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The effect of sea ice on the oceanographic structure and phytoplankton biomass in the Nemuro Strait, a nursery area of salmon *1

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Abstract: Coastal waters of the Okhotsk Sea and the Nemuro Strait of east Hokkaido are important nursery grounds for salmon fry released from hatcheries to the rivers of these districts. As an annual event in these coastal regions, sea ice drifting from the north of the Okhotsk Sea covers the area in winter and phytoplankton blooms occur following the retreat of sea ice in the spring. Spring phytoplankton blooms are thought to be important precedents to zooplankton production which supports the growth of salmon fry during their first oceanic stage. With establishment of a better management scheme of salmon resources as the ultimate goal, the objective of this study is to fill the gaps in our knowledge about mechanisms through which sea ice affects hydrography and phytoplankton production in the Nemuro Strait.

Through analyzing water temperature, salinity, nutrients (nitrate, phosphate and silicate) and chlorophyll *a* collected during January and July in 1998–2002, the water under the ice cover was revealed as being nutrient-rich. As judged by nutrient ratios (N: P=11.2 and Si: P=23), the origin of the water under sea ice was considered to be Okhotsk Intermediate Cold Water which entered the Nemuro Strait before sea ice encroached. Nutrient-poor Soya Warm Water was found in the Nemuro Strait during summer only.

Intensive study in 1998 revealed that massive phytoplankton blooms occurred after sea ice retreat in late March. Size fractionated chlorophyll a data showed the majority of phytoplankton was composed of >10 μ m size, but small size fractions (2–10 μ m and <2 μ m) increased as the season progressed. Zooplankton abundance peaked following the spring phytoplankton bloom in 2001, and the most dominant component was Copepoda, followed by Sagittoida or jellyfishes.

Massive phytoplankton blooms occurred after sea ice retreat in most years with the exception of 1999 when sea ice retreat was delayed to late April. The major mechanism of the onset of the phytoplankton blooms is the water column stratification due to ice melt combined with the development of a deep mixing layer within the critical depth. A moderate phytoplankton bloom in 1999 was attributed to a shallow mixing depth which limited nutrient availability for phytoplankton.

The present results regarding the effect of the timing of sea ice retreat on the magnitude of phytoplankton blooms are opposite to those predicted from Hunt *et al.*'s hypothesis for the Bering Sea. This difference in the consequences of sea ice-phytoplankton bloom relationships between the Nemuro Strait and the Bering Sea may be reconciled if one takes into account of dissimilar daily solar radiation at equivalent seasons which would have a dissimilar effect on sea ice melting. The Bering Sea is located at higher latitudes than the Nemuro Strait, hence daily solar radiation in the former are much less than in the latter, and in the former early retreat of sea ice is not associated with meltwater leading to water column stratification.

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Analysis of historical data showed that accumulated ice concentration has both positive and negative effects on fisheries resources. The return rates (percentage of mature salmon returning relative to the total number of fry released) of chum and pink salmon were negatively correlated with accumulated ice concentrations. Return rates of chum salmon were high in the years when their fry were released well after the sea ice retreat. Provision of food for fry before release improved the return rate of mature chum salmon, but the rate has been variable year to year due to reasons which are unknown at present.

To improve the return rate of mature salmon, future study should be directed to ward evaluating the change of food environments for salmon juveniles (zooplankton) in relation to the force of sea ice, especially during periods of sea ice retreat. Given that migration of salmon juveniles from the coastal waters into the Okhotsk Sea represents the first stage of their oceanic life, zooplankton production cycles in the Okhotsk Sea should be evaluated in order to diagnose feeding conditions of salmon juveniles, which affect their subsequent survival.

Key Words: sea ice, phytoplankton, salmon, Nemuro Strait, Okhotsk Sea

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Chapter 1. Introduction

Sea ice is distributed in high latitude seas, typically Antarctic and Arctic waters, covering an area of up to 7 % of the surface of the earth in winter (Comiso *et al.*, 1990). Our knowledge about the impacts of sea ice on biological process in the pelagic ecosystem has increased rapidly in both the Arctic (Wassman *et al.*, 2006) and Antarctic Oceans (Smith and Nelson, 1985; Garrison *et al.*, 1987; Sakshaug and Skjoidal, 1989; Comiso *et al.*, 1990; Lancelot *et al.*, 1991; Riebesell *et al.*, 1991; Bianchi *et al.*, 1992; Schloss and Estrada, 1994; McMinn, 1996; Dunbar *et al.*, 1998).

In the northern North Pacific Ocean, sea ice occurs during part of the year (winter) in the Bering and Okhotsk Seas. Intensive studies have been made on the effect of sea ice on the production cycle in the Bering Sea (Alexander, 1980; Alexander and Niebauer, 1981; Schandelmeier and Alexander, 1981; Niebauer and Alexander, 1985; Niebauer et al., 1990; Niebauer et al., 1995; Stabeno et al., 1998; Hunt Jr. et al., 2002). While comparable studies in the Okhotsk Sea are still lacking, results from other ice covered pelagic ecosystems show that ice meltwater enhances the density stratification during ice retreat in the spring and facilitates phytoplankton blooms (Alexander and Niebauer, 1981). Biological processes other than phytoplankton in sea ice covered areas were reviewed by Diekmann and Hellmer (2003).

As an area which is covered by ice in winter in the North Pacific, the Nemuro Strait located in the southern Okhotsk Sea is of special interest in this study because it is an area in which hatchery-raised fry are released to rivers flowing into the strait in order to improve management of salmon resources. Chum salmon (Onchorhynchus keta) fry are released in the spring, spend their early life in the coastal waters of the Nemuro Strait, and then migrate into the Okhotsk Sea to spend their first summer. Chum salmon move to the western subarctic gyre for their first winter, then they migrate between summer feeding grounds in the Bering Sea and wintering grounds in the Alaskan Gyre for a period of up to four years, and finally return to their mother rivers to spawn (Ueno and Ishida, 1996; Urawa, 2000). A historical record of salmon hatcheries in this district which goes back to the 1950s shows a strong relationship between the seasonal occurrence of sea ice and the return of mature salmon to mother rivers as discussed in this study (see Chapter 5).

The objective of this study is to fill gaps in our knowledge about the effects of sea ice on the oceanographic conditions and phytoplankton growth through the collection and analysis of field data in the Nemuro Strait. As the first attempt in the Nemuro Strait, field surveys were carried out during ice-covered periods using icebreaking vessels and in so doing seasonal sequences of water mass, nutrient regime, chlorophyll *a* and zooplankton abundance data were collected (Chapter 2). Special attention

was paid to the incidence of phytoplankton blooms during the ice retreat season (Chapter 3), and the mechanism determining the year-to-year variations in the magnitude of phytoplankton blooms was explored (Chapter 4). To link these data to salmon resources, historical data on sea ice coverage, hatchery production, and fishery yields of salmon and other commercial species were summarized and analyzed (Chapter 5). As a synthesis, future study needed for the establishment of a better management scheme of salmon resources through adjusting the activities of hatcheries is proposed (Chapter 6).

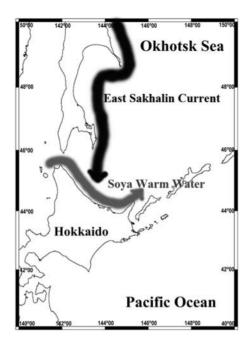
Chapter 2. Oceanographic Conditions in the Nemuro Strait during the Ice Season

Sea ice begins to form in coastal waters of the northern Okhotsk Sea off Magadan province in Russia early in the winter. The southward advance of sea ice is affected by a seasonal wind in winter and by the East Sakhalin Current of which volume transport reaches a maximum in December-January (Itoh and Ohshima, 2000; Ohshima et al., 2002; Ito et al., 2003). Sea ice advances southward and reaches the coast of the Okhotsk region of east Hokkaido. The coastal waters of the Okhotsk region and the Nemuro Strait of east Hokkaido are covered with sea ice between late January and middle or late March of every year. As a hydrographical feature of the southwestern Okhotsk Sea and the Nemuro Strait, these regions are under the influence of the Soya Warm Current which flows along the Okhotsk Sea coast of Hokkaido (Aota, 1979; Aota and Takizawa, 1994). Thus, the hydrography of the Nemuro Strait is complicated by the effect of not only sea ice but also by the warm current.

In this chapter, the properties of water masses prevailing in the Nemuro Strait are discussed with special reference to the winter ice season.

2.1 Materials and methods

Oceanographic observations were conducted at six stations on a transect (0.5, 1, 2, 4, 6 and 8 km from coast) off Rausu in the northern Nemuro Strait in January (before sea ice reaches the coasts) through July (no ice) in 1998-2002 (Fig. 2-1). An



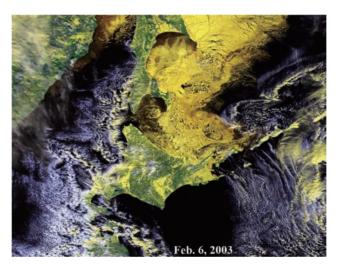


Fig. 2-1. Nemuro Strait (arrowed) as a marginal sea of the southwestern Okhotsk Sea (*top*), and MODIS satellite image of sea ice extension to the Okhotsk Sea and the Nemuro Strait in winter (*bottom*). The East Sakhalin Current and Soya Warm Current are superimposed in the top panel.

extensive sampling program was conducted in 2002 (9 times including 20 March; 9, 16 and 23 April; 8 and 22 May; 5 and 26 June; and 17 July) during the period in which there occurred an ice edge bloom and an open water bloom of phytoplankton. Under sea ice observations were made on board the Japan Coast Guard icebreaker *Teshio* on 4 April in 1999. Water temperature and salinity were measured

with a Memory STD (Alec Electronic Co., Ltd.). Transparency was measured with a Secchi disk. Water samples were routinely collected from 9 depths in the top 200 m (0, 10, 20, 30, 50, 75, 100, 150 and 200 m) with a Rigo-B sampler (Rigosha Co., Ltd.). At the stations shallower than 200 m, the number of sampling depths was reduced accordingly. Sampled water was filtered through

Whatman GF/F filters. Nutrient (nitrate, phosphate and silicate) concentrations were analyzed by using a Hitachi 100-60 spectrophotometer (Hitachi Co., Ltd.) and Flow Injection Analyzer 5020 (Tecater Co., Ltd.). Chlorophyll *a* was extracted from filters with methanol solutions (Otsuki *et al.*, 1987) and quantified with Turner AU-10 fluorometer (TurnerDesign Co., Ltd.).

Continuous monitoring of water temperature, salinity, dissolved oxygen concentration, current direction and speed in real time was accomplished through use of the Coastal Area information Network System (CANS), which was located 5 km off Shibetsu in the southern Nemuro Strait at a depth of 15 m (Fig. 2-2). A sediment trap bottle (diameter; 15 cm, length; 40 cm, filled with 8 % formalin-40 psu salted water to prevent advection of the fixative from the bottle) was mounted on the CANS to collect zooplankton, which was recovered seven times at two week intervals. Zooplankton thus collected are so called "swimmers" (cf. Seiler

and Brandt, 1997) and assumed to be an index of zooplankton abundance in the water column in this study. The entire observation period ranged between late January and late July in 2001.

2.2 Results

2.2.1 Water mass

Continuous temperature and salinity records at 15 m depth at the station off Shibetsu showed that although salinity was >33 psu from mid February to the end of March, it decreased rapidly to 32 psu in early April and this low salinity was maintained until the end of April (Fig. 2-3). It is noted that the station was ice-covered from early February to late March. In the northern Nemuro Strait, temperature was about -2°C (close to the freezing point of seawater) and salinity was around 33 psu during the ice-covered season (Figs. 2-4 and 2-5). Salinity decreased suddenly to 32 psu and temperature increased to 0°C in early April when the sea ice

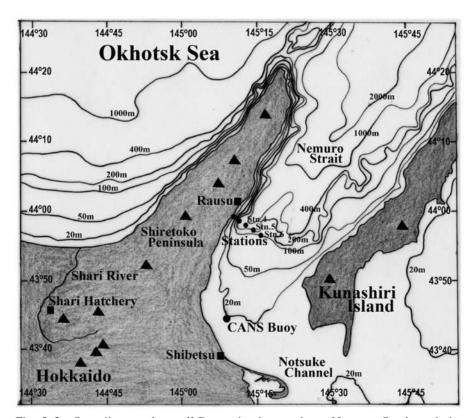


Fig. 2–2. Sampling stations off Rausu in the northern Nemuro Strait and the location of CANS buoy off Shibetsu in the southern Nemuro Strait.

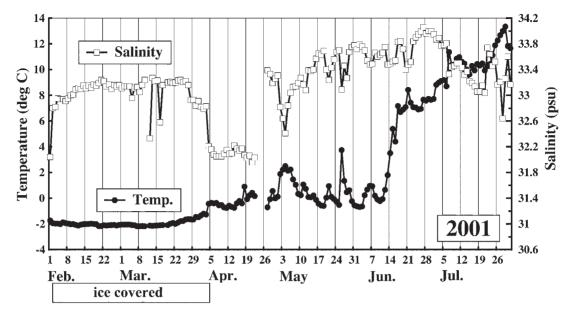


Fig. 2-3. Continuous records of temperature and salinity measured with a CTD fixed at 15 m depth at CANS buoy station located 5 km off Shibetsu during February-July 2001.

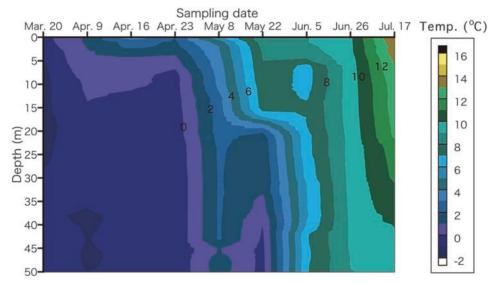


Fig. 2-4. Vertical profile of water temperature at the station 2 (1 km off Rausu) in the Nemuro Strait during March-July 2002.

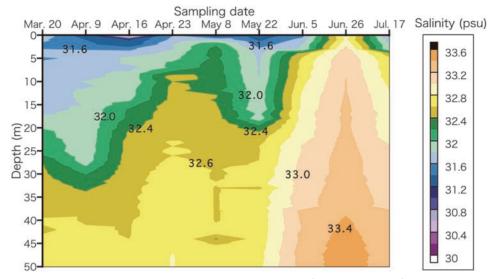


Fig. 2–5. Vertical profile of salinity at the station 2 (1 km off Rausu) in the Nemuro Strait during March-July 2002.

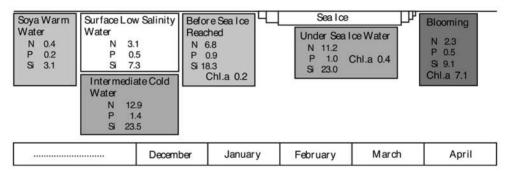


Fig. 2-6. Schematic presentation of seasonal sequences of water masses in the Nemuro Strait and associated changes in nutrient regimes and chlorophyll a in 1998 and 1999. See text for details.

retreated from Rausu. Temperatures continued to rise in early May. Phytoplankton blooms were observed late April when salinity decreased. Water temperatures of less than 0° C were seen until early April, after which they increased gradually and reaching 1-7°C in mid June.

