# Tight coupling between primary productivity, export production, and the growth of benthic scallops in the coastal region of the Okhotsk Sea along Hokkaido.

Running title: primary production and scallop growth in Okhotsk Sea

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## Abstract

Scallop culture is conducted worldwide, nonfeeding and depending on the natural phytoplankton production for the diet. It is necessary for sustainable culture of this species to understand how the phytoplankton production and subsequent vertical transport to the bottom (export production) are regulated by environmental factors. A three-year time series monitoring of chlorophyll and temperature, as well as sinking particle flux, was conducted to elucidate the relationship between surface primary production, the subsequent export, and the growth of benthic cultured scallops in spring in the coastal region of the Okhotsk Sea along Hokkaido, Japan. Five times larger export fluxes were observed in 2013 than those in other years. *Coscinodiscus* spp., diameter > 200 μm, was the quantitatively dominant phytoplankton in 2013. This species contributed to the high export flux due to a higher settling velocity. The sudden drops in temperature by > 2°C were observed during the study period. These indicated that the supply of nutrients from Intermediate Cold Water (ICW), a cold and nutrients rich water mass, accelerated the primary productivity in this area. This intensity was strongest in 2013, contributing to the high export flux. The large export flux in 2013 provided a more sufficient food to the benthic cultured scallops, resulting in a two times higher growth of the scallops than in other years. This study demonstrated that the size

of the dominant diatom species and the supply from ICW strongly influenced the export ratio and the growth of cultured scallops.

Keywords: Nutrient, diatom, *Coscinodiscus*, sediment trap, scallop, export production, pelagic-benthic coupling

## 1. INTORODUCTION

The global scallop production was 900,000 tons in 1990 and increased to 2,816,000 tons in 2017 (FAO, 2018). This increase was mainly brought by the development of scallop aquaculture in China. The assessment and management of carrying capacity for bivalve culture is necessary for sustainable culture in the future (McKindsey et al., 2006). The Japanese scallop, *Patinopecten (Mizuhopecten) yessoensis*, is a commercially important subarctic species cultured extensively in the coastal areas of northern Japan. Hokkaido is the largest landing base for this species. The annual landing in 2017 was about 300,000 tons (33% of the total fishery production in Hokkaido). The culturing method of scallop is either to hang the shell by string in the water column (hanging culture) or to sow in the seabed (sowing culture). In the coastal area of the Okhotsk Sea, scallops are cultivated by sowing culture using the 4-year (hereafter, yr) rotational harvesting system, where one of four culture zones is seeded with juveniles (naturally collected spats of 1-yr aged hanging cage cultured individuals) and leaving three years before harvest. The number of juveniles sown was the same each year and the population density was 5-14 individuals per $m^2$ (Paturusi et al., 2002). This scallop production has been relatively constant since the 1990s, but has still fluctuated and experienced a lower production during several years (Hokkaido Prefecture, https://www.pref.hokkaido.lg.jp/sr/sum/62097.html).

Food and feeding studies of scallops have shown that they ingest phytoplankton (Shumway et al., 1997; Zhou et al., 2006; Aya & Kudo, 2007) or settling particles in their natural habitats (Cranford & Grant, 1990; Aya & Kudo, 2010). Scallops grow well from spring to summer, consuming the organic matter produced during the spring bloom (Miyoshi et al, 2015). The growth ceases after summer due to the short of diet supply. Miyoshi et al. (2015) preliminarily reported 1.5-times higher growth of cultured scallops in 2013 than the average. As for the scallops growing on the seafloor, their food supply mainly relies on the vertical transport of organic matter as settling particles

(export production) from the surface euphotic layer; the coupling between primary production and export production is important for evaluating the diet condition. This food supply (i.e., feeding environment) may be influenced by the fluctuation of the primary production in spring. Sediment traps have been employed to measure the export flux of settling particle organic matter in the water column as an estimate of food supply (Smith Jr, et al., 2001). The predictive model for the harvest failure of sowing cultured scallop indicates that the growth of benthic scallop is mostly explained by the Chl *a* at the bottom in spring (Shinada et al., 2005)

The study site, in the vicinity of the Okhotsk Sea in Hokkaido, is known to as the southern limit where drifting sea ice can be seen in the northern hemisphere. According to the definition by Takizawa (1982), water masses in the vicinity of the Okhotsk Sea in Hokkaido are distinguished by salinity and temperature as follows, Soya Warm Water (SWW): salinity > 33.6 and temperature 7-20°C; Forerunner of Soya Warm Water (FSWW): salinity > 33.8 and temperature 2-6°C; Okhotsk Surface Water (OSW): salinity < 32.5 and temperature < 18°C; Intermediate Cold Water (ICW): salinity 32.8-33.4 and temperature -1.8-2°C and East Sakhalin Current Water (ESCW): salinity < 32.0 and temperature < 7°C.

Several studies on feeding environment reported seasonal changes of nutrients and chlorophyll *a* (Chl *a*) in the southwestern Okhotsk Sea (Maita & Toya, 1986; Shiomoto, 1997; Sorokin & Sorokin, 2002; Mustapha & Saitoh, 2008; 2009; Kasai et al., 2010; Kudo et al., 2011). The physical environment of scallop culture ground is judged to fluctuate seasonally, but basically under SWW (Takizawa, 1982). SWW current flows southeastward along the study area of the Okhotsk Sea. In the offshore region, OSW is found at the surface and ICW presents below OSW. Nutrients were generally low in SWW, moderate in OSW, and rich in ICW. Spring blooms are generally observed in temperate and subarctic coastal areas. Sizable new production occurs during the spring bloom (Kudo & Matsunaga, 1999; Kudo et al., 2015). The development of the spring bloom occurs in a short period of time in response to the favorable ambient conditions. Less frequent, i.e., monthly observations could miss the opportunity to identify the peak of the spring bloom. A continuous time series observation is necessary to characterize the full sequence of the spring bloom.

Based on these characteristic features of the coastal area of Okhotsk Sea in Hokkaido, we address two hypotheses in this study: (i) The drifting sea ice retreat and

the presence of ICW, unique features of the Okhotsk Sea, could influence the spring bloom occurrence and primary production in this area and (ii) the timing for the onset of the spring bloom, as well as the vertical export of organic matter, might relate to the growth of the benthic cultured scallops from spring to summer. A three-year continuous time series monitoring of chlorophyll and temperature, as well as settling particle flux, was conducted to elucidate the relationship between surface primary production, the subsequent export, and the growth of cultured scallops. The objectives of this study are to report the detailed results of this observation and discuss the above mentioned relationship.

## 2. MATERIALS & METHODS

### 2.1 Sampling and water analyses

Sampling and mooring were conducted using research vessels at two stations, Mombetsu (44°24'N, 143°25'E, depth 40 m) and Tokoro (44°10'N, 143°57'E, depth 42 m) in the coastal region of the Okhotsk Sea along Hokkaido (Fig. 1). Sampling at Mombetsu was conducted on 31 March, 14 April, 10 and 17 May in 2011, 23 March, 3 and 16 April, 1 and 14 May in 2012 and 15 March, 1 and 15 April, 1 and 15 May in 2013 at interval of twice a month. Sampling at Tokoro was conducted on 13 April, 15 and 31 May in 2011, 19 April, 11 and 29 May in 2012 and 18 April and 13 May in 2013 at about once a month.

Temperature and salinity profiles were obtained by a CTD (Conductivity, Temperature and Depth) profiler (ASTD 650, JFE Advantech). Water samples for Chl *a* and nutrients were taken vertically from the surface to 5 m above the bottom at interval of 5 m with a 5 L van Dorn sampler (Rigo).

An aliquot of sample for Chl *a* was filtered onto a Whatman GF/C filter. The filter was stored frozen in *N,N*-dimethylformamide to extract plant pigments (Suzuki & Ishimaru, 1990). The extracted Chl *a* was measured with a Turner 10-AU (Welschmeyer, 1994). The samples for $NO_3^-$, $NO_2^-$, $NH_4^+$, $PO_4^{3-}$, and $Si(OH)_4$ analyses were stored frozen for subsequent analyses with a QuAAtro (Bran+Luebbe) (Grasshoff et al. 1999). The precision (coefficient of variation, CV) of the nutrient analyses was about 1% for all nutrients by replicate analyses of samples at natural concentration levels. Detection limits were estimated at 0.01 μM based on three times the standard deviation of the lowest concentration of samples.

