/145°05'E	28	5,519	0:07–1:18(N)	0–49, 49–145, 145–248, 248–500, 500–999
12	39°30'N/146°07'E	26	5,191	5:34–6:10(D)	0–50, 50–153, 153–248, 248–500, 500–1,000
12	39°29'N/146°05'E	26	5,219	1:05–2:00(N)	0–47, 47–145, 145–246, 246–497, 497–996
14	39°28'N/147°02'E	27	5,211	10:12–10:50(D)	0–49, 49–152, 152–250, 250–502, 502–996
14	39°30'N/146°58'E	26	5,191	22:33–23271(N)	0–49, 49–152, 152–250, 250–502, 502–996

^{*1}Day, ^{*2}Night, ^{*3}Dawn

Table 4-3. Locations of stations, times of samplings and sampling depth using MOCNESS-I in Tohoku waters during 1-8 September 1998

St.	Approx. tow location	Date	Depth (m), when towing commenced	Tow time	Tow range (m)
1	40°30'N/142°05'E	1	264	15:56–16:13(D ^{*1})	0–17, 17–23, 23–47, 47–97, 97–150, 150–221
2	40°33'N/143°43'E	4	2,455	8:36–11:56(D)	0–26, 26–51, 51–152, 152–252, 252–401, 401–601, 601–995
2	40°33'N/143°39'E	2	2,354	2:06–4:04(N ^{*2}–DWN^{*3})	0–23, 23–46, 46–151, 151–249, 249–388, 388–575, 575–1,000
3	40°26'N/144°57'E	3	5,977	15:13–17:42(D)	0–26, 26–53, 53–153, 153–254, 254–385, 385–603, 603–1,001
5	41°24'N/143°22'E	3	1,708	12:16–14:24(D)	0–26, 26–53, 53–154, 154–253, 253–402, 402–602, 602–1,042
5	41°24'N/143°21'E	3	1,638	20:50–23:37(N)	0–24, 24–51, 51–148, 148–249, 249–401, 401–602, 602–994
6	39°36'N/143°32'E	4	2,671	20:53–23:25(N)	0–25, 25–49, 49–149, 149–249, 249–400, 400–600, 600–995
7	38°30'N/143°25'E	5	2,745	14:22–16:16(D)	0–24, 24–49, 49–153, 153–254, 254–401, 401–595, 595–1,007
7	38°29'N/143°25'E	5	2,773	20:55–23:12(N)	0–25, 25–50, 50–152, 152–251, 251–400, 400–598, 598–997
8	37°29'N/143°34'E	6	6,073	8:11–10:03(D)	0–25, 25–50, 50–151, 151–252, 252–399, 399–599, 599–1,000
9	36°30'N/143°23'E	7	6,618	7:38–9:21(D)	0–25, 25–51, 51–149, 149–251, 251–398, 398–600, 600–996
9	36°30'N/143°23'E	6	6,669	20:39–22:39(N)	0–26, 26–52, 52–151, 151–250, 250–400, 400–599, 599–988
10	37°28'N/141°34'E	8	205	6:24–6:49(D)	0–25, 25–51, 51–98, 98–149, 149–171
10	37°29'N/141°34'E	7	199	19:15–19:29(DSK ^{*4})	0–24, 24–50, 50–97, 97–147, 147–169

^{*1}Day, ^{*2}Night, ^{*3}Dawn, ^{*4}Dusk

Table 4-4. Locations of stations, times of samplings and sampling depth using MOCNESS-I in Tohoku waters during 26-30 November 1999

St.	Approx. tow location	Date	Depth (m), when towing commenced	Tow time	Tow range (m)
2	36°26'N/143°28'E	26	6,468	8:38–10:51(D ^{*1})	0–24, 24–52, 52–151, 151–251, 251–401, 401–602, 602–1,000
4	38°37'N/143°38'E	27	3,177	22:33–0:01(N ^{*2})	0–25, 25–51, 51–150, 150–256, 256–394, 394–588, 588–757
5	39°20'N/143°25'E	28	2,832	8:48–11:31(D)	0–51, 51–151, 151–251, 251–401, 401–602, 602–995
6	40°23'N/143°40'E	29	2,448	22:02–0:03(N)	0–24, 24–51, 51–152, 152–250, 250–400, 400–600
8	42°23'N/144°50'E	30	1,723	17:27–19:47(N)	0–24, 24–50, 50–150, 150–250, 250–401, 401–599, 599–996

^{*1}Day, ^{*2}Night

mocline developed near the surface in August, in 100-200m depth in October and in 200-250m depth in December over the survey area. Chlorophyll *a* concentration was higher than 3 μ g l^{-1} in the surface layer at 50m isobath and in the surface and benthic layers at 300m isobath, but decreased gradually over the survey area from April to December. In February, higher chlorophyll *a* concentration than 1 μg l^{-1} dominated over the total water column at 50-150m isobaths and a concentration higher than 6 μ g l^{-1} occurred in the benthic layer at 50m isobath.

Pelagic immature stage collected by the ORI net occurred mainly at 150m isobath in April (Fig. 4-4). It was most abundant at 300m isobath in June. It occurred mainly at 200 and 300m isobaths after June, but rarely occurred over the survey area in December and February. Benthopelagic immature stage collected by the beam-trawl net was rarely observed over the survey area in April, but was most abundant during daytime at 300m isobath in June (Fig. 4-5). It occurred mainly at 200 and 300m isobaths after June, but rarely occurred over the survey area in December and February.

Pelagic adults were most abundant at 100m isobath during daytime and 150m isobath at night in April (Fig. 4-6). However it occurred mainly at 200 and 300m isobaths after April. Benthopelagic adults were rarely observed over the survey area in April, but were most abundant during daytime at 300m isobath in June (Fig. 4-7). They occurred mainly at 200 and 300m isobaths after June, but rarely occurred over the survey area in February.

At the coastal stations (100 and 150m isobaths), 15-19mm size classes were dominant to the total abundance both in the pelagic and benthopelagic *E. pacifica* in April (Fig. 4-8). However, <10mm size classes were dominant both in pelagic and benthopelagic *E. pacifica* after June.

At the offshore stations (200 and 300m isobaths), 12-18mm size classes during daytime and 15-21mm size classes at night were dominant in the pelagic *E. pacifica* in April (Fig. 4-9). 15-19mm size classes during daytime and 15-21mm size classes at night were dominant in the benthopelagic *E. pacifica* in April. In June, <10mm size classes occurred abundantly both in pelagic and benthopelagic *E. pacifica* but 15-19mm size classes were most abundant during daytime in the benthopelagic *E. pacifica.* >15mm size classes gradually decreased in abundance both in the pelagic and benthopelagic *E. pacifica* after August. Then, < 10mm size classes also decreased after December.

Distribution of *E. pacifica* off northeastern Japan in April

Sts. 1 and 2 were located near the warm-core ring centering at 37°10' N, 143°40' –141°58'E (Kato *et al.,* 2000). Surface temperature of these stations was 14.5-17.1℃ (Figs. 4-10-12). The first branch of the Oyashio Current came close to the coastal areas at 38°30' –39°N and 40°N. The thermal front of the Oyashio Current occurred between St. 2 and St. 3. Water with about 1℃ occurred at about 100m depth at Sts. 4, 5, 6, 8 and 9 and lower temperatures than 2 ℃ were dominant from the surface to 100 or 200m at Sts. 6, 8 and 9. Coastal stations (Sts. 12-15) were located near the marginal area of the first branch of the Oyashio Current, and the surface temperatures of these stations were 6.2–8.5℃. The chlorophyll *a* concentration in the surface layer was higher than 1 μg l^{-1} at all offshore stations except St. 9, especially 0-10m layers at St. 5 and 20-30m layers at St. 6 showed a concentration higher than 6 μg l^{-1}. The chlorophyll *a* concentration in the surface layer was higher than 1 μg l^{-1} at Sts. 13 and 15 but lower than 0.7 μg l^{-1} at Sts. 12 and 14.

Eggs were abundant at Sts. 1, 2, 3 and 5 but scarce at Sts. 6, 8 and 9 and at each coastal station except St. 12 (Figs. 4-11 and 12). Calyptopis was abundant at Sts. 1 and 2 but was scarce at other stations. Furcilia was abundant at Sts. 1 and 12-14, but was scarce at the offshore stations in waters colder than 5℃ isotherm at 100m depth. Immature stage occurred mainly at coastal stations but was scarce at offshore stations. Adults occurred over the survey area including stations in waters colder than 2 ℃ isotherm at 100m depth and were abundant at Sts. 6, 8, 12-15 at night. The abundance of adults collected at night was higher than that collected during daytime for each station except St. 5; especially the abundance collected at night was 452-fold higher than that collected during daytime at St. 14.

In the offshore area, median depth of eggs was shallower than 50m during day and night at each

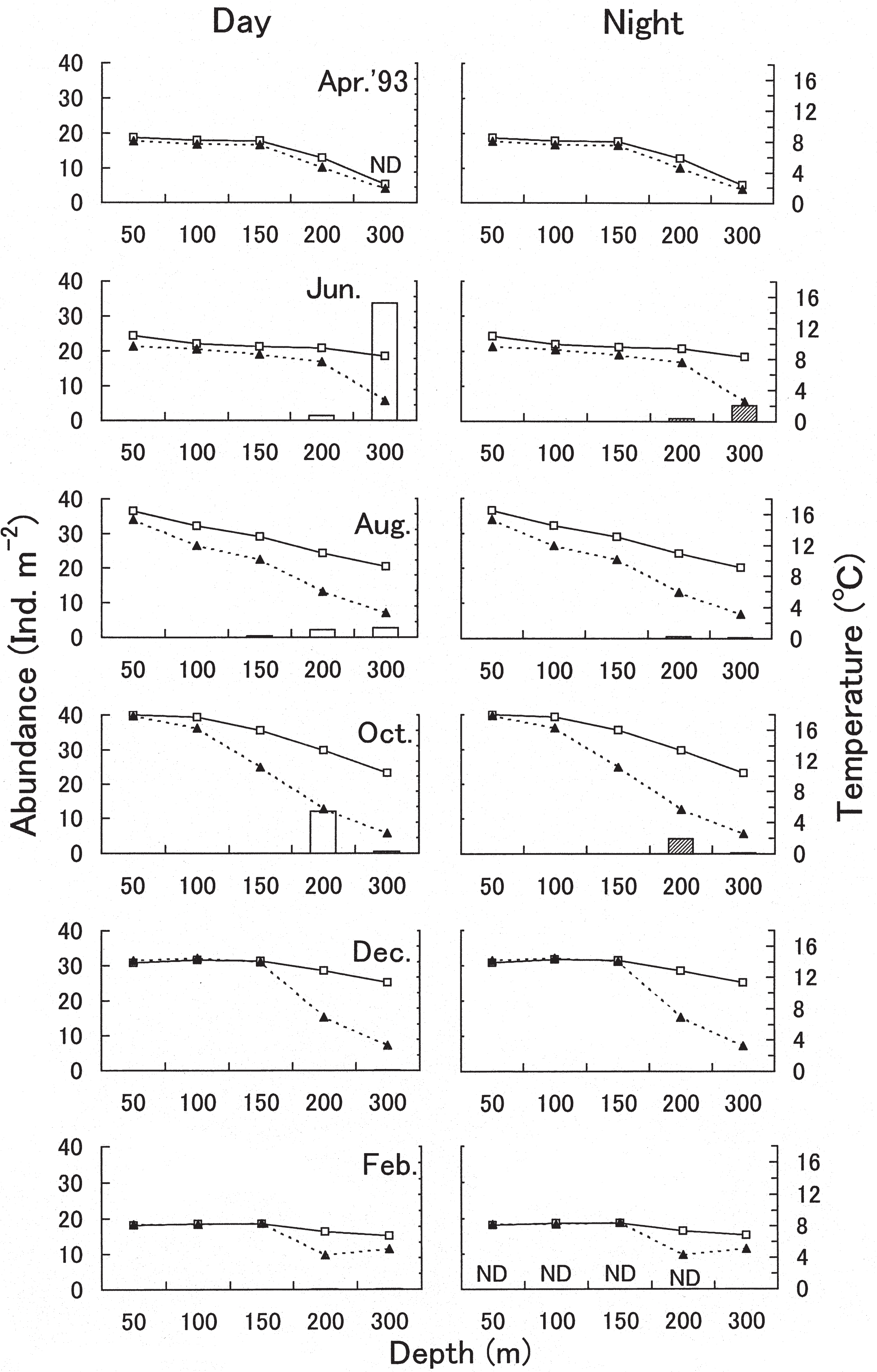

Fig. 4-5. Seasonal changes in the abundance of immature *Euphausia pacifica* sampled by beam-trawl nets. Symbols as in Fig. 4-4.

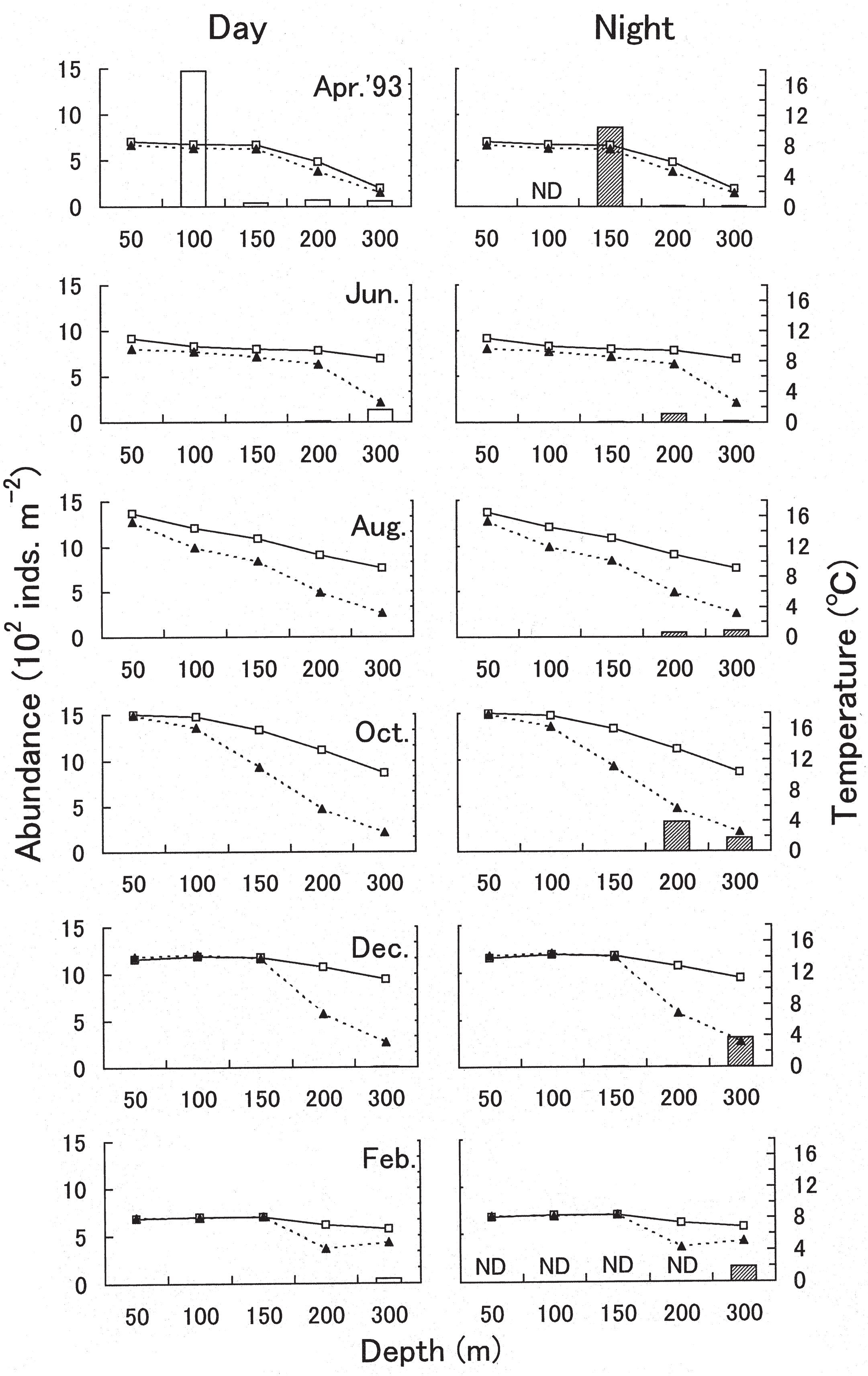

Fig. 4-6. Seasonal changes in the abundance of adult *Euphausia pacifica* sampled by ORI net. Symbols as in Fig. 4-4.

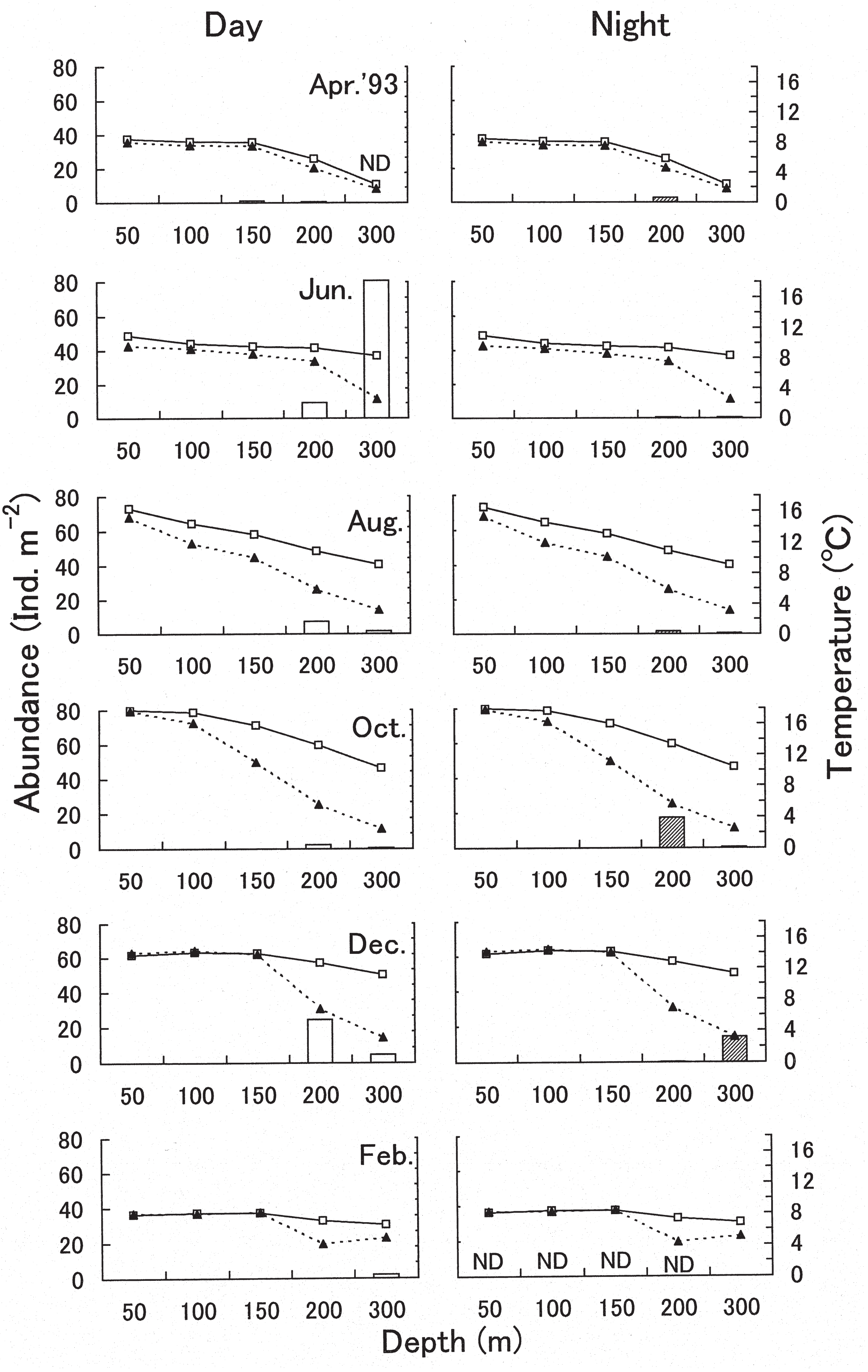

Fig. 4-7. Seasonal changes in the abundance of adult *Euphausia pacifica* sampled by beam-trawl nets. Symbols as in Fig. 4-4.

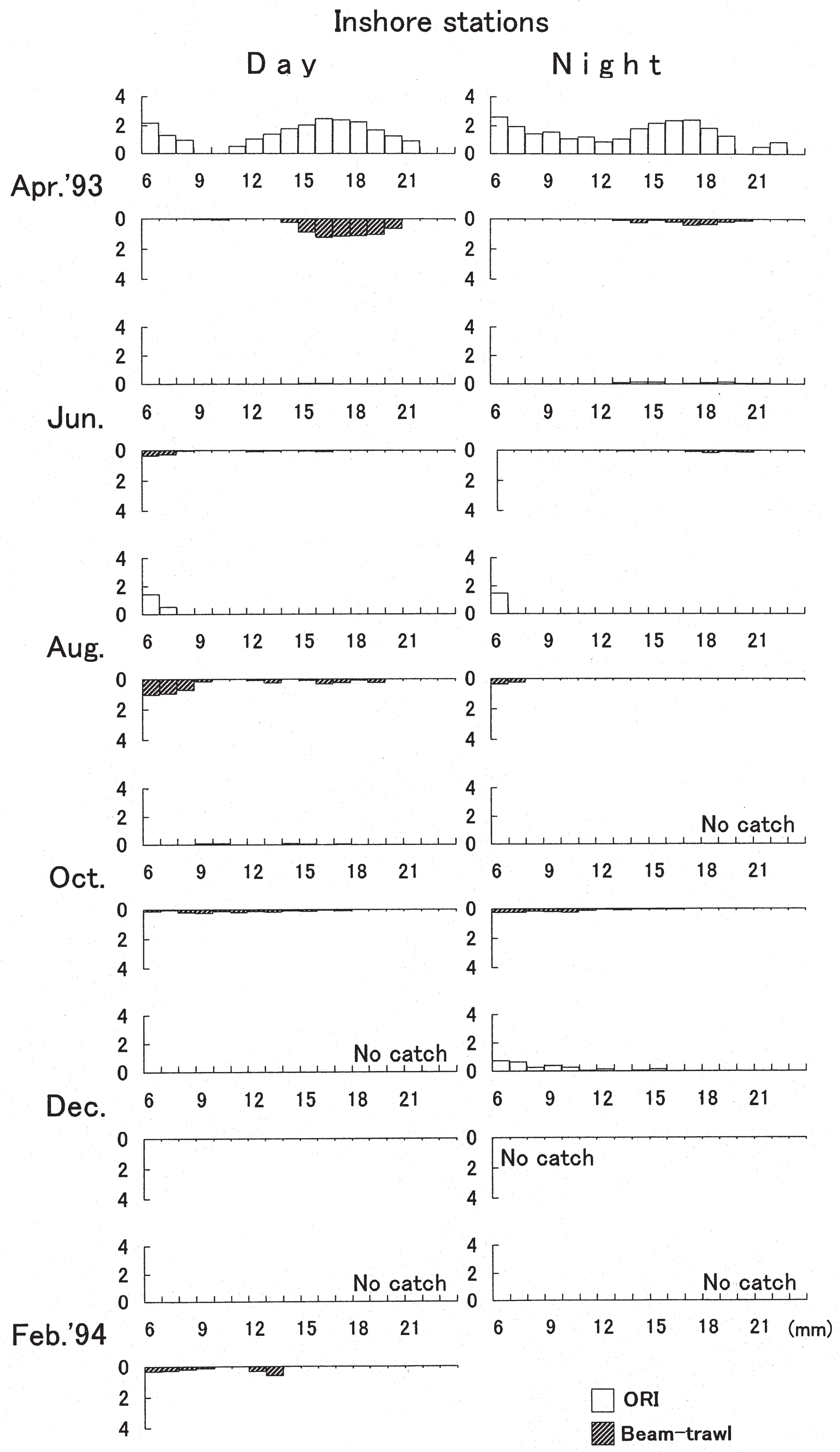

Fig. 4-8. Length frequency distribution of *Euphausia pacifica* at inshore stations (100m and 150m depth). Upward and downward bars show the abundance sampled by ORI and beam-trawl nets, respectively. Vertical bar shows abundance (ORI collection: log (no. m^{-2}+1), Beam-trawl: log (10^2 no. m^{-2}+1)).

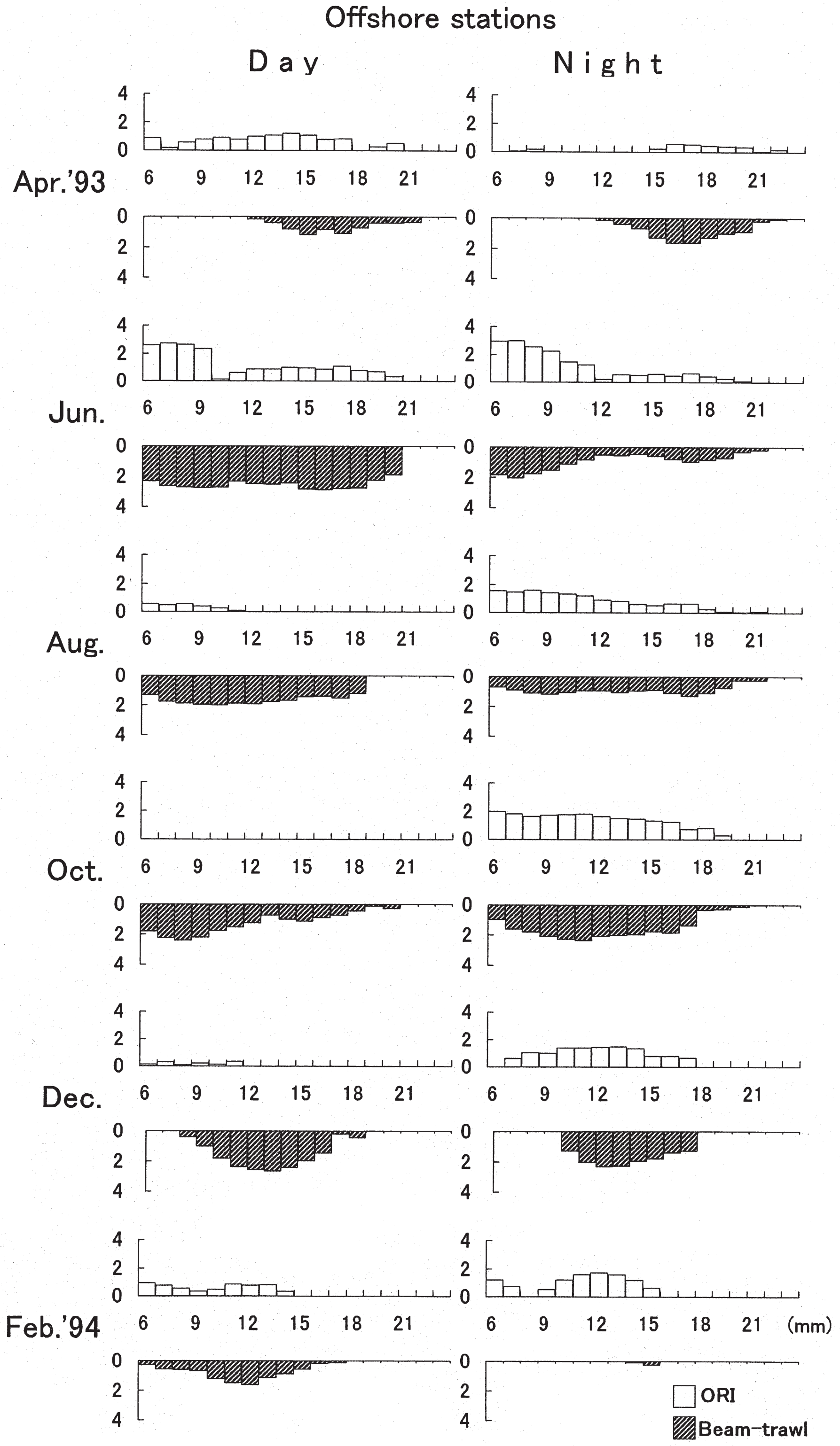

Fig. 4-9. Length frequency distribution of *Euphausia pacifica* at the offshore stations (200m and 300m depth). Upward and downward bars show abundances sampled by ORI and beam-trawl nets, respectively. Vertical bar shows abundance (ORI collection: log (no. m^{-2}+1), Beam-trawl: log (10^{20} no. m^{-2}+1)).