The nutrients and chlorophyll a were measured in 1998 and 1999. Mean nitrate–N, phosphorus-P, silicate–Si and chlorophyll a concentrations in the top 10 m across the six stations were 6.8 μ mol N, 0.9 μ mol P, 18.3 μ mol Si and 0.2 μ g chl a l⁻¹, respectively, before the sea ice area was reached. Under the sea ice, respective figures were 11.2 μ mol N, 1.0 μ mol P, 23.0 μ mol Si and 0.4 μ g chl a

 Γ^{-1} , and during phytoplankton blooms concentrations were 2.3 μ mol N, 0.5 μ mol P, 9.1 μ mol Si and 7.1 μ g chl a Γ^{-1} (Fig. 2–6).

2.2.2 Phytoplankton blooms and zooplankton

Phytoplankton blooms occurred at the ice edge, and then in open water at the Station 2 off Rausu in 2002 (Fig. 2–7). The ice edge bloom was already underway when the present sampling program was initiated on 20 March 2002, and the chlorophyll a maximum (8–9 μ g chl a Γ^1) observed at 5–10 m depth deepened to 20–25 m depth on 9 April, and then collapsed on 16 April. On 23 April, moderate concentrations of chlorophyll a (3–4 μ g chl a Γ^1)

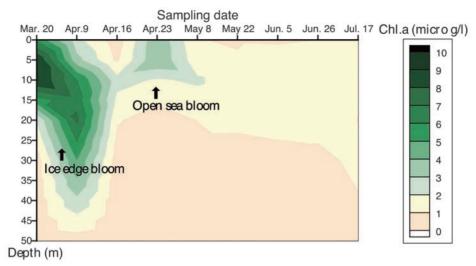


Fig. 2–7. Vertical profile of chlorophyll *a* at the station 2 (1 km off Rausu) in the Nemuro Strait during March–July 2002.

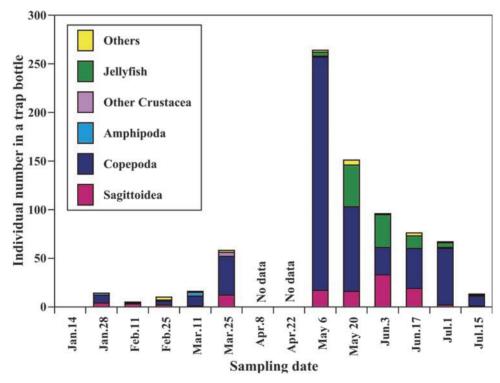


Fig. 2-8. Zooplankton abundance and composition at CANS buoy station located 5 km off Shibetsu in the Nemuro Strait during January–July 2001.

were detected in the top 10 m (open sea bloom), but this was not observed in the next sampling on 8 May (Fig. 2-7).

Zooplankton samples collected in the sediment trap located at a depth of 15 m were composed of Copepoda, Ampipoda, other Crustacea, Sagittoidea, jellyfish and others (Fig. 2-8). Because of the nature of the collection method (sediment trap), the results cannot be regarded as quantitative, but may still reflect their abundance in the water column. Numbers of zooplankton were low from January to March, increasing gradually during the ice season, and forming a peak in early May. After the peak, zooplankton numbers decreased toward the end of the sampling program of this year (15 July 2001). Throughout the samples, the most dominant zooplankton taxon was Copepoda, followed by Sagittoidea or jellyfish (Fig. 2-8).

2.3 Discussion

A rapid increase in water temperature from 0 to 8°C was seen in mid June 2001, accompanied by moderate increase in salinity from 33.6 to 34 psu (Fig. 2-3). The water mass of salinity >33.6 psu observed in the Okhotsk coast of Hokkaido has been identified as the Soya Warm Water (Aota, 1979). The main factor affecting the transport volume of the Soya Warm Water is the difference in water levels among the northern Japan Sea, Soya Strait and Shiretoko Peninsula (Aota, 1984). The current from the Japan Sea coast of Hokkaido to the Nemuro Strait has been evaluated by tracking floating

objects (Aota, 1984; Aota and Matsuyama, 1987). The present results of a rapid increase in water temperature and salinity in mid June off Shibetsu (Fig. 2-3) are indicative of inflow of the Soya Warm Water into the Nemuro Strait.

The ratios of nutrients (N:P and Si:P) may be used as a marker of water masses occurring in the Nemuro Strait (Table 2-1). From this perspective, the Soya Warm Water and the Surface Low Salinity Water are characterized by low N:P ratio and low Si:P ratio, respectively. According to Aota (1979) and Aota and Takizawa (1994), the Sova Warm Water is usually replaced with the Surface Low Salinity Water in late autumn before sea ice reaches the Okhotsk coast of Hokkaido in the following year. The Soya Warm Current is nutrient poor (0.4μ) mol N, 0.2 μ mol P and 3.1 μ mol Si; Maita and Toya, 1986). Itoh and Ohshima (2000) suggested that the sea level at the Hokkaido coast of the Okhotsk Sea reaches its maximum in December due to the intrusion of cold East Sakhalin Current Water. From these seasonal sequences, it is clear that the nutrient-rich Intermediate Cold Water of the Okhotsk Sea (12.9 μ mol N, 1.4 μ mol P and 23.5 μ mol Si; Maita and Toya, 1986) reaches the Okhotsk coast of Hokkaido before the sea ice does, and remains under the sea ice during the winter season (Fig. 2-6).

The open water bloom of phytoplankton (Fig. 2-7) was observed in the top 10 m during mid to late April 2002 (Fig. 2-7) when salinity decreased suddenly to <32 psu (Fig. 2-5). According to

Table 2-1.	Mean ratios	of nutrients	(N/P and	Si/P) a	and water	masses	occurred in	1 the
Nemuro Str	rait.							

Water Mass	N/P	Si/P	Chlorophyll a (µg/l)	Reference
Soya Warm Water	2.0	15.5	-	Maita and Toya (1986)
Surface Low Salinity Water	6.2	14.6	-	Maita and Toya (1986)
Intermediate Cold Water	9.2	16.8	-	Maita and Toya (1986)
Before Sea ice Reached	7.6	20.3	0.2	This study
Under Sea Ice Water	11.2	23.0	0.4	This study
After Sea Ice Retreated (Blooming)	4.6	18.2	7.1	This study

Alexander and Niebauer (1981), melting ice at the ice edge facilitates phytoplankton blooms in the Bering Sea. This is because lowered salinities caused by melting ice increase stability of the water column. Niebauer et al. (1990) suggested also that stratification in the ice edge blooms resulted from salinity gradients, while in open water, stratification resulted from thermal gradients. Veth et al. (1992) considered that the meltwater lens produced during the spring ice retreat in the marginal ice zone of the northwestern Weddell Sea was the main contributor to the stability of the water column when surface temperatures were low. Such sea ice-phytoplankton bloom interactions have also been reported by other researchers (Stabeno et al., 1998; Smith and Nelson, 1986; Sakshaug and Skjoldal, 1989). All these results strongly suggest that the mechanism determining the open water blooms of phytoplankton observed in the Nemuro Strait (Fig. 2-7) is similar to those being reported in the Bering and Weddell Seas.

All of these results of water mass and associated nutrient regimes and chlorophyll *a* concentrations in the Nemuro Strait are summarized in Fig. 2-6. While the abundance and composition of zooplankton was investigated only in 2001 (Fig. 2-8), its seasonal variation pattern characterized by an abundance or biomass peak in spring is a commonly reported feature from the Oyashio region (Seki and Shimizu, 1997; Saito *et al.*, 2002; Ikeda *et al.*, in press). At its peak, zooplankton abundance or biomass is largely composed of copepods whose spawning or development is accelerated by the phytoplankton blooms.

Chapter 3. Chlorophyll *a* and Nutrient Concentrations in the Nemuro Strait after Sea Ice Retreat

The northern Nemuro Strait is covered with sea ice from January to March or April. Sea ice has been thought to be a cause of high primary production in spring season in this region (Aota, 1986; Kudo, 1996). Spring phytoplankton blooms have been confirmed through shipboard chlorophyll *a* measurements in coastal waters of the Okhotsk Sea (Watanabe, 1989; Nishiyama, *et al.*, 1989; Shimizu *et al.*, 1989), especially in April when sea

ice retreats. Ice algae may act as a seed population for a spring phytoplankton bloom after ice melt (Taguchi, 1993), but the relationship between sea ice and phytoplankton growth in the Okhotsk Sea has not yet been well established. Kudo and Matsunaga (1999) have reported that the development of a spring bloom in Funka Bay located in southwestern Hokkaido is highly dependent on the timing of the intrusion of the Oyashio water into the bay.

In this chapter, possible factors controlling the incidence of spring phytoplankton blooms in coastal waters in the northern Nemuro Strait are discussed based on chlorophyll *a* data collected during the period mid March-July in 1998.

3.1 Material and methods

Starting before sea ice retreat on 21–23 March in 1998 (Sea Ice Information Center, First Regional Maritime Safety Headquarters), samplings were carried out at 6 stations on a transect on 17 March, 14 April, 12 May, 9 June and 8 July in 1998. The six stations are 0.5 (Stn.1), 1 (Stn.2), 2 (Stn.3), 4 (Stn.4), 6 (Stn.5) and 8 km (Stn.6) distant from Matsunori located 4 km southwest of the town of Rausu on the Shiretoko peninsula (all stations fall in an area delineated by 43° 56.2N to 43° 57.7N and 145° 14.8E to 145°12.5E) (Fig. 3–1).

Vertical profiles of temperature and salinity were obtained with an Alec Memory STD AST-200. Transparency was determined with a Secchi disc (SDR) at the stations where observations were carried out during the daytime, and the extinction coefficient k (m^{-1}) was computed from an equation where k = 1.7/SDR (Poole and Atkins, 1929). The depth of the euphotic layer (EL) was defined as the depth where 1 % of the surface light penetrated (EL = $-\ln (0.01)/k$).

Seawater samples for measuring chlorophyll *a* and nutrient concentrations were collected from the surface, and at 5, 10, 20, 30, 50, 75, 100, 150 and 200 m depths using a Rigo-B water sampler. For chlorophyll *a*, 200 ml to 250 ml aliquots of seawater were filtered through a 47 mm Whatman GF/F glass fiber filter. Chlorophyll *a* was size-fractionated at all stations during April and July. For the size fractionation, additional seawater samples (50 ml) were filtered through 25 mm Nuclepore filters of

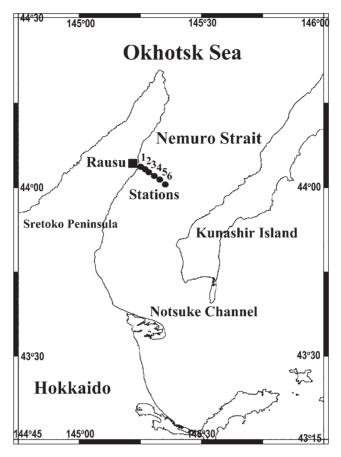


Fig. 3-1. Sampling stations off Rausu in the northern Nemuro Strait during March-July 1998.

 $10~\mu$ m, $2~\mu$ m and $0.2~\mu$ m pore size and the vacuum pressure applied was less than 100 mm Hg (Joint and Pomroy, 1983). Chlorophyll a concentrations were measured with the same method described in Chapter 2.1

3.2 Results

3.2.1 Water temperature, salinity and nutrients

Temporal variations of water temperature and salinity were generally well synchronized at the six stations during the observation periods. Across stations and depths, water temperature varied from -1.66 to -0.21°C on 17 March, from -1.26 to 0.16°C on 14 April, from 0.07 to 4.66°C on 12 May, from 0.06 to 9.32°C on 9 June, and from 4.50 to 14.08°C on 8 July (Fig. 3-2). Across stations and depths, salinity varied from 32.07 to 32.62 psu on 17 March, from 31.90 to 32.86 psu on 14 April, from 32.05 to 33.16

psu on 12 May, from 32.02 to 33.12 psu on 9 June, and from 31.69 to 33.56 psu on 8 July (Fig. 3-3). Temperature and salinity were vertically uniform on 17 March. Low salinity water (<32.0 psu) was observed in the upper 30 m with a weak salinity gradient below 40 m depth on 14 April. A weak temperature gradient was observed in the upper 30 m water column and saline water (>33.0 psu) occurred below about 80 m depth during the period of 12 May - 9 June. A steep temperature gradient was seen in the upper 10 m and saline water (>33.4 psu) appeared below about 40 m depth at Stns. 1 to 5, and below about 70 m depth at Stn.6 on 8 July.

The Okhotsk Intermediate Cold Water (temperature; -1.5 to 1.5°C, salinity; <33.0 psu) defined by Maita (1986) was observed below 80 m depth in March, in the upper 100 m depth in April and between 30 and 80 m depth in May. The temperature and salinity between 40 and 80 m

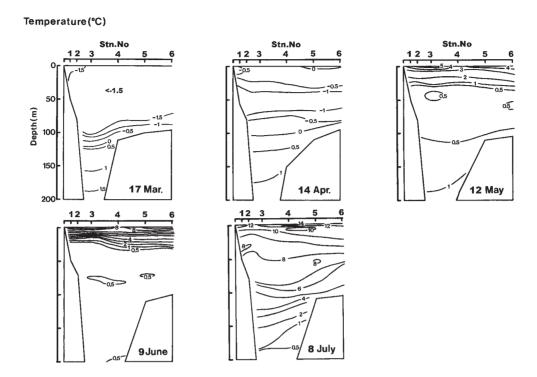


Fig. 3-2. Vertical profiles of temperature ($^{\circ}$ C) at Stns. 1-6 off Rausu in the Nemuro Strait during March-July 1998.

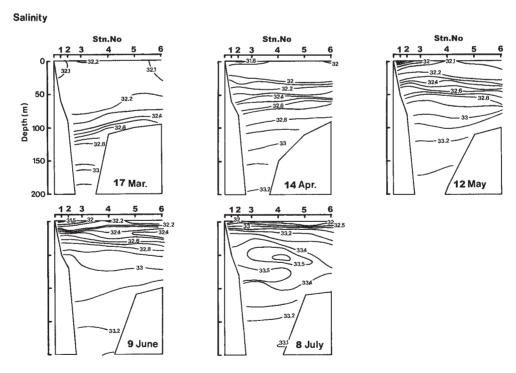


Fig. 3-3. Vertical profiles of salinity (psu) at Stns. 1-6 off Rausu in the Nemuro Strait during March-July 1998.

depth in July were 6.5-8.3°C and 33.4-33.6 psu, respectively, which was considered to be indicative of its origin in the Sova Warm Water (temperature: $7.3-13^{\circ}$ °C and salinity; 33.6-34.0 psu, cf. Maita 1986). The depth of the surface mixed layer was defined as the depth where the vertical gradient of sigma-t reached its maximum. The depth of the surface mixed layer at six stations was 79-93 m in March, 24-32 m in April, 26-31 m in May, 7-16 m in June and 7-10 m in July, thus showing a trend of decreasing depth as the season progressed. Secchi disk readings at six stations were 13-21 m in March, 6-10 m in April, 11-13 m in May, 7.7-10.8 m in June, and 7-9 m in July. Hence, the depths of the euphotic layer were calculated to be 35.2-56.9 m in March, 16.3-27.1 m in April, 29.8-35.2 m in May, 20.9-29.3 m in June, and 19.0-24.4 m in July. The depth of the surface mixed layer greatly exceeded that of the euphotic layer in March and was slightly deeper in April, but in May through July the euphotic layer was deeper than the surface mixed layer.

