

Spatial variations in time-integrated plankton metabolic rates in Sagami Bay using triple oxygen isotopes and O₂:Ar ratios

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Abstract

Plankton metabolic rates, such as rates of gross, net community production and community respiration, were measured in the surface waters using triple oxygen isotopes and O₂:Ar ratios. The ¹⁷Δ anomaly showed clear coastal and offshore gradients that were consistent with the distribution of chlorophyll *a* and oxygen saturation. Gross primary production (GPP) rates in coastal regions were several times higher than offshore regions, and the net-to-gross production ratio (N:G) indicated that coastal regions were net autotrophic, whereas offshore regions were net heterotrophic. On a seasonal scale, about 73% of the phytoplankton-produced carbon was respired. Based on floating-sediment-trap data, export production to the aphotic zone was about 12–20% of the GPP; the rest accumulated as dissolved organic carbon (DOC) or was respired.

Marine primary production accounts for about 50% of total carbon fixation in the biosphere (Field et al. 1998). About 60–90% of primary production is respired by heterotrophs in the upper few meters of the ocean (Laws et al. 2000). The ocean ecosystem is sustained by excess of gross primary production (GPP) over community respiration (R), which is termed net community production (NCP); the balance between GPP and R (the net metabolic status) dictates whether oceans are net sources or sinks of CO₂ to the atmosphere. Several studies have suggested that metabolic processes are substantially out of balance in the open-ocean regions, i.e., respiration is higher than production (del Giorgio and Duarte 2002; Williams et al. 2004), while coastal oceans are net autotrophic (Ducklow and McAllister 2005). Williams (1997) compared depth-integrated GPP and R and found that they are substantially in balance. However, both opinions are hotly debated. For instance, dissolved O₂ incubation experiments in the oligotrophic subtropical ocean (Hawaii Ocean Time Series

Station; HOTS) suggested that heterotrophy is dominant in the photic zone (Williams et al. 2004). If this is so, it raises the question: what is the carbon source that supports heterotrophy in excess of production? Karl et al. (2003) observed that incubation experiments miss relatively short and infrequent occurrences of episodic high-productivity events, which may support net heterotrophy in oligotrophic regions. Clearly, the importance of such events cannot be assessed accurately on the basis of any single sampling because of the short time period covered by incubations. Therefore, a lack of data for episodic high-productive events and the inherent limitations of incubation experiments (Williams et al. 2004) prevent us from understanding whether metabolic rates are in balance or not.

Most of our knowledge of primary production and production-to-community respiration ratios are based on incubation experiments using tracers, such as ¹⁴C (Steeman Nielsen 1952), and ¹⁸O (Grande et al. 1989), and concentration changes of dissolved oxygen or dissolved inorganic carbon in light and dark bottles. Each one of these techniques has its strengths and weaknesses due to problems involved in bottle incubations (the effect of lack of mixing on growth of bacteria and phytoplankton) and loss or recycling of labeled tracer (Bender et al. 1987; Howarth and Michaels 2000). Bender et al. (1987) suggested that the gross production, based on ¹⁸O labeling, might give accurate estimates because enrichment of ¹⁸O in dissolved O₂ through respiration does not seriously influence production estimates. However, Ostrom et al. (2005) found that primary production by ¹⁸O incubation was significantly lower than ¹⁴C and light and dark bottle incubations in eutrophic and mesotrophic

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environments and attributed this to consumption of labeled O_2 within cells or evolution of extraneous O_2 . Therefore, data derived using incubation techniques may seriously underestimate production. Recently, triple oxygen isotopes of dissolved O_2 and the dissolved O_2 :Ar ratio have been used as a tracer to estimate GPP and net-to-gross production ratios (N:G) in different regions (Hendricks et al. 2004; Juranek and Quay 2005; Sarma et al. 2005, 2006a). Unlike bottle incubation methods, this multiple-tracer approach measures changes in ambient dissolved O_2 without enclosure in a bottle; thus, the resulting isotope and concentration data reflect all productivity and respiration that occurred over the residence time of O_2 in the water column. In other words, if the residence time of O_2 is 1 week, then the isotope and concentration values that are measured reflect the average production and respiration that occurred in that time frame, which is significantly longer than that of traditional incubations, which typically last 6–12 h. In order to understand more accurately how the time integrated plankton metabolic balance changes from eutrophic coastal regions to oligotrophic open-ocean regions, high-spatial-resolution sampling was carried out in Sagami Bay during the end of the spring bloom period. Here, we report the first measurements of plankton metabolism in Sagami Bay on a basinwide basis.

