

Effects of phytoplankton vertical migration on the formation of oxygen depleted water in a shallow coastal sea

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ABSTRACT

In this paper, oxygen budget was estimated for the lower layer of water column in a semi-enclosed bay, Ago Bay, Japan. Benthic oxygen consumption rates were measured directly with an *in situ* measurement device from 13 July to 16 August 2004. Oxygen budget was calculated based on physical, chemical and biological processes using the observed data. Along with the change of the water column structure at the time of a hit of typhoon, dominant phytoplankton species shifted from the diatom *Skeletonema costatum* to the dinoflagellate *Heterocapsa circularisquama*. During the diatom-dominating period, oxygen supply rate in the lower layer due to photosynthesis was comparable to or slightly lower than the sediment oxygen consumption rate. In contrast, during the dominance of the dinoflagellate, net oxygen budget was significantly negative in the lower layer while it was positive in the upper layer. This could be attributed to the migration behavior of the dominant dinoflagellate *H. circularisquama* that swim up to the upper layer and produce oxygen in daytime, and swim down to the lower layer and consume oxygen in nighttime. The results of the present study suggest that phytoplankton migration behavior can enhance the development of oxygen depleted water mass in the lower layer of eutrophic shallow coastal seas.

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1. Introduction

It is widely known that oxygen depletion in the lower layer of water column during summer stratified season is mainly caused by higher decomposition rate of organic matter and lower oxygen supply. Coastal seafloor, in general, is an active site of decomposition of organic matter sank from the upper water column and supplies remineralized inorganic nutrients to the water column. In those processes, such as decomposition of organic matter and nitrification, oxygen is consumed in the bottom water (Justić et al., 2002; Christensen et al., 2003; Giles et al., 2006). Dissolved oxygen in bottom water is supplied physically by horizontal/vertical advection and diffusion. During the stratified season, pycnocline prevents oxygen supply from the surface layer to the lower layer, while oxygen consumption rate by sediments becomes higher due to increase in temperature (Thamdrup et al., 1998). In case of lower

layer thicker than 5 m, oxygen depletion is driven primarily by planktonic respiration rather than sediment consumption (Kemp et al., 1992). In intertidal and littoral shallow areas whose bottom is illuminated with sunlight, phytoplankton in the lower water can be the oxygen producer. Kamizono et al. (1996) calculated the oxygen budget in the lower layer below pycnocline in Suo-Nada (avg. depth 9 m), Japan, and reported that oxygen production exceeded consumption during the period of phytoplankton species, the diatom *Chaetoceros* spp. dominated in the lower layer. However, vertical migration of phytoplankton has not been taken into consideration on oxygen budget in the water column. Needless to say, it is recognized that dinoflagellates take up nutrients in the bottom layer during the night and return to the upper layer in order to perform photosynthesis during the day (Yamamoto et al., 2002). In other words, in the lower layer, dinoflagellates only consume oxygen in nighttime, whereas diatoms do not only consume oxygen but also produce in daytime.

Ago Bay is a small semi-enclosed coastal bay in Japan and is located in the central part of Honshu Island, Japan (34°N, 136°E) with the surface area of 26 km² and the average depth of 10 m. There are no major industrial facilities in the vicinity, and relatively

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small rivers carrying agricultural runoffs and sewage are the major sources of artificial nutrient inputs to the bay. The experimental station is located in the inner eastern part of the bay (Fig. 1) where there is no fresh water input from rivers. The rias coastline provides calm sea condition for pearl oyster culture facilities. The pearl oyster culture was started about a century ago and the production reached maximum in the 1960s, and has decreased to date. The intensive pearl oyster culture may have deteriorated the sediment quality. Chemical oxygen demand of the sediment has been increasing for recent 30 years exceeding the limit defined as polluted sediment by JFRCA (Nakanishi et al., 2001), whereas the decline occurred in the pearl culture production during the same period. One of the possible causes of the decline in the production is occurrence of *Heterocapsa circularisquama*. The red tide of *H. circularisquama* occurred in Ago Bay for the first time in 1992, and damaged about 3 billion yen (23 million US\$) due to mass mortality of pearl oysters (Nakanishi et al., 1999). Until now, *H. circularisquama* has formed red tides every summer, and damaged the pearl oyster culture (Masuda et al., 2004). It is suspected that the outbreak of *H. circularisquama* may be caused by nutrient regeneration from the sediment due to oxygen depletion (Shiraishi et al., 2007).

In the present study, we focus on the effect of phytoplankton vertical migration on the formation of oxygen depleted water mass in the lower layer below pycnocline. Hence, we directly measured benthic oxygen consumption rates and observed water quality, and estimated that the oxygen budget during the period of diatom-dominating and dinoflagellates-dominating periods.

2. Materials and methods

2.1. In situ continuous water observation system

Dissolved oxygen concentration, water temperature, salinity, chlorophyll fluorescence and turbidity were measured from 10 July to 16 August 2004, with an *in situ* continuous water observation system at the inner area of Ago Bay at 9.5 m depth (Fig. 1). The observation system was equipped with an electric winch to pull up and down the sensors which electric power is supplied by a solar

panel on the wooden raft. Water quality of the water column was monitored at an hourly interval from the surface (0.2 and 0.5 m) to the bottom with 1 m interval.

2.2. Bell-jar type oxygen measurement system

Benthic community oxygen consumption rate, which includes macrobenthos respiration, benthic algae photosynthesis, aerobic decomposition by bacteria, and chemical oxygen consumption, was measured using an *in situ* bell-jar type oxygen measurement system (ADO2000, JFE Alec) developed by Nagao et al. (2000). The ADO2000 consists of a transparent acrylic bell-jar which can be moved up and down by a cylinder that is deployed in the center of the flame. A stirring assembly for water circulation is mounted inside in the bell-jar.

Two sets of temperature, salinity, and fluorescent oxygen sensors are mounted inside and outside of the bell-jar. The set of sensor outside was used as a reference to monitor the ambient natural condition. The distance between these sensors and the seafloor is 20 cm. In addition, chlorophyll and light intensity sensors are deployed on the flame at the height of 30 cm and 60 cm above the seafloor, respectively.

