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An early spring bloom of large diatoms in the ice-covered Saroma-ko Lagoon, Hokkaido, Japan

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*Saroma-ko Lagoon, the largest body of water that has complete ice coverage during winter in Japan, was not completely covered by ice in the winter of 2009. This condition is considered to be a result of the progression of global warming. A bloom of large diatoms was observed in the ice-free area between February and April. This early spring bloom seemed to have started in the latter part of January, and lasted for about three months. The maximum chlorophyll-*a *(Chl* a*) concentration of about 10 mg m^{-3} was observed in March, and was similar to the level of 5–20 mg m^{-3} previously reported for the ordinary spring bloom in Saroma-ko Lagoon. The maximum primary production of 786 mgC m^{-2} day^{-1} and the maximum Chl* a*-specific primary production, an index of the phytoplankton growth rate, were also found in March. Species changes from* Thalassiosira *spp. to* Chaetoceros *spp. were observed during the bloom. This early spring bloom could extend into the ordinary spring bloom period. Its duration was obviously longer than that of the spring bloom, which is typically about one month. These results show the phytoplankton condition that could be expected during winter and spring as global warming progresses.*

Keywords: early spring bloom, large diatoms, primary production, chlorophyll-*a*, ice-covered aquatic area, shortening of ice coverage, global warming

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INTRODUCTION

A trend towards a shortening of the duration of ice coverage due to global warming has been reported in many rivers, ponds and lakes around the world (Schindler *et al.*, 1990, 1996; Magnuson *et al.*, 2000; Futter, 2003). Because ice coverage inhibits the input of solar radiation into the water, this shortening results in increased light conditions in the water beneath the ice. In ice covered waters, ice algae account for a substantial proportion of primary production (Horner & Schrader, 1982; Arrigo *et al.*, 1997; Gosselin *et al.*, 1997; Hattori *et al.*, 2001; Lizotte, 2001), although the potential capacity of primary production is generally low in ice algae compared to its phytoplankton counterparts (Rivikin *et al.*, 1989; Irwin, 1990; Smith & Sakshaug, 1990; Ban *et al.*, 2006). The shortening of the ice coverage period therefore implies a possible decrease in the relative importance of ice algae as primary producers, and an increase in the relative importance of phytoplankton. The shortening also implies an increase of wintertime primary production in the ice covered rivers, ponds and lakes. Changes in primary producers could have pronounced effects on the structure and function of a given aquatic ecosystem (e.g. Parsons *et al.*, 1984; Lalli & Parsons, 1993). Accordingly, global warming can possibly change ecosystems and biological production during winter and spring in ice-covered aquatic areas.

Saroma-ko Lagoon, with a surface area of 150 km^2 and a maximum depth of 19.5 m, is located on the north-east coast of Hokkaido, Japan, and is connected to the Okhotsk Sea by two narrow channels. In total, 14 rivers flow into the lagoon. This lagoon is the largest of the lakes, marshes and lagoons that are characterized by complete ice coverage during winter in Japan. During the ice coverage period, sporadic studies in the past have shown that the chlorophyll-*a* concentration (phytoplankton biomass) in the water was low, on the order of 0.5 mg m^{-3} or less, under the ice (Fukuchi *et al.*, 1989; Satoh *et al.*, 1989; Tada *et al.*, 1993; Niimura *et al.*, 2000); production by ice algae was far greater than that by phytoplankton (Hattori *et al.*, 2001). The spring bloom has been observed in the lagoon after disappearance of ice in April (Fukuchi *et al.*, 1989; Nishihama *et al.*, 1989; Tada *et al.*, 1993). Chlorophyll-*a* concentrations reached 5–20 mg m^{-3} in the spring blooms, although the blooms lasted for only one month (Fukuchi *et al.*, 1989; Nishihama *et al.*, 1989; Tada *et al.*, 1993). Although little is known about the primary production and species composition of phytoplankton during this bloom, diatoms dominated in both the ice algae and the phytoplankton communities in the lagoon in winter (Takahashi, 1981; McMinn *et al.*, 2008).

The duration of the period of complete ice coverage has tended to decrease since 1964 in Saroma-ko Lagoon, and

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years with incomplete ice coverage have been frequently observed since 1990 (e.g. Shirasawa *et al.*, 2001; Aquaculture Fisheries Cooperation of Lake Saroma, http://homepage3.nifty.com/saromako/). Thus, the same trend that is being reported globally for ice-coved aquatic areas has also been noted in Saroma-ko Lagoon. In winter 2009, the lagoon was only partly covered by ice, at about 64% of its surface (see Figure 1), a condition that is considered to be a result of global warming. We carried out an emergency observation of the ice-free area of the lagoon during winter and spring 2009, and noted a wintertime diatom bloom that continued through to spring. Our observations suggest that the occurrence of these types of blooms will continue as incomplete ice coverage occurs frequently. This paper, although it reports only one series of observations, provides important details of the algal bloom that should be helpful in the prediction of the influence of global warming progression on ecosystems and biological production during the winter and spring in ice-covered aquatic areas, because incomplete ice coverage is rarely observed. In addition, since Saroma-ko Lagoon has been the site of successful shellfish culture operations for scallops and oysters (e.g. Kurata *et al.*, 1991; Nishihama, 1994) this paper will also allow the prediction of possible effects of global warming on aquaculture in the ice-covered aquatic areas.

