Phytoplankton distribution during the winter convective season in Sendai Bay, Japan

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Abstract

We investigated the elevated chlorophyll-*a* (Chl-*a*) zone found along the coast in winter in Sendai Bay, Japan, using hydrographic observations and a one-dimensional ecosystem model. Chlorophyll-*a* distribution was vertically homogeneous with a horizontal gradient and could be approximated as a power function of bottom depth; Chl-*a* concentration drastically increased with decreasing bottom depth, despite temperature and salinity being almost vertically and horizontally homogeneous. The observed results revealed significant correlations among Chl-*a* and nutrients concentrations proportional to the Redfield ratio. Diatoms accounted for more than 99 % of the detected total cells, indicating the occurrence of a diatom bloom. A one-dimensional ecosystem model, which incorporated vertical mixing and the self-shading effect of phytoplankton, revealed that bottom depth was responsible for the occurrence of the bloom during the convective season in coastal area where vertical mixing reached the bottom and that there existed the critical bottom depth where the integrated Chl-*a* in the water column remained constant. A bloom could occur where the bottom depth is shallower than the critical bottom depth, not when the depth of the mixed layer is shallower than the classical critical depth and the stratification is established. From the observational and model results, it is suggested that the diatom bloom was induced by oceanic water intrusion, which transported nutrients to the bay and the elevated Chl-*a* zone was formed within a month after the intrusion.

1. Introduction

Sendai Bay is one of the major bays located in the Tohoku region of Japan on the Pacific coast, with a width of 60 km. Most of the bay is on the continental shelf, with an average depth of approximately 50 m. Five major rivers flow into the bay; the Abukuma, Natori, Yoshida, Naruse and Kyu-Kitakami Rivers. The total river discharge is approximately $1000 \text{ m}^3 \text{ s}^{-1}$. The Bay also widely opens to the Pacific Ocean and is affected by oceanic water derived from the Oyashio, the Kuroshio and the Tsugaru Warm Water (Kudo, 1971). Especially, the Oyashio has an important role to supply nutrients to the Bay because its nutrient concentrations are high. The Bay is famous for oyster and seaweed farming, which are both harvested in winter. It is thus extremely important to understand the spatial and temporal variations in phytoplankton productivity and nutrient concentrations in this season. Since oysters feed on phytoplankton, the winter bloom could promote oyster growth. In contrast, the photosynthesis of seaweed is inhibited by the consumption of required nutrients by phytoplankton. Further, the depletion of nutrients owing to the winter bloom causes discoloring of cultured rhodophyte seaweed and degrades the quality of the product (Kakinuma et al., 2008).

In Sendai Bay, Yokouchi et al. (1998) reported that chlorophyll-*a* (Chl-*a*) started to increase before the mixed layer became shallower than the critical depth, which was proposed by Sverdrup (1953). Indeed, high Chl-*a* concentrations, up to 10 mg m^{-3} , are often observed in winter on Moderate-resolution Imaging Spectroradiometer (MODIS) derived satellite Chl-*a* images (Fig. 1). Chl-*a* zone is found approximately 20 km off the coast. The phytoplankton

bloom in winter was reported to be formed in river plumes in Biscay Bay (Gohin et al., 2003). Also in Sendai Bay, phytoplankton blooms driven by riverine nutrient inputs are possibly to occur, because several rivers flow into the bay (Fig. 2). However, high Chl-*a* is also distributed along the coast of the Fukushima Prefecture where freshwater input is lower. This indicates that, processes other than fresh water input might contribute to the formation of high Chl-*a* zones. Yokouchi et al. (1998) reported the timing and magnitude of the bloom changed inter-annually and indicated that oceanic intrusion might induce the inter-annual difference.

In coastal regions, Cloern (1991) reported phytoplankton biomass increased during neap tides corresponding to the enhancement of the stratification. The onset of stratification retains the phytoplankton in the upper layer where there is enough light for photosynthesis, which then leads to a vast increase in phytoplankton (Sverdrup, 1953; Riley, 1957). Taylor and Ferrari (2011) showed that the onset of a bloom could also be triggered by a reduction in turbulent mixing even in the convective condition, through the increased residence time of phytoplankton in the euphotic layer. Lucas et al. (1998) reported that enhanced tidally driven mixing in the shallower system may have stronger negative effects on phytoplankton population growth by removing phytoplankton biomass from the euphotic layer. Similarly, in the convective season, as vertical mixing induced by heat loss at the sea surface dominates, phytoplankton tends to be moved to the aphotic layer where light intensity is insufficient for photosynthesis and its biomass is apt to decrease (Findlay et al., 2006). The light availability, which depends on the turbidity or transparency, also regulates photosynthesis through changing the depth of the euphotic layer (Cloern, 1999). Hitchcock and Smayda (1977)

indicated unusual low light intensity induced the delay of the bloom inception. Pennock (1985) stated that phytoplankton blooms were regulated both spatially and temporally by light availability. Cases that the vertical mixing enhances the phytoplankton biomass are also reported (Behrenfeld, 2010). It is suggested that the reduction in grazing pressure on phytoplankton, owing to dilution by mixing, is greater than the decrease in photosynthetic rate, and thus net growth rate remains positive (Yoshie et al., 2003; Rousseaux et al., 2012). Thus, phytoplankton populations in the convective season are controlled by a combination of factors related to the net growth rate of phytoplankton and it is important to clarify the mechanisms which induce blooms in this season.