The ADO2000 was settled by SCUBA divers to ensure that the chamber was inserted into the sediment properly and that resuspension of sediment did not occur inside. Data collections were made every 10 min during 13 July–16 August 2004. On 29 July, the ADO2000 was temporary salvaged to change batteries and to wipe out attachments on sensors and acrylic bell-jar, ensuring for the data quality.

During the observation, the bell-jar was down onto the sediment surface to measure oxygen consumption rate for 2 h and was up to renew the water inside for 1 h, repeatedly. The measuring area of the surface sediment covered by the bell-jar is 0.066 m² and measuring volume of the overlying water is 15.5 L. Water in the bell-jar was circulated with a flow rate of 2 cm s⁻¹ which is the average rate observed around the site.

Oxygen consumption rate in the bell-jar was calculated by the slope of the regression of least squares fitting against time during the first 60 min in each measurement, and the benthic community

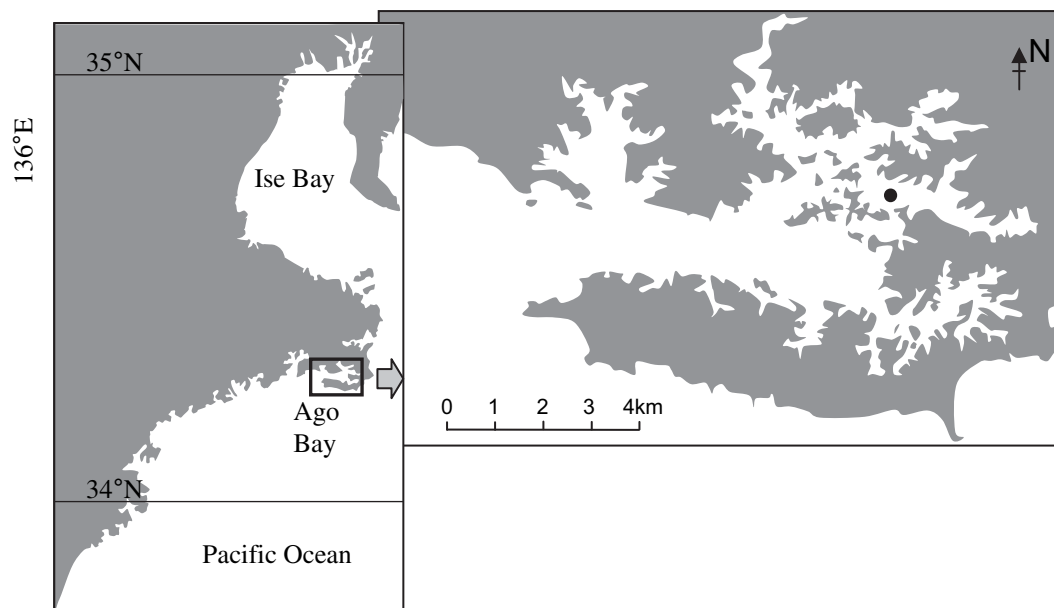


Fig. 1. Map showing the study site (filled circle) in the inner area of Ago Bay, Japan.

oxygen consumption (F_B) was estimated by the oxygen consumption rate in the water volume (15.5 L) divided by the measuring surface area (0.066 m²).

2.3. Air–sea oxygen flux (F_S)

The oxygen flux from the atmosphere to seawater was computed using the equation proposed by Stigebrandt (1991), which takes into account the effect of gas transfer due to bubbles:

$$F_S = V(1.025C'_S - C_S) \quad (1)$$

where F_S is the oxygen flux from the air to sea (g O₂ m⁻² d⁻¹), C'_S is the oxygen saturation value (g O₂ m⁻³), and C_S is the observed surface oxygen concentration (g O₂ m⁻³, 0.2 m). The transfer velocity, V (m d⁻¹), was calculated by the semi-empirical relationship between wind speed and gas transfer velocity given by Liss and Merlivat (1986):

$$V = 5.9 Sc^{-2/3}(0.17W), \text{ for } W < 3.6 \quad (2)$$

$$V = 5.9 Sc^{-1/2}(2.85W - 9.65), \text{ for } 3.6 < W < 13 \quad (3)$$

At oxygen saturation levels above 125%, Eqs. (2) and (3) were multiplied by $(C_S/C'_S)^2$ to take into account the oxygen surplus.

where Sc is Schmidt number, and W is wind speed (m s⁻¹) measured at Ugata fire station which is located 2 km away from the observing station. The Schmidt number, the ratio between the kinematic viscosity and the molecular diffusivity, of oxygen was calculated using the equation derived by Stigebrandt (1991).

$$Sc = 1450 - 71T_S + 1.1T_S^2 \quad (4)$$

where T_S is the water temperature at 0.2 m depth.

2.4. Vertical diffusion and oxygen flux through the pycnocline (F_P)

Vertical diffusivity (K_z ; m² s⁻¹) was calculated by one-dimensional diffusion equation of heat with respect to depth (Takeoka et al., 1986). In this study, pycnocline virtually divided water column into two water bodies.

$$H_L dT_L/dt = K_z(T_U - T_L)/\Delta h \quad (5)$$

where H_L and Δh is the thickness of the lower layer (m) and vertical distance between of the upper and lower layers (m), respectively. T_U and T_L are the average water temperature (°C) in the upper and lower layers, respectively, and t the time. Using the daily averaged data of T_U and T_L , K_z was calculated each day during the observation period.

Oxygen transport by vertical diffusion (F_P ; g O₂ m⁻² d⁻¹) was estimated using the following equation (Takeoka et al., 1986).

$$F_P = K_z(C_U - C_L)/\Delta h \quad (6)$$

where C_U and C_L are the concentration of dissolved oxygen of the upper and lower layers (g O₂ m⁻³), respectively. Positive value represents the flow from upper layer to lower layer.

