Metabolic balance of gross primary production and community respiration in Sagami Bay, Japan

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ABSTRACT: Gross primary production (GPP), community respiration (CR) and net community production (NCP) were studied for about 3 yr (September 2001 to June 2004) within the euphotic layer in the center of Sagami Bay, Japan. Oxygen fluxes exhibited seasonal and annual variations linked to the seasonal cycle of water column conditions and solar irradiance. GPP was >1 mmol O_2 m^{-3} d^{-1} above ca. 30 m in summer. CR exhibited seasonal patterns coupled to the variation in GPP. NCP at the surface was generally positive and maximum throughout the observation period, whereas at the subsurface layer it was negative, suggesting a balanced relationship between production and consumption of oxygen in the euphotic zone. GPP, CR and NCP integrated within the euphotic zone ranged from 44 to 264 (mean ± SE: 111 ± 13), 10 to 311 (100 ± 15) and –94 to 112 (11 ± 8) mmol O_2 m^{-2} d^{-1}, respectively. GPP and CR showed distinct seasonal patterns, and both tended to be higher from spring to summer (high productivity, HP) than from fall to winter (low productivity, LP). The threshold GPP for metabolic balance of the community (i.e. GPP:CR, $P:R$ = 1) was higher during the HP period (4.1 mmol O_2 m^{-3} d^{-1}) than during the LP period (0.4 mmol O_2 m^{-3} d^{-1}), with a mean value of 1.4 mmol O_2 m^{-3} d^{-1}. These results suggest the importance of organic carbon produced in the past or elsewhere in sustaining a relatively high background CR rate during the HP period in Sagami Bay.

KEY WORDS: Gross primary production · Community respiration · Net community production · Seasonal variation · Sagami Bay

INTRODUCTION

Carbon exchange by photosynthesis and respiration is the largest biogeochemical cycle in aquatic systems. Almost all estimates of oceanic primary production have been obtained by the ^{14}C tracer *in vitro* incubation technique (Steemann-Nielsen 1952). While this technique gives an approximate estimate of primary production, it does not give any information on heterotrophic processes by microorganisms, which play an important role in carbon cycles via microbial food webs (Azam et al. 1983). However, oxygen-based measurements offer a unique insight into physiological and biogeochemical processes that other tracers cannot provide.

The metabolic balance between gross primary production (GPP) and community respiration (CR) determines the net community production (NCP). It is very important to investigate the metabolic balance since the processes of GPP and CR are responsible for major flows of carbon in the upper waters of most aquatic systems. The balance between GPP and CR in oceanic systems determines whether the biological pump acts as a net source or sink of carbon (Williams 1993). However, this balance is variable on geographical, temporal and seasonal scales (del Giorgio et al. 1997, Geider 1997, Duarte & Agustí 1998, Williams 1998, del Giorgio & Duarte 2002), highlighting the need for ecosystem functioning over smaller scales to be studied in order to determine the trophic status on a global scale (Serret et al. 1999, González et al. 2001).

The GPP threshold (i.e. GPP at GPP = CR) separates the net autotrophic from net heterotrophic communities. The threshold is affected greatly by the heterotrophic respiratory rate. When bacterial and protozoan respiratory rates are low, the threshold becomes low. The threshold is relatively high (50 mmol O_2 m^{-3} d^{-1}) in coastal regions, whereas in the open sea it is relatively low (<3 mmol O_2 m^{-3} d^{-1}) (Duarte & Agustí 1998, González et al. 2001, Serret et al. 2001, Agustí et al. 2004, Agustí & Duarte 2005). Recently, Duarte et al. (2004) reported a value of about 4 mmol O_2 m^{-3} d^{-1} in a Spanish coastal area of the northwestern Mediterranean. However, knowledge about variation of the seasonal threshold is meager. It is also important to evaluate the depth of compensation irradiance (percentage irradiance at NCP = 0) related to the GPP threshold (Agustí & Duarte 2005).

Some studies on NCP succession have monitored GPP and CR in time series >1 yr (Smith & Kemp 2001, Berman et al. 2004, Duarte et al. 2004). Time series of the metabolism in productive coastal communities have shown that GPP and CR may be in balance over annual time scales (Sherr & Sherr 1996, Serret et al. 1999). Recently, it has been reported that the metabolic status of ecosystems also reflects net heterotrophy in coastal regions (Duarte et al. 2004). However, these studies have been carried out in areas very close to the shore, under eutrophic conditions, or under strong tidal influence within estuaries or fjords, situations well removed from steady-state conditions. Furthermore, some studies were restricted only to surface NCP measurements (e.g. Blight et al. 1995).

The seasonal variability of heterotrophic metabolism may be coupled to that of primary production (Duarte et al. 2004, Agustí & Duarte 2005), while others report no evidence of this coupling (Findlay et al. 1991, Agustí et al. 2004). The decoupling between CR and GPP is possibly related to the physical condition of the water column and/or to organic inputs.

Here, we present data on the spatial and temporal variations of GPP, CR and NCP within the euphotic zone over about 3 yr in the center of Sagami Bay, and examine the relationships between these parameters. We show that the photic zone of the bay has a net autotrophic character for most of the year, with a brief period of net heterotrophy in late spring and/or summer.

