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Relationship between net and gross primary production in the Sagami Bay, Japan

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Abstract

Net and gross primary production (GPP), based on the incorporation of ^{13}C-labeled inorganic carbon into particulate carbon and O_2 production, were compared from September 2001 to July 2003 in Sagami Bay, Japan. Euphotic zone integrated GPP, ^{13}C uptake, and their ratio (^{13}C uptake : GPP) ranged from 40 to 331, 14 to 163 mmol C m^{-2} d^{-1}, and 0.34 to 0.69, respectively. The ^{13}C uptake : GPP ratios were relatively lower in summer (low nutrient, LN) than from fall to spring (high nutrient, HN), with a mean value (±standard error) of 0.52 ± 0.03 during the study period. The mean value of the ratio in the upper water column above which 20% of surface light penetrates was higher during HN than during LN periods. On the contrary, no significant differences were observed between HN and LN periods in the depths at which <10% light penetrates. Algal respiration was 36% of GPP in the study periods. The sum of ^{13}C uptake and algal respiration accounted for 58–100% of GPP, with a mean value of 80%. This implies that about 20% of GPP might have been excreted as dissolved organic cargon and/or mineralized as light respiration.

Primary production is one of the most important components of the biogeochemical carbon cycle in aquatic systems. Generally, the primary production is estimated from the rate of uptake of inorganic carbon into particulate carbon and/or the rate of evolution of oxygen into the water. In incubations of 24 h, the former method is considered to provide the values closest to net primary production (NPP), while the latter comes closest to gross primary production (GPP) (e.g., Falkowski and Raven 1997). It is important to estimate ratios of NPP : GPP in order to understand the ecosystem and carbon balance in the ocean. This ratio provides information on the ability of an ecosystem to retain production and to set an upper limit on the amount of production that can be exported from the euphotic zone (Dickson et al. 2001). Taking various factors into account, Laws et al. (2000) calculated the theoretical ratio of 0.48 for the Arabian Sea. However, little is known about how this ratio varies with season. Difference between particulate organic carbon (POC) production and GPP is due to not only (light+dark) respiration but also to excretion of dissolved organic carbon (DOC). The excretion rate of DOC by phytoplankton is affected by nutrient concentration (Williams 1990). Consequently, it is expected that the ratios of POC production to GPP vary seasonally.

We measured the incorporation rate of ^{13}C into particulate material only as well as the oxygen evolution rate using the light–dark bottle method. Unfortunately, no $DO^{13}C$ measurements were made during our experiments. In this article, we present the seasonal variations of ^{13}C uptake, GPP, and $PO^{13}C$: GPP ratios in the Sagami Bay for a period of approximately 2 yr.

Materials and methods

Sampling—Time-series observations were carried out in the Sagami Bay from September 2001 to July 2003 at Sta. S3 on board the R/V *Seiyo Maru* from the Tokyo University of Marine Science and Technology (Fig. 1). Hydrographic data (water temperature, salinity) and water samples were collected using a CTD (Falmouth Scientific) rosette system fitted with Teflon-coated Niskin bottles of 8-liter capacity. The vertical photosynthetically active radiation (PAR) profiles were measured using a natural fluorescence sensor (PNF 2300, Biospherical Instruments). The samples for determination of ^{13}C uptake and GPP were collected from six depths corresponding to 100%, 30%, 20%, 10%, 5%, and 1% of the surface irradiance with reference to the PAR profile. The seawater samples for nutrient analysis were collected from