2.5. Oxygen production in the water column

Net production of oxygen in the upper and lower layer was calculated by the balance of the inflow, outflow and daily change of oxygen content in each layer.

$$V_U dC_U/dt = V_U P_U + SF_S - SF_P \quad (7)$$

$$V_L dC_L/dt = V_L P_L + SF_P - SF_B \quad (8)$$

where V_U and V_L represent a volume for the upper and lower layer (m³), respectively. P_U and P_L represent the net production rates in each layer. S is the area of the interface (m²) between the upper layer and the lower layer. Oxygen production rate was calculated on the basis of hourly data during daytime (5:00–19:00) and nighttime (19:00–5:00), assuming that F_S , F_P , and F_B were constant during a day.

We ignored the horizontal advection terms in present analysis, because no horizontal differences of the environmental conditions were observed for most of the observation period in the simultaneous work (Haraguchi et al., 2008). For a diatom-dominating phase, it was selected that the period from 13 July at the time when the benthic oxygen measurement started until the water mixing by typhoon starting at 29 July 2004. For a dinoflagellate-dominating phase, it was selected that the period from 6 August at the time when the distinct diel change in vertical profile of chlorophyll *a* was observed until 11 August 2004 before the water advection occurred.

3. Results

3.1. Water column structure and oxygen distribution

Temporal variations of temperature, salinity, density (sigma-*t*), dissolved oxygen (DO) and chlorophyll *a* concentrations obtained from 10 July to 16 August 2004 are shown in Fig. 2. A strong thermocline/pycnocline was found at 4 m depth (Fig. 2a and 2c). Since the water depth is 9 m, the pycnocline virtually divides the water column into two water bodies of approximately equal volumes. From 10 July to 29 July, water temperature in the upper (0–4 m) and the lower (4–9 m) layers underwent a continual warming from 25 to 29 °C and 22–26 °C, respectively, their difference was about 3 °C. From 30 July to 2 August, stratification was temporarily destroyed and the water temperature became to 27 °C in the whole water column due to strong wind caused by a hit of the typhoon NAM-THEUN (T0410). After the typhoon passage, the water temperature increased again by surface heating.

Salinity in the surface layer decreased to 33.5–32.5 due to the heavy rainfall by the pass of the typhoon (Fig. 2b). On 29 and 30 July, precipitation of 43–90 mm d⁻¹ was recorded at the Ago Metrological Observatory Station. Except for the typhoon event, precipitation was low during the study period with no rainfall from 10 July to 28 July and only 2.7 ± 5.2 mm d⁻¹ from 6 to 11 August during the dinoflagellates-dominating period.

DO concentrations at 1 m above the seafloor gradually decreased but still remaining 3.0–4.0 mg L⁻¹ before the typhoon event. After the typhoon passed, DO concentration rapidly decreased to the level of 1.0–2.0 mg L⁻¹ by 11 August (Fig. 2d). Further, the oxygen depleted water mass (<3 mg L⁻¹) extended to the middle layer of the depth at 4 m from 9 August. On the other hand, DO at the upper layer increased to 10 mg L⁻¹ or higher the level of over saturation.

3.2. Chlorophyll *a* and phytoplankton abundance

Before the mixing on 30 July, chlorophyll *a* concentration was high with 10–20 µg L⁻¹ in the lower layer (4–9 m) compared to those in the upper layer 2.0–3.0 µg L⁻¹ (Fig. 2e). By the microscopic observation, the diatom species *Skeletonema costatum* dominated below the pycnocline before the typhoon passage (Mie Prefecture, 2005). In this period, the cell density of diatoms reached highest at $0.8\text{--}4.7 \times 10^6$ cells L⁻¹ in the lower layer. This was 1–2 orders