MATERIALS AND METHODS

Study area. Sagami Bay, situated on the eastern coast of Japan, covers an area of 2700 km^2, with a mean depth of 750 m (Fig. 1). Fresh water flows into Sagami Bay from 2 main rivers (Sagami and Sakawa) and other minor rivers. The amount of fresh water is greater in summer (7 to 10 × 10^6 m^3 d^{-1}) than in winter (3 to 5 × 10^6 m^3 d^{-1}) (Iwata 1985). Counterclockwise currents along the coast are dominant in the bay, independent of the season.

Sampling. Time-series observations were carried out monthly from September 2001 to June 2004 at Stn S3 in the center of Sagami Bay by the RV 'Seiyo Maru' of the Tokyo University of Marine Science and Technology and the RV 'Tansei Maru' of the Japan Agency for Marine-Earth Science and Technology (Fig. 1). Hydrographic data (water temperature, salinity) and water samples were collected with a CTD (Falmouth Scientific) rosette system fitted with Teflon-coated Niskin bottles of 8 l capacity. The vertical photosynthetically active radiation (PAR) profiles were measured using a natural fluorescence sensor (PNF 2300, Biospherical Instruments). The samples for determination of GPP were collected from the depths corresponding to 100, 30, 20, 10, 5, and 1 or 0.2% of the surface irradiance with reference to the PAR profile. The seawater samples for nutrient concentration analysis were collected from 9 depths above 100 m. The incident solar radiation was monitored with a LiCor 2 sensor during the incubation experiments.

Chlorophyll a. A total of 200 to 300 ml samples were filtered onto 25 mm Whatman GF/F filters under gentle aspiration (<250 kPa). Chlorophyll a (chl a) was immediately extracted by immersing the filter in N,N-dimethylformamide (Suzuki & Ishimaru 1990), and the samples were preserved at –20°C until on-shore analysis. 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 to the depth of 1% surface incident irradiance.
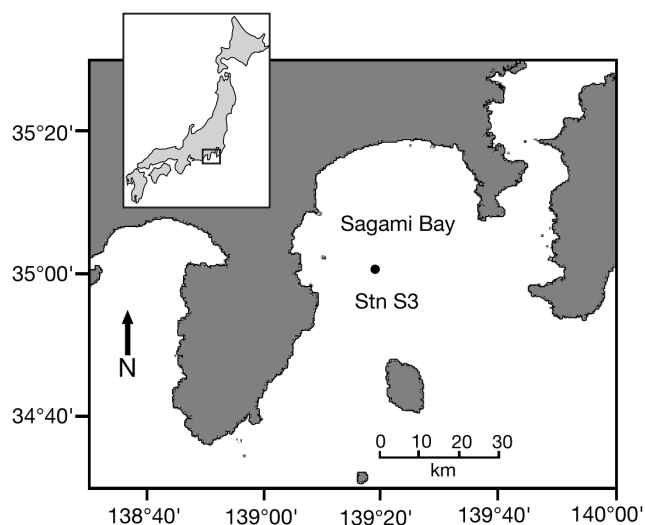
Fig. 1. Sampling location in Sagami Bay, Japan

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

GPP, CR and NCP. GPP and CR were 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 the Niskin bottle by means of a silicone tube. From each depth, 3 dark bottles and 3 light bottles 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. The dark bottles were wrapped with aluminum foil and were kept within dark bags, and the light bottles were incubated under irradiance conditions that simulated those of the original sampling depth. After incubation, the light and dark bottles were fixed immediately. Fixing and storage, reagents and standardization followed the recommendations of Carritt & Carpenter (1966). Dissolved oxygen concentration was measured by automated precision Winkler titration performed with a Metrohm 785 DMP Titrino, utilizing a potentiometric end point (Oudot et al. 1988). The average coefficient of variation (CV) of the dissolved oxygen concentration in triplicated bottles was about 0.05%. Euphotic-zone-integrated values were calculated as the standing stock of chl *a*. CR was determined from the oxygen change in the dark bottles, NCP was determined from the oxygen change in the light bottles, and GPP was calculated as the sum of CR and NCP.

RESULTS

Physicochemical condition

Comparison of PAR from September 2001 to August 2002, September 2002 to August 2003 and September 2003 to June 2004 showed lower values in June/July 2003 than in June/July of the other years (Fig. 2). PAR in June/July 2003 was equal to that in winter. The surface temperature ranged from 15 to 27°C and was >20°C in May/June to October (summer) and about 15°C from January to March (winter) (Fig. 3a,b). Water mass of high temperature–low salinity was present at the surface in summer and low temperature–high salinity in winter. In summer, the thermocline was at 20

to 40 m, while in winter the depth of the upper mixed layer deepened by >100 m. This was similar to the data reported previously for Sagami Bay (Kamatani et al. 1981, Kanda et al. 2003). The low salinity in the surface layer in summer is thought to be due to the influence of riverine water, as mentioned in the 'Introduction'. Regional upwelling was sporadically observed in October 2001, June/July and November 2002, July/August 2003 and May 2004 (Fig. 3a). Takahashi et al. (1980) reported that local upwelling occurs in Sagami Bay. The euphotic layer and upper mixed layer were found at depths of 30 to 67 and 10 to 131 m, respectively. The euphotic layer depth tended to be deeper than the upper mixed layer depth from spring to summer and shallower from fall to winter.