In the top 30 m, a rapid decline in nutrients was observed during March and April ; e.g. nitrate from >7 μ mol (all stations) to <3 μ mol (Stns. 2–5) (Fig. 3–4), phosphate from 1.3 μ mol to <0.7 μ mol (Stn.4 to Stn. 6) or to <1.0 μ mol (Stns. 1–3) (Fig. 3–5), and silicate from >8 μ mol (Stns. 4–6) to <8 μ mol (Stns. 4–6) (Fig. 3–6). Silicate concentrations in the upper 20 m depth at Stns. 1–3 were very high (11–17 μ mol) but decreased to 8–13 μ mol in April. Nitrate was >25 μ mol throughout the water column on June 9 when the water temperature was uniform below about 40 m depth.

The mean concentrations of nitrate, phosphate and silicate in the euphotic layer during each month were as follows; $8.82 \pm 0.84~\mu$ mol, $1.28 \pm 0.08~\mu$ mol and $11.19 \pm 2.93~\mu$ mol, respectively, in March; $2.42 \pm 1.09~\mu$ mol, $0.53 \pm 0.11~\mu$ mol and $9.05 \pm 3.50~\mu$ mol, respectively, in April ; $5.38 \pm 2.40~\mu$ mol, $0.63 \pm 0.23~\mu$ mol and $12.92 \pm 3.36~\mu$ mol, respectively, in May; $5.14 \pm 4.49~\mu$ mol, $0.30 \pm 0.31~\mu$ mol and $4.80 \pm 5.13~\mu$ mol, respectively, in June; and $0.66 \pm 0.41~\mu$ mol, $0.10 \pm 0.07~\mu$ mol and $4.27 \pm 1.63~\mu$ mol, respectively, in July.

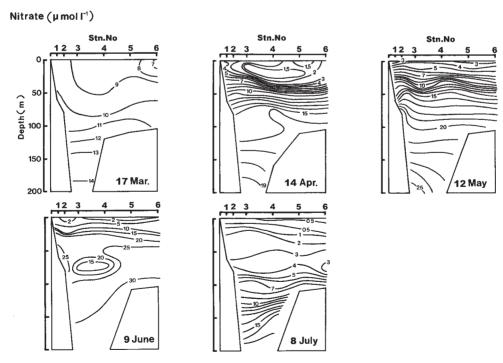


Fig. 3-4. Vertical profiles of nitrate concentration (μ mol) at Stns. 1-6 off Rausu in the Nemuro Strait during March-July 1998.

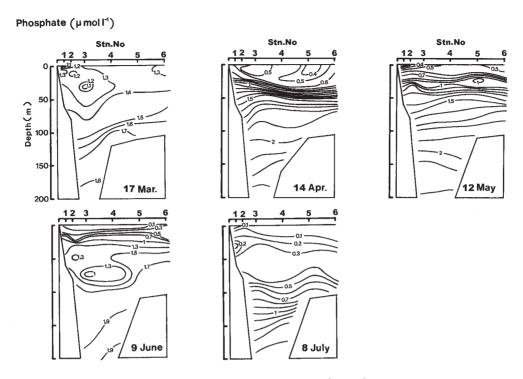


Fig. 3–5. Vertical profiles of phosphate concentration (μ mol) at Stns. 1–6 off Rausu in the Nemuro Strait during March–July 1998.

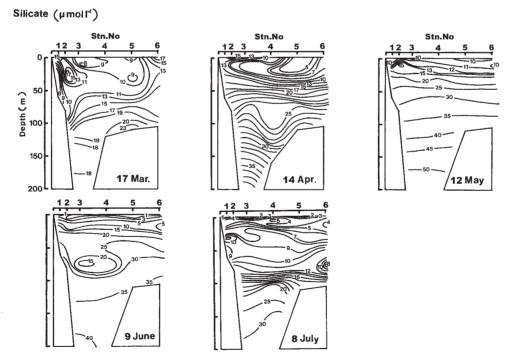


Fig. 3–6. Vertical profiles of silicate concentration (μ mol) at Stns. 1–6 off Rausu in the Nemuro Strait during March–July 1998.

3.2.2 Phytoplankton biomass and its size composition

Chlorophyll *a* concentration began to increase in the surface layer in March at Stn.6 close to Kunashiri Island (Fig. 3–7). Chlorophyll *a* increased rapidly at 10–20 m depth intervals at Stns. 2–6 in April (maximum; <12 μ g l⁻¹), then decreased suddenly in May. Chlorophyll *a* returned to previous levels at 5–10 m depths at Stns. 3–6 in June with some higher concentrations extending to >30 m depth. The mean chlorophyll *a* concentrations in the euphotic layer over the six stations were 1.45 ± 0.85 μ g l⁻¹ in March, 6.97 ± 2.99 μ g l⁻¹ in April, 0.66 ± 0.25 μ g l⁻¹ in May, 1.48 ± 0.85 μ g l⁻¹ in June, and 1.26 ± 0.39 μ g l⁻¹ in July.

The size compositions of chlorophyll a in the euphotic layer were characterized by the predominance of the large fraction (>10 μ m) which composed of 94 to 95 % of the total chlorophyll a. (Fig. 3-8). In May, the proportion of the large fraction decreased, and the medium (2-10 μ m) and the small size fractions (<2 μ m) increased to 25 and 33 %, respectively, of the total chlorophyll

a. In June, the medium and small size fractions were 24–28 % and 15–19 %, respectively, of the total chlorophyll a. The large size fraction increased again from June to July and composed of 59–79 % of the total chlorophyll a.

3.3 Discussion

The depth of the Nemuro Strait becomes rapidly shallow in either directions towards Shiretoko peninsula or Kunashiri Island (Fig. 3-1). Given this topographical feature, wind-driven upwelling may be a mechanism to transport nutrients to surface layers and upwelling is considered to occur under the influence of the southwest wind in the Nemuro Strait. According to Otani (1986), such upwelling is induced by continuous winds of speeds exceeding 5 m s⁻¹. The number of days in which the southwest wind velocity exceeded 5 m s⁻¹ (daily mean of the previous ten days) during the present field survey was zero in March, two days (7.3 ms⁻¹) in April, five days (7.3 ms⁻¹) in May, zero in June and one day (5.3 ms⁻¹) in July (the data from Nemuro Meteological Station). These results, suggesting possible

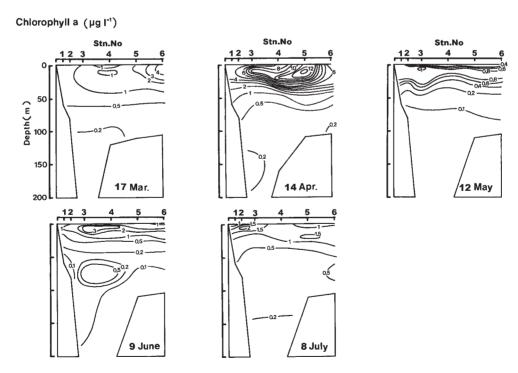


Fig. 3-7. Vertical profiles of chlorophyll a concentration (μ g Γ^{-1}) at Stns. 1-6 off Rausu in the Nemuro Strait during March–July 1998.

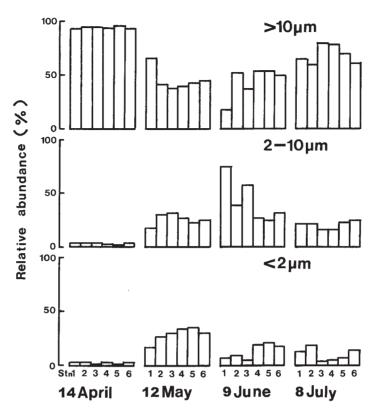


Fig. 3-8. Size fractionated chlorophyll a in the euphotic layer at Stns. 1-6 off Rausu in the Nemuro Strait during April–July 1998.

upwelling in May, are consistent with those of high nutrients observed at 50-200 m depths in May (Figs. 3-4 through 3-6).

Temperature was homogenous below 30 m depth and a weak salinity gradient was observed below 50 m depth in June (Fig. 3-3). Based on temperature and salinity data, the density (sigma-t) of seawater was calculated (cf. Sudo, 1974). Sigma-t below 50 m depth was 25.84-26.70 in March, 25.96-26.62 in April, 26.20-26.72 in May, 26.41-26.70 in June, and 26.05-26.60 in July (data not shown). Judging from the narrowest range of the sigma-t in June, a mixed layer might be formed below 50 m depth bringing nutrients from the deeper layer to the intermediate layer in that month. Relationships between salinity and nitrate, phosphate and silicate concentrations within the euphotic layer are shown Fig. 3-9. Except for March and April when salinities were vertically uniform, nutrient concentrations increased with salinity during May and July. Since

salinity increased with depth in the euphotic layer, this suggests that nutrients were supplied from the deep layer to the euphotic layer between May and June.