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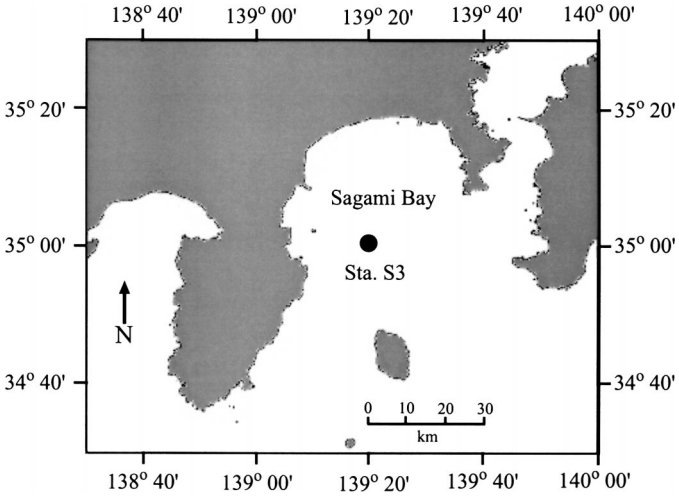

Fig. 1. Sampling location in the Sagami Bay, Japan.

8 to 11 depths above 200 m in depth. The incident solar radiation was monitored with a LiCor 2 sensor during the incubation experiments.

Chlorophyll a—Aliquots of 200–300-mL samples were filtered onto 25-mm Whatman GF/F filters under gentle aspiration (<200 kilopascals). Chlorophyll *a* (Chl *a*) was immediately extracted by immersing the filter in *N*,*N*-dimethylformamide (Suzuki and Ishimaru 1990), and the samples were preserved at −20°C until on-shore analysis was performed. Chl *a* concentrations were determined using a Turner Design Model 10-AU fluorometer calibrated with commercial Chl *a* (Wako Pure Chemical Industries), according to the method of Parsons et al. (1984). Euphotic zone integrated standing stocks were obtained by trapezoidal integration of the volumetric data down to the depth of 1% surface incident irradiance.

Nitrate+nitrite—Samples were collected in polystyrene bottles, frozen immediately after collection, and stored at −20°C until analysis. Nitrate+nitrite concentrations were measured with a Bran and Luebbe AACS III.

Photosynthetic ^{13}C incorporation—Seawater samples from each depth were immediately transferred into three transparent 250-mL acid-cleaned polycarbonate bottles. Seawater in the bottle was spiked with a ^{13}C–$NaHCO_3$ (99 atm% ^{13}C; Shoko Corporation) solution. The ^{13}C enrichment was about 10% of the total inorganic carbon in the ambient water. Incubation experiments were begun within about 1 h after sample collection. The samples were incubated for 24 h in an on-deck incubator that simulated the irradiance at the original sampling depths by use of various combinations of neutral-density and blue plastic filters. The deck incubator was equipped with a cooling and heating system so as to keep the water temperature within ±0.5°C during incubation. During hours of darkness, the incubators were covered with opaque screens to prevent artifacts due to the ship's deck light. Immediately following incubation, the samples were filtered directly through precombusted (450°C for 4 h) Whatman GF/F filters under gentle vacuum (<200 kilopascals), and the particulate matter on the Whatman GF/F filters was rinsed with prefiltered seawater. The filtered samples were immediately frozen and stored at −20°C until isotope analysis was performed on land. The filters were treated with HCl fumes for 4 h to remove inorganic carbon and were completely dried in a vacuum desiccator. The isotopic ratios of ^{13}C to ^{12}C and particulate organic carbon were determined by a combined system of an EA1110 (CE Instruments) elemental analyzer and a DELTA Plus (Finigan MAT) mass spectrometer. Primary productivity was calculated according to the equation described by Hama et al. (1983). Euphotic zone integrated values were calculated as the standing stock of Chl *a*.

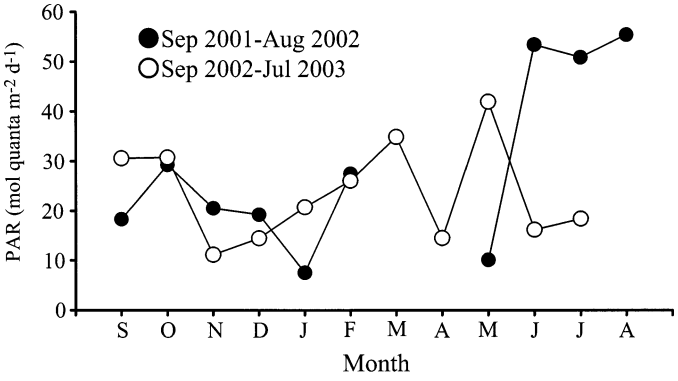

Fig. 2. Seasonal variation in PAR at Sta. S3 in the Sagami Bay.