Nitrate + nitrite concentrations were >5 µmol l^{-1} during fall to winter in the water column, while the concentrations were <1 µmol l^{-1} in the upper 20 m during spring to summer (Fig. 3c). In particular, the concentrations were <0.5 µmol l^{-1} in the upper 10 m from June to October 2002 and in the upper 20 m from May to September 2003. This is due to the seasonal thermocline that suppresses vertical mixing. The nitrate + nitrite concentration of >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). The distributions of spatial and temporal variations in phosphate concentrations were also similar to those of nitrate + nitrite concentrations (Fig. 3d). However, phosphate concentrations >0.05 µmol l^{-1} were in the upper 10 m, where nitrate + nitrite concentrations were <0.5 µmol l^{-1}, indicating that N:P ratios were <16.

The percentage of oxygen saturation (%O$_2$ sat.) in the upper layer is a valuable indicator broadly summarizing the recent history of biological activity (Najjar & Keeling 1997). High levels of %O$_2$ sat. (>100%) were observed near the surface in summer (Fig. 4a). Low levels of %O$_2$ sat. (<100%) were found in subsurface waters in summer and in the water column during fall to spring, when the surface mixed layer was deep (Fig. 4a).
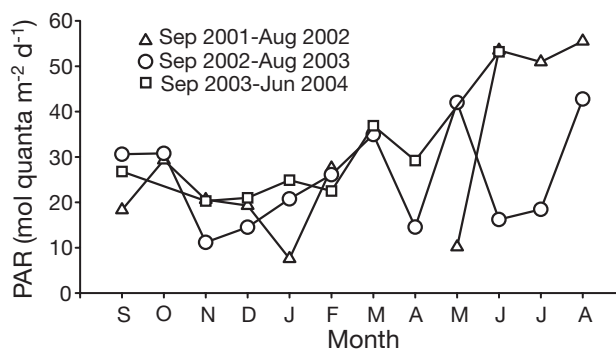

Fig. 2. Seasonal variation in photosynthetically active radiation (PAR) at Stn S3 in Sagami Bay

Phytoplankton biomass

Chl *a* concentrations reached values >1.5 mg m^{-3} in the subsurface layer in June/July and November 2002, June to October 2003 and April to June 2004 (Fig. 4b).

The fluctuation of chl *a* vertically integrated in the euphotic zone was irregular and did not show obvious seasonal variation (Kamatani et al. 1981) (Fig. 5). The mean value of chl *a* from September 2003 to June 2004 was the highest among the 3 studied years (Table 1).
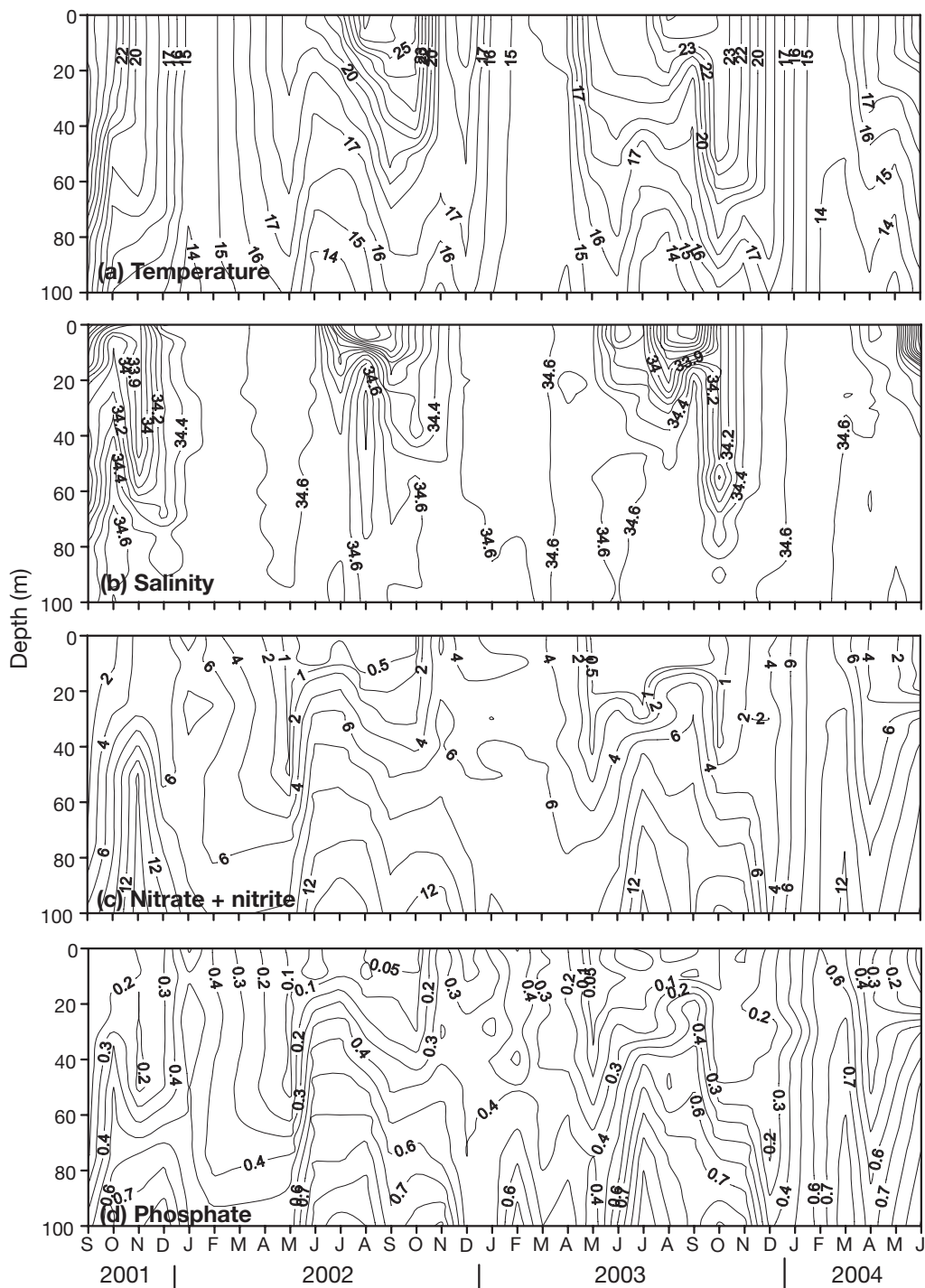

