



# Seasonal variation in metabolic rate of plankton community in the inner part of Tokyo Bay

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## Abstract

Understanding the environmental factors that shape planktonic communities is essential to understand the diversity of aquatic ecosystems. Gross primary production (GPP), community respiration (CR), and net community production (NCP) were measured from May to December in the inner part of Tokyo Bay, and the metabolic balance between GPP and CR was analyzed. Environmental variability was also analyzed by measuring temperature, salinity, nutrient, and chlorophyll *a* (Chl *a*) concentrations. The results showed a threshold GPP (GPP at GPP=CR) of 14.2 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup> in the inner bay, while the mean value of CR was 41.0 mmol O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup>, six times higher than the mean values reported previously for coastal areas. This indicates that the surface layer of the inner bay is biologically productive with a highly heterotrophic population. In contrast, all NCPs were positive (NCP > 0, GPP/CR ratio: 3.80 ± 0.82) throughout the study period. NCP was strongly correlated with Chl *a*, indicating that the metabolic balance of the planktonic community in the inner part of Tokyo Bay is controlled by factors regulating the autotroph community, such as nutrient (especially phosphate) supply and water temperature.

**Keywords** Gross primary production · Community respiration · Net community production · Plankton metabolic balance · Tokyo Bay

## 1 Introduction

The coastal oceanic region has the highest biological productivity due to the significant input of terrestrial mineral and organic matter from river run-off. Eutrophication due to excessive nutrient loading from land induces large phytoplankton blooms and subsequent deposition of large amounts of organic carbon to benthic waters. Dissolved oxygen (DO) decreases as the settled organic matter decomposes, and regenerates into nutrients, generating anaerobic water masses. The regenerated nutrients return to the surface layer by wind and current mixing, and are reused by the phytoplankton for growth.

Elucidation of the environmental factors that regulate planktonic community formation is essential for understanding the current and future planktonic community changes in marine ecosystems. Metabolism in oceans plays a significant

biogeochemical role on Earth, mainly through plankton communities and bacteria. Plankton communities play an important role in the carbon cycle, influencing O<sub>2</sub>–CO<sub>2</sub> air–sea exchange and providing energy to the marine food web through their metabolic processes (Gazeau et al. 2005; Calleja et al. 2013).

The metabolic rate of planktonic communities consists of organic matter production and respiration. The metabolic balance between gross primary production (GPP) and community respiration (CR) determines the net community production (NCP = GPP – CR). Depending on the dominance of each of these processes, ecosystems or communities may be classified as: autotrophic, in which organic matter is produced more than respiration requirements, or heterotrophic, which consumes more organic matter through the respiratory processes that they have, or in balance when production and respiration are of equal magnitudes. Several external factors, such as water temperature, nutrient concentrations, and solar irradiance, directly and indirectly, affect the primary production and metabolism of plankton communities in the ocean (Parsons et al. 1984a). As GPP and CR are the primary

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carbon flows in the surface layer, investigating metabolic balance is very important for predicting future ecosystems.

Tokyo Bay (central Japan) is enclosed by metropolitan areas, with a population of approximately 31 million living in its watershed. Nitrogen and phosphorus discharged from the Tokyo Bay watershed by human activities enter the bay through rivers, sewage treatment plants, and factories (Takada 1993). In the Tokyo Bay watershed, the major rivers (Tama, Arakawa, Edo, and Sumida) are mainly concentrated on the northwestern side of the bay, accounting for approximately 80% of the total freshwater inflow into the bay (Matsumura and Ishimaru 2004). Tokyo Bay is a semi-enclosed inner bay with an average depth of 15 m, resulting in eutrophic conditions and very high chlorophyll *a* (Chl *a*) concentrations above 100 mg m<sup>-3</sup> by nano- to micro-sized phytoplankton, such as diatoms, raphidophytes, and dinoflagellates, from spring to summer, making it one of the areas with the highest primary production worldwide (Yamaguchi et al. 1991; Nomura 1998; Cloern et al. 2014). In the benthic layer of Tokyo Bay, large anoxic water masses form from summer to autumn (Kajiyama and Uto 2016; Ando et al. 2021; Yokoyama and Iimura 2022). Anoxic water masses induce “blue tides” (rising sulfide-rich anoxic benthic waters), which often have a significant impact on commercially valuable benthic organisms, such as clams and fish species, which inhabit the coastal areas of Tokyo Bay (Kajiyama 2019). Upwelling phosphate-rich water formed by elution from sediments under anaerobic conditions can also cause anomalous phytoplankton blooms in surface layers (Uchiyama et al. 1998; Nakane et al. 2008). In addition to the loss of fishing grounds in shallow waters due to land reclamation, Tokyo Bay’s total catch has decreased since the mid-1960s (Kakino et al. 2011). Understanding Tokyo Bay’s current marine environment and ecosystem is essential for contributing to conserving and restoring the bay and evaluating future fishery resources.