Oxygen production (GPP)—GPP was determined from in vitro changes in dissolved oxygen after 24-h light and dark bottle incubations. Seawater was carefully siphoned into nine 100-cm^3 gravimetrically calibrated borosilicate glass bottles from Niskin bottles by means of a silicone tube. From each depth, three dark and light bottles were placed in the same incubator as ^{13}C uptake experiments. The dark bottles were wrapped with aluminum foil and were kept in the dark bags, and the light bottles were incubated under irradiance conditions that simulated those of the original sampling depth as the ^{13}C uptake bottle. After incubation, the light and dark bottles were fixed immediately. Fixing, storage, reagent preparation, and standardization were followed the recommendations of Carritt and Carpenter (1966). Dissolved oxygen concentration was measured with automated precision Winkler titration performed with a Metrohm 785 DMP Titrino, utilizing a potentiometric end point. Euphotic zone integrated values were calculated as the standing stock of Chl *a*. Laws (1991) reported a photosynthetic quotient between 1.1 and 1.4. For convenience, the photosynthetic quotient using this conversion was assumed to be 1.2 (Smyth et al. 2004).

Results and Discussion

PAR ranged from 7.6 to 55.5 mol quanta m^{-2} d^{-1} during the experimental period (Fig. 2). When PAR was compared between September 2001 and August 2002 and September 2002 and July 2003, it was greatly different from May until

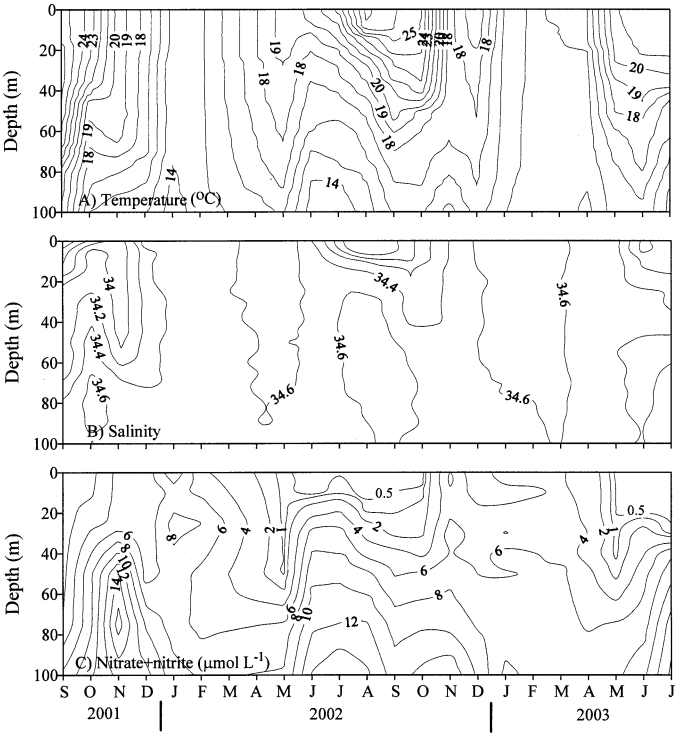

Fig. 3. Vertical and temporal distribution of (A) temperature, (B) salinity, and (C) nitrate+nitrite concentration from September 2001 to July 2003.