Fig. 3. Vertical and temporal distribution of (a) temperature (°C), (b) salinity, (c) nitrate + nitrite concentrations (µmol l^{-1}) and (d) phosphate concentrations (µmol l^{-1}) from September 2001 to June 2004

Oxygen flux and *P:R* balance

GPP ranged from 0.1 to 50.2 mmol O_2 m^{-3} d^{-1} within the euphotic layer during the observed period (Fig. 4c). Generally, GPP was >1 mmol O_2 m^{-3} d^{-1} above ca. 30 m in summer. The spatial and temporal variations in GPP normalized to chl *a* concentration were also similar to that of GPP (data not shown). GPP and %O_2 sat. were positively related (*t*-test, p < 0.001). This result reveals that the oxygen supersaturation at
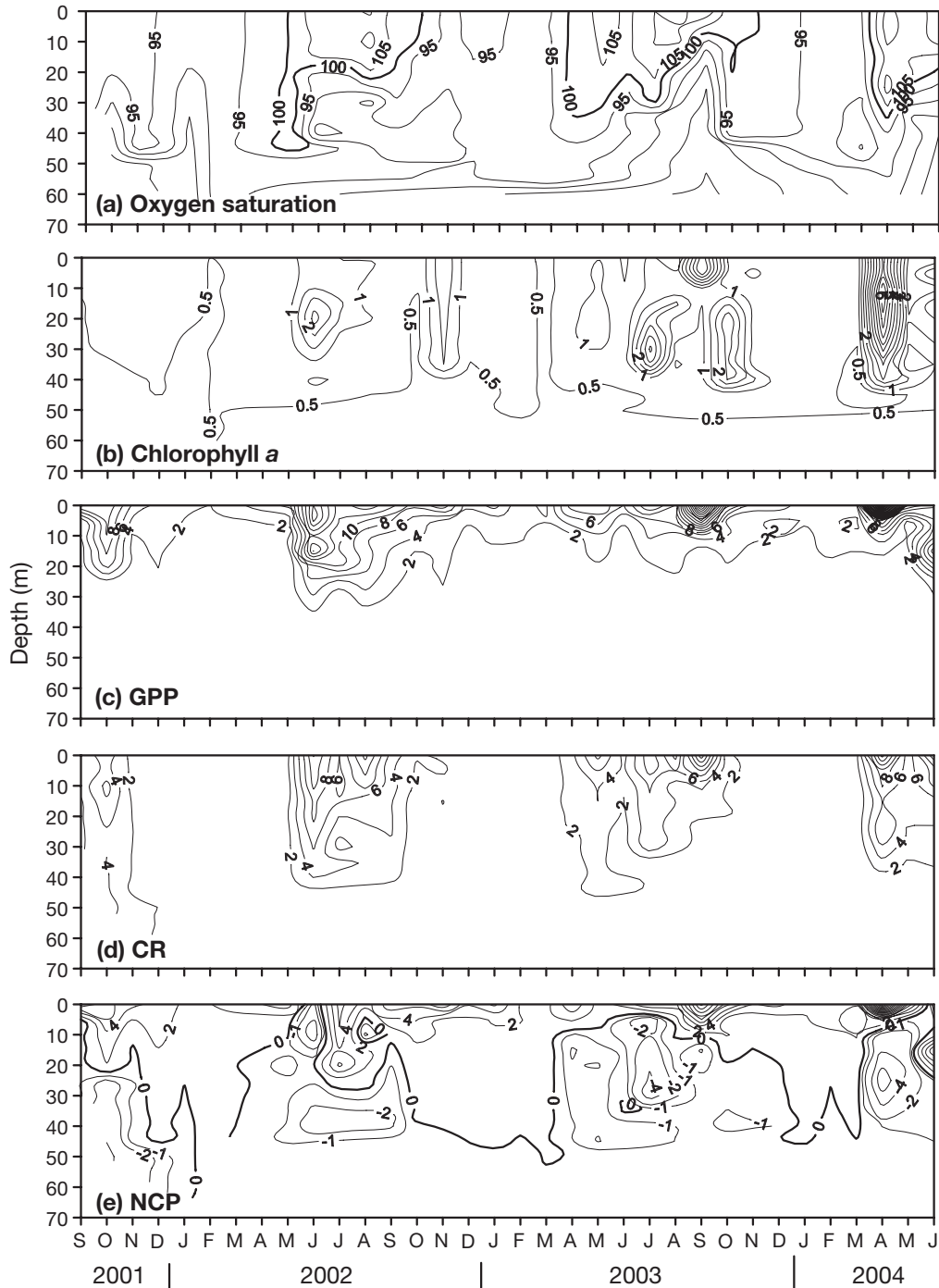