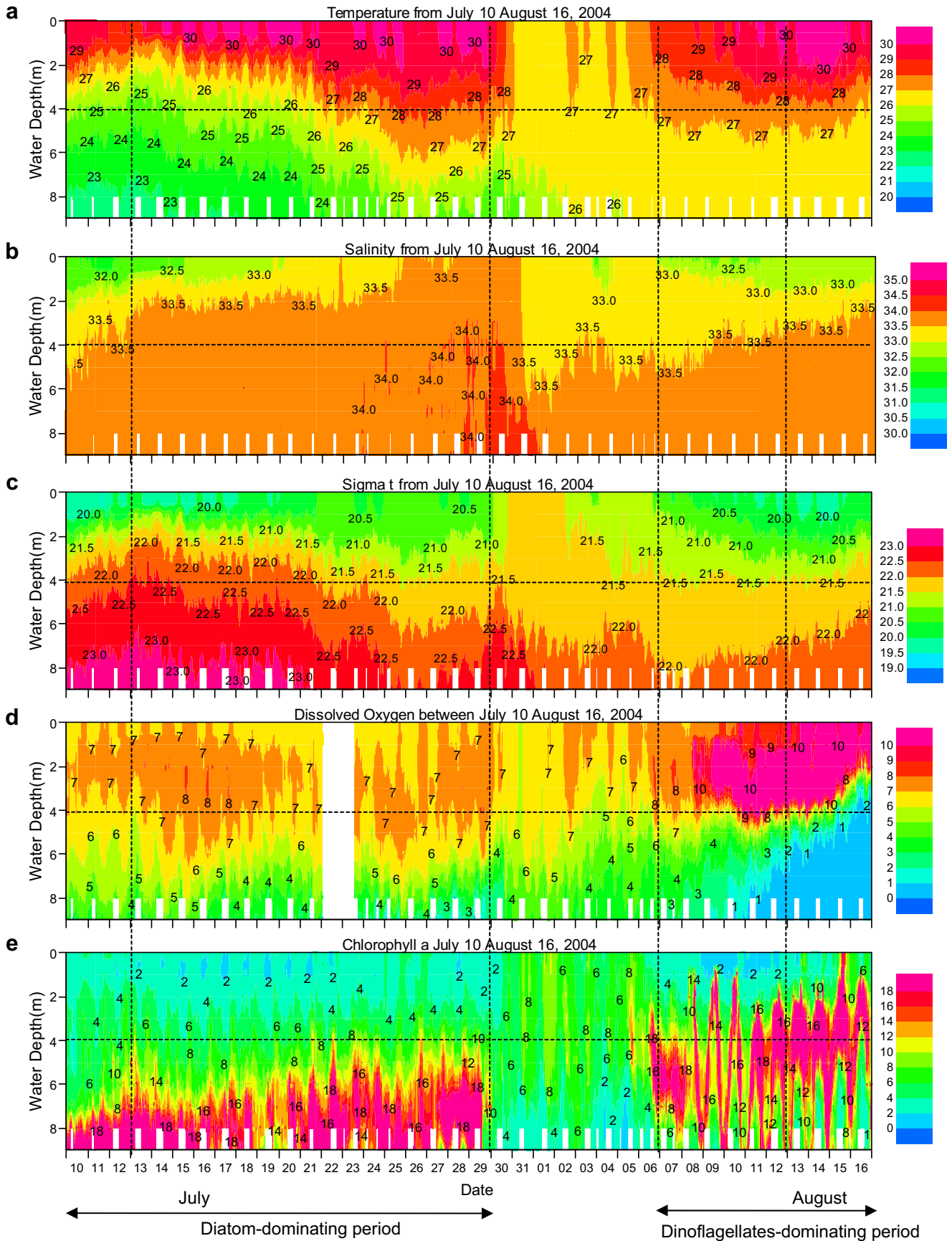


Fig. 2. Temporal variations in the vertical distribution of (a) temperature, (b) salinity, (c) density (σ - t), (d) dissolved oxygen, (e) chlorophyll a from 10 July to 16 August 2004.

of magnitude higher than those in the upper layer ($0.02\text{--}1.2 \times 10^6$ cells L^{-1}).

After the mixing, a distinct diel change in vertical profile of chlorophyll *a* with the concentration of above $20 \mu\text{g L}^{-1}$ was observed from 6 August (Fig. 2e). It is suggested that the diel change in the chlorophyll *a* vertical profile was due to diel vertical migration of dinoflagellates not by a tidal movement of water mass because such diel changes were not observed in the water temperature and salinity. The microscopic observation revealed that the dominant species was shifted to a dinoflagellate *Heterocapsa circularisquama* from *Skeletonema costatum* (Mie Prefecture, 2005). The cell density of dinoflagellates showed a maximum value of 1.4×10^7 cells L^{-1} at 2 m depth on 10 August. Depth-integrated abundance reached highest at 4.2×10^{10} cells m^{-2} . This was 2 order of magnitude higher than that in the diatom-dominating period ($2.6\text{--}8.3 \times 10^8$ cells m^{-2}). In the beginning of the dinoflagellates-dominated bloom coincided with the increase of water temperature from 25 to 27 °C in the lower layer due to wind induced mixing (Fig. 2a).

Duration of sunshine recorded at the Ago Metrological Observatory Station was not different between diatom-dominating period from 10 July to 29 July (7.6 ± 3.1 h) and dinoflagellate-dominating period from 6 August to 11 August (7.7 ± 3.7 h). However, we observed a different in the maximum light intensity measured at 60 cm above the seafloor between diatom and dinoflagellate-dominating period. Maximum light intensity of $64 \pm 24 \mu\text{mol m}^{-2} \text{s}^{-1}$ in diatom-dominating period went down to the $24 \pm 8 \mu\text{mol m}^{-2} \text{s}^{-1}$ in dinoflagellate-dominating period (Figure not shown).

3.3. Diffusion across the air-sea interface

Daily mean wind speed data and estimated air-sea oxygen flux (F_S) are shown in Fig. 3. Positive value of F_S means that the oxygen flux is from the atmosphere to the sea. Except for the cloudy weather during typhoon passage, the flux was directed toward the atmosphere, because of high oxygen concentration due to photosynthesis in the upper layer. Higher wind speed enhanced oxygen flux from the saturated surface water, and the F_S showed the minimum value of $-1.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ on 30 July at the time when the wind speed was strongest (5.8 m s^{-1}). Oxygen flux from the water increased by one order magnitude from 10 August and reached maximum on 14 August. Diffusive flux across the air-sea

interface during 6–11 August ($-0.09 \pm 0.09 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) when dinoflagellate-dominating period was higher than those during 13–29 July ($-0.03 \pm 0.01 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) when diatom-dominating period (Mann–Whitney Rank test, $p = 0.027$).

3.4. Oxygen transport by vertical diffusion through the pycnocline

In our simultaneous study, vertical diffusivity (K_z) was measured by a free-rising type of Micro Scale Profiler (TurboMap 4, JFE Alec) in 4 August 2004 (Nagao et al., 2005). They repeatedly measured K_z at the same site in present study (Fig. 1), and reported the range from 0.1 to $1 \text{ cm}^2 \text{ s}^{-1}$. Our calculation result ($0.14 \text{ cm}^2 \text{ s}^{-1}$) at present shows good agreement with the direct measurement (Fig. 4a).

The K_z temporarily increased during the hit of typhoon. Mean K_z was the same level between the diatom-dominating period ($0.18 \pm 0.16 \text{ cm}^2 \text{ s}^{-1}$) and the dinoflagellate-dominant period ($0.15 \pm 0.11 \text{ cm}^2 \text{ s}^{-1}$). However, oxygen transport by vertical diffusion through the pycnocline (F_P , $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) during the dinoflagellate-dominating period ($1.23 \pm 0.61 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) was 2.5 times higher than those during the diatom-dominating period ($0.54 \pm 0.35 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) (t -test, $p = 0.002$). The F_P increase was responsible for the large difference of oxygen concentration between upper and lower layer in the dinoflagellate-dominating period.

3.5. Oxygen consumption in the bottom sediment

In most cases, oxygen concentration in the bell-jar decreased linearly during first 60 min after closing the bell-jar, and gradually decreased in the next 60 min. When the bell-jar was up to renew the water inside, oxygen concentration in the bell-jar returned closely to the reference within 20 min. An example of the measurement in the bell-jar on 14 July was shown in Fig. 5 in open circle.