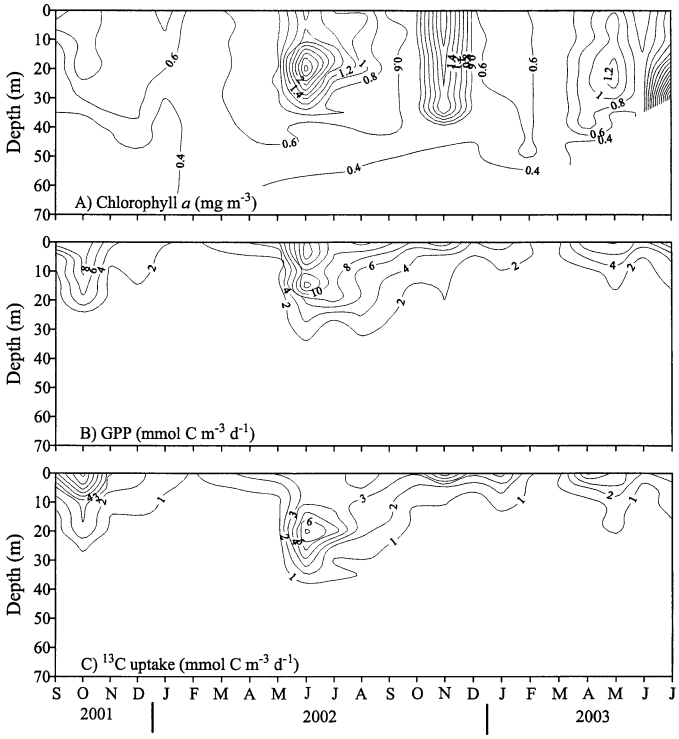

Fig. 4. Vertical and temporal distribution of (A) chlorophyll *a* concentration, (B) gross primary production (GPP), and (C) ^{13}C uptake from September 2001 to July 2003.

July in both years, although the variation was similar from September to February in the next year. Spatial and temporal variations of temperature and salinity are shown in Fig. 3A and B. The surface temperature was 15–27°C and more than 20°C in May/June–October (summer) and about 15°C during January–March (winter). The surface layer was high temperature–low salinity in summer and low temperature–high salinity in winter. In summer, the thermocline existed at 20–40 m, while the depth of the upper mixed layer deepened to more than 100 m in winter. A similar phenomenon was reported previously in the Sagami Bay (Kamatani et al. 1981). Regional upwelling was sporadically observed in October 2001, June–July and November 2002, and July 2003 (Fig. 3A). Takahashi et al. (1980) reported that local upwelling occurs in the Sagami Bay in summer. Depths of the euphotic layer and the mixed layer were from 30–67 and 10–131 m, respectively. The euphotic layer depth tended to be deeper than the mixed layer depth from spring to summer and shallower from fall to winter.

Nitrate+nitrite concentrations were more than 5 μmol L^{-1} during fall to winter in the water column, while the concentrations were less than 1 μmol L^{-1} in the upper 20 m during spring to summer (Fig. 3C). In particular, the concentrations were less than 0.5 μmol L^{-1} in the upper 10 m from June to October 2002 and in the upper 20 m from May to July 2003 by developed seasonal thermocline. The nitrate+nitrite of more than 5 μmol L^{-1} was brought to the vicinity of 40 m by upwelling in October 2001, June–July and November 2002, and July 2003 (Fig. 3C).

Chl *a* concentrations ranged from 0.2 to 3.6 mg m^{-3} within the euphotic zone during the observed period. Subsurface chlorophyll maximum (>1.5 mg m^{-3}) was found during June–July, November 2002, and June–July 2003 (Fig. 4A). High Chl *a*–concentration periods were associated with upwelling. Therefore, the variations of Chl *a* concentration are likely to be related to upwelling in the Sagami Bay.

GPP and ^{13}C uptake rates ranged from 0.1–16.9 and 0.1–9.4 mmol C m^{-3} d^{-1} within the euphotic layer during the observed period (Fig. 4B,C). Distributions of the GPP and ^{13}C uptake rates showed, generally, the maximum values at the surface and were different from that of the Chl *a* concentration. Although the nitrate+nitrite concentrations were less than 0.5 μmol L^{-1} in the upper 10 m from May to October 2002 and in the upper 20 m from May to July, the GPP and ^{13}C uptake rates were relatively higher than during any other period. This implies that phytoplankton growth is not greatly affected by nitrate+nitrite concentration in the Sagami Bay.