Fig. 4. Vertical and temporal distributions of (a) percentage of oxygen saturation (%), (b) chlorophyll *a* concentration (mg m^{-3}), (c) gross primary production (GPP; mmol O_2 m^{-3} d^{-1}), (d) community respiration (CR; mmol O_2 m^{-3} d^{-1}) and (e) net community production (NCP; mmol O_2 m^{-3} d^{-1}) from September 2001 to June 2004
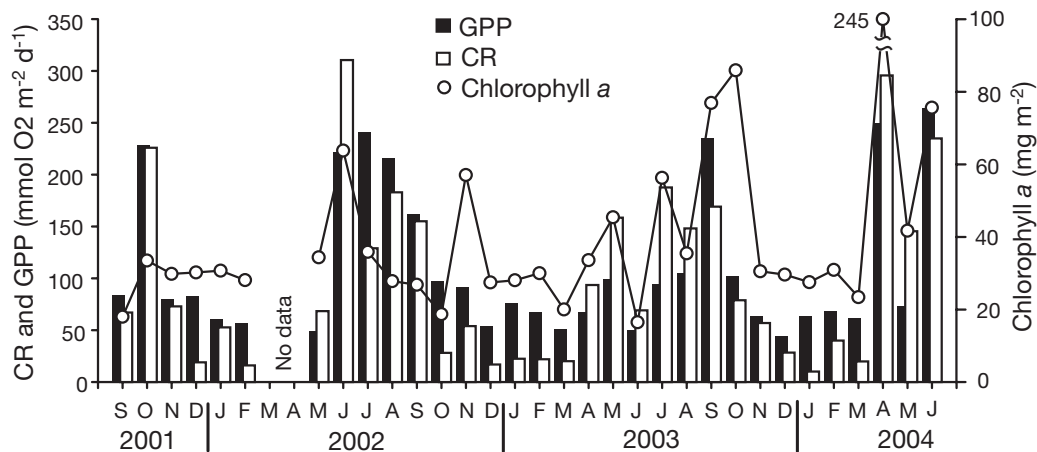
Fig. 5. Temporal variations in vertically integrated chlorophyll *a*, gross primary production (GPP), and community respiration (CR) from September 2001 to June 2004

the surface is partially due to the photosynthetically produced oxygen by phytoplankton.

CR exhibited seasonal patterns coupled to the variation in GPP (Fig. 4d). CR generally showed maximum values at the surface, and was >1 mmol O_2 m^{-3} d^{-1} from spring to fall, while it was <1 mmol O_2 m^{-3} d^{-1} in winter throughout the euphotic zone (Fig. 4d). In Fig. 4e, zero represents community compensation depth (CCD). CCD was relatively deep in winter (ca. 50 m) and shallow from spring to fall (10 to 30 m). NCP was generally positive and showed maximum values at the surface throughout the observation period (Fig. 4e). In contrast, NCP in the subsurface layer was negative. In particular, when GPP was >10 mmol O_2 m^{-3} d^{-1} at the surface, NCP was <–1 mmol O_2 m^{-3} d^{-1} in the subsurface layer (Fig. 4e).

GPP and CR vertically integrated in the euphotic zone showed distinct seasonal patterns, and both tended to be higher from spring to summer (April to October) than from fall to winter (November to March) (Fig. 5). The seasonal trend of CR generally coincided with that of GPP. There were a few months in which CR exceeded GPP even when GPP was >100 mmol O_2 m^{-2} d^{-1}. The mean values of GPP and CR from September 2001 to August 2002 were the highest of the 3 studied years (Table 1). Hence, the experimental time

was separated into a high-productivity (HP) period (April to October) and a low-productivity (LP) period (November to March). The mean values of GPP and CR in the HP period from September 2003 to June 2004 were the highest of the 3 studied years (Table 2). The mean values of CR during the HP period were higher than those of GPP from September 2002 to August 2003 and September 2003 to June 2004, though GPP from September 2001 to August 2002 was slightly higher than CR (Table 2). The difference in mean values of GPP during the HP periods between September 2002 to August 2003 and September 2003 to June 2004 was 88 mmol O_2 m^{-2} d^{-1}, while that of CR was 65 mmol O_2 m^{-2} d^{-1}. In contrast, the mean values of GPP during the LP period were higher than those of CR over the 3 yr period and approximately equal, unlike those in the HP period (Table 2).

NCP was generally positive during summer–winter and negative in spring (Fig. 6). However, in 2003, NCP was negative not only in spring but also in summer. The mean value of NCP during the HP period over the 3 studied years was negative (–6 mmol O_2 m^{-2} d^{-1}), whereas that of the LP period was positive (33 mmol O_2 m^{-2} d^{-1}; Table 2).

The compensation irradiance (i.e. percentage irradiance at $P:R = 1$) during the observed 3 yr period was

Table 1. Mean values (±SE) of chlorophyll *a* (chl *a*), gross primary production (GPP), community respiration (CR) and net community production (NCP) calculated by trapezoidal integration from the surface to the 1% light depth