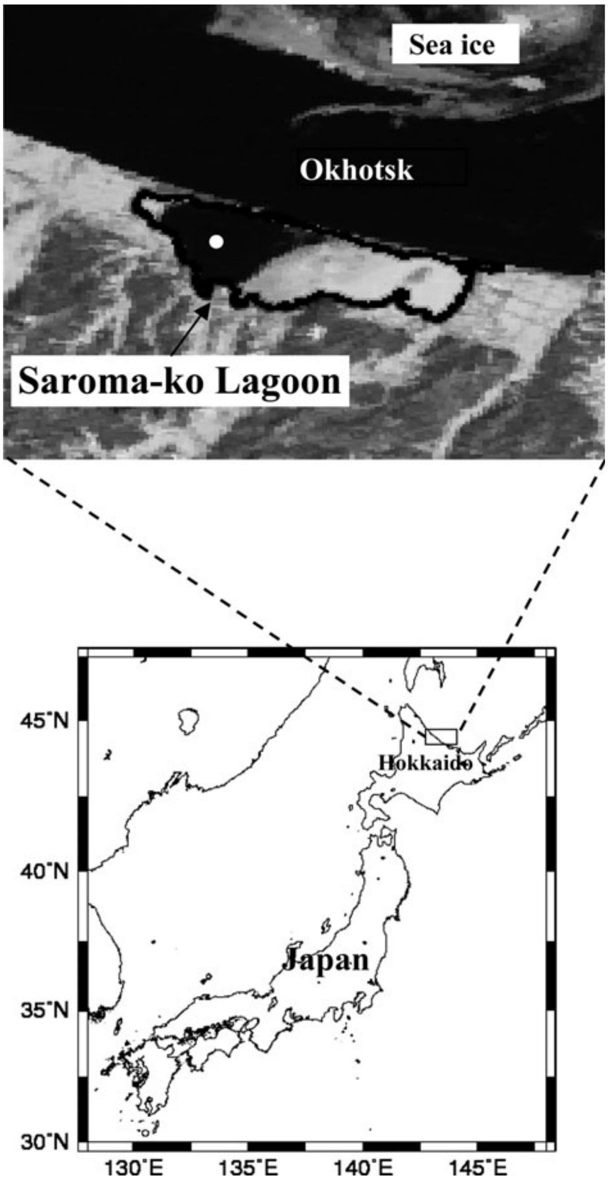

Fig. 1. MODIS image on 3 March 2009, and the location of Station 21 (solid circle; 44°09′N 143°51′E) in Saroma-ko Lagoon. Observations were carried out on 16 February, 18 March and 17 April 2009. Black and white areas in the lagoon show ice-free and ice-covered areas, respectively. The percentage contribution of ice coverage was highest on 3 March and accounted for 64% of the whole surface area in the lagoon.

MATERIALS AND METHODS

Observations were conducted at Station 21 (44°09′ N 143°51′ E) with the depth of 15 m, located near the central part in Saroma-ko Lagoon, during February to April, 2009 (Figure 1). Water samples were collected between 8:00 am and 10:00 am from four depths corresponding to 100, 37, 17 and 1% light depths using an acid cleaned Niskin X sampler hung on a non-metal wire (polyethylene). The light depths were determined 30 minutes before each sampling with a quantum sensor (Alec AL30-CMP).

Chlorophyll-*a* (Chl *a*) concentrations of total and size-fractionated samples were measured with fluorometry using a Turner Designs 10-AU fluorometer according to Welschmeyer (1994). Size separated samples (0.2–0.5 l) were prepared by filtration through Nuclepore filters with pore sizes of 10 and 2 µm and a Whatman GF/F (about 0.7-µm pore size: total). Chl *a* was extracted with N, N-dimethylformamide (Suzuki & Ishimaru, 1990). Calibration of the fluorometer was performed with a commercially available Chl *a* standard (Sigma-Aldrich Co.). Chl *a* concentrations for the <2, 2–10 and >10 µm fractions were obtained from the differences between the total and 2 µm, 2 and 10 µm, and total and 10 µm, respectively.

Primary production (photosynthetic rate) was measured by the simulated *in situ* method using the ^{13}C uptake technique (Hama *et al.*, 1983). The samples (1 l) were dispensed into two 1-l polycarbonate bottles at each light depth and enriched with ^{13}C-NaHCO$_3$ (99 atom% ^{13}C; Shoko Co. Ltd.) to about 10% of the total inorganic carbon in ambient water within 30 minutes after collection of the samples, and then incubated *in situ* for 24 hours. Dark bottle uptake is similar to the zero-time blank in the ^{13}C technique (Shiomoto *et al.*, 1998), and thus no dark bottles were used. Bottles of seawater samples inoculated with ^{13}C-NaHCO$_3$ were held in the coastal surface water in Saroma-ko Lagoon, at irradiances corresponding to the depths at which the samples were taken, using black mesh screens. The temperatures in the coastal surface water were about 2°C higher than the *in situ* temperatures (−1.5–5°C) of the samples that were collected. Shiomoto (2009) showed that a 2°C increase relative to the *in situ* temperature (0.2°C) induced increases of about 20% in photosynthetic rates for small size phytoplankton and little increase for larger phytoplankton using samples from the coastal area of Hokkaido. The primary production obtained in this study was considered to be almost equal to the *in situ* values. Immediately following incubation, seawater samples in bottles were directly filtered through pre-combusted (450°C for 4 hours) 47-mm Whatman GF/F filters. The particulate matter on the Whatman GF/F filters