2.2 Continuous monitoring

Data loggers (Infinity-CLW, JFE Advantech) were moored at 5 m above the bottom at Mombetsu and Tokoro, recording Chl fluorescence, turbidity, and temperature at an interval of one hour from February to May for four months in 2012 and 2013 (for two months from April to May in 2011). These loggers were moored before sea ice cover in 2012 and 2013. The loggers were equipped with a wiper blade to clean the observation window prior to the fluorescence measurement. Chl fluorescence was calibrated against the discretely measured Chl *a* concentration sampled at the same time and depth. An additional logger (AEM-HR, Alec Electronics) was moored at 5 m below the surface at Tokoro, recording temperature, current speed and direction in 2011 and 2013.

The intrusion of ICW was judged to occur when the temperature decreased by > 2 °C.

2.3 Settling flux

A sediment trap (SMC7S-500, NGK) was moored to collect settling particles at 5 m above the bottom at Tokoro. The trap had an opening area of 0.018 $m^2$ with a baffle and was equipped with seven collection cups that were automatically changed at an interval of 10 days. The cups were filled with 4% neutralized formaldehyde containing seawater with 4 g $L^{-1}$ of NaCl to increase density. The settling flux was calculated dividing the total amount of materials in each cup by the opening area and the days of collection.

The retrieved trap samples were sieved through 1-mm mesh to remove swimmers (zooplankton captured alive). An aliquot of sample was filtered onto a pre-combusted and tare weighed GF/F filter. The filter was washed with Milli-Q water and then freeze-dried (DC41, Yamato). The filter was weighed several times until a constant value was obtained. The filter was further processed in HCl fumes to remove particulate inorganic carbon for 1 d and then neutralized in a desiccator containing NaOH for 2-3 weeks. The filter was used for the measurement of POC and PON with an elemental analyzer (NA-1500, Fisons). Diatom cells in the trap were counted with a microscope (BX-51, Olympus). Diatoms were identified and counted by genus, *Chaetoceros, Thalassiosira,* and *Coscinodiscus*, and unidentified diatoms were counted as either other centrics or other pennates. The cell volume was calculated based on the cell height and valve diameter in cylinder form (centrics) and the short and long axis lengths in elliptic prism

form (pennates) (Hillebrand et al., 1999). The conversion from the cell volume to C content followed by Strathmann (1967) method.

2.4 Scallop growth

The adductor muscle wet weight of 30 individuals was measured monthly for 2-, 3-, and 4-yr-old scallops at Tokoro. The age of scallops was denoted as 1-yr old scallops just sown in the seabed. The number for each cohort indicates the year sown. The scallop growth rate was expressed as the rate of increase in adductor muscle wet weight (ww g $d^{-1}$), calculated as the difference in the averaged weight between April and August divided by the days. The law data of wet weight measurements were provided by Tokoro Fisheries Cooperative Association.

2.5 Drifting sea ice information

The last day of drifting sea ice cover off Mombetsu was obtained from the Okhotsk Sea Ice Museum of Hokkaido website (http://giza-ryuhyo.com/ryuhyoinfo/ryuhyotop.html).

3. RESULTS

3.1 Environmental conditions: Temperature, salinity, nutrients and Chl *a*

The vertical distributions of temperature and salinity at Mombetsu were shown in Fig. 2a, b (2011), Fig. 3a, b (2012) and Figs. 4a,b (2013). The time-course changes in temperature and Chl *a* obtained by continuous monitoring in 2011, 2012 and 2013 were shown in Figs. 5a,b, c (Mombetsu) and Figs. 6a, b, c (Tokoro). The temperature and salinity at Mombetsu were vertically uniform at 0-3 °C and < 33.0 in March, 2011 (Fig. 2a, b). The temperature increased to 6°C at the middle of May and salinity also increased to > 33. The temperature near the bottom at the beginning of April 2011 was 4°C at Mombetsu (Fig. 5a). Small variations in temperature were observed until the end of April. A sharp decrease in temperature to < 3°C was observed on April 25 and this lower temperature remained for a few days. This decrease coincidently occurred at the surface and the bottom at Tokoro (Fig. 6a). After this, the temperature rose to 5°C, but a similar temperature drop in a short period occurred in May.

The temperature at bottom showed some fluctuations between -1.8 and 2°C in February and March 2012 when sea ice covered the surface at Mombetsu (Fig. 5b). The

temperature sharply increased to 4°C on April 18, two weeks after the last day of sea ice cover and thereafter gradually increased to 6°C until the beginning of May. A sharp decrease in temperature to 3°C occurred in the middle of May. The salinity at the surface in April 2012 was < 32.0, indicating the influence of freshwater discharge (Fig. 3b).

The temperature was < 0°C during the period of drifting ice cover until March 11, 2013, the last day of sea ice cover in Mombetsu (Fig. 5c). The temperature in 2013 was similar to that in 2012, but increased to 2°C on April 1 at depths below 25 m while salinity increased to 33.5 within the same depth range (Fig. 4a,b). The temperature gradually increased from this date to 6°C in the middle of April. A sharp drop in temperature from 6 to 2°C occurred at the end of April and this lower temperature continued for about 20 days. The sequence of temperature at the surface was the same as the bottom in Tokoro (Fig. 6c). Temperature increased more gradually in 2013 than in 2012. The similar pattern of change and vertical homogeneity in temperature and salinity from March to May was observed at Mombetsu in three years.

The DIN ($NO_3^-$+$NO_2^-$+$NH_4^+$) and $Si(OH)_4$ at 5 m were high at 10-14 μM and 18-25 μM in March and April in 2012 and 2013 at Mombetsu (Fig. 7a). DIN and $Si(OH)_4$ was vertically homogeneous. $NH_4^+$ and $NO_2^-$ concentrations were low at < 1 μM (not shown); thus DIN mainly consisted of $NO_3^-$. The DIN and $Si(OH)_4$ at 5 m in 2012 increased to 14 μM and 25 μM in April and then dropped to < 2 μM and < 5 μM in May. Those in 2013 decreased gradually in April and dropped to the same level of 2012 by May. Those at Mombetsu in 2011 were low at the beginning of April and maintained this level until the end of May. The values and temporal change of DIN and $Si(OH)_4$ at Tokoro (Fig. 7b) were the same as those at Mombetsu except in the middle of April in 2013 when DIN and $Si(OH)_4$ were depleted at Tokoro, but high at Mombetsu.

Chl *a* fluctuated at < 2 μg $L^{-1}$ in April, but increased to 5 μg $L^{-1}$ at the beginning of May 2011 (Fig. 5a). Chl *a* was low at < 2 μg $L^{-1}$ in February and fluctuated up to 3 μg $L^{-1}$ in March at Mombetsu in 2012 during the cover of sea ice. Chl *a* showed two peaks at the end of April and May and remained > 2 μg $L^{-1}$ for about one week in 2012 at Mombetsu. The temporal change in temperature and Chl *a* at Tokoro (Fig. 6b) were similar to that at Mombetsu. The peak of Chl *a* was 8 μg $L^{-1}$ at Tokoro, which was two times higher than that in Mombetsu. Chl *a* concentration showed an increase at the end of April just after the sharp drop in temperature. The highest Chl *a* concentration

reached > 10 μg $L^{-1}$. Chl *a* concentration during the period of the dropped temperature was valuable and more than two times higher at Tokoro than that at Mombetsu. There were the several occasions of sudden temperature drop in May and increase in Chl *a* afterward in three years (Figs. 5 & 6).

3.2 Settling flux

A time series of total mass, as well as C and N settling fluxes, for three years at Tokoro showed an inter-annual variation (Figs. 8a, b, c). The total mass fluxes in 2011 and 2012 ranged from 0.9 to 9.3 g $m^{-2}$ $d^{-1}$ with the highest flux at the end of April for 2011 and in early May for 2012. The total mass flux in 2013 showed a distinct peak from the end of April to the beginning of May. The maximum flux was 119 g $m^{-2}$ $d^{-1}$ at the beginning of May and the second largest flux was 49.5 g $m^{-2}$ $d^{-1}$ at the end of April. This maximum value was an order of magnitude higher than that observed in 2011 and 2012. The total mass fluxes in other periods of 2013 were similar to those in 2011 and 2012. The organic C and N fluxes showed a similar trend to that of the total mass flux. Distinctly large fluxes were observed in 2013, with the maximum values of 1,165 mg C $m^{-2}$ $d^{-1}$ and 142 mg N $m^{-2}$ $d^{-1}$ at the beginning of May. The average C:N ratios in the settling particles were 11.41 ± 2.49, 8.86 ± 0.49, and 9.17 ± 0.58 in 2011, 2012, and 2013, respectively. The average C:N ratios in 2011 was statistically higher than those in 2012 ($p = 0.026$, Turkey-Kramer method)

The diatom cell flux showed that dominant species were different for the three years (Fig. 9a). *Thalasiosira* spp. were dominant in 2011, while *Chaetoceros* spp. were dominant in 2012. *Chaetoceros* spp. and other centric and pennate diatoms were dominant in cell number in 2013; however, *Coscinodiscus* spp. (mainly, *Coscinodiscus wilesii;* Miyoshi et al., 2015*)*, a large diatom with > 200 μm diameter was found at the end of April and the beginning of May in 2013. The diatom fluxes in 2013 had a maximum value of about 1,000 mg C $m^{-2}$ $d^{-1}$ while those in 2011 and 2012 were < 50 mg C $m^{-2}$ $d^{-1}$ (Fig. 9b). The maximum C converted diatom flux by *Coscinodiscus* spp. in 2013 accounted for the observed maximum C flux of 1,165 mg C $m^{-2}$ $d^{-1}$in 2013.