Daily benthic oxygen production rates averaged over 8 times measurements per day always showed negative values presenting consumption (Fig. 6c). The consumption rates were almost the same before and after the mixing by the typhoon. However, from 8 August, oxygen consumption rate decreased to almost zero owing to lack of oxygen. Although oxygen measured by ADO2000 at 20 cm above the seafloor almost exhausted, oxygen measured by

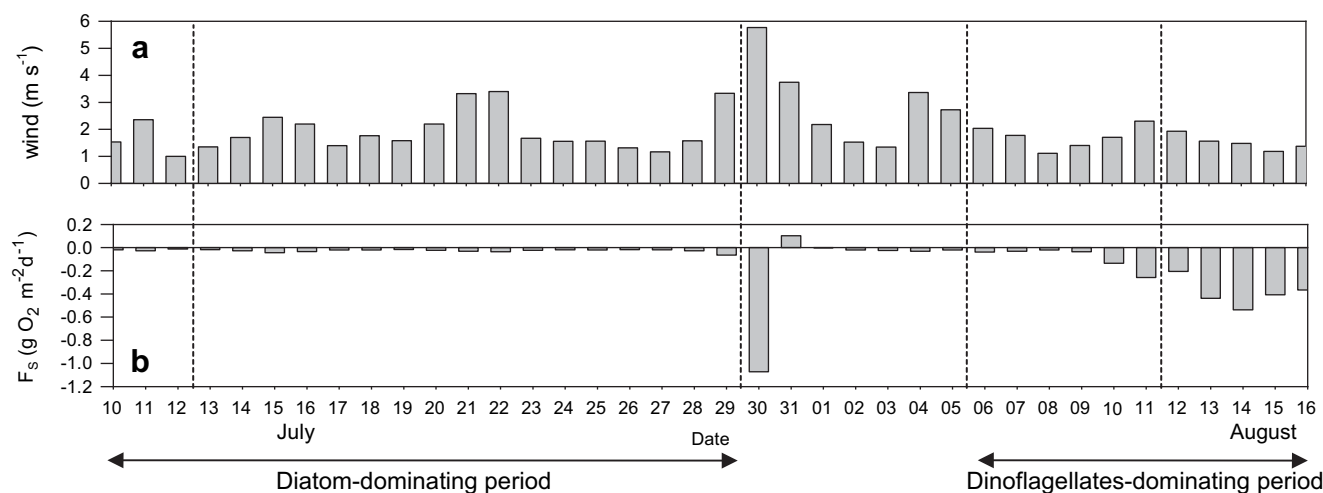


Fig. 3. Temporal variations in (a) the wind speed and (b) air-sea oxygen flux (F_S) from 10 July to 16 August 2004. Positive value of F_S indicates that the oxygen flux is from the atmosphere to the sea.

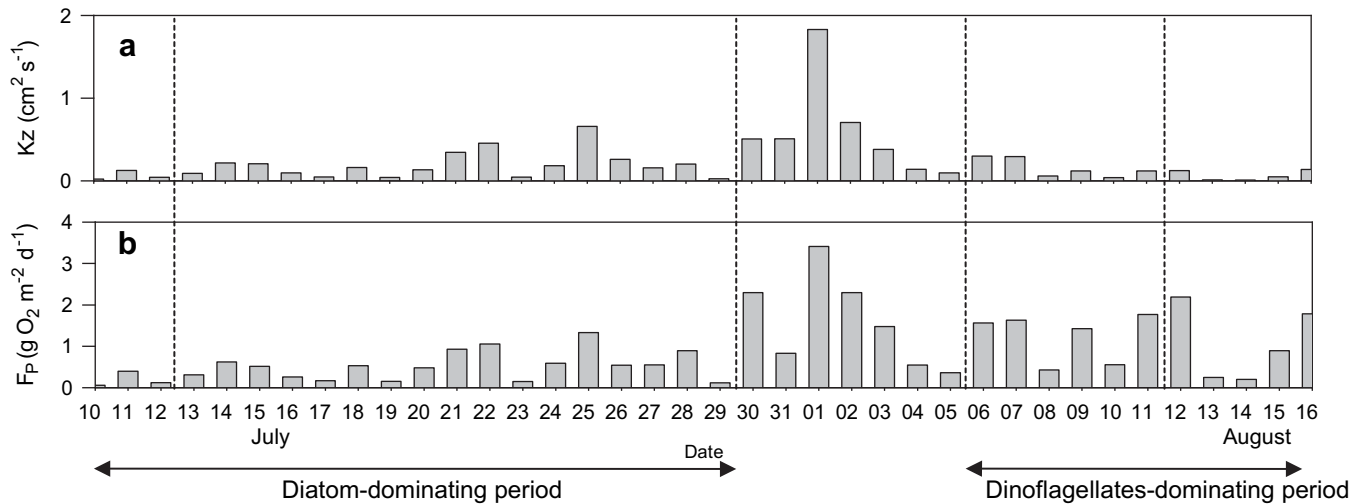


Fig. 4. Temporal variations in (a) vertical diffusivity (K_z) and (b) diffusive oxygen flux through pycnocline (F_p) from 10 July to 16 August 2004. Positive value of F_p indicates that the oxygen flux is from the upper layer to the lower layer.

water observation system at 50 cm above the seafloor remained 1.0–2.0 mg L⁻¹ until 11 August (Fig. 2d).

3.6. Net oxygen production in the water column

In our simultaneous study, no horizontal differences in the environmental conditions were observed during the present observation period except on 12 August and onward (Haraguchi et al., 2008). This indicates that horizontal advection and diffusion are not determinative to oxygen transportation in horizontal direction before 11 August. A rapid increase of salinity in the bottom water accompanied by increases in nitrate and dissolved oxygen concentrations were observed at the bay mouth in 6 August 2004 (Haraguchi et al., 2008). This water mass intruded into the bay center and pushed central water to the innermost part closed to the experimental site at 12 August 2004. With the above reason, we calculated the oxygen budget for the period of 13 July–11 August.