Methods

Sample collection, purification, and measurements of triple oxygen isotopes—Continuous shipboard sampling for measurement of triple oxygen isotopes and O_2 :Ar ratios was conducted on board R/V *Tansei-maru* from 02 May to 09 May 2006 in Sagami Bay, central Japan. Bubble-free surface waters were collected through the ship's seawater-intake supply line, which was located at the bow at a nominal depth of 4 m. Dissolved gases were extracted using a 12-cm-long, hollow-fiber, membrane-degassing module (SEPAEL® PF-001D, Dainippon Ink and Chemicals), which consisted of fibers made of poly-4-methylpenten-1 (PMP) with thicknesses of 0.04 mm and pores of 30×10^{-6} mm diameter covered with a surface skin layer of 0.001 mm thickness. Under high vacuum, the membrane allows passage of only gas molecules and minimal passage of liquids. Dissolved O_2 , Ar, and N_2 were collected with a molecular sieve at liquid nitrogen temperature and sealed in a glass tube, after which they were brought to the shore-based laboratory for further extraction and isotopic analysis of dissolved gases. Sarma et al. (2006b) provide more details of the continuous shipboard sampling system and comparisons with traditional equilibration techniques. Dissolved O_2 and Ar were quantitatively separated and purified from other dissolved gases using gas chromatography according to the method by Sarma et al. (2003), and isotopic ratios were measured using a Delta Plus (Finnigan, ThermoQuest) mass spectrometer. Masses 32, 33, and 34 were measured against a standard mixture of O_2 and Ar to determine $\delta^{17}O$ and $\delta^{18}O$ (δ^xO [per mil] = $[10^3(xO/^{16}O)_{\text{sample}}/(xO/^{16}O)_{\text{air}} - 1]$). The O_2 :Ar ratio in the sample is directly proportional to the ratio of mass 32 to mass 40. The proportionality constant was determined by measurements of a compressed air standard. Each sample was analyzed for 10 cycles, where each cycle consisted of 10 runs

to achieve high precision in the delta values; it took about 4 h to complete the entire analysis of each sample. All isotope values are reported with respect to the isotopic and gas ratio composition of atmospheric air. Temperature and salinity were measured using a thermosalinograph, and chlorophyll *a* (Chl *a*) was estimated using a Turner Fluorometer. Dissolved O_2 was measured following Carritt and Carpenter (1966) using automated precision Winkler titration by Metrohm 785 DMP Titrino, and a potentiometric end point.

Gross oxygen production by ^{18}O spike incubation—Incubation experiments were conducted for measuring in situ GPP at six depths in the upper 40 m (0, 5, 10, 15, 25, and 40 m), four times (03, 04, 07, and 08 May 2006) in central Sagami Bay ($35^\circ N$, $139.5^\circ E$). Two samples per depth were collected for initial $\delta^{18}O$ determination of dissolved O_2 , and two samples per depth were spiked with 100 μL of 95 atom% enriched ^{18}O -labeled water (Cambridge Isotope Laboratories) and incubated for 24 h in the primary production array (Bender et al. 1987). After incubation, ~ 100 mL of subsample were drawn into pre-evacuated gas extraction vessels and capped.

Daily GPP was calculated from the isotopic composition of dissolved oxygen (DO) in initial and incubated samples using the following equation (Bender et al. 2000)

$$GPP = \{ [\delta^{18}O(O_2)_f - \delta^{18}O(O_2)_i] / [\delta^{18}O_{\text{water}} - \delta^{18}O(O_2)_i] \} \times (O_2)_i \quad (1)$$

where the subscripts *i* and *f* refer to the isotopic composition of O_2 in initial and final samples, $(O_2)_i$ is the oxygen concentration of the initial water sample, and $\delta^{18}O_{\text{water}}$ is the isotopic composition of the enriched water. The CO_2 equilibration method was used for measuring $\delta^{18}O$ of enriched water samples with a precision better than 0.1 per mil. $(O_2)_i$ was determined by the Winkler method with precision of $\pm 0.2 \mu\text{mol kg}^{-1}$.