3.3 Scallop growth

The muscle weight of scallop in each cohort increased from spring to summer (Fig. 10). The scallop growth ceased from summer and the muscle weight did not change or

decreased in some cohorts from fall to the next spring (2008 cohort in 2012, and 2009 cohort in 2012 and 2013).

The growth rate of scallops from April to August varied inter-annually, showing the lowest rate at 0.038 ww g $d^{-1}$ for the 2-yr scallop of 2011 and the highest one at 0.13 ww g $d^{-1}$ for the 4-yr scallop of 2013 (Fig. 11). Statistical tests were conducted for growth rates within the same age cohort (Tukey-Kramer method). The growth rates for the 2-, 3-, and 4-yr scallops in 2013 were significantly higher than those in 2011 and 2012 ($p < 0.01$). The rates for the 2- and 4-yr scallops in 2011 and 2012 were not significantly different ($p > 0.05$).

## 4. DISCUSSION

### 4.1 The timing of spring bloom occurrence, water mass exchange, and consumption of nutrients

Salinity observed at Mombetsu in March ranged from 32.5 to 33.5. Based on the criteria defined by Takizawa (1982), salinity of OSW, ESCW and FSWW are < 32.5 , <32.0 and 33.8-34.2, respectively. Judging from salinity, the water mass seemed the mixture of FSWW and either OSW or ESCW. Water mass was replaced by SWW, a more saline and higher temperature water mass. This transition in 2012 occurred abruptly on April 18, rising > 4°C in a few hours and then temperature gradually increased from 4 to 7°C in 10 days (Fig. 5b).

Explosive increase in biomass of phytoplankton, which is close to their maximal growth, is observed in spring due to the relaxation of a limiting factor for growth, called spring bloom (Baretta-Bekker et al., 1998). The prominent feature of the spring bloom is the rapid increase in Chl *a* accompanied by the drawdown of nutrients. The continuous monitoring of Chl *a* at 5 m above the bottom was conducted to evaluate the diet condition for scallop (Shinada et al., 2005). The nutrient drawdown is another additional index to judge the timing of the spring bloom occurrence although nutrient concentration may change by water mass exchange. The initial DIN and $Si(OH)_4$ at Mombetsu in March, 2012 and 2013 were almost the same at 10-14 μM and 18-25 μM (Fig 7a). In 2011, those were low at < 1μM on April 1, suggesting that the spring bloom had occurred before this date. The high bottom Chl *a* at > 4 μg $L^{-1}$ was observed at the beginning of April at Tokoro (Fig, 6a). In 2012 and 2013, DIN and $Si(OH)_4$ were sharply dropped at the end of April, indicating that the spring bloom occurred after the

middle of April. In 2012 at Mombetsu and Tokoro, bottom Chl *a* at the end of April showed the peaks at > 2 μg $L^{-1}$ (Figs. 5b & 6b). In 2013, DIN concentration was 11.5 μM on March 15 at Mombetsu, decreased to 6 μM on April 1 and further decreased to 2.5 μM on May 1 (Fig. 7a). This decrease in nutrients seemed to be not only due to the actual utilization by phytoplankton, but also apparently due to changes in the water mass. A plot of DIN vs salinity off Mombetsu in 2013 indicated a conservative mixing of DIN between the mixed water mass of OSW or ESCW, and FSWW from March 15 to April 15 (Fig. 12). The end member concentration of DIN for the mixed water mass of OSW and ESCW, and FSWW was estimated as 10-14 μM and 6 μM, respectively from the regression line obtained from DIN vs salinity prior to April 15. However, DIN drawdown of 6-10 μM was observed from April 15 to May 1 without changing salinity. The Chl *a* concentration increased to 2-4 μg $L^{-1}$ on May 1. Thus, the spring bloom occurred in the mixed water mass between the mixed water mass of OSW and ESCW, and FSWW in the middle of April 2013. The bottom Chl *a* at Mombetsu and Tokoro showed the peaks from the middle to the end of April in 2013 (Figs. 5c & 6c).

Judging from the timing of DIN and $Si(OH)_4$ drawdown and bottom Chl *a*, the spring bloom occurred the earliest in 2011. The temperature started increasing after the retreat of drifting sea ice. The retreat and the temperature rise were observed three weeks earlier in 2013 than in 2012. However, the spring bloom occurred at the similar timing in 2012 and 2013. The thermal stratification of the water column is generally a triggering factor for spring bloom occurrence (Simpson & Sharples, 2012). However, this area is vertically well mixed due to a strong current > 20 cm $s^{-1}$ (Miyoshi unpublished). Thus, the onset timing of the spring bloom was not affected by that of the drifting sea ice retreat nor that of water column stratification of water column. The occurrence of spring bloom was reported in the absence of vertical water column stratification (Townsend et al, 1992, 1994; Kudo & Matsunaga 1999). The irradiance condition is the triggering factor for the spring bloom occurrence in these studies. The underwater irradiance was not measured in the present study, thus we could not discuss further for this.

4.2 Role of ICW in refueling nutrients

ESCW and OSW usually occupies the coastal region of the Okhotsk Sea along Hokkaido from December to March and from April to October, respectively. These

water masses move offshore when the strength of FSWW starts increasing in spring (Takizawa, 1982). There were the several occasions of sudden temperature drop in May and increase in Chl *a* afterward (Figs. 5 & 6). This event indicated the mixing with ICW when this water mass approached the near shore. ICW is characterized by properties such as temperature < 0°C and a high concentration of nutrients ($NO_3^-$ > 30 μM, $PO_4^{3-}$ > 1.5 μM and $Si(OH)_4$ > 100 μM), which originates from the ejection of sea salt during the formation of sea ice (Kasai et al., 2010; Kudo et al., 2011). The mixing with ICW replenished nutrients in the area where nutrients were low or depleted. This supply of nutrients can stimulate the growth of phytoplankton. On board incubation experiments demonstrated that the mixing of SWW with ICW stimulates phytoplankton growth, especially for large-sized (> 10 μm) cells (Kudo et al., 2011). This event was prominent at Tokoro at the end of April 2013 (Fig. 6c). Temperature lowered < 2°C for more than two weeks and Chl *a* increased > 10 μg $L^{-1}$. This event was fueled with the intrusion of ICW and led to a massive growth of *Coscinodiscus* spp. and the subsequent export to the bottom at Tokoro.

We deployed the continuous monitoring sensors at Mombetsu and Tokoro to monitor a fine scale change in temperature and Chl *a*. The values of temperature and Chl *a* obtained from the deployed instrument were consistent with those obtained from the discreate sampling. The short-term change in temperature and subsequent increase in Chl *a* was missed to observe by the discreate sampling conducted at the interval of twice (Mombetsu) and once (Tokoro) a month but was able to be elucidated by the continuous monitoring.

4.3 Regulation of export by diatom species composition

A three-year sediment trap mooring in the coastal area of the Okhotsk Sea revealed the relatively large inter-annual variation in the settling flux. The maximum values of the total mass flux and organic C and N fluxes in 2013 were more than five times higher than those in 2011 and 2012 (Fig 8a, b, c). Oceanographic conditions such as temperature, salinity, and nutrient concentrations in March were similar for the three years. *Coscinodiscus* spp. was the quantitatively dominant phytoplankton (Fig. 9a, b) and the diameter of the cell valve was > 200 μm. The sinking rate of a phytoplankton cell is a function of cell size (Smayda, 1970). A particle with a diameter (r) of 100 μm will settle at ~12 m $d^{-1}$. The other diatom species found in this study had a diameter <

10 μm. Decreasing the size of the particle by a factor of 10 lowers sinking rates by a factor of 100 because of the $r^2$ dependence on the sinking rate (Middelburg, 2019). Comparing sinking rates, the other diatom species would have an order of magnitude lower rate than that of *Coscinodiscus* spp. *Coscinodiscus* spp. (*C. wailesii*) was also found in the coastal area of the Sea of Japan in spring 2013 (Shimada et al., 2014).