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was rinsed with pre-filtered lagoon water, and the filters were immediately frozen for the later isotope analysis ashore. Before the isotope analysis, filters were treated with HCl fumes for 4 hours to remove inorganic carbon and completely dried in a vacuum desiccator. The isotopic ratios of ^{13}C to ^{12}C and particulate organic carbon contents were determined using a mass spectrometer (ANCA SL, CerCon). The total inorganic carbon in the water was measured with an infrared analyser (Shimadzu TOC 5000). The primary production rate was calculated according to the equation described by Hama *et al.* (1983). The rates in the two polycarbonate bottles at each light depth were averaged.

Vertical profiles of temperature and salinity were determined using an Alec memory conductivity–temperature–depth probe (ASTD 687). Nutrient concentrations were measured with a BLTEC Auto Analyzer SWAAT after storing samples at −20°C. Incident insolation (photosynthetically active radiation, PAR, 400–700 nm) was monitored every two minutes with a quantum sensor (Alec MDS MKV/L) during the incubation. For phytoplankton species examination, a 1-l seawater sample was taken and fixed with neutralized formalin (2% vol/vol). These samples were concentrated to 10 ml by siphoning off excess solution after three days of settling. Aliquots (1/20–1/10 of each sample) were examined, depending upon the cell density, using a light microscope equipped with interference and phase contrast optics. Phytoplankton were identified to species level when possible, or otherwise grouped by genera.

RESULTS

Physical and chemical conditions of the lagoon during the observation period

In the winter of 2009, the surface of the lagoon only had a maximum of 64% ice cover (Figure 1). Solar radiation during incubation was nearly equal in February and March, and an increase was observed in April (Figure 2A). The depth of the euphotic zone (1% light depth) shallowed from February (15 m) to April (7.5 m). The depth of the euphotic zone extended through the whole water column in February.

Water temperatures were almost constant throughout the whole water column in February and March, and almost constant to near bottom in April (Figure 2B). The temperatures within the euphotic zone were about −1.5°C in February, about 0°C in March and about 5°C in April. Salinity was also almost constant from surface to bottom in February, whereas it increased with depth in the other months (Figure 2C). A remarkable decrease of salinity in the surface layers was found in April, probably due to a supply of

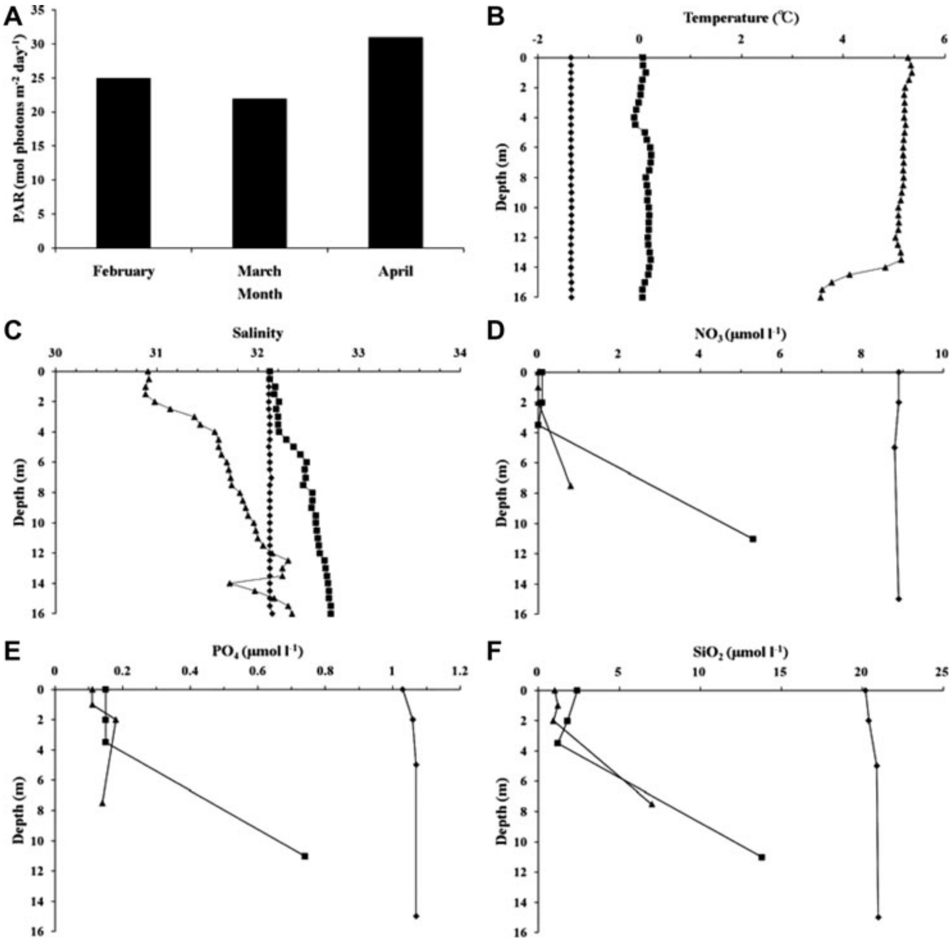

Fig. 2. Change in the daily total photosynthetic active radiation (PAR: 400–700 nm) during incubation experiments (A) and vertical profiles of temperature (B), salinity (C), nitrate (NO_3; D), phosphate (PO_4; E) and silicate (SiO_2; F) in February (◆), March (■) and April (▲). The data of temperature and salinity were obtained at 0.5 m intervals.