Gross oxygen production by dissolved-oxygen, light and dark bottle method—Seawater samples were carefully siphoned into nine ~ 100 mL gravimetrically calibrated borosilicate glass bottles from each Niskin bottle. From each depth, three light and three dark bottles were incubated along with ^{18}O -enriched bottles in the primary production array for in situ incubation. The dark bottles were wrapped with aluminum foil. After 24 h, DO in both light and dark bottles was fixed using Winkler reagents following Carritt and Carpenter (1966). DO concentrations were measured using the Metrohm 785 DMP Titrino, with potentiometric end-point detection with a standard deviation of $\pm 0.07\%$. Changes in DO concentrations in the light bottle were taken as net community production (NCP), and DO changes in the dark bottle were taken as community respiration (R).

Results and Discussion

The spatial distributions of sea-surface temperature (SST), salinity (SSS), Chl *a*, and O_2 saturation are shown in Fig. 1. SST showed strong spatial variations in Sagami Bay (16.3 to $19.2^\circ C$; Fig. 1a). SST warmed from coastal to

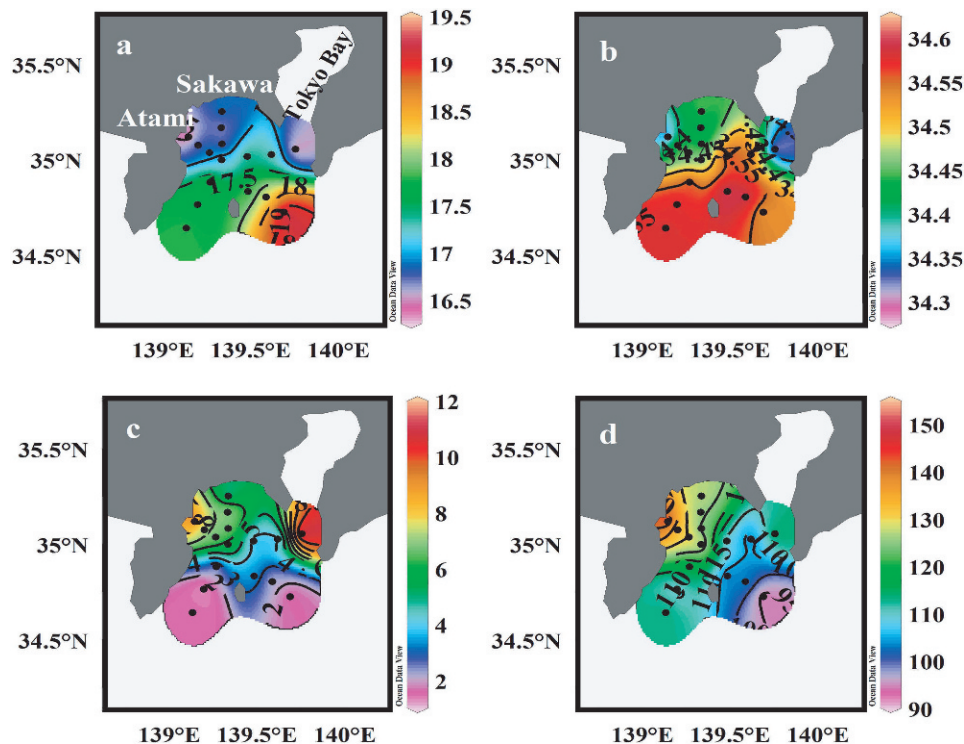


Fig. 1. Spatial variations in (a) sea-surface temperature ($^{\circ}\text{C}$), (b) salinity, (c) chlorophyll *a* (mg m^{-3}), and (d) dissolved oxygen saturation (%) in the surface waters of Sagami Bay during May 2006.

offshore and showed relatively low temperatures off Atami and Tokyo Bay. SSS varied in a similar way, showing lower-saline waters (0.3 lower) in the coastal compared to offshore regions (Fig. 1b). Freshwater discharge by rivers has a strong influence on the surface salinity of Sagami Bay during the summer. Two major rivers, Sagami and Sakawa, open into Sagami Bay in the north. The amount of discharge of freshwater is greater in summer ($7\text{--}10 \times 10^6 \text{ m}^3 \text{ d}^{-1}$) than in winter ($3\text{--}5 \times 10^6 \text{ m}^3 \text{ d}^{-1}$; Iwata 1985). Counterclockwise currents along the coast are dominant during entire year and mix coastal low-saline waters with high-saline offshore waters. The mixed-layer depth, defined as the depth where temperature decreases by 0.5°C from that of surface, varied from 18 to 40 m, with relatively deeper mixed layers in central Sagami Bay. The euphotic zone depth was similar to the mixed-layer depth. Wind speeds varied from 0.5 to 10.3 m s^{-1} , and relatively higher values occurred off Tokyo Bay. Otherwise, wind speeds were less than 7 m s^{-1} over the entire bay. Surface Chl *a* concentrations ranged from 1 to 10 mg m^{-3} and decreased from coastal to offshore regions (Fig. 1c). The highest Chl *a* value was observed off Atami and Tokyo Bay. This pattern is consistent with low SST and SSS, suggesting that vertical mixing might have enhanced nutrients inputs and, thus, Chl *a*. One day prior to our first sampling, the highest winds ($\sim 10 \text{ m s}^{-1}$) were observed off Tokyo Bay, which might have led to enhanced nutrient supply through vertical mixing. Tokyo Bay also receives discharges of domestic sewage, which contains much nitrogen and phosphorus from surrounding big