Salinity in the study area was > 33.5 in April and May of 2013, indicating FSWW, connecting with the current from the Sea of Japan. Thus, the seed population of *Coscinodiscus* spp. seemed to be supplied from the Sea of Japan. Such large cells seemed to sink faster below the euphotic zone under the less turbulent environment. SWW, a fast southeast current at > 20 cm $s^{-1}$ flowed steadily at the study site in spring, providing turbulent mixing conditions.

Diatoms form massive blooms and sink rapidly in nutrient-rich areas. In such regions, export production accounts for more than 50% of the total carbon fixation (Sancetta et al., 1991; Berger & Herguera, 1992; Bienfang & Ziemann, 1992; Buesseler, 1998; Heiskanen & Leppänen, 1995). The nutrient-rich condition was formed in 2013 by refueling the nutrients from ICW. Thus, the high export flux in 2013 was brought by the combination of the seed supply of *Coscinodiscus* spp. from the Sea of Japan and the acceleration of the primary productivity refueling nutrients from ICW.

The settling fluxes under seasonal sea ice were reported at a nearby location in the Okhotsk Sea (Hiwatari et al., 2008). Total mass flux and organic C flux ranged from 0.2 to 1.2 g $m^{-2}$ $d^{-1}$ and from 20 to 120 mg C $m^{-2}$ $d^{-1}$, respectively. These fluxes under sea ice were an order of magnitude lower than those after the sea ice retreat observed in the present study. The organic C flux under sea ice was composed of mainly fecal pellets in January and ice algae in March just after the retreat of sea ice (Hiwatari et al., 2008). In the present study, neritic phytoplankton were the main contributors to the settling organic C flux in spring.

### 4.4 Factors affecting the growth of scallops

Scallop cultures in the Okhotsk Sea are conducted by sowing 1-y juveniles into a 4-part segmented seabed and harvesting 4-yr adults using dragging gear. Scallops mainly consume phytoplankton (Shumway et al., 1987, 1997; Lorrain et al., 2002) and detritus (Cranford & Grant, 1990). The growth rate of scallops from April to June varied inter-annually, showing the lowest rate at 0.04 g $d^{-1}$ for a 2-yr scallop of 2011 and the highest

one at 0.13 g $d^{-1}$ for a 4-yr scallop of 2013 (Fig. 11). The growth rates for 2, 3 and 4-yr scallops in 2013 were significantly higher than those in 2011 and 2012 ($p < 0.01$). The temperature at the bottom of Tokoro showed a similar pattern from April to June in 2011, 2012 and 2013. The temperature ranged from 2.4°C in April 2012 to 10.2°C in June 2011. The ingestion efficiency of scallops does not change from -2 to 10°C (Kurata et al., 1991). Thus, the temperature was not the factor explaining the difference in growth of scallops in the three years.

The timing of the spring bloom occurrence is a posssible factor influencing the growth of scallops. Early occurrence of the spring bloom may provide available food to scallops earlier. The spring bloom occurred earliest in 2011 and later at the similar timing in 2012 and 2013. The growth of scallops did not seem to be affected by the timing of the spring bloom.

Japanese scallops, *P. yessoensis,* belong to Pectinidae and are filter-feeding bivalves. They do not possess any sorting function for ingesting food (Beninger et al., 1988). The dominant phytoplankton in the settling flux in 2013 was *Coscinodiscus* spp., a centric diatom with a diameter of > 200 µm. *Coscinodiscus* spp. cells sunk rapidly and contributed to the large settling flux of organic matter in 2013 (Fig. 9b). This large flux provided a more food source for benthic scallops than in other years, resulting in the highest growth of scallops in 2013. The hanging culture of scallops is conducted in Lake Saroma, which is brackish lagoon connected to the Okhotsk Sea (Fig. 1). Although the dominant phytoplankton in 2013 was also *Coscinodiscus* spp. in Lake Saroma, the growth of hanging cultured scallops was not better than in normal years (Miyazono pers comm). This could be explained by a shorter residence time of the *Coscinodiscus* spp. cells in the water column due to a faster sinking rate. Thus, hanging cultured scallops in Lake Saroma could not consume *Coscinodiscus* spp. cells during their suspension in the water column. The effect of the settling flux on the growth of scallops in the Okhotsk Sea appeared more clearly for the 3 and 4-yr age classes in 2013 than for the 2-yr class (Fig. 11). This is due to the age or size dependent difference in the efficiency of ingestion for larger cells of > 200 µm (Aya & Kudo, 2017).

## 5. CONCLUSION

Close coupling between primary production, the subsequent export, and the growth of benthic cultured scallops was observed through a time series monitoring over three

years. High growth of scallops was observed in 2013 when *Coscinodiscus* spp., whose cell valve diameter was > 200 μm, was quantitatively dominant. This species contributed to the higher export flux due to a higher settling velocity. The supply of nutrients from ICW, a characteristic water mass in the Okhotsk Sea with high nutrients, accelerated the primary production after the spring bloom. This supply was prominently high in 2013 and enhanced the growth of *Coscinodiscus* spp. This study demonstrated that the combination of the seed supply of *Coscinodiscus* spp. from the Sea of Japan and the acceleration of the primary productivity refueling nutrients from ICW strongly influenced the export and the pelagic-benthic coupling in the coastal area. The settling organic matter monitoring by the sediment trap is important for assessing the growth potential or the carrying capacity of scallop sowing culture.

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CONFLICT OF INTERESTS

The authors confirm that they have no conflicts of interest to declare in the preparation or publication of this research.

AUTHOR CONTRIBUTIONS

Takayuki Terumoto contributed to the sample analysis and to the data analysis. Isao Kudo contributed to the design of the research, to the analysis of the results, and to the writing of the manuscript. Koji Miyoshi contributed to the design of the research and to the sampling. Akiyoshi Shinada contributed to the design of the research and to the phytoplankton analysis. Akira Miyazono contributed to the design of the research and to the sampling. All authors reviewed and approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Figure legends

Figure 1 Map showing Mombetsu and Tokoro, sampling and mooring locations (○).

Figure 2 Temporal change in temperature (a) and salinity (b) at Mombetsu in 2011.

Figure 3 Temporal change in temperature (a) and salinity (b) at Mombetsu in 2012.

Figure 4 Temporal change in temperature (a) and salinity (b) at Mombetsu in 2013.

Figure 5 Time series of temperature, Chlorophyll *a* by a mooring logger and temporal change in Chlorophyll *a* (■) by a discrete sampling at 5 m above the bottom in 2011 (a), 2012 (b) and 2013 (c) at Mombetsu. The blue bars on the x-axis indicate the period when the influence of ICW was observed.

Figure 6 Time series of temperature, Chlorophyll *a* by a mooring logger and temporal change in Chlorophyll *a* (■) by a discrete sampling at 5 m above the bottom in 2011 (a), 2012 (b) and 2013 (c) at Tokoro. Time series of temperature at 5 m (surface) was shown in 2011 and 2013. The blue bars on the x-axis indicate the period when the influence of ICW was observed.

Figure 7 Temporal change in DIN and $Si(OH)_4$ at 5 m of Mombetsu (a) and Tokoro (b).

Figure 8 Time series of total flux (a), C flux (b) and N flux (c) in 2011, 2012 and 2013 at Tokoro.

Figure 9 Time series of diatom cell number flux (a) and diatom C converted flux (b) in 2011, 2012 and 2013 at Tokoro. Thal: *Thalasiosira*, Chaet: *Chaetoceros*, Cos: *Coscinodiscus*, centric: other centrics and pennate: pennate diatoms.

Figure 10 Temporal change in muscle weight of scallops for each cohort. Number for each cohort indicates the year sown. Error bar indicates the standard error from 30 samples.

Figure 11 Growth rate of benthic cultured scallop for 2, 3 and 4-yr age at Tokoro in 2011, 2012 and 2013. Different alphabet indicates significant difference ($p < 0.05$) within the same age. Statistical analysis was conducted by Tukey-Kramer method.

Figure 12 Relationship between salinity and DIN concentration in 2013 at Mombetsu. The dashed line indicates the regression line obtained data from March 15, April 1 and April 15. The circles indicate the endmember for the water mass in March (MWM: Mixed Water Mass) and FSWW.