Relationships between nitrate (N), phosphate (P) and silicate (Si) in the euphotic layer were analyzed by plotting the data (Fig. 3-10) and calculating linear regression equations and correlation coefficients. Since the data for March did not show any significant relationships, means \pm SD were computed as 8.82 \pm 0.84 μ mol for nitrate (N), 1.28 \pm 0.08 μ mol for phosphate (P), and 11.19 \pm 2.93 μ mol for silicate (Si) (all n=32). For months other than March, the following regression equations were obtained;

```
\begin{array}{lll} {\rm P=}0.087{\rm N}+0.315 & (r=0.83,\,p<0.001),\\ {\rm P=}0.019{\rm Si}+0.354 & (r=0.58,\,p<0.05) \ {\rm in\ April\ (n=23)}\\ {\rm P=}0.085{\rm N}+0.166 & (r=0.87,\,p<0.001),\\ {\rm P=}0.055{\rm Si}-0.090 & (r=0.79,\,p<0.001) \ {\rm in\ May\ (n=29)} \end{array}
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P=0.064N-0.033 (r=0.94, p<0.001),

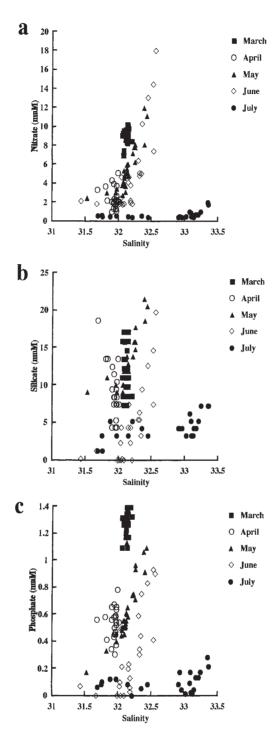


Fig. 3-9. Relationships between salinity and concentrations of nitrate (a), silicate (b), and phosphate (c) in the euphotic layer off Rausu in the Nemuro Strait during March-July 1998.

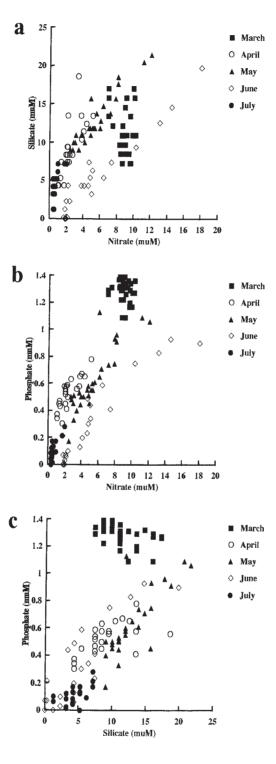


Fig. 3-10. Relationships between nitrate and silicate (a), nitrate and phosphate (b), and silicate and phosphate (c) in the euphotic layer off Rausu in the Nemuro Strait during March-July 1998.

P=0.053Si+0.042 (r=0.86, p<0.001) in June (n=24) P=0.026N-0.012 (r=0.59, p<0.05),

P=0.136Si+0.008 (r=0.79, p<0.001) in July (n=23) The slopes of the regression lines denote the uptake ratio of nutrients by phytoplankton (Shiomoto and Hashimoto, 1999). Therefore, the ratios (Si:N:P) in the euphotic layer were 9:7:1 in March, 52:11:1 in April, 18:12:1 in May, 19:16:1 in June and 39:7:1 in July. The nutrient Si:N:P ratios below the euphotic layer were 10:7:1 in March, 14:7:1 in April, 21:11:1 in May, 18:16:1 in June and 31:10:1 in July. Comparing the uptake ratios by phytoplankton in the euphotic layer, it was suggested that the phytoplankton community in April took Si at a higher rate than the rate supplied below the euphotic layer. The Si and N relationship in April was expressed as Si=2.43N+3.19 (r=0.76, p<0.001, n=23), indicating that Si was removed 2.4 times faster than N. The positive intercept (3.19) of the regression equation means that silicate is left when nitrate is used up. In other words, phytoplankton growth in the Nemuro Strait is possibly limited by N. At the same time, the present results suggest that the Okhotsk Intermediate Cold Water containing high levels of Si is of special importance for phytoplankton blooms in the Nemuro Strait.

The chlorophyll a of the size fraction >10 μ m reached a maximum in mid April and contributed 94-95% of the total chlorophyll a biomass (Fig. 3-8). According to a seasonal study of the size composition of chlorophyll a in Monbetsu harbor on the Okhotsk coast of Hokkaido, the proportion of the large size fraction (>10 μ m) peaked in March when the harbor was covered with sea ice (Hamasaki et al., 1998). The major component of the large and medium size fractions may be diatoms and flagellates, and the small size fraction is believed to be composed of cyanobacteria and other picophytoplankton (Odate, 1994). Unfortunately, no microscopic observation on phytoplankton species was made in this study to confirm this.

According to the Sverdrup model (1953), phytoplankton net production occurs in the water column when the critical depth is greater than the depth of the surface mixed layer. To test this model, the critical depth (D_{cr} ; m) was estimated from the simplified equation (Takahashi *et al.*, 1996);

$$D_{cr} = 0.5 I_0 / (I_c \times k)$$

where I_0 is the surface light intensity (Ein m^{-2} h^{-1}), k is the extinction coefficient (m^{-1}) and I_c is the compensation light intensity (Ein m^{-2} h^{-1}). The calculation of k was based on k=1.7SDR (Pool and Atkins, 1929). For I_c , 0.023 Ein m^{-2} h^{-1} converted from 0.002 ly min^{-1} (Parsons *et al.*, 1984) was substituted. Data on total daily sunlight intensity and day length were those collected by the Nemuro Meteological Station. Energy-heat conversion factors were: 1 joule= 10^7 erg, 1 g cal= 4.185×10^7 erg, and 1 einstein $=52 \times 10^3$ g cal.

The daily values averaged over ten days: I_0 (Ein m^{-2} h^{-1}) were 0.233 in March, 0.270 in April, 0.334 in May, 0.333 in June and 0.237 in July. I_0 increased from March to May. Calculated D_{cr} values were 48–56 m in March, 27–32 m in April, 54–63 m in May, 38–44 m in June and 72–85 m in July. During the present study, the depths of the surface mixed layer were 24–32 m in April, 26–28 m in May, 7–10 m in June and 8 m in July. Thus, comparing D_{cr} with the surface mixed layer (27–32 m vs 24–32 m), the Sverdrup model predicts the occurrence of the phytoplankton bloom to be in April in the northern Nemuro Strait was observed in this study, in other wards there is good agreement between model predictions and field observations.

Although moderate concentrations of phytoplankton $(1.65-2.12 \mu g \text{ chl } a \text{ l}^{-1})$ and high concentration of nutrients were observed in mid March (Figs. 3-4 through 3-7), the peak of the phytoplankton bloom occurred in April rather than March. The compensation light intensity of phytoplankton was influenced by water temperatures and decreased with decreasing temperature (Takahashi et al., 1996). The temperature was below 0°C in the entire water column in March, hence the compensation light intensity of phytoplankton in March is suspected to have been low. The critical depth (D_{cr}) was calculated for March using Ic values of ice algae $(6.48 \times 10^{-4} \text{--} 3.6 \times 10^{-3} \text{ Ein m}^{-2} \text{ h}^{-1} \text{ converted from})$ $0.18-1.0 \ \mu \, \text{Ein m}^{-2} \, \text{s}^{-1}$) (cf. Kirk, 1994). The D_{cr} in March was 305-1,692 m, which is much deeper than the depth of the surface mixed layer, indicating that the net gain in photosynthetic products (phytoplankton biomass) was negative in mid March despite the presence of rich nutrients.

Chapter 4. Between-Year Variations in Chlorophyll a and Nutrients in the Nemuro Strait after Sea Ice Retreat

Sea ice begins to be formed in the coastal waters of the northern Okhotsk Sea off Magadan province, Russia in early winter. Sea ice advances southward by the influence of seasonal winds and the East Sakhalin current (Itoh and Oshima, 2000; Oshima et al., 2001; Oshima et al., 2002; Itoh et al., 2003). On the coast of Nemuro Strait, sea ice arrives in late January and retreats in mid to late March in most years, but the effects of year-to-year variation in the dates of sea ice departure on the phytoplankton growth and the underlying mechanisms have been little studied. The data available prior to the present study were those of Shiomoto et al. (1998) who compared chlorophyll a concentrations in the southern Okhotsk Sea during late fall in 1993 and 1996 before the arrival of sea ice, but not during sea ice retreat in the spring.

From the viewpoint of enhancement of salmon resources, the Okhotsk coastal waters of Hokkaido and Nemuro Strait are the most important nursery areas for juveniles. Survival and growth of juvenile chum salmon depends on the abundance and availability of food (Karpenko, 2003). Coastal environmental conditions including food organisms have been reported as major factors affecting the survival success of juvenile salmon in the first oceanic period of life (Ryding and Skalski, 1999; Willette et al., 1999; Fukuwaka and Suzuki, 2002). Clearly, the environmental conditions of the coastal regions of the Okhotsk Sea and the Nemuro Strait for salmon could vary from one year to the next because of interannual variations of the incidence of phytoplankton blooms as discussed above.

As typical cases for years with and without massive phytoplankton blooms in the Nemuro Strait, the results from 1998 mentioned in Chapter 3.2 are compared with those from 1999 below.

4.1 Materials and methods

Sampling stations, treatment of samples and analytical methods were identical to those described above (Chapter 3.1). Sampling dates were 4 and 21 April, 18 May, 1 and 22 June and 13 July in 1999.

Days of bright sunshine and solar radiation were calculated based on the data in the Monthly Bulletins of the Nemuro Meteorological Station, Sapporo District Meteorological Observatory. The data of the first and the last dates when sea ice were recognized along the Okhotsk Sea coast were provided by the Abashiri Meteorological Station, Sapporo District Meteorological Observatory. The dynamics of sea ice along the Okhotsk Sea coast (the first and the last dates of sea ice recognized) were estimated from the images of a radar network of Esashi-Monbetsu-Abashiri and the accumulated daily sea ice concentrations (% day) along the Okhotsk Sea coast of Hokkaido reported by the Sea Ice Laboratory of the Institute of Low Temperature Science, Hokkaido University. "Sea ice concentration" is defined as percent coverage of sea ice in the sea area studied. According to Aota et al. (1993), the force of sea ice along the Okhotsk Sea coast of Hokkaido may be defined as the accumulated ice concentration. The information of sea ice distribution in the Okhotsk Sea was compiled from the home page of the Meteorological Bureau (http://www.data.kishou.go.jp/kaiyou/db/seaice. html). The information on the period between the first and last date when sea ice was recognized in the Okhotsk Sea coast of Hokkaido was obtained from the home page of the Ice Information Center, First Regional Coast Guard Headquarters (http://w ww1.kaiho.mlit.go.jp/KAN1 /1center.html).

4.2 Results

4.2.1 Dynamics of sea ice

The period of sea ice is given in days from the date when sea ice first reached the coast to the date when sea ice last left the coast. The period of sea ice in the Okhotsk Sea coast of Hokkaido was 61 days (from January 26 to March 27) in 1998, and 113 days (from January 13 to April 25) in 1999. From the inflection point of the accumulated ice concentration curve, the area of sea ice area shifted to a decreasing phase on 8 March (Julian Day = 67) in 1998 and April 15 (Julian Day = 105) in 1999 (Fig. 4-1). Therefore, the dates when sea ice began

to retreat in the Okhotsk Sea coast of Hokkaido in 1998 and 1999 were early March and mid April, respectively.

4.2.2 Light condition

Taking into account daily variations, there was no appreciable difference in the seasonal patterns of daily solar radiations between January and July in 1998 and 1999. In early April, when sea ice was retreating in 1998 but not retreating in 1999, the daily solar radiation was much higher in 1998 (18.48 MJ m $^{-2}$) than in 1999 (15.40 MJ m $^{-2}$) (Fig. 4–2). Such district between-year differences were not observed in the mean daily solar radiations during mid April and early May in 1998 (17.79 MJ m $^{-2}$) and 1999 (17.25 MJ m $^{-2}$).

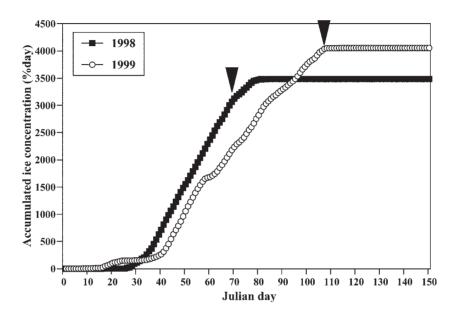


Fig. 4-1. Accumulated daily ice concentration with progress of season in the Okhotsk coastal area of Hokkaido in 1998 and 1999 (sea ice radar observation of Hokkaido University). Arrows denote inflection points.

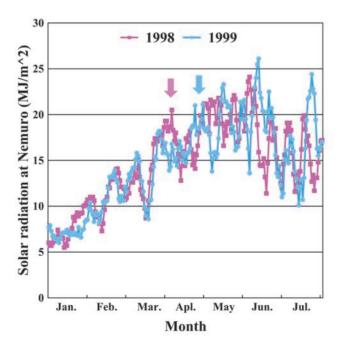


Fig. 4-2. Seasonal changes in daily solar radiation at the Nemuro Meteorological Station in 1998 and 1999. Arrows denote the dates when solar radiation first exceeded 20 MJ m⁻² of each year.

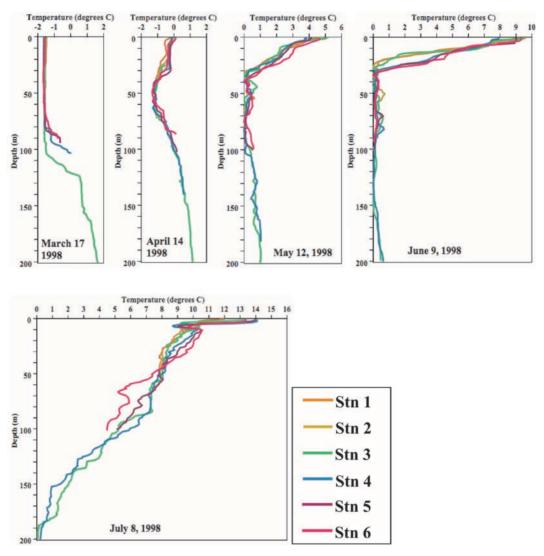


Fig. 4-3. Vertical profiles of temperatures at Stn. 1-6 off Rausu in the Nemuro Strait during March-July 1998.

4.2.3 Water temperature

While no data was available in March in 1999, the results from April through July showed that the vertical profiles of water temperatures at six stations in 1998 (Fig. 4-3) and 1999 (Fig. 4-4) were more or less similar when compared interannually by month. No appreciable between-station differences were detected. From April onward, a thermocline developed in the top 40 m. In early June, the thermocline was well established in the top 30-40 m, and water temperature was homogeneous below the thermocline. In July, the water temperature of the entire water column increased, forming a gradual declining pattern from the surface to 200 m depth. Very cold water (0°C or less) seen at 50-100 m depths during April and June was observed only at

