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INITIAL DYNAMIC PROCESSES AND STRUCTURE OF DEEP CHLOROPHYLL-A MAXIMA

By

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SYNOPSIS

Deep chlorophyll-a maxima (DCM) around the thermocline is sometimes observed in lakes or seas. However, the various factors, such as physical, chemical, and biological processes, that affect their formation and maintenance are not well known. In this paper, the initial dynamics and structure of DCM processes with and without a thermocline were investigated by experimental studies. These experiments were conducted under controlled physical conditions. Water samples for experiments were collected from the surface of a field pond, and zooplankton were removed by a filtering apparatus. Vertical distributions of water temperature and chlorophyll-a were measured during experiments. DCM were observed to be formed only at the thermocline. By making a comparison with previous studies, we concluded that a reduction of the settling rate of phytoplankton around the thermocline was an important mechanism for the formation of DCM.

INTRODUCTION

Many studies have been conducted on the occurrence and the formation of deep chlorophyll-a maxima (DCM) (1), (7), (8), (9), and many studies have also been conducted on phenomenon such as red tides and water blooms of blue-green

algae (2), (3), (4). Large numbers of phytoplankton cells are produced by eutrophication of stagnant water bodies such as lakes, marshes, reservoirs, and enclosed bays, and this has posed several water quality issues that have developed into social problems. Mature phytoplankton show a marked trend toward a local existence in space (1). As an example of localization of phytoplankton, researchers have long been known that deep chlorophyll-a maxima (DCM) are found not in the water surface layer receiving much light but around the thermocline of the lower photic-zone layers (5), (6).

Previous studies have revealed several possible mechanisms of the occurrence of DCM, such as adaptation to the low light environment of phytoplankton, their preference of deep-water environments where both inorganic nutrients and light are present, and the flotation and settling of cells (1), (7), (8), (10). Coon et al. (7) reported that many DCM studies conducted in the past did not clearly distinguish the initial DCM formation process from the processes that maintain them. One characteristic of DCM is that stable DCM are formed over a period of several months. On the other hand, the process involved in the formation has not been extensively studied because of difficulties encountered in 1) creating a thermocline, which is deemed to be a necessary condition for the formation of true DCM in the laboratory, and 2) studying the initial formation process at the appropriate time at a measurement site. Pick et al. (11) reported that the formation of a chlorophyll-a peak around the thermocline was due to cyst germination, but it appears that such a general explanation is insufficient. The purpose of this study was to determine experimentally the processes involved in the formation of DCM. In this study, experiments were performed using equipment that can vary water density (by changing water temperature); this system allowed us to examine only the vertical distribution of water temperatures.

MATERIALS AND METHODS

Experimental Setup

The aim of the experiment was to investigate the accumulation of phytoplankton around the thermocline by using the apparatus shown in Fig. 1. This experimental apparatus included two different-sized cylindrical water tanks. The smaller water tank (hereafter called the "proliferation water tank") was 90 cm in diameter and height and was used to measure various parameters, such as water temperature and chlorophyll-a and PO_4-P concentrations, which are indicators of phytoplankton growth. The larger water tank (hereafter referred to as an "external water tank") was 106 cm in diameter and 126 cm in height and was used to control the water temperature of the proliferation water tank. A thermocline can be formed at any depth by cooling the water using water from the external water tank.

Water Sample

Approximately 1,000 L of water was collected from the surface of a regulated pond at Tokyo Denki University. Due to the presence of zooplankton in the sample, the water sample was filtered by using an external filtering apparatus for 36 h prior to the start of the experiments. The mesh size of the external filtering apparatus was about 50 μm. In addition, some species of phytoplankton, such as the green algae "*Scenedesmus,*" (existence rate in water sample based on cell number: 75%), diatom "*Fragilaria,*" (4%), and green algae "*Coelastrum*" (2%) were observed in the water sample using a microscope. Two days before starting experiment, nitrogen (in the form of potassium nitrate: 10.1 mg^{-N}/L) and phosphorus (in the form of sodium phosphate: 2.45 mg^{-P}/L) were added to the water sample in accordance with the Redfield ratio.