In this paper, we examine the mechanisms responsible for the formation of high Chl-*a* zones along the coast of Sendai Bay in the convective season, focusing on bottom depth regulating the occurrence of phytoplankton blooms. We conducted hydrographic observations to examine the vertical structure of Chl-*a* and parameters related to photosynthesis. Based on the observed results, a one-dimensional ecosystem model was used to examine the observed distribution of Chl-*a* and the mechanisms of formation of high Chl-*a* zone. We demonstrated that a phytoplankton bloom induced by the oceanic water intrusion during the convective season in coastal area without riverine input or the onset of the stratification. We clarified the critical bottom depth, which is corresponding to the Sverdrup's critical depth in open ocean, was responsible for the occurrence of the blooms. The mechanisms revealed by our study will contribute to a better understanding of phytoplankton dynamics in coastal regions.

2. Methods

2.1. Hydrographic observation

Hydrographic observations were conducted in Sendai Bay between the 6 and 10 January 2012, by the R/V *Dainana-Kaiyo-Maru* chartered by the Tohoku National Fisheries Research Institute. In Sendai Bay, 41 stations were established on two transects; the C line which ran from stations C1 to C22 was a cross-shore line located off the Abukuma River, and the P line from stations P1 to P17 was an alongshore line at approximately 30 m depth (Fig. 2). Measurements of temperature, salinity, dissolved oxygen, Chl-*a* fluorescence and light intensity by aqua quality sensor AAQ (AAQ-1186; JFE Advantech, Japan) were carried out at all stations, either to the bottom or 100 m depth. At half of the stations, measurements with a Conductivity, Temperature, Depth and dissolved Oxygen (CTDO) sensor (SBE 19 with SBE43; Sea Bird Instruments, Washington) were conducted from the sea surface to near the bottom. At the same stations, water samples were taken at the surface, at depths 10, 30 and 50 m, and at 5 m above the bottom, using a 6-L Van Dorn water sampler equipped a pinger to monitor depth and to take samples at precise depths.

Salinities measured with the CTDO sensor were calibrated with water sample salinities measured with a salinometer (AUTOSAL 8400B; Guildline, Canada). The root mean square (RMS) error between the salinity measured by the salinometer and the calibrated salinity of CTDO was 0.0033. The salinities of the AAQ were calibrated with calibrated salinities of the CTDO.

Samples for nutrients measurements were collected in duplicate from the Van Dorn sampler

at each depth. Samples were stored frozen at -40°C until analysis in the laboratory. Nutrient concentrations were determined by the method of Parsons et al. (1984a) using a continuous flow analyzer (QuAatro 2-HR; BLTEC Inc., Japan). The RMS differences between duplicate samples were 0.16, 0.03, 0.19, 0.05 and $0.76\ \mu\text{mol L}^{-1}$ for NH_4 , NO_2 , NO_3 , PO_4 and SiO_2 , respectively. We define dissolved inorganic nitrogen (DIN) as the sum of NH_4 , NO_2 and NO_3 .

Water samples for Chl-*a* analysis were immediately filtered through a 25 mm Whatman GF/F glass fiber filter, preserved in DMF (*N*, *N'*-dimethylformamide) and frozen until analysis. Fluorometric measurements of Chl-*a* were performed using the Welschmeyer method (Welschmeyer, 1994) with a Turner Designs fluorometer (10-AU; Turner Designs, Canada). The calibration of the fluorometer was conducted using the Turner Designs solid standard. Measured Chl-*a* concentrations were used for the calibration of the fluorescence sensor of the AAQ by linear regression.

Samples for analysis of species composition of phytoplankton community were collected from the sea surface and 30 m depth at stations C5 and C12. The samples were fixed with Lugol's solution (4 %) and preserved at 4°C . Samples were concentrated by a reverse filtration through $2\ \mu\text{m}$ nucleopore filter. In the concentrated samples, each species of phytoplankton was identified following Tomas (1997) and its cell numbers were counted under a light microscopy.

2.2. One-dimensional ecosystem model

To calculate the temporal evolution of phytoplankton biomass, the relevant processes were

formulated as follows. The time derivative of phytoplankton concentration (Chl) is

$$\frac{\partial Chl}{\partial t} = PS - RS, \quad (1)$$

where PS is the photosynthesis rate and RS is the respiration rate. PS is expressed as

$$PS = G_{max} \cdot F_I \cdot F_T \cdot F_N \cdot Chl, \quad (2)$$

where G_{max} is the maximum growth rate, F_I , F_T and F_N are terms of limitation owing to light, temperature and nutrients, respectively. F_I is denoted as

$$F_I = \frac{I}{I_{opt}} \exp(1 - \frac{I}{I_{opt}}), \quad (3)$$

where I is light intensity and I_{opt} is the optimum light intensity (Steele, 1962). The vertical distribution of I is expressed as

$$I(z) = I_0 \exp(-kz), \quad (4)$$

where z is the depth defined as zero at the sea surface and positive downward (m), I_0 is the light intensity at the sea surface ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and k is the light extinction coefficient (m^{-1}).