During the diatom dominant period, oxygen gradually decreased but still remaining 3.0–4.0 mg L⁻¹ in the bottom layer at the end of this species dominance (Fig. 2d). Oxygen budget analysis revealed that *in situ* planktonic photosynthesis produced 2.1 ± 2.1 g O₂ m⁻² d⁻¹ in the lower layer during 13–29 July during the diatom-dominating period (Fig. 6b). Therefore, biological net production was 4 times higher exceeding physical supply of 0.54 ± 0.35 g O₂ m⁻² d⁻¹. The total supply rate (2.6 g O₂ m⁻² d⁻¹) was comparable to or lower than the sediment oxygen consumption rate

(3.4 g O₂ m⁻² d⁻¹). As a result, oxygen decreased gradually and was still remaining in the lower layer. During this period, the net oxygen production in the upper layer was also positive (0.64 ± 0.84 g O₂ m⁻² d⁻¹) and was lower than the values in the lower layer (*t*-test, $p < 0.001$).

In contrast, after the mixing, during 6–11 August when the dinoflagellate-dominated, average net oxygen production in the upper layer increased to 4.9 ± 3.2 g O₂ m⁻² d⁻¹, which was higher than that of 0.64 g O₂ m⁻² d⁻¹ during the diatom dominant period (Fig. 6a). In the lower layer, however, oxygen production showed negative value (-2.4 ± 3.0 g O₂ m⁻² d⁻¹). Negative value means the oxygen consumption in the layer. During daytime (5:00–19:00), oxygen production rate was 2.8 times higher in the upper layer (0.58 ± 0.28 g O₂ m⁻² h⁻¹) than that in the lower layer (0.21 ± 0.17 g O₂ m⁻² h⁻¹) (Fig. 7). During nighttime (19:00–5:00), however, oxygen consumption rate in the lower layer (0.48 ± 0.20 g O₂ m⁻² h⁻¹) was 1.7 times large compared to that in the upper layer (0.29 ± 0.26 g O₂ m⁻² h⁻¹). On a daily basis, oxygen production showing negative values in the lower layer was responsible for the decreased daytime production and increased nighttime consumption.

During dinoflagellates-dominating period daily planktonic oxygen consumption rate was 2 folds higher than the physical supply from the upper layer. As a result, oxygen consumption rate in the lower layer including sediment increased with 5 times higher rate (-3.7 g O₂ m⁻² d⁻¹) compared with the diatom-dominating

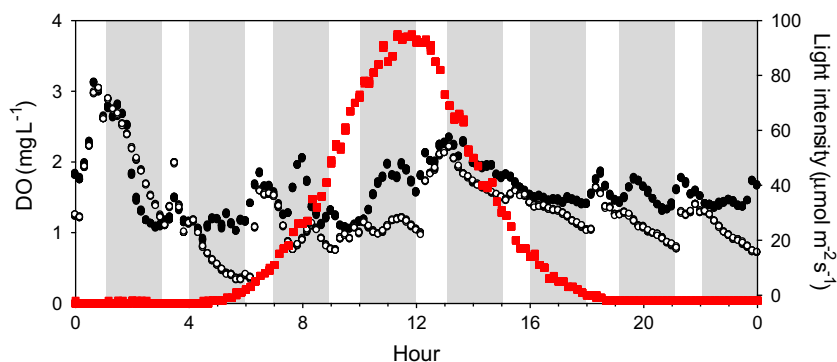


Fig. 5. Temporal changes in the oxygen concentration in the bell-jar (open circle) and reference (solid circle) of *in situ* bottom water and light intensity on the seafloor (solid square) in the inner area of Ago Bay in 14 July 2004. Gray and white areas denote close and open state of the bell-jar, respectively.