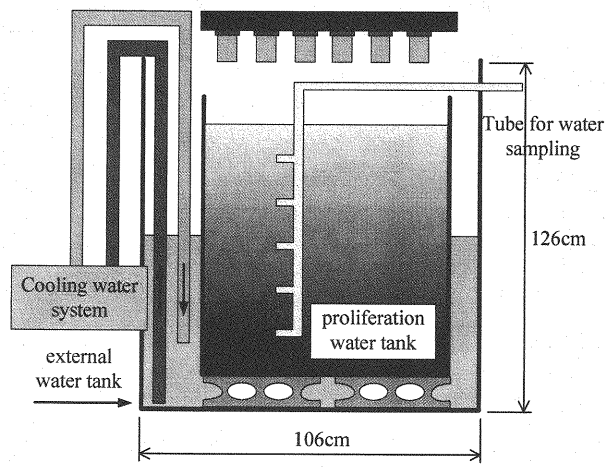

Fig. 1 Schematic of experimental apparatus

Experimental Conditions

Two experimental conditions were examined. The difference in the experiments was only the sampling day (case 1: 2008/6/14, case 2: 2008/6/21). The light intensity and irradiation time for phytoplankton growth was controlled by using white fluorescent lamps. The illumination intensity was set at 7000 lux because it was the best intensity for the growth of *Scenedesmus* spp. (12). To recreate daylight and night hours, a fluorescent lamp was turned on for 13 h from 6 am to 19 pm and turned off for 11 hours from 19 pm to 6 am.

Measurements

PO_4-P, chlorophyll-a (Chl-a), and water temperature were measured. The distribution of water temperatures was measured by using a thermistor at 1 cm intervals from the surface of the water to the bottom. The PO_4-P and Chl-a distributions in the proliferation water tank were measured everyday at 11 am using a sampling tube to collect the water sample. Measurements were conducted around the thermocline at 5 cm intervals in depth, and the other parts of the tank were measured at 10 cm intervals in depth.

EXPERIMENTAL RESULTS

Figs. 2 and 3 show the experimental results for the cases with and without a thermocline, respectively. The results show the variations in the vertical distribution of water temperature and chlorophyll-a.

Formation of Thermocline

The results for the cases with a thermocline (left-hand of Figs. 2 and 3) indicate that at the start of the experiment, there was almost no vertical variation in water temperature. One day after the start of the experiments, the water temperature at 40 cm depth was 15°C. Convection currents gradually decreased the temperature over the next four days. However, light irradiation and heat transfer from the air resulted in the formation of a stable thermocline of about 25°C near

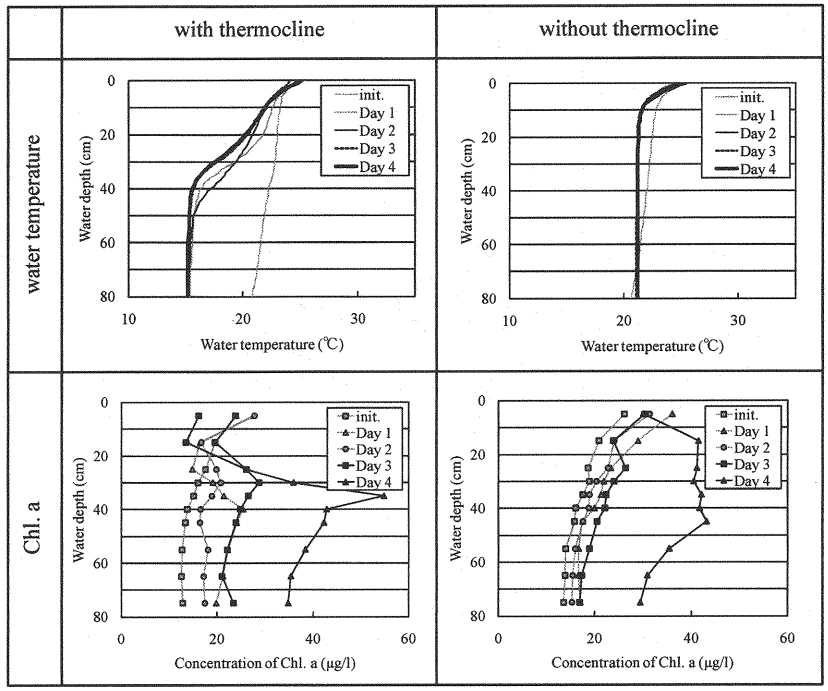

Fig. 2 Experimental results of vertical distribution of water temperature and chlorophyll-a in case 1