cities, resulting in eutrophication (Nomura and Yoshida 1997). Advection of Chl *a*-rich Tokyo Bay waters to the study site was also possible. The spreading of high-Chl *a* contours from the coastal to offshore areas suggests advection of coastal waters into central Sagami Bay (Fig. 1c). Oxygen saturation in the upper layer broadly summarizes the recent history of biological activity (Hendricks et al. 2004). O_2 supersaturation was observed in the entire bay (100–122%), except in the southwestern portion of the bay ($\sim 97\%$) (Fig. 1d), which showed higher oxygen saturation in the coastal compared to offshore regions, presumably due to biological production exceeding community respiration, but also perhaps due to the high flux of oxygen from the atmosphere. The fact that the distribution of oxygen saturation was similar to that of Chl *a* suggests that oxygen saturation was mainly due to phytoplankton production. Based on the mixed-layer depth and sea-to-air flux of O_2 , the residence time of oxygen in the mixed layer varied from 8 to 14 d.

Three processes control $\delta^{18}\text{O}$ distribution in surface waters: biological oxygen production, community respiration, and air–sea exchange. Since lighter $\delta^{18}\text{O}$ is produced during photosynthesis ($\delta^{18}\text{O} = -22.96$ per mil with reference to atmospheric O_2), higher rates of production relative to respiration result in lower $\delta^{18}\text{O}$ values. Community respiration increases $\delta^{18}\text{O}$ due to the preferential consumption of ^{16}O (Bender 1990), while air–sea exchange drives dissolved $\delta^{18}\text{O}$ toward close to atmospheric equilibrium ($\delta^{18}\text{O} = 0.8$ per mil at 25°C). Therefore, the distribution $\delta^{18}\text{O}$ in dissolved oxygen in the surface waters

Table 1. Spatial variations in SST, SSS, $\delta^{17}\text{O}$, $\delta^{18}\text{O}$, and $^{17}\Delta$ anomaly in Sagami Bay.

Sta.	Latitude (°N)	Longitude (°E)	SST (°C)	SSS	$\delta^{17}\text{O}$ (per mil)	$\delta^{18}\text{O}$ (per mil)	$^{17}\Delta$ anomaly (per meg)
A0	35.119	139.145	16.258	34.304	-0.951	-2.135	155.657
A1	35.075	139.199	16.766	34.460	-0.322	-0.802	93.566
A2	35.037	139.263	16.932	34.464	-0.186	-0.554	100.786
S0	35.253	139.334	16.948	34.460	-0.030	-0.279	114.749
S1	35.167	139.332	16.576	34.382	-0.531	-1.242	112.304
S2	35.082	139.335	16.503	34.404	-0.539	-1.300	134.515
S3	34.999	139.333	17.220	34.467	-0.259	-0.687	96.907
T4	35.017	139.479	17.456	34.586	-0.293	-0.736	87.895
T5	35.028	139.618	17.310	34.567	-0.156	-0.462	83.520
T6	35.055	139.755	16.397	34.287	0.306	0.406	95.743
O4	34.834	139.482	17.771	34.600	0.229	0.373	35.992
O5	34.804	139.586	18.176	34.600	0.099	0.114	40.446
O6	34.726	139.688	19.337	34.525	0.313	0.496	56.324
I04	34.883	139.268	17.961	34.580	0.629	1.143	37.634
I05	34.764	139.196	17.597	34.578	0.479	0.870	28.437
I06	34.642	139.131	17.792	34.578	0.779	1.442	32.881

indicates which process (primary production, respiration, or atmospheric exchange) is predominant in the water column. The distribution of $\delta^{18}\text{O}$ values (Table 1) shows that coastal waters have relatively lower $\delta^{18}\text{O}$ values (< -0.3 per mil) than offshore waters (> -0.1 per mil), suggesting higher production in the coastal regions (Fig. 2a). The lowest $\delta^{18}\text{O}$ value (< -1 per mil) was found off Atami and Tokyo Bay, suggesting that the highest rates of production occurred in these two regions. The $\delta^{18}\text{O}$ values were slightly more than equilibrium (0.9 to 1.1 per mil) in the southwestern bay, where O_2 undersaturation was observed, which could be due to dominance of respiration over production.