In Tokyo Bay, most focus is on autotrophic communities via photosynthetic processes (primary production). Primary production in Tokyo Bay has apparent seasonal variation, being higher in spring and summer and lower in winter (Shibata and Aruga 1982; Brandini and Aruga 1983; Yamaguchi et al. 1991; Bouman et al. 2010). However, the community respiration rates occupied by heterotrophs and their seasonal variation are not well known in Tokyo Bay. Furthermore, there have been few reports on the metabolic balance of planktonic communities. The balance between GPP and CR determines the amount of carbon supplied to the coastal food web. It also defines the metabolic state of the ecosystem, involving both autotrophic and heterotrophic metabolic activities.

In this study, we measured plankton metabolism (GPP, CR, and NCP) to clarify the seasonal variation of GPP and CR in the inner part of Tokyo Bay. In addition, we measured

the water temperature, salinity, nutrients, and Chl *a* concentration, and discussed the factors that maintain high primary production.

## 2 Materials and methods

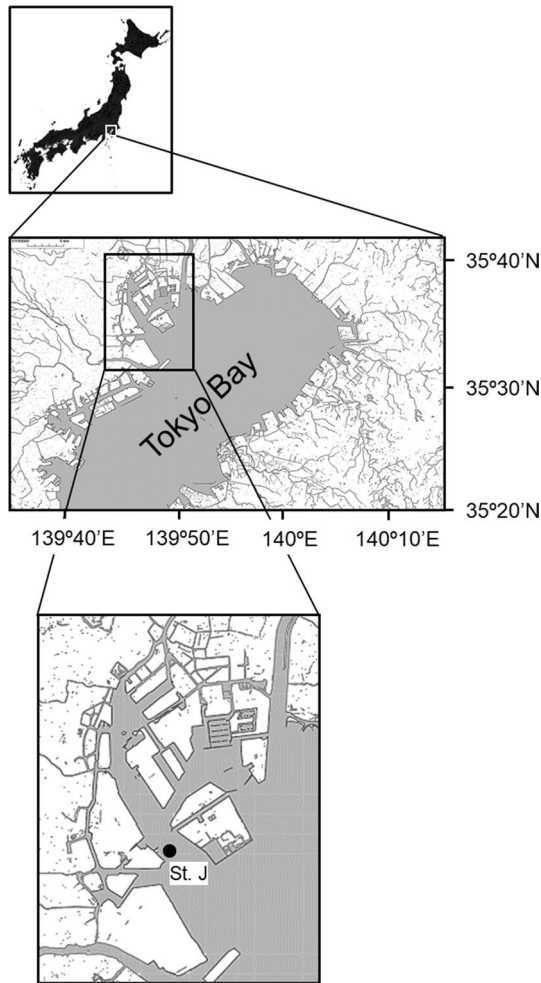
We conducted time-series observations between May and December 2021 (Table 1) in the vicinity of Jonanjima Seaside Park (St. J: 35°35'00" N, 139°47'00" E) in the northwestern part of the inner part of Tokyo Bay. (Fig. 1). Water samples were collected from a depth of 0.5 m with a Niskin bottle to measure GPP, CR, Chl *a* concentration, and nutrient (nitrate + nitrite, ammonium, and phosphate) concentrations. Water temperature and salinity were measured using a digital thermometer (Hanna Instruments HI98501) and a digital salinometer (Hanna Instruments HI98319). Saturated DO was estimated from the water temperature and salinity (García and Gordon 1992). Daily meteorological data, such as temperature, precipitation, wind direction and speed, and total solar radiation, during the observation period were derived from the Automated Meteorological Data Acquisition System (AMeDAS) of the Tokyo Meteorological Observatory.

### 2.1 Nutrients and Chl *a*

Seawater samples were transferred to polystyrene bottles, flash-frozen, and stored at -20 °C until analysis. The analyses of nitrate + nitrite, ammonium and phosphate were performed using a UV-Visible spectrometer (Genesys 10S UV-VIS, Thermo Scientific, USA) following the standard analytical methods described by Parsons et al. (1984b). The detection limits of nitrate + nitrite was 0.3 µM, ammonium 1.0 µM, and phosphate 0.2 µM. 200–300 mL of the collected sample was filtered through a 47 mm Whatman GF/F filter under gentle suction (< 250 kPa). The filters were soaked

**Table 1** Twelve sampling dates in 2021 at St. J in the inner part of Tokyo Bay

Sampling date
5 May
18 May
1 Jun
6 Jul
3 Aug
21 Aug
11 Sep
25 Sep
30 Oct
13 Nov
27 Nov
11 Dec



**Fig. 1** Map of the study area in Tokyo Bay. St. J indicates the location of the sampling site in this study

in 90% acetone, and Chl *a* was immediately extracted (Parsons et al. 1984b). Chl *a* concentrations were measured according to the method described by Parsons et al. (1984b) using a Turner Design Model 10-AU fluorometer calibrated with commercially available Chl *a* (Wako Pure Chemical Industries).