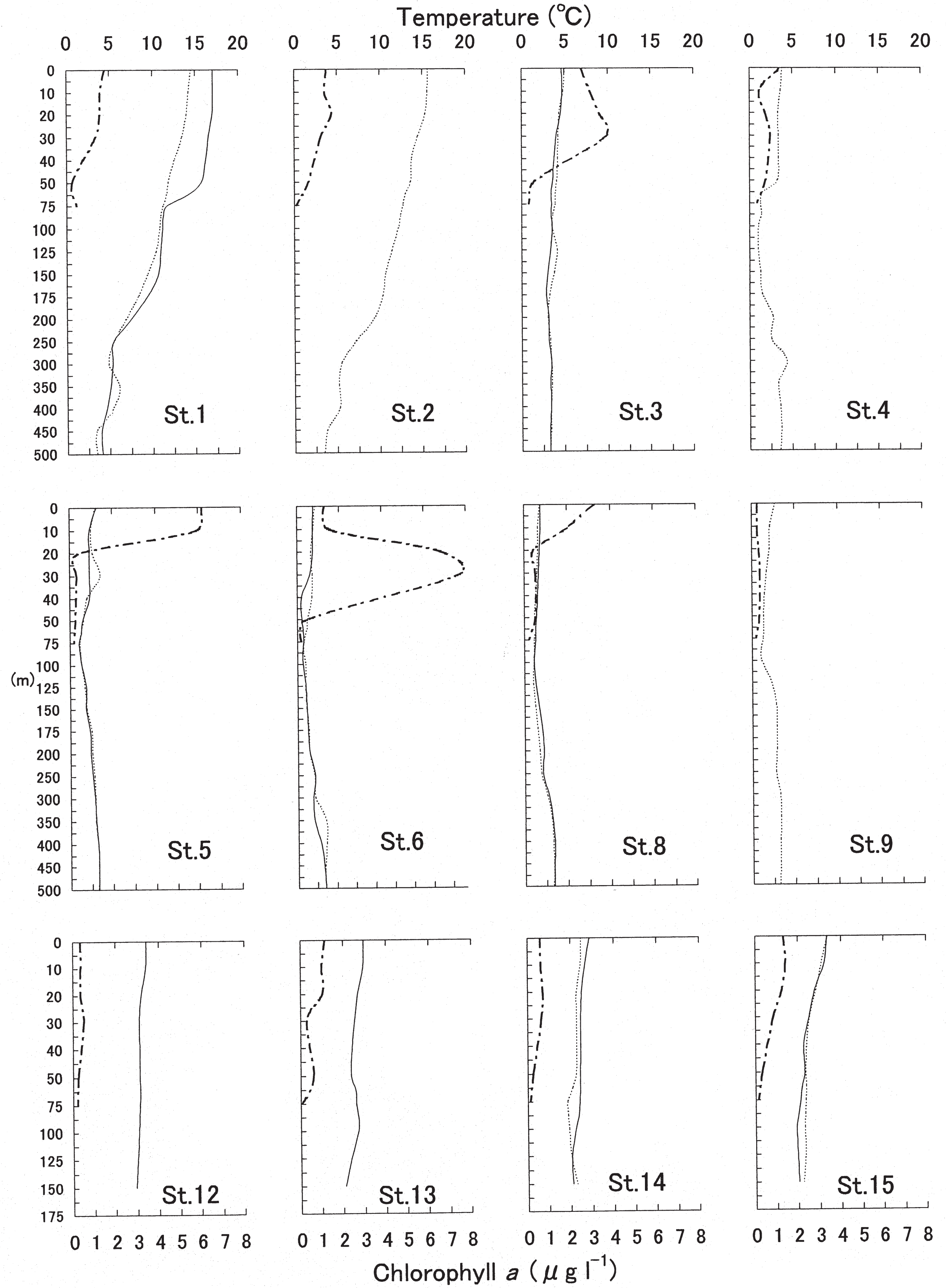

Fig. 4-10. Vertical profiles of temperature and chlorophyll *a* at each station in April 1998. Temperatures obtained from CTD in MOCNESS-I. Chained, solid and broken lines show chlorophyll *a*, night (twilight) temperature and day temperature, respectively.

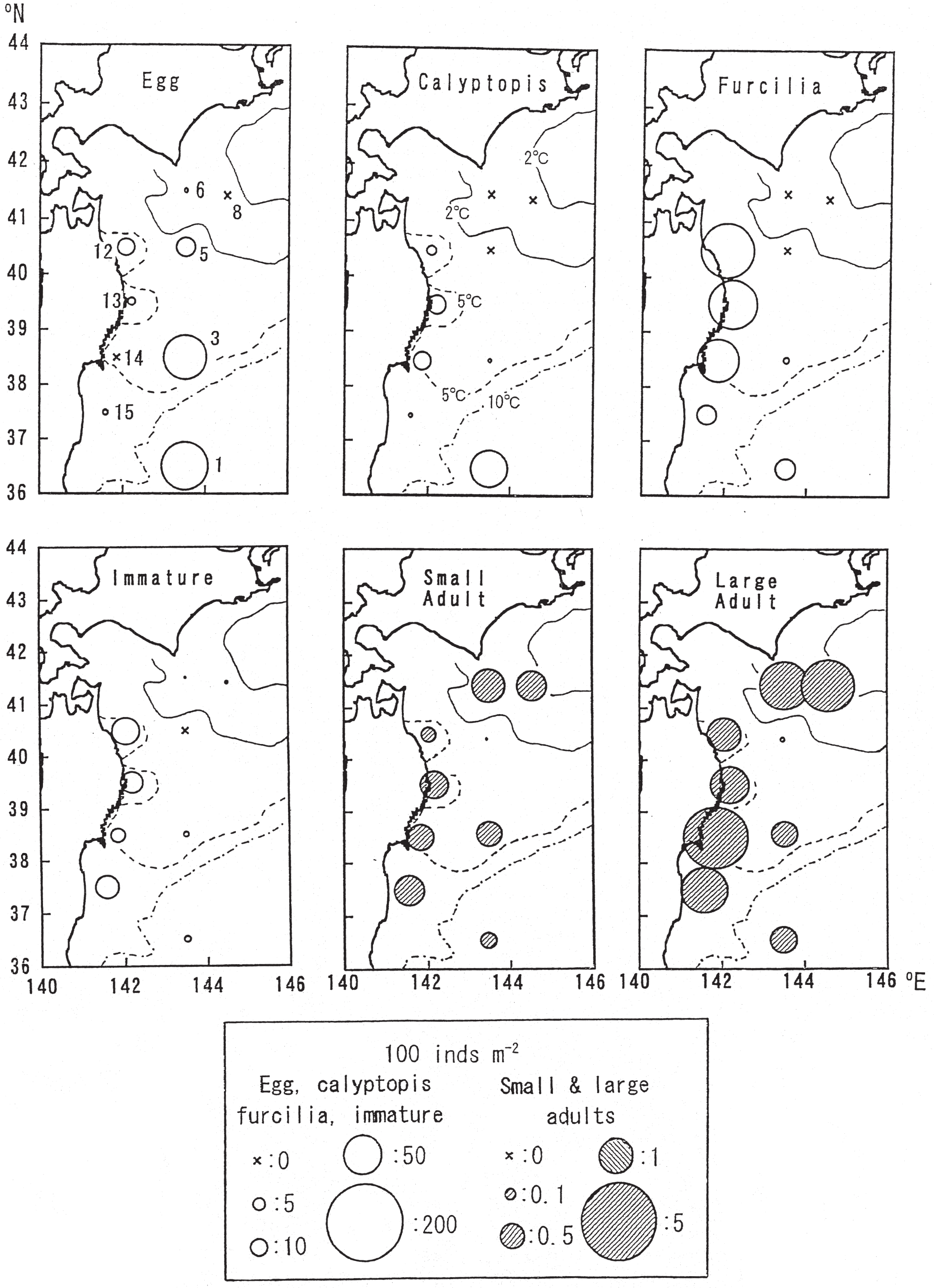

Fig. 4-11. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at night (except for St. 5 at twilight time) and temperature gradients at 100m depth in April, 1998. The scales as in legend. Stations are numbered in "egg".

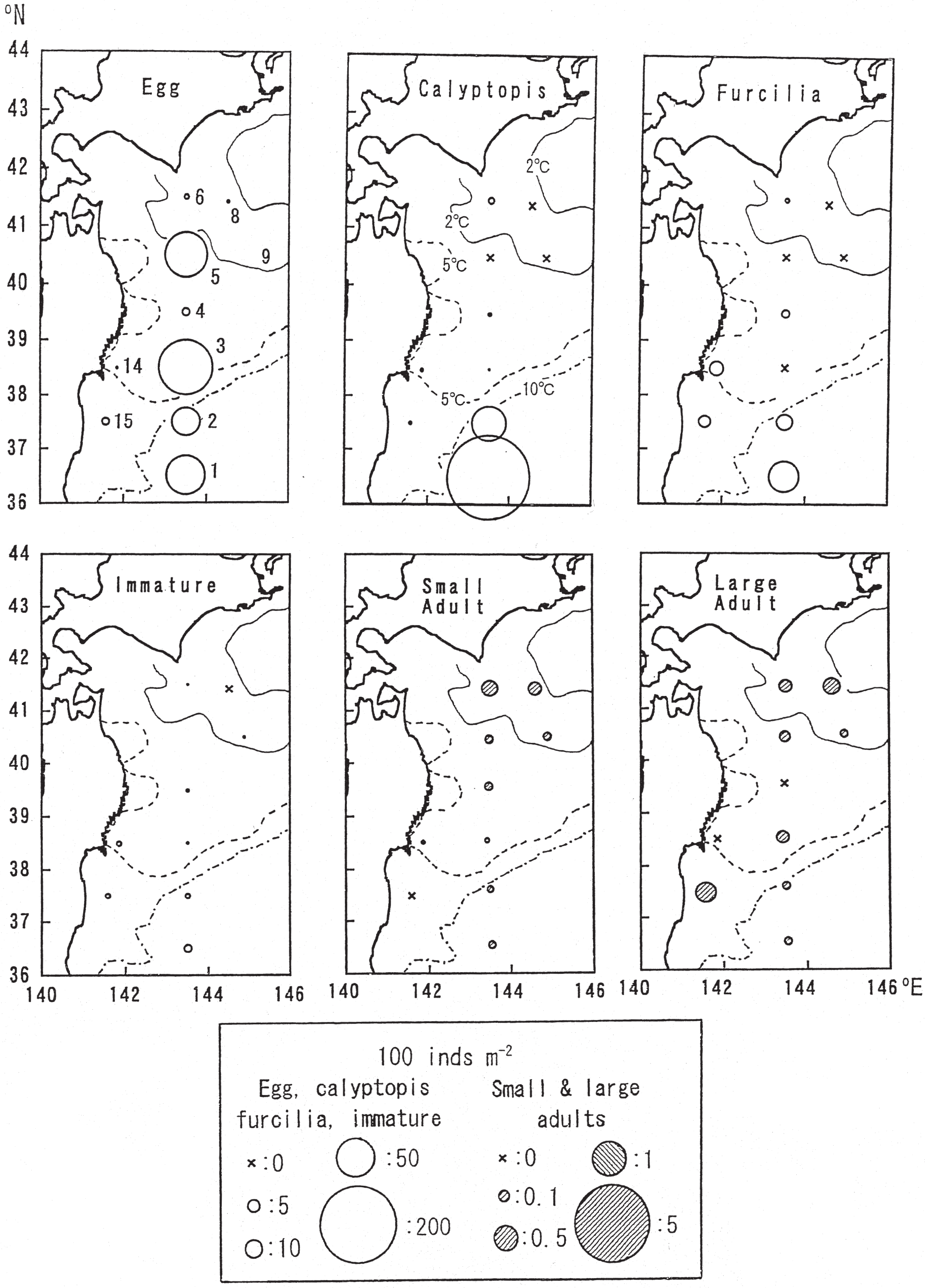

Fig. 4-12. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at day and temperature gradients at 100m depth in April 1998. The scales as in legend. Stations are numbered in "egg".

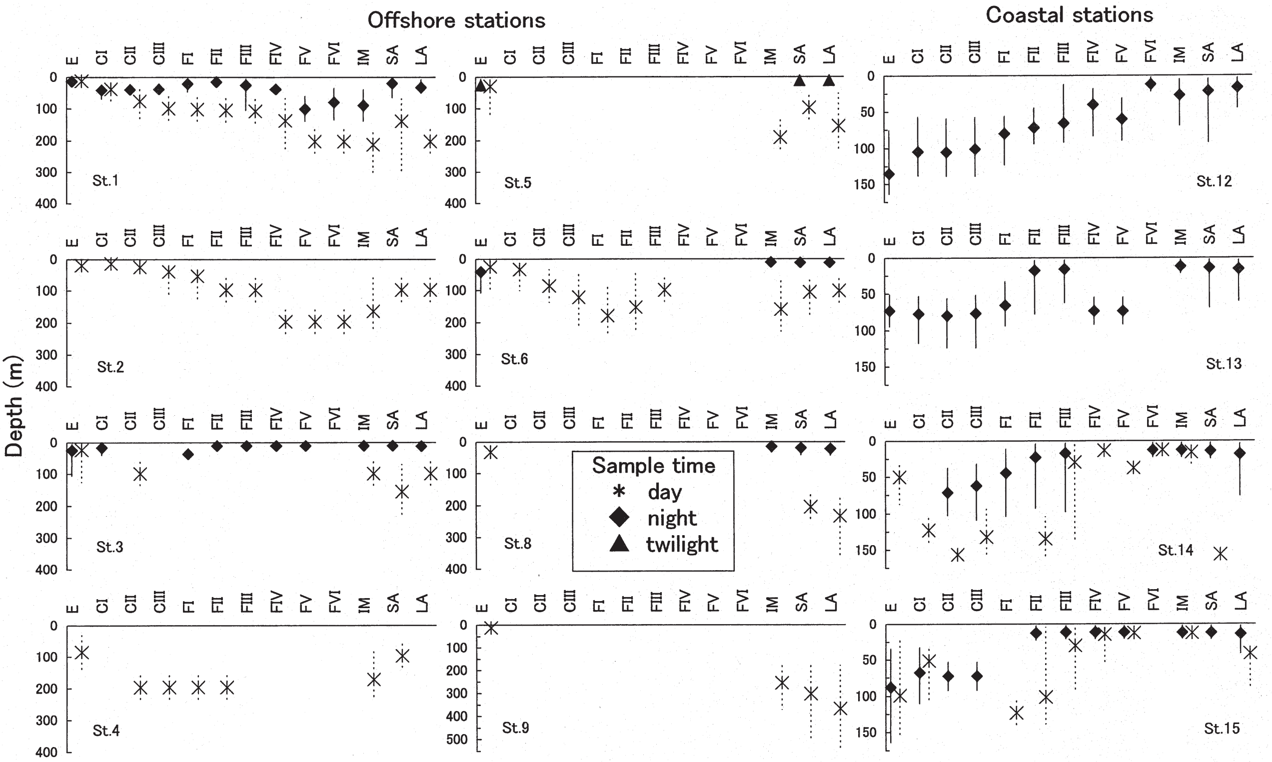

Fig. 4-13. Vertical distributions by developmental stage form egg to adult of *Euphausia pacifica* in each station in April 1998. Symbols show median depth. Vertical bar shows the range of 80% of abundance. SA and LA = small (≦15mm) and large (>15mm) adult, respectively.

station (Fig. 4-13). Median depth of other stages at night was shallower than 50m at all stations except at St. 1 where median depth of fifth and sixth furcilia and immature stage occurred at about 100m depth. Median depth of first calyptopis during daytime was also shallower than 50m at all stations, but median depth during daytime tended to increase with the developmental stages from second calyptopis. However, the deepening trend with developmental stages stopped at about 200m depth from fifth furcilia at St. 1, sixth furcilia at St. 2, second calyptopis at St. 4 and first furcilia at St. 6. Median depth of adults during daytime was generally at 100-200m but at about 300m at St. 9.

In the coastal area, median depth of eggs was deeper than 50m during day and night at each station (Fig. 4-13). Median depth of calyptopis at night was deeper than 50 m and deepest among all developmental stages except eggs at each station. Median depth of later stages than furcilia at night tended to be shallower with the developmental stages and median depth of immature and adult stages was shallower than 25m at each station. Depth of the lower limit of 80% abundance in calyptopis and first to third furcilia during daytime was deeper than 100m at Sts. 14 and 15 and their median depth was deepest among all developmental stages. Median depth of later stages than third furcilia during daytime was shallower than 50m at each station except at St. 14 where median depth of small adults were at about 150-170m. Median depth of large adults during daytime was at about 40m at St. 15.

Distribution of *E. pacifica* off northeastern Japan in July

It appears that Sts. 6, 8 and 10 were located at the northern side of the warm-core ring (Inagake *et al.,* 1997), with St. 8 closest to the center of the ring among these stations (Figs. 4-14-16). St. 5 was located within the influence of the first branch of the Oyashio Current while Sts. 12 and 14 were under the influence of the second branch of the Oyashio Current. A strong thermocline appeared between 0 to 50m and water cooler than 2.9℃ occurred below 50m. Eggs were abundant at St. 10 during daytime and St. 5 and 14 at night (Figs. 4-15 and 16).

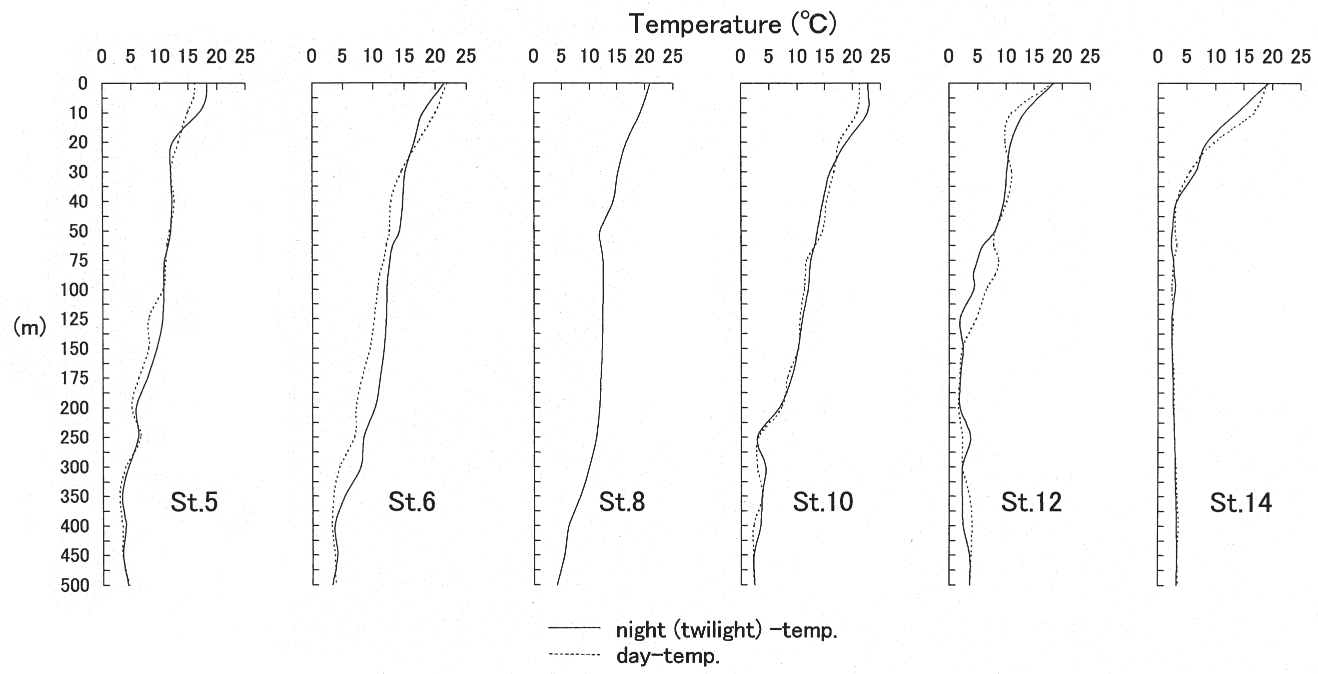

Fig. 4-14. Vertical profiles of temperature by station in July 1995. Solid and dotted lines show the night (twilight) and day temperatures, respectively. Temperatures obtained from CTD in MOCNESS-I.

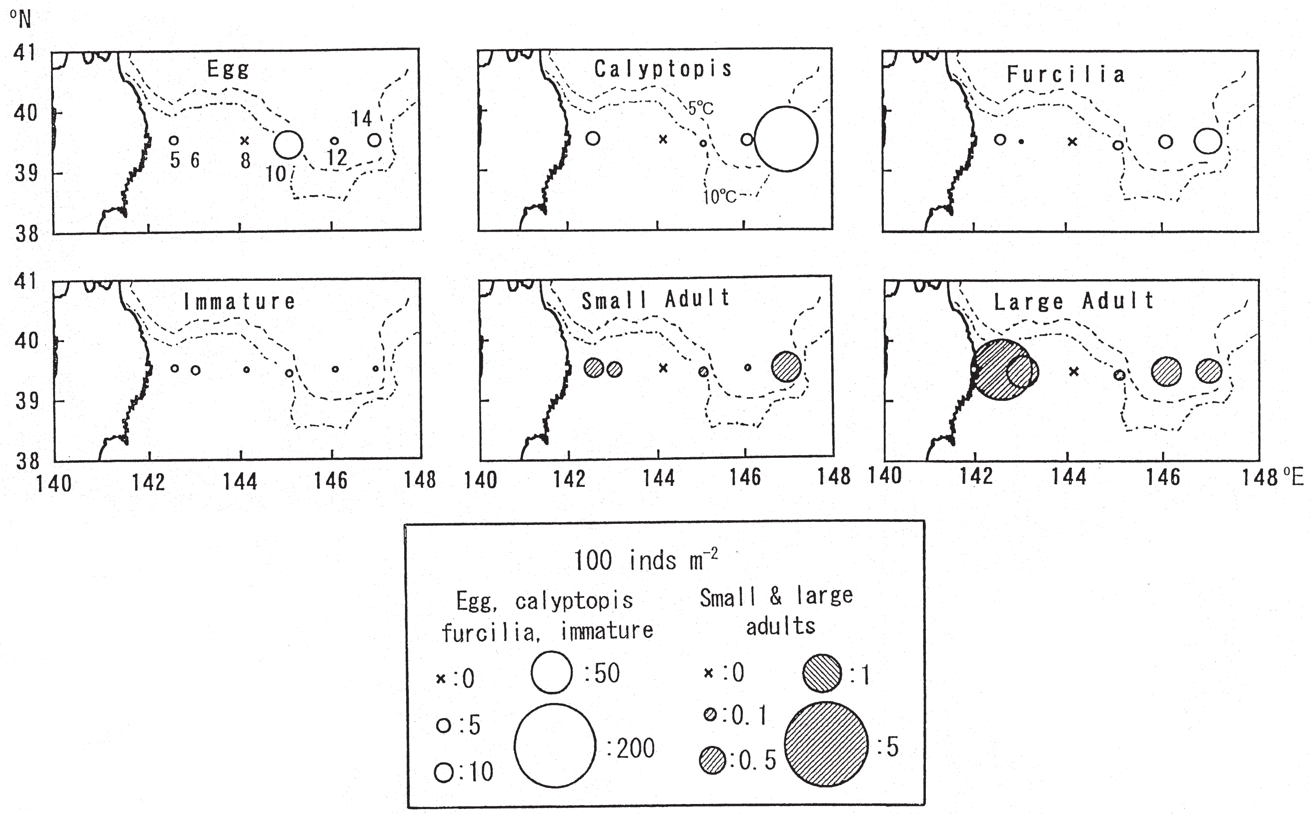

Fig. 4-15. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at night (except for St. 6 at twilight time) and temperature gradients at 100m depth in July 1995. The scales as in legend. Stations arenumbered in "egg".

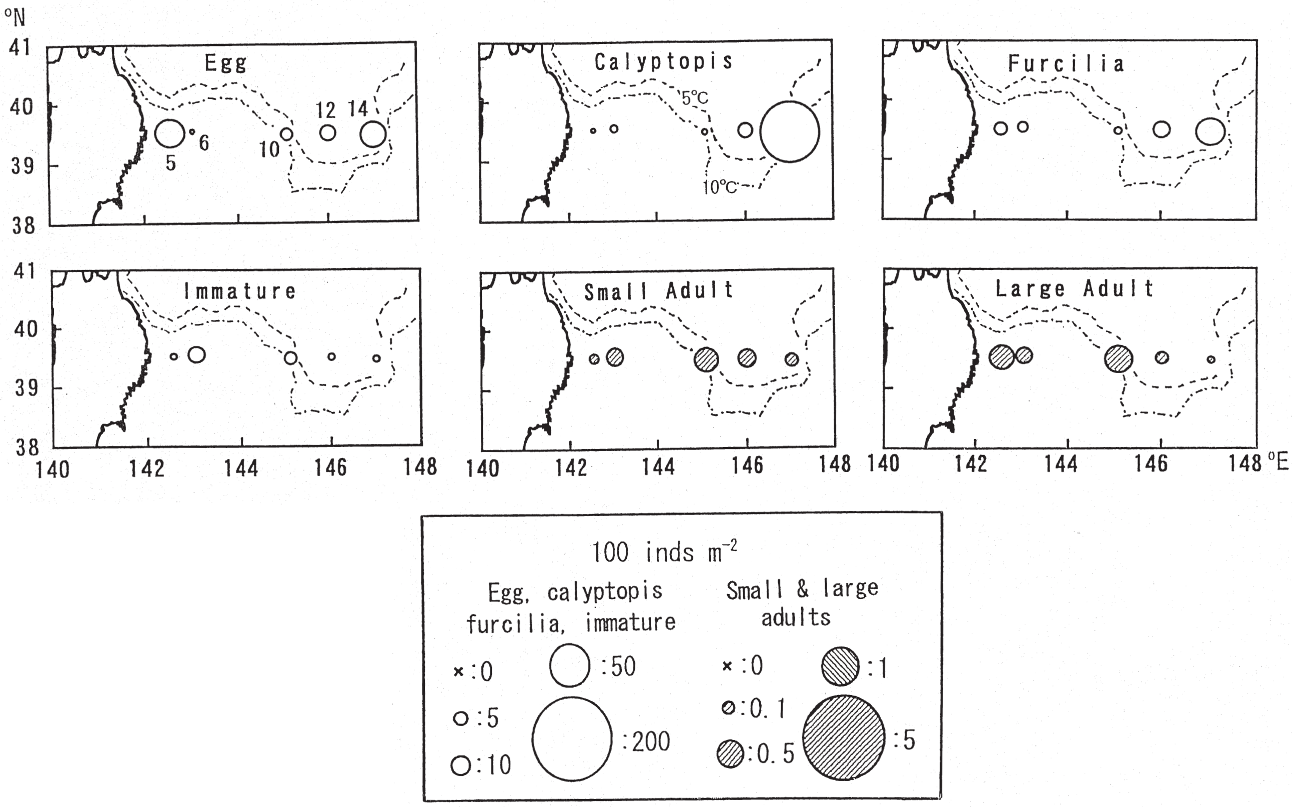

Fig. 4-16. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at day and temperature gradients at 100m depth in July 1995. The scales as in legend. Stations are numbered in "egg".