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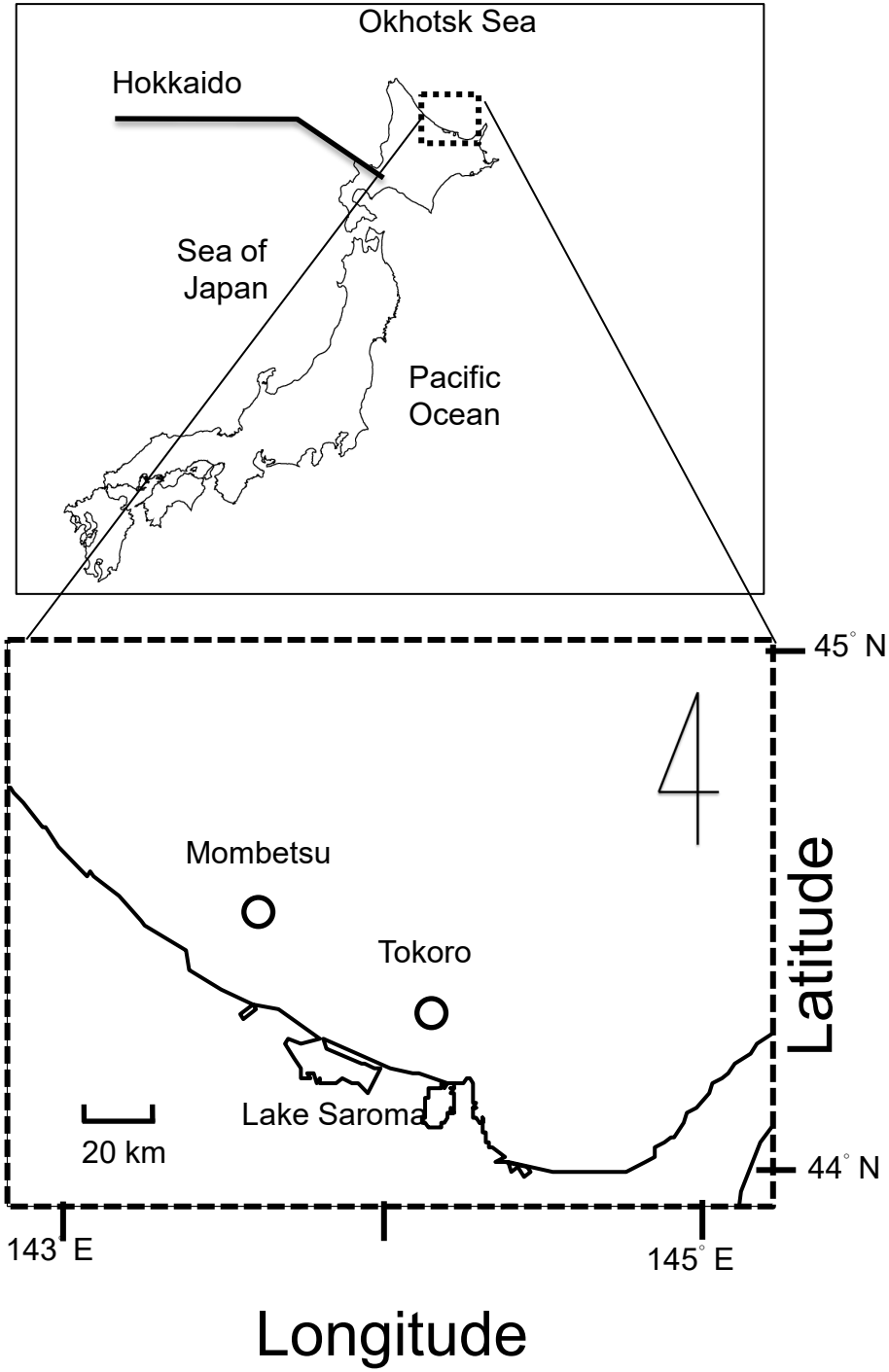

Okhotsk Sea
Hokkaido
Sea of
Japan
Pacific
Ocean
45° N
4
Mombetsu
Tokoro
Latitude
Lake Saroma
20 km
44° N
143° E
145° E
Longitude

Fig.1

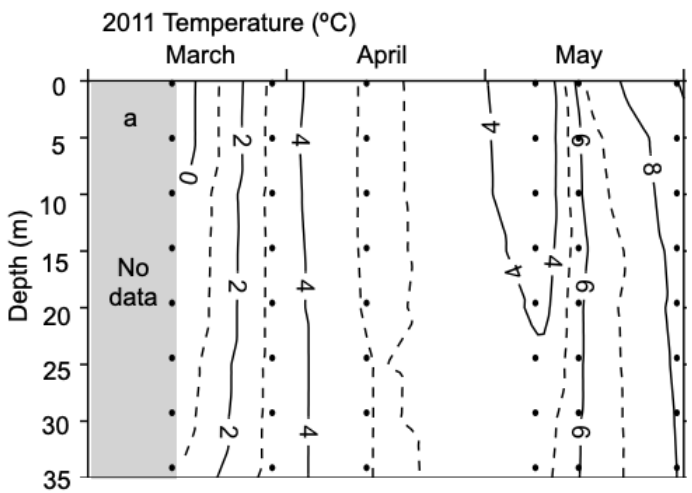



Fig. 2a

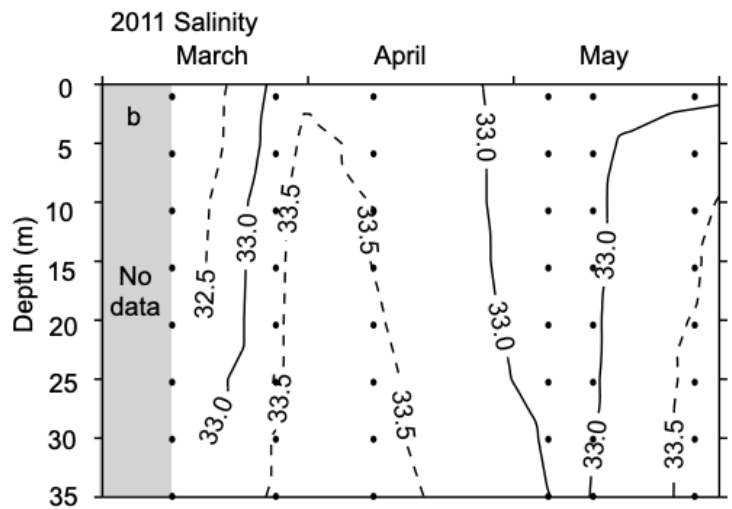



Fig. 2b

Fig.2

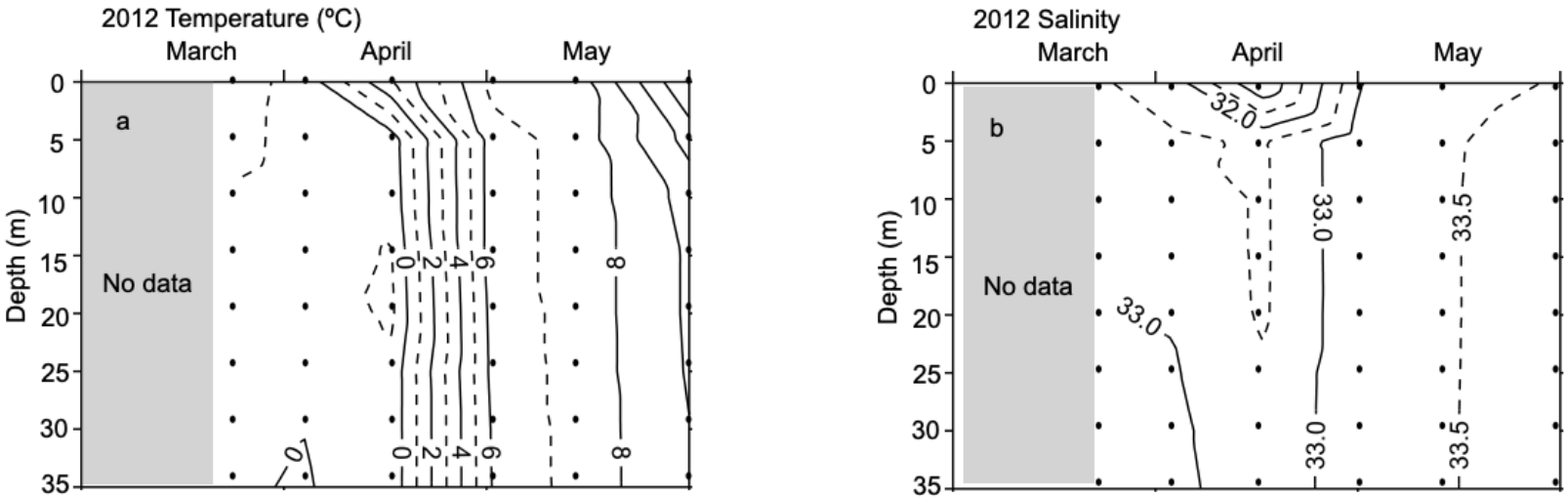

2012 Temperature (ºC)
March
April
May
a
No data
Depth (m)
0
5
10
15
20
25
30
35
0
2
4
6
8
2012 Salinity
March
April
May
b
No data
Depth (m)
32.0
33.0
33.5