Spatial variations in $^{17}\Delta$ anomaly and plankton metabolic rates—The $^{17}\Delta$ anomaly was computed following Angert et al. (2003):

$$^{17}\Delta = 10^6 \{ \ln[(\delta^{17}\text{O}/1000) + 1] - 0.518 \ln[(\delta^{18}\text{O}/1000) + 1] \} \quad (2)$$

The constant (0.518) is the slope of $\delta^{17}\text{O}$ vs. $\delta^{18}\text{O}$ for mass-dependent processes and represents consumption of oxygen during respiration (Luz and Barkan 2005).

The $^{17}\Delta$ anomaly ranged from 27 to 155 per meg relative to atmospheric O_2 (Fig. 2b). The highest anomaly (155 per meg) was found off Atami, and the lowest values were offshore (27 to 57 per meg) (Fig. 2b). There were clear gradients in the $^{17}\Delta$ anomaly from offshore to coastal regions. The $^{17}\Delta$ anomaly in the mixed layer is influenced by in situ GPP and influx of oxygen from the atmosphere. However, the distribution of the $^{17}\Delta$ anomaly is consistent with that of Chl *a* and oxygen saturation distributions, suggesting a predominant influence of biological production on the $^{17}\Delta$ anomaly relative to air-sea exchange. The average measured wind speeds over one week were used for computation of GPP using the following equation (Luz and Barkan 2000):

$$\text{GPP} = k\text{Co}(\Delta^{17}\text{O} - \Delta_{\text{eq}}) / (\Delta_{\text{max}} - \Delta^{17}\text{O}) \quad (3)$$

where GPP is the gross O_2 production ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), k is the piston velocity, Co is the equilibrium O_2 concentration, Δ_{eq} is the $^{17}\Delta$ of dissolved O_2 at equilibrium solubility (16 ± 5 per meg), and Δ_{max} is a specific value of photosynthetically produced O_2 (249 ± 15 per meg; Luz and Barkan 2000). Oxygen saturation was computed based on Garcia and Gordon (1992), and the piston velocity was derived from Wanninkhof (1992) using weekly average observed wind speeds.

Previous studies in central Sagami Bay have shown that the variation in the $^{17}\Delta$ anomaly within the mixed layer is smaller than measurement errors (Sarma et al. 2005, 2006a). Thus, the $^{17}\Delta$ anomaly in samples collected from 4-m depth are taken to be the mixed-layer average. GPP estimates based on Eq. 3 varied from 34 to 963 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in the mixed layer, where the higher production rates were observed in the coastal regions (Fig. 2c). Production off Atami ($963 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) was ~ 15 times higher than offshore regions ($34.2\text{--}143 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), and GPP was positively correlated with Chl *a* ($p < 0.001$; $n = 16$) and oxygen saturation ($p < 0.001$; $n = 16$), suggesting that oxygen saturation in the surface layers might partially be due to the photosynthetically produced oxygen. In this model, it is assumed that vertical mixing with subsurface water has no influence on the $^{17}\Delta$ anomaly in the mixed layer. However, Sarma et al. (2005, 2006a) showed that a small amount of the $^{17}\Delta$ anomaly increase was possibly due to vertical mixing, and this contribution becomes significant at higher wind speeds ($\sim 10 \text{ m s}^{-1}$). Since wind speeds were relatively low ($< 7 \text{ m s}^{-1}$) during our study period, except off Tokyo Bay, the contribution from vertical mixing was probably insignificant.