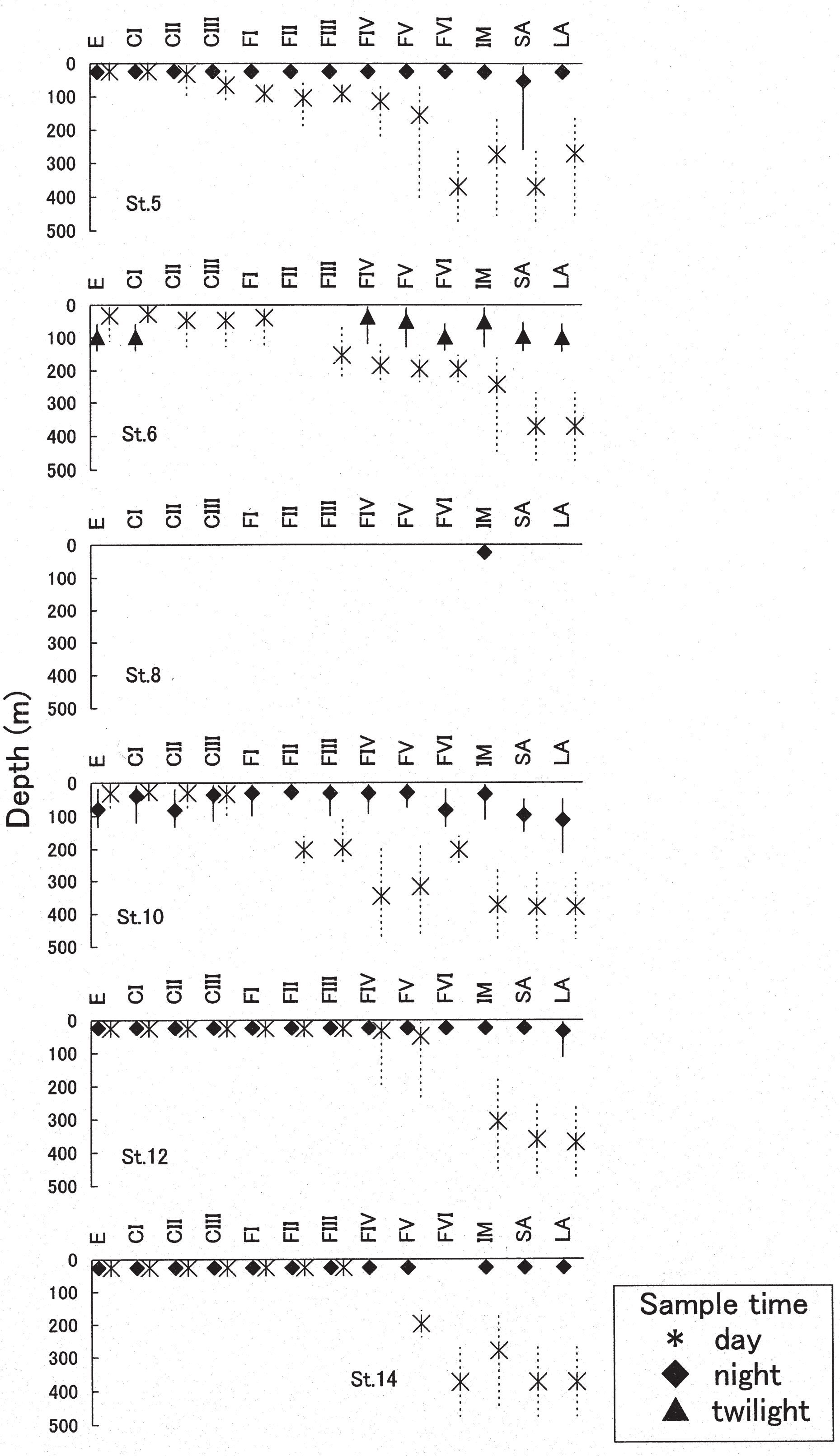

Fig. 4-17. Vertical distributions by developmental stage from egg to adult of *Euphausia pacifica* by station in July 1995. Symbols show median depth. Vertical bar shows the range of 80% of abundance. SA and LA = small (≦15mm) and large (>15mm) adult, respectively.

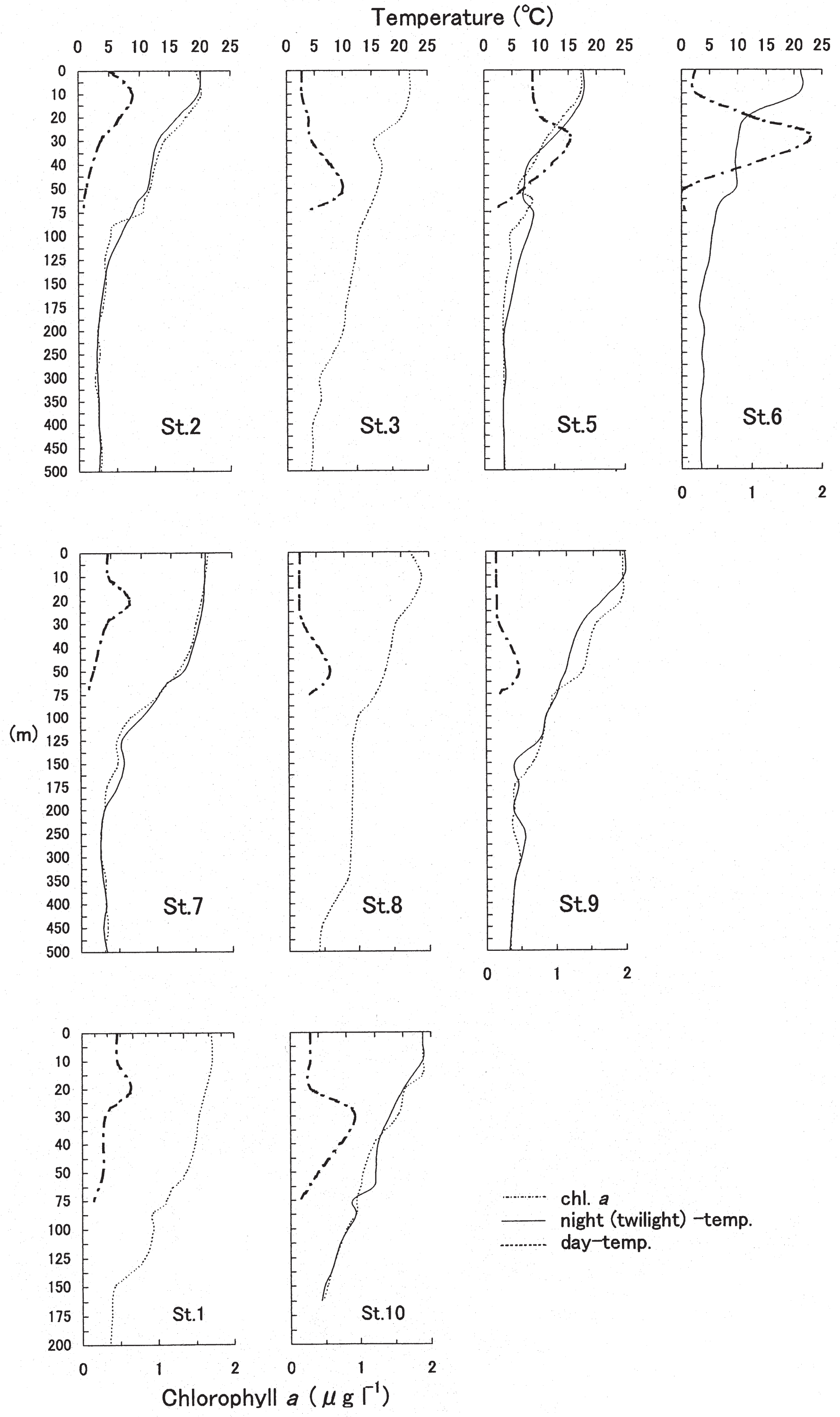

Fig. 4-18. Vertical profiles of temperature and chlorophyll *a* at each station in September 1998. Temperatures obtained from CTD in MOCNESS-I.

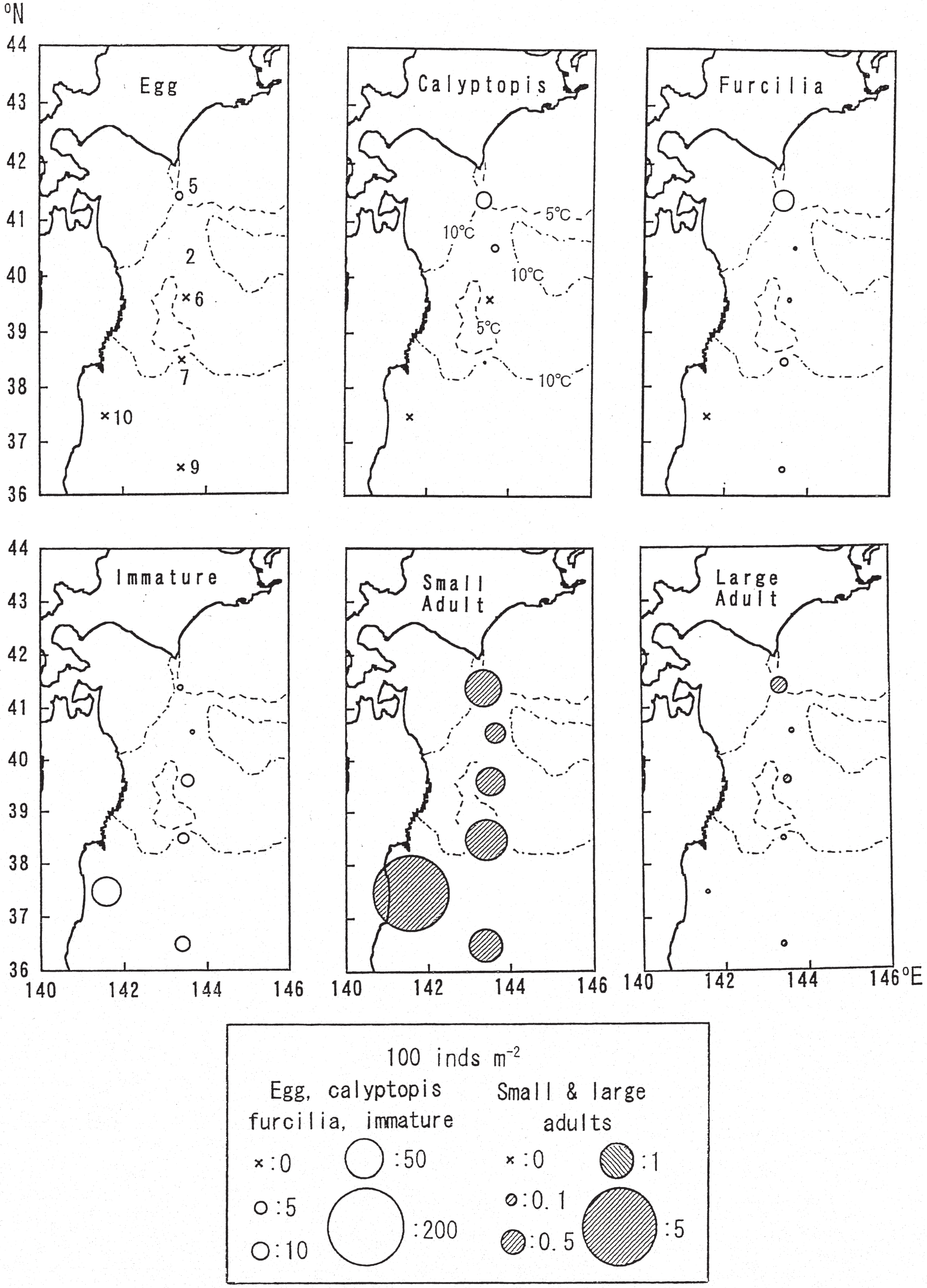

Fig. 4-19. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at night (except for St. 2, 10 at twilight time) and temperature gradients at 100m depth in September 1998. The scales as in legend. Stations are numbered in "egg".

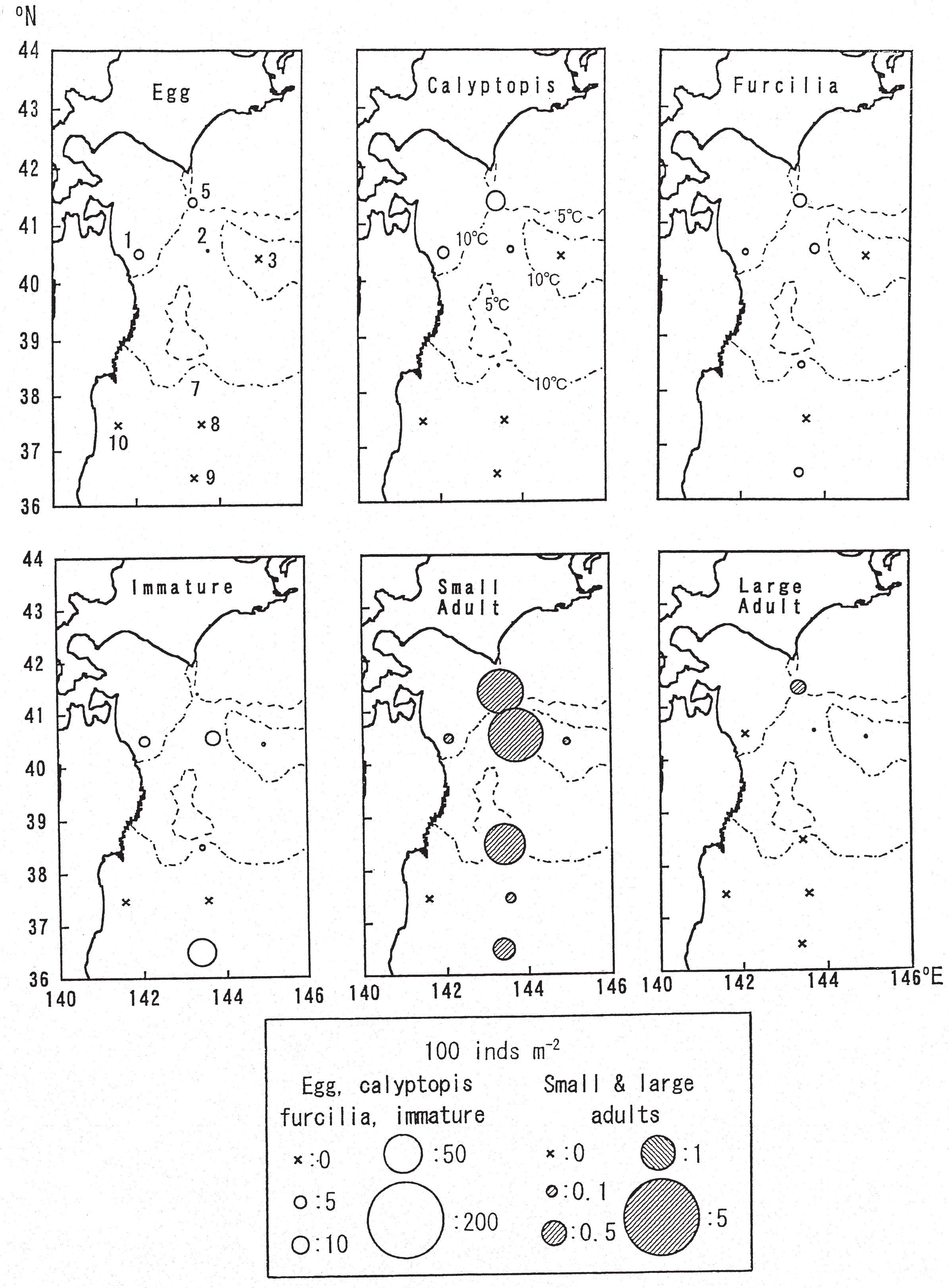

Fig. 4-20. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at day and temperature gradients at 100m depth in September. The scales as in legend. Stations are numbered in "egg".

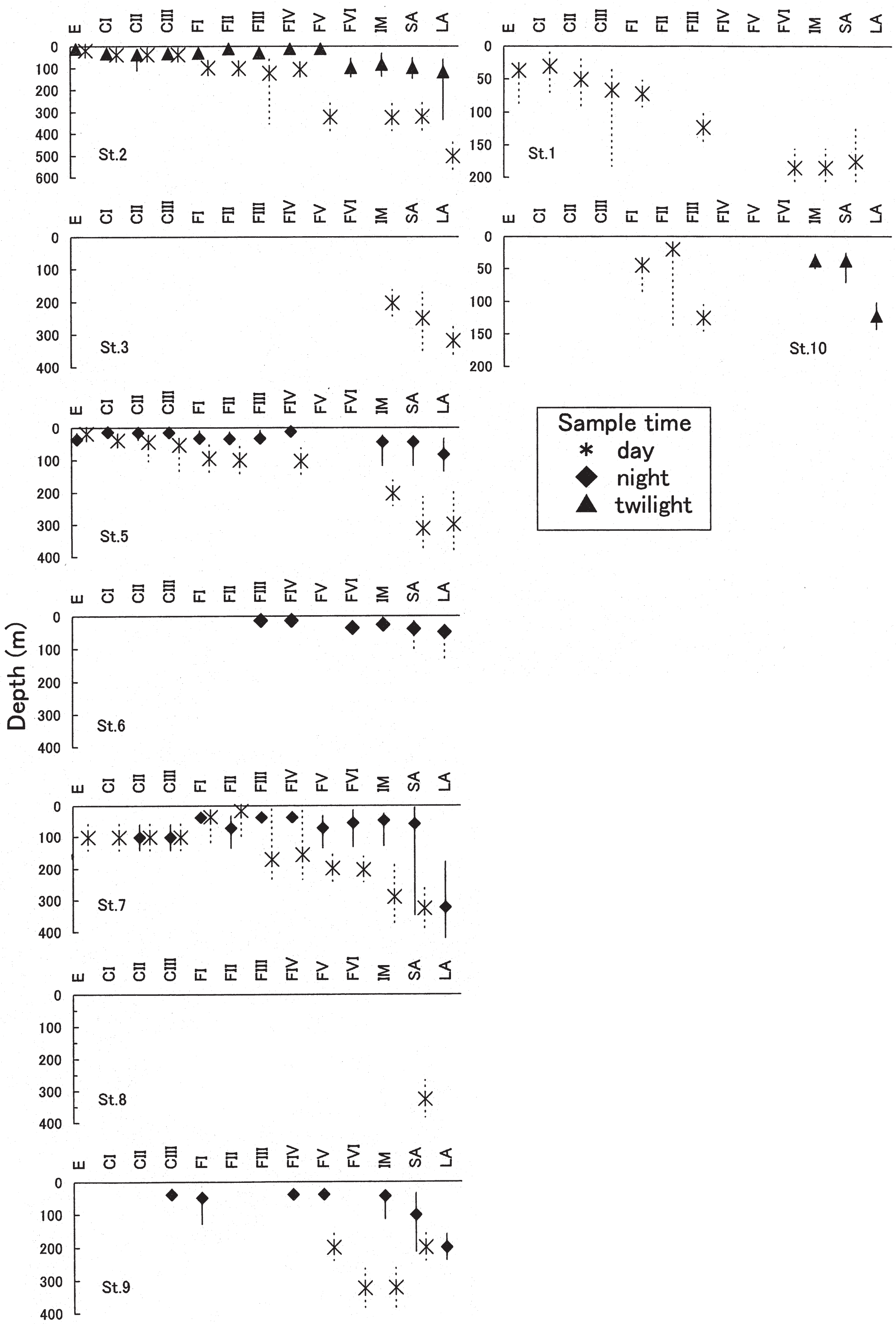

Fig. 4-21. Vertical distributions by developmental stage from egg to adult of *Euphausia pacifica* by station in September1998. Symbols show median depth. Vertical bar shows the range of 80% of abundance. SA and LA = small (≦15mm) and large (>15mm) adult, respectively.

Calyptopis and furcilia stages were abundant at St. 14 at night. Immature stage was abundant at Sts. 6 and 10 during daytime. Small adults were abundant at St. 10 during daytime and St. 14 at night. Large adults were abundant at St. 5 at night. Only immature euphausiids occurred at St. 8.

The median depth of each developmental stage at night was generally shallower than 50m at each station (Fig. 4-17). However, the median depth of developmental stages from eggs to second calyptopis and from fourth furcilia to adults at Sts. 6 and 10 at night was about 100m. The median depth of euphausiids during daytime increased with the developmental stages from calyptopis or early stages of furcilia at Sts. 5, 6 and 10. However, the depth increased with the developmental stages from fourth or fifth furcilia and younger stages stayed in the shallow layer even during daytime at Sts. 12 and 14.

Distribution of *E. pacifica* off northeastern Japan in September

Sts. 3 and 8 were located near the center of the warm-core rings (37°30'N, 144°E and 40°20'N, 145°10'E, respectively; Kato *et al.*, 2000) and higher temperatures than 10 ℃ occurred above 200m at St. 3 and above 350m at St. 8 (Figs. 4-18-20). Sts. 7 and 9 were located along the marginal area of the warm-core rings and higher temperatures than 16 ℃ occurred above 50m at both stations. St. 5 was located between the first branch of the Oyashio Current and Tsugaru Warm Current. St. 6 was located on the east side of the cold-core ring. Lower temperatures than 10℃ occurred below 30m at Sts. 5 and 6. St. 2 was located between warmer and colder water masses. St. 1 was strongly affected by the Tsugaru Warm Current (Kato *et al.*, 2000). St. 10 was located south of 10℃ isotherm at 100m depth and water with about 23℃ occurred above 20m at this station. Maximum chlorophyll *a* concentration occurred below the thermocline (generally at 30–50m) at each station except Sts. 2 and 7. Higher than 1 μ g l^{-1} occurred at 30m at Sts. 5 and 6, but maximum concentration was lower than 1 μ g l^{-1} at other stations.

A few eggs occurred at Sts. 1 and 5 but rarely occurred at other stations (Figs. 4-19 and 20). A few larvae of calyptopis and furcilia occurred at St. 5 but rarely occurred at the other stations. Immature stage and small adults occurred widely and were most abundant at St. 10 at night. Large adults occurred mainly at St. 5 at night, but rarely occurred at other stations. Every developmental stage rarely occurred at Sts. 3 and 8.

In the offshore areas, median depth of *E. pacifica* at night tended to increase with the developmental stages from fifth furcilia or immature stage at each station (Fig. 4-21). Especially, median depth of large adults was significantly deep at St. 7 (323m) and St. 9 (201m), and upper limit depth of their 80% abundance occurred below the thermocline at both stations. Median depth of euphausiid during daytime tended to increase with the developmental stages from first-third furcilia. Median depth of adults during daytime was generally about 300m at each station, but that of large adults was 501m at St. 2 and that of small adults was 200m at St. 9.

At St. 1, median depth of *E. pacifica* during daytime tended to increase with the developmental stages from second calyptopis and immature and adult stages occurred in the benthopelagic layer (Fig. 4-21). Median depth of large adults (124m) at night was deeper than that of immature and small adults (39 m) at St. 10. Immature and adult stages did not occur during daytime at St. 10.

Distribution of *E. pacifica* off northeastern Japan in November

Sts. 2 and 4 were located under the influence of the Kuroshio Extension, and higher temperatures than 15℃ occurred above 150m at St. 2 and above 200m at St. 4 (Figs. 4-22-24). Sts. 5 and 6 were located along the marginal area of the cold-core ring. Thermocline occurred between 75 and 150m at St. 5 where the temperatures were about 13℃ above 75m and about 3 ℃ below 150m. Apparent thermocline did not occurred at St. 6. St. 8 was located under the influence of the Oyashio Current and had a thermocline between 50 and 100m with lower temperature than 4℃ below 100m. Chlorophyll *a* concentration tended to be higher in the northern stations and showed 0.7～0.9 μ g l^{-1} between the surface and 50m at St. 8.

Eggs, calyptopis and furcilia stages occurred limitedly along the marginal area of the cold-core ring and were most abundant at St. 5 (Figs. 4-23 and 24).

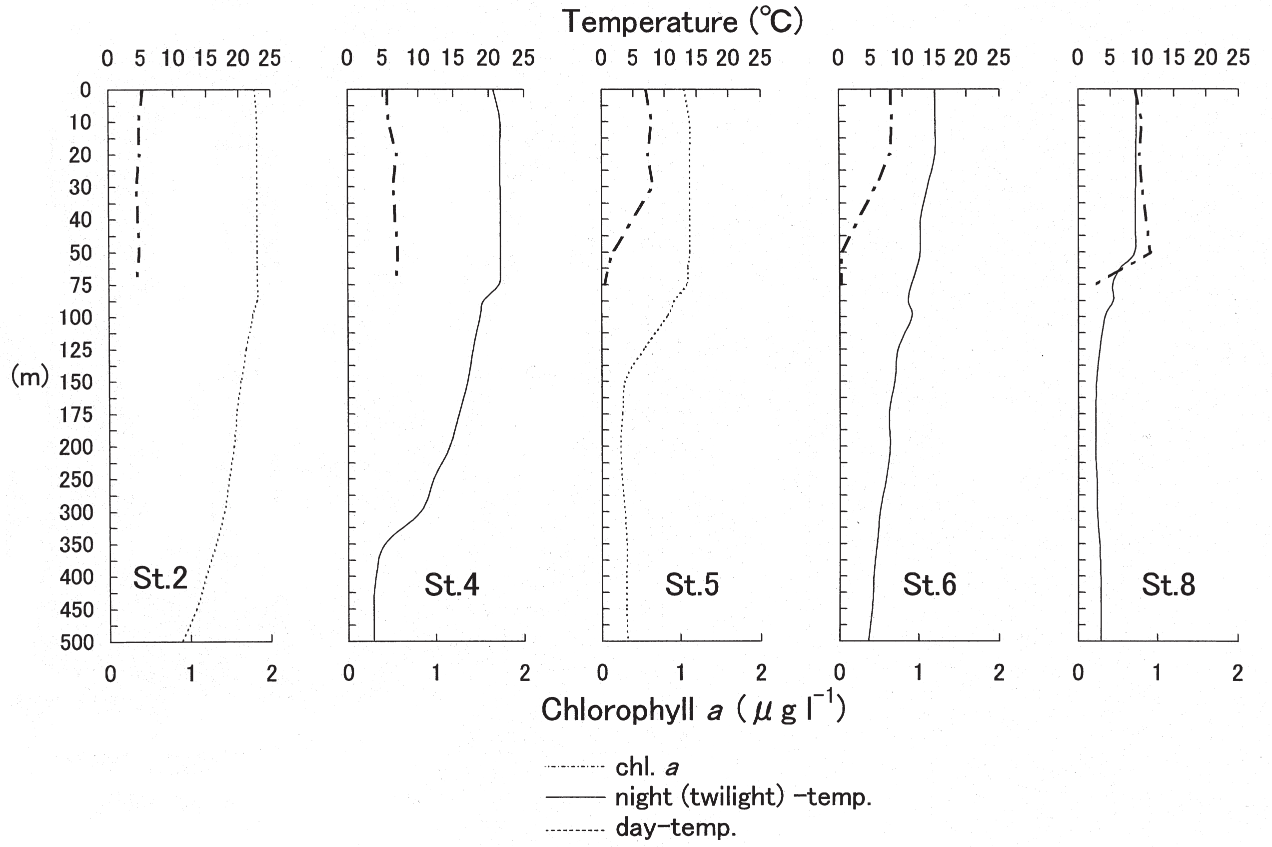

Fig. 4-22. Vertical profiles of temperature and chlorophyll *a* at each station in November 1999. Temperatures obtained from CTD in MOCNESS-I.

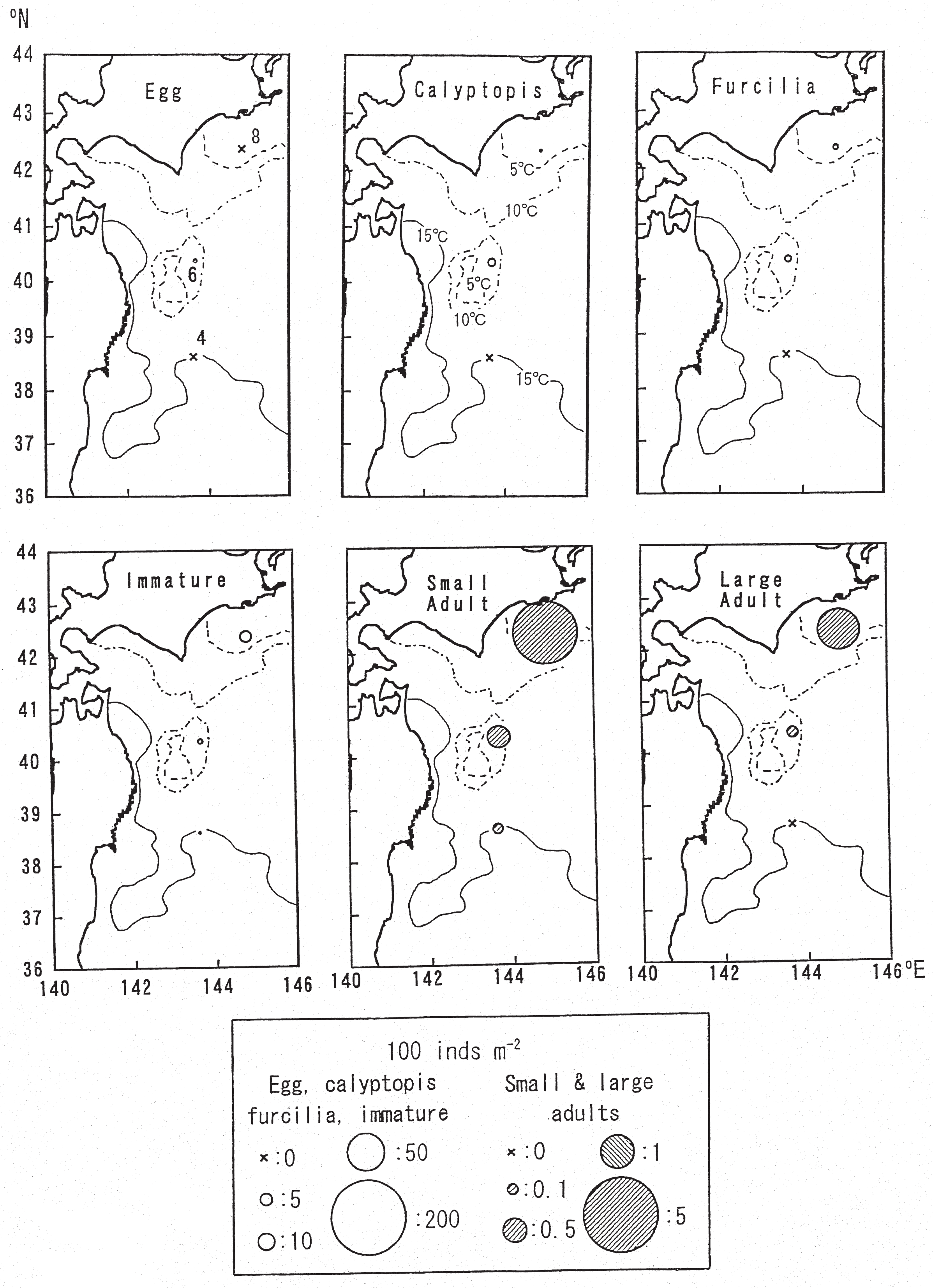

Fig. 4-23. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at night and temperature gradients at 100m depth in November. The scales as in legend. Stations are numbered in "egg".