Fig. 3b

Fig.3

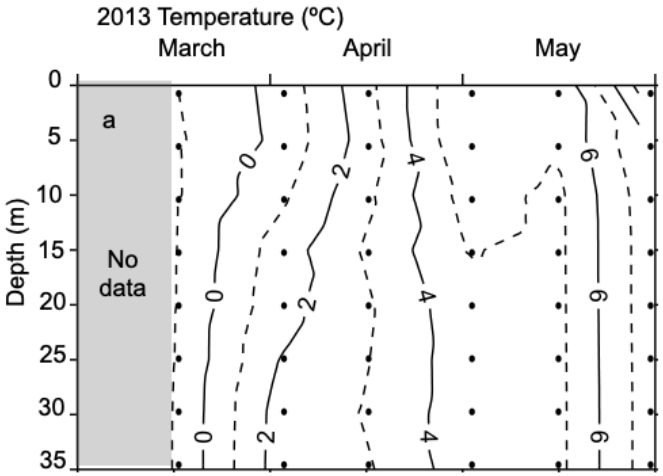



Fig. 4a

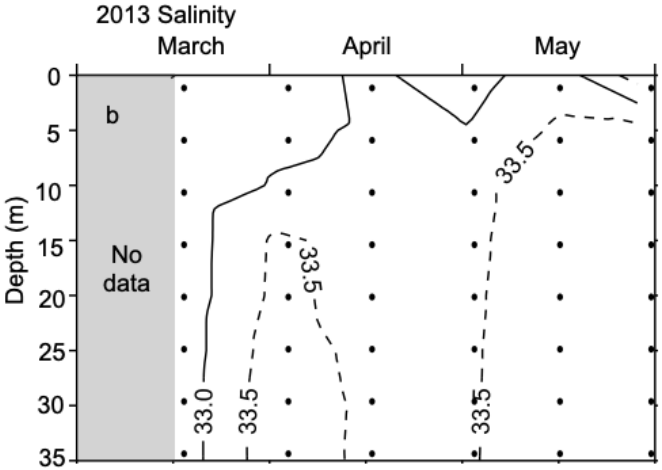



Fig. 4b

Fig.4

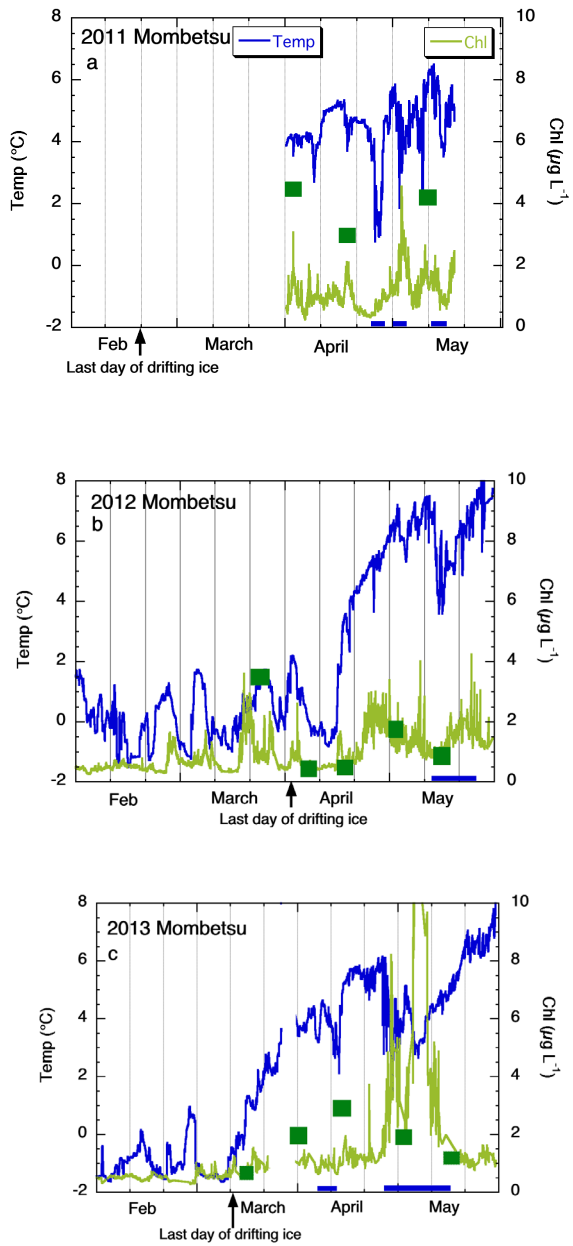

2011 Mombetsu
a
Temp
Chl
Temp (°C)
Chl (μg L-1)
Feb
March
April
May
Last day of drifting ice
2012 Mombetsu
b
Temp (°C)
Chl (μg L-1)
Feb
March
April
May
Last day of drifting ice
2013 Mombetsu
c
Temp (°C)
Chl (μg L-1)
Feb
March
April
May
Last day of drifting ice

Fig.5

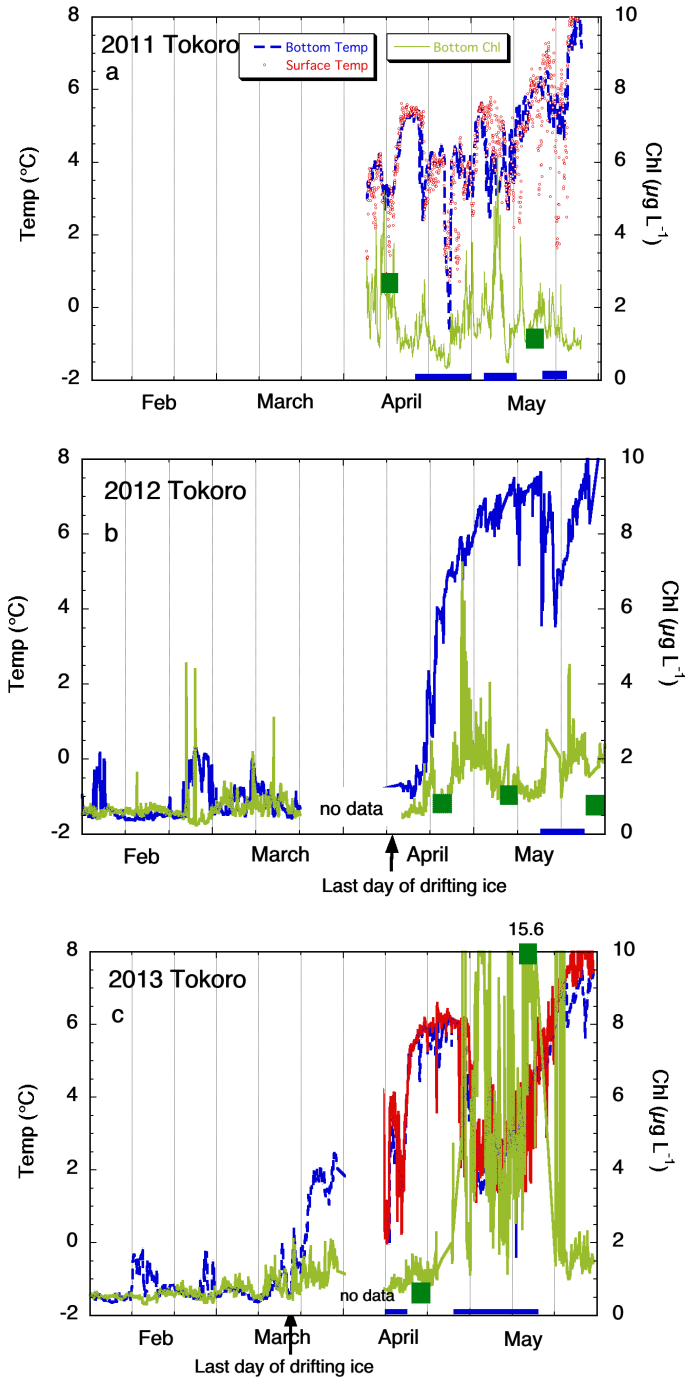

2011 Tokoro
a
Bottom Temp
Surface Temp
Bottom Chl
Temp (°C)
Chl (μg L⁻¹)
Feb
March
April
May
2012 Tokoro
b
no data
Last day of drifting ice
2013 Tokoro
c
15.6
no data
Last day of drifting ice