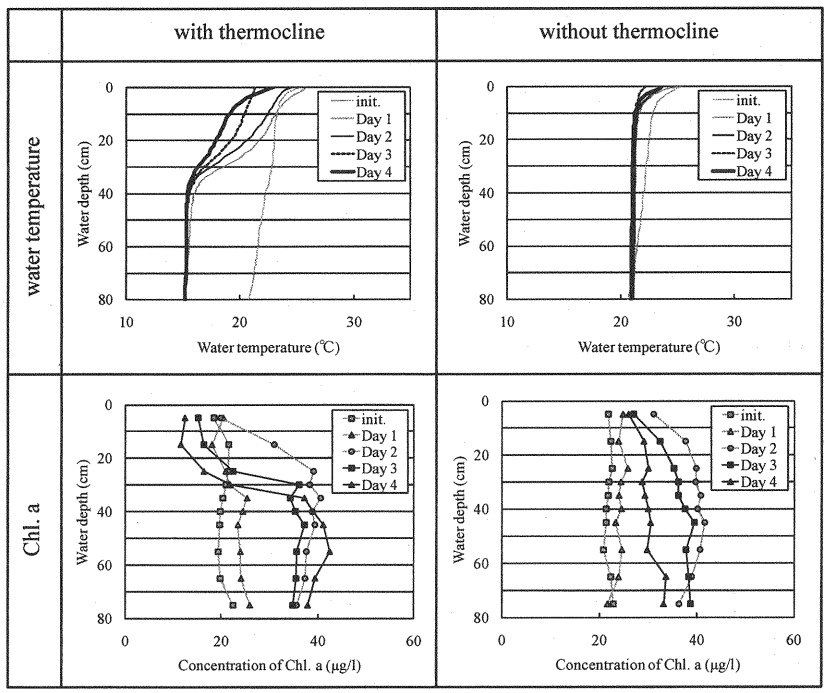

Fig. 3 Experimental results of vertical distribution of water temperature and chlorophyll-a in case 2

the water surface. During the experiments, the water temperature in the transverse direction was also measured at 11 am everyday at 3.5 cm intervals and at 60 cm in depth. The temperature was observed to be constant spatially. This observation confirmed that convection currents had not been generated in the proliferation water tank. In addition, the experiment was performed in a dark room, and there was no mixing of water at the surface due to wind.

On the other hand, experimental cases without the thermocline (right-hand of Figs. 2 and 3) indicate that for the

duration of the experiment, there was no noticeable change in the vertical distribution of water temperatures. However, a thin thermocline layer near the water surface was affected by light irradiation and air heat transfer, resulting in a slight increase in water temperature. Because the thin thermocline layer that formed near the water surface was stable, it was determined that this did not result in convection currents in the experimental water tank. A notable characteristic of the vertical distribution of water temperatures is that the thermocline was formed in two layers (near the water surface and in a deep layer). This differs from formations of a thermocline in lakes and marshes, which form in water circulation layers, thermocline layers, and in deep layers. This is because in the experimental system, there were no external forces, such as wind, that play a role in the creation of the water circulation layer. Because DCM tend to form in the thermocline and at greater depths, our study is aimed at determining the processes associated with the formation of DCM.

Vertical Distribution of Chlorophyll-a

At the start of the experiment, the vertical distribution of chlorophyll-a was constant in both cases (cases 1 and 2 with the thermocline), but the concentrations of chlorophyll-a gradually increased with time. The increase in the deeper layer was more gradual than in the thermocline. In this paper, the deeper layer will be referred to as the DCM. On the other hand, for cases 1 and 2 without a thermocline (right side of Figs. 2 and 3), the patterns were slightly different, and the distribution of chlorophyll-a had no DCM without a thermocline. In addition, the total amounts of chlorophyll-a in case 1 and 2 were almost the same.

Case 1 showed a high concentration of chlorophyll-a near the water surface regardless of the presence or absence of a thermocline during the experiment. A possible reason for this was the presence of the dinoflagellate *Peridinium*, which swim and accumulate at the water surface. On the other hand, case 2 (with a thermocline) showed a lower concentration of chlorophyll-a near the water surface than case 1 (see left side of Fig. 2 and Day 4). This phenomenon might be due to the existence of a smaller number of the *Peridinium* than in Case 1.

During this experiment, the processes involved in the initial formation of DCM occurred in the deeper layers beneath the thermocline. This result implied that the thermocline played a role in DCM formation. In the following section, we will examine the mechanism by which a thermocline contributes to DCM formation along with other factors that may affect the DCM formation process.