## 2.2 GPP, CR, and NCP

Seawater was carefully collected from a Niskin bottle using silicone tubing and placed into 12 calibrated borosilicate glass 100 mL bottles. Four were fixed immediately, and the initial DO was measured, another four were incubated in the light. The last four were incubated in the dark in an incubator (Daiwa Industries Ltd. CDB-14LA). Incubation experiments began within approximately one hour of sample collection. After collection, the light bottles were incubated at in situ temperature in a temperature-controlled incubator under white fluorescent light (Hitachi FL20SD) of

$350 \mu\text{mol m}^{-2} \text{s}^{-1}$  photosynthetically active radiation (PAR: 400–700 nm) (Bocaniov and Smith 2009) from dawn to dusk on the collection day. Light bottles were also incubated in the dark at in situ temperature from dusk to dawn. Dark bottles were wrapped in aluminum foil, stored in dark bags, and incubated for 24 h at in situ temperatures. After incubation, DO in the light and dark bottles were fixed immediately. Reagent preparation and standardization were performed following the method described by Carritt and Carpenter (1966). DO was measured by automatic precision Winkler titration with a Metrohm 785 DMP Titrino using a potential difference (Oudot et al. 1988), while light-saturated GPP was determined from in vitro changes in DO after 24 h of light/dark bottle incubation. CR was determined using the oxygen change in dark bottles (initial DO—dark DO), and NCP using the oxygen change in light bottles (light DO—initial DO). GPP was calculated as the sum of the CR and NCP. The maximum standard error (SE) for the initial DO during this study period was  $\pm 1.1 \text{ mmol m}^{-3}$ , light DO was  $\pm 4.0 \text{ mmol m}^{-3}$ , and dark DO was  $\pm 2.8 \text{ mmol m}^{-3}$ . As a result, the maximum SE for GPP, CR, and NCP were estimated to be  $\pm 2.8$ ,  $\pm 1.9$ , and  $\pm 2.7 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ , respectively.