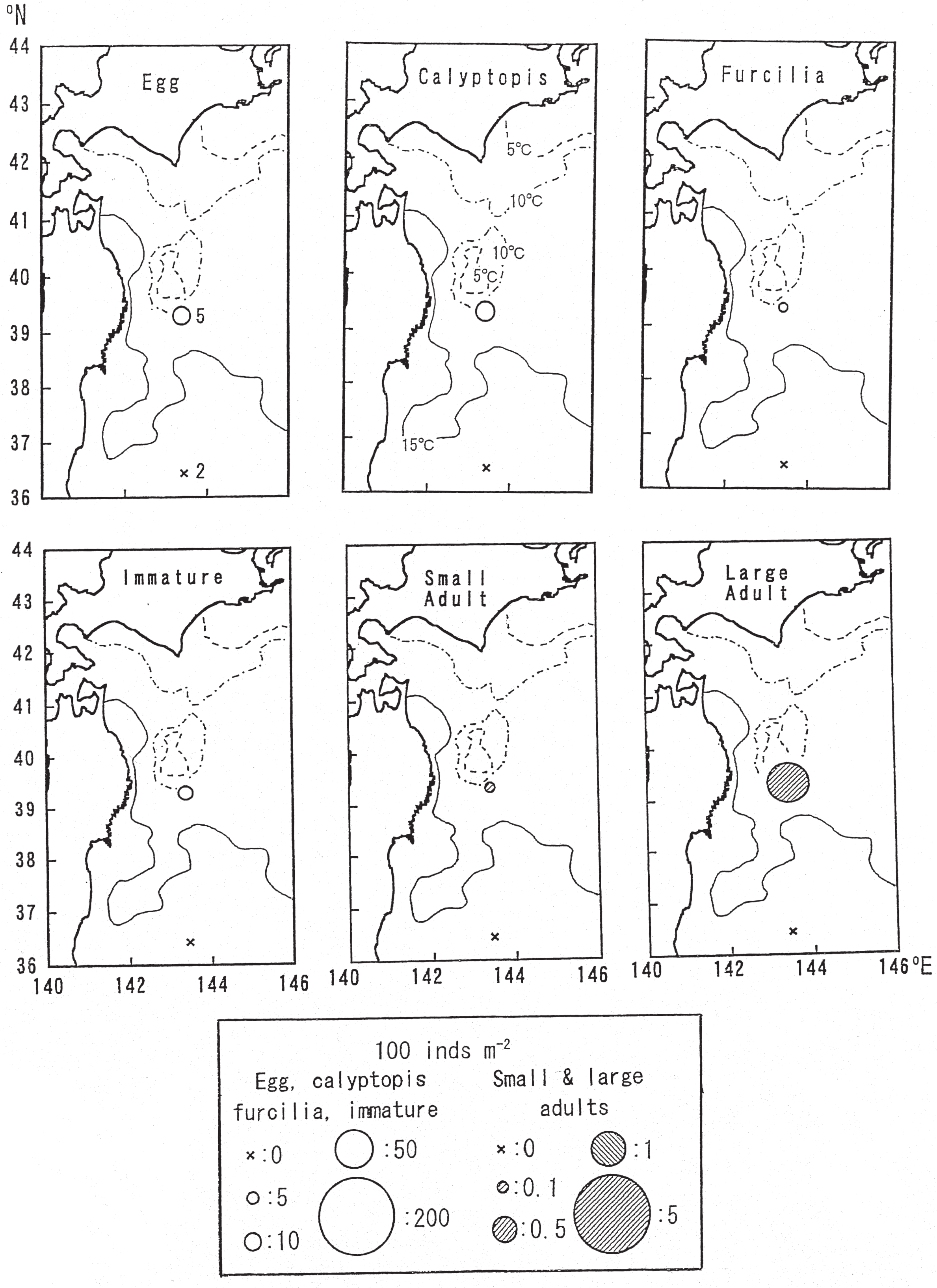

Fig. 4-24. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at day and temperature gradients at 100m depth in November. The scales as in legend. Stations are numbered in "egg".

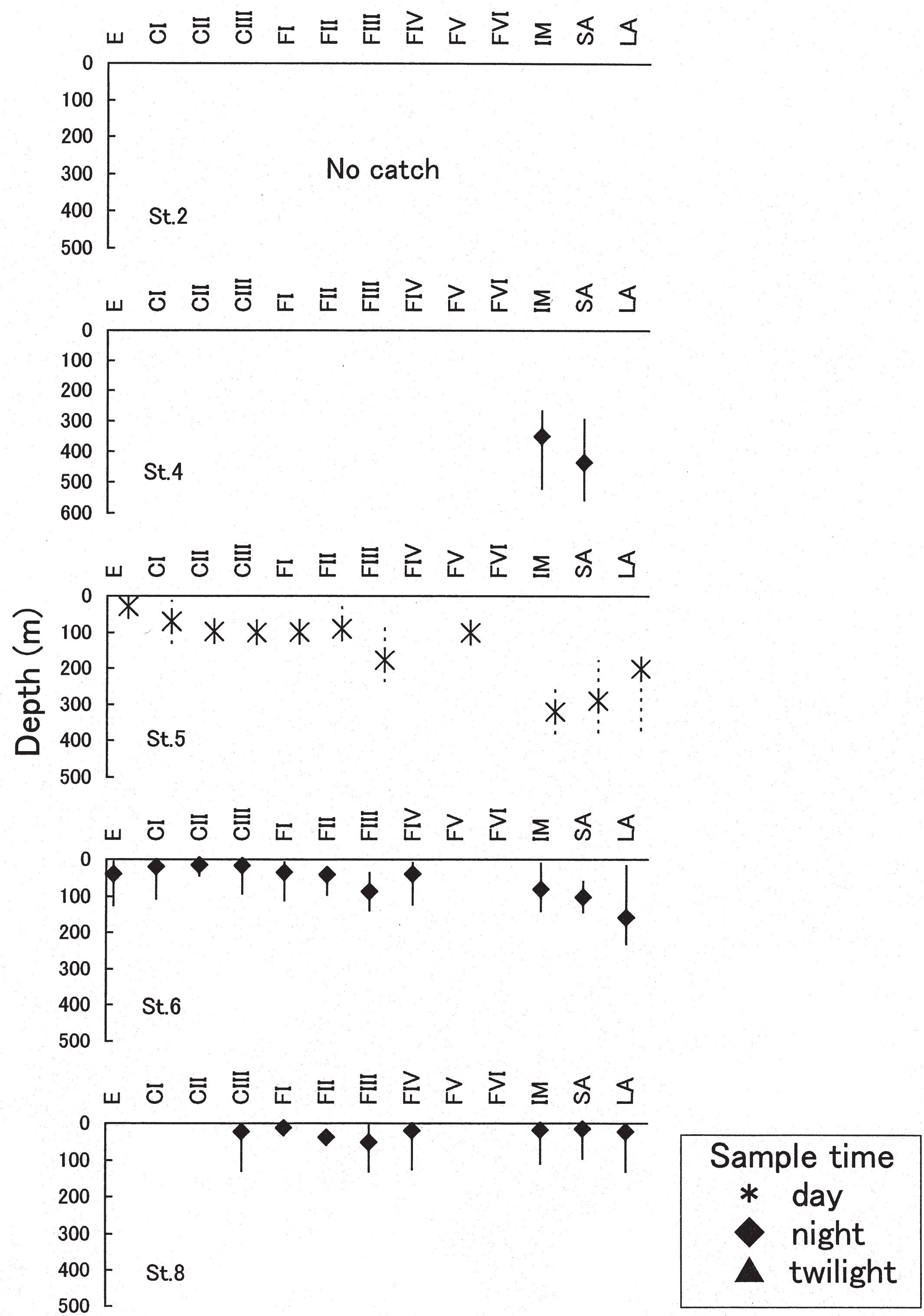

Fig. 4-25. Vertical distributions by developmental stage from egg to adult of *Euphausia pacifica* by station in November 1999. Symbols show median depth. Vertical bar shows the range of 80% of abundance. SA and LA = small (≦15mm) and large (> 15mm) adult, respectively.

Immature stage occurred at Sts. 5 and 8. Small and large adults were abundant at St. 8. Every developmental stage rarely occurred at Sts. 2 and 4.

Median depth of each developmental stage at night was shallower than 50m at St. 8 (Fig. 4-25). Median depths of *E. pacifica* at night increased with the developmental stages from immature stage and that of large adult was 232m at St. 6. Median depth of immature and small adults at night was significantly deeper (436m each) and upper limit depth of 80% abundance occurred at 267 and 294m, respectively, which were slightly shallower than the thermocline (300–350m).

Discussion

Characteristics of the pelagic and benthopelagic *E. pacifica* in the Sanriku coastal waters

From the ORI and beam-trawl net surveys, immature and adult *E. pacifica* seem to be distributed mainly on the upper slope where cold temperatures ≦8℃ occurred in the near bottom layer, forming a benthopelagic population from early summer to fall in the Sanriku coastal waters (Figs. 4-3-9). On the other hand, adult *E. pacifica* seems to form dense aggregations above the continental shelf where water with 7–8℃ dominates in the total water column and are pelagic throughout the day in spring (Figs. 4-3-9). MOCNESS-I net survey in the coastal waters in spring supported the latter conclusion, i.e. adults occurred mainly above 100m at St. 15 both during day and night in April (Fig. 4-13). On the other hand, immature and adult *E. pacifica* did not occur in the total column during day although they occurred abundantly at night at St. 10 in September (Figs. 4-19-21). Endo (2000) observed that benthopelagic *E. pacifica* aggregations occurred in the sea depth range from 160-400m off Sanriku in summer and their thickness was a few meters from the sea bed. Therefore no collection of immature and adult stages during day at St. 10 may be due to sampling failure of the benthopelagic *E. pacifica* by MOCNESS-I net of which deepest tow depth was ca. 30 m above the sea bed.

Greene *et al*. (1988) suggested that *Meganyctiphanes norvegica* reaches the sea bed and forms benthopelagic aggregations in coastal waters during day at depths less than the usual diurnal vertical migration in the offshore waters. Daytime depth (300–400m) in the offshore waters in summer and fall seems to cause the formation of benthopelagic population on the upper slope for *E. pacifica*. On the other hand, adults were abundantly collected by beam-trawl net even at night in October and December (Fig. 4-7). This may be due to 1) contaminated sampling with pelagic *E. pacifica* during the retrieval of the net from the sea bed to the surface or 2) the collection of genuine benthopelagic population at night because the occurrence of the thermocline in the middle-deeper layer prevented *E. pacifica* from ascending toward the upper layer as observed in the warm offshore waters (Figs. 4-21 and 25). A trawl net survey using a closing net mechanism is necessary to confirm the accurate time of formation of benthopelagic aggregations.

Benthopelagic *E. pacifica* on the upper shelf was most abundant in June. This was perhaps originated from 1) the active recruitment of the spring-hatched cohort because recruitment time from hatching to immature or adult stages takes ca. 2 months (e.g. Endo, 1981) and 2) abundant overwintered individuals which formed dense pelagic populations in the Sanriku waters in spring.

The trophic significance of *E. pacifica* in the Sanriku coastal waters is suggested from the results of the present study as follows. In spring, *E. pacifica* plays an important role as food for plankton-feeding fishes living in the shallow waters such as sand lance and sea-birds such as *Aethia cristatella* and *Cerorhinca monocerata* (Odate, 1991), because it forms dense aggregations in the shallow layers on the continental shelf during day. On the other hand, from early summer to fall, *E. pacifica* plays an important role as food for demersal fishes such as walleye pollack, because it forms a benthopelagic population on the upper slope. Fujita (1994) showed that demersal fishes in the coastal waters off Otsuchi, Iwate Prefecture and off Sendai Bay, Miyagi Prefecture ingested *E. pacifica* most actively from May to July. In the present study, benthopelagic *E. pacifica* on the upper shelf was most abundant in June. So, demersal fishes seem to make the most of benthopelagic *E. pacifica* as food in early summer when it is most abundant. The abundance of *E. pacifica* in early summer may have a strong effect on the life history of these demersal fishes.

Joint samples of plankton and predators are necessary to further quantify these relationships.

Characteristics of seasonal horizontal distribution in the offshore waters

There are apparently three tendencies in the horizontal distribution in the offshore waters as follows. 1) Eggs and larval stages were most abundant in the transitional area off Sanriku and Joban in April but rarely occurred in the Oyashio area off southern Hokkaido in the same months (Figs. 4-11 and 12). 2) Small adults occurred widely in the Oyashio and transitional areas in each month although large adults rarely occurred in the warmer waters of the transitional area (10℃ < T_{100}≦15℃ ; Figs. 4-19 and 20). 3) Every developmental stage rarely occurred in the Kuroshio area (Figs. 4-23 and 24). These evidences are consistent well with the results obtained by the horizontal distribution survey in Chapter 3.

Diurnal vertical migration of each developmental stage

Euphausiid eggs are generally thought to have a higher specific gravity than sea water and sink after liberation from gravid female (Mauchline and Fisher, 1969) but eggs of *E. pacifica* seem to be rather neutral because they were generally distributed within 100m or so in vertical range (Figs. 4-13, 17, 21 and 25).

Annual average median depth of each developmental stage of *E. pacifica* during day and night for all offshore stations in the MOCNESS-I net survey is shown in Fig. 4-26. The average median depth at night was shallower in eggs, calyptopis and early and middle stages of furcilia and tended to increase with the developmental stages from middle stages of furcilia to large adults, while that during day was shallowest in eggs and first calyptopis and tended to increase with developmental stages from first calyptopis to sixth furcilia. Gradual extension of the vertical range with developmental stages is well consistent with the trend reported in other populations (Brinton, 1967; Bollens *et al.,* 1992; Iguchi, 1995).

Annual average water temperature at the median depth of each developmental stage during day and night is shown in Fig. 4-27. The average water temperature at night was highest at about 12 ℃ in calyptopis and furcilia stages, and was 9.8, 10.2, 9.0, 8.0 ℃ in eggs, immature and small and large adults, respectively, while that during day was highest of 9.2, 11.2℃ in eggs and first calyptopis, respectively, and gradually decreased with the developmental stages from first calyptopis to immature (ca. 4℃). The change in pattern with developmental stages at night is well consistent with both that for the horizontal distribution by water mass (Table 3-2) and that for the vertical distribution (Fig. 4-26). This suggests that the vertical distribution at night of each developmental stage relates closely to the respective suitable temperatures. On the other hand, the change in pattern with developmental stages during day is well consistent with that for the verti-

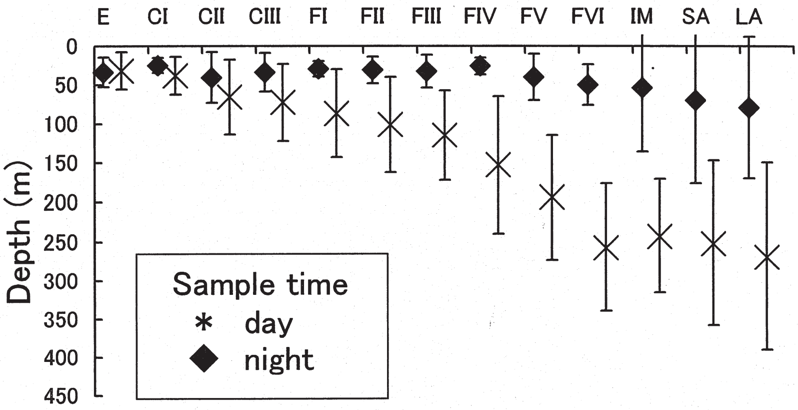

Fig. 4-26. Average vertical distribution by development stage from egg to adult of *Euphausia pacifica* for offshore stations in July 1995, April and September 1998, and November 1999. Symbols show the average median depth. Vertical bar shows standard deviation.

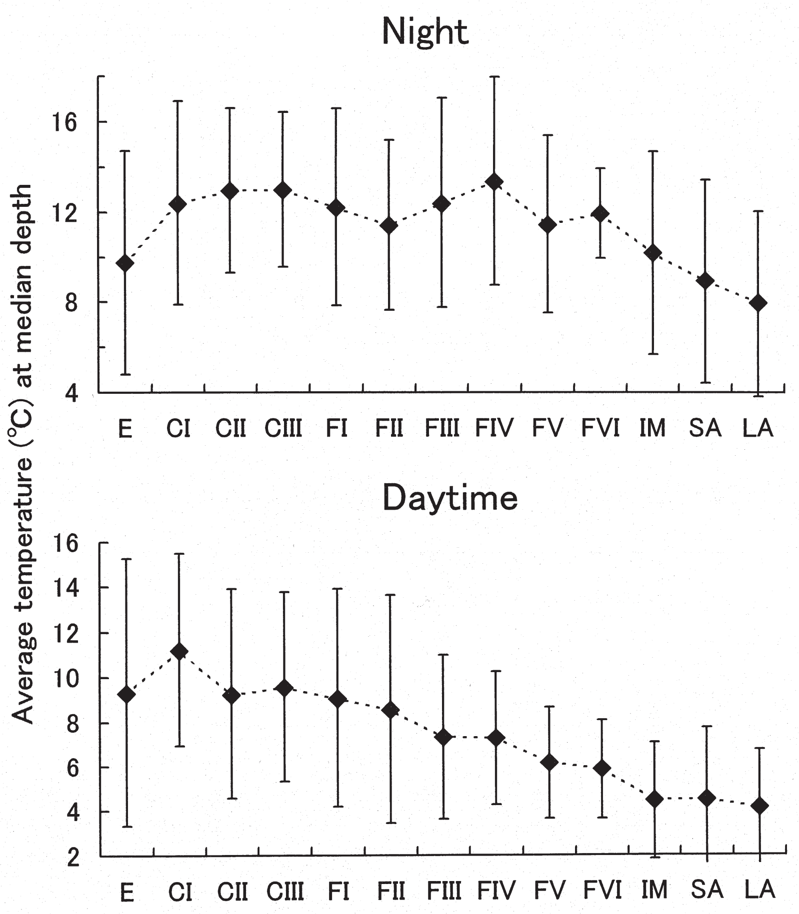

Fig. 4-27. Average water temperature at the median depth of each developmental stage of *Euphausia pacifica* for offshore stations in July 1995, April and September 1998, and November 1999. Vertical bar shows standard deviation.

cal distribution (Fig. 4-26). The vertical distribution of each developmental stage during day is thought to be related to not only the suitable temperatures but also swimming ability because larval stages are generally considered to take place diurnal vertical migration in the shallower layer in order to effectively utilize phytoplankton in the surface layer due to their weak swimming ability (Mauchline and Fisher, 1969; Iguchi, 1995). However, the reason why pre-third furcilia stages stayed in the surface layer even during daytime in the Oyashio area in July seems to be due to avoidance of cold temperatures of <4 ℃ that occurred below the thermocline and acceleration of growth in the warm surface layer (see Ross, 1981).

Median depth of *E. pacifica* both during day and night tended to be deepest in eggs or calyptopis and become shallow with the developmental stages from calyptopis to advanced stages at coastal stations in April, which was quite different from the diurnal vertical migration pattern with developmental stages usually found at the offshore stations (Fig. 4-13). According to Nakagawa *et al.* (2001), adult *E. pacifica* can ingest copepods with prosome length of 2.1mm which almost equals to the total length of the third calyptopis. Therefore, it is suggested that copulated females liberate their eggs in the deeper layers and larval stages avoided adults by controlling their diurnal vertical migration to minimize cannibalism by the adults abundantly distributed in the surface layer. A change in diurnal vertical migration pattern of furcilia stage in *E. pacifica* according to the abundance of predators was also observed in Dabob Bay, off western USA (Bollens *et al.,* 1992).

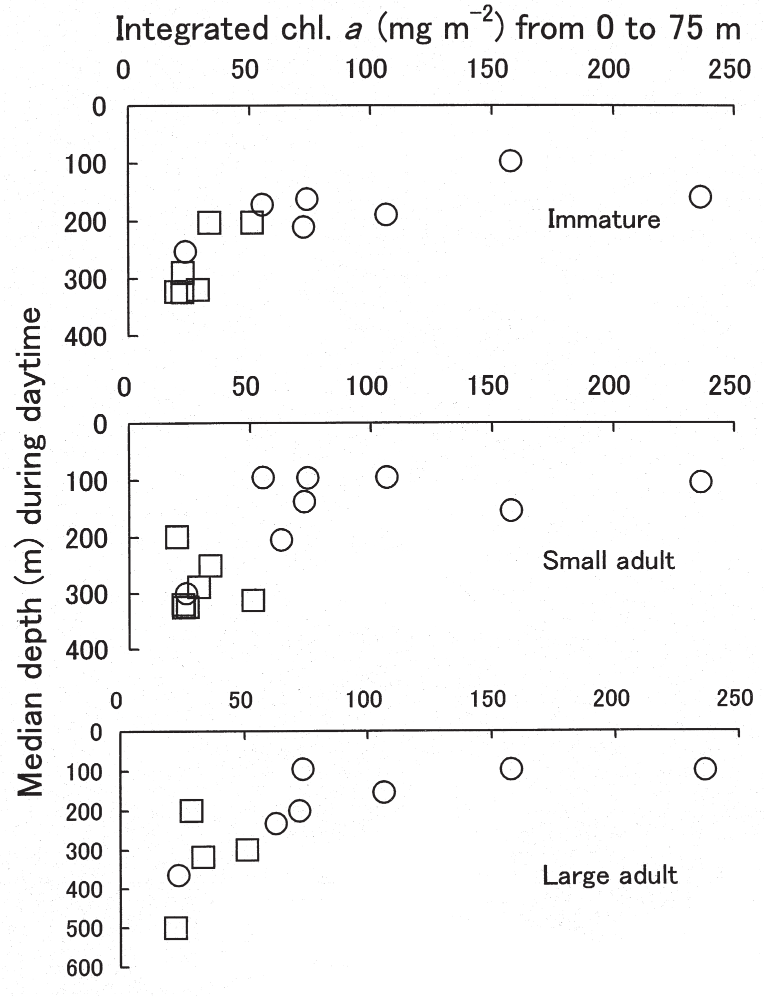

Fig. 4-28. Relationship between median depth during daytime of immature, small and large adult *Euphausia pacifica* for offshore stations and the integrated concentration (mg m^{-2}) of chlorophyll *a* from 0 to 75m depth. Circle: station in April 1998, square: station in July 1995, September 1998 and November 1999.

Characteristics of diurnal vertical migration of immature and adult stages

Iguchi *et al.* (1993) suggested that post larval stages of *E. pacifica* avoid ascending into the surface high temperatures at night during summer and fall in Toyama Bay. The results of Iguchi *et al.* (1993) seems to be consistent with the present study; i.e. median depth at night of immature and adult stages tended to be deeper in the warmer areas in summer and fall, especially large adults hardly reached beyond the thermocline in the mid layer (Figs. 4-21 and 25). However, median depth at night of adults at St. 6 in November was significantly deeper than that at St. 1 in April, although the vertical distribution of water temperatures was similar between the two stations (Figs. 4-10, 13, 22 and 25). Therefore, seasonal difference in nighttime depth of adult *E. pacifica* may be due to not only temperatures but also other factors such as seasonal food conditions because adult *E. pacifica* tends to ingest diatoms positively when they are abundant in the surface layer as mentioned later in **Chapter 6**.

Endo (1981) suggested that adult *E. pacifica* needs not to descend to deeper layers in the colder regions because it can reduce metabolic expenditure in the shallow cold layers, while it needs to descend to the deeper layers below the thermocline in the warmer regions, referring to the hypothesis by McLaren (1963). Endo's results seems to be consistent with the present ones, i.e. median depth during daytime of immature and adult stages in April, where the thermocline did not develop, was significantly shallower ($P < 0.01$; Mann-Whitney) than that in other months and thus distance of diurnal vertical migration tended to be shorter in April (Fig. 4-13). However, median depth during daytime of large adults was shallow (97m) at St. 2 where the surface temperature was higher than 15℃, while that was quite deep (326) m at St. 9 where temperatures lower than 3℃ dominated in the total water column (Fig. 4-13). In addition, median depth during daytime of immature and adult stages was quite deep (250-500m) in spite of the occurrence of a thermocline above 50m depth at St. 14 in July (Fig. 4-17). On the other hand, median depth during daytime of immature and adult stages at the offshore stations where the concentration of chlorophyll *a* from 0 to 75m was higher than 50mg m^{-2} was significantly shallower ($P < 0.05$; Mann-Whitney) than that where concentration was lower than 50mg m^{-2} (Fig. 4-28). Therefore, it is suggested that the median depth during daytime depends not only vertical distribution of temperatures but also on the illumination caused by the density of phytoplankton which could affect the vulnerability to visual predators in the shallow layer.

Chapter 5. Biomass, production and metabolism of *Euphausia pacifica*

Euphausia pacifica is an important fisheries resource and food item for many fishes off the northeastern Pacific coast, and their biomass and production has been actively studied (Brinton and Reid, 1986; Gomez-Gutierrez and Robinson, 1997; Heath, 1977; Tanasichuk, 1998a). Off the Japanese coast, biomass and production of the species have been studied only in Toyama Bay, Japan Sea (Iguchi and Ikeda, 1999), but such studies have not yet been conducted off the Pacific coast of northeastern Japan.

In this chapter, biomass, production (growth, eggs, moults) and metabolism (routine and diurnal vertical migration) of *E. pacifica* were investigated along the coastal waters off northeastern Japan, and characteristics of carbon budgets of *E. pacifica* off northeastern Japan are discussed comparing with the same species from other regions as well as other euphausiid species.

Materials and Methods

The analyses of biomass and production of *Euphausia pacifica* were based on bimonthly samples collected using Norpac nets (diameter: 0.45m; mesh size: 0.34mm) and 5.5m long cylindrical-conical nets (diameter: 1.3m; mesh size: 0.45mm; Watanabe, 1992) along the coastal waters off southeastern Hokkaido (41°-43°N), Sanriku (38°-41°N) and Joban (36°-38°N) on the R. V. *Wakataka-maru* (Tohoku National Fisheries Research Institute, Fisheries Research Agency), *Tankai-maru* and *Hokko-maru* (Hokkaido National Fisheries Research Institute, Fisheries Research Agency) from March 1997 to February 1998. The March survey was conducted only off Sanriku. The abundance of eggs and calyptopis stage (ca. <1 to 2mm body length) was determined from the Norpac net collections, those of furcilia (ca. > 2 to 6mm), immature (ca. >6 to 10mm) and adult (ca. >10mm) stages were determined from the cylindrical-conical net collections. Norpac nets were vertically towed from 150m to the surface at 1m s^{-1}. The cylindrical-conical nets were obliquely towed at a ship speed of 2 knots from 15m above the sea bottom to 0m where the sea depth was shallower than 300m, and towed from 150 to 0m where the sea depth was deeper than 300m. Cylindrical-conical net was towed only at night at all stations because post-calyptopis stages migrate below the 150m depth in the daytime, but mostly occur at < 150m depth at night (see **Chapter 4**), except at stations along the zigzag acoustic survey lines between 100 and 300m isobaths off Sanriku and Joban in March and April (Miyashita *et al.,* 1998). Water temperature and salinity from 0 to 300m depth were measured by CTD (Sea-Bird). More details on sampling methods, the results of seasonal changes in oceanographic features and the distribution and spawning activity of *E. pacifica* using the same samples can be found in **Chapter 3**.

The body length (BL: the distance between the tip of the rostrum and distal end of the telson) was divided into 1mm increments (24 size classes over the entire range of <1 to 24mm BL). The relationship between BL (mm) and dry weight (DW) for *E. pacifica* was calculated as $\mathrm{DW} = 9.954 \times 10^{-4}\mathrm{BL}^{3.156}$, according to Iguchi and Ikeda (Iguchi and Ikeda, 1995). Carbon contents of each developmental stage and size class of *E. pacifica* were calculated according to Iguchi and Ikeda (1998).

Average biomass (B) of each coastal area and entire survey area during entire survey period was calculated as

$$B = \sum_{i=1}^{s} \left((B_i + B_{i+1}) \times d_{i,\, i+1}/2 \right) / \sum d_{i,\, i+1} \quad (5.1)$$

where B_i is biomass of ith survey, $d_{i,\, i+1}$ is days between ith survey and $(i+1)$th survey. The entire study period was 313 days (six sampling periods) for the coastal areas off southeastern Hokkaido and Joban, and 356 days (seven sampling periods) for the coastal area off Sanriku. The entire study period for the entire survey area was presumed to be 356 days (seven sampling periods) on the assumption that the biomass and production off Sanriku in March 1997 stands for the average off all three coastal areas in the same month.