DISCUSSION

Main Cause of Initial DCM Formation

(a) Effect of Light Conditions

One of the main causes of initial DCM formation is probably the proliferation of phytoplankton, which prefer a low-light environment (13), (14), at the deeper water level. Field observations showed that in many cases the DCM were formed at the bottom of the euphotic zone (1), (5), (6). Therefore, to calculate the extinction coefficient of light, the location of the euphotic zone was verified in the proliferation water tank using a quantum light meter. The extinction coefficient was calculated by applying the Lambert-Beer law. The light intensity in the water tank is given by

$$I(z) = I_0 \exp(-\varepsilon z) \quad (1)$$

where I = the light intensity; ε = the extinction coefficient; and z = the water depth. The extinction coefficient of light was 2.72 m^{-1}. Therefore, the euphotic zone was estimated to be at a depth of about 1.7 m corresponding with a light intensity of 1%. However, in this experiment, the DCM formed in deep water (about 40 cm deep), and thus the formation of DCM did not depend on the light conditions.

(b) Effect of Nutrients

The nutrient concentration of the water around the thermocline was low in some of the field cases. A low nutrient concentration is a possible factor in the formation of DCM (1), (8). However, the concentration of PO_4-P exceeded 0.05 mg/L at all times during the experiment. This amount of concentration is sufficient for phytoplankton growth. Therefore, the formation of DCM was not caused by a nutrient limitation in our experiments.

(c) Settling Velocity

Fig. 3 shows that the rate of phytoplankton settling was reduced by a decrease in the water temperature from Day 2 to Day 4. The concentration of phytoplankton near the water surface decreased due to their settling, and a high concentration of phytoplankton in the deeper layer also moved downward. In addition, the rate of phytoplankton settling gradually decreased on Days 2, 3, and 4. Based on these results, it appears that the initial formation of DCM in this experiment was due to the effect of the thermocline on the rate of phytoplankton settling.

In addition, the possibility that a change in the turbulent diffusion coefficient in the vertical direction resulted in the formation of the DCM (5), (6) can be ruled out because no turbulence was generated in the water tank during this experiment. The quantitative relationship between the decrease of water temperature and the rate of phytoplankton settling will be described in more detail in the next section.

Relationship Between Phytoplankton Settling Rate and Water Temperature

We have already reported that the DCM formation seemed to be due to the effect of the thermocline on the settling of phytoplankton in this experiment. However, the phytoplankton settling was qualitatively demonstrated by assuming that there was movement of the boundary between the area of low chlorophyll-a concentration near the water surface and the area of high chlorophyll-a concentration in the deeper layer. We will now compare and discuss the settling rate of phytoplankton according to qualitative calculations using both experimental results and the value calculated applying Stokes' law.

(a) Relationship Between Water Temperature and Settling Rate (Stokes' law)

The density of phytoplankton cells is generally higher than that of water except for *Microcystis aeruginosa*, which have gas vesicles (15). Therefore, the mature phytoplankton near the water surface pass through the thermocline to the bottom of the tank. The settling rate of phytoplankton calculated by applying Stokes' law shows that the rate decreases around the thermocline where the density of the water increases rapidly due to the rise in water temperature (Fig. 4). This may result in the retention of phytoplankton.

Fig. 4 shows the relationship between the water temperature and settling rate that was calculated by applying Stokes'

law:

$$S_{pp} = \frac{1}{18\mu}(\rho_{pp} - \rho_w)gd^2 \quad (2)$$

where S_{pp} = the settling rate; μ = the water viscosity coefficient; ρ_{pp} and ρ_w = the densities of phytoplankton and water, respectively; g = the gravitational acceleration; and d = the diameter of globular phytoplankton.

Eq.2 shows that the settling rate depends on the density and viscosity of water, which change with water temperature. Fig. 4(a) shows the relationship between water temperature and the density and viscosity of water.

Fig. 4(b) shows the relationship between water temperature and the settling rate calculated by adopting Eq.2, with the density of phytoplankton 'ρ_{pp}' set as a parameter. Although the density of phytoplankton differs according to its species or physiological state, the example seen in the calculation [Fig. 4(b)] used general values of 1020−1200 kg/m^3. The diameter of *Scenedesmus*—the dominant species in the water sample—was 10 μm; in the calculation, the same value was used as the phytoplankton diameter '*d*'.