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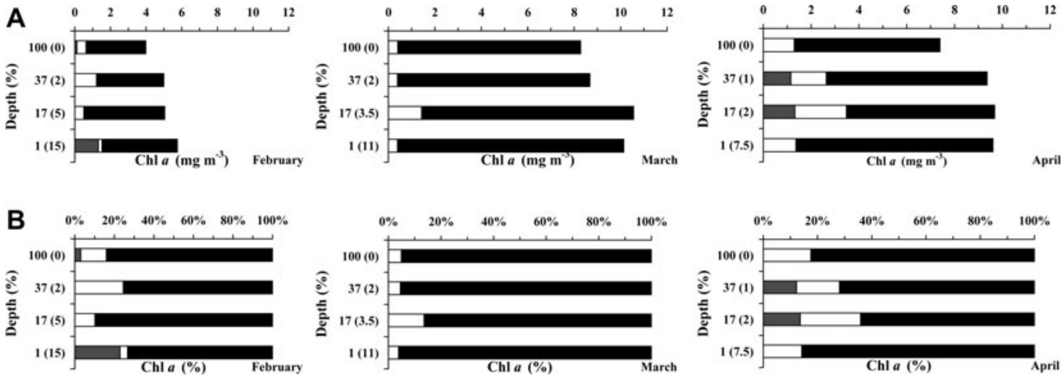

Fig. 3. Vertical profiles of size-fractionated chlorophyll-*a* concentration (A) and chlorophyll-*a* size composition (B) in February, March and April. ▨, <2 μm; ☐, 2–10 μm; ■, >10 μm. Figures in parentheses on the vertical axis show the depth in metres.

inflow of snow melt water from the terrestrial environment as well as the melting water from the ice.

Nitrate was almost constant throughout the water column with concentrations of about 9 μmol l^{-1} in February (Figure 2D). In the other months, although nitrate was almost exhausted in the upper layers of 17% light depth within the euphotic zone, relatively high concentrations compared with the upper layers were found at the 1% light depths. The concentrations at the 1% light depth decreased from March to April. The results imply a nutrient supply from lower layers to the upper layers and less supply in April than in March. Ammonium concentrations were generally lower than 0.4 μmol l^{-1} within the euphotic zone (not shown). The same temporal changes during February to April as well as the same vertical profiles were observed in phosphate and silicate within the euphotic zone (Figure 2E, F). However, they were not completely exhausted in the upper layers within the euphotic zone even in March and April.

Chlorophyll-*a* concentrations and size distributions

Total Chl *a* concentrations within the euphotic zone were nearly constant in every month (Figure 3A). The Chl *a* concentrations increased two to three times from February (4–6 mg m^{-3}) to March (8–11 mg m^{-3}). Maximum values during the observation were found in March. Almost equal values as in March were observed in April (7–10 mg m^{-3}).

Large size phytoplankton, >10 μm fraction, dominated the total Chl *a* concentrations in every depth and every month (Figure 3B). The percentage contributions of the large size phytoplankton were nearly constant within the euphotic zone. The phytoplankton accounted for 70–90% of the total Chl *a* concentrations in February, 90–95% in March and 60–90% in April. The maximum contribution of the large size phytoplankton to total Chl *a* concentration was observed in March when total Chl *a* concentrations were maximum in this study.

Primary production

Primary production was nearly constant at the 17% light depth and above in February, whereas it decreased with depth in March and April (Figure 4A). The production rates at the 1% light depth were extraordinarily lower than those at the upper light depths in every month (<1.5 mgC m^{-3} day^{-1}). The primary production values in this study ranged from 25 to 165 mgC m^{-3} day^{-1} except for the 1% light depth. The maximum value was found at the 100% light depth in March.

The daily primary production in the water column, calculated by the trapezoidal integration from the surface to the 1% light depth, was in the range of 298 and 786 mgC m^{-2} day^{-1} (Table 1). The maximum daily primary production was