The somatic production of *E. pacifica* was computed as the sum of growth increments of 24 size classes multiplied by the abundance of each size class:

$$P_g = \sum_{i=1}^{s} \left((CW_{i+1} - CW_i) / D_i \times N_i \right) \quad (5.2)$$

where P_g is the daily somatic production (mg C m^{-2} day^{-1}), i is the size class, CW_i and CW_{i+1} are carbon weight (mg C) at the beginning and end of the size interval, D_i is the developmental time (days) from CW_i to CW_{i+1}, N_i is the average abundance (ind. m^{-2}) of each size class and s is 24.

To obtain CW, BL data were converted to dry weight (DW) using the allometric equation, then to carbon units by multiplying carbon content data for each BL class mentioned above. Monthly size-frequency distribution of *E. pacifica* along the three coastal areas is shown in Fig. 5-1. *E. pacifica spawns* near the marginal area of the Oyashio Current ($T_{100} = 5$℃) throughout the year (see **Chapter 3**), so continual occurrence of small size individuals off Sanriku and Joban throughout the year (Fig. 5-1) may be due to transportation from the adjacent spawning area, although spawning occurs limitedly in spring in the both areas (see **Chapter 3**). Discrete cohorts are difficult to follow on the basis of such considerable overlap of small size ranges. Therefore, the growth rates of individuals for ≦10mm size classes (corresponding to larval and immature size) were estimated to be 0.1mm day^{-1} throughout the year as reported by many field studies (Heath, 1977; Bollens *et al.,* 1992; Brinton, 1976; Iguchi *et al.,* 1993; Smiles and Pearcy, 1971). The growth rates for > 10mm size classes (corresponding to adult size) were estimated from the population size-frequency distributions of adult stage over the whole coastal area using the software application (Macdonald and Green, 1988), assuming that the seasonal growth rate was common in the three coastal areas because adult *Euphausia pacifica* could migrate between coastal areas with the seasonal change of waters masses according with the Oyashio Current and may not spend its entire life history in each individual area (see **Chapter 3**).

The estimations of moult and egg production needed the assumption of habitat temperatures for each developmental stage of *E. pacifica.* The median depths of eggs and the calyptopis stage are shallower than 50 m in the Sanriku waters in both spring and summer regardless of the difference of water masses, except along the coastal waters in spring (7-8℃ dominated throughout the water column) where their median depths are deeper than 100 m (see **Chapter 4**). The median depths of the furcilia stage are at the surface layer at night and shallower than 150m during daytime in the Sanriku waters in both spring and summer regardless of the water masses. Therefore, the daily average temperature that *E. pacifica* encounters was estimated to be the average temperature from 0 to 50m for eggs and calyptopis stage and from 0 to 150m for furcilia stage for each coastal area in each month. The median depths of immature and adult stages are at the surface layer at night and about 150m during daytime in the Sanriku waters in spring (see **Chapter**

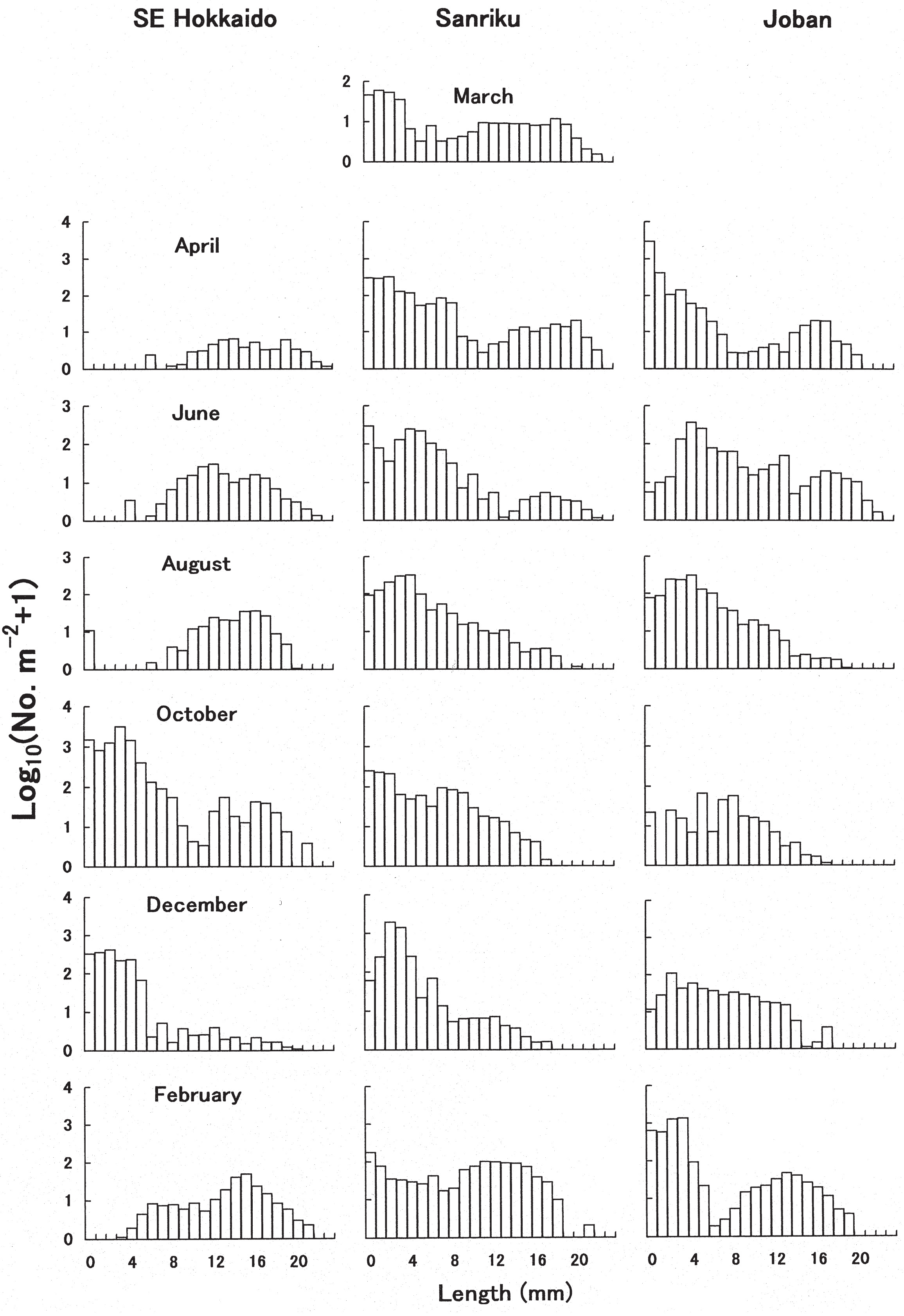

Fig. 5-1. Monthly size-frequency distribution of *Euphausia pacifica* from March 1997 to February 1998 along the three coastal areas: off southeastern Hokkaido, Sanriku and Joban.

4), therefore the daily average temperature for immature and adult stages was estimated to be the average temperature from 0 to 150m for each coastal area in March, April 1997 and February 1998. In summer, their median depths during daytime are about 300m, and those depths at night are deeper than the surface layer due to avoidance of high surface temperatures (see **Chapter 4**). The average temperature at the upper limit depth of $D_{80\%}$ (80% range of abundance from the median depth; Pennak, 1943) at night in summer was 17.4, 14.8 and 9.9℃ for immature stage, small adults (≦ 15mm) and large adults (>15mm), respectively. Therefore, the daily average temperature was estimated to be the average temperature from the depth of 17℃ to 300m for immature stage, from the depth of 15℃ to 300m for small adults and from the depth of 10℃ to 300m for large adults during June-December 1997.

The production of moults is given by the equation:

$$P_e = \sum_{i=1}^{S} (a \times \mathrm{DW}_i \times \mathrm{N}_i) / IP_i \quad (5.3)$$

where P_e is the moult production (mg C m^{-2} day^{-1}), DW_i is the dry weight of each size class, N_i is the average abundance of each size class, a is the percent loss in body DW per moulting (4.0%; Iguchi and Ikeda, 1999) multiplied by carbon content of moults (23% of dry weight; Iguchi and Ikeda, 1998), and IP_i is the intermoult period (days) of immatures and adults (>6mm) estimated from $\log_{10}IP_i = 0.321\mathrm{BL} + 10^{0.034-0.0435T}$, where T is in ℃ (Iguchi and Ikeda, 1995).

The production of eggs was computed by the equation:

$$P_r = E \times CW_e / D_e \quad (5.4)$$

where P_r is the egg production (mg C m^{-2} day^{-1}), E is the average abundance of eggs (number m^{-2}), De is the average hatching time calculated from De = 8.0925 × $e^{-0.1389T}$ [estimated from the relationship between hatching times and temperatures (Table 1 in Iguchi and Ikeda, 1994)] and CWe is the carbon weight of an egg (2.4 μg C; Iguchi and Ikeda, 1998).

The metabolism (M; mg C m^{-2} day^{-1}) was partitioned into two components; routine metabolism (M_{rtn}) and diurnal vertical migration metabolism (M_{div}) developed by Iguchi and Ikeda (1999). M_{rtn} was represented by the mean routine oxygen consumption rate (R: μl O_2 $\mathrm{indiv.}^{-1}$ hr^{-1}) of *E. pacifica* placed in a pressurized (40 atm) and unpressurized (1 atm) annular respirometer by Torres and Childress (1983), combined with the body exponent (0.85) of oxygen consumption rates obtained for an allied species *E. superba* by Ikeda (1984), i. e. $R = a\ \mathrm{DW}^{0.85}$. a = 1.03 at 8℃ (Torres and Childress, 1983). M_{div} is the amount of oxygen consumed in the diurnal vertical migration (R': μl O_2 $\mathrm{indiv.}^{-1}$ km^{-1}), which was calculated from the equation of net cost of transport as a function of weight (mg DW) of animals established for pelagic crustaceans ("multiple-paddle" propulsive system as compared with "undulatory" propulsion system of fish): $R' = 28.74\ \mathrm{DW}^{0.72}$ (Torres, 1984; the original equation based on energy units was modified using the oxycalorific equivalent of 1 cal = 208.33 μl O_2 and water content of *E. pacifica* (80%) by Iguchi and Ikeda (1999)). R' is independent of temperature in theory (cf. Morris *et al.*, 1990). Thus, each metabolism is given by equation:

$$M_{\mathrm{rtn}} = a \times 24 \times 10^{-3} \times b \times \Sigma\ \mathrm{DW}_i^{0.85} \times N_i \quad (5.5)$$

$$M_{\mathrm{div}} = d \times 10^{-3} \times 28.74 \times b \times \Sigma\ \mathrm{DW}_i^{0.72} \times N_i \quad (5.6)$$

where a (1.03 at 8℃) for each habitat temperature mentioned above is computed using the mean Q_{10} = 2.1 obtained in the experiment of Torres and Childress (1983), b (0.97 × 12/22.4) is conversion factor for oxygen (volume) to carbon (weight) assuming protein metabolism (RQ = 0.97; Gnaiger, 1983), DW_i is the dry weight of each size class, N_i is the average abundance of each size class, d is diurnal vertical migration distance (km) defined as above.

The carbon assimilated by *E. pacifica* (A: mg C m^{-2} day^{-1}) is defined as $A = P + M = P_g + P_e + P_r + M_{\mathrm{rtn}} + M_{\mathrm{div}}$, assuming no leakage of soluble organic matter from the body. The amount of ingested carbon (I: mg C m^{-2} day^{-1}) was computed by adopting an assimilation efficiency value of 84 % determined on *E. pacifica* by Lasker (1966), i.e. $I = A/0.84$.

Each production and metabolism (PM) of each coastal area and entire survey area during entire survey period was calculated as

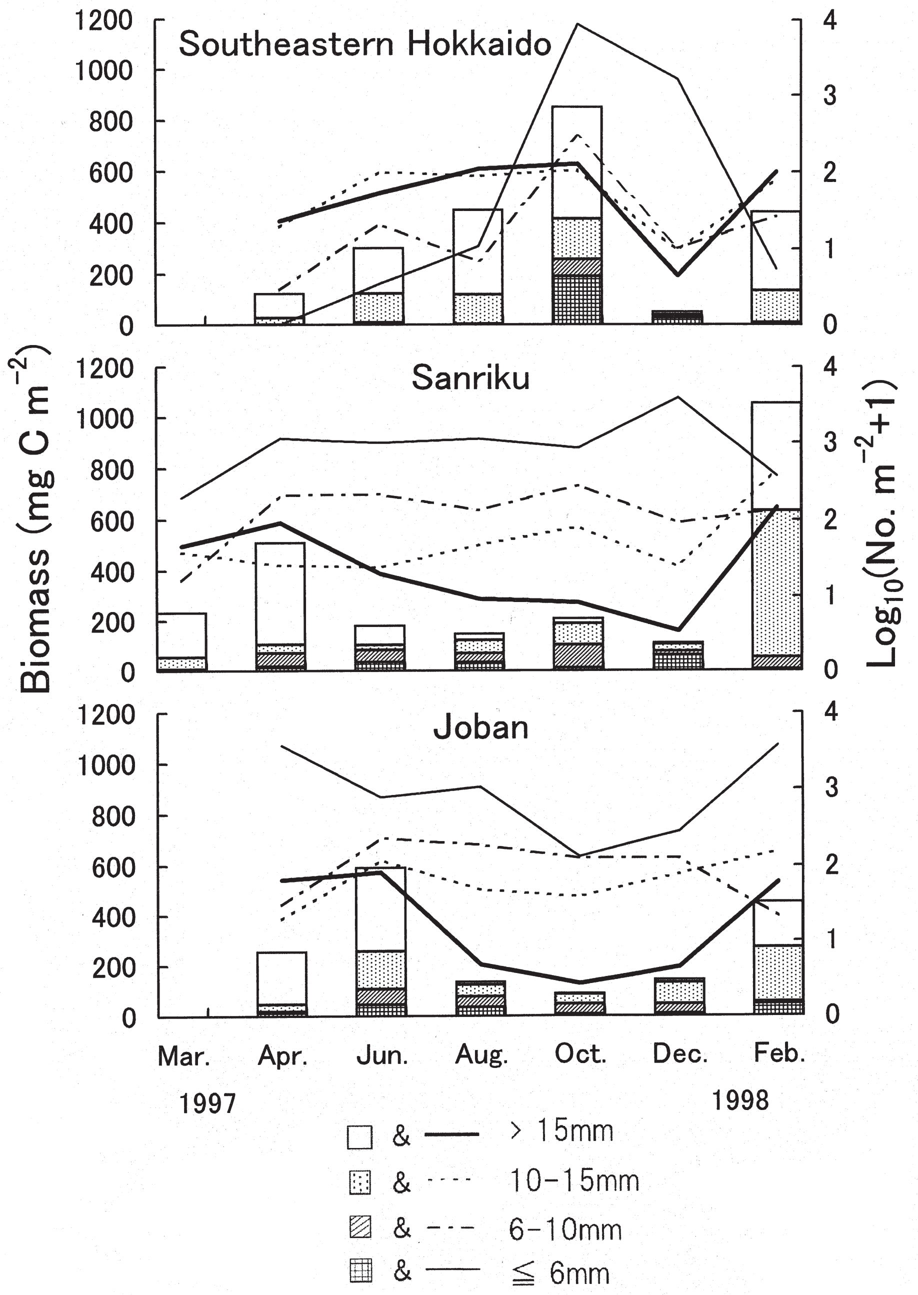

Fig. 5-2. Seasonal changes in the monthly average biomass (bars) and abundance (lines) by size class of *Euphausia pacifica* along the three coastal areas off northeastern Japan.

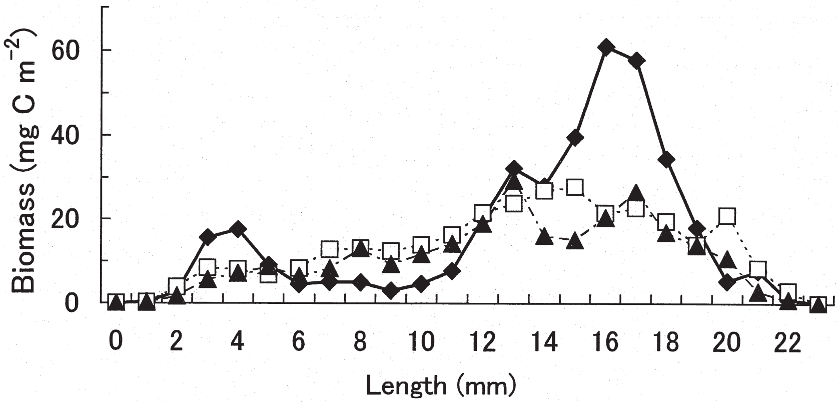

Fig. 5-3. Mean biomass for each size class of *Euphausia pacifica* along the three coastal areas off northeastern Japan. ◆: southeastern Hokkaido, □: Sanriku, ▲: Joban.

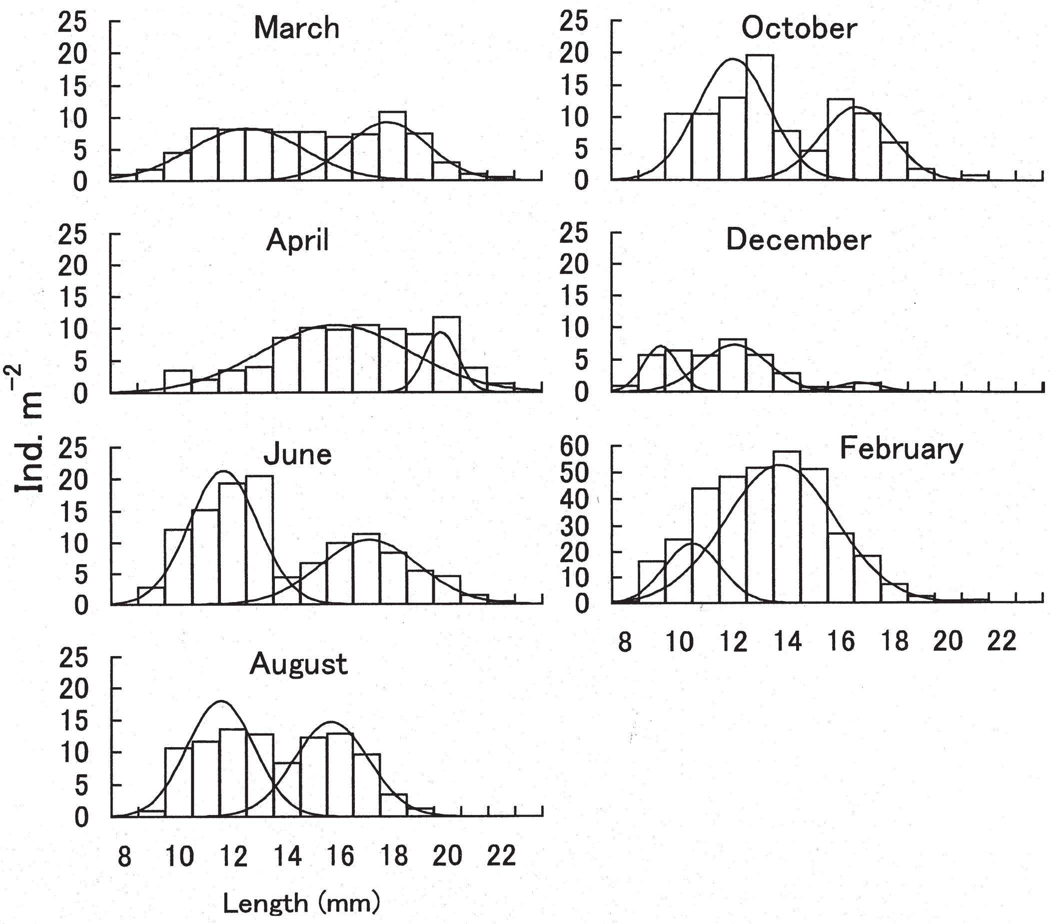

Fig. 5-4. Size-frequency distribution of adult *Euphausia pacifica* in the entire survey area off northeastern Japan. Hypothetical distribution curve of each cohort is superimposed using a computer program devised by Macdonald and Green (1988).

$$PM = \sum_{i=1}^{S} \left((PM_i + PM_{i+1}) \times d_{i,\, i+1}/2 \right) \quad (5.7)$$

where PM_i is daily each production and metabolism of ith survey, $d_{i,\, i+1}$ is days between ith survey and $(i+1)$th survey.

Results

Biomass

Off southeastern Hokkaido, the monthly biomass of *E. pacifica* increased from April to October, peaked at 852mg C m^{-2} in October and decreased after that (Fig. 5-2). Off Sanriku, the biomass was high in April (509mg C m^{-2}) and February (1,055 mg C m^{-2}), but was low from June through December (112-209 mg C m^{-2}). Off Joban, the biomass was high in April (254mg C m^{-2}), June (591mg C m^{-2}), and February (453mg C m^{-2}), but was low from August through December (90-104mg C m^{-2}). The relative contribution of large adults (>15mm) to the total biomass tended to be high in each coastal area when the total biomass was high.

Large adults of *E. pacifica* were most abundant in October off southeastern Hokkaido, and abundant in February, April and June off Sanriku and Joban (Fig. 5-2). So, high biomass tended to be recognized when large adults were abundant in each coastal area.

Annual mean biomass was 381mg C m^{-2}, 314mg C m^{-2} and 258mg C m^{-2} off southeastern Hokkaido, Sanriku and Joban, respectively (Table 5-1).

Annual mean biomass peaked among 13-19mm size classes commonly in each coastal area, with a

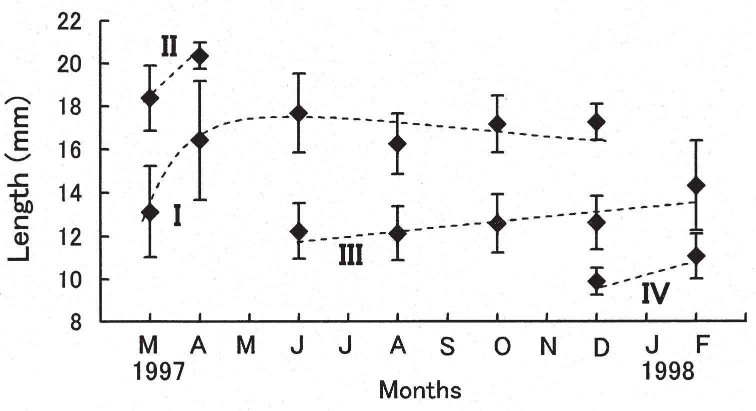

Fig. 5-5. Seasonal changes in the average length of each cohort of adult *Euphausia pacifica* estimated by size-frequency distributions in all coastal areas off northeastern Japan. Roman numerals indicate the cohort number. Lines: Hypothetical growth. Vertical bars: SD.

Table 5-1. Carbon budget (mg C m^{-2}) of *E. pacifica* along the three coastal areas off northeastern Japan during the survey period (313 or 356 days)

	SE Hokkaido (313 days)			Sanriku (356 days)			Joban (313 days)			Entire area (356 days)		
Mean biomass (B)	381			314			258			309		
		(% of P)	(% of A)		(% of P)	(% of A)		(% of P)	(% of A)		(% of P)	(% of A)
Somatic production (P_g)	1971	51.5%	25.7%	2178	56.3%	28.3%	1591	70.9%	30.0%	1983	57.7%	27.8%
Egg production (P_r)	1636	42.7%	21.3%	1414	36.5%	18.4%	410	18.3%	7.7%	1199	34.9%	16.8%
Moult production (P_e)	221	5.8%	2.9%	280	7.2%	3.6%	243	10.8%	4.6%	255	7.4%	3.6%
Gross production ($P=P_g+P_r+P_e$)	3829		49.9%	3872		50.3%	2243		42.3%	3438		48.2%
Routine Metabolism (M_{rtn})	2520		32.8%	2783		36.1%	2257		42.5%	2614		36.7%
Diurnal vertical migration metabolism (M_{div})	1325		17.3%	1044		13.6%	805		15.2%	1074		15.1%
Gross metabolism ($M=M_{rtn}+M_{div}$)	3846		50.1%	3827		49.7%	3062		57.7%	3688		51.8%
Assimillation ($A=P+M$)	7674			7699			5306			7126		
Ingestion ($I=A/0.84$)	9136			9166			6316			8483		
P_g:B	5.17			6.94			6.17			6.41		
P:B	10.05			12.34			8.70			11.12		
P:M	1.00			1.01			0.73			0.93		

second smaller peak among 3-5mm size classes off southeastern Hokkaido (Fig. 5-3). The relative biomass of size classes >10mm was considerably high, contributing 76.6-83.6% to the total in each coastal area.

Monthly mean biomass in all survey stations varied between 104 mg C m^{-2} (in December) to 685mg C m^{-2} (in February), and the annual mean biomass was 309mg C m^{-2} (Table 5-1).

Seasonal growth pattern

In the monthly average length-frequency distributions of adult *E. pacifica* in the all three coastal areas, two modal size groups were generally recognized (Fig. 5-4). It was difficult to rationally divide the size distribution for February into two modal groups based only on the length-frequency data. The groups for February were divided by considering the sequence of modal groups from June to December. Based on the modal growth pattern, average growth follows this pattern (Fig. 5-5): cohort I of

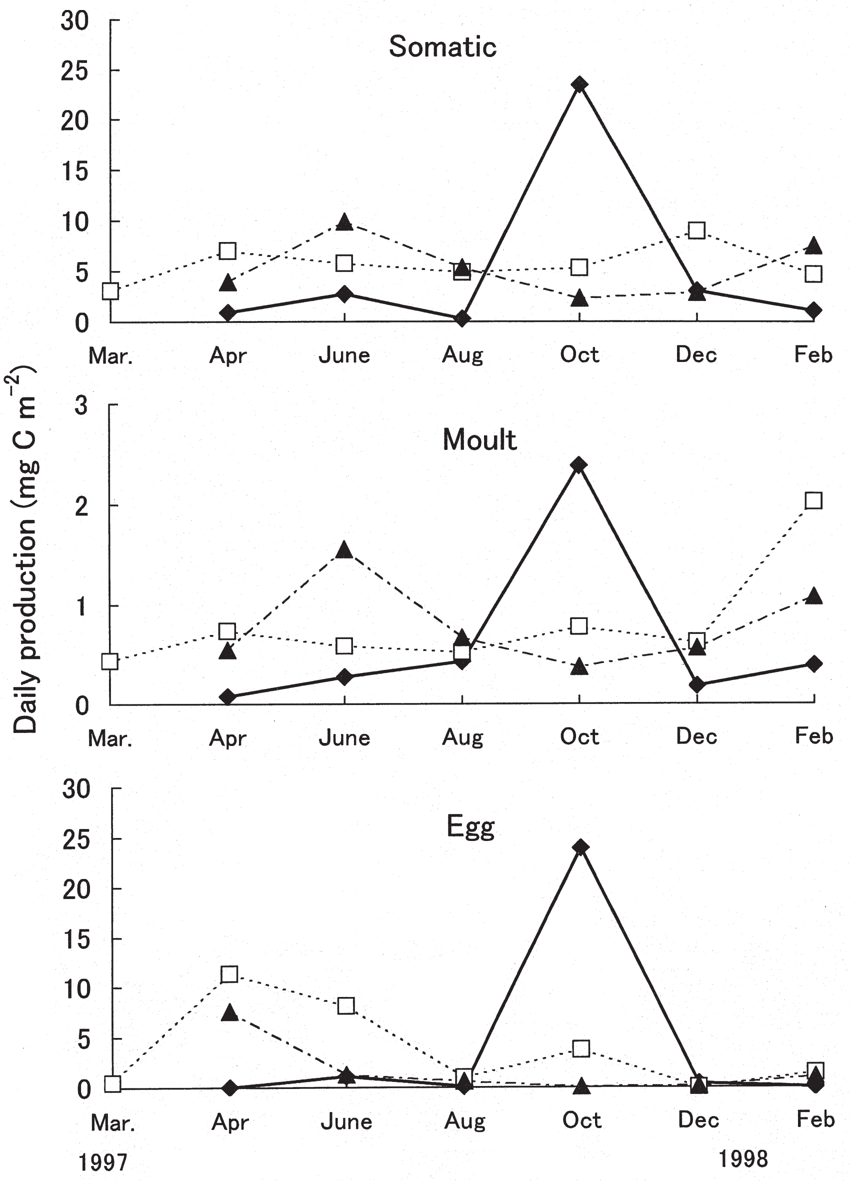

Fig. 5-6. Seasonal changes in daily production of somatic, moult and egg of *Euphausia pacifica* along the three coastal areas off northeastern Japan. The symbols are the same as shown in Fig. 5-3.