The diurnal variation of light intensity at the sea surface, I_0 , is given as the third power of the sine function from sunrise to sunset, following Ikushima (1967). The daytime length was set to 10 hours from 7:00 to 17:00, as was the standard during the observation period in the study area. I_0 is expressed from I_{max} , which is I_0 at the time of culmination, as follows:

$$\begin{aligned} I_0 &= I_{max} \sin^3(\pi \frac{t_h - 7}{10}) \quad (7\text{h} \leq t_h \leq 17\text{h}), \\ I_0 &= 0 \quad (0\text{h} \leq t_h < 7\text{h} \text{ or } 17\text{h} < t_h < 24\text{h}) \end{aligned} \quad (5)$$

where t_h is time (h) of each day of calculation. F_T was assumed, following Eppley (1972), as

$$F_T = \exp(k_T \cdot T), \quad (6)$$

where T was given as a constant at 10°C according to the observational result (Fig. 3A). F_N

was adopted from the Michaelis-Menten formula and expressed using the half saturation rate (k_P).

$$F_N = P/(P + k_P) . \quad (7)$$

Here, we estimated F_N from only PO_4 concentration (P), because the observed DIN and PO_4 were highly correlated in wide range of their concentrations and the slope of the regression line (DIN/ PO_4) was 18.9, approximately consistent with the Redfield ratio (Redfield et al., 1963). The details are described in section 3.1. The time derivative of P is

$$\frac{\partial P}{\partial t} = -R_{CP} \cdot (PS - RS) , \quad (8)$$

where R_{cp} is the Chl-*a*/ PO_4 ratio. Respiration rate was assumed to be proportional to phytoplankton concentration.

$$RS = k_{RS} \cdot Chl . \quad (9)$$

The self-shading effect was incorporated through k of equation (4), following Shigesada and Okubo (1981), as

$$k = \alpha_1 + \alpha_2 Chl , \quad (10)$$

where α_1 is the light extinction rate of sea water and α_2 is the self-shading coefficient.

3. Results

3.1. Observational results

Sectional distributions of temperature, salinity and Chl-*a* measured along the C line by calibrated AAQ are illustrated in Fig. 3. Temperature was completely homogeneous vertically, to the bottom or 100 m depth, and had quite weak horizontal gradients at 10.0–11.0°C.

Salinity was homogeneous both vertically and horizontally at 33.90–33.95. The exception for both temperature and salinity was at C1–C3, which was slightly cooler and less saline. In contrast, the distribution of Chl-*a* was mostly homogeneous vertically, but varied horizontally. A strong gradient in Chl-*a* was formed between C11 and C12. In the inshore region of this boundary, high Chl-*a* concentrations ($> 3.0 \text{ mg m}^{-3}$) were observed, especially around C4 where the concentration exceeded 6.0 mg m^{-3} . The Chl-*a* concentration offshore of the boundary gradually decreased with increasing bottom depth, by 1.0 mg m^{-3} . The observed distributions of Chl-*a* were consistent with those observed by satellite (Fig. 1B).

The DIN, PO_4 and SiO_2 were similarly distributed along the C line (Fig. 4). Between C7 and C10, a strong horizontal gradient was formed and nutrient concentrations were low in the inshore region of the boundary, and high in the offshore region. Between C4 and C7, local minimas were observed, with values of less than 2.0, 0.25 and $6.0 \mu\text{mol L}^{-1}$ for DIN, PO_4 and SiO_2 , respectively. In contrast, at C1, which is in the vicinity of the mouth of the Abukuma River, concentrations of DIN and PO_4 were at their minimum, while local maxima was observed in SiO_2 . These differences are thought to be induced by fresh water inputs, because low salinity water was observed there (Fig.3A).

The relationships among Chl-*a*, nutrients, temperature and salinity on the C line (except for C1 where fresh water influence was found) are shown in Fig. 5. There is a significant positive correlation between DIN and PO_4 ($r = 0.97$, $p < 0.001$, $df = 27$) with a slope of $18.9 \mu\text{mol}/\mu\text{mol}$ and the slope, that is to say, the ratio of DIN/ PO_4 is approximately consistent with the Redfield ratio, which is typically 16 (Redfield et al., 1963). SiO_2 also has significant

positive relationships with DIN and PO₄ ($r > 0.99$, $p < 0.001$, $df = 27$). There were significant negative relationships between Chl-*a* and the nutrients DIN, PO₄ and SiO₂ ($r < -0.93$, $p < 0.001$, $df = 27$). The slopes of these linear regression lines were -1.3 , -26.1 and -0.9 $\mu\text{g}/\mu\text{mol}$, respectively. There was a significant negative correlation between temperature and Chl-*a* ($r = -0.86$, $p < 0.001$, $df = 27$). Salinity, which showed a homogeneous distribution, had no significant relationship with Chl-*a*.

Community structure of phytoplankton in the surface water at C5 was as follows. The Fragilariaceae (*Asterionellopsis glacialis*) was dominant at this site, comprising 57 % of total cells. The Chaetocerotaceae (*Chaetoceros debilis* and *Chaetoceros compressus*) and Thalassiosiraceae (*Thalassiosira gravida*) were sub-dominant families, comprising 27 and 12 % of total cells, respectively. More than 99 % of the detected total cells were diatoms. The species present and the composition ratio of identified phytoplankton observed at the surface at C5 were similar to those at 30 m depth at C5 and at the surface and 30 m depth at C12, indicating that diatoms drove the observed Chl-*a* and nutrients distributions.

Light intensity is known as one of limiting factors for photosynthesis. The vertical distributions of the ratio of light intensity measured by AAQ to the sea surface value are shown in Fig. 6. Here, only stations where the sea surface light intensity was greater than 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ are depicted. In some stations, the profiles near the sea surface were complex, while in all stations the ratios decreased exponentially (linearly in logarithmic axis) with depth in the layer lower than the middle depth of each station. The boundary where slopes of light dissipation in the lower layer differ between inshore and offshore regions is around

C11–C14. We estimated k in the lower layer using equation (4). There were significant differences ($p < 0.01$, $df = 7$) in k , which was 0.122 and 0.077 m^{-1} in the inshore and offshore regions, respectively. The high k is suggested to be induced by high Chl-*a* concentrations, because a significant positive relationship ($r = 0.90$, $p < 0.001$, $df = 7$) was found between vertically averaged Chl-*a* and k in the lower layer (Fig. 7). In the inshore region, although k is high, the light intensity at the deepest depth is higher than in the offshore region; that is to say, more light is available in the whole water column.