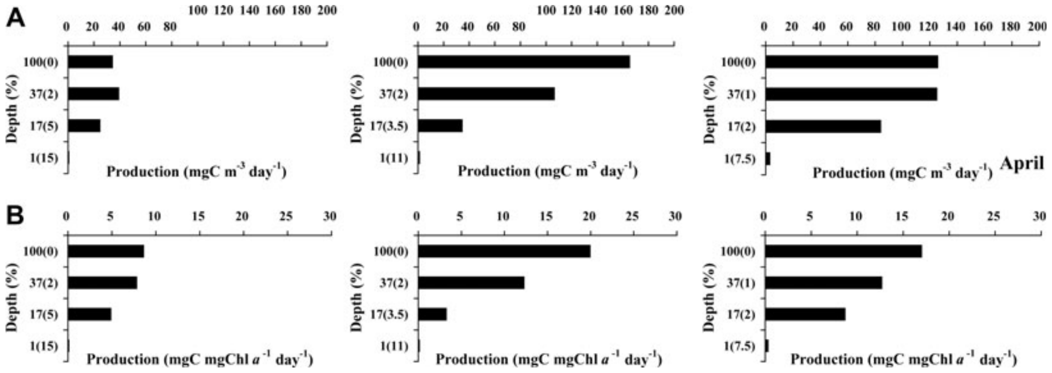

Fig. 4. Vertical profiles of primary production (A) and chlorophyll-*a*-specific primary production (B) in February, March and April. Figures in parentheses on the vertical axis show the depth in metres.

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Table 1. Daily primary production in February, March and April.

	February	March	April
Primary production (mgCm^{-2} day^{-1})	298	786	471

observed in March, and the maximum value was about three times higher than that in February and about two times higher than that in April.

Chl *a*-specific primary production, an index of phytoplankton growth rate (e.g. Lalli & Parsons, 1993), decreased with depth in every month, and abrupt decreases were found at the 1% light depth (Figure 4B). The Chl *a*-specific primary production at the 17% light depth and above increased from February (4.9–8.7 mgC mgChl a^{-1} day^{-1}) to March (3.3–20.0 mgC mgChl a^{-1} day^{-1}), whereas the values were nearly equal in March and April (8.7–17.0 mgC mgChl a^{-1} day^{-1}). The change in Chl *a*-specific primary production from February to April was similar to those in total Chl *a* and in primary production.

Phytoplankton species

Diatoms accounted for almost 100% of all living cells counted by the light microscope at every light depth in every month. The cell numbers of diatoms increased extraordinarily from February (0.7–1.6 × 10^5 cells l^{-1}) to April (1.2–4.3 × 10^6 cells l^{-1}) through to March (5.6–9.7 × 10^5 cells l^{-1}) (Figure 5A). Marked maximum values were found at the 100% light depth in April. The temporal variation in diatom cell numbers was not the same as those in Chl *a* concentration and in primary production.

Thalassiosira spp. were dominant at every light depth in February, accounting for 70–90% of all cell numbers of diatom (Figure 5B). Both *Thalassiosira* spp. and *Chaetoceros* spp. were dominant in March with maximum Chl *a* and daily primary production; the former and latter species accounted for 30–40% and 40–60% of all diatom cells, respectively. In April, *Chaetoceros* spp. were remarkably dominant, accounting for more 95% of all diatom cells. Succession of dominant diatom species, *Thalassiosira* spp. to *Chaetoceros* spp., was observed during February to April.

DISCUSSION

Saroma-ko Lagoon was often completely covered by ice during winter in the past. In such a situation, the spring phytoplankton bloom occurs in the ice melting season, April, in the lagoon (Fukuchi *et al.*, 1989; Nishihama *et al.*, 1989; Tada *et al.*, 1993). Chl *a* concentrations were between 0.5 and 1 mg m^{-3} in the water before ice coverage (December), and concentrations were generally less than 0.5 mg m^{-3} in the water below the ice (Fukuchi *et al.*, 1989; Satoh *et al.*, 1989; Tada *et al.*, 1993; Niimura *et al.*, 2000). The Chl *a* concentrations reached 5–20 mg m^{-3} in the spring bloom, and the bloom usually continued for about one month (Fukuchi *et al.*, 1989; Nishihama *et al.*, 1989; Tada *et al.*, 1993). In this study, the Chl *a* concentrations within the euphotic zone were about 5 mg m^{-3} in February and reached a maximum of about 10 mg m^{-3} in March (Figure 3A). Maximum daily primary production was observed in March (Table 1) and maximum Chl *a*-specific primary production (growth rate) was also observed in March (Figure 4B). Relatively high phytoplankton biomass and production were maintained in April (Figures 3A & 4B; Table 1). In addition, large size phytoplankton (Figure 3B) and diatoms contributed significantly to phytoplankton communities during observations. The results show that large size diatom bloom occurred in early spring and continued to spring in the ice-free area of the lagoon; namely the occurrence of an early spring bloom was observed.

Ice coverage and overlying snow inhibit incident solar radiation into the water below the ice, and the relative incident solar radiation reaching below the sea ice was less than 10% in Saroma-ko Lagoon (Satoh *et al.*, 1989; Kishino, 1993; Hattori *et al.*, 2001; Ikeya *et al.*, 2001). Rises in irradiance have been reported to increase phytoplankton production and biomass in the water below the ice in Antarctic lakes (Lizotte & Priscu, 1992; Lizotte *et al.*, 1996). Observations in Antarctica (Rivkin *et al.*, 1989) and on the Labrador Shelf (Irwin, 1990) have shown that phytoplankton beneath the ice have the potential capacity to increase primary production remarkably when light conditions are extraordinarily improved, i.e. dim to bright conditions. Furthermore, Ikeya *et al.* (2000) found the same potential capacity in *Chaetoceros* sp. isolated from the water in Saroma-ko Lagoon immediately after ice melting in April. An ice-free condition, i.e. improvement of light condition in the water,