200 m depth in July in both years.

4.2.4 Salinity and density

Vertical profiles of salinities were characterized by the surface minimum (30–32 psu) and a gradual increase with increasing depth from April through June in both 1998 (Fig. 4–5) and 1999 (Fig. 4–6). The vertical profile in July was somewhat different from those of the preceding months in that the salinity maxima (33.5–33.6 psu) was seen at 40–100 m depths and salinity decreased beyond that depth. Between-station differences were not appreciable in 1998, but lower values were seen in offshore stations during April and May in 1999.

Vertical profiles of sigma-t during March-July in 1998 (Fig. 4-7) and April-July in 1999 (Fig. 4-8)

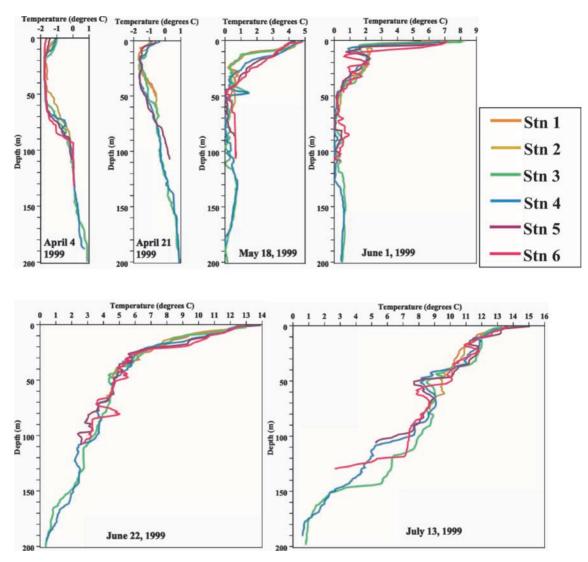


Fig. 4-4. Vertical profiles of temperatures at Stn. 1-6 off Rausu in the Nemuro Strait during April-July 1999.

were 24-25 in the surface layer and increased gradually toward 200 m (sigma-t: 26-27). Vertical profiles of sigma-t were similar to those of salinity, with the exception of the profile in July in both years. Specifically, the mid-depth maxima seen in the salinity profile in July (Figs. 4-5 and 4-6) was not seen in sigma-t profiles for that month.

4.2.5 Mixed layer, euphotic zone and critical depth

The mixed layer depth can be defined as the depth at which the density reaches a maximum when a vertical profile of density is constructed by plotting at depth intervals of 1 m (Mann and Lazier, 1996). Mixed layer depth estimated using this

method after sea ice retreated in 1998 (Fig. 4-7) and 1999 (Fig. 4-8) was 8-30 m and 4-13 m, respectively (Table 4-1). During the same period, the euphotic zone depth and critical depth ranged from 22 to 33 m and from 25 to 52 m, respectively, in 1998, and from 28 to 42 m and from 33 to 50 m, respectively, in 1999 (Table 4-1). Mixed layer depths became shallower as the season progressed, but such a pattern was not detected in the euphotic zone depth and critical depth.

4.2.6 Nutrients

The first sampling dates in 1998 (17 March) and in 1999 (21 April) were before the onset of

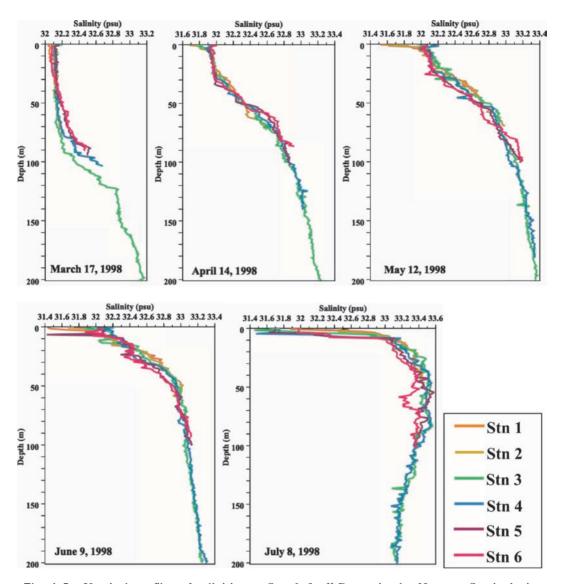


Fig. 4–5. Vertical profiles of salinities at Stn. 1–6 off Rausu in the Nemuro Strait during March–July 1998.

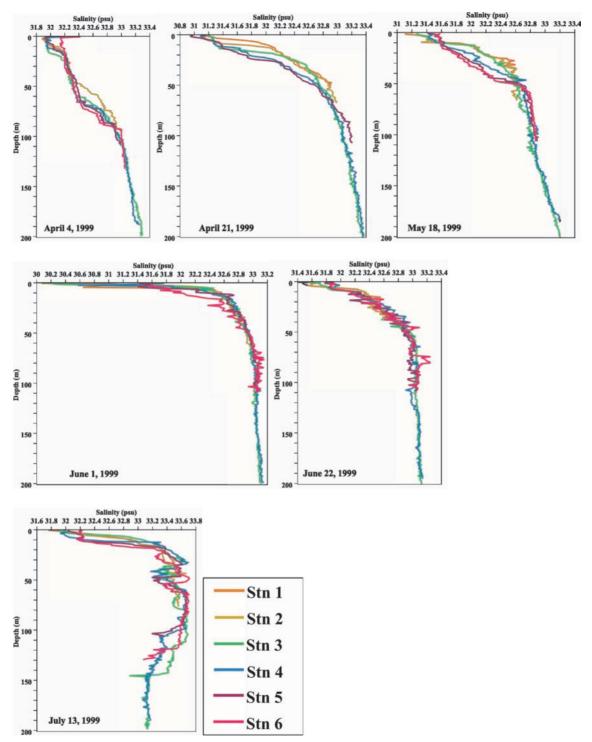


Fig. 4-6. Vertical profiles of salinities at Stn. 1-6 off Rausu in the Nemuro Strait during April-July 1999.

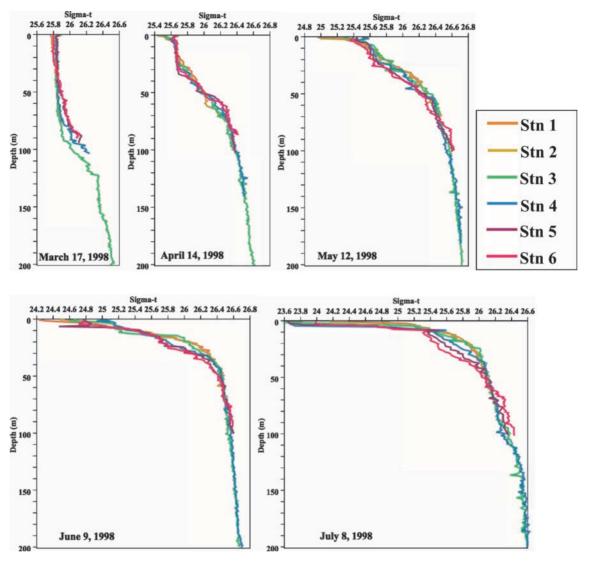


Fig. 4-7. Vertical profiles of sigma-t at Stn. 1-6 off Rausu in the Nemuro Strait during March-July 1998.

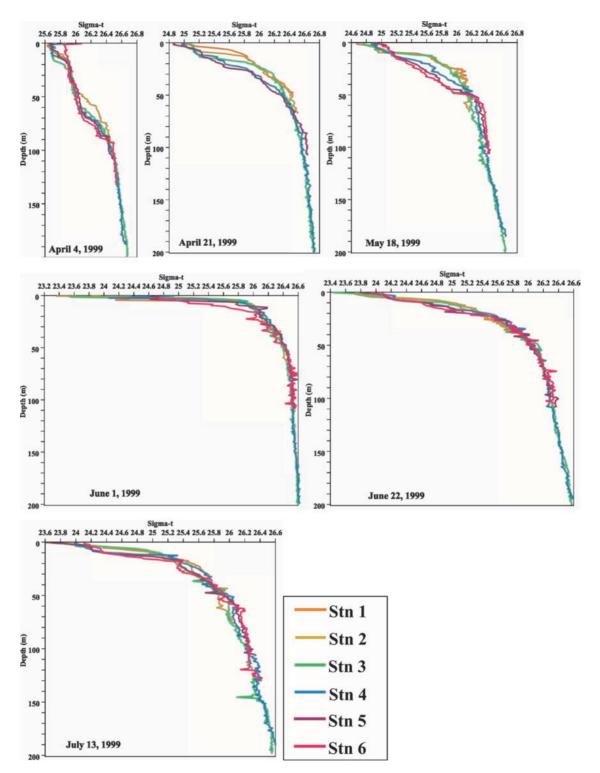


Fig. 4-8. Vertical profiles of sigma-t at Stn. 1-6 off Rausu in the Nemuro Strait during April-July 1999.

Table 4-1. Seasonal variations in critical depth, euphotic layer and mixed layer in 1998 and 1999 off Rausu in the Nemuro Strait. Each value represent mean at 6 stations.

Year	Date (Critical depth	Euphotic layer	Mixed layer	
1998	March 17	51 m	46 m	84 m	
	(March 21 - 23 Sea i		ce retreated from the coast)		
	April 14	29 m	23 m	30 m	
	May 12	52 m	33 m	27 m	
	June 9	38 m	24 m	12 m	
	July 8	25 m	22 m	8 m	
1999	April 4	33 m	41 m	91 m	
	April 21	87 m	63 m	76 m	
	(April 26 - 28	8 Sea ice retreated from the coast)			
	May 18	50 m	42 m	13 m	
	June 1	38 m	28 m	4 m	
	June 22	48 m	34 m	10 m	
	July 13	33 m	31 m	9 m	

Table 4-2. Seasonal variations in nutrients and chlorophyll *a* concentrations in the euphotic layer off Rausu in the Nemuro Strait in 1998 and 1999. Each value represents mean at 6 stations.

Year	Date	Nitrate (µmol/l)	Phosphate (µmol/l)	Silicate (µmol/l)	Chlorophyll a (µg/l)
1998	March 17	8.82	1.28	11.19	1.45
	(March 21 - 23	Sea ice retreat	ted from the coast)		
	April 14	2.42	0.53	9.05	6.97
	May 12	5.38	0.63	12.92	0.66
	June 9	5.14	0.30	4.80	1.48
	July 8	0.66	0.10	4.27	1.26
1999	April 4	9.35	0.92	18.30	0.65
	April 21	6.11	0.68	15.46	0.99
	(April 26 - 28	Sea ice retreate	ed from the coast)		
	May 17	2.35	0.40	7.78	1.77
	June 1	5.16	0.31	15.62	0.98
	June 22	1.10	0.13	8.09	0.73
	July 13	1,22	0.02	3.17	0.80

phytoplankton bloom. Nitrate, phosphate and silicate in the euphotic layer were all high in these first sampling dates in both years (Figs. 4-9 through 4-14, Table 4-2). As the season progressed, all these nutrients were more or less consumed by a phytoplankton bloom in the euphotic layer. Nitrate, phosphate and silicate decreased from 8.82 to 2.42 μ mol, from 1.28 to 0.53 μ mol, and from 11.19 to 9.05

 μ mol, respectively, between 17 March and 14 April in 1998 (Table 4-2), and from 6.11 to 2.35 μ mol, from 0.68 to 0.40 μ mol and from 15.46 to 7.78 μ mol, respectively, between 21 April and 17 May in 1999 (Table 4-2). Nutrients in the euphotic layer reached at minimum levels in June and/or July in both years. Below the euphotic layer, high nutrients were maintained throughout the study periods, and

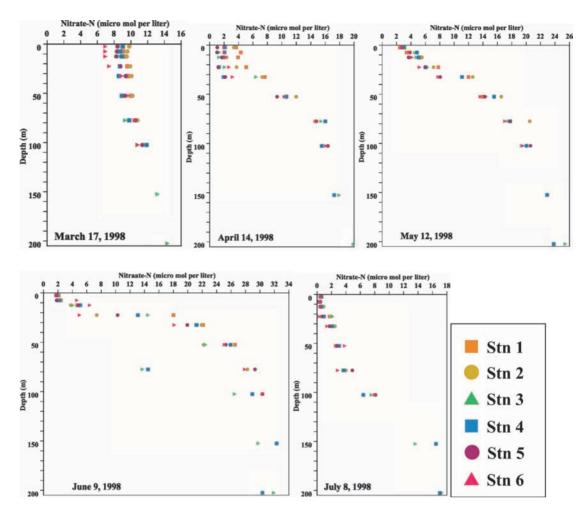


Fig. 4-9. Vertical profiles of nitrate concentrations at Stn. 1-6 off Rausu in the Nemuro Strait during March-July 1998.

no appreciable differences were seen between 1998 and 1999.

4.2.7 Chlorophyll a

While chlorophyll a concentration in the mixed layer reached as high as $13 \mu g \Gamma^1$ in April after sea ice retreated on 21--23 March in 1998 (Fig. 4-15), the concentration barely exceeded $3 \mu g \Gamma^1$ after sea ice retreated on 26--28 April in 1999 (Fig. 4-16). Average chlorophyll a in the euphotic zone ranged from 0.66 to $6.97 \mu g \Gamma^1$ between March and July in 1998, and from 0.65 to $1.77 \mu g \Gamma^1$ between April and July 1999 (Table 4-2).

4.3 Discussion

During the sea ice retreat in 1998 and 1999,

no appreciable differences were seen in daily solar radiation levels (Fig. 4-2) and nutrient concentrations in the euphotic zone (Table 4-2). Nevertheless, a massive plankton bloom was observed in 1998 when sea ice retreated earlier (late March) than in 1999 (late April). Assuming that there were no changes in water mass, the nutrient utilization by a phytoplankton bloom can be estimated by the difference between the nutrient concentrations when sea ice began to retreat (before blooming) and concentrations remaining after the bloom. On this basis, possible yield of chlorophyll a in the euphotic layer in 1998 and 1999 was estimated from nutrient data (N and P, Table 4-2) combined with the nutrient-chlorophyll a ratio of diatoms (Brzezinski, 1985). The decrease in N or P

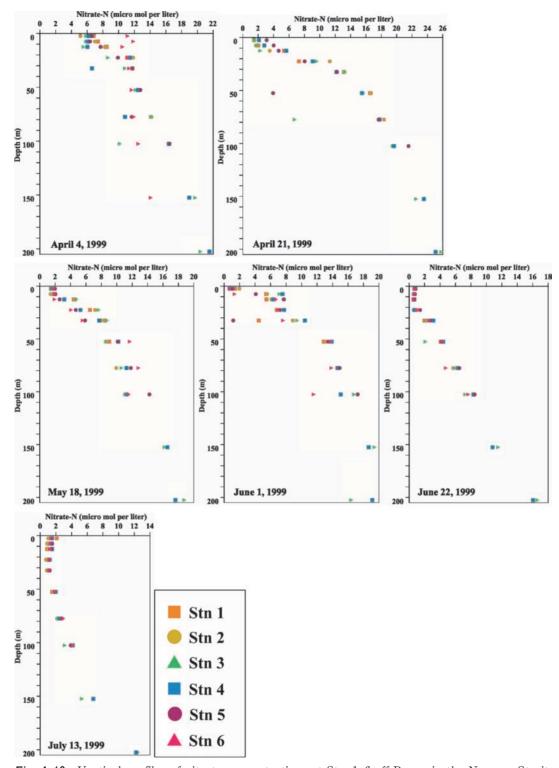


Fig. 4–10. Vertical profiles of nitrate concentrations at Stn. 1–6 off Rausu in the Nemuro Strait during April–July 1999.

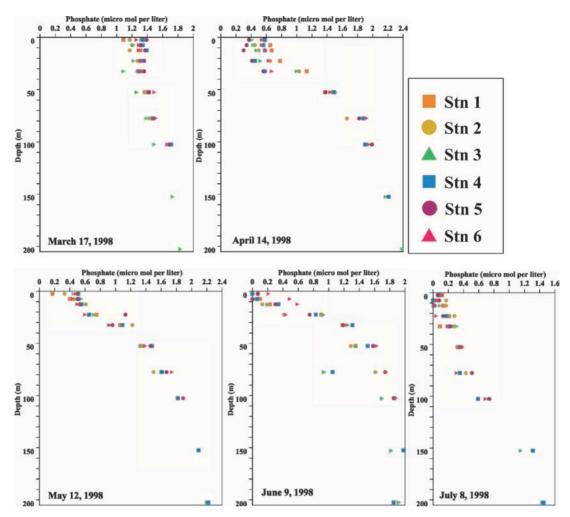


Fig. 4-11. Vertical profiles of phosphate concentrations at Stn. 1-6 off Rausu in the Nemuro Strait during March-July 1998.

concentrations during the bloom season was fitted to a regression model;

N or
$$P = a \times D + b$$
,

where D is Julian days since the beginning of sea ice retreat, and a and b are constants. Resultant regression equations are, N = -0.066D + 14.15 ($R^2 = 0.895$) and P = -0.011D + 2.065 ($R^2 = 0.991$) for 1998, and N = -0.079D + 16.05 ($R^2 = 0.897$) and P = -0.009D + 1.714 ($R^2 = 0.985$) for 1999. The amounts of N or P utilized by phytoplankton were calculated from these equations and converted to chlorophyll a using a set of conversion factors including C:

Chl. a=30 (Banse, 1977) and C: N: P = 106: 16: 1 (Redfied ratio, cf. Parsons *et al.*, 1984). The total amounts of N and P utilized by the phytoplankton bloom during the study period (Julian Day = 104) in 1998 were 4.90 μ mol and 0.422 μ mol, respectively, which equate 5.3–7.0 μ g chlorophyll a l⁻¹. The same calculation in 1999 showed that the total N and P utilized by phytoplankton during the study period (Julian Day = 138) in 1999 was 2.78 μ mol and 0.072 μ mol, respectively, which is equivalent to 1.19–3.0 μ g chlorophyll a l⁻¹. Observed chlorophyll a maxima were 6.97 μ g l⁻¹ in 1998 and 1.77 μ g l⁻¹

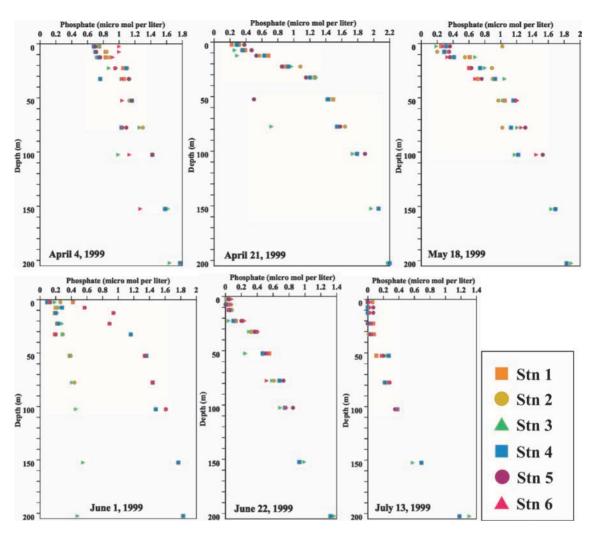


Fig. 4–12. Vertical profiles of phosphate concentrations at Stn. 1–6 off Rausu in the Nemuro Strait during April–July 1999.

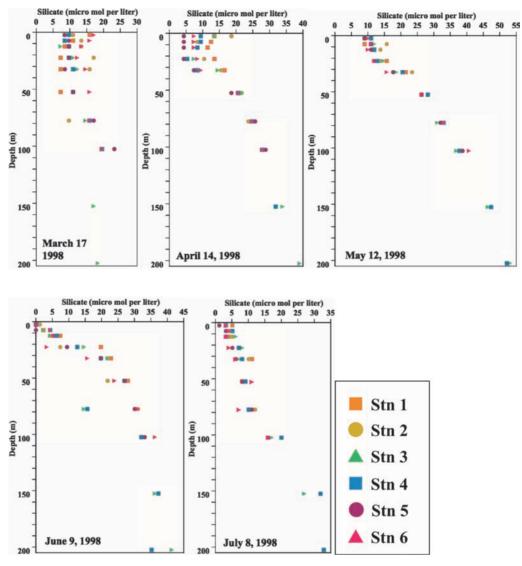


Fig. 4–13. Vertical profiles of silicate concentrations at Stn. 1–6 off Rausu in the Nemuro Strait during March–July 1998.

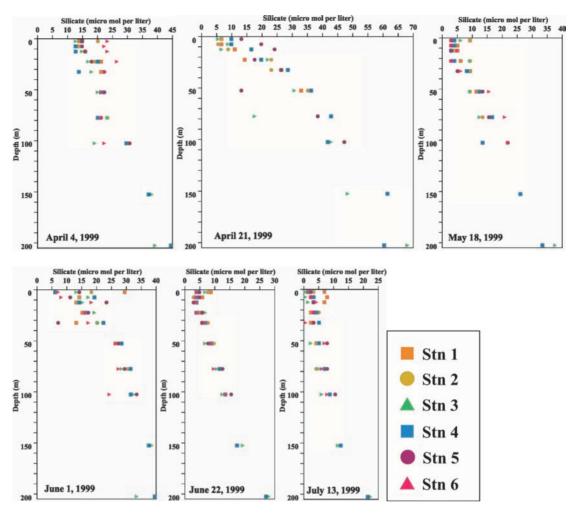


Fig. 4-14. Vertical profiles of silicate concentrations at Stn. 1-6 off Rausu in the Nemuro Strait during April-July 1999.

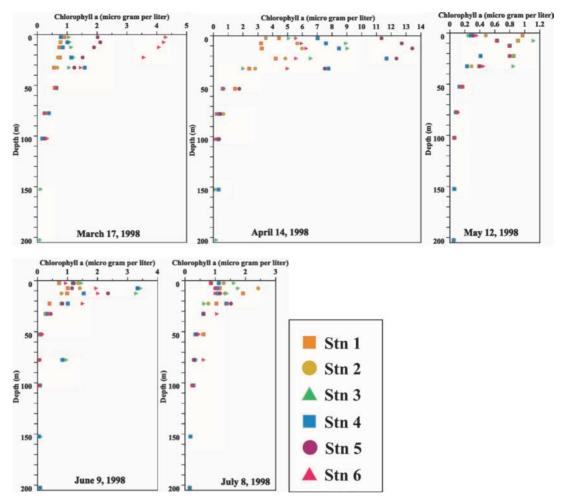


Fig. 4–15. Vertical profiles of chlorophyll a concentrations at Stn. 1–6 off Rausu in the Nemuro Strait during March–July 1998.

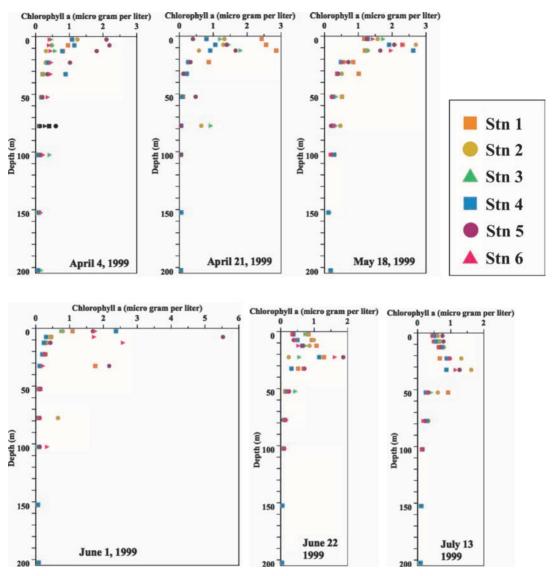


Fig. 4–16. Vertical profiles of chlorophyll a concentrations at Stn. 1–6 off Rausu in the Nemuro Strait during April–July 1999.

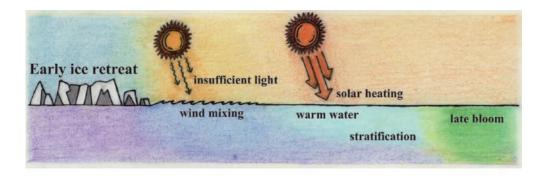
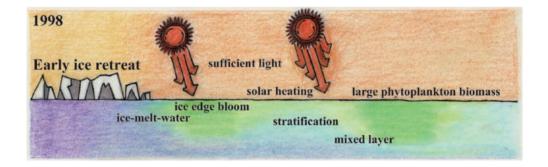




Fig. 4–17. Possible mechanism for the consequences of early and late sea ice retreat to the development phytoplankton bloom in the Bering Sea (Hunt's hypothesis).



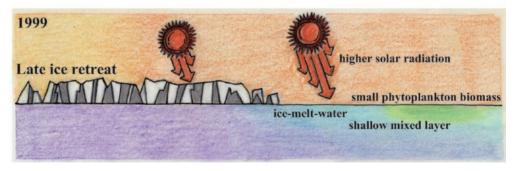


Fig. 4–18. Possible mechanism for the consequences of early and late sea ice retreat to the development phytoplankton bloom in the Nemuro Strait.

in 1999 (Table 4-2), which fall within the range predicted from the decrease in nutrients.

Comparing the depth of the mixed layer after sea ice retreat, the mixed layer depth just after the ice retreat in 1998 was deeper (14 April; 30 m) than that (18 May; 13 m) in 1999 (Table 4-1). As compared with the depth of mixed layer, the depth of euphotic zone at the same date was slightly shallower (23 m) in 1998 but much deeper (42 m) in 1999. The critical depth was nearly similar (29 m) in 1998 but much deeper (50 m) in 1999. The magnitude of primary production is governed by the thickness of the mixed layer (nutrient pool) on the premise that the bottom of the mixed layer is not light limited (shallower than the critical depth). While the daily solar radiation during sea ice retreat periods in 1998 and 1999 was similar (Fig. 4-2), the radiation in early March 1998 was less than that in early April 1999, suggesting that the sea ice melted slowly in 1998 but quickly in 1999 as judged by vertical profiles of salinity and density in each year (Figs. 4–7 and 4–8).

In the Bering Sea, delayed incidence of phytoplankton blooms in open water is characteristic of years in which sea ice retreated early, while phytoplankton blooms occurring immediately in open water is characteristics of a year in which sea ice retreat was delayed (Hunt et al., 2002: Hunt and Drinkwater, 2005) (Fig. 4-17). According to the hypothesis in years of late sea ice retreat, phytoplankton accumulates in cold meltwater, because there is sufficient light to support the bloom in a stabilized water column. In contrast, when sea ice retreats early in the spring, there is insufficient light to support phytoplankton growth and strong seasonal winds prevent water column stratification. In contrast to this hypothesis, early retreat of sea ice in 1998 in the Nemuro Strait led to a massive phytoplankton bloom, and late retreat of sea ice in 1999 in the Nemuto Strait led to a less marked phytoplankton bloom.

The Bering Sea (52-62°N) is located at higher latitudes than the Nemuro Strait (43.7-44.3°N). This means that daily solar radiation in the former region is less than that in the latter region (Sathyendranath and Platt, 1988). Lower daily solar radiation in the Bering Sea suggests a deeper mixed layer because

of slow sea ice melting during years of early sea ice retreat. The meltwater lens produced during sea ice retreat in the marginal ice zone has been considered as the main contributor to the stability of the water column (Veth et al., 1992), a necessary precedent to the onset of a phytoplankton bloom. In contrast to the Bering Sea, sea ice melts quickly even in years of early sea ice retreat because of higher daily solar radiation, which facilitates stratification of the water column and leads to the onset of a phytoplankton bloom. In years during which sea ice retreat is delayed, sea ice melts rapidly and the resultant low salinity water spreads at shallow depths (=shallow mixed layer) leading to a less marked phytoplankton bloom (Fig. 4-18). Thus, the fundamental difference in sea ice-phytoplankton growth relationships between the Bering Sea and the Nemuro Strait lie in the differences in latitudes at the two locations which in turn govern daily solar radiation levels at the sea surface.