Fig. 4(b) indicates that the settling rate increased with increasing water temperature regardless of the density of the phytoplankton. It also shows that higher densities of phytoplankton and higher water temperatures result in a greater increase in the settling rate.

Fig. 4(c) shows the variation in the dimensionless settling rate of phytoplankton with density, in which a settling rate of 'S_{pp0}' corresponds to the water temperature 0°C. It indicates that the dimensionless phytoplankton settling rate increases with water temperature and that the density of phytoplankton is only marginally affected in low temperature areas. However, this effect is greater for temperatures higher than 15°C. Generally, a difference of 5−10°C in water temperature was observed around the thermocline when DCM formed in a field site. According to Fig. 4(c), when a thermocline is present, the phytoplankton settling rate in the lower layer may decrease by about 30% as compared with that in the upper layer, e.g., when the temperature in the upper layer is 25°C and in the lower layer is 15°C.

(b) Comparison of Experimental and Theoretical Settling Rates

The phytoplankton settling rate in the experiment was calculated using the equation:

$$S_{pp-obs} = \frac{\Delta h}{\Delta t} \quad (3)$$

where S_{pp-obs} = the settling rate calculated from the experimental result; Δh = the settling depth [m]; and Δt = the elapsed time. The settling depth Δh is defined by the depth difference between the source to the point of the rapidly changing concentration of chlorophyll-a.

Fig. 5 shows the relationship between the settling rate calculated using Eq.3 and the water temperature in the experiment. The average settling rate and water temperature are plotted in the figure. In addition, it shows the relationship between the settling rate calculated using Eq.2 and the water temperature, assuming that the cell density ρ_{ss} is 1020 kg/m^3.

Comparing the settling rate obtained from the experimental results with the rate calculated using Eq.2 shows reveals close agreement between the two, and in both cases, there is a positive correlation between the settling rate and the water temperature. This finding seems to support the hypothesis that DCM formation resulted from the effect of the thermocline on the phytoplankton settling rate. Here, the settling velocity was fast because water temperature was high. However,

the chlorophyll-a concentration tended to increase in the water tank. Therefore, the entire water tank was thought to have a strong influence on growth processes.

However, a close analysis of both cases indicates that the water temperature had a smaller effect on the settling rate that was calculated using Stokes' law than the settling rate determined experimentally. One reason for this difference is that it might be caused by the indirect calculation of the settling rate for the experiments. The other reason is the assumption that the shape of phytoplankton was globular in calculating the settling rate using Stokes' law.

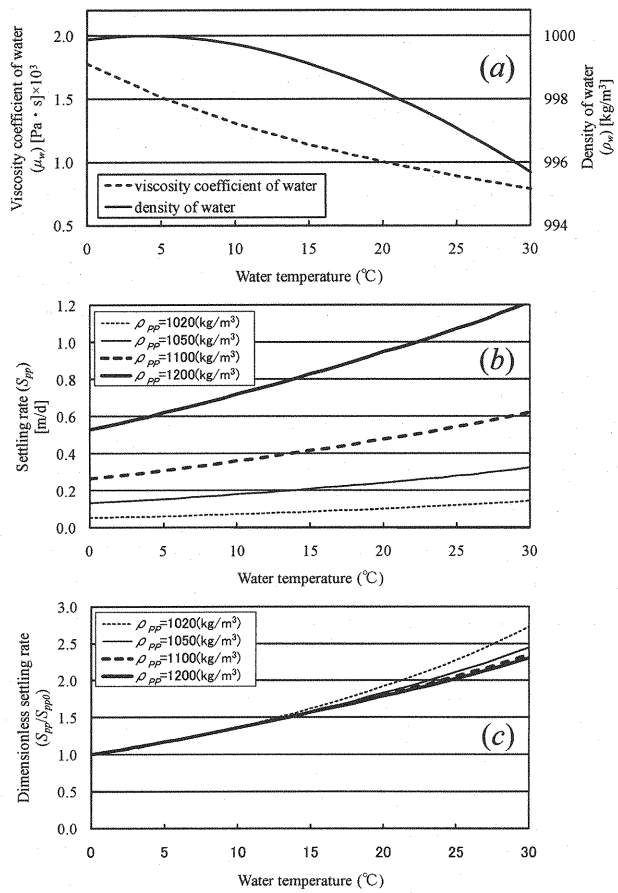

Fig. 4 Correlation between water temperature, viscosity coefficient of water, density of water, and settling rate