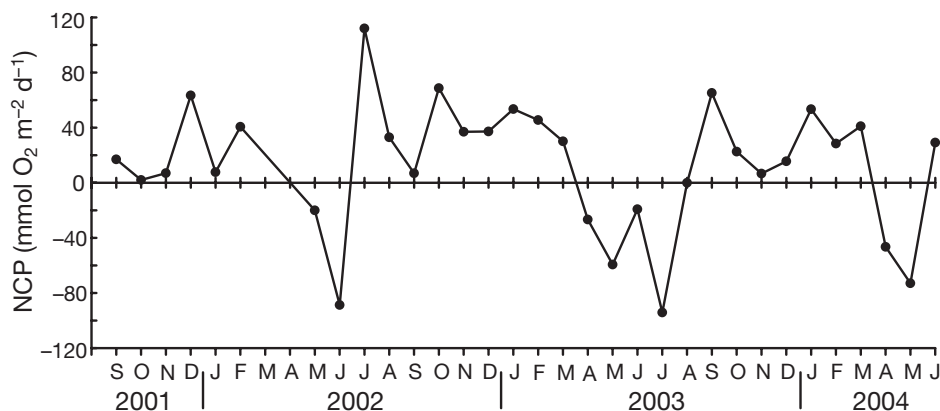|	Sep 2001–Aug 2002	Sep 2002–Aug 2003	Sep 2003–Jun 2004	Sep 2001–Jun 2004
Chl *a* (mg m^{-2})	33 ± 4	33 ± 4	52 ± 9	39 ± 4
GPP (mmol O_2 m^{-2} d^{-1})	132 ± 26	84 ± 9	122 ± 28	111 ± 13
CR (mmol O_2 m^{-2} d^{-1})	114 ± 31	81 ± 19	108 ± 31	100 ± 15
NCP (mmol O_2 m^{-2} d^{-1})	17 ± 17	3 ± 15	14 ± 14	11 ± 8

Fig. 6. Temporal variation in vertically integrated net community production (NCP) from September 2001 to June 2004

located at 8% of the ambient irradiance, and, during HP and LP, the percentage irradiance was 20 and 1%, respectively (Fig. 7).

There was a positive relationship between the $P{:}R$ ratio and GPP (Fig. 8). An overall threshold GPP was 1.4 mmol O_2 m^{-3} d^{-1}, to reach a state of balanced metabolism (i.e. $P{:}R = 1$), and, during HP and LP, the threshold GPP was 4.1 and 0.4 mmol O_2 m^{-3} d^{-1}, respectively.

Annual fluxes of oxygen and $P{:}R$ balance

In this study, annual GPP was higher than that in the Bay of Biscay and in the North Pacific subtropical gyre, whereas annual CR was approximately equal (Serret et al. 1999, Williams et al. 2004) (Table 3). Annual rates of GPP were higher than those of CR from September 2001 to August 2002 and September 2003 to June 2004, resulting in $P{:}R$ ratios of 1.3 and 1.2, respectively. In contrast, GPP was nearly equal to CR from September 2002 to August 2003, resulting in a $P{:}R$ ratio of 1.0. Therefore, annual NCP was not negative in the euphotic zone during the 3 yr period (Table 3).

DISCUSSION

In this study, a seasonal pattern was observed for GPP (Figs. 4c & 5). GPP correlated positively with PAR (t-test, $p < 0.01$). This implies that the rate of oxygen evolution is related to the light intensity. While the nitrate + nitrite concentrations were <0.5 µmol l^{-1} in the upper 10 m from May to October 2002 and in the upper 20 m from May to September 2003, the phosphate concentrations were >0.05 µmol l^{-1} (Fig. 3c,d). However, GPP was higher relative to other periods. This suggests that phytoplankton growth is not greatly limited by nutrient concentrations in Sagami Bay. Nutrient concentrations, supporting relatively high GPP, may have been supplied from riverine water due to low salinity and a strong thermocline (Fig. 3a,b). The temporal variation in primary production is likely to be affected by light intensity and nutrient concentration in Sagami Bay.

The variations in CR are likely to be coupled to those in GPP from a dataset compiled from 100s of stations worldwide (e.g. Duarte & Agustí 1998, Williams 1998), in contrast to reports that CR is independent of GPP because of the reduced bacterial and protozoan respiratory rates during periods of high phytoplankton

Table 2. Mean values (±SE) of chl *a*, GPP, CR and NCP during the high-productivity (April to October) and low-productivity (November to March) periods

	Sep 2001–Aug 2002	Sep 2002–Aug 2003	Sep 2003–Jun 2004	Sep 2001–Jun 2004
High productivity				
Chl *a* (mg m^{-2})	36 ± 7	36 ± 6	76 ± 11	46 ± 6
GPP (mmol O_2 m^{-2} d^{-1})	173 ± 38	96 ± 14	184 ± 45	146 ± 20
CR (mmol O_2 m^{-2} d^{-1})	164 ± 43	120 ± 23	185 ± 42	153 ± 20
NCP (mmol O_2 m^{-2} d^{-1})	9 ± 29	−24 ± 21	0 ± 29	−6 ± 14
Low productivity				
Chl *a* (mg m^{-2})	30 ± 1	33 ± 6	28 ± 1	30 ± 2
GPP (mmol O_2 m^{-2} d^{-1})	70 ± 6	68 ± 7	60 ± 4	66 ± 3
CR (mmol O_2 m^{-2} d^{-1})	40 ± 12	27 ± 6	31 ± 7	32 ± 5
NCP (mmol O_2 m^{-2} d^{-1})	30 ± 12	41 ± 4	29 ± 8	33 ± 4

production in Antarctic waters (Agustí et al. 2004). In Sagami Bay, the variations in CR generally coincided with that of GPP (Figs. 4c,d & 5), suggesting a balanced relationship between production and consumption of oxygen in the euphotic zone of Sagami Bay, i.e. when GPP was relatively high, NCP was not relatively high (Figs. 5 & 6).