Since water properties such as temperature and salinity were vertically homogeneous throughout the water column (Figs. 3, 4), continuous vertical mixing is considered to have occurred, owing to convection induced by heat loss at the sea surface. Vertical mixing means that the phytoplankton was also stirred vertically and could not stay at a certain depth. As a result, the light intensity that the phytoplankton received changed constantly with their changing depth. The abundance of phytoplankton in the inshore region could increase, even near the bottom, because sufficient light for photosynthesis was available throughout the water column. In contrast, photosynthesis in the offshore region was restricted since the light availability was low during the phytoplankton was advected to the deeper layer by vertical mixing.

The bottom depth affected the observed Chl-*a* concentration, when the plotted values of Chl-*a* were vertically averaged, owing to only minor variations from near-homogeneity in the observed profile (Fig. 8). The relationship between bottom depth (D) and observed Chl-*a* (Chl_{obs}) can be approximated as a power function:

$$Chl_{obs} = 188.35D^{-1.006} \quad (r = 0.99, p < 0.001, df = 18), \quad (11)$$

thus, as the bottom depth shallows, Chl-*a* concentration drastically increases.

To clarify the mechanisms for the formation of high Chl-*a* zones in the inshore region and the effect of bottom depth on the diatom bloom in the convective season, we created a one-dimensional ecosystem model representing the Chl-*a* profile.

3.2. Results of the model

The notation of parameters and their values for the ecosystem model are given in Table 1. Values of several parameters were determined according to the observed results in this study. We adopted 26.1 g/mol for R_{cp} following the observed relationship between PO_4 and Chl-*a* (Fig. 5E). We used 0.0565 m^{-1} and $0.0136 \text{ mg}^{-1} \text{ m}^2$ for α_1 and α_2 , respectively, following the observed relationship between Chl-*a* and k (Fig. 7). Values of other parameters were determined based on Kawamiya et al. (1995). As Chl-*a* and PO_4 and other properties were distributed homogeneous vertically, the vertical distribution of Chl and P was assumed to be homogeneous throughout the water column owing to strong vertical mixing. As the observation period is winter, heat loss at the sea surface makes the surface water denser than the lower water. A strong vertical mixing can be induced to neutralize the density reverse and the mixing reaches the bottom in the condition of vertically homogeneous from the sea surface to the bottom as recognized in Fig. 3. To introduce the effect of strong vertical mixing, vertical distributions of Chl and P were calculated with equations (1) or (8), and then homogenized vertically at each time step. Here, the vertically homogenized Chl was

calculated by

$$Chl_{hmg} = \frac{1}{D} \int_0^D Chl(z) dz . \quad (12)$$

Multiple cases for 60 days were run with different initial conditions and parameter values. Initially, *Chl* (Chl_0) and *P* were given as vertically homogeneous, and various values (from 0.1 to 4.0 by 0.1 mg m⁻³ for Chl_0) were adopted following the observed relationship between them (Fig. 5E). Although light limitation strongly affects photosynthesis, the related parameters are difficult to determine because I_{max} can vary with cloudiness and I_{opt} can change with phytoplankton species. As F_I is expressed as a function of I_{max}/I_{opt} , we used various values of I_{max}/I_{opt} (from 0.1 to 2.0 by 0.1) for the case studies. Here, we assumed that I_{max} represents averaged light intensity since we focused on relatively a short period (within 2 months) and I_{opt} was constant because most of the detected cells were diatoms. To understand the influence of bottom depth on the occurrence of a phytoplankton bloom, multiple cases with different bottom depths (from 10 to 160 by 5 m) were performed.

We assessed the model reproducibility using the RMS error (RMSE) of horizontal distribution between the observed Chl-*a* and calculated *Chl* at corresponding bottom depths on each days of calculation. Figure 9 shows the combination of Chl_0 and I_{max}/I_{opt} on each day of calculation, under which calculated *Chl* agreed well with the observed Chl-*a* (RMSE ≤ 0.3 mg m⁻³). The high agreement could only be achieved with a few combinations of Chl_0 and I_{max}/I_{opt} , and the integration time to obtain the high agreement depended on the combinations of Chl_0 and I_{max}/I_{opt} . When the initial Chl_0 was relatively low (1.0–1.7 mg m⁻³), high I_{max}/I_{opt} (1.1–1.4) was essential and it took 20 days integration to achieve good agreement with the

observations. With values of Chl_0 increased, decreased I_{max}/I_{opt} and longer integration time were needed to reproduce reasonable horizontal Chl distribution. When the initial Chl_0 was relatively high ($> 3.8 \text{ mg m}^{-3}$), low I_{max}/I_{opt} (0.6-0.7) was essential and it took 50 days of integration to achieve high agreement with the observed $Chl-a$.