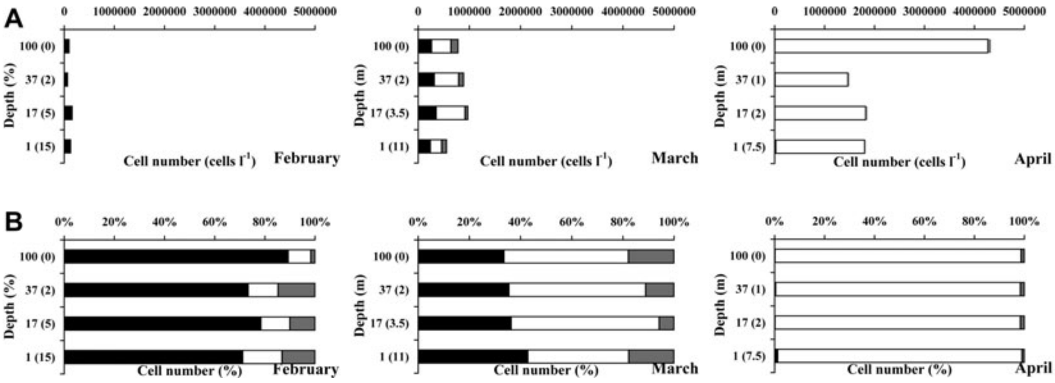

Fig. 5. Vertical profiles of cell numbers of diatom (A) and percentage contributions of *Thalassiosira* spp. (■), *Chaetoceros* spp. (□) and other diatoms (▨) to total diatom cell numbers (B) in February, March and April. Figures in parentheses on the vertical axis show the depth in metres.

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is considered to be a primary factor for the onset of the observed early spring bloom.

Winter blooms have been observed in sub-Arctic coastal regions without ice coverage (Keller *et al.*, 1999; Labry *et al.*, 2001; Townsend & Thomas, 2001; Oviatt *et al.*, 2002; Glé *et al.*, 2007; Álvarez *et al.*, 2009). Light was considered to be the trigger for the onset of the winter bloom (Legendre, 1990; Labry *et al.*, 2001). Labry *et al.* (2001) showed that the winter bloom occurred when the depth-averaged irradiance (E_m) received by phytoplankton in the mixed layer was above light saturation parameter (E_K; Talling, 1957; Sakshaug *et al.*, 1997) which is an index of the onset of light-saturation for P_{max}. The early stage of the early spring bloom is considered to have occurred during February, and we calculated E_m (Riley, 1957) and E_K (Sakshaug *et al.*, 1997) in February as follows for investigating the relationship between the two parameters:

$$E_m = (E_o - E_o \times e^{-KZ_m})/KZ_m \qquad (1)$$

where E_o is the total surface incident irradiance (incident PAR; μmol photons m^{-2} s^{-1}), K is the vertical attenuation coefficient for PAR (m^{-1}) and Z_m is the depth of mixed layer (m) . Based on the measurement of the vertical profiles of PAR in the water, K in February was calculated to be 0.24 m^{-1} from the linear relationship between ln(PAR) in water and the depth. E_o was 25 mol photons m^{-2} day^{-1} and Z_m was 15 m in February:

$$E_K = P_{max}/\alpha \qquad (2)$$

where P_{max} and α are the maximum primary production and the initial slope in the relationship between light intensity and primary production, respectively. Diatoms dominated phytoplankton communities within the euphotic zone in February, March and April, and diatom species compositions were almost equal among four light depths in each month (Figure 5B). The four light depths represent four light intensities. Accordingly, the vertical profiles of Chl *a*-specific primary production in each month are considered to indicate the relationship between light intensity and primary production of phytoplankton community. The primary production increased to the maximum light intensity (100% light intensity: 20–30 mol photons m^{-2} day^{-1}) in February, March and April, i.e. during the period of the early spring bloom (Figure 4B). The relationship between light intensity and primary production can be represented by the hyperbolic tangent equation as follows (Jassby & Platt, 1976):

$$P = P_{max} \times \tanh(\alpha \times E/P_{max}) \qquad (3)$$

where P and E are Chl *a*-specific primary production and light intensity, respectively, and P_{max} and α are maximum primary production and the initial slope in the relationship between light intensity and primary production, respectively. Optimal values of P_{max} and α were obtained by applying the data to Equation (3) by nonlinear least-squares fitting, using the Microsoft Excel Solver. P_{max} and α in February were estimated to be 8.7 mgC mgChl a^{-1} day^{-1} and 1.33 mgC mgChl a^{-1} day^{-1} (mol photons m^{-2} $day^{-1})^{-1}$, respectively. As a result, the E_m and E_K were calculated to be 6.8 mol quanta m^{-2} day^{-1} and 6.6 mol quanta m^{-2} day^{-1}, respectively, and both of the values were almost equal. It is thus probable that light availability was satisfied for the bloom diatoms, supporting that light was a primary factor for the early spring bloom.