Fig.6

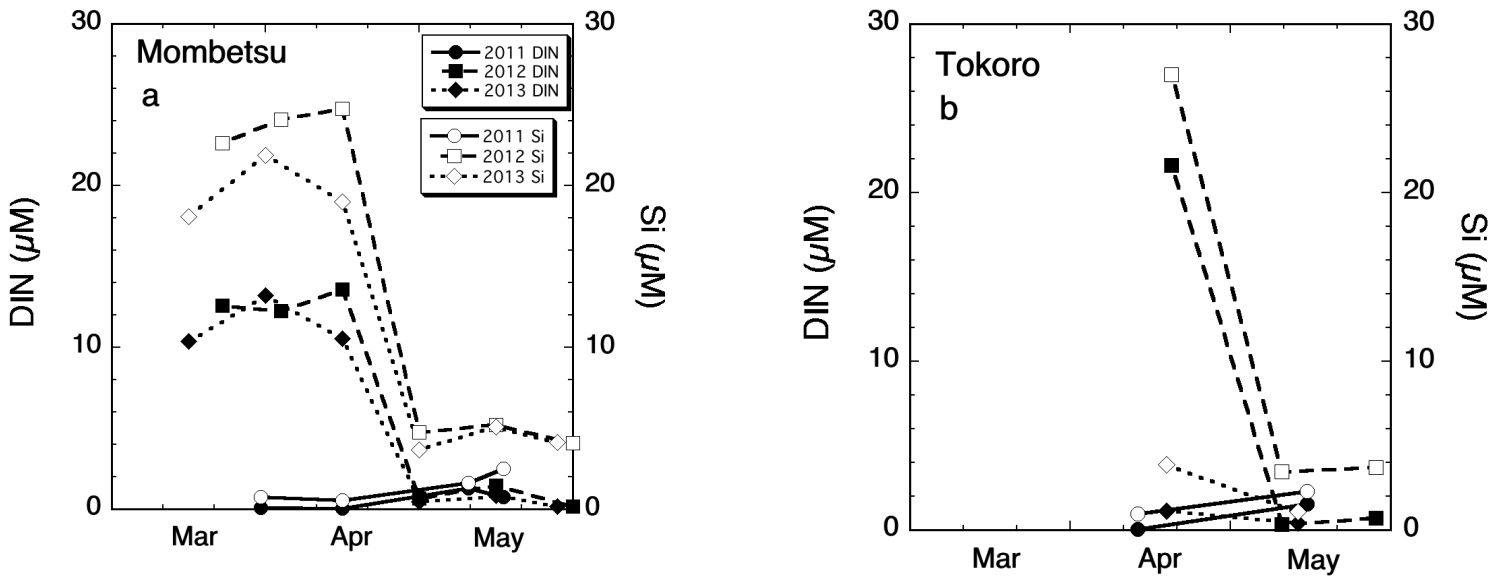

Mombetsu
a
2011 DIN
2012 DIN
2013 DIN
2011 Si
2012 Si
2013 Si
DIN (μM)
Si (μM)
30
20
10
0
Mar
Apr
May
Tokoro
b
DIN (μM)
Si (μM)
30
20
10
0
Mar
Apr
May

Fig.7

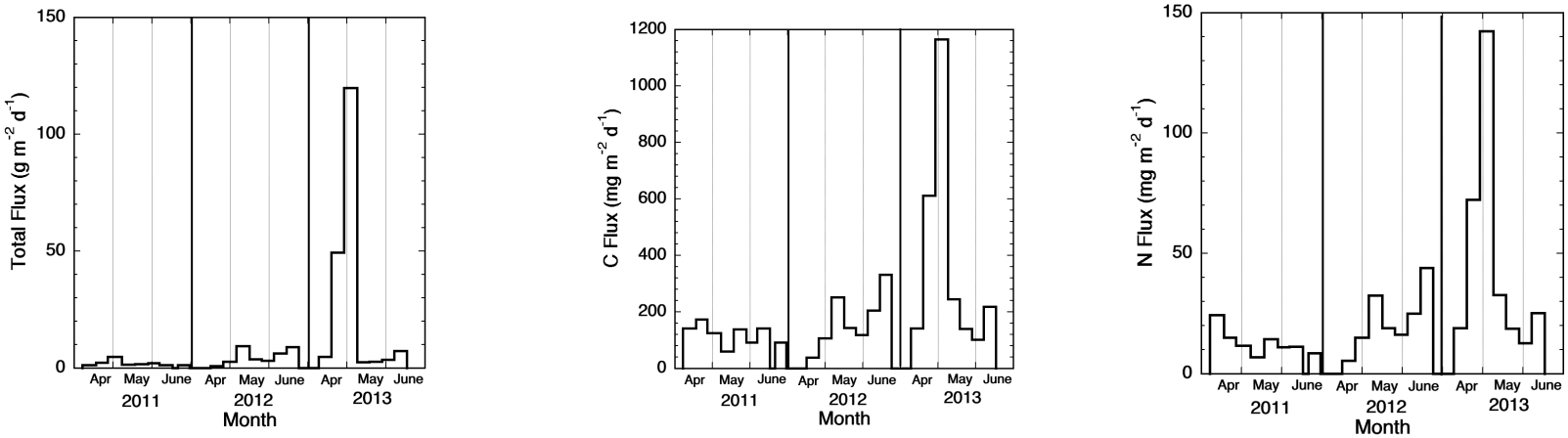
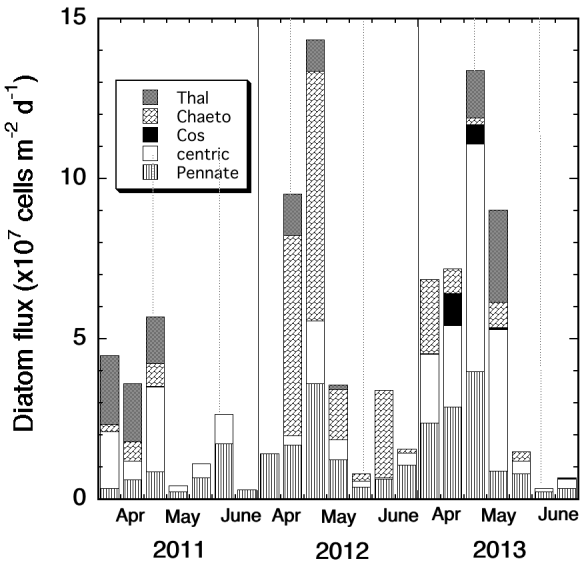

Total Flux (g m-2 d-1)
150
100
50
0
Apr May June Apr May June Apr May June
2011 2012 2013
Month
C Flux (mg m-2 d-1)
1200
1000
800
600
400
200
0
Apr May June Apr May June Apr May June
2011 2012 2013
Month
N Flux (mg m-2 d-1)
150
100
50
0
Apr May June Apr May June Apr May June
2011 2012 2013
Month

Fig.8


Diatom flux (x10$^7$ cells m$^{-2}$ d$^{-1}$)
15
10
5
0
Thal
Chaeto
Cos
centric
Pennate
Apr
May
June
Apr
May
June
Apr
May
June
2011
2012
2013

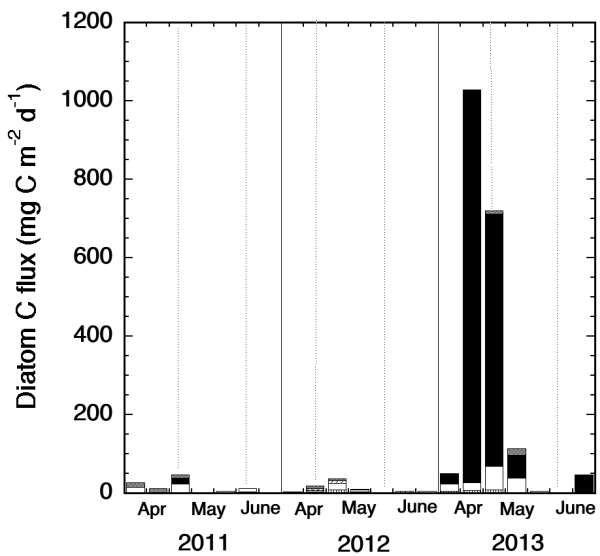

Diatom C flux (mg C m$^{-2}$ d$^{-1}$)
1200
1000
800
600
400
200
0
Apr
May
June
Apr
May
June
Apr
May
June
2011
2012
2013