The CCD varied seasonally (Fig. 4e). The algal compensation depth (ACD) is conventionally taken as the depth to which 1 % of the surface irradiance penetrates

(euphotic zone). Our observations of NCP allow us to determine the CCD. The difference between the 2 compensation depths is an expression of the relative contributions of algal and heterotrophic respiration (Williams & Purdie 1991). Therefore, when heterotrophic respiration becomes more important than algal respiration, CCD becomes shallow. In contrast, when heterotrophic respiration becomes less important than algal respiration, CCD approaches the ACD. The CCD (1 % light depth: 40 to 50 m) during the LP period was
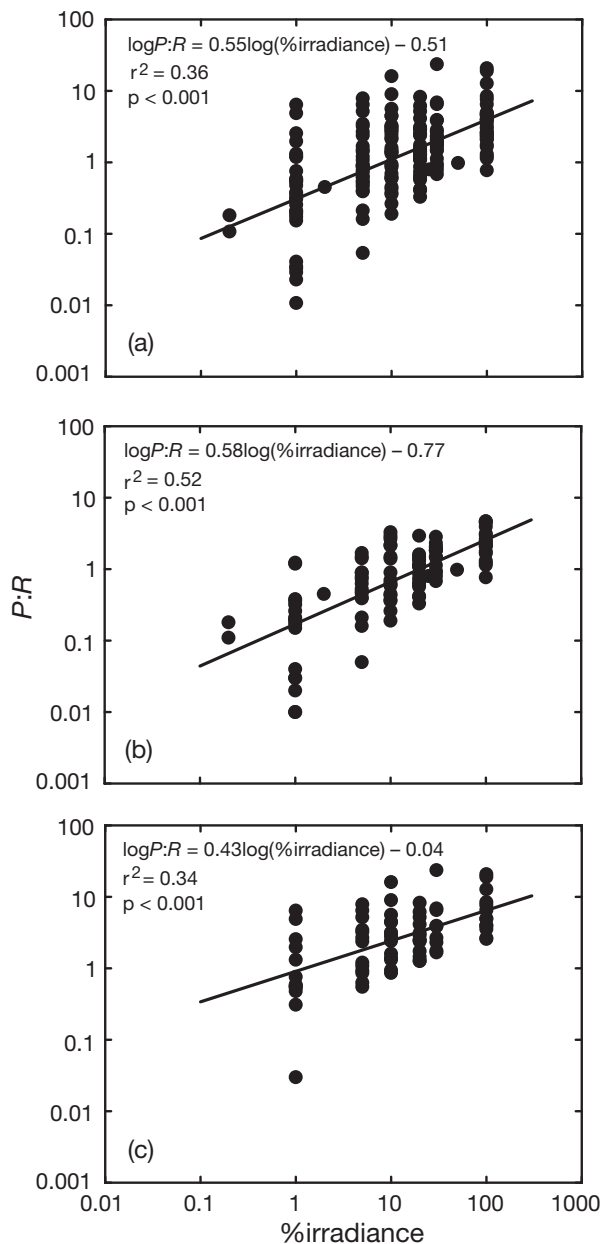

Fig. 7. Relationship between the P:R ratio and the percentage of surface irradiance during (a) total, (b) high-productivity (April to October) and (c) low-productivity (November to March) periods
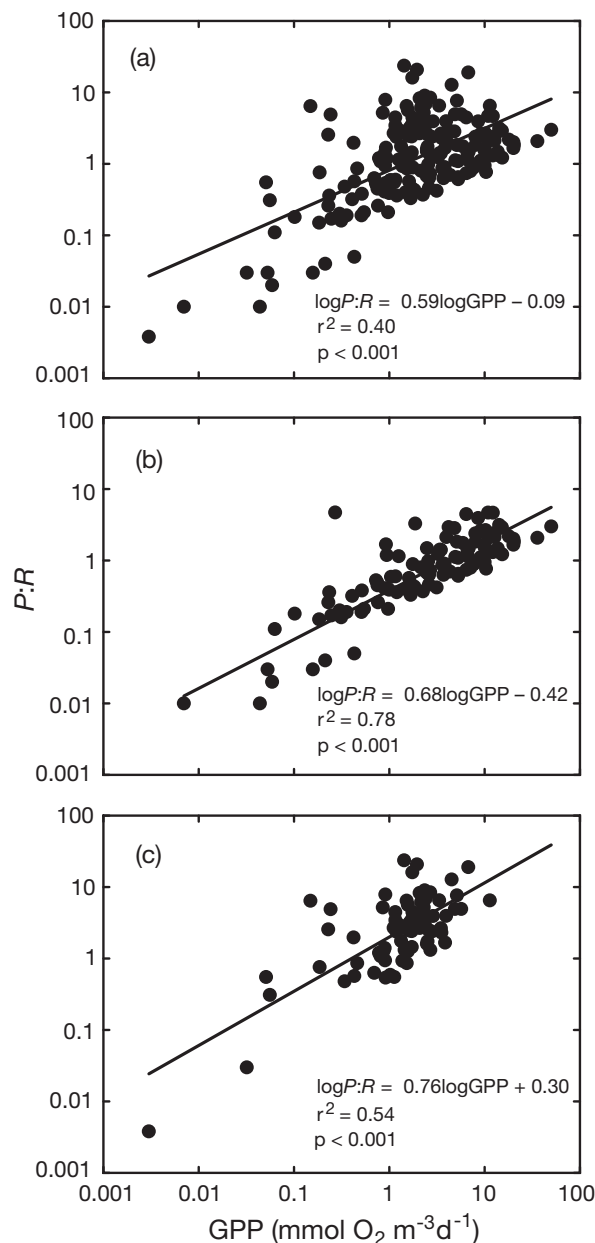