Net-to-gross production ratios (N:G) were computed based on the equation from Hendrick et al. (2004)

$$\text{N} : \text{G} = [(\text{O}_2/\text{O}_{2 \text{ sat}}) - 1] \times (\Delta_{\text{max}} - \Delta^{17}\text{O}) / (\Delta^{17}\text{O} - \Delta_{\text{eq}}) \quad (4)$$

where $\text{O}_2/\text{O}_{2 \text{ sat}}$ is biological oxygen saturation. Biological oxygen supersaturation is defined as O_2 supersaturation in

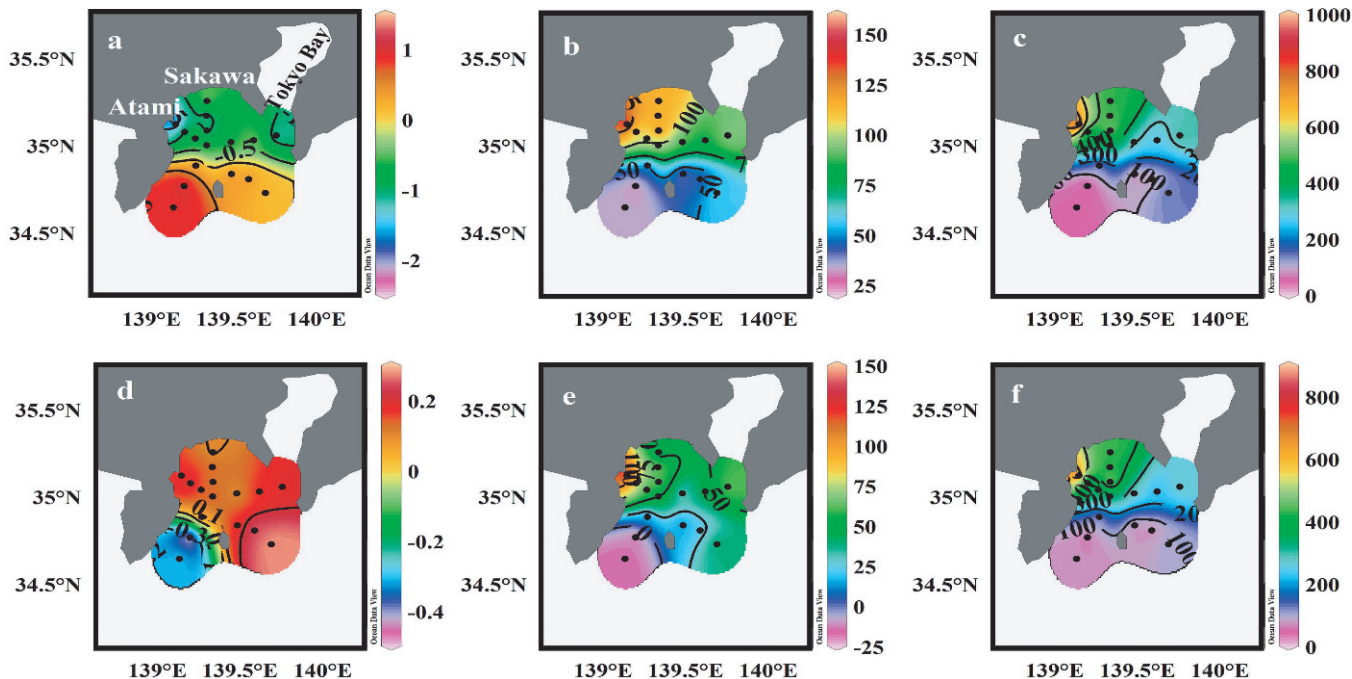


Fig. 2. Spatial variations in time-integrated (a) $\delta^{18}\text{O}$ (per mil), (b) $^{17}\Delta$ anomaly (per meg), (c) GPP ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), (d) N:G ratio, (e) NCP ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), and (f) community respiration ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) in the surface waters of Sagami Bay during May 2006.

excess of Ar supersaturation, and it is equal to biological oxygen saturation minus one. It can be derived as $\text{O}_2:\text{Ar}$ ratio divided by the $\text{O}_2:\text{Ar}$ ratio at saturation, $([\text{O}_2]/[\text{Ar}])/([\text{O}_2]_{\text{sat}}/[\text{Ar}]_{\text{sat}})$. The extent of saturation of O_2 and Ar is a function of temperature and salinity (Weiss 1970). The other terms in Eq. 4 are same as in Eq. 3.