Temporal variations of Chl *a*, GPP, and ^{13}C uptake vertically integrated in the euphotic zone are shown in Fig. 5. The values of Chl *a*, GPP, and ^{13}C uptake were 16–64 mg m^{-2} and 40–331 and 14–163 mmol C m^{-2} d^{-1}, respectively, and were the highest in June 2002. The fluctuation of Chl *a* was irregular and did not show obvious seasonal variation (Kamatani et al. 1981). On the other hand, the variation of GPP tended to be relatively high in summer. The seasonal trend of GPP almost matched that of ^{13}C uptake (*t*-test, $r = 0.96$, $p < 0.001$). The values of GPP and ^{13}C uptake were relatively low in June–July 2003. PAR was excessively low in June–July 2003 (Fig. 2). The low GPP and ^{13}C uptake

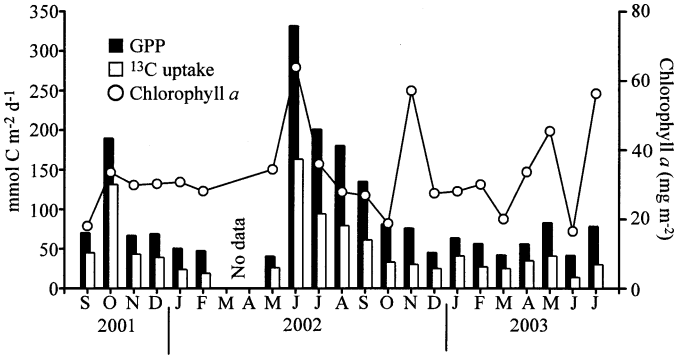

Fig. 5. Temporal variations in vertically integrated chlorophyll *a*, gross primary production (GPP), and ^{13}C uptake.

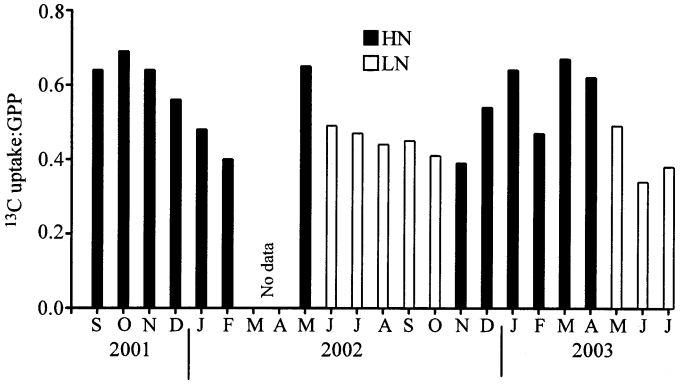

Fig. 6. Seasonal variation in the ratio between ^{13}C uptake and gross primary production (GPP).

rates could be due to low PAR. Chlorophyll-specific primary productivity is an index of growth rate. The variations of chlorophyll-specific GPP and ^{13}C uptake were 15–78 and 6–47 mg C mg Chl^{-1} d^{-1}. The chlorophyll-specific GPP and ^{13}C uptake rates positively correlated with PAR (*t*-test, $p < 0.01$). Consequently, the temporal variation of primary productivity is likely to be affected more greatly by light intensity than by nutrient concentration in the Sagami Bay (Smyth et al. 2004).