Chapter 5. Historical Data Analysis

According to Hokkaido fishery statistics 2002 (Hokkaido, 2004), the production of scallops, chum salmon and seaweed was valued at 54.3 billion yen (20.8 % of the total fishery production of Hokkaido), 34.2 billion yen (13.1 %) and 25.7 billion yen (9.9 %), respectively. The production value of these three fishery resources exceeded 40 % of the total value of the entire Hokkaido fisheries production (260.5 billion yen). Within Hokkaido, fishery production of scallops, chum salmon and seaweed in the Ohkotsk Sea coast and the Nemuro Strait region in 2002 was valued at 35.0 billion yen (42.0 % of total fishery value of Hokkaido), 17.4 billion yen (20.9 %) and 2.8 billion yen (3.3 %), respectively, and all together accounted for more than 60 % of the total fishery production (valued at 83.2 billion yen) in these two regions. It is noted that the production of chum salmon alone in these two regions accounts more than 50 % of that of Hokkaido as a whole.

Salmon juveniles are released from hatcheries around Hokkaido and the northern part of Honshu Island and migrate to and feed in the Ohkotsk Sea from early summer to late autumn of their first year before they migrate out of the Okhotsk Sea (Ueno et

al., 1995; Urawa, 2000). Compared with the Pacific Ocean, the Okhotsk Sea is a preferable habitat for salmon juveniles in that food zooplankton is very abundant (Seki et al., 1995), less saline-surface water lessen osmotic stress (Shimizu et al., 1995), and Hokkaido, Sakhalin, the Eurasian continent, Kamchatka and the Kuril Islands are natural barriers to prevent dispersion of the population (Hanawa, 1996). As mentioned above, the environmental conditions of the Okhotsk Sea coast and the Nemuro Strait region are characterized by sea ice cover in winter, but the relationship between high salmon production and sea ice has never been addressed before.

5.1 Sea ice and fishery production along the Okhotsk coast of Hokkaido

Sea ice exerts negative effects on local fisheries in one sense in that it makes operation of fishing boats difficult, and it damages seaweeds and cultivation facilities. In another way though, the inevitable restriction of fishing boat operations may protect fishery resources from over exploitation.

Walleye pollack (*Theragra chalcogramma*), flatfish (*Pleuronectidae* spp.), giant Ezo scallop (*Patinopecten yessoensis*) and Arabesque greenling (*Pleurogrammus azonus*) are major fishery resources in the coastal waters of the Abashiri district in the southeastern Okhotsk Sea.

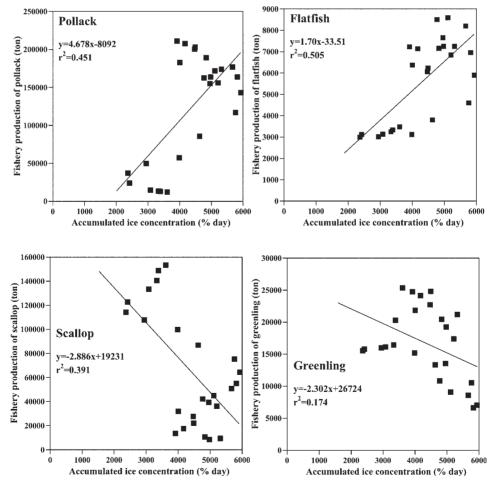


Fig. 5–1. Relationship between the accumulated ice concentrations and annual fishery production of pollack, flatfish, scallop and greenling in the Okhotsk coast during 1969–1998.

The relationship between the accumulated ice concentration off the Okhotsk Sea coast and the fishery production of walleve pollack, flatfish, giant Ezo scallop and Arabesque greenling from 1969 to 1998 were analyzed (Fig. 5-1). Since most of the fisheries target of fish species including salmon which are 4> years old, year-to-year variations were smoothed by calculating a moving average (for five years) before attempting correlations with sea ice. A positive correlation was shown between the two parameters for flatfish and pollack (p<0.001) while a negative correlation was found for scallop (p<0.001) and greenling (p<0.05). The accumulated ice concentration off the Okhotsk Sea coast has been showing a decreasing trend for a long time to date. Therefore, a positive correlation indicates a decreasing trend of the fishery resource and a negative correlation indicates an increasing trend of

the fishery resource.

5.2 Salmon returned to the Okhotsk Sea coast of Japan

The kinds of salmon dealt with in this study are largely chum salmon (*Oncorhynchus keta*), but pink salmon (*O. gorbuscha*) is also referenced for comparison. Data on the number of salmon captured along coasts and in the rivers, and the annual records of hatching and breeding of salmon in the hatcheries were compiled from the yearbooks of the Hokkaido Salmon Hatchery from 1950 to 1996, and the reports of the National Salmon Resources Center (NASREC) from 1997 to 2002. In the yearbooks and reports, detailed data from the Shari hatchery of the Kitami branch of NASREC located in the upper reaches of the Shari River draining into the Abashiri coast region are of special interest (Fig.

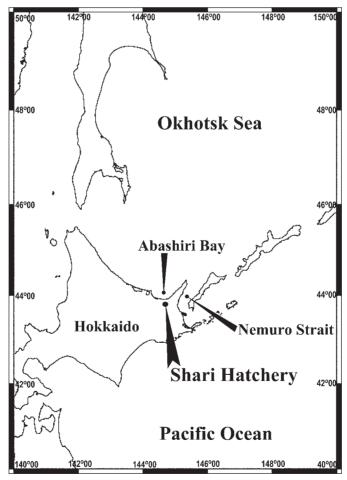


Fig. 5–2. Location of the Shari hatchery (arrowed) on the Okhotsk Sea coastal region of Hokkaido.

5–2). Fisheries production data and its commercial values in Hokkaido were compiled from statistical yearbooks of the Hokkaido Department of Fisheries and Forestry.

The number of chum salmon fry released from hatcheries in Hokkaido increased rapidly from 300 million in the 1960s to one billion in the 1980s. A total of about 200 million chum salmon fry have been released from rivers in each of the five districts of Hokkaido; the Okhotsk Sea, Nemuro, the Japan Sea, and east and west Erimo Peninsula. Accordingly, the returning number of mature chum salmon has increased rapidly since the latter half of the 1970s. During the 1980s, the sum of returning mature chum salmon increased remarkably except in the Okhotsk Sea and Nemuro districts. This reflects the fact that the increase in the number of released salmon fry was less in these two districts as compared with those in the other three districts. In the Okhotsk district, the number of released salmon fry in fact

even decreased from the 1980s to the 1990s although this resulted in the improvement of the number of returning mature chum salmon in this district in the 1990s (Fig. 5-3).

The percentage of returning mature salmon from the total number of released fry is the "return rate", which is on average 1.1 % in the 1950s, 1.6 % in the 1960s, 2.5 % in the 1970s, 3.2 % in the 1980s and 5.3 % in the 1990s in Hokkaido. Within Hokkaido, the return rate in the Nemuro district was less than the average in the 1950s and the 1960s but greater than the average after the 1970s. In the Okhotsk Sea district, the figure was 3.1 % which is greater than the average through the 1970s, decreased to 2.1 % in the first half of the 1980s, recovered to 3.8 % in the latter half of the 1980s and afterwards increased as high as 8.5 % in the 1990s. As a result, the sum of salmon fishery production by set net fisheries off Abashiri and Shari in the eastern Okhotsk Sea coast and off Rausu and Shibetsu in the

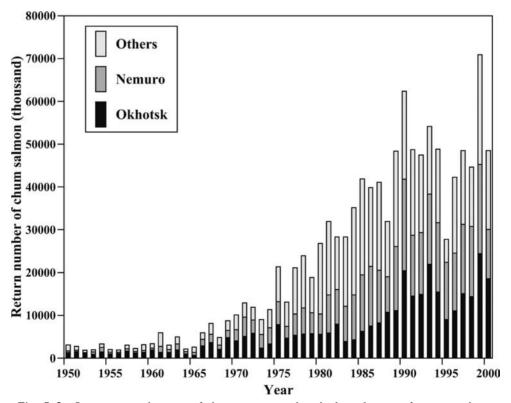


Fig. 5-3. Long-term changes of the return number in brood year of mature chum salmon (*Oncorhynchus keta*) in the Okhotsk Sea, Nemuro and other coast districts (total of the Japan Sea, west coast of Erimo Peninsula and east coast of Erimo Peninsula) around Hokkaido.

Nemuro Strait region has exceeded 40 % of that of Hokkaido as a whole since the 1990s.

5.3 Sea-ice and return of mature salmon

Annual data of the accumulated sea ice concentration along the Okhotsk Sea coast from 1969 to 2004 used in this analysis are those from the sea ice observation radar operated by the Sea Ice Laboratory of Hokkaido University at Mombetsu, and those along the Abashiri coast from 1930 to 2004 are from observations by the Abashiri Meteorological Observatory. For detailed accounts of the area covered by the radar and the observations, see Aota *et al.* (1993). The dates sea ice reached and retreated from the coasts during the period 1950 to 2004 were from the Okhotsk Sea Ice Museum of Hokkaido homepage (http://giza-ryuhyo.com).

The relationship between sea ice distribution off the Abashiri coast and off the Okhotsk Sea coast of Hokkaido was examined. Because the extent of sea ice is indicated by a value integrated over daily-accumulated ice concentration, the

extent of sea ice was assumed to be large when the annual accumulated ice concentration is high (Aota and Ishikawa, 1993). There was a positive and significant correlation (p < 0.001) between the accumulated ice concentration off the Abashiri coast (by observation) and the summed values of the accumulated ice concentration off the Okhotsk Sea coast of Hokkaido (observed with radar at Esashi, Mombetsu and Abashiri). In other words, the annual variation in sea ice concentration off the Abashiri coast reflected that of the Okhotsk Sea coast of Hokkaido. Subsequently the relationship between the extent of sea ice and the return rate of mature chum salmon to their home rivers on the Abashiri coast was analyzed using long-term data. The five-year moving average of the accumulated ice concentration off the Abashiri coast showed a clear trend of decline from 1930 to 2004 (p<0.001). Three peaks, each approximately 20 years apart, were observed (Fig. 5-4). The years of 1945 and 1985 correspond to the cold years broadly seen in the waters around Japan (Sakurai et al., 2000). While a trend of decrease is seen between the 1930s

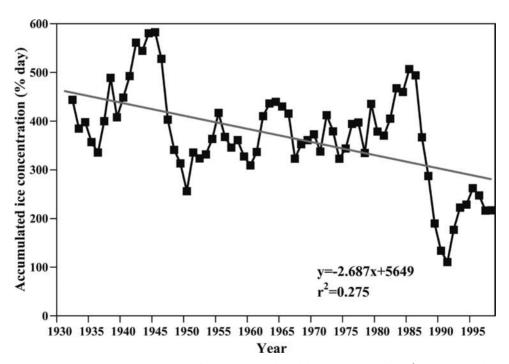


Fig. 5-4. Long-term changes of the accumulated ice concentration (5-year moving averages) off Abashiri coast by watching observations during 1932–1998.

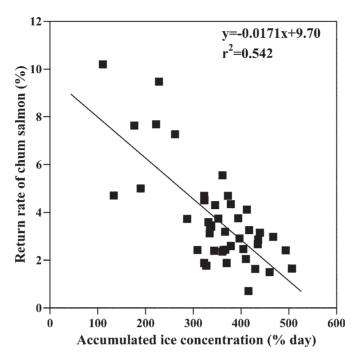


Fig. 5-5. Relationship between the return rate of mature chum salmon (*Oncorhynchus keta*) and the accumulated ice concentration in release year (5-year moving averages) off Abashiri (Okhotsk Sea) during 1951-1995.

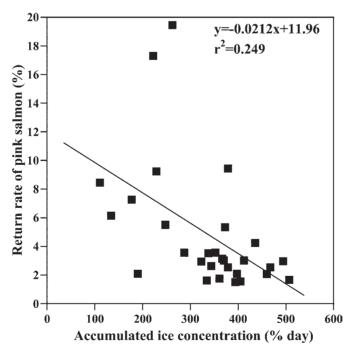


Fig. 5-6. Relationship between the return rate of mature pink salmon (*Oncorhynchus gorbuscha*) and the accumulated ice concentration in release (5-year moving averages) off Abashiri (Okhotsk Sea) during 1968-1996.

and the 1990s, large year-to-year variations in the extent of sea ice are also evident.

The return rate of mature chum salmon on the Okhotsk Sea coast was negatively correlated with the annual accumulated ice concentration off the Abashiri coast (Fig. 5-5); the number of returned chum salmon was less in years in which the amount of sea ice was extensive. The same negative relationship was also confirmed for the return rate of mature pink salmon (Fig. 5-6). In Fig. 5-6, two anomalously high-return cohorts were those released in 1993 and 1995, which may reflect higher survival during their coastal lives although the reasons for this potentially higher survival are unknown (perhaps high zooplankton abundance, large juvenile size, etc.).

The relationship between the duration of sea ice cover along the coasts and the release timing of salmon fry was examined. The duration of sea ice coverage can be defined in two ways; one is the number of days between the first appearance of sea ice appeared and its complete disappearance; and the other is the number of days between the date of sea ice reaching the coast and the date of sea ice starting to retreat from the coast (Fig. 5–7). The duration of sea ice coverage in the

1960s, 1970s, 1980s and 1990s were 92, 95, 91 and 78 days, respectively, along the Abashiri coast by the first definition, and were 55, 59, 49 and 46 days, respectively, along the Abashiri coast by the second definition. Under either definition, a trend of shortening of sea ice coverage in recent years is evident in the waters around Abashiri. Analyzing a historical data set (1930–1992), Aota *et al.* (1993) noted a positive correlation between the duration of sea ice coverage and the accumulated ice concentration. This positive correlation was confirmed in the present study by adding data since 1993 to those used in Aota *et al.*'s (1993).

5.4 Sea ice and artificial salmon enhancement