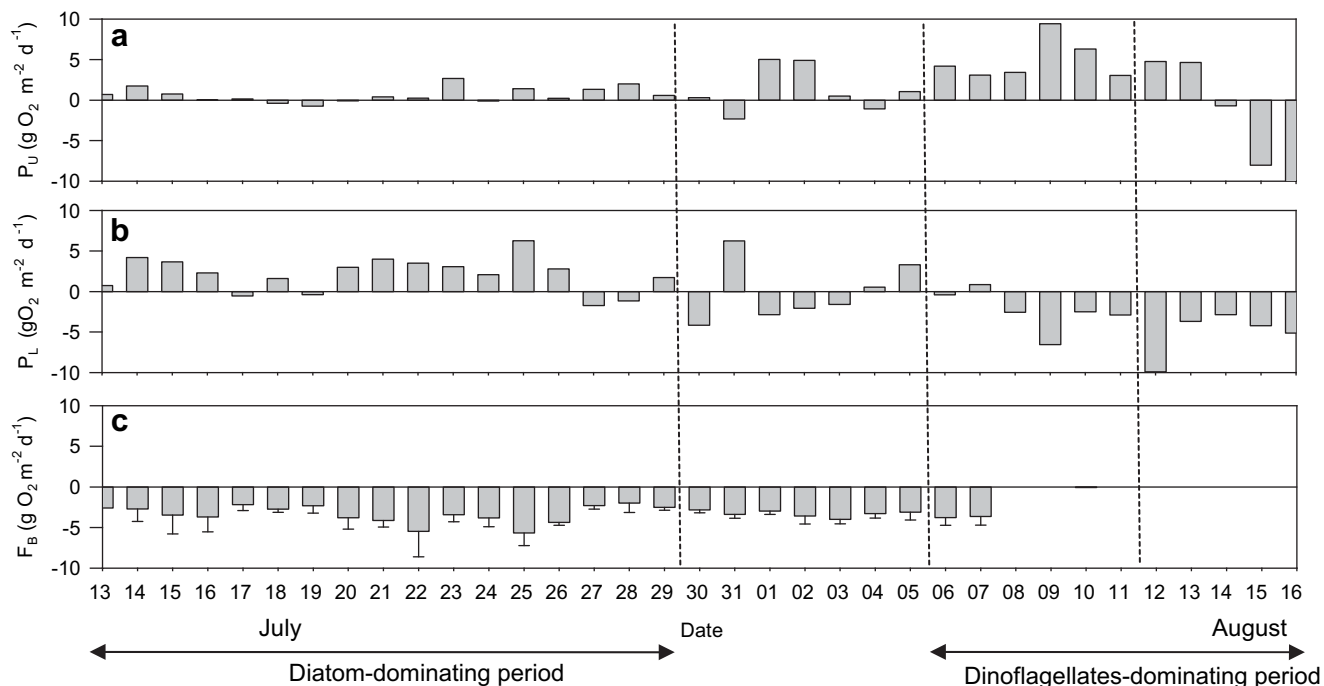


Fig. 6. Temporal variations in planktonic net oxygen production rate in (a) the upper (P_U) and (b) the lower layer (P_L), and (c) benthic community oxygen consumption rate (F_B) from 13 July to 16 August 2004.

period ($-0.76 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$). During the dinoflagellate-dominating period, oxygen rapidly decreased and the oxygen depleted water mass extended to the middle layer (Fig. 2d).

4. Discussion

4.1. Physical oxygen supply

Oxygen flux through the air–sea interface (F_S) was also not an important oxygen supply process to the water column, because the F_S always directed toward the atmosphere except for a hit of

typhoon as shown in Fig. 3b. Particularly, the F_S was 3-folds greater in the dinoflagellate-dominating period than in the diatom-dominating period (Fig. 8). This could be attributed to vertical migration behavior of *Heterocapsa circularisquama* dominated during the period. Although oxygen production by phytoplankton photosynthesis was primarily occurs in the upper layer of the water column, produced oxygen was considered to be prevented to transport to the lower layer by the robust thermal stratification. Compared to the oxygen flux by vertical diffusion through the pycnocline (F_P), the benthic oxygen demand (F_B) was 2–6 folds higher (Fig. 4b, 6c, and 8). Therefore, the diffusive oxygen transport through the

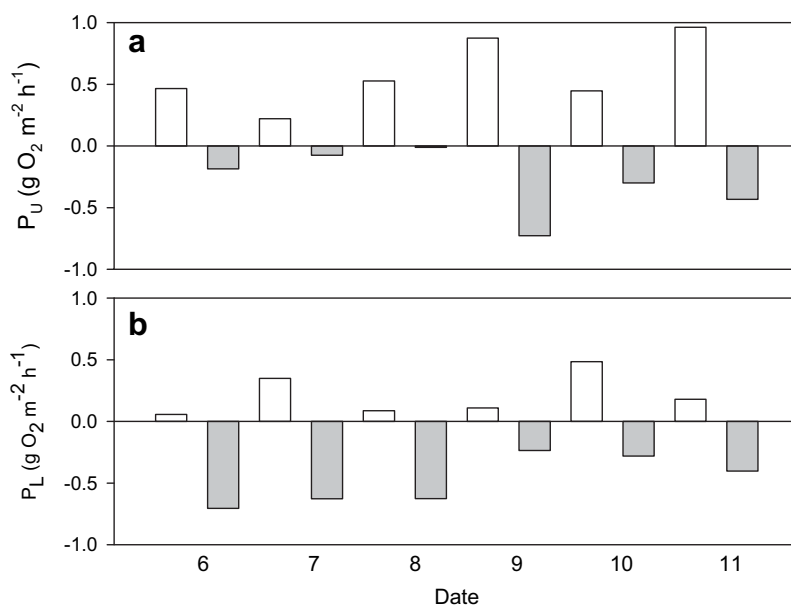


Fig. 7. Temporal variations in planktonic net oxygen production rate in (a) the upper (P_U) and (b) the lower layer (P_L) from 6 to 11 August 2004. Open and filled columns represent the rates during daytime (5:00–19:00) and nighttime (19:00–5:00).

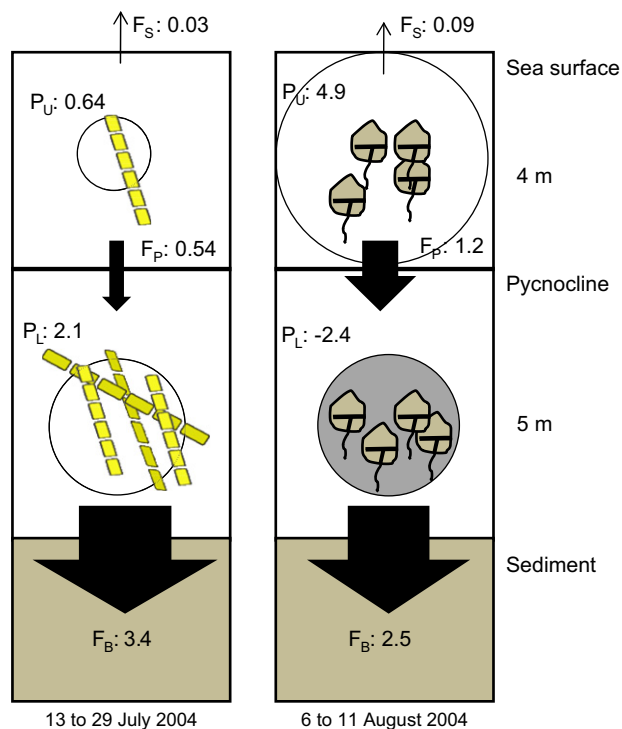


Fig. 8. Schematic drawing for oxygen budgets during the diatom-dominating period and the dinoflagellate-dominating period in the inner area of Ago Bay. The black arrows of air-sea oxygen flux (F_S), diffusive oxygen flux through pycnocline (F_P) and benthic community oxygen consumption rate (F_B) indicate flow of oxygen in unit of $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$. The white and black circles indicate production and consumption of oxygen, respectively, in the upper (P_U) and (b) lower layer (P_L) unit of $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$.

thermocline could not prevent the proceeding of oxygen depletion in the lower layer.