The time evolution of vertically averaged Chl concentration is illustrated as Fig. 10. Here, the figure shows the case where Chl_0 is 1.6 mg m^{-3} and I_{max}/I_{opt} is 0.95, under which the calculated Chl had the highest agreement with the observed $Chl-a$ on the 25th day of calculation (RMSE = 0.25 mg m^{-3}). Consistent with the observed results, the relationship between the bottom depth (D) and Chl concentration could be approximated as a power function:

$$Chl = aD^b \quad (13)$$

where a and b are constants which depend on Chl_0 , I_{max}/I_{opt} and the days of calculation. Under initial conditions (days of calculation = 0), Chl concentration is horizontally homogenous. As the calculation advances, Chl increased and decreased in shallower and deeper regions, respectively. The boundary of bottom depth was 110 m. Since Chl concentration was temporally stable at the boundary, the depth of the boundary is critical relevant to the occurrence of phytoplankton blooms. Hereafter we call the depth of the boundary as the critical bottom depth. The critical bottom depth is defined as the depth of the intersection of lines drawn by the equation (13) on various days of calculation under a certain combination of Chl_0 and I_{max}/I_{opt} (Fig. 10). In other words, PS equals RS in the equation (1), that is, the vertically integrated growth and decrease of phytoplankton balance out there. The critical

bottom depth depends on Chl_0 and I_{max}/I_{opt} . The critical bottom depth becomes deep (shallow) under the conditions of relatively low (high) Chl_0 and high (low) I_{max}/I_{opt} (Fig. 9).

The bottom light intensity at the critical bottom depth was 0.02 % of its surface value in the case with the highest agreement with the observed Chl-*a*. The bottom light intensity in the region shallower than the critical bottom depth was higher than that in the deeper region although *Chl* concentration and *k* in the shallower region was higher than the deeper region. This result gave good agreement with the observed horizontal distribution of Chl-*a* and *k* (Fig. 6, 7). In the region shallower than the critical bottom depth, *Chl* drastically increased until the 25th day of calculation (Fig. 10). In contrast, after the 25th day, *Chl* remains almost temporally stagnant. The model results revealed that the stagnation of phytoplankton growth was induced by nutrient limitation.

For the cases initial Chl_0 was relatively low (1.0–1.7 mg m⁻³), the critical bottom depths were relatively deep (120–160 m) as shown in Fig. 9. In these cases, high I_{max}/I_{opt} was needed to achieve reasonable reproducibility. This means that there was a large area where enough light is available for photosynthesis even near the bottom. The bottom light intensities at the critical bottom depth were < 0.01 % of its surface value, suggesting phytoplankton bloom could occur by either strong surface light (high I_{max}) or efficient light utilization (low I_{opt}) which makes high I_{max}/I_{opt} value. In these cases, the high agreement with the observed Chl-*a* distribution was achieved by power functional increases in *Chl* in the region shallower than the critical bottom depth. In this region efficient photosynthesis occurred, owing to plenty of light (high I_{max}/I_{opt}). For the cases initial Chl_0 was relatively high (>3.8 mg m⁻³), the critical

bottom depths were relatively shallow (50–60 m). The bottom light intensities at the critical bottom depth were $> 0.4 \%$ of its surface value, suggesting that either surface light is not enough (low I_{max}) or inefficient light utilization (high I_{opt}). In these cases, since the initial Chl_0 is high, the high agreement was achieved by the reduction of Chl in the region deeper than the critical bottom depth, where phytoplankton was stirred vertically between the euphotic and aphotic layers because of low I_{max}/I_{opt} , and thus RS exceeds PS in the equation (1), that is, the decrease of phytoplankton overcomes its growth. It takes many days to reduce the Chl concentration from initial value to observed one in this region.

4. Discussion

We observed a vertically homogeneous $Chl-a$ distribution, with a strong horizontal gradient, in the convective season in Sendai Bay. The negative correlation between $Chl-a$ and nutrients, and the ratio of DIN/PO_4 corresponding closely to the Redfield's N:P ratio (Redfield et al., 1963), suggest that the patterns observed were dependent on photosynthesis by phytoplankton. A simple ecosystem model of photosynthesis and respiration indicate that light intensity and vertical mixing reasonably represent the observed relationship between the bottom depth and $Chl-a$ concentration; $Chl-a$ drastically increased with decreasing depth and was approximated as a power function of bottom depth (Fig. 10). Power functional distribution of $Chl-a$ forms a strong horizontal gradient around C12 (70 m depth), because the slant of the bottom depth became steeper (Fig. 2), that is the $Chl-a$ abruptly decreased with increasing bottom depth around the station and the $Chl-a$ drastically increased in the region shallower than the station.

If the horizontal gradient of *Chl-a* and nutrients was formed by the conservative horizontal mixing of the two end members, where one has high *Chl-a* and low nutrients derived by photosynthesis (left-upper in Fig. 5DEF) and another has low *Chl-a* and high nutrients derived by respiration or decomposition (right-lower in the same figures), the relationship between the bottom depth and *Chl-a* concentration would become closer to linear, not a power function.

In the open ocean, classically, when the depth of the mixed layer becomes shallower than the critical depth, conditions allow for the onset of phytoplankton growth (Parsons et al, 1984b). However, our study revealed that bottom depth was responsible for the occurrence of the bloom in the convective season in coastal area where vertical mixing reached the bottom and there existed the critical bottom depth where vertically integrated *Chl* concentration remained constant. A bloom could occur where the bottom depth is shallower than the critical bottom depth, not just when the depth of the mixed layer is shallower than the classical critical depth. Our model result which had the highest agreement with the observed *Chl-a* revealed the bottom light intensity was 0.02 % of its sea surface value at the critical bottom depth and increased with decreasing bottom. In the region shallower than the critical bottom depth, phytoplankton was stirred vertically mainly in the euphotic layer receiving sufficient light for continuous photosynthesis, which resulted that the vertically integrated growth overcame phytoplankton decrease, because of the shallow depth, despite light extinction being large owing to the self-shading effect from the high *Chl-a* concentration. In the region deeper than the critical bottom depth, although *Chl-a* concentration and light extinction were low, the

temporally averaged light intensity which phytoplankton received was lower than that in the region shallower than the critical bottom depth, because phytoplankton was stirred vertically not only the euphotic layer but also aphotic layer, which resulted that the vertically integrated phytoplankton decrease overcame the growth, as found by Findlay et al. (2006). As a result, high *Chl-a* zones were formed along the coast.