The Shari River is the main river supporting the salmon resources of the Abashiri coastal region and is one of the important salmon enhancement rivers in the Okhotsk Sea coastal region (Fig. 5-2). The Shari hatchery of the Kitami branch of the National Salmon Resources Center is located in the upper reaches of the Shari River and has a long history of salmon enhancement which goes back to 1950. The entire history may be divided into three periods from the viewpoint of treatment of salmon fry before release (Fig. 5-8). From 1950 to 1966, none of the

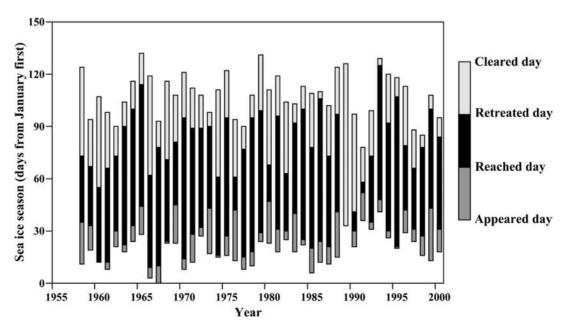


Fig. 5-7. Long-term changes of ice-covered season off Abashiri. See text for details.

salmon fry were fed in the hatchery before release to the river (Non-feed period). From 1967 to 1986, part of salmon fry were fed and the other part were not fed, before release to the river (Transitional period). The Transitional period may be subdivided into "First" and "Second" by the difference in the starting dates of fry release to the stream (First: released late, Second: released early). From 1987 until the present, all salmon fry were fed in a hatchery before being released to the river (Feed period).

In Fig. 5-8, the release date in a given year was shown by the number of days counted from January first (Julian day). For example, the release date during the Non-feed period was between 89-120 days, meaning the release of salmon fry started on the 89th day and finished on 120th day. The release dates during the Transitional period were 68-145 days, and during the Feed period were 107-149 days. It is noted that the starting date and ending date of fry release were earlier during Non-feed period than Feed-period. The duration of

release was the longest during Transitional period because the number of fry and the proportion of fed fry increased gradually. The breeding duration of female salmon inevitably became longer when salmon fry were fed during the Feed period.

The return rate of mature chum salmon and the body weight of released fry during each period are compared. The return rate and the body weight of fry were 2.9 % and less than 0.5 g during Non-feed period, 3.6 % and 1.2 g during First Transitional period, 2.4 % and 0.5–0.7 g during Second Transitional period, and 7.0 % and 0.9–1.4 g during Feed period. The return rate of mature chum salmon during Second Transitional period was the lowest because a large number of the fry were needed to release over the longer period (including early in the season) due to the limited capacity of hatchery facilities.

Chapter 6. General Discussion

While the present results clearly suggest that the

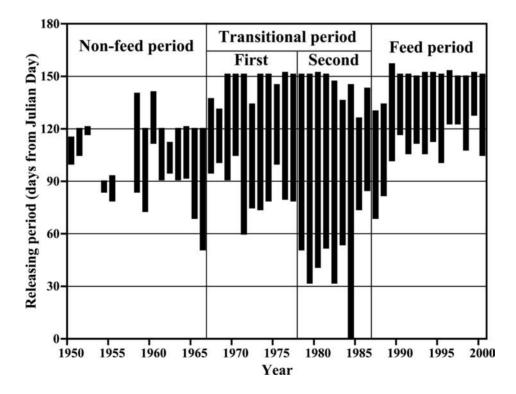


Fig. 5-8. Historical accounts of raising procedures of chum salmon fry after hatching to release in the Shari hatchery during 1950–2000.

effects of sea ice on salmon of hatchery origin was mediated by hydrography, phytoplankton blooms and zooplankton (food for salmon) in the coastal environments, the expression of these effects may vary depending on the physiological characteristics of different salmon species. There was a negative correlation between the accumulated sea ice concentration off the Abashiri coast and the return rate of mature chum salmon in the Okhotsk Sea coast off Hokkaido (Fig. 5-5). Compared with chum salmon, the correlation was weak in pink salmon (Fig. 5-6). Chum salmon are different from pink salmon in that the former spawn in spring water and the latter in river water. Pink salmon can adapt to lower temperature environments than can chum salmon (Kobayashi, 1968). This means that pink salmon is able to endure lower temperatures in the coastal regions in the course of their downstream migration. The growth and maturation of pink salmon are much faster than chum salmon and pink salmon return to home rivers for spawning in two years (Heard, 1991). Because of this shorter generation time, the return rate of pink salmon is expected to be higher than that of chum salmon if they are not food limited during their oceanic lives. Nevertheless, a large year-to-year variation in the return rates of pink salmon may be indicative of rather adverse food conditions during their oceanic lives.

The return rate of mature chum salmon decreased when chum salmon fry were released during the period of sea ice (Fig. 5-5 and 5-6). In addition, the period of sea ice coverage was extended when the force of sea ice was strong (Aota *et al.*, 1993).

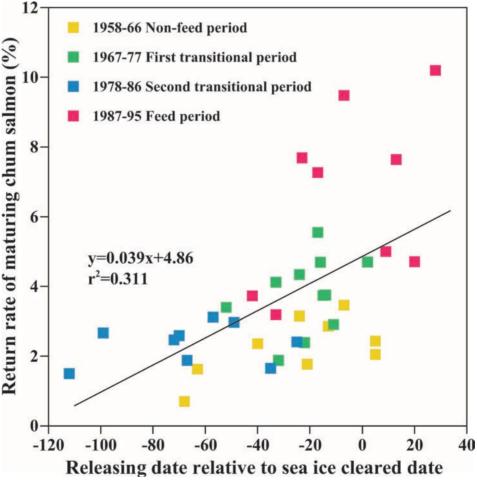


Fig. 6-1. Relationship between the return rate in brood year of mature chum salmon in the Okhotsk Sea coast and the releasing date of chum salmon fry from the Shari hatchery relative to the sea ice cleared date off Abashiri.

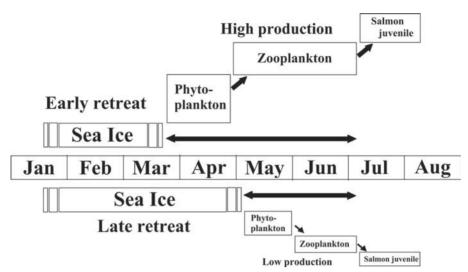


Fig. 6-2. Schematic diagram of two scenarios regarding the timing of sea ice retreat which lead high or low production of phytoplankton, zooplankton and survival of salmon juveniles through food chain in the Nemuro Strait.

The relationship between the release date of salmon fry from the Shari hatchery relative to the date of sea ice disappearance from the Abashiri coast and the return rate of mature chum salmon in the brood year in the Okhotsk Sea coastal region was examined (Fig. 6-1). A positive correlation (p<0.001) between these two parameters in Fig. 6-1 indicates that the return rate increased when chum salmon fry were released after the sea ice retreated from coastal regions. For this reason, food (zooplankton) for salmon fry is considered to be abundant because of a preceding phytoplankton bloom, especially in years when sea ice retreated early in the spring (Fig. 6-2).

In examining records taken from 1958 to 1995, it was noted that the return rate of mature salmon remained low in the Second Transitional period (1978–1986, Fig. 6–1). Despite the fact that the fry were fed prior to release, low return rates may be due to the strong force of sea ice (Fig. 5–4), earlier release of fry (Fig. 5–8), and small body size of the fry released (as mentioned above) during these years. Shimizu *et al.* (1989) reported that water temperatures off Yubetsu, located in the north of Abashiri, were low during 1983 and 1985. It is therefore considered that salmon fry released in the Second Transitional period might encounter low

temperature conditions in the Okhotsk coastal region and suffer a high mortality during their early oceanic life (Shimizu, 1998). While the provision of food for the fry prior to the release could improve their return rate as mature salmon (Kobayashi, 1987), the present results strongly indicate that the return rates are also affected by coastal environments (temperatures, food zooplankton etc.) encountered downstream. Analyzing the relationship between the return rate of chum salmon and sea surface temperatures as determined by satellite images in the coastal waters around Hokkaido, Miyakoshi et al. (2007) noted that the return rate was low in years of low temperature. It is suggested that the low sea surface temperature is results from delayed sea ice retreat; if so, the suggestion by Miyakoshi et al. (2007) is consistent with the relationship between the return rate and accumulated ice concentration of this study (Fig. 5-5).

In this dataset the return rates of chum salmon fry which were released after the sea ice retreated from the coastal regions are still variable (Fig. 6-1), suggesting that the causes of fry mortality observed as high as >90% during their oceanic lives are still largely unknown. Yatsu and Kaeriyama (2003) analyzed causes affecting survival of Hokkaido chum salmon during their oceanic migrations and

concluded that while the body size at release was positively correlated the effects of the number of fry released, oceanic sea surface temperatures (SST) and climate (Aleutian Low Pressure) were all not significant. It has also been suggested that the survival salmon fry in coastal waters is affected by climate (regime shift) (Kaeriyama, 2003).

As a next step to improve the return rate of mature salmon, study should be directed to the feeding conditions of salmon fry during the sea ice retreat season in the coastal waters of the Nemuro Strait (Shimizu and Aota, 2000; Shimizu et al., 2001; Shimizu et al., 2007). Since zooplankton are the major food component of salmon fry, zooplankton production cycles in coastal waters and in the Okhotsk Sea need to be studied as a basis to evaluate the mechanism of survival during their first oceanic year. Today, salmon hatchery programs aimed at enhancement of the resources have a number of problems aside from technological issues. These problems include environmental and economic issues posed by coexistence of hatchery-raised and wild populations as target of salmon fisheries; how to maintain genetic diversities; how to avoid imbalance of the ecosystem; how to secure the economies of local salmon fishermen under fluctuating demand-supply relationships, etc (Kaeriyama, 1994, 1996), although all these issues are outside of the scope of this study.

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References

- Alexander V., 1980: Interrelationship between the seasonal sea ice and biological regimes. *Cold Regions Sci. Technol.*, **2**, 157-178.
- Alexander V. and Niebauer H. J., 1981: Oceanography of the eastern Bering Sea ice-edge zone in spring. *Limnol. Oceanogr.*, 26, 1111–1125.
- Aota M., 1979: Oceanographic conditions in the coastal area of southwestern Okhotsk Sea. Bull. Coastal Oceanogr., 17, 1–11 (in Japanese).
- Aota M., 1984: Oceanographic structure of the Soya Current. Bull. Coastal Oceanogr., **22**, 30–39 (in Japanese).
- Aota M., 1986: Okhotsk Sea and sea ice. Gekkan Kaiyo, 18 (2), 66-74 (in Japanese).
- Aota M. and Ishikawa M., 1993: Data on the variations of ice concentration in the Okhotsk Sea coast of Hokkaido. Umi to Sora, **69**, 95-108 (in Japanese).
- Aota M., Ishikawa M., Murai K., and Hirata T., 1993: Variation of accumulated ice concentration off Abashiri, Okhotsk Sea coast of Hokkaido. Umi no Kenkyu, **2**, 251–260 (in Japanese).
- Aota M. and Matsuyama M., 1987: Tidal current fluctuations in the Soya Current. *J. Oceanogr.*, **43**, 276–282.
- Aota M. and Takizawa T., 1994: Research of Soya

- Warm Current and cooperative observation between Japan and Russia-Soya Project. Symposium-Japan Sea, GekkanKaiyo, 194, 819-823 (in Japanese).
- Banse K., 1977: Determining the carbon-to-chlorophyll ratio of natural phytoplankton. *Mar. Biol.*, **41**, 199–212.
- Bianchi F., Boldrin A., Cioce F., Dieckmann G.,
 Kuosa H., Larsson A. M., Nothig E. M., Sehlstedt
 P. I., Scocal G., and Syvertsen E. E., 1992:
 Phytoplankton distribution in relation to sea ice,
 hydrography and nutrients in the northwestern
 Weddell Sea early spring 1988 during EPOS.
 Polar Biol., 12, 225-235.
- Brzezinski M. A., 1985: The Si:C:N ratio of marine diatoms: Interspecific variability and the effect of some environmental variables. *J. Phycol.*, **21**, 347–357.
- Comiso J. C., Maynard N. G., Smith Jr. W. O., and Sullivan C. W., 1990: Satellite ocean color studies of antarctic ice edges in summer and autumn. *J. Geophys. Res.*, **95** (C6), 9481–9496.
- Dieckmann G. S. and Hellmer H. H., 2003: The importance of sea ice: an overview, in "Sea Ice, an introduction to its physics, chemistry, biology and geology" (ed. by Thomas D. N. and Dickmann G. S.), Blackwell, Oxford, pp. 1–21.
- Dunbar R. B., Leventer A. R., and Mucciarone D. A., 1998: Water column sediment fluxes in the Ross Sea, Antarctica: Atmospheric and sea ice forcing. *J. Geophys. Res.*, 103 (C13), 30741-30759.
- Fukuwaka M. and Suzuki T., 2002: Early sea mortality of mark-recaptured juvenile chum salmon in open coastal waters. *J. Fish Biol.*, **60**, 3-12.
- Garrison D. L., Buck K. R., and Fryxell G. A., 1987: Algal assemblages in Antarctic pack ice in ice-edge plankton. *J. Phycol.*, **23**, 564-572.
- Hamasaki K., Ikeda M., Ishikawa M., Shirasawa K., and Taguchi S., 1998: Seasonal variability of size-fractionated chlorophyll *a* in Monbetsu Harbor, Hokkaido, northern Japan. *Plankton Biol. Ecol.*, **45**, 151–158.
- Hanawa K., 1996: Location of the research of the Okhotsk Sea in the research of the North Pacific Ocean. Gekkan Kaiyo, **28**, 526–533 (in Japanese).