Vertical advection is one of the physical transport processes. However, we assumed that vertical advection could be ignored because the amount of oxygen transport was estimated to be small from the previous work (Chiba and Yamagata, 2008). In the study, horizontal and vertical diffusion coefficients and upwelling velocities were estimated for ten blocks in Ago Bay using a box model analysis. A two-layer model divided at 4 m depth (pycnocline) was applied for the stratified period from July to October 2003. The upwelling velocity at the same site in the present study was calculated to be -0.4 to 1.4 m d^{-1} with the average 0.4 m d^{-1} . Assuming the same average upwelling velocity to that calculated for the period of 2004, oxygen flux from the lower layer to the upper layer was $0.55 \pm 0.04 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in the diatom-dominating period and was $0.38 \pm 0.06 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in the dinoflagellate-dominating period. These values were counteracted by the oxygen transport by vertical diffusion (F_P).

4.2. Biological oxygen supply during diatom-dominating period

The diatom, *Skeletonema costatum*, is one of the dominant species often forms blooms in this bay (Masuda et al., 2008). In our observation, the bloom of this species lasted for about three weeks by the hit of typhoon. Our experimental station is located in the inner area of Ago Bay (Fig. 1) where there are no major rivers as source of fresh water. Growth of diatoms was observed in the lower layer but it was not significant in the upper layer. This may be due to exhaustion of nutrients in the upper layer reported by Haraguchi et al. (2008), which is supported by the record of no rainfall during this period. In the lower layer, meanwhile, ammonium and phosphate concentrations were high, which may be generated by

decomposition of organic matter. Mean light intensity at 0.6 m above the seafloor was $64 \pm 24 \mu\text{mol m}^{-2} \text{ s}^{-1}$, that was higher than the compensation irradiance defined as the light intensity below which no growth of *S. costatum* can occur ($1.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$) (Langdon, 1987). This also suggests that oxygen production was occurring even below the pycnocline in the shallow area of 9 m depth or less.

Photosynthetic efficiency of diatom is explained by chlorophyll *a* concentration and light intensity (Langdon, 1987). They reported that the chlorophyll *a*-based gross photosynthetic efficiency and maintenance respiration efficiency at zero growth rate for *Skeletonema costatum* are $0.02 \mu\text{mol O}_2 (\mu\text{g chl } a)^{-1} (\mu\text{mol photon m}^{-2} \text{ s}^{-1}) \text{ h}^{-1}$ and $0.002 \mu\text{mol O}_2 (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$, respectively. Daily net production was calculated to be $0.40 \text{ mg O}_2 \text{ L}^{-1} \text{ d}^{-1}$ ($2.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) using the *in situ* light intensity ($64 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$) and chlorophyll *a* ($10 \mu\text{g chl } a \text{ L}^{-1}$). The value estimated from the oxygen budget ($2.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) in Fig. 8 is well corresponding to the value calculated from the light intensity and chlorophyll *a* for *S. costatum*.

4.3. Biological oxygen consumption during dinoflagellate-dominating period

Respiration rates of dinoflagellates with large size were generally higher than those of diatoms with small size (Burris, 1977; Falkowski and Owens, 1978). Maintenance respiration of phytoplankton is always explained by cell biomass regardless of species (Langdon, 1987). Langdon (1988) proposed that a formula for maintenance respiration rates of phytoplankton as a factor of 6.6×10^{-4} multiplied by carbon content (pg C cell^{-1}) powered by 0.54. Carbon content of *Heterocapsa circularisquama* was calculated from the equation proposed by Menden-Deur and Lessard (2000) as a factor of 0.76 multiplied by cell volume (μm^3) powered by 0.819. For this calculation, cell volume was computed using the geometric formula for spheroid. Average cell length ($23.9 \mu\text{m}$) and width ($17.3 \mu\text{m}$) of this species were reported by Horiguchi (1995). Ten-hours average respiration rate at the night of 10 August when *H. circularisquama* dominated in the lower layer was calculated to be $0.42 \text{ mg O}_2 \text{ L}^{-1} \text{ night}^{-1}$ ($2.1 \text{ g O}_2 \text{ m}^{-2} \text{ night}^{-1}$) using chlorophyll *a* concentration of $100 \text{ mg chl } a \text{ m}^{-2}$ in the lower layer at midnight. This value is in good agreement with the value of $2.8 \text{ g O}_2 \text{ m}^{-2} \text{ night}^{-1}$ estimated from the oxygen budget (Fig. 7).

This study indicates that dinoflagellates can affect on the formation of oxygen depleted water. Under the anoxic condition, major nutrients such as phosphorous and trace metal as well as easily eluted from sediments (Cowan and Boynton, 1996). Benthic nutrient flux plays an important role in the pelagic nutrient cycle in semi-enclosed bay (Sarker et al., 2005). The occurrence of *Heterocapsa circularisquama* might be related to the oxygen-deficient water with nutrient-rich condition as pointed out by Shiraishi et al. (2007). Our results suggest that respiration of dinoflagellates provides favorable growth condition for them with plenty nutrient under low oxygen condition.

5. Conclusion

During the diatom dominant period, oxygen supply rate to the lower layer was calculated to be $2.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ by *in situ* planktonic net oxygen production and $0.54 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ by physical process from the upper layer (Fig. 8). Therefore, biological net production was 4 times higher than the physical supply. The total supply rate, $2.6 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, was comparable to or lower than the sediment oxygen consumption rate, $3.4 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$. As a result, oxygen decreased gradually but was still remaining in the lower layer by the end of diatom-dominating period.

In contrast, after the mixing, the average net oxygen production in the upper layer during the dinoflagellate-dominating period was $4.9 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, which was higher than that during the diatom-dominating period ($0.64 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) (Fig. 8). In the lower layer, however, oxygen consumption rate increased 5 times higher compared to the diatom-dominating period. During the time, planktonic oxygen consumption rate was 2 folds higher than the physical supply rate from the upper layer. The results of this study indicate that a mechanism for the development of oxygen depleted water mass due to vertical migration of dinoflagellates plays an important role in the stratified coastal seas.

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