As mentioned in the introduction, the light availability affects phytoplankton production through the change of the depth of the euphotic layer (Cloern, 1999) and regulates the onset of phytoplankton bloom both spatially and temporally (Hitchcock and Smayda, 1977; Pennock, 1985). The limitation of light is frequently reported in highly turbid estuary where the depth of the euphotic layer is relatively shallow (Irigoien and Castel, 1997; Cloern, 1999). In coastal ecosystems which are regulated by light limitation, we propose a new theory for the onset of phytoplankton bloom based on our results. The bloom occurs when a strong vertical mixing dominates, neither when the mixed layer depth becomes shallower than the critical depth (Sverdrup, 1953; Riley 1957; Parsons et al., 1984b) nor when turbulent mixing is reduced (Taylor and Ferrari, 2011). The theory is applicable for the region where the winter mixed layer reaches the bottom, that is, the transparency is relatively high, and the depth of the euphotic layer is approximately same as the bottom depth. In the region satisfied these conditions, there exists the critical bottom depth, a bloom can occur where the bottom depth is shallower than the critical bottom depth and power functional distribution of *Chl-a* with bottom depth is formed. The trigger of the bloom is discussed below.

The initial *Chl* condition (Chl_0) under which the calculated *Chl* showed the highest

agreement with the observed Chl-*a* was 1.6 mg m^{-3} . This concentration was similar to the lowest value observed, which was found in the oceanic region in Sendai Bay (Figs. 1 and 4). Kudo (1971) reported that oceanic water frequently intruded into Sendai Bay and induced intermittent water exchange. Considering this intrusion of oceanic water and our observed results and model, the water in the bay became vertically and horizontally homogeneous, with low Chl-*a* concentration and high nutrient concentrations owing to the intrusion of oceanic water. The supply of nutrients to the region shallower than the critical bottom depth promoted photosynthesis. As the bottom depth shallowed, more photosynthesis was promoted, and thus the horizontal gradient of Chl-*a* and nutrients were formed. Under our theory, relationships among Chl-*a* and nutrients proportional to the Redfield ratio were produced from the homogeneous initial conditions of Chl-*a* and nutrients by spatial difference of photosynthesis rate. That is, the slopes among Chl-*a* and nutrients (Fig. 5) are equivalent to the so-called ratios among $\Delta\text{Chl-}a$ and $\Delta\text{nutrients}$ (Δ indicates temporal change in concentration). From the model results, we presume that the observed distribution was formed 25 days after the intrusion of oceanic water. Of course, as the observed relationship between the bottom depth and Chl-*a* concentration could be reproduced by various combination of Chl_0 and $I_{\max}/I_{\text{opt}}$ and durations, the properties of the intruding oceanic water might differ from those mentioned above. However, according to our observations and model results, it is unlikely that the formation of the high Chl-*a* zone was induced by the intrusion of oceanic water with high Chl-*a* and low nutrients, as the zone appeared a relatively long time after the intrusion (> 40 days). Such water masses were not observed in the offshore region, and it is thought that the

formation of the zone occurred within approximately a month. The fact that the oceanic water intruded within a month is demonstrated as follows.

At the beginning of December 2011, we carried out hydrographic observations similar to this study on the R/V *Wakataka-Maru* of the Tohoku National Fisheries Research Institute. Temperature, salinity and Chl-*a* distributions acquired with AAQ are shown in Fig. 11, using the same calibration method as this study. Temperature was vertically homogeneous, with a horizontal gradient similar to this study; however, it was more than 3°C warmer. Salinity was 33.0–34.0, except for in the upper layer of C1–C3. The salinity obtained by *Wakataka-Maru* was lower in value and stronger in its horizontal gradient than that obtained at the beginning of January 2012. Chlorophyll-*a* distribution obtained by *Wakataka-Maru* was also different from that obtained by *Dainana-Kaiyo-Maru*; Chl-*a* concentration was high between C7–C14 at 2.0–2.8 mg m⁻³, which corresponded to a salinity of 33.6–33.8, and low in the region shallower than C7 at 1.0–2.0 mg m⁻³ in December 2011. Nutrients obtained in December 2011 were distributed vertically homogeneous (stratified) in the region shallower (deeper) than 60 m depth. Nutrients obtained in January 2012 were higher than that obtained in December 2011 except for near the bottom of C19. The results that the structure and concentration of water properties were different between two cruises suggest the probability of oceanic water intrusion with nutrients supply after *Wakataka-Maru* cruise. Stimulated by the nutrient supply, the phytoplankton bloom occurred between two cruises, thus within a month, which strongly supports our inference based on the model results.

We used a one-dimensional model to represent the observed horizontal distribution of Chl-*a*.

While a two-dimensional model might be more accurate, this model reasonably reproduced the horizontal gradient of Chl-*a*. We neglected horizontal mixing and calculated the vertical distribution of Chl-*a* at various bottom depths using a one-dimensional model. The strong horizontal gradient in Chl-*a* distribution observed supports the theory that horizontal mixing was weak. These conditions of weak horizontal mixing, could lead to the observed negative relationship between temperature and Chl-*a* (Fig. 5G). The more the bottom depth shallowed and the Chl-*a* concentration increased, the more the seawater was cooled. Although temperature had become homogeneous both horizontally and vertically by the intrusion of oceanic water, as temperature was cooled under the low horizontal mixing condition, temperature in the shallower region decreased more than in the deeper region and the horizontal temperature gradient (Fig.3A) could be formed.