- Heard W. R., 1991: Life history of pink salmon, in "Pacific Salmon Life Histories" (ed. by Croot C. and Margolis L.), Univ. British Columbia, Vancouver, pp. 120–230.
- Hokkaido, 2004: Fisheries statistics of Hokkaido in 2002 (in Japanese).
- Hunt G. L. Jr and Drinkwater K. F., 2005: Ecosystem studies of sub-Arctic seas (ESSAS) science plan, GLOBEC Report No.19, viii, 60 pp.
- Hunt G. L. Jr, Stabeno P., Walters G., Sinclair E., Brodeur R. D., Napp J. M., and Bond N. A., 2002: Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Res. II*, 49, 5821–5853.
- Ikeda, T., Shiga N., and Yamaguchi A., Structure, biomass distribution and trophodynamics of the pelagic ecosystem in the Oyashio region, western subarctic Pacific. *J. Oceanogr.*, in press.
- Itoh M. and Ohshima K. I., 2000: Seasonal variations of water masses and sea level in the southwestern part of the Okhotsk Sea. *J. Oceanogr.*, **56**, 643–654.
- Itoh M., Ohshima K. I., and Wakatsuchi M., 2003: Distribution and formation of Okhotsk Sea Intermediate Water: An analysis of isopycnal climatological data. J. Geophys. Res., 108 (C8) 14, 1-18.
- Joint I. R. and Pomroy A. J., 1983: Production of picoplankton and small nanoplankton in the Celtic Sea. *Marine Biol.*, 77, 19–27.
- Kaeriyama M., 1994: Variation of fishery production of salmon in Japan. Gekkan Kaiyo, **26**, 466–470 (in Japanese).
- Kaeriyama M., 1996: Reproduction of salmonid fishes and optimum releasing techniques. Gekkan Kaiyo, 28, 589-594 (in Japanese).
- Kaeriyama M., 2003: Does regime shift affect biomass dynamics and life history of salmonid fishes? Gekkan Kaiyo, **35**, 131–136 (in Japanese).
- Karpenko V. I., 2003: Review of Russian marine investigations of juvenile Pacific salmon. *N. Pacif. Anadr. Fish. Comm. Bull.*, No. 3, 69-88.
- Kirk J. T. O., 1994: Light and Photosynthesis in Aquatic Ecosystems, 2nd ed., Cambridge University Press, Cambridge, 509 pp.
- Kobayashi T., 1968: Some observation on the natural spawning ground of chum and pink salmon in

- Hokkaido. Sci. Rep. Hokkaido Salmon Hatchery, **22**, 7–13 (in Japanese).
- Kobayashi T., 1987: Salmon fishery and resource enhancement, Suisanshinko, Vol.20, No. 3 (219), 36 pp (in Japanese).
- Kudo S., 1996: Sea ice ecosystem-seasonal sea ice ecosystems developing in Saroma-ko lagoon in winter-. *Aquabiology*, **102**, 21–27.
- Kudo I. and Matsunaga K., 1999: Environmental factors affecting the occurrence and production of the spring phytoplankton bloom in Funka Bay, Japan. *J. Oceanogr.*, **55**, 505–513.
- Lancelot C., Billen G., Veth C., Becquevort S., and Mathot S., 1991: Modeling carbon cycling through phytoplankton and microbes in the Scotia-Weddell Sea area during sea ice retreat. *Mar. Chemist.*, **35**, 305-324.
- Maita Y., 1986: Chemistry of the Okhotsk Sea. Gekkan Kaiyo, **188**, 117-122 (in Japanese).
- Maita Y. and Toya K., 1986: Characteristics on the distribution and composition of nutrients in subarctic regions. Bull. Fish. Oceanogr., 50, 105-113 (in Japanese).
- Mann K. H. and Lazier J. R. N., 1996: Vertical Structure of the Open Ocean: Biology of the mixed layer, in "Dynamics of Marine Ecosystem", Blackwell Science, 394 pp.
- McMinn A., 1996: Preliminary investigation of the contribution of fast-ice algae to the spring phytoplankton bloom in Ellis Fjord, eastern Antarctica. *Polar Biol.*, **16**, 301-307.
- Miyakoshi Y., Saitoh S., Matsuoka A., Takada M., Asami H., Fujiwara M., and Nagata M., 2007: Comparison of release timing of hatchery-reared juvenile chum salmon (*Oncorhynchus keta*) to spring coastal sea surface temperature during high and low survival period. *GIS/Special Analysis in Fishery and Aquatic Science*, 3, 227-240.
- Niebauer H. J. and Alexander V., 1985: Oceanographic frontal structure and biological production at an ice edge. *Cont. Shelf Res.*, 4, 367-388.
- Niebauer H. J., Alexander V., and Henrichs S., 1990: Physical and biological oceanographic interaction in the spring bloom at the Bering Sea marginal ice edge zone. *J. Geophys. Res.*, 95

- (C12). 22229-22241.
- Niebauer H. J., Alexander V., and Henrichs S., 1995: A time-series study of the spring bloom at the Bering Sea ice edge, I. Physical processes, chlorophyll and nutrient chemistry. *Cont. Shelf Res.*, 15, 1859-1877.
- Nishihama U., Kurata M., and Tada M., 1989: Seasonal change of chlorophyll concentration lagoon Saroma-ko and Notoro-ko and off Abashiri. *Bull. Fish. Oceanogr.*, **53**, 52-54 (in Japanese).
- Odate T., 1994: Plankton abundance and size structure in the northern North Pacific Ocean in early summer. *Fish. Oceanogr.*, **3**, 267–278.
- Ohshima K. I., Mizuta G., Itoh M., Fukamachi Y., Watanabe T., Nabae Y., Suehiro K., and Wakatsuchi M., 2001: Winter oceanographic conditions in the southwestern part of the Okhotsk Sea and their relation to sea ice. *J. Oceanogr.*, 57, 451-460.
- Ohshima K. I., Wakatsuchi M., and Fukamachi Y., 2002: Near-surface circulation and tidal currents of the Okhotsk Sea observed with satellite-tracked drifters. *J. Geophys. Res.*, 107 (C11), 3195–3224.
- Otani K., 1986: Coastal upwelling generated by the impulsive longshore wind. Bull. Coastal Oceanogr., 23, 155-165 (in Japanese).
- Otsuki A., Watanabe M. M., and Sugahara K., 1987: Chlorophyll pigments in methanolextracts from ten axenic cultured diatoms and three green algae as determined by reverse phase HPLC with fluorometric detection. *J. Phycol.*, 23, 406-414.
- Parsons T. R., Takahashi M., and Hargrave B., 1984: Biological Oceanographic Processes, 3rd ed., Pergamon Press, Oxford, 330 pp.
- Poole H. H. and Atkins M. R. G., 1929: Photoelectric measurements of submarine illumination throughout the year. *Mar. Biol.*, **16**, 297–324.
- Riebesell U., Schloss L., and Smetacek V., 1991: Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. *Polar Biol.*, 11, 239–248.
- Ryding K. E. and Skalski J. R., 1999: Multivariate regression relationships between ocean conditions and early marine survival of coho

- salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci., **56**, 2374–2384.
- Saito H., Tsuda A., and Kasai H., 2002: Nutrient and plankton dynamics in the Oyashio region of the western subarctic Pacific Ocean. *Deep-Sea Res. II*, **49**, 5463–5486.
- Sakshaug E. and Skjoldal H. R., 1989: Life at the ice edge. *AMBIO*, **18**, 60-67.
- Sakurai Y., Kiyofuji H., Saitoh S., Goto T., and Hiyama Y., 2000: Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions. *ICES J. Mar. Sci.*, 57, 24-30.
- Sathyendranath S and Platt T., 1988: The spectral irradiance field at the surface and in the interior of the ocean: a model for applications in oceanography and remote sensing. *J. Geophys. Res.*, **93**, 9270–9280.
- Schandelmeier L. and Alexander V., 1981: An analysis of the influence of ice on spring phytoplankton population structure in the southeast Bering Sea. *Limnol. Oceanogr.*, 26, 935-943.
- Schloss I. and Estrada M., 1994: Phytoplankton composition in the Weddell-Scotia Confluence area during austral spring in relation to hydrography. *Polar Biol.*, **14**, 77-90.
- Seiler D. and Brandt A., 1997: Seasonal occurrence of planktonic Cristacea in sediment trap samples at three depth horizons in the Greenland Sea. *Polar. Biol.*, 17, 337–349.
- Seki J. and Shimizu I., 1997: Distribution of zooplankton communities during spring to early summer in the Pacific coastal waters near Hiroo, Hokkaido. Bull. Plankton Soc. Japan, 44, 21-30.
- Seki J., Shimizu I., Ueno Y., Kawasaki H., and Kono T., 1995: Composition and distribution of zooplankton in the south Okhotsk Sea and western North Pacific Ocean off the Kuril Islands in October and November, 1993. Report on the 1993 R/V Kaiyo-maru Juvenile Salmon Research, Salmon Rep. Ser., 40, 45-56 (in Japanese).
- Shimizu I., 1998: Fishery resource and water environment, in "Water environment and water resource in the snowfall and cold regions" (ed.

- by Tachibana H.), Shinzansha-Scitec, Tokyo. pp. 311-322 (in Japanese).
- Shimizu I. and Aota M., 2000: Does sea ice bring high biological production in early spring? 15th Intern. Symp. Okhotsk Sea and sea ice, OSCORA, 15, 273–277.
- Shimizu I., Aota M., and Saitoh S., 2001: The scale of a primary production caused by the change in the period of retreat and the area of sea ice. 16th Intern. Symp. Okhotsk Sea and sea ice, OSCORA, **16**, 174–180.
- Shimizu I., Saito T., and Seki J., 2007: Influence of sea ice on spring phytoplankton and foraging period of juvenile salmon in Nemuro Strait. *N. Pac. Anadr. Fish Comm. Tech. Rep.*, 7, 101–104.
- Shimizu I., Seki J., Ueno Y., Kawasaki H., and Kono T., 1995: Distribution of nutrients and chlorophyll a in the Okhotsk Sea and the Pacific Ocean off the Kuril Islands during the feeding migration of juvenile salmon. Report on the 1993 R/V Kaiyo-maru Juvenile Salmon Research, Salmon Rep. Ser., 40, 30-44 (in Japanese).
- Shimizu I., Seki J., Mayama H., and Urawa S., 1989: Oceanic structure of the coastal area off Yubetsu in the Okhotsk Sea in spring, in "Abstract of 1989 Spring Conference Oceanogr. Soc. Japan", pp. 5-6 (in Japanese).
- Shiomoto A. and Hashimoto S., 1999: Relationship between chlorophyll *a* and nutrients in Suruga Bay, central Japan May 1996. Bull. Fish. Oceanogr., **63**, 1-7 (in Japanese).
- Shiomoto A., Tanaka H., Seki J., Shimizu I., and Shibuya Y., 1998: Chlorophyll-a concentration in the southern Okhotsk Sea in late autumn: a comparison between 1993 and 1996. *Plankton Biol. Ecol.*, **45**, 139–149.
- Smith W. O. and Nelson D. M., 1985: Phytoplankton bloom produced by a receding ice edge in the Ross Sea: Spatial coherence with the density field. *Science*, **227**, 163–166.
- Smith Jr. W. O. and Nelson D. M., 1986: Importance of ice edge phytoplankton production in the Southern Ocean. *BioScience*, **36**, 251–257.
- Stabeno P. J., Schumacher J. D., Davis R. F., and Napp J. M., 1998: Under-ice observations of water column temperature, salinity and spring phytoplankton dynamics: Eastern Bering Sea

- shelf, 1998, J. Mar. Res., 56, 239-255.
- Sudo H., 1974: Polynomials for computing potential temperature, density, specific volume and pressure of sea water. *Bull. Tokai Reg. Fish. Res. Lab.*, 77, 113–131.
- Sverdrup H. U., 1953: On conditions for the vernal blooming of phytoplankton. *J. du Conseil*, **18**, 287–295.
- Taguchi S., 1993: Production and vertical flux of ice algae. Bull. Coastal Oceanogr., 31, 3-16 (in Japasese).
- Takahashi M., Furuya K., and Ishimaru T., 1996: Biological Oceanographic Processes, 3rd ed., Vol. 2, Tokai Univ. Press, 90 pp (in Japanese).
- Ueno Y. and Ishida Y., 1996: Summer distribution and migration routes of juvenile chum salmon (*Oncorhynchus keta*) originating from river in Japan. Bull. Nat. Res. Inst. Far Seas Fish., 33, 139-147.
- Ueno Y., Seki J., Shimizu I., Urawa S., Kaeriyama M., and Kojima Y., 1995: The origins of chum salmon juveniles distributed in the Sea of Okhotsk and Pacific coasts off the Kuril Islands. Report on the 1993 R/V Kaiyo-maru Juvenile Salmon Research, Salmon Rep. Ser., 40, 65-87 (in Japanese).
- Urawa S., 2000: Estimation of migration routes of

- Japanese salmon by genetic characterization and further research on resource variation. Nat. Salmon Resources Center Newsletter, **5**, 3–9 (in Japanese).
- Veth C., Lancelot C., and Ober S., 1992: On process determining the vertical stability of surface waters in the marginal ice zone of the north-western Weddell Sea and their relationship with phytoplankton bloom development. *Polar Biol.*, 12, 237-243.
- Wassman P., Reigstad M., Haug T., Rudels B., Carroll M. L., Hop H., Gabrielsen G. W., Falk-Petersen S., Denisenko S. VG., Arashkevich E., Slagstad D., and Pavlova O., 2006: Food webs and carbon flux in the Barents Sea. *Prog. Oceanogr.*, 71, 232–287.
- Watanabe T., 1989: Environmental characteristics in the Northern Hokkaido. Bull. Fish. Oceanogr., 53, 47–52 (in Japanese).
- Willette T. M., Cooney R. T., and Hyer K., 1999: Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. *Can. J. Fish Aquat. Sci.*, **56**, 364-376.
- Yatsu A. and Kaeriyama M., 2005: Linkages between coastal and open-ocean habitat and dynamics of Japanese stocks of chum salmon and Japanese sardine. *Deep-Sea Res. II*, **52**, 727–737.