Table 5-2. Relative contribution (%) of each size class of *E.pacifica* to mean biomass (B), somatic producition (P_g), moult production (P_e), routine metabolism (M_{rtn}), diurnal vertical migration metabolism (M_{div}) and assimilation (A) achieved during survey period off SE Hokkaido

Development stage*	Size Class (mm)	%B	%P_g	%P_e	%M_{rtn}	%M_{div}	%A
Calyptopis	0～1	0.004	0.8	0.03	0.04	0	
	1～2	0.1	2.2	0.5	0.5	0	
	2～3	0.7	8.3	3.1	2.3	0.9	
Furcilia	3～4	4.1	30.3	17.3	12.4	6.0	
	4～5	4.6	24.5	16.1	11.2	6.4	
	5～6	2.4	9.8	5.8	4.2	3.5	
Immatures	6～7	1.2	4.0	2.1	1.6	2.7	
	7～8	1.3	3.9	2.2	1.8	2.5	
	8～9	1.3	3.3	2.0	1.6	2.0	≦10 mm
	9～10	0.8	1.7	0.9	0.8	1.2	40.6
Small adults	10～11	1.2	0.9	1.1	1.1	1.5	
	11～12	2.0	1.7	1.5	1.7	2.5	
	12～13	5.3	2.5	4.3	4.6	6.5	
	13～14	8.5	2.3	7.5	7.7	9.6	
	14～15	7.4	0.8	5.0	5.8	6.5	
Large adults	15～16	10.5	0.7	5.6	7.6	8.5	
	16～17	16.1	0.7	8.9	11.8	14.0	
	17～18	15.2	0.5	8.2	11.2	12.9	
	18～19	9.1	0.4	4.7	6.6	7.0	
	19～20	4.8	0.4	2.0	3.1	3.3	
	20～21	1.4	0.2	0.4	0.8	0.9	
	21～22	2.0	0.1	0.7	1.3	1.3	
	22～23	0.2	0.03	0.1	0.1	0.2	> 10 mm
	23～24	0.04	0	0.01	0.02	0.02	59.4
	Total	100	100	100	100	100	100

*Developmental stages should be considered as a rough guide.

Table 5-3. Relative contribution (%) of each size class of *E.pacifica* to mean biomass (B), somatic producition (P_g), moult production (P_e), routine metabolism (M_{rtn}), diurnal vertical migration metabolism (M_{div}) and assimilation (A) achieved during survey period off Sanriku

Development stage*	Size Class (mm)	%B	%P_g	%P_e	%M_{rtn}	%M_{div}	% A
Calyptopis	0～1	0.002	0.4	0.01	0.02	0	
	1～2	0.1	1.5	0.3	0.3	0	
	2～3	1.2	12.2	3.8	3.4	3.2	
Furcilia	3～4	2.7	16.8	7.7	6.3	6.8	
	4～5	2.6	11.6	6.5	5.2	4.9	
	5～6	2.1	7.4	5.2	4.1	3.4	
Immatures	6～7	2.6	7.7	4.6	3.8	6.0	
	7～8	4.0	10.0	6.7	5.5	6.6	
	8～9	4.2	9.0	5.9	5.0	6.3	≦10 mm
	9～10	3.9	7.5	5.4	4.7	5.1	44.6
Small adults	10～11	4.4	1.8	5.0	4.6	5.5	
	11～12	5.2	1.4	5.3	5.1	5.5	
	12～13	6.8	1.3	6.4	6.3	6.6	
	13～14	7.6	1.2	6.4	6.7	6.6	
	14～15	8.6	1.4	6.5	7.1	6.5	
Large adults	15～16	8.9	1.5	6.1	7.0	6.0	
	16～17	6.9	1.1	4.4	5.3	4.7	
	17～18	7.2	1.4	4.2	5.4	4.6	
	18～19	6.2	1.8	3.3	4.4	3.7	
	19～20	4.4	1.5	2.1	3.0	2.4	
	20～21	6.7	1.1	2.7	4.3	3.7	
	21～22	2.7	0.4	1.2	1.8	1.5	
	22～23	1.0	0.1	0.4	0.6	0.5	> 10 mm
	23～24	0.002	0	0.001	0.001	0.001	55.4
	Total	100	100	100	100	100	100

*Developmental stages should be considered as a rough guide.

Table 5-4. Relative contribution (%) of each size class of *E.pacifica* to mean biomass (B), somatic producition (P_g), moult production (P_e), routine metabolism (M_{rtn}), diurnal vertical migration metabolism (M_{div}) and assimilation (A) achieved during survey period off Joban

Development stage*	Size Class (mm)	%B	%P_g	%P_e	%M_{rtn}	%M_{div}	% A
Calyptopis	0～1	0.007	1.0	0.02	0.03	0	
	1～2	0.1	1.4	0.2	0.3	0	
	2～3	0.7	6.8	1.7	1.7	1.4	
Furcilia	3～4	2.2	13.4	4.3	4.0	4.9	
	4～5	2.8	12.3	6.3	5.3	4.8	
	5～6	3.4	11.7	7.1	5.8	5.3	
Immatures	6～7	2.5	7.2	4.3	3.6	5.1	
	7～8	3.2	7.9	5.1	4.3	5.6	
	8～9	5.0	10.8	7.5	6.4	7.6	≦10 mm
	9～10	3.6	6.8	4.8	4.2	5.4	46.9
Small adults	10～11	4.5	2.8	5.7	5.1	6.0	
	11～12	5.5	2.3	6.3	5.8	6.4	
	12～13	7.3	2.9	7.4	7.2	7.6	
	13～14	11.4	5.4	10.1	10.3	10.6	
	14～15	6.2	0.9	4.8	5.2	4.9	
Large adults	15～16	5.8	1.0	3.9	4.5	3.7	
	16～17	7.9	1.6	5.0	6.0	4.8	
	17～18	10.3	1.8	6.1	7.7	6.0	
	18～19	6.6	0.9	3.8	4.9	3.8	
	19～20	5.4	0.7	2.8	3.8	3.2	
	20～21	4.2	0.4	2.1	3.0	2.2	
	21～22	1.1	0.1	0.5	0.8	0.7	
	22～23	0.4	0.03	0.2	0.3	0.2	> 10 mm
	23～24	0	0	0	0	0	53.1
	Total	100	100	100	100	100	100

*Developmental stages should be considered as a rough guide.

about 13mm in March shows rapid growth through about 16mm in April to about 18mm in June with the growth rate being 0.077mm day^{-1} from March to April and 0.019mm day^{-1} from April to June. This cohort then shows no growth after June to December, and is likely to connect to cohort II of about 18mm in March if the seasonal growth pattern could be supposed to be invariable between years. Cohort II showed rapid growth (0.046mm day^{-1}) to about 20mm in April. There are two new cohorts in June (cohort III) and December (cohort IV) which seem to be spring-hatched and fall-hatched, respectively (see **Chapter 3**). Cohort III of about 12mm in June shows slow growth (0.008mm day^{-1}) to about 14mm in February. Cohort IV of about 10mm in December also shows slow growth (0.016mm day^{-1}) to about 11mm in February. Both of these newly-appearing cohorts are likely to connect to the cohort I of about 13mm in March if the seasonal growth pattern could be supposed to be invariable between years.

Production

Off southeastern Hokkaido, the production due to growth (P_g) was remarkably high (23.5mg C m^{-2}) in October, but was almost less than 3mg C m^{-2} in other months (Fig. 5-6). Higher P_g was observed in April (7.0mg C m^{-2}) and December (9.0mg C m^{-2}) off Sanriku and in June (9.9mg C m^{-2}) and February (7.6mg C m^{-2}) off Joban. The seasonal change off Sanriku and Joban was less dramatic than off southeastern Hokkaido. High P_g tended to be observed when high abundance of larvae occurred in each coastal area, and vice versa (see **Chapter 3**).

Off southeastern Hokkaido, the production due to moults (P_e) was high (2.4mg C m^{-2}) in October, but was almost less than 0.5mg C m^{-2} in other months (Fig. 5-6). Higher P_e was observed in February (2.0mg C m^{-2}) off Sanriku and, in June (1.6mg C m^{-2}) and next February (1.1mg C m^{-2}) off Joban. The seasonal change of P_e synchronized well with that of the biomass (Fig. 5-2) in each coastal area.

Off southeastern Hokkaido, the production due to eggs (P_r) was remarkably high (24.0mg C m^{-2}) in October, but was remarkably low in other months (Fig. 5-6). Off Sanriku, P_r was 11.3mg C m^{-2} in April and 8.1mg C m^{-2} in June, but was remarkably low in other months. Off Joban, P_r was 7.6mg C m^{-2} in April but remarkably low in other months. The seasonal change of P_r depended strongly on that of abundance of eggs in each coastal area (see **Chapter 3**).

The total production ($P = P_g + P_e + P_r$) during the survey period off southeastern Hokkaido (3,829mg C m^{-2}) was comparable with that off Sanriku (3,872mg C m^{-2}), but rather higher than that off Joban (2,243mg C m^{-2}) (Table 5-1). The rank of $P : B$ ratio during the survey period was Sanriku (12.34) > southeastern Hokkaido (10.05) > Joban (8.70). The production due to growth during the survey period ranged from 2,178mg C m^{-2} off Sanriku to 1,591mg C m^{-2} off Joban, contributing the highest proportion (51.5-70.9%) to the total production in each coastal area. The production due to moults during the survey period ranged from 280mg C m^{-2} off Sanriku to 221mg C m^{-2} off southeastern Hokkaido, contributing the lowest proportion (5.8-10.8%) to

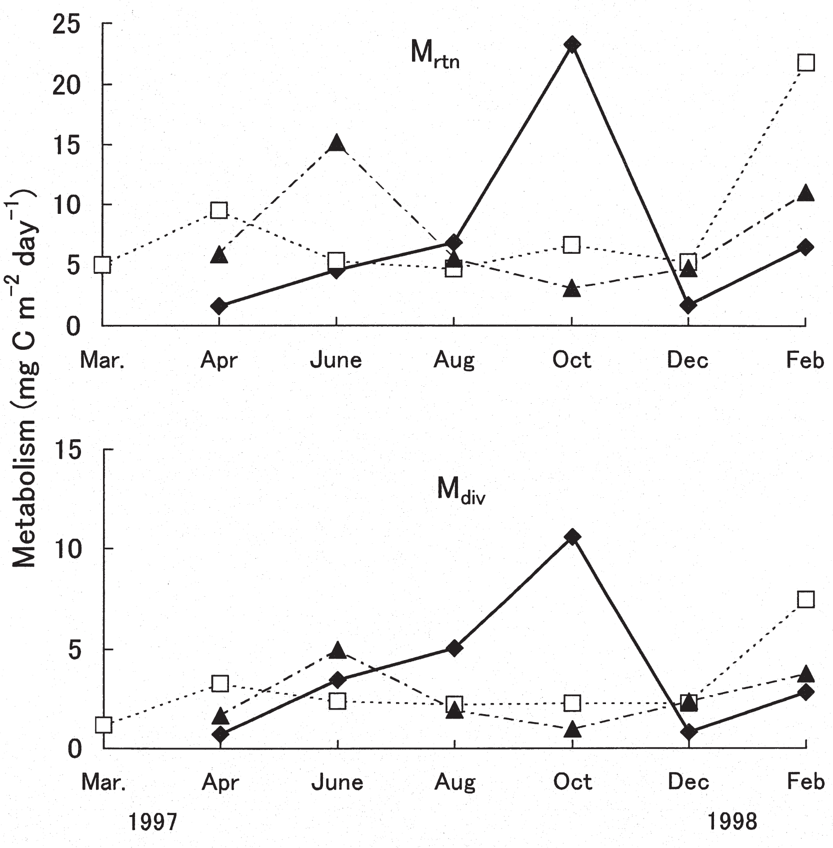

Fig. 5-7. Seasonal changes in carbon loss due to routine metabolism (M_{rtn}) and diurnal vertical migration metabolism (M_{div}) of *E. pacifica* along the three coastal areas off northeastern Japan. The symbols are the same as shown in Fig. 5-3.

Table 5-5. Relative contribution (%) of each size class of *E.pacifica* to mean biomass (B), somatic producition (P_g), moult production (P_e), routine metabolism (M_{rtn}), diurnal vertical migration metabolism (M_{div}) and assimilation (A) achieved during survey period off entire surveyarea

Development stage*	Size Class (mm)	%B	%P_g	%P_e	%M_{rtn}	%M_{div}	% A
Calyptopis	0~1	0.004	0.6	0.02	0.01	0	
	1~2	0.1	1.6	0.3	0.2	0	
	2~3	0.9	9.5	2.9	2.3	1.9	
Furcilia	3~4	2.8	19.0	8.8	7.1	5.8	
	4~5	3.1	15.0	8.6	6.6	5.3	
	5~6	2.4	8.9	5.8	4.4	3.7	
Immatures	6~7	2.0	6.4	3.8	3.0	4.5	
	7~8	2.8	7.6	5.0	4.0	4.8	
	8~9	3.3	7.8	5.3	4.4	5.0	≦10 mm
	9~10	2.5	5.2	3.8	3.1	3.5	42.4
Small adults	10~11	3.2	1.8	4.0	3.6	4.0	
	11~12	4.0	1.8	4.6	4.2	4.5	
	12~13	6.1	2.2	6.0	5.8	6.6	
	13~14	8.2	2.7	7.5	7.6	8.3	
	14~15	7.5	1.4	5.6	6.2	6.2	
Large adults	15~16	8.8	1.4	5.5	6.7	6.6	
	16~17	10.0	1.3	5.8	7.4	8.1	
	17~18	10.6	1.5	6.0	7.9	8.0	
	18~19	7.9	1.6	4.3	5.8	5.3	
	19~20	5.5	1.4	2.7	3.9	3.4	
	20~21	5.2	0.8	2.4	3.6	2.8	
	21~22	2.4	0.3	1.1	1.7	1.4	
	22~23	0.7	0.1	0.3	0.5	0.4	> 10 mm
	23~24	0.02	0	0.004	0.01	0.01	57.6
	Total	100	100	100	100	100	100

*Developmental stages should be considered as a rough guide.

the total production in each coastal area. The production due to eggs (1,636mg C m^{-2}) during the survey period off southeastern Hokkaido was slightly higher than that off Sanriku (1,414mg C m^{-2}), but about 4 times higher than that off Joban (410mg C m^{-2}). The total production across the entire survey area was 3,438mg C m^{-2} and the $P:B$ ratio was 11.12.

The relative contribution of each size class to the total somatic production during the survey period was high among 3-5mm size classes (25.8-54.8%) commonly in each coastal area (Tables 5-2-4). However, the relative contribution of size classes > 10mm was only 11.1-20.7% in each coastal area. The relative contribution of each size class to the total exuvial production during the survey period was high among 3-5mm size classes (33.4%) and 13-19mm (39.9%) off southeastern Hokkaido (Table 5-2). On the other hand, it was nearly constant across the wide size range (3-18mm) off Sanriku and Joban (Tables 5-3 and 4).

Metabolism

Off southeastern Hokkaido, the routine metabolism (M_{rtn}) was highest (23.3mg C m^{-2}) in October, but was less than 2mg C m^{-2} in April and December (Fig. 5-7). Higher M_{rtn} was observed in February (21.9mg C m^{-2}) off Sanriku and in June (15.2mg C m^{-2}) and February (11.1mg C m^{-2}) off Joban. The seasonal change of M_{rtn} synchronized well with that of the biomass (Fig. 5-2) in each coastal area.

Off southeastern Hokkaido, the diurnal vertical migration metabolism (M_{div}) was highest (10.6mg C m^{-2}) in October, but was less than 1mg C m^{-2} in

April and December (Fig. 5-7). Higher M_{div} was observed in February (7.5mg C m^{-2}) off Sanriku and in June (5.0mg C m^{-2}) off Joban. The seasonal change of M_{div} synchronized well with that of the biomass (Fig. 5-2) and M_{rtn} in each coastal area. The total metabolism ($M = M_{rtn} + M_{div}$) during the survey period off southeastern Hokkaido (3,846mg C m^{-2}) was comparable with that off Sanriku (3,827mg C m^{-2}), but higher than that off Joban (3,062mg C m^{-2}) (Table 5-2). The routine metabolism during the survey period ranged from 2,783mg C m^{-2} off Sanriku to 2,257mg C m^{-2} off Joban, contributing the highest proportion (32.8-42.5%) to the assimilation in each coastal area. The diurnal vertical migration metabolism during the survey period ranged from 1,325mg C m^{-2} off southeastern Hokkaido to 805mg C m^{-2} off Joban, contributing 13.6-17.3% to the assimilation in each coastal area. The total metabolism across the entire survey area was 3,688mg C m^{-2}, contributing 51.8% to the assimilation.

The relative contribution of each size class to the total routine metabolism during the survey period was high among 3-5mm size classes (23.6%) and 16-18mm (23.1%) off southeastern Hokkaido, but it was nearly constant across the wide size range (3-18mm) off Sanriku and Joban (Tables 5-2-4). The relative contribution of each size class to the total diurnal vertical migration metabolism during the survey period was similar to that to the total routine metabolism in each coastal area, but the relative contribution among 16-18mm (27%) was about 2 times higher than that among 3-5mm (12.4%) off southeastern Hokkaido.

Assimilation and ingestion

The assimilation (A) during the survey period off southeastern Hokkaido (7,674mg C m^{-2}) was comparable with that off Sanriku (7,699mg C m^{-2}), but rather higher than that off Joban (5,306mg C m^{-2}) (Table 5-1). The assimilation across the entire survey area was 7,126mg C m^{-2}. The ingestion (I) during the survey period ranged from 9,166mg C m^{-2} off Sanriku to 6,316mg C m^{-2} off Joban, and the ingestion across the entire survey area was 8,483mg C m^{-2}.

The relative contribution of larval size class ($\leqq$ 10mm) to the assimilation (thus also to the ingestion) during the survey period ranged from 41 to 47% in the coastal areas (Tables 5-2-5).

Discussion

Characteristics of biomass

High biomass was recognized when large adults were abundant in each coastal area (Fig. 5-2). The relative contribution of large adults to the total annual mean biomass was 51% across the entire survey area, while their relative contribution to the total annual mean abundance was only 2.6%. Therefore, the biomass is thought to be strongly affected by the occurrence of large adults which have a relatively high weight per individual. Annual mean biomass was low in the low latitudes due to the influence of the warmer Kuroshio waters through summer and fall which large adults avoid (see **Chapter 3**).

The biomasses of several euphausiid species from several regions are shown in Table 5-6. Water content and carbon content are assumed to be 80 % and 43 %, respectively and converted to carbon weight (mg) per square meter or dry weight (mg) per 1,000 cubic meters from original units in the literature (Brinton and Reid, 1986; Gomez-Gutierrez and Robinson, 1997; Heath, 1977; Tanasichuk, 1998a; Gomez-Gutierrez *et al.,* 1996; Hirota *et al.,* 1982; Lavaniegos, 1995; Mauchline, 1977; Siegel, 2000; Tanasichuk, 1998b). The annual mean biomass of *E. pacifica* in the coastal waters off northeastern Japan was lower than that at Saanich Island (Heath, 1977) and off Oregon (Mauchline, 1977) in the upstream California Current, but higher than that off southern California (Brinton, 1976) and off Baja California (Gomez-Gutierrez and Robinson, 1997) in downstream California Current. The tendency for the biomass of *E. pacifica* to be higher in the higher latitudes of the eastern Pacific is identical with the trend along the coastal waters off northeastern Japan.

The annual mean biomass of 1,090mg C m^{-2} for *E. pacifica* in Toyama Bay was about three times higher than that found along the coastal waters off northeastern Japan (Iguchi *et al.,* 1993). The annual mean abundance of eggs of *E. pacifica* was 2,749 inds m^{-2} in Toyama Bay (calculated from Table 1 in Iguchi *et al.* (1993)), which is nearly identical with

Table 5-6. Biomass and *P:B* ratios of euphausiids from net sampling surveys [*1]

Species	Geographic region	Biomass (mg C m^{-2})	*P*:*B* from growth	*P*:*B* from moults	*P*:*B* from eggs	References
Euphausia pacifica	Saanich Island, Canada	2025.3[*2]	2.6[*3]			Heath (1977)
Euphausia pacifica	Barkley Sound, Canada	301–624 (384)[*4]	6.4–16.7(11.0)	0.9–1.4 (1.2)[*5, 6]		Tanasichuk (1998a)
Euphausia pacifica	Oregon, USA	1125[*7]	8.7			Mauchline (1977)
Euphausia pacifica	Southern California, USA (Jan.)	17–163 (112)[*8]				Brinton and Reid (1986)
Euphausia pacifica	Southern California, USA (Apr.)	77–166 (107)[*8]				Brinton and Reid (1986)
Euphausia pacifica	Baja California, Mexico	38[*4]				Gomez-Gutierrez& Robinson (1997)
Euphausia pacifica	Toyama Bay, Japan	1,090	3.8	1.1	1.1	Iguchi and Ikeda (1999)
Euphausia pacifica	Northeastern Japan	258–381(309) [3,362–5,852 (4,300)][*9]	5.2–6.9 (6.4)	0.6–0.9 (0.8)	1.6–4.5 (3.9)	This study
Euphausia similis	Sagami Bay, Japan	102	4.8			Hirota *et al*. (1990)
Euphausia nana	Sagami Bay, Japan	25[*8]				Hirota *et al*. (1982)
Euphausia lucens	Benguela Current	[9,750–47,290 (22,480)][*9]	3.9–8.9 (6.9)	3.2–3.3 (3.3)[*5]	0.3–1.0 (0.6)[*10]	Stuart and Pillar (1988)
Euphausia superba	Antarctic Peninsula	387–527 (457)	0.83–1.1 (1.0)			Siegel (1992)
Euphausia superba	Elephant Island	86–2,683(903)[*8]				Siegel (2000)
Euphausia superba	Antarctic, Indian Ocean		1.53			Miller *et al*. (1985)
Meganyctiphanes norvegica	North Atlantic and North Sea	[140–13,990 (1,983)][*9]	1.3–6.3 (3.5)			Lindley (1982)
Meganyctiphanes norvegica	Rockall Trough, Britain		1.6			Mauchline (1985)
Nematoscelis microps	Sagami Bay, Japan	30[*8]				Hirota *et al*. (1982)
Nematoscelis gracilis	Sagami Bay, Japan	11[*8]				Hirota *et al*. (1982)
Nematoscelis megalops	Rockall Trough, Britain		3.4			Mauchline (1985)
Nematobrachion boopis	Rockall Trough, Britain		1.2			Mauchline (1985)
Nyctiphanes simplex	Baja California, Mexico	44[*4]	12.7	2.1[*5]	0.3[*10]	Lavaniegos (1995)
Nyctiphanes simplex	Baja California, Mexico	17[*4]	6.99			Gomez-Gutierrez *et al*. (1996)
Nyctiphanes australis	Storm Bay, Tasmania	[5,389][*9]	14.5	4.2[*5]	0.9[*10]	Hosie and Ritz (1983)
Nyctiphanes couchi	North Sea	[150–2,070 (700)][*9]	4.0–5.5 (4.5)			Lindley (1982)
Stylocheiron maximum	Rockall Trough, Britain		2.5			Mauchline (1985)
Thysanopoda acutifrons	Rockall Trough, Britain		2.3			Mauchline (1985)
Thysanoessa spinifera	British Columbia	147–547 (323)[*4]	11.1–35.0 (18.7)	0.8–1.8 (1.0)[*5, 6]		Tanasichuk (1998b)
Thysanoessa inermis	North Sea & east coast of USA	[690–2,370 (1,112)][*9]	1.4–6.1 (2.8)			Lindley (1980)
Thysanoessa longicaudata	North Atlantic	[70–2,360 (1,088)][*9]	1.2–11.6 (4.1)			Lindley (1978)
Thysanoessa longicaudata	Rockall Trough, Britain		6.4			Mauchline (1985)
Thysanoessa raschi	Gulf of St. Lawrence	[470][*9]	3.8			Berkes (1977)
Thysanoessa raschi	North Sea & east coast of USA	[310–1,600 (778)][*9]	1.3–10.4 (4.0)			Lindley (1980)

[*1] Note that mean values are shown in parentheses, and some values are converted from original ones to compare with the standardized units or assumptions described in the literature or below this table.

[*2] Conversion from mg WW m^{-3}

[*3] Recalculated value by Iguchi and Ikeda (1999)

[*4] Conversion from mg DW m^{-2}

[*5] Assuming that moult carbon content to be 23 % of DW.

[*6] Assuming that proportion of body DW lost per molting to be 4% becaue of the possibility of overestimating of the proportion (10.6–11.6 %) in the literature (see Iguchi and Ikeda (1999)) .

[*7] Conversion from mg DW $1000m^{-3}$

[*8] Conversion from mg WW m^{-2}

[ ][*9] mg DW $1000m^{-3}$

[*10] Assuming that proportion of egg carbon content to be 47 % of DW.

the value of 2,894 inds m^{-2} for the entire survey area off northeastern Japan. However the annual mean abundance of adults in Toyama Bay (822 inds m^{-2}) is about seven times higher than that of the entire survey area off northeastern Japan (122 inds m^{-2}), so such large difference in annual mean biomass is thought to attribute to the large difference in annual mean abundance of adults. The mortality rate of fall-winter hatching may be higher than that of spring hatching off northeastern Japan because of unfavorable feeding condition during fall and winter as shown by the low abundance of phytoplankton, microzooplankton and mesozooplankton (Kasai *et al.,* 2001; Kotani *et al.,* 1996; Odate, 1994). Therefore, the annual average recruitment rate off northeastern Japan is suggested to be lower than that in Toyama Bay where spawning occurred limitedly in spring phytoplankton bloom (Iguchi *et al.,* 1993).

Off the Pacific coast of Japan, the biomass of *E. pacifica* is much higher than that of southern warmer species in Sagami Bay (Hirota *et al.,* 1982; Hirota *et al.,* 1990) (Table 5-6). However, no latitudinal trend is found between different species in the global level. For example, the biomass of subarctic species such as *Thysanoessa rachi* and *T. inermis* in the north Atlantic (45-60°N) is much lower than the mean biomass of subarctic-transitional *E. pacifica* off northeastern Japan (36-43°N). It should noted, however, that subarctic species in the north Atlantic studied by Lindley (1978; 1980; 1982) were only sampled the upper 10m layer by day and night, which may have led to underestimation of euphausiid biomass due to the vertical migratory behavior. The survey using with the same gear and methods is needed to compare the biomass of euphausiid species correctly.

Characteristics of production and assimilation

The relative contribution of larval and immature specimens (＜10mm) of *E. pacifica* to the total somatic production during the survey period was high (79-89%), although their contribution to the total annual mean biomass was only 14-24% in each coastal area. This is due to the high growth rate of larvae and immature specimens as compared to adult specimens. This tendency was also recognized for *E. pacifica* from Barkley Sound, where the annual production due to growth and moults of larval and immature specimens (＜9mm) showed the high proportion to the total (25-72% and 7-46%), although their annual mean biomass showed the low proportion to the total (14-24%) from 1991 to 1997 (Tanasichuk, 1998a).

Annual $P_g : B$, $P_e : B$ and $P_r : B$ ratios of several euphausiids are shown in Table 5-6. The previous measurements were standardized to carbon units by assuming the same carbon content as *E. pacifica* in this study: 43% of DW for the body, 23% of DW for moults, and 47% of DW of eggs.

The annual $P_g : B$ ratio tends to be high (ca. 9-15) for euphausiids that show continuous occurrences of larvae throughout the year and high growth rates, such as *E. pacifica* and *Thysanoessa spinifera* off Barkley Sound (Tanasichuk, 1998a; 1998b), *E. pacifica* off Oregon (Mauchline, 1977), *N. simplex* off Baja California (Gomez-Gutierrez and Robinson, 1997; Lavaniegos, 1995) and *Nyctiphanes australis* off Storm Bay, Tasmania (Hosie and Ritz, 1983). Meanwhile, the annual $P_g : B$ ratio tends to be low (ca. 1-4) for euphausiids which have short spawning periods and slow or long stagnated growth, such as *E. superba* (Miller *et al.,* 1985; Siegel, 1992), *M. norvegica* (Lindley, 1982; Mauchline, 1985) and *Thysanoessa spp.* (except for *T. longicaudata* in the North Atlantic Ocean) (Lindley, 1978; 1980). The $P_g : B$ ratio (5.2-6.9) of *E. pacifica* along the coastal waters off northeastern Japan was intermediate between these two groups due to the stagnant growth of adults during summer-winter coupled with the continuous occurrence of larvae which show high growth rate throughout the year off Sanriku and Joban and the considerably numerous larvae occurring in October off southeastern Hokkaido (see **Chapter 3**). In Toyama Bay seasonal growth pattern of adult *E. pacifica* is similar to that off northeastern Japan but the occurrence of larval stages was limited only in spring (Iguchi *et al.,* 1993). So, $P_g : B$ ratio in Toyama Bay (3.8) is rather lower than that off northeastern Japan (Table 5-6).