We estimated F_N from only PO_4 because the observed DIN and PO_4 were highly correlated in wide range of their concentrations, including low concentrations. The fact that the slope of the regression line was 18.9 (Fig. 5A), slightly higher than the Redfield ratio (Redfield et al., 1963), supports the PO_4 base model is valid (Koerselman and Meuleman, 1996). However, the offset of the regression line was negative (Fig 5A). We presumed the negative offset was derived from the nutrients consumption owing to the photosynthesis according to the relatively higher DIN/ PO_4 ratio than Redfield ratio. To make assurance the influence of DIN, we constructed the DIN base model using the relationship between DIN and Chl-*a* (Fig.5 D) and confirmed that the results did not differ than the PO_4 base model except in the relatively long period of days of calculation (> 40 days) when nutrient were exhausted. This implies that

the nutrient limitation did not affect the onset the bloom in this study.

Since the relationship between DIN and PO_4 was approximately consistent with the Redfield ratio (Redfield et al., 1963), and both nutrients were negatively correlated with Chl-*a*, the high Chl-*a* concentration is likely because of the phytoplankton bloom. As the Redfield ratio for C:N (C:P), is 106:16 (106:1) mol/mol, we can estimate the C/Chl-*a* ratio from the observed Chl-*a*/DIN (Chl-*a*/ PO_4) ratio, which was 1.3 (26.1) g/mol. Using this value, we estimate the C/Chl-*a* ratio as 52.7 (48.7) g/g. Similar values are reported in the North Pacific and in a coastal region of Japan (Behrenfeld et al., 2005; Yamaguchi and Imai, 1996), confirming our assumption that the increase in Chl-*a* concentration accompanied with nutrient decrease was caused by photosynthesis by phytoplankton. As SiO_2 was also negatively correlated to Chl-*a*, and diatoms such as Fragilariaceae and Chaetocerotaceae were identified from the samples fixed with Lugol's solution, the bloom was likely induced by diatoms. Brzezinski (1985) proposed that the Redfield ratio for diatoms was Si:N:P=14:16:1. As the observed ratios of SiO_2 /DIN and SiO_2 / PO_4 were 1.4 and 27.7 $\mu\text{mol}/\mu\text{mol}$, respectively, much more Si was used for photosynthesis than N and P, relative to the Redfield ratio. However, the Si/N ratio reported was greater than the typical ratio under conditions of depleted iron, insufficient light and nutrient limitation (Takeda, 1998; Saito and Tsuda, 2003). As the high linear correlation between Si and N (P) was found at a wide range of nutrients concentration, it is considered that the relatively high Si/N (Si/P) ratio was not induced by nutrient limitation. Since light intensity near the bottom was low (less than 1 % of the sea surface value; Fig. 6), even in the region shallower than the critical bottom depth, light limitation might induce the relatively

high Si/N (Si/P) ratio.

We conducted case studies using various values of I_{max}/I_{opt} (0.1–2.0 by 0.1) because it was difficult to determine the value of I_{max} and I_{opt} . The observed light intensity at the sea surface around noon was 75–167 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and climatological solar radiation was reported at 340 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at winter (Watanabe and Kobayashi, 1985). I_{opt} adopted by general ecosystem models are 210–420 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Kawamiya et al., 1995; Kishi et al., 2007). From these values, I_{max}/I_{opt} is calculated at 0.1–1.6 and our setting (0.1–2.0) is valid. Using the observed I_{max} (75–167 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and the value of I_{max}/I_{opt} under which the calculated *Chl* had the highest agreement with the observed *Chl-a* of 0.95, I_{opt} is estimated as 79–175 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Shikata et al. (2010) reported that the growth of diatom (Fragilariaceae, Chaetocerotaceae and Thalassiosiraceae) saturated at a light intensity of 80–150 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The similarity of the reported value to our estimated I_{opt} suggests that the diatom bloom occurred as mentioned above.

Previous studies report that a reduction in the grazing pressure on phytoplankton is responsible for the onset of the bloom (Yoshie et al., 2003; Behrenfeld, 2010). Models incorporating mortality and grazing are commonly used for understanding phytoplankton dynamics (Kawamiya et al., 1995; Kishi et al. 2007). However, we were able to model the observed *Chl-a* distribution without incorporating these parameters, because we focused on a relatively short period in which phytoplankton rapidly grew. Mortality and grazing may be responsible for the process of phytoplankton decline after the bloom, and thus reducing *Chl-a* concentration. However, in Sendai Bay frequent water exchange can flush out the water in the

bay and may be responsible for the declination in Chl-*a* concentration. When calculated under the conditions of relatively high Chl_0 and low I_{max}/I_{opt} , our model results had high agreement between the calculated Chl and observed Chl-*a* for a relatively long period (>40 days; Fig. 9). The high agreement was associated with Chl-*a* reduction by RS in the equation (1). Incorporating mortality and grazing, which induce Chl-*a* reduction similar to RS , could achieve high agreement between the calculated Chl and observed Chl-*a* in a short period (approximately 30 days). However, as high Chl-*a* was not found in the offshore region of Sendai Bay, it is unlikely that oceanic water with a high Chl-*a* concentration intruded.