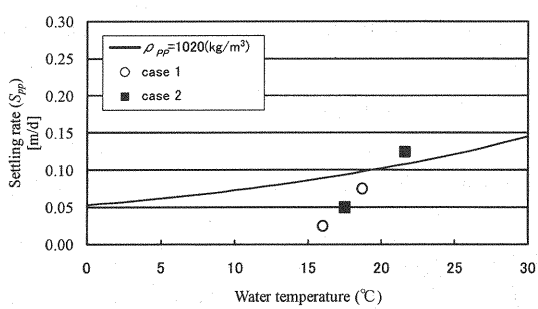

Fig. 5 Relationship between water temperature and settling rate

Comparison of Experimental Results with Previous Studies

In previous studies on the formation of DCM and the mechanism responsible for maintaining its presence, it was reported that physical elements such as the settling rate and turbulent diffusion coefficient in the vertical direction may play important roles. However, no conclusion was reached because of the complex elements involved (5), (6), (16). Steele et al. (6) considered the possibility that a decrease in the settling rate underneath the thermocline might have led to the formation of DCM. However, because the settling rate of phytoplankton determined using Stokes' law was two to three times larger than the value observed in the water, it was eventually concluded that biological factors have a greater effect on the value (6). Studies were conducted to investigate the mechanism responsible for the continuous presence of DCM, which were similar to the observations of the DCM formation process. Subsequently, studies investigating changes in the settling rate revealed a response to biological stimuli such as nutrients, salt, and light conditions at deeper depths (17), (18), but there have been few studies of the physical processes involving the relationship between the phytoplankton settling phenomenon and DCM formation.

Although the focus of our study was on an area that has been investigated for some time, the novelty of this research is that it uses knowledge of a simple phenomenon (phytoplankton settling) to explain the mechanism behind the formation of DCM. The DCM were formed using *Scenedesmus*, which was the dominant species in the water sample used in the experiment. However, in natural environments, DCM are usually formed by diatom phytoplankton (19), (20). Hence, the *Scenedesmus* observed in this experiment is not representative of the species that occur more commonly in water bodies. Although, from the viewpoint of DCM formation due to phytoplankton settling, it is important to consider whether the phytoplankton can swim and float. Hence, the dominant species *Scenedesmus*, which is similar to diatoms, is the correct species to analyze this phenomenon because it does not have the ability to swim and float.

Thus, the physical settling phenomenon plays an important role in the formation of DCM, and the settling rate of phytoplankton in the water varies with its physiological state or chemical composition (15), (18). Therefore, to more accurately estimate the settling rate of phytoplankton in water by using a dynamic model, further investigations are necessary. To verify the factors identified as being important for the formation of DCM, new techniques such as increasing the extinction coefficient to match the photic layer to the upper layer should be implemented. To change the vertical profile, nutrient salts may be added to the lower layer. It will also be necessary to measure the volume of dissolved oxygen to evaluate the activity of phytoplankton in experimental water tanks. Understanding the above experimental observations on the formation of DCM and the mechanism by which its presence is maintained in water is essential for developing a model that integrates the phytoplankton's physiological state and variation in its chemical composition. This is a topic for future study.

CONCLUSION

The aim of this study was to examine experimentally the formation of the DCM observed in stagnant water and to investigate the formation mechanism. To reproduce field phenomenon in a simplified experimental model, the thermocline, light conditions, and concentration of nutrients were controlled in the experimental equipment. After filtering a water sample that had been collected from a regulated pond at Tokyo Denki University, the experiment was performed over a period of four days. It was found that the formation of DCM was due to only a physical condition—the

existence of a thermocline. When the phytoplankton settled underneath the thermocline, we observed that the mechanism responsible for the formation of the DCM was a decrease in the settling rate, which was in turn due to a decrease in water temperature.

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APPENDIX – NOTATION

The following symbols are used in this paper:

$I(z)$	=light intensity at z;
I_0	=light intensity at water surface;
ε	= extinction coefficient;
z	=water depth;
S_{pp}	= settling rate;
μ	= viscosity coefficient of water;
ρ_{pp}	=density of phytoplankton;
ρ_w	=density of water;
g	=gravitational acceleration;
d	=diameter of globular shaped phytoplankton;
S_{pp-obs}	=settling rate calculated from the experimental result;
Δh	= settling depth at the point where the inflection point of concentration of chlorophyll-a; and
Δt	=elapsed time.

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