The annual $P_e : B$ (ca. 1.0) of *E. pacifia* both in the eastern and western Pacific Ocean was much lower than that of *N. australis* (4.2) in Storm Bay and *E. lucens* (3.2-3.3) in the Benguela Current. This was mainly due to the long interval of moults in *E. pacifica* as compared with that in *N. australis* and *E. lucens.* The interval in *E. pacifica* was 3-10 days for larvae-immatures and 8-22 days for adults along the coastal waters off northeastern Japan, and was 3-4 days for larvae-immatures and 4-6 days for adults in *N. australis* and *E. lucens.*

Iguchi and Ikeda (1999) showed that the relative proportion of egg production to the total production ($P_g + P_e + P_r$) in *E. pacifica* was 20.6% in Toyama Bay, which is comparable to the value of 26.5% for the same species in the northern North Pacific (Lasker, 1966) and thus supposed that *E. pacifica* is a euphausiid characterized by a higher investment of carbon in egg production. *E. pacifica* along each coastal area off northeastern Japan also showed high proportion of egg production (18-43%) to the total production despite the limited spawning season. The low exuvial production due to relatively long interval of moults mentioned above is thought to increase the relative proportion of egg production in *E. pacifica.* The annual $P_r : B$ ratio (1.6-4.5) of *E. pacifica* along the coastal waters off northeastern Japan was higher than that (1.1) in Toyama Bay. This may attribute to unfavorable recruitment or underestimation of biomass due to cohesive aggregation along the coastal waters off northeastern Japan as compared with Toyama Bay mentioned above.

Metabolism of *E. pacifica* had been only calculated for Toyama Bay population by Iguchi and Ikeda (1999). $P : M$ ratio (0.73-1.0) along each coastal waters off northeastern Japan during survey period was significantly higher than that in Toyama Bay (0.41) (Table 5-1). One of the reasons attribute to higher $P_g : B$ and $P_r : B$ ratios off northeastern as mentioned above. The other reason is that both $M_{\mathrm{rtn}} : B$ and $M_{\mathrm{div}} : B$ ratios along the coastal waters off northeastern Japan (6.7-8.9 and 3.1-3.5, respectively) is lower than that in Toyama Bay (10.0 and 4.8, respectively). Lower $M_{\mathrm{rtn}} : B$ and $M_{\mathrm{div}} : B$ ratios off northeastern Japan attribute to lower habitat temperatures or lower coefficient a in equations (5. 5) (e. g. average of 6.7℃ off northeastern Japan vs. 8.0℃ in Toyama Bay for large adults) and shorter diurnal vertical migration or coefficient d in equation (5. 6) (e.g. average of 0.31km off northeastern Japan vs. 0.4-0.6km in Toyama Bay for large adults), respectively. However it should be noted that the shorter diurnal vertical migration is closely related to shallow sea bottom depths at onshore stations which could interrupt descending toward deeper depths in daytime usually conducted in offshore area.

Chapter 6. Feeding of *Euphausia pacifica*

Endo (1981) and Nakagawa *et al.* (2001) studied the seasonal changes in stomach contents of *Euphausia pacifica* in Sanriku waters. Off northeastern

Table 6-1. Locations of stations, times of sampling, number of samples and total length of *Euphausia pacifica* examined for the southeastern Hokkaido and Joban waters

	Latitude	Longitude	Depth (m)	Day	Time	Number of samples	Range of total length (mm)	Mean total length ±SD
SE Hokkaido	42°20'N	143°45'E	295	Apr. 15 '97	2:47	20	13.5–21.0	17.4±2.6
	42°30'N	145°00'E	1790	Jun. 21,'97	21:58	9	11.7–18.9	16.1±2.3
	42°40'N	144°55'E	540	Aug. 6,'97	21:29	20	13.3–19.5	16.4±1.6
	42°40'N	144°55'E	540	Oct. 1,'97	0:08	20	12.6–18.5	16.7±1.6
	42°40'N	144°55'E	540	Dec. 9,'97	18:21	10	12.0–18.4	14.6±2.0
	42°40'N	144°55'E	540	Feb. 25,'98	22:04	20	14.5–20.3	16.4±1.5
Joban	37°35'N	141°36'E	219	Apr. 22,'97	0:43	20	13.2–18.1	15.8±1.2
	36°50'N	141°15'E	179	Jun. 24,'97	0:09	20	12.5–22.3	16.8±2.2
	36°50'N	141°16'E	200	Aug. 2,'97	1:26	20	10.1–14.3	11.8±1.1
	36°50'N	141°17'E	208	Oct. 5,'97	20:43	20	12.0–17.0	13.4±1.3
	36°50'N	141°17'E	208	Dec. 11,'97	22:40	8	10.0–12.6	11.2±1.0
	36°50'N	141°16'E	200	Feb. 28,'98	22:35	20	14.0–17.2	15.7±1.0

Japan, however, the food habits of *E. pacifica* have been studied only in Sanriku waters. Studies on the comparison of the food habits of *E. pacifica* between different water masses is important to understand the structure of marine ecosystems off northeastern Japan.

In this chapter, seasonal changes in stomach contents of *E. pacifica* was surveyed in the coastal waters off southeastern Hokkaido and Joban. From the results, how diets and feeding behavior change according to ambient food conditions were examined. In addition, the significance of ingestion of copepods by *E. pacifica* was compared between the coastal waters off northeastern Japan.

Materials and Methods

Cylindrical-conical net samples collected bimonthly from April 1997 to February 1998 in the southeastern Hokkaido waters (about 42°40'N) and the Joban waters (about 36°50'N) (see **Chapter 3**) were used for the analysis of stomach contents of *Euphausia pacifica* (Table 6-1). The profiles of temperature and salinity were determined using CTD (Sea-Bird) or STD (Alec Electronics).

A 100 ml water sample was collected from each of 6 depths (0, 10, 20, 30, 50, 75m), filtered through a Whatman GF/F glass fiber filter, and analyzed by the method of Yentsch and Menzel (1963) with a Hitachi 139 spectrofluorometer for chlorophyll *a*. *Chlorophyll a* was integrated over the upper 75 m, and then averaged for each cruise.

Eight to ten adult *E. pacifica* were sorted randomly from each station, and their total length, from the anterior tip of the rostrum to the distal end of the telson, was measured. A total of 207 stomachs were dissected out and the contents spread on glass slides. Stomachs were examined under a dissecting microscope, and scored into 5 classes based on their fullness: empty stomachs (class 0), less than 25% full (class I), 25-50% full (class II), 50-75% full (class III), more than 75% full (class IV).

Food organisms were identified, enumerated and dimensions measured to allow calculation of both the total carbon content of the stomach contents and the relative contribution of the various prey types. The carbon contents of diatoms and dinoflagellates were estimated from cell volumes according to Strathmann (1967). Tintinnid carbon was estimated from the lorica volume according to Verity and Langdon (1984). Invertebrate eggs found in the stomachs were thought to be copepod eggs and carbon content was estimated from the egg size using a conversion factor of 0.14 pgC μm^{-3} (Kiorboe *et al.*, 1985). Copepods in the stomach were identified from their hard structures, mandibles, and their number was determined from the number of pairs of mandible blades of a given size. Total length of copepods was measured when found intact in the stomach. The carbon content of copepods was obtained by estimating the prosome length from the width of the mandible blades using the equation of Karlson and Bamstedt (1994), then calculating the dry mass from the prosome length of the copepod and assuming that 46% of the dry mass was carbon (Vidal, 1980). The carbon contents of intact copepods in the stomach were calculated from the total length using the equation of Hirota (1986).

Body carbon of *E. pacifica* was estimated from the total length using the equation of total length vs. dry weigh from Iguchi and Ikeda (1995) and conversion factor from the dry weight to carbon weight in different size classes of *E. pacifica* from Iguchi and Ikeda (1998).

Daily carbon ingestion of *E. pacifica* was calculated based on the gut passage time of 1.08 hr (Willason and Cox, 1987) and constant feeding limited from sunset to sunrise.

Results

Along the coastal waters off southeastern Hokkaido, waters with temperatures less than 2℃ occurred from the surface to 300m depth and coastal Oyashio waters with salinities less than 33.0 PSU occurred in the upper layer shallower than 100m in April (Fig. 6-1). Surface water temperatures rose from April to October. Surface water temperature was about 13℃ but less than 5℃ in the deeper layer than 75m in October. The surface water temperatures dropped after October and coastal Oyasshio waters with temperatures less than 1℃ and salinities less than 33.0 PSU in the upper layer than 50m. Along the coastal waters off Joban, water temperature in the total water column rose from April to October and the surface water temperature was about 22℃ in August and October. Waters with temperatures higher than 5℃ and salinities higher than 33.7 PSU were dominant from April to December. However, waters with temperatures less than 7℃ and salinities less than 33.7 PSU occurred in the upper layer than 30m.

Along the coastal waters off southeastern Hokkaido, chlorophyll *a* concentration was extremely high, 11.7 μ gl^{-1} in the surface layer in April and it was 4.2 μ gl^{-1} in 30m (Fig. 6-1). However, it was less than 0.5 μ gl^{-1} over the total water column in August. It was 1.4 μ gl^{-1} over the surface layer in October and 0.8 μ gl^{-1} in the upper layer than 50min December. It was less than 0.4 μ gl^{-1} in the total water column in February. Along the coastal waters off Joban, chlorophyll *a* concentration was 1.7 μ gl^{-1} in the surface layer in April and it was 0.7-0.9 μ gl^{-1} in 30-50m. However, it was less than 0.3 μ gl^{-1} in the total water column from August to December. It was 0.91-0.96 μ gl^{-1} in 30-50m. Thus, chlorophyll *a* concentration off the southeastern Hokkaido tended to be higher than that off Joban throughout the year.

Along the coastal waters off southeastern Hokkaido, the percentage of *E. pacifica* with a half or more stomach fullness (classes III and IV) was 100 % in February and it was 80 % in April and August (Fig. 6-2). On the other hand, the percentage of *E. pacifi-*

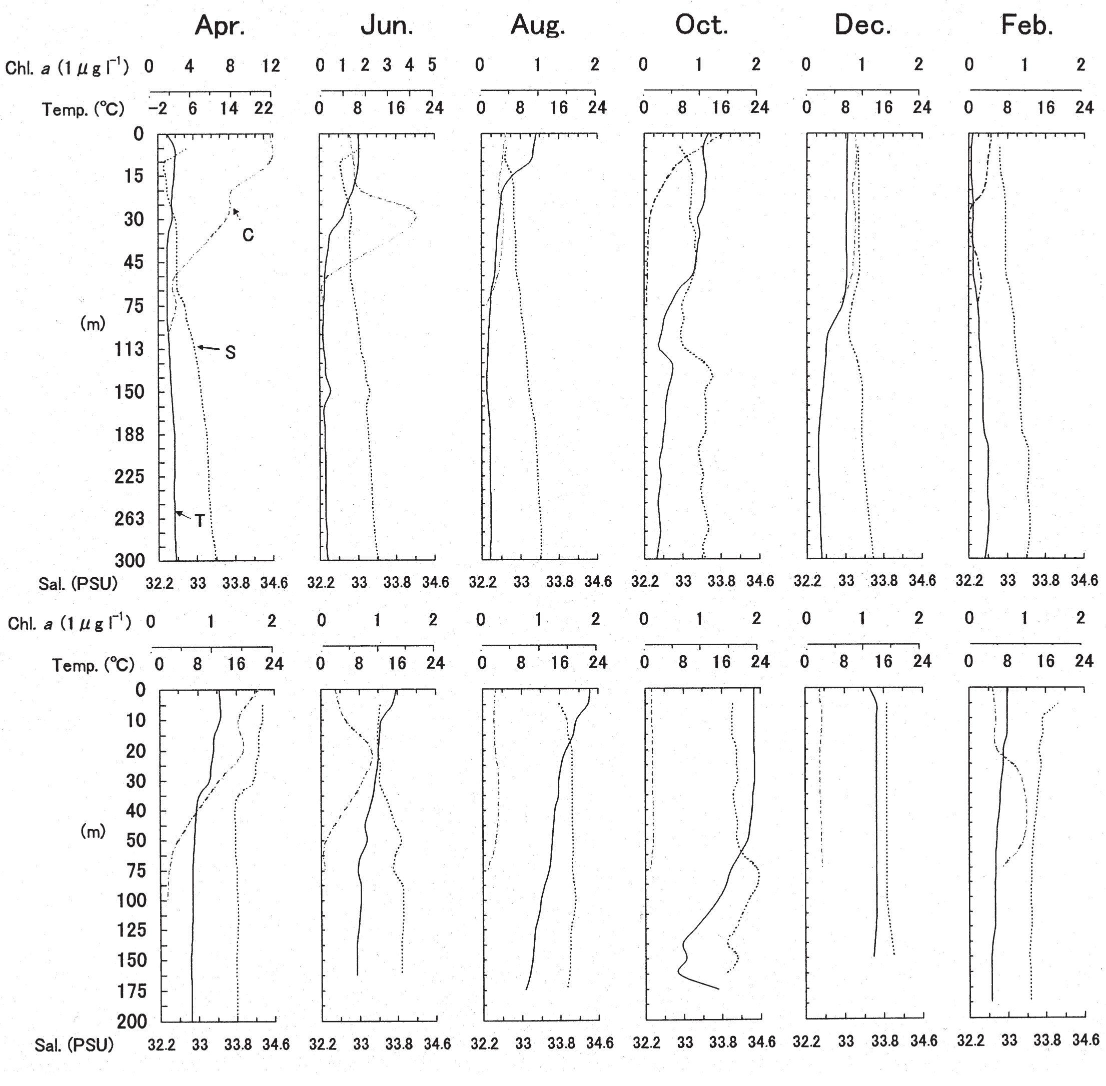

Fig. 6-1. Vertical profiles of water temperature, salinity and chlorophyll *a* in the southeastern Hokkaido waters (top) and Joban waters (bottom).

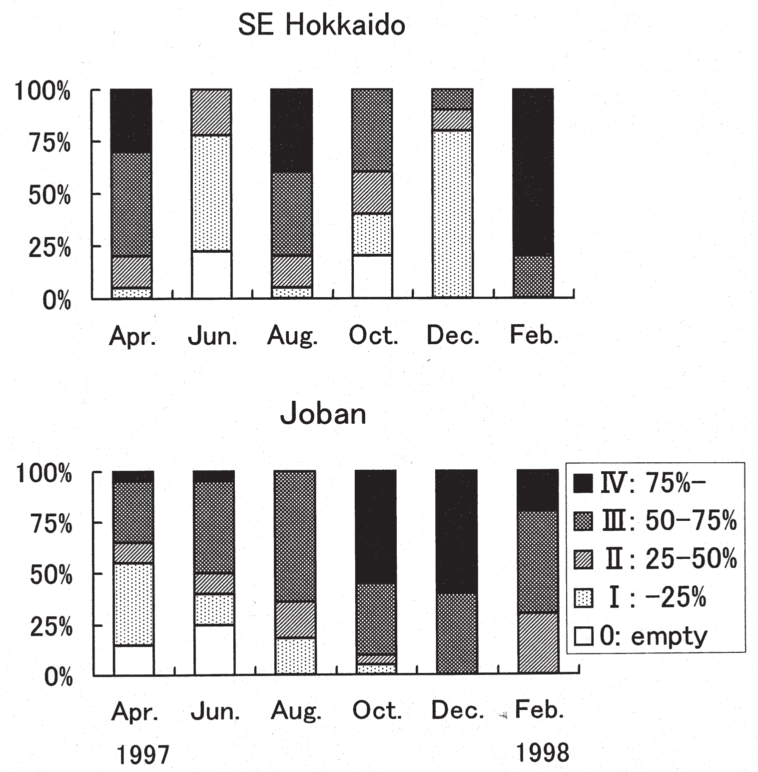

Fig. 6-2. Seasonal change in the stomach fullness composition of *Euphausia pacifica*.

ca with empty or a quarter stomach fullness (classes 0 and I) was 79 % and 80 % in June and December, respectively. Along the coastal waters off Joban, the percentage of *E. pacifica* with a half or more stomach fullness (classes III and IV) was 90 % and 100 % in October and December, respectively. On the other hand, the percentage of *E. pacifica* with empty or a quarter stomach fullness (classes 0 and I) was 65 % and 40 % in April and June, respectively.

Identifiable food items found in the stomach contents of *E. pacifica* were classified into 9 groups (diatoms, dinoflagellates, tintinnids, invertebrate eggs, copepod mandibles, foraminiferans, silicoflagellates, copepod nauplii and appendicularian houses). Frequency of occurrence of diatoms, dinoflagellates and tintinnids tended to be high throughout the year off both coastal waters and that of diatoms was generally higher than 70% off the southeastern Hokkaido (Table 6-2). The frequency occurrence of copepod mandibles off Joban was higher than that off southeastern Hokkaido throughout the year except February and August. Copepod nauplii occurred only in August off Joban and in October off southeastern Hokkaido.

Along the coastal waters off southeastern Hokkaido, diatoms in the stomach of *E. pacifica* were abundant (154 cells krill^{-1}) (Fig. 6-3). Dinoflagellates were abundant in August (24 cells krill^{-1}) and February (14 cells krill^{-1}). Tintinnids were abundant in October (19 cells krill^{-1}) and February (21 cells krill^{-1}). Invertebrate eggs were abundant in October (0.5 inds krill^{-1}) and February (0.4 inds krill^{-1}). Copepods were abundant in August and October (both 0.4 inds krill^{-1}) but were lower than those off Joban throughout the year.

Along the coastal waters off Joban, diatoms in the stomach of *E. pacifica* were abundant in February (121 cells krill^{-1}) and October (25 cells krill^{-1}) (Fig. 6-3). However they were scarce from April to August and in December. Dinoflagellates were abundant from April to August (3.4-8.5 cells krill^{-1}) but were scarce from October to February (0.9-1.6 cells

Table 6-2. Frequency of occurrence (%) of identifiable food items in gut contents of *Euphausia pacifica*

	Apr.'97	Jun.'97	Aug.'97	Oct.'97	Dec.'97	Feb.'98
Diatoms						
SE Hokkaido	100	67	90	75	80	80
Joban	80	5	15	90	100	100
Dinoflagellates						
SE Hokkaido	65	0	100	75	20	100
Joban	45	30	40	55	100	100
Foraminiferans						
SE Hokkaido	0	0	9	5	10	80
Joban	5	5	0	20	13	10
Tintinnids						
SE Hokkaido	45	44	100	75	70	100
Joban	10	45	30	10	50	70
Invertebrate eggs						
SE Hokkaido	15	0	40	20	20	45
Joban	0	15	35	20	30	25
Copepod mandibles						
SE Hokkaido	0	11	35	10	0	25
Joban	20	35	15	35	25	20
Copepod nauplii						
SE Hokkaido	0	0	0	5	0	0
Joban	0	0	35	0	0	0
Silicoflagellates						
SE Hokkaido	5	0	5	70	0	10
Joban	35	0	10	5	100	45
Appendicularian houses						
SE Hokkaido	0	0	10	10	0	0
Joban	35	5	0	70	88	0

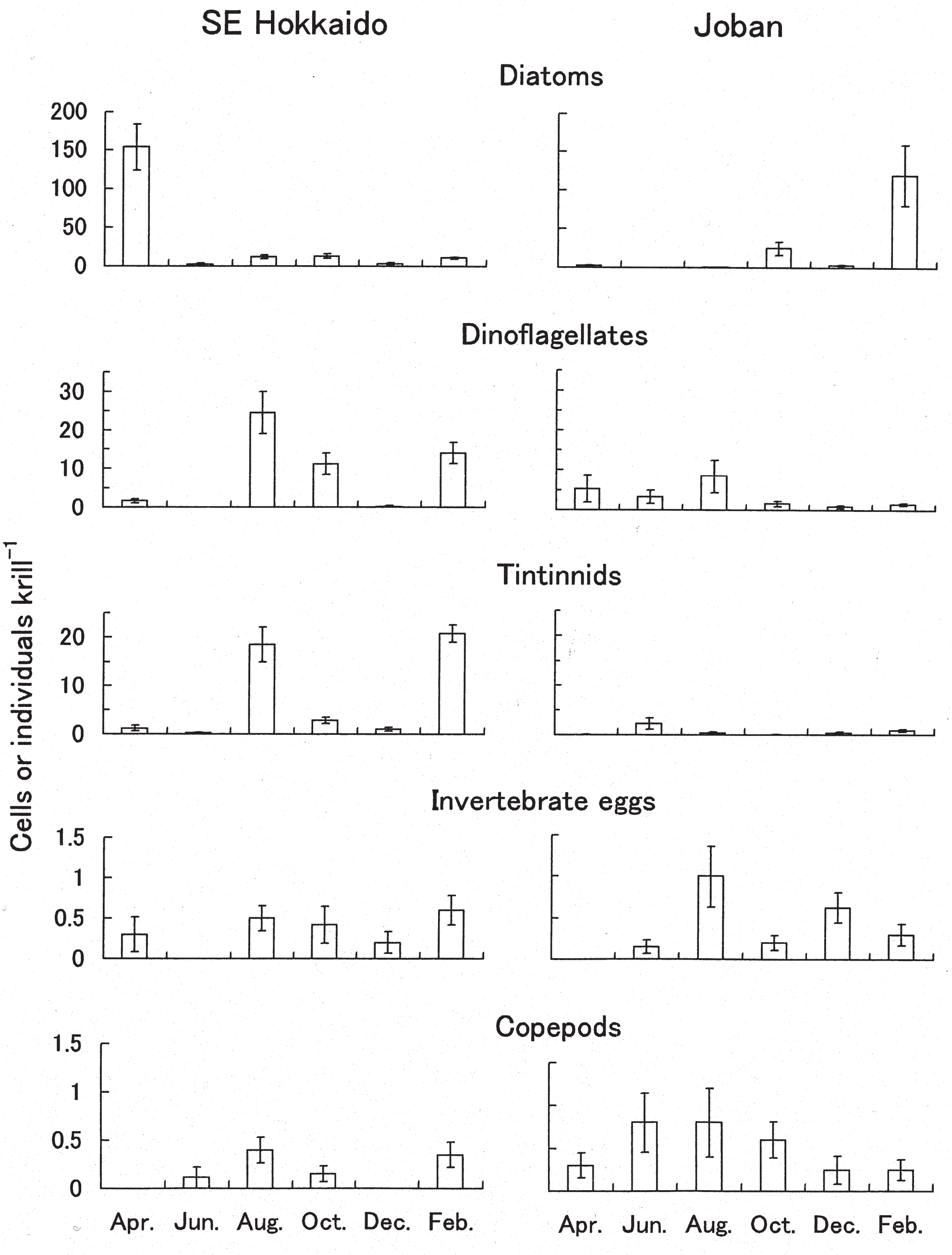

Fig. 6-3. Seasonal change in mean number of each identifiable food item in the gut contents of *Euphausia pacifica* individuals. Vertical bar represents ±1 SE.

Table 6-3. Mean total volumes of diatoms, dinoflagellates and tintinnids, mean diameter of invertebrate eggs, and mean prosome length of copepods in the stomach of *Euphausia pacifica* individuals.

	Apr.'97	Jun.'97	Aug.'97	Oct.'97	Dec.'97	Feb.'98
Diatom volume ($\times 10^3 \mu m^3$)						
SE Hokkaido	11.2(0.3)*	3.7(1.7)	2.4(0.3)	9.9(1.0)	6.3(2.0)	3.5(0.4)
Joban	6.8(1.3)	0.3(0)	5.2(3.4)	1.8(0.2)	6.3(1.7)	1.6(0.1)
Dinoflagellate volume ($\times 10^3 \mu m^3$)						
SE Hokkaido	37(7)		3(2)	10(3)	2(1)	18(3)
Joban	8(3)	51(34)	25(10)	32(13)	319(191)	219(72)
Tintinnid volume ($\times 10^3 \mu m^3$)						
SE Hokkaido	167(34)	190(32)	19(4)	208(48)	398(116)	131(6)
Joban	761	18(1)	36(9)	66	20(3)	203(20)
Invertebrate egg diameter (μm)						
SE Hokkaido	184(133)		114(92)	80(46)	76(74)	117(68)
Joban		160(133)	35(18)	107(83)	85(54)	65(49)
Copepod prosome length (μm)						
SE Hokkaido		1163	525(109)	279(89)		432(117)
Joban	701(231)	541(90)	232(34)	470(130)	715(28)	351(82)

*Mean (standard error)

Table 6-4. Calculated carbon content (μ g C Krill-1) of each indentifiable food item in the stomach contents of *Euphausia pacifica* *

		Diatoms	Dinoflagellates	Tintinnids	Invertebrate eggs	Copepods	Total
SE Hokkaido	Apr.	0.061	0.005	0.011	0.138	0.000	0.215
	Jun.	0.000	0.000	0.002	0.000	3.130	3.133
	Aug.	0.001	0.006	0.056	0.054	1.776	1.893
	Oct.	0.004	0.008	0.034	0.015	0.184	0.246
	Dec.	0.001	0.000	0.020	0.007	0.000	0.027
	Feb.	0.002	0.019	0.156	0.070	1.672	1.933
Joban	Apr.	0.001	0.004	0.002	0.000	4.773	4.781
	Jun.	0.000	0.010	0.003	0.045	7.085	7.143
	Aug.	0.000	0.013	0.001	0.003	0.547	0.567
	Oct.	0.002	0.004	0.000	0.018	5.010	5.035
	Dec.	0.001	0.016	0.001	0.028	2.285	2.331
	Feb.	0.008	0.018	0.010	0.006	0.565	0.608

*Note that carbon content of food items, except copepods of which figure could be estimated from indigested mandible, was considerably underestimated because they were easily broken by digestion.

Table 6-5. Average body carbon, stomach contents carbon, and daily ration of *Euphausia pacifica* of total identifiable bood items and copepods

		Average body C (mg C)	Stomach contents C (μ g C krill^{-1})	Total daily ration (% Body C d^{-1})	Daily ration of copepods (% Body C d^{-1})	Copepod contribution (%)
SE Hokkaido	Apr.'97	3.77	0.21	0.06	0.00	0.0
	Jun.'97	2.92	3.13	0.86	0.86	99.9
	Aug.'97	3.01	1.89	0.56	0.52	93.7
	Oct.'97	3.18	0.25	0.09	0.07	74.7
	Dec.'97	2.13	0.03	0.02	0.00	0.0
	Feb.'98	2.99	1.93	0.78	0.67	86.5
Joban	Apr.'97	2.62	4.78	1.79	1.79	99.8
	Jun.'97	3.33	7.14	1.85	1.84	99.2
	Aug.'97	1.07	0.57	0.49	0.47	96.9
	Oct.'97	1.60	5.04	3.60	3.58	99.5
	Dec.'97	0.90	2.33	3.44	3.37	98.0
	Feb.'98	2.58	0.61	0.28	0.26	92.9

Table 6-6. Ingestion by adult size of *E. pacifica* of copepods estimated by the stomach contents and total foods estimated by carbon budgets necessary for production and metabolism during feeding survey period (313 days) from April 1997 to February 1998

		Biomass of >10mm (mg C) (A)	Daily ration of copepods (% Body C) (B)[*1]	Daily ingestion of copepods (mg C) (A × B)	Ingestion of copepods from Apr. to Feb. (mg C) (D)[*2]	Total ingestion from Apr. to Feb. (mg C) (E)	Copepod contribution (D/E)
SE Hokkaido							
	Apr.	123	0.0	0.0			
	Jun.	293	0.9	2.5			
	Aug.	447	0.5	2.3			
	Oct.	595	0.1	0.4			
	Dec.	23	0.0	0.0			
	Feb.	436	0.7	2.9			
					395	5431	7.3%
Sanriku							
	Apr.	439	0.4	1.8			
	Jun.	97	3.1	3.0			
	Aug.	79	2.5	2.0			
	Oct.	106	1.2	1.3			
	Dec.	34	1.7	0.6			
	Feb.	1003	1.1	11.0			
					867	4480	19.3%
Joban							
	Apr.	237	1.8	4.2			
	Jun.	484	1.8	8.9			
	Aug.	59	0.5	0.3			
	Oct.	43	3.6	1.5			
	Dec.	98	3.4	3.3			
	Feb.	398	0.3	1.0			
					1007	3356	30.0%
Entire survey area	Apr.	316	0.5	1.7			
	Jun.	278	1.7	4.7			
	Aug.	177	0.9	1.6			
	Oct.	212	0.5	1.1			
	Dec.	49	2.4	1.2			
	Feb.	650	0.9	5.7			
					768	4206	18.2%

[*1] Daily ingestion rate of copepods off Sanriku is from Table 3 in Nakagawa *et al.* (2001).

[*2] $\sum((CI_j+CI_{j+1}) \times d_{j,j+1}/2)$: CI_j is daily ingestion of copepods for jth survey, $d_{j,j+1}$ is days between jth survey and (j+1)th survey.

krill^{-1}). Tintinnids were scarce throughout the year. Invertebrate eggs were abundant in August (1.0 inds krill^{-1}) and December (0.6 inds krill^{-1}). Copepods occurred throughout the year and were abundant in August and October (both 0.8 inds krill^{-1}) but were scarce (0.25 inds krill^{-1}) in February when diatoms were abundant.