Nutrient supply from oceanic water intrusion is responsible for the successful seaweed farming in the area. Further, the formation of a high Chl-*a* zone after the intrusion is important for oyster farming. The environment suitable for both seaweed and oyster farming in this area could be formed by the frequent intrusion of oceanic water inducing phytoplankton blooms, which would support high fishery production in Sendai Bay. Further studies are needed to understand the frequency of the intrusion and the underlying mechanisms.

5. Conclusions

A combination of field data with a simple one-dimensional ecosystem model was used to elucidate the mechanisms responsible for winter plankton blooms in Sendai Bay in the coast of Japan. A vertically homogeneous Chl-*a* distribution with a strong horizontal gradient was observed and the distribution could be approximated as a power function of bottom depth. Chl-*a* increased with decreasing the bottom depth and vice versa, and there existed the critical

bottom depth where Chl-*a* was temporally stable. The bottom light intensity was 0.02 % of its surface value at the critical bottom depth and increased with decreasing bottom depth, despite Chl-*a* and *k* also increased. This indicates that light penetrates to the bottom and photosynthesis is possible even near the bottom in the region shallower than the critical bottom depth. Stirred vertically mainly in the euphotic layer, phytoplankton distributed in the region shallower than the critical bottom depth could increase its biomass. On the contrary, in the region deeper than the critical bottom depth, since phytoplankton was stirred vertically between the euphotic and aphotic layers, its biomass decreased.

The observed winter bloom was formed by increase of diatom such as Fragilariaceae and Chaetocerotaceae. Our model results suggested that the bloom was possibly to be induced by the intrusion of oceanic water with low Chl-*a* and high nutrient concentrations, that photosynthesis was promoted by the nutrient supply especially in the region shallower than the critical depth, and that the high Chl-*a* zone was formed within a month. Indeed, in the hydrographic observations conducted a month before the bloom, high Chl-*a* distribution was not observed and salinity distribution was different from that after the bloom, supporting our inference derived from model results.

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Table 1. Notations used in the model and parameter values.

G_{max}	maximum photosynthetic rate at 0°C	1.00	day ⁻¹
k_t	temperature coefficient for photosynthetic rate	0.063	°C ⁻¹
k_p	half saturation coefficient for PO ₄	0.18	μmol L ⁻¹
R_{cp}	Chl-a/PO ₄ ratio	26.1	g/mol
k_{RS}	respiration rate	0.05	day ⁻¹
α_1	light extinction rate of sea water	0.0565	m ⁻¹
α_2	self-shading coefficient	0.0136	mg ⁻¹ m ²
I_{opt}	optimum light intensity	not constant	μmol m ⁻² s ⁻¹
I_{max}	light intensity at the sea surface at noon	not constant	μmol m ⁻² s ⁻¹
I_{opt}/I_{max}		0.1 – 2.0	
H	bottom depth	20 – 160	m
Chl_0	initial condition of Chl	0.1 – 4.0	mg m ⁻³
dz	vertical resolution	1.0	m
dt	time step	600	s

Figure Legends

- Fig. 1. Chl-*a* concentration around Sendai Bay derived from MODIS Aqua, acquired on (A) 3 January 2011 and (B) 3 January 2012.
- Fig. 2. Locations of observation stations and bathymetry in Sendai Bay.
- Fig. 3. Cross-sectional distributions of (A) temperature, (B) salinity and (C) Chl-*a*, observed by aqua quality sensor (AAQ) along the C line (Fig. 2) at the beginning of January 2012.
- Fig. 4. Cross-sectional distributions of (A) DIN, (B) PO₄ and (C) SiO₂ along the C line (Fig. 2) at the beginning of January 2012.
- Fig. 5. Relationships among Chl-*a*, nutrients, temperature and salinity on the C line (Fig. 2), except for C1. (A) PO₄ vs. DIN, (B) PO₄ vs. SiO₂, (C) DIN vs. SiO₂, (D) DIN vs. Chl-*a*, (E) PO₄ vs. Chl-*a*, (F) SiO₂ vs. Chl-*a*, (G) Chl-*a* vs. temperature and (H) Chl-*a* vs. salinity. Solid line indicates linear regression line.
- Fig. 6. Vertical distributions of the ratio of light intensity to the sea surface value, observed by aqua quality sensor (AAQ).
- Fig. 7. Relationship between vertically averaged Chl-*a* and the light extinction coefficient (*k*) in the lower layer. Solid line indicates linear regression line.
- Fig. 8. Relationship between bottom depth and vertically averaged Chl-*a*. Solid line indicates regression curve.
- Fig. 9. Shaded area indicates combinations of Chl_0 and I_{max}/I_{opt} under which calculated Chl showed good agreement with the observed Chl-*a* ($RMSE \leq 0.3 \text{ mg m}^{-3}$). Numerals

indicate the days of calculation. Contours indicate the critical bottom depth under combinations of Chl_0 and I_{max}/I_{opt} .

Fig. 10. Time evolution of Chl for each bottom depth (solid lines). The highest agreement with the observed $Chl-a$ (RMSE = 0.25 mg m⁻³) was achieved on the 25th day of calculation, when Chl_0 was 1.6 mg m⁻³ and I_{max}/I_{opt} was 0.95. Circles indicate the observed relationship between bottom depth and $Chl-a$.

Fig. 11. Cross-sectional distributions of (A) temperature, (B) salinity and (C) $Chl-a$ measured by aqua quality sensor (AAQ) along the C line (Fig. 2), at the beginning of December 2011.

Fig. 12. Cross-sectional distributions of (A) DIN, (B) PO₄ and (C) SiO₂ along the C line (Fig. 2) at the beginning of December 2011.

Fig. 1

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