It is well known that the phytoplankton bloom occurs when the mixed layer depth (Z_m) is shallower than the critical depth (Z_{cr}) (Sverdrup, 1953; Parsons *et al.*, 1984). Labry *et al.* (2001) showed that such a water column condition was necessary for the occurrence of the winter bloom, and hence we investigated the relationship between Z_m and Z_{cr} in February which was considered to be the initial stage of the early spring bloom in Saroma-ko Lagoon. The depth of the euphotic zone (15 m), where the net primary production is positive and there is 1% surface radiation (Parsons *et al.*, 1984), was almost equal to the depth of water (16 m) in February, and the water was well mixed throughout the water column (see uniform vertical profiles of temperature and salinity in February in Figure 2B, C). Z_{cr} is deeper than the depth of the euphotic zone (Sverdrup, 1953; Parsons *et al.*, 1984), and hence the mixed layer depth was considered to be shallower than the critical depth in February, meaning that the water column condition was satisfied for occurrence of the early spring bloom. The mixed layer depth does not become deeper than the depth of water. The shallow depth of water in Saroma-ko Lagoon (19.5 m at deepest) possibly plays an important role in the occurrence of the early spring bloom after all.

The concentrations of nitrate and phosphate within the euphotic zone were about 9 and 1 μmol l^{-1}, respectively, in February, probably at the initial stage of the bloom (Figure 2D, E). The concentrations were nearly equal to those in the water below the ice in February (before the spring bloom) in the complete ice coverage years (nitrate + nitrite: about 10 μmol l^{-1}; phosphate: about 1.3 μmol l^{-1}; Tada *et al.*, 1993). The maximum Chl *a* concentrations in the early spring bloom, about 10 mg m^{-3} (Figure 3A), were nearly equal to those in the spring bloom (5–20 mg m^{-3}; Fukuchi *et al.*, 1989; Nishihama *et al.*, 1989; Tada *et al.*, 1993). Nutrients regulate phytoplankton productivity and biomass, and Chl *a* concentration reflects phytoplankton productivity and biomass. Consequently, the similarity between the nutrient concentrations and maximum Chl *a* concentrations in this study and the previous studies circumstantial evidence that the phytoplankton (large diatoms) in the early spring bloom had the same potential growth capacity as the phytoplankton in the usual spring bloom.

This study, furthermore, revealed the bloom of large size phytoplankton and succession of dominant species in the early spring bloom in Saroma-ko Lagoon (Figures 3 & 5). Unfortunately little is known about phytoplankton species in the spring bloom in the lagoon, though *Detonula confervacea*, *Nitzschia* spp., *Odontella aurita* and *Thalassiosira* spp. existed dominantly beneath the ice in February (Watanabe *et al.*, 1993; Ikeya *et al.*, 2001) and *Chaetoceros* spp. and *Thalassiosira* spp. dominated in the water a few days after sea-ice disappearance in April (Kashino *et al.*, 1998). On the other hand, the dominance of *Thalassiosira* spp. and *Chaetoceros* spp. was observed in the spring diatom bloom after the ice melt in Notoro-ko Lagoon which is geographically proximate to Saroma-ko Lagoon, i.e. about 25 km south-west of it, and is connected to the Okhotsk Sea (Asami & Imada, 2001). In addition, *Thalassiosira* spp. and *Chaetoceros* spp. were recorded as dominant large size diatoms in the spring

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blooms in the coastal regions of Hokkaido (Nakata, 1984; Taguchi *et al.*, 2000), and the succession from *Thalassiosira* spp. to *Chaetoceros* spp. was also reported (Nakata, 1984). Saroma-ko Lagoon is connected to the Okhotsk Sea by the two channels and the lagoon water is significantly affected by the coastal water in the Okhotsk Sea (Shibanuma *et al.*, 1995), suggesting that there is analogy in the spring bloom phytoplankton between the lagoon and the Hokkaido coastal region. The same results as the previous studies of the spring bloom were obtained in this study. Consequently, there is a great possibility that the dominant diatoms in the early spring bloom are similar to those in the spring bloom in Saroma-ko Lagoon. Therefore, the same potential growth capacity and dominant diatoms show that the early spring bloom observed in this study front-loaded the spring bloom.

Our observations began from the middle of February, by which time the early spring bloom had already started. The time increase in the phytoplankton community can be estimated under the assumption that logarithmic growth is maintained as follows (e.g. Parsons *et al.*, 1984):

$$N_2 = N_1 \exp[\mu(t_2 - t_1)] \quad (4)$$

where N_1 and N_2 are phytoplankton biomass (Chl *a* concentration) at times t_1 and t_2 (days), respectively, and μ is the specific phytoplankton growth rate (day^{-1}). Biomass is usually expressed as carbon content ($mgC\ m^{-3}$), but here the initial biomass was measured as the Chl *a* concentration ($mg\ m^{-3}$). Chl *a* concentration was converted to the carbon content of the phytoplankton by multiplying the slope between the concentrations of Chl *a* and the particulate organic carbon before incubation. A significant linear regression line was obtained with a slope of 60 ($P < 0.001$). The value was within the range of the carbon to Chl *a* ratios of phytoplankton assemblages in previous culture and field studies (25–100 $mgC\ mgChl\ a^{-1}$; e.g. Parsons *et al.*, 1984; Furnas, 2002). In this study, N_1 as Chl *a* was assumed to be 0.5 $mg\ m^{-3}$ because Chl *a* concentrations in the water before ice coverage (December) were reported to be 0.5–1 $mg\ m^{-3}$ (Fukuchi *et al.*, 1989; Satoh *et al.*, 1989; Tada *et al.*, 1993; Niimura *et al.*, 2000). N_2 as Chl *a* was 5.0 $mg\ m^{-3}$ because Chl *a* concentrations at the four light depths within the euphotic zone in February were averaged to be 4.95 $mg\ m^{-3}$. N_1 and N_2 as Chl *a* were converted to 30 and 300 $mgC\ m^{-3}$, respectively. The specific growth rate is calculated by the following equation (e.g. Parsons *et al.*, 1984):