The temporal variations of ^{13}C uptake : GPP ratio are shown in Fig. 6. The ratios varied from 0.34 to 0.69, with a mean value (±standard error [SE]) of 0.52 ± 0.03. This implies that 50% of inorganic carbon taken up by phytoplankton is fixed as POC in the cell. The issue of what ^{13}C or ^{14}C incubations measure is highly controversial. There are reports in the eutrophic and oligotrophic regions in which 12-h to 24-h ^{14}C incubation measured something closer to gross production (e.g., Williams et al. 1983). On the other hand, it is also reported that the ^{14}C method gives an estimate that is close to net production when the incubation is 12–24 h long (e.g., Marra and Barber 2004). Our results were close to the net production. The ratios of ^{14}C uptake : GPP were found to be 0.48 in the Atlantic Ocean (Kiddon et al. 1995), 0.45 in the equatorial Pacific Ocean (Bender et al. 1999), and 0.45–0.65 in the Arabian Sea (Laws et al. 2000; Dickson et al. 2001). Our value in the Sagami Bay was close to those of the other regions. The ratios tended to be relatively lower during summer than during fall to spring. Nutrient concentration directly affects photosynthesis, especially carbon fixation (Falkowski and Raven 1997). When the nitrate+nitrite concentrations were less than 0.5 μmol L^{-1} in the upper 10 m, the ratios were less than 0.5. Hence, the experimental time was separated into a low-nutrient (LN) period (<0.5 μmol L^{-1}, June–October 2002 and May–July 2003) and a high-nutrient (HN) period (>0.5 μmol L^{-1}, the other months) by nitrate+nitrite concentration in the upper 10 m. The mean value (±SE) during the LN period was 0.44 ± 0.02 and during the HN period was 0.57 ± 0.03. Significant statistical difference was found between the ratios during the LN and the HN periods (*U*-test, $p < 0.01$). The ratios were higher in the HN than in the LN period (Fig. 6).

The spatial variations of ^{13}C uptake : GPP ratio within the euphotic layer are shown in Fig. 7. The mean values of the ratio in the upper 20% light depth were higher during the HN than during the LN period (Fig. 7). On the other hand, the values below 10% light depth were nearly equal between the HN and LN periods. Therefore, the difference between the HN and LN periods, as shown in Fig. 7, was due to that of the ratio in the upper 20% light depth. The ratio lowers by phytoplankton respiration and excretion of $DO^{13}C$. There is maintenance respiration and growth-rate–dependent respiration in dark respiration of phytoplankton (Langdon 1993). Most of the dark respiration in the surface layer is growth-rate–dependent respiration (Falkowski and Raven 1997). As described before, phytoplankton growth is not greatly affected by nitrate+nitrite concentration in the Sagami Bay. However, the excretion of DOC by phytoplankton is larger during the LN condition than during the HN condition (e.g., Williams 1990). The 20% light depth corresponds to approximately 10-m depths. Further, respiration rates in the light exceed those in the dark due to autotrophic metabolic processes, such as photoenhanced mitochondrial respiration, chlororespiration, and/or the Mehler reaction (Bender et al. 1999). The light intensity in the LN period was higher than in the HN period (*U*-test, $p < 0.05$). Consequently, the differences in the ratio in the upper 20% light depth are likely to be due to the excretion rate of DOC and/or light respiration. The ratios tended to decrease from 10% light depth to 1% light depth in the HN and LN conditions,

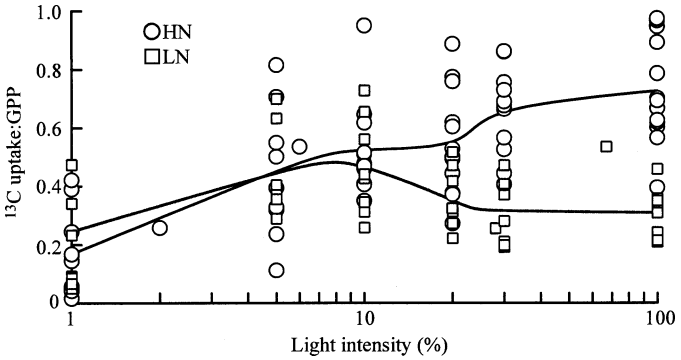

Fig. 7. Vertical change of the ratio between ^{13}C uptake and gross primary production (GPP) during the high-nutrient (HN) and the low-nutrient (LN) periods. Solid lines represent the mean values at each depth.

though the nutrient was replete below 10% light depth (Figs. 3C and 7). This is due to the fact that the proportion of maintenance respiration increased with decrease of the light intensity.