Fig.9

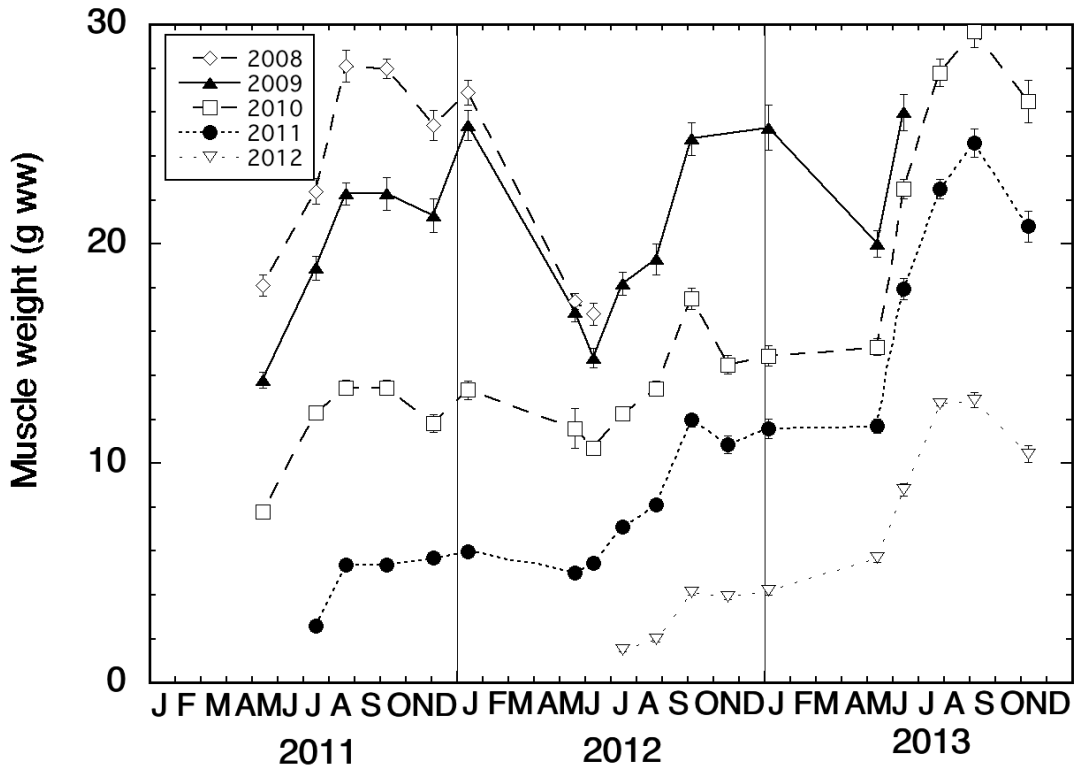

Muscle weight (g ww)
30
20
10
0
2008
2009
2010
2011
2012
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
2011
2012
2013

Fig.10

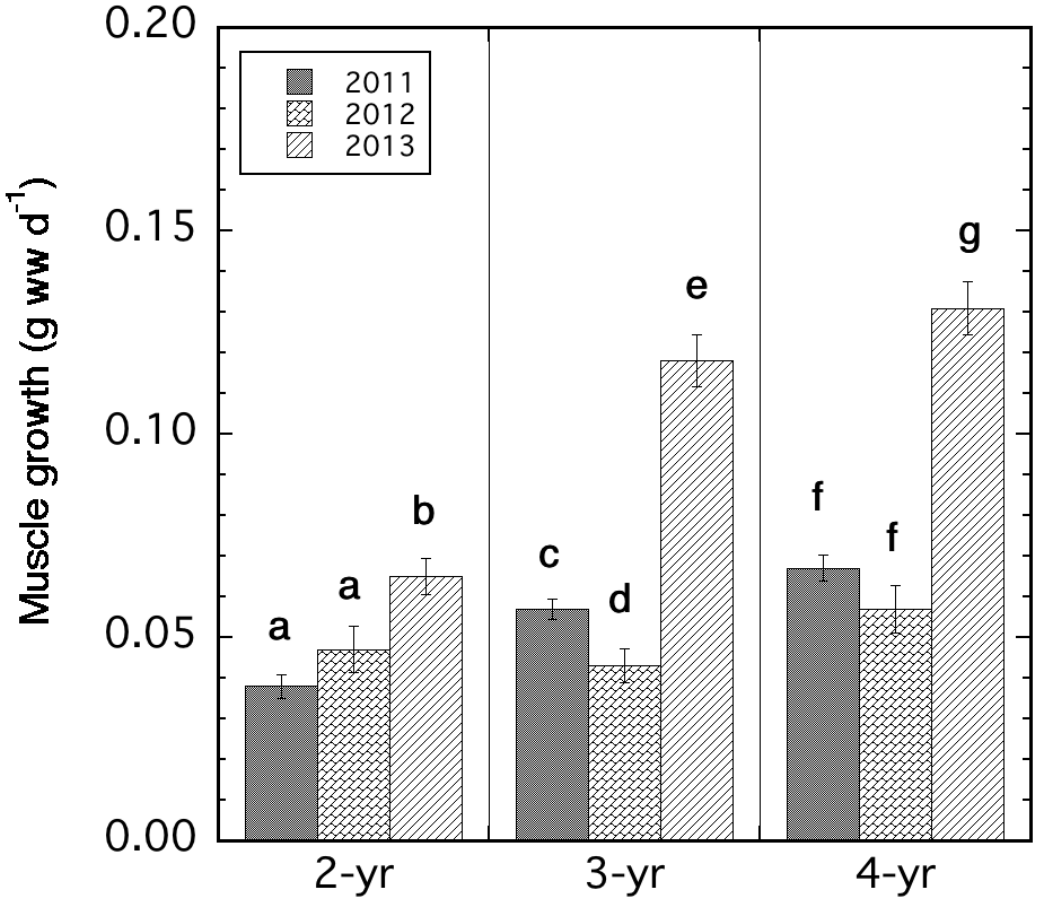

0.20
0.15
0.10
0.05
0.00
Muscle growth (g ww d-1)
2011
2012
2013
a
a
b
c
d
e
f
f
g
2-yr
3-yr
4-yr

Fig.11

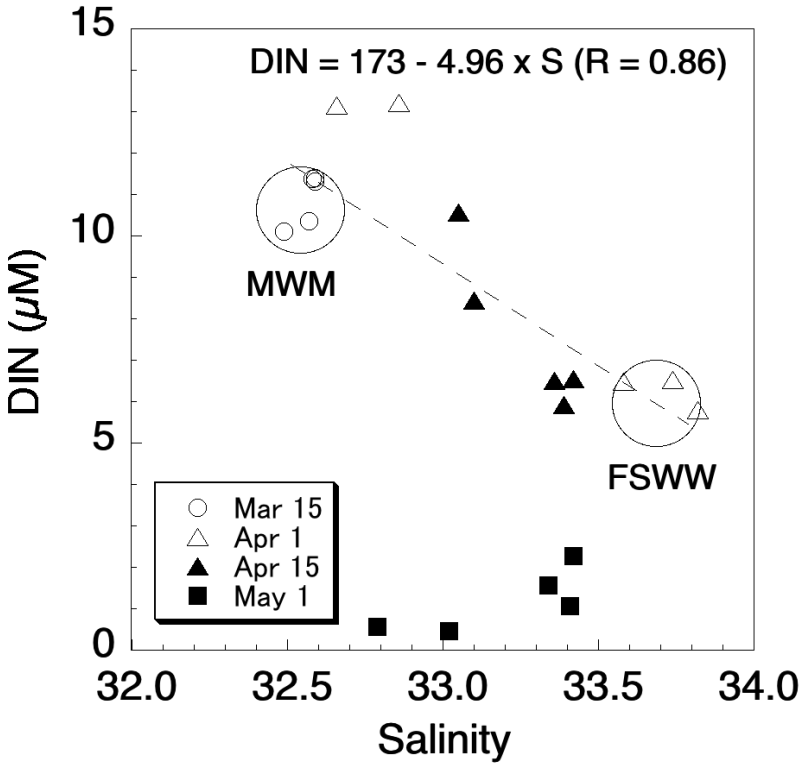

DIN = 173 - 4.96 x S (R = 0.86)
MWM
FSWW
Mar 15
Apr 1
Apr 15
May 1
DIN (μM)
Salinity
15
10
5
0
32.0
32.5
33.0
33.5
34.0

Fig.12