Fig. 8. Relationship between the P:R ratio and the gross primary production (GPP) during (a) total, (b) high-productivity (April to October) and (c) low-productivity (November to March) periods

Table 3. Annually integrated rates and mean values (±SE) of GPP, CR and NCP, and the ratio of GPP to CR (*P*:*R*)

	Sep 2001–Aug 2002	Sep 2002–Aug 2003	Sep 2003–Jun 2004	Mean ± SE
GPP (mol O_2 m^{-2} yr^{-1})	45	30	37	37 ± 4
CR (mol O_2 m^{-2} yr^{-1})	35	29	32	32 ± 2
NCP (mol O_2 m^{-2} yr^{-1})	10	1	5	5 ± 3
P:*R*	1.3	1.0	1.2	1.2 ± 0.1

almost equal to the ACD (Fig. 4e). CR may have been reduced during the LP period because of low water temperature. In contrast, the CCD (20% light depth: 10 to 30 m) during the HP period was much shallower than during the LP period (Fig. 7), suggesting that the relative contributions of heterotrophic respiration to algal respiration were greater during the HP period than during the LP period. Therefore, the seasonal variations in CCD imply that the relative contributions of algal and heterotrophic respiration in CR vary seasonally.

NCP was negative in spring 2002, 2003 and 2004. It is thought that net heterotrophy in the water column is due to organic inputs from rivers and/or a temporary imbalance of autotrophic production and heterotrophic consumption. Salinity in spring did not decrease and was >34 (Fig. 3b). Therefore, the negative values of NCP in spring may not be dependent on the effect of allochthonous inputs of organic matter. In spring, vertical mixing was still active (Fig. 3a,b), so that phytoplankton production was relatively low because of low light conditions. Sherr & Sherr (2003) reported that bacterial activity increased with an increase in temperature. In our study, temperature was higher in spring than in winter (Fig. 3a), suggesting that bacterial production was greater in spring than in winter. CR showed a positive correlation with temperature (*t*-test, p < 0.001). Consequently, the negative values in spring are likely to be due to a temporary imbalance of autotrophic production and heterotrophic consumption.

In 2003, NCP was negative not only in spring, but also in summer. In coastal regions, the inputs of the allochthonous dissolved organic matter (DOM) from rivers may lead to negative NCP (Duarte et al. 2004). Salinity decreased in summer (Fig. 3b), indicating that the influence of river water in Sagami Bay was greater in summer than in winter (Iwata 1985), as mentioned in the 'Introduction'. Allochthonous DOM from rivers may have been discharged into Sagami Bay in summer. Further, GPP in the summer of 2003 was relatively low compared with that in other years because of low solar irradiance (<20 mol quanta m^{-2} d^{-1}; Fig. 2). Consequently, the negative NCP in the summer of 2003 is likely to be due to the influx of allochthonous DOM and the low GPP.

During the LP period of each year, GPP and CR were approximately constant, but were very variable during the HP period (Table 2). This implies that the seasonal

and annual changes of GPP and CR are dependent on those of the HP period. The mean value (–6 mmol O_2 m^{-2} d^{-1}) of NCP during the HP period over the 3 studied years was negative (Table 2), representing a characteristic of the HP period. Consequently, CR, which exceeds GPP during the HP period, must be supported by organic carbon produced in the past or elsewhere.

The *P*:*R* ratio of the community increased with increasing GPP, consistent with results across other aquatic ecosystems (Duarte & Agustí 1998). The threshold GPP values (LP: 0.4 mmol O_2 m^{-3} d^{-1}; HP: 4.1 mmol O_2 m^{-3} d^{-1}) for metabolic balance (i.e. GPP at *P*:*R* = 1) were surprisingly low in comparison with the value (50 mmol O_2 m^{-3} d^{-1}) in coastal regions reported by Duarte & Agustí (1998). The mean value of threshold GPP was 1.4 mmol O_2 m^{-3} d^{-1} over the 3 yr study (Fig. 8), close to the estimate of 1.1 mmol O_2 m^{-3} d^{-1} required to render open ocean communities net autotrophic (Duarte & Agustí 1998, González et al. 2001). The threshold during the HP period was 10-fold higher than during the LP period. The value during the HP period was close to a threshold value (3.95 mmol O_2 m^{-3} d^{-1}) reported for the Mediterranean oligotrophic littoral by Duarte et al. (2004). During the LP period, the threshold GPP value was lower than the mean value, but, during the HP period, it was about 3 times higher than the mean value. This indicates the importance of organic carbon produced in the past or elsewhere in sustaining a relatively high background CR rate during the HP period. Consequently, GPP and CR during the HP period are likely to be supported partially by nutrient and allochthonous DOM from rivers.

In the present study, annual GPP and CR were variable from year to year (Table 3). The CV of GPP (20%) is higher than that of CR (9%), implying that the variation in annual NCP is greatly dependent on that in annual GPP. Annual GPP was higher than annual CR in the euphotic zone in Sagami Bay during the 3 studied years (Table 3). Consequently, the positive value of annual NCP in Sagami Bay is due to variation in annual GPP. del Giorgio & Duarte (2002) mentioned that the integrated respiration rate in the 200 to 1000 m layer should range from 30 to 130% of the integrated respiration in the 0 to 200 m layer. The organic carbon exceeding the needs for CR in the euphotic zone may be consumed by organisms living below the euphotic layer of Sagami Bay.

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