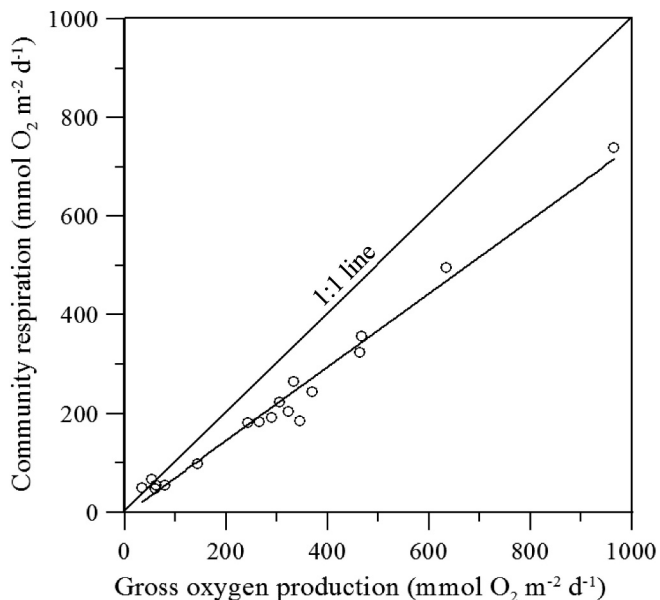


Fig. 3. Relationship between gross oxygen production and community respiration in Sagami Bay.

The ratio of net-to-gross production (N:G) indicates the fate of photosynthetic products in the upper layer. A higher N:G ratio indicates that a large portion of photosynthetically produced carbon is eventually exported to deeper layers, whereas a lower ratio indicates that most of the product is consumed in the upper layers and a lower fraction is exported (Dickson et al. 2001). In addition, a negative value for N:G suggests that the system is heterotrophic, i.e., community respiration is greater than primary production. N:G ratios in Sagami Bay varied from -0.5 to 0.28 , where higher ratios occurred in the southeastern bay (0.17 to 0.28) and the lowest ratios were in the southwestern bay (0.09 to -0.49); in the rest of the bay, it varied from 0.07 and 0.26 (Fig. 2d). Negative N:G ratios in the southwestern bay are consistent with low oxygen saturation ($\sim 97\%$) and heavier $\delta^{18}\text{O}$ (~ 1.1 per mil), suggesting that community respiration was dominant over production. N:G ratios were exceptionally low in the northern basin (0.07 to 0.1) where the Sakawa River discharged. Shiah et al. (2006) found that bacterial growth rate increases with increase in river discharge from the Chang-Jiang River to the East China Sea. The low ratios in the northern basin could thus be due to enhanced bacterial respiration associated with freshwater discharge. In upwelling areas, off Atami and Tokyo Bay, where GPP was several times higher than elsewhere in the bay, N:G ratios were relatively higher (~ 0.2) (Fig. 2d).

Net community production (NCP), computed from gross production and N:G ratio ($\text{GPP} \times \text{N:G}$), ranged from -17 to $146.5 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, and the highest and

Table 2. Hydrography, GPP, N:G, and P:R ratios using incubation technique and $^{17}\Delta$ anomaly and $O_2:Ar$ at sta. S3 in the central Sagami Bay.

Parameter	03 May 2006	04 May 2006	07 May 2006	08 May 2006	$^{17}\Delta$ anomaly & $O_2:Ar$
Temperature	18.00	17.24	17.00	16.76	16.82
Salinity	34.57	34.51	34.49	34.47	34.51
NO_3	2.22	2.36	1.21	1.37	1.87
GPP	300.2	318.6	267.6	393.3	345.2
N:G	0.66	0.61	0.18	0.57	0.47
P:R	2.92	2.55	1.22	2.34	1.87

lowest net production rates occurred in the upwelling regions and western entrance of Sagami Bay, respectively (Fig. 2e). This suggests that heterotrophic conditions prevailed in the western bay mouth, whereas autotrophy dominated in the rest of the bay. Advection of excess carbon in the coastal regions may support heterotrophy in the offshore regions. Community respiration rates, computed as the difference between GPP and NCP, varied from 50.2 to 739.5 $mmol O_2 m^{-2} d^{-1}$; clear coastal and offshore gradients were observed (Fig. 2f). The relationship between time- and depth-integrated GPP to R (Fig. 3) was similar that of Williams (1997), and the slope is close to unity (0.75), which is almost the same as that observed by Williams (1997). Most of the values lie well below the 1:1 line (the point of metabolic balance, where heterotrophy matches autotrophy), suggesting that a significant amount of carbon is available for either accumulation in the mixed layer or export to deeper layers (Fig. 3).