Mean total volumes of diatoms, dinoflagellates and tintinnids, mean diameter of invertebrate eggs and mean prosome length of copepods in the stomach of *E. pacifica* varied between months and areas (Table 6-3). Mean total volumes of diatoms off southeastern Hokkaido tended to be higher than those off Joban, but mean total volumes of dinoflagellates off Joban tended to be higher than those off southeastern Hokkaido throughout the year. Mean prosome length of copepods off southeastern Hokkaido (488 μm) was not significantly smaller than that off Joban (502 μm) (Mann-Whitney: $P > 0.05$).

Copepods were the dominant food item by carbon content when they occurred in the stomach (Table 6-4). Stomach content carbon off Joban tended to be higher than that off southeastern Hokkaido. Stomach content carbon off Joban was highest in June (7.1 μg) and higher in April and October (both higher than 4 μg). On the other hand, stomach content carbon off southeastern Hokkaido was significantly lower in April, October and December. The low carbon in August off Joban was due to the small mean prosome length of copepods (232 μm) (Table 6-3) despite the high number of copepods in the stomach (Fig. 6-3). On the other hand, the high carbon content in October off southeastern Hokkaido was due to just one copepod with large prosome length (1,163 μm) in the stomach.

The daily ration (% body carbon day^{-1}) off southeastern Hokkaido was less than 1 % and tended to be lower than that off Joban throughout the year (Table 6-5). On the other hand, the daily ration off Joban was high in October (3.6%), December (3.4%).

Discussion

Nakagawa *et al.* (2001) showed that copepods are the most important food item, in terms of carbon, for most of the year in Sanriku waters but *E. pacifica* might have shifted its food preference to the abundant diatoms in spring, rather than feed on copepods whose escape behavior likely costs the euphausiids additional energy expenditure to catch and ingest them. *E. pacifica* tended to consume many diatoms when a high chlorophyll *a* concentration occurred in the surface or subsurface layers but tended to consume large number of copepods when the chlorophyll *a* concentration was low in the total water column both in southeastern Hokkaido and Joban waters (Fig. 6-3). This tendency is well consistent with that of *E. pacifica* off Sanriku (Nakagawa *et al.,* 2001). Therefore, it is suggested that *E. pacifica* flexibly switches the feeding behavior according to ambient food conditions in the wide range off northeastern Japan.

Both the numerical number and carbon of copepods in the stomach of *E. pacifica* off Joban were generally higher than those off southeastern Hokkaido throughout the year (Fig. 6-3 and Table 6-5). Copepods may be a more important food item for *E. pacifica* off Joban where phytoplankton abundance is lower than that off southeastern Hokkaido throughout the year.

Assimilation of adult size (>10mm) of *E. pacifica* during the entire feeding survey period (313 days) was calculated to be 4,562mg C m^{-2} and 2,819mg C m^{-2} off southeastern Hokkaido and Joban, respectively (gross metabolism multiplied by relative contribution of >10mm for each area [see Tables 5-1-5]). Assuming the assimilation efficiency of ingested food to be 0.84 (Lasker, 1966), ingestion by adult *E. pacifica* during the entire feeding survey period was estimated to be 5,431mg C m^{-2} (4,562/0.84) and 3,356mg C m^{-2} (2,819/0.84) off southeastern Hokkaido and Joban, respectively (Table 6-6). On the other hand, ingestion of copepods by adult size *E. pacifica* during the entire feeding survey period is estimated to be 395mg C m^{-2} and 1,007mg C m^{-2} off southeastern Hokkaido and Joban, respectively, using data of the daily ration of copepods (% Body C d^{-1}; Table 6-5) and biomass of adult size (Fig. 5-2) in each month (Table 6-6). Therefore, the copepod contribution to the total food ingestion for adult size of *E. pacifica* is estimated to be 7.3% (395/5,431) and 30.0% (1,007/3,356) off southeastern Hokkaido and Joban, respectively.

Assimilation and ingestion by adult size of *E. pa-*

cifica over the entire feeding survey period (313 days) is estimated to be 4,480 mg C m^{-2} and 3,763 mg C m^{-2}, respectively off Sanriku by using the same calculations as mentioned above (Table 6-6). On the other hand, ingestion by adult size of *E. pacifica* of copepods during the entire feeding survey period off Sanriku is estimated to be 867 mg C m^{-2}, using data of the daily ration by *E. pacifica* of copepods in Table 3 in Nakagawa *et al.* (2001) and biomass of adult size (Fig. 5-2) in each month (Table 6-6). Then, the copepod contribution to the total ingestion during the entire feeding survey period is estimated to be 19.3 % (867/4,480) off Sanriku. Therefore, the importance of copepods as a food item for *E. pacifica* is assumed to increase with the warmer waters.

Several quantitative problems arise by the examination of stomach contents with a dissecting microscope. Phytoplankton cells are broken by mastication and only a small fraction remains intact in the stomach. Gut pigment analysis could help estimate the amount of phytoplankton ingested. Daily ingestion of copepods was calculated by assuming a gut passage time of 1.08 h (Willason and Cox, 1987) in this study. However, different passage times have been reported for phytoplankton and copepods for *E. lucens* (Stuart and Pillar, 1990). So, the gut passage times for major food items by *E. pacifica* have to be determined experimentally in the future. Copepods were suggested to be entirely consumed by *E. pacifica* in this study. However, the copepod *Pseudocalanus sp.* was not entirely consumed by *E. pacifica* in feeding experiments (Ohman, 1984). So, there is a possibility that ingestion of copepods by *E. pacifica* is overestimated by the present method.

In this study, unidentifiable detrial contents were frequently found in the stomachs of *E. pacifica*. They may be organisms without shells such as naked flagellates and ciliates, marine snow, or other digested organisms. The contribution of naked ciliates as a food source of *E. pacifica* cannot be neglected because the biomass ratio of naked ciliates/tintinnids ranged from 3 to 123 in Sanriku waters (Kato, 1995). Nakagawa *et al.* (2004) suggested that *E. pacifica* ingests many naked ciliates and plays a role in linking the microbial food webs to the classical grazing food chains. In addition, Dilling *et al.* (1998) found that *E. pacifica* assimilates natural marine snow with a relatively high efficiency, similar to the values observed when feeding on diatoms. Marine snow, therefore, can be one of the factors that were not included in the calculation of the carbon content of food items.

As mentioned above, *E. pacifica* is found to be able to utilize a wide variety of food sources. This could sustain the continuous spawning (see **Chapter 3**) throughout the year and make *E. pacifica* one of dominant zooplankton species off northeastern Japan. However, it should be noted that the main resources for spawning in the Oyashio area and its frontal area during summer and autumn might not be copepods but phytoplankton and microzooplankton (Fig. 6-3) and ingestion of copepods might be more important foods for small adults in the warmer waters where they can not obtain foods sufficiently in the surface layer during the same seasons.

Chapter 7. General discussion

In this chapter, three key points are discussed from the results obtained in **Chapters 2-6.** First, the significance of the seasonal migration of *Euphausia pacifica* off northeastern Japan is discussed from the point of view of feeding, reproductive maturation and segregation between developmental stages, comparing with the cases in *Euphausia superba.* Secondly, the mechanism of formation of fishing ground in *E. pacifica* in the Sanriku and Joban coastal waters is discussed in relation to its seasonal horizontal and vertical distribution pattern and physical environments. Finally, the impact on the primary and secondary production by *E. pacifica* off northeastern Japan was estimated and is discussed in comparison with *Neocalanus* species.

Significance of seasonal migration of *Euphausia pacifica* off northeastern Japan

It appears that seasonal change in the distribution of adult *Euphausia pacifica* is clearly affected by that of the Oyashio waters off northeastern Japan (Table 3-2; Figs. 3-15-17). The northward shift of the Oyashio waters along with that of the Kuroshio waters during early summer and fall seems to accelerate large adults to shift their distribution toward more northern, colder waters as mentioned in Chapter 3. However, simultaneously, this shift might provide them with more productive waters where they can select mainly phytoplankton and microzooplankton as food items (Fig. 6-3) which do not require high energy costs to be ingested compared with copepods, along with the reduction of metabolic requirements in the colder conditions (MacLaren, 1963). In addition, Oyashio area during summer and fall, which is the main distributional area for adult *E. pacifica* (Fig. 3-4), provides them with rather favorable feeding conditions partly because predominant macrozooplankton such as *Neocalanus species* are dormant in the Oyashio area during these seasons (Odate, 1994; Tsuda *et al.,* 1999; 2004). These favorable feeding conditions seem to enable adult *E. pacifica* to conduct active copulation and spawning in the Oyashio area during summer and fall (Figs. 3-4, 10 and 11).

Eggs of *E. pacifica* seem to be rather neutrally buoyant because they were generally distributed within 100 m or so in vertical range (Figs. 4-13, 17, 21 and 25). So, eggs of *E. pacifica* liberated in the surface layer could remain to stay and hatch in the warm surface layer in the Oyashio area during summer and fall (Figs. 3-2 and 19). In addition, larval stages also seem to stay throughout the day in the shallow warmer layer by controlling their diurnal vertical migration (Fig. 4-17) and might accelerate their developmental time in the warmer conditions (Ross, 1981). Thus, this summer-fall hatching could accelerate the growth and reduce the mortality during its early developmental stages in the warmer condition and then contribute to maintaining the population of *E. pacifica* off northeastern Japan.

Euphausia superba off the Antarctic Peninsula is suggested to conduct a seasonal migration between the continental shelf area and oceanic waters for spawning (Ichii *et al.,* 1998) and feeding (Ichii *et al.*, 1998; Siegel, 2000). This causes the segregation in horizontal distribution between the developmental stages, which might have a great effect on the reduction of intraspecific competition and parental cannibalism (Siegel, 2000). On the other hand, the segregation in horizontal distribution might be attributable mainly to the difference of suitable temperature range between developmental stages for *Euphausia pacifica* off northeastern Japan. That is to say, spawning and larval stages occur in the warmer side of the distribution of adult (Table 3-2) and segregate their vertical distribution with that of adults by the suitable temperature range (Fig. 4-27) at night when adults mainly feed (Endo, 1981; Ponomareva, 1963). This horizontal and vertical segregation by water temperatures between developmental stages might contribute to the reduction of intraspecific competition and also cannibalism by adults.

On the other hand, when a suitable temperature range overlaps in the total water column between larval stages and adults such as in the coastal waters off Sanriku in spring, copulated females might liberate their eggs in the deeper layers and larval stages might control their diurnal vertical migration to avoid encountering the aggregation of adults (Fig. 4-13).

In conclusion, seasonal change in distribution of adult *E. pacifica* are affected by water temperatures. This might provide adults with favorable feeding condition to realize reproductive maturation after spring and might cause the segregation of the horizontal and the vertical distribution between developmental stages which contributes to reduce the intraspecific competition and also cannibalism by adults.

Characteristics of formation of fishing ground of *E. pacifica*

Kodama (1995a) and Odate (1991) suggested that the fishing ground tend to be formed at the surface temperatures >5℃ because the cold water temperatures <5℃ are not suitable for *E. pacifica* based on empirical data. In March 2001, the fishing ground seemed to be formed avoiding the 0℃ isotherm close to the shore (Fig. 2-18), so such extreme cold temperatures may not be favorable for *E. pacifica.* These cold temperatures may cause *E. pacifica* to migrate southward toward off Sanriku and Joban regions along with the southward advection by the Oyashio Current during late winter and spring, which is well supported by the results in the cylindrical-conical net survey (Figs. 3-15-17). However, the lower limit of suitable temperature range for *E. pacifica* seemed to be much lower than 5℃ from the result in the cylindrical conical net survey (Fig.

3-19). On the other hand, it might be advantageous for spawning adults to migrate toward warmer waters because warm conditions accelerate the development of eggs and larval stages (Ross, 1981; Iguchi and Ikeda, 1994) and might consequently contribute to the reduction of mortality during early stages.

The benthpelagic swarms off Joban were usually formed in the area with high surface temperatures up to 15℃ after early summer (Figs. 2-13, 14 and 17). Fishing conditions of *E. pacifica* have been predicted generally using surface temperatures in Sanriku (Kodama, 1995a) but using benthic temperatures in Joban (Ebisawa, 1995). Because temperatures at daytime depth of adult *E. pacifica* are generally below 8℃ (Figs. 4-7) and its distribution needed lower temperatures <8℃ in the benthic layer in the Sanriku coastal waters (Figs. 4-6 and 7), lower temperatures <8℃ are considered to be necessary for its habitat. Fig. 7-1 shows the seasonal change of average water temperatures at 0, 100 and 200m from January to July throughout 18 years off Nakaminato, Ibaraki Prefecture, one of the main ports. The surface temperatures abruptly rose from May, but the cold waters <8℃ derived from the Oyashio Current intruded at 200m depth from May to June when the fishing grounds are mainly formed in the Joban coastal waters. On the other hand, daytime depth of adult *E. pacifica* is generally above 150m in spring when thermocline is undeveloped and phytoplankton is abundant, but is below 200m from summer to autumn (Figs. 4-13, 17, 21 and 25). Therefore, it is suggested that daytime depth of adults shifts to deepen in early summer. From this evidence, the typical seasonal pattern of formation of fishing ground in the Joban coastal waters is as follows. The distribution of adult *E. pacifica* is blocked by the waters with warmer temperatures >8℃ in the shallow layers, usually located north of Oshika Peninsula (ca. 38°20' N) and is not likely to extend to the Joban coastal waters during late winter and spring. In early summer, however, adult *E. pacifica* shift to deepen its daytime depth below 200m, and then a part of them, whose southward distribution has been blocked by the warmer waters in the shallow layer by early summer, might encounter the cold water mass in the mid-layer, which intrudes toward the Joban coastal waters, during the daytime and be advected southward by this water mass. And then, this advected population may mainly form the fishable benthic swarms in the Joban coastal waters.

Odate (1991) showed that fishing depths in Joban were shallower than 50 m depth from 1981 to 1984 when the southward shift of the Oyashio Current

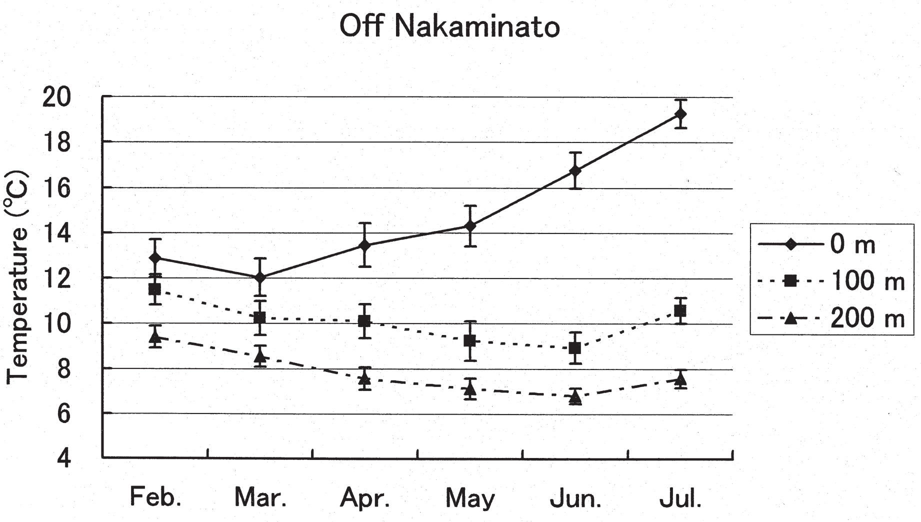

Fig. 7-1. Average temperature (℃) at 0, 100, 200m depth off Nakaminato, Ibaraki Prefecture (36°34' N, 141°04' E).

was strong. The fishing period in these years was significantly earlier than other years (Fig. 2-9). So, it is suggested that adult *E. pacifica* were advected by the surface layer with low temperatures <8 ℃ toward the Joban coastal waters simultaneously to the Sanriku coastal waters during late winter and spring in such strong Oyashio years.

However, it may be difficult for large adults to survive after summer in the benthopelagic form in the warm Joban coastal waters as mentioned above. This is also well supported by the low catch and CPUE after July at Otsu Port (Fig. 2-11).

In conclusion, it is suggested that the fishing ground or fishable aggregations in spring are mainly formed in the cold waters of the transitional area as mentioned in the previous reports perhaps due to the facilitation of copulation, spawning and growth of larval stages in the warmer conditions. On the other hand, the fishing ground in the Joban coastal waters in early summer might be due to the encounter of *E. pacifica* which shift to deepen the daytime depth with the intrusion of cold water mass derived from the Oyashio Current in the mid-layer, and the southward advection of *E. pacifica* toward the Joban coastal waters by this intrusion.

Impact on the primary and secondary productions by ingestion of *E. pacifica* off northeastern Japan

Other than *Euphausia pacifica*, *Neocalanus species* (*N. cristatus, N. plumchrus* and *N. flemingeri*) are also the dominant large grazing copepods occurring off northeastern Japan and predominant components of the zooplankton biomass (Conover, 1988; Mackas and Tsuda, 1999; Kobari *et al.,* 2003). Kobari *et al.* (2003) estimated that the annual production and ingestion in carbon in *Neocalanus species* is 19.3 and 38.9 g C m^{-2} in the southeastern Hokkaido region. Therefore, production and carbon ingestion by *E. pacifica* during the survey period (3.8 and 9.1g C m^{-2}) corresponds to about one fifth and one fourth of annual production and ingestion by *Neocalanus species,* respectively, in this region (Table 5-1). Taniguchi (1981) showed that the annual primary production in the subarctic and polar frontal (transitional) area in the northwestern Pacific is 100-150 g and 80-100g C m^{-2}, respectively. Therefore, annual carbon ingestion by *E. pacifica* off southeastern Hokkaido (ca. 9.1g C m^{-2}; Table 5-1) is estimated to correspond to ca. 6-9% of the annual primary production in the subarctic area. While, the annual carbon ingestion by *E. pacifica* off Sanriku and Joban (ca. 9.2 and 6.3g C m^{-2}; Table 5-1) is estimated to correspond to ca. 6-11% of the annual primary production in the polar frontal area.

Carbon ingestion by adult size of *E. pacifica* during the survey period off southeastern Hokkaido, Sanriku and Joban is estimated to be 5.4, 5.1 and 3.4g C m^{-2} (9.1×0.594, 9.2×0.554 and 6.3×0.531; Tables 5-1 and 5), respectively. While, carbon ingestion by adult size of *E. pacifica* of copepods is calculated to correspond to 7.3, 19.3 and 30.0% of the total off southeastern Hokkaido, Sanriku and Joban during the feeding survey (Table 6-6). So, carbon ingestion during the entire survey period off southeastern Hokkaido, Sanriku and Joban is estimated to be 0.4, 0.98 and 1.01g C m^{-2} (5.4 × 0.073, 5.1 × 0.193 and 3.4 × 0.3), respectively. Taniguchi (1981) showed that secondary production in the subarctic and polar frontal area in the northwestern Pacific is 6.0-18.2g and 4.0-10.8g C m^{-2}, respectively. Therefore, the annual carbon ingestion by adult size *E. pacifica* of copepods off southeastern Hokkaido is estimated to correspond to ca. 2-7% of the annual secondary production in the subarctic area. On the other hand, annual carbon ingestion by adult size *E. pacifica* of copepods off Sanriku and Joban is estimated to correspond to ca. 9-25 % of the annual secondary production in the polar frontal area.

If carbon ingestion other than copepods is supplied from phytoplankton, annual carbon ingestion by adult size *E. pacifica* of phytoplankton off southeastern Hokkaido is calculated to correspond to ca. 3-5% of the annual production in the subarctic area. While, if so, annual carbon ingestion by adult size *E. pacifica* of phytoplankton off Sanriku and Joban is calculated to correspond to ca. 2-5% of the annual production in the polar frontal area. So, ingestion impact by adult *E. pacifica* on secondary production is suggested to be rather higher than that on the primary production in the polar frontal area.

In conclusion, annual impact on primary production by adult *E. pacifica* does not seem to be as high as compared to that by *Neocalanus species* in the Oyashio area. On the other hand, ingestion by small adults might have a significant effect on the secondary production in the transitional area during summer and fall. Conversely, secondary production in the transitional area during summer and fall may sustain the survival of small adults during the same seasons, which could allow their active participation in spawning in the transitional area during the following spring.

Acknowledgements

I would like to express my sincere gratitude to Professor Makoto Terazaki, Tokyo University, for his continuous guidance and invaluable suggestions throughout the course of the present study. I am grateful to Professor Takanari Sugimoto, Tokai University and Professors Ichiro Aoki, Shuhei Nishida, Yoshiro Watanabe, Tokyo University, for their kindness in critical readings of the manuscript and invariable comments for the manuscript.

I would like to express my sincere thanks to Associate Professor Yoshinari Endo, Tohoku University for his guidance to euphausiid biology and invaluable suggestions on the present study.

I am also grateful to Shigeyuki Kawahara, Hiroya Sugisaki, Takashi Ogishima, Yuichi Kotani, Naoki Iguchi, Kaoru Nakata and Taro Ichii, Fisheries Research Agency, Kazuko Odate, formerly of Fisheries Research Agency, Associate Professor Atsushi Tsuda, Sean Toczko and Travis Johnson, Tokyo University and Masatoshi Moku, National Fisheries University, for their invaluable comments in the present study. I can never thank enough Hiroshi Itoh, *Suidosha* Co. Ltd. and Yoshizumi Nakagawa, Kinki University, for their kind advice on the stomach content analysis of *Euphausia pacifica.*

I would like to express my sincere gratitude to officers and crew of the R. V. *Wakataka-maru, Tankai-maru* and *Hokko-maru,* Fisheries Research Agency, for their devoted assistance with the collection of samples. This thesis would not have been possible without the cooperation of them.

I am grateful to Kiyoshi Nozawa, Iwate Prefectural Fisheries Technical Center, Nasumi Tomikawa, Miyagi Prefecture Fisheries Research and Development Center, Tadahiro Saotome, Fukushima Prefecture Fisheries Experimental Station and Ryuji Ando, Ibaraki Prefecture Fisheries Experimental Station, for providing me with both the fishery data of *Euphausia pacifica* and the Norpac net samples. I also thank Kitaro Abe, Hajime Kimura and Katsuji Abe, Izushima Fishermen's Association, Miyagi Prefecture, Masayuki Minato, Fishermen's Association for Coastal Fishing Boats in Iwate Prefecture, and Sadanobu Sengoku and Katsumi Ishikawa, National Federation of Fisheries Co-operative Association, for providing me with much useful data and information on the *Euphausia pacifica* fishery. Thanks are also due to Makoto Fujita and Masahiro Asano, Japan Fisheries Information Service Center, and Tomowo Watanabe and Yugo Shimizu, Fisheries Research Agency, for providing me with oceanographic data in the Tohoku Sea waters.

Finally, I would like to express my sincere gratitude to Kuniaki Okuda and Mitsuyuki Hirai, Fisheries Research Agency, for their grateful encouragements to complete this thesis.

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本州東方海域におけるツノナシオキアミの漁業及び生活史に関する研究

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ツノナシオキアミは北太平洋における優占するオキアミ類であり，本邦太平洋側ではオホーツク海南西部から駿河湾にかけて分布している。本種は冬春季の三陸・常磐沿岸において重要な漁獲対象種である。1992～2001年の年間平均漁獲量，漁獲金額はそれぞれ６万６千トン，31億円である。年間漁獲量，漁期及び漁獲金額の年変動は大きいため，安定した経営及び流通のため正確な資源量の評価及び漁況予測が求められている。一方，本種は，多くの固有種，回遊種の重要な餌となり，生態系における鍵種である。また，その大きな生物量を考慮すると，低次生産に対する捕食圧も大きなものと推察される。このように，本種が北太平洋において低次栄養段階から高次栄養段階への物質の輸送に重要な役割を果たしていることを考慮すると，海洋生態系の構造を理解するうえで，本種の分布，生活史及び炭素収支に関する定性・定量的な研究が重要となる。そこで，本研究では本州東方域における本種の漁業，水平・鉛直分布，生活史，生物量，炭素収支（生産量及び代謝量），食性を検討した。

まず，海況変動がツノナシオキアミの漁況にどのように影響してきたか明らかにするために，本漁業の発展や漁獲規制を考慮しつつ，単位努力当り漁獲量（CPUE）等の漁況指数の経年変化を親潮第一分枝等の海況指数との関係で調べた。その結果，漁況と海況の関係では次のような傾向が認められた。すなわち，親潮第一分枝の南下が弱い年には，漁況は岩手県沿岸域では比較的安定するが，宮城県沿岸域及び常磐沿岸域では低いCPUEを示したり初漁日が遅くなったりして不漁を呈した。一方，親潮第一分枝の南下が強い年には，宮城県沿岸域及び常磐沿岸域では岩手県沿岸域と同様に高いCPUEを示したり初漁日が早くなったりして好漁を呈した。

本州東方域におけるツノナシオキアミの水平分布及び生活史の平均像を明らかにするために，ノルパックネットと新稚魚ネットを用いて広域（約36－43°N，145°E以西）における本種の産卵域，分布，成長の季節変化及び寿命を調べた。その結果，交尾と産卵は周年親潮域と親潮系冷水域で行われ，春季にその盛期を迎え，晩秋～冬季に停滞気味であった。成長については，小型成体（越冬前）において３～６月に明確な成長が認められた。寿命は，雄で24ヶ月，雌で28ヶ月と推定された。発育段階間の分布については，ファーシリア期から成体にかけて徐々に冷水域側に分布を拡げる一方，大型成体（越冬個体）で暖水域側に出現しなくなる傾向が認められた。また，産卵域や各発育段階の地理的な分布パターンは季節的な水塊の配置と密接な関係を有した。

ツノナシオキアミの鉛直分布の実態及びそれを規定する物理・生物的環境要因を明らかにするため，ORI，ビームトロール，MOCNESSネット標本を用いて本州東方域の三陸沿岸域（陸棚及び陸棚斜面上部）及び沖合域における本種の鉛直分布の季節変化を調べた。まず三陸沿岸域では，水温躍層が発達し近底層に８℃未満の冷水が存在する６～12月の陸棚斜面上部に本種の底付群が形成されていた。しかし，春季には全水柱をほぼ７－８℃で覆われる陸棚域で漂泳群が多く出現し，底付群は全沿岸域においてほとんど認められなかった。沖合域では，全測点平均でみると，夜間の分布深度（中央値）はファーシリア中期から大型成体にかけて発育するにつれて徐々に深くなる傾向が認められた。一方，昼間の分布深度はファーシリアⅠ期から同Ⅵ期にかけて発育するにつれて徐々に深くなる傾向が認められた。夏～秋季の暖水域における夜間の未成体及び成体の分布深度は深くなる傾向が認められ，特に大型成体は中層の躍層より上部をほとんど超えることができなかった。一方，春季の日中の未成体及び成体の分布深度は夏～秋季（300－400m）に比べ浅く（約150m），その結果鉛直幅の短くなる傾向が認められた。

ツノナシオキアミの炭素収支の特徴を明らかにするため，道東〜常磐沿岸域における本種の生物量，生産量及び代謝量を調べた。生物量は，道東域では夏〜秋季，三陸・常磐域では晩春〜初夏に高かった。年平均生物量は，道東，三陸，常磐域でそれぞれ381，314，258mg C m^{-2}であった。ほぼ年間の全生産量（成長＋脱皮＋産卵）は，道東域（3,829mg C m^{-2}）と三陸域（3,872mg C m^{-2}）で同様であったが，両海域とも常磐域（2,243mg C m^{-2}）より顕著に高かった。各海域において成長生産量が全生産量の占める割合（51.5－70.9%）が最も高かった。全代謝量（基礎代謝＋鉛直移動による代謝）は3,062〜3,486mg C m^{-2}で，同化量（全生産量＋全代謝量）の50.1－57.7%を占めた。このうち，基礎代謝量（2,257〜2,783mg C m^{-2}）は同化量の32.8－42.5%と，各海域とも最も高い割合を占めた。

環境中の餌生物に応じてツノナシオキアミ成体の食性や摂餌様式がどのように変化するか明らかにするため，道東域及び常磐域における本種の胃内容物の季節変化を調べた。ツノナシオキアミは，環境中のクロロフィル*a*濃度が高い時に多くの珪藻を摂餌し，クロロフィル*a*が低い時にカイアシ類を摂餌する傾向が認められた。一般に，胃内容中のカイアシ類の個体数及び炭素量とも常磐域の方が道東域より高かった。全摂餌量に対するカイアシ類の割合は道東域で7.3%，常磐域で30%と推定され，緯度の低い温暖な海域ほどカイアシ類の餌としての重要性が高まると考えられた。

以上得られた結果をもとに，同属の南極オキアミや*Neocalanus*属のカイアシ類と比較しながら，ツノナシオキアミの季節的回遊の重要性，三陸・常磐沿岸域における本種の漁場形成機構，本種の摂餌が低次生産に与える影響について論議した。

No.18, 41-165（2006）