According to Steemann Nielsen and Hansen (1959), dark respiration of phytoplankton at the saturation light is about 10% of the average of the maximum gross photosynthetic rate. Therefore, algal respiration often has either been considered to be insignificant relative to heterotrophic respiration or has not been taken into account as an important component of community respiration. However, this value is reported to be an underestimate (Langdon 1993). As for the daily dark respiration : gross photosynthetic ratio, diatom population is 21%; cyanophyte-, prymensiophyte-, or chlorophyte-dominated populations are 30–36%; and dinoflagellate population is 70–90% (Langdon 1993). We roughly estimated algal respiration with phytoplankton population data in the Sagami Bay reported by Hashihama (2003) and daily dark respiration : GPP ratios obtained from Langdon (1993) using the following equation:

$$\text{Algal respiration} = \text{GPP} \times (0.21 \times \text{diatom proportion} + 0.80 \times \text{dinoflagellate proportion} + 0.33 \times \text{other phytoplankton proportion})$$

Respiratory quotient was assumed to be 1. Algal respiration was estimated to be from 14 to 121 mmol C m^{-2} d^{-1} from June 2002 to July 2003 and accounted for 31–38% of GPP, with a mean value of 36%. Grande et al. (1989) found that dark loss of $PO^{14}C$ (12–24 h) accounted for 26–36% of ^{14}C assimilation into particulate matter during the preceding 12-h incubation in the light. Duarte and Cebrián (1996) calculated that the average proportion of GPP respired by autotrophs from 154 reports was 35%. Kiddon et al. (1995) estimated that daily algal respiration accounted for 32% of GPP. Our value was close to the values reported previously. This indicates that phytoplankton respiration plays an important role on carbon cycle in the ocean.

What percentage does the total of ^{13}C uptake and algal respiration amount to with regard to GPP? The sum accounted to 58–100% of GPP and tended to be higher during the HN period (mean value: 92%) than during the LN period (mean value: 72%). The mean value throughout HN and LN periods was 80%. These results imply that a mean 28% of GPP may have been excreted as DOC and/or mineralized as light respiration by phytoplankton during the LN period and a mean 8% in the HN period. The mean deficiency throughout HN and LN periods was estimated to be 20% of GPP. Baines and Pace (1991) reported that an average percent of DOC was 13% from a regression model based on 225 observations. DOC excretion was from less than 10% to over 60% of GPP and varied greatly by environmental condition and phytoplankton species, although the extent of excretion was inversely proportional to nutrient concentration (Williams 1990). Recently, Marañón et al. (2004) reported that the average value of DOC production within the water column was 19%. Our speculated value was close to the value reported by Marañón et al. (2004). The DOC production would play an important role for the bacterial production. In the future, if excretion rates of DOC are measured simultaneously with ^{13}C uptake rates and GPP values, algal respiration will be estimated more precisely than our it was in our speculation.

Recently, the Fast Repetition Rate Fluorometer (FRRF) method to estimate primary production, nondestructively and continuously without bottle incubation, was developed (Suggett et al. 2001; Smyth et al. 2004). This technique can measure the GPP when the fluorometer is moved up and down in the water column. Sarma et al. (2005) reported that the GPP estimated by the FRRF method was approximately similar to that of the light and dark O_2 method. The estimate of primary production obtained from satellite remote sensing depends greatly on the calibration data, which are based on carbon incorporation into particulate material (Morel and Antoine 2002). However, the validation data related to remote sensing is very deficient. If the FRRF is used to the verification data about the primary production estimation from the satellites, our data will be useful for the transformation from GPP to NPP.

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