GPP was always higher than R in Sagami Bay except in the southwestern bay. The production-to-respiration ratio (P:R) ranged from 0.68 to 1.87 (mean 1.25 ± 0.07). Recently, Hashimoto et al. (2006) observed summer mean P:R ratios in central Sagami Bay (sta. S3) of 1.2 ± 0.1 based on 4 yr of data, which is consistent with our observations. Hoppe et al. (2002) found that large oceanic regions are dominated by net heterotrophy, whereas autotrophy prevails in the high latitudes. Ducklow and McAllister (2005) observed that major portions of coastal regions are net autotrophic. Our results, therefore, indicate that net heterotrophy in open-ocean regions may be supported by excess carbon delivered from coastal regions through lateral advection (del Giorgio and Duarte 2002).

In order to assess the way in which short-term variability in plankton metabolic rates could influence our measurements, ^{18}O -enriched and DO incubation experiments were conducted in central Sagami Bay (sta. S3) for 4 d, and results were used to obtain estimates of GPP, N:G, and P:R ratios in the upper 40 m. GPP ranged from 267.6 to 393.3 (mean 319.9 ± 26) $mmol O_2 m^{-2} d^{-1}$, N:G ratios ranged from 0.18 to 0.66 (mean 0.51 ± 0.08), and P:R ratios varied from 1.2 to 2.9 (2.25 ± 0.36). Mean rates are consistent with estimates based on oxygen isotopes and $O_2:Ar$ ratios (345 ± 72 , 0.47 ± 0.04 , and 1.87 ± 0.31 , respectively) (Table 2). This strongly suggests that the oxygen-isotope technique captures short-term variations in

plankton metabolic rates. Short-term variations in plankton metabolic rates (Table 2) may be due to changes in environmental conditions, water mass structure, or problems involved in the incubation techniques. For example, the incubation experiments imply that variations in plankton metabolism and its balance are up to 13–23%, since significantly higher production rates were observed on 08 May 2006 (about 23%), and lower rates were observed during 07 May 2006 (by 13%) from that of mean GPP by $^{17}\Delta$ anomaly. Hence, the experimental conditions on the day of incubation reflect results that might lead to either under- or overestimation of the given process and, therefore, their metabolic balance. Hence, time-integrated metabolic rates are required to understand organic carbon balance in the ecosystem.

The important remaining question is whether the estimated excess of production over consumption in the upper water column is sufficient to sustain export production. Our understanding of deep-water metabolism is very limited, but a number of studies have attempted to determine export production as a fraction of surface-water production. The broad generalization has been made (Berger et al. 1989) that 10–20% of primary production is exported from the euphotic zone, with the likelihood that a greater percentage is exported in areas of high production. Community respiration linearly correlates with GPP, and its slope suggests that community respiration consumes up to ~73% of the GPP in Sagami Bay, where the rest is exported to the aphotic zone as sinking particulates or accumulates in the water column as dissolved organic carbon. The sinking organic carbon fluxes measured below the mixed layer (~40 m) using floating sediment traps over an 8-d period suggest that 12% of GPP sinks to the aphotic zone as particulate organic carbon (Y. Yamada pers. comm.). However, Honda et al. (2006) suggested that the trapping efficiency of floating sediment traps could be as low as 20% to 30%. Even if 30% of the sinking organic carbon were trapped by the floating sediment traps, export production could account for only 20% of GPP; hence, a significant amount of carbon presumably accumulates as DOC in the water column and might be available for respiration. Therefore, the fate of the dissolved organic carbon in the upper layers of the bay is an important element in the overall carbon balance in Sagami Bay.

Earlier studies based on incubation experiments at the time-series station in central Sagami Bay (Hashimoto et al. 2006) suggested that net heterotrophy exists from April to August and net autotrophic conditions prevail in other months. However, our results during May at the same stations showed large daily variations in plankton metabolic rates; for instance, the P:R ratio varied from 1.2 to 2.9 from 03 to 08 May 2006. Therefore, short-term integrated rates might lead to misinterpretation of the long-term process in the system. On the other hand, the first measurements of spatial variations of time-integrated plankton metabolic rates and their balance in Sagami Bay revealed that net autotrophy exists in the eutrophic coastal waters, and net heterotrophy exists in the oligotrophic open-ocean regions. The export of excess

carbon from the coastal regions to the open sea might support open-sea net heterotrophy in Sagami Bay. On the other hand, Karl et al. (2003) observed a short-term increase in dissolved O₂ in the subtropical North Pacific at HOTS and attributed this to episodic high-production events driven by winds, which are difficult to observe in incubation experiments. Such episodic high-production events can now be measured using the triple isotope method, which allows accurate long-term measurements of plankton metabolic balance, leading to better understanding of global rates.

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