$$\mu = \ln[(N_0 + \Delta N)/N_0] \quad (5)$$

where N_0 is the initial biomass of the phytoplankton and ΔN is the biomass increased by net photosynthesis per day ($mgC\ m^{-3}\ day^{-1}$). N_0 was the phytoplankton biomass in February, i.e. N_2 (300 $mgC\ m^{-3}$). ΔN (43.5 $mgC\ m^{-3}\ day^{-1}$) was obtained by multiplying P_{max} in February (8.7 $mgC\ mgChl\ a^{-1}\ day^{-1}$) by the mean Chl *a* (5.0 $mg\ m^{-3}$), meaning that the value was potential growing capacity of phytoplankton in February. As a result, the growth rate (μ) in February was calculated to be 0.14 day^{-1}. Supposing that the growth rate was constant (0.14 day^{-1}) during the onset of the early spring bloom to the day of the February observation (16 February), $t_2 - t_1$, the duration of increase in Chl *a* concentration from 0.5 to 5.0 $mg\ m^{-3}$, was calculated to be 16 days using Equation (4). t_2 was 16 February and thus the early spring bloom was estimated to have occurred by 31 January at the latest, because the maximum growth rate during the 16 days after the onset of the bloom was used for the calculation. Accordingly, the early spring bloom was thus considered to have continued for almost three months. The duration of the early spring bloom was longer than that of the spring bloom (about one month).

Maximum phytoplankton biomass and production were observed in March (18 March) and nearly equal values as in March were found in April (17 April; Figures 3A & 4; Table 1), reflecting that the prime time of the early spring bloom lasted about one month at least. Nevertheless, nutrients, especially nitrate, were exhausted in the upper layers of the 17% light depth within the euphotic zone in March and April (Figure 2B, C & D). In contrast, relatively high concentrations were found at the 1% light depth (Figure 2B, C & D). The results imply that the nutrient supply to the upper layers from the lower layers was related to the maintenance of the continuation of the bloom. However, concentration gradients of all nutrients between the 17% and 1% light depths diminished markedly from March to April (0.71 to 0.15 $\mu mol\ l^{-1}\ m^{-1}$ for nitrate, 0.0791 to 0.0036 $\mu mol\ l^{-1}\ m^{-1}$ for phosphate and 1.7 to 1.1 $\mu mol\ l^{-1}\ m^{-1}$ for silicate). On the other hand, markedly low salinity was found in the upper layers in April (Figure 2C). The low salinity was probably due to a supply of inflow of snow melt water from the terrestrial environment as well as melting water of ice. Consequently, nutrient supply through the rivers probably played a large part in the maintenance of the prime time of the bloom.

Progression of global warming would be expected to induce incomplete ice coverage. In winter 2009, the lagoon was only partly covered by ice (Figure 1). Thus the front-loading of the ordinary spring bloom observed in this study shows the phytoplankton state during winter and spring in the lagoon that can be expected as global warming progresses. Improvement in the light condition in the water was considered to be a primary factor responsible for the front-loading. It is not difficult to expect that the progression of global warming induces temporal and spatial expansion of the ice-free area, and hence improvement of the light condition in the water. This appears to result in front-loading of the ordinary spring bloom in areas that normally would be ice-covered and where the spring bloom normally occurs only after ice-melting. The front-loaded bloom could possibly continue through to the regular spring bloom when nutrients are supplied.

Progression of the shortening of ice coverage and frequent incomplete ice coverage means temporal and spatial expansion of the ice-free area, and hence an increase of contribution in the ice-free area to the overall primary production during winter. Based on limited data for wintertime primary production in Saroma-ko Lagoon, the primary production is higher in the ice-free area (298–786 $mgC\ m^{-2}\ day^{-1}$ in February, March and April in this study; Table 1) than in the ice-covered area (198 $mgC\ m^{-2}\ day^{-1}$; Hattori *et al.*, 2001). The potential capacity of primary production of phytoplankton in the water below the ice has been reported to be higher than that of ice algae (Rivikin *et al.*, 1989; Irwin, 1990; Smith & Sakshaug, 1990; Ban *et al.*, 2006). Therefore, the progression of global warming may possibly result in increases in primary production during the winter and spring, thereby affecting the ecosystem and water quality in Saroma-ko Lagoon, as well as in other aquatic areas normally covered by ice. Continued monitoring of the ice condition and

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primary production in Saroma-ko Lagoon will therefore be important to confirm this possibility and for further prediction of the influence of global warming on ice-covered aquatic areas throughout the world.

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