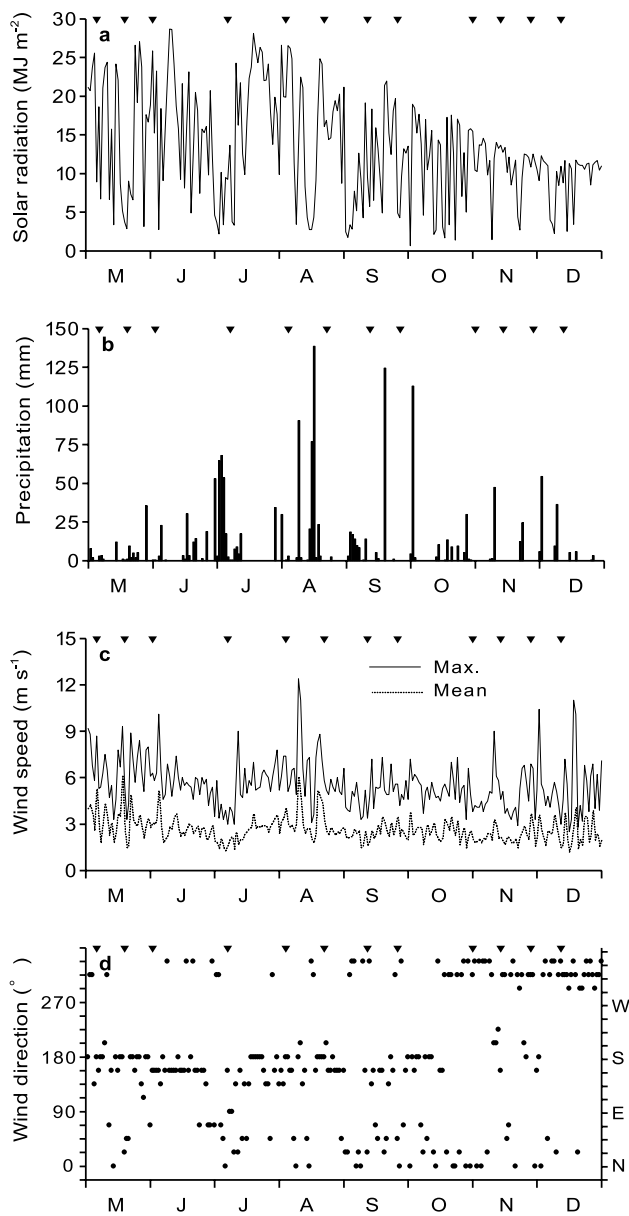
## 3 Results

### 3.1 Weather conditions

Solar radiation decreased from late June to early July with values above  $20 \text{ MJ m}^{-2}$  from May to August, decreasing through December (Fig. 2a). Continuous precipitation was observed in early July, mid-August, and early September (Fig. 2b) with a total of 206 mm recorded in Tokyo from 1 to 5 July before the survey date (6 July) (Fig. 2b). The total precipitation for five days before the observation date was less than 50 mm. Winds were predominant from the south-southeast or the south from May to mid-October, with an average wind speed of approximately  $3 \text{ m s}^{-1}$ , with occasionally northerly winds (Fig. 2c, d). Northerly winds with a maximum speed of approximately  $5 \text{ m s}^{-1}$  were blowing continuously from 31 August to 9 September before 11 September (Fig. 2c, d). Northerly winds were also observed before 6 July, 30 October, and 11 December; however, the average wind speed was approximately  $3 \text{ m s}^{-1}$  or less.

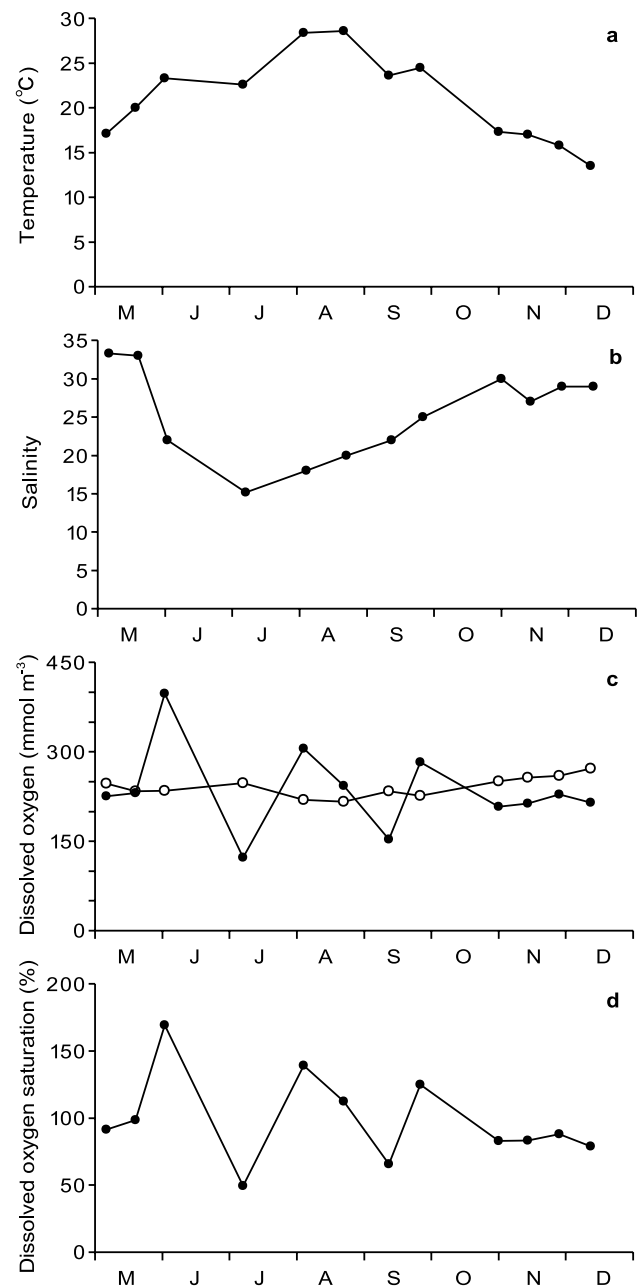
### 3.2 Water temperature, salinity and DO

The surface water temperature during the study period ranged from 13.5 to 28.6 °C (mean  $\pm$  SE:  $21.0 \pm 1.4$  °C), with values of 28 °C during August (Fig. 3a). Seasonal variations in water temperature were generally similar to those in solar radiation. Salinity ranged from 15.2



**Fig. 2** Temporal variations in solar radiation (a), precipitation (b), wind speed (c), and wind direction (d) from 1 May to 31 December 2021. Closed triangles indicate survey dates in this study

to  $33.3$  ( $25.3 \pm 1.6$ ), decreasing from May to July and remaining below 20 from July to August. Salinity then increased in December (Fig. 3b). The DO ranged from 122 to  $398 \text{ mmol m}^{-3}$  ( $236 \pm 20 \text{ mmol m}^{-3}$ ), with the highest value recorded on 1 June and saturated DO ranged from 217 to  $272 \text{ mmol m}^{-3}$  (Fig. 3c). On 6 July and 11 September, DO was lower than  $160 \text{ mmol m}^{-3}$ , much lower than the values observed on other days and the saturation rate of oxygen was 49 and 66%, respectively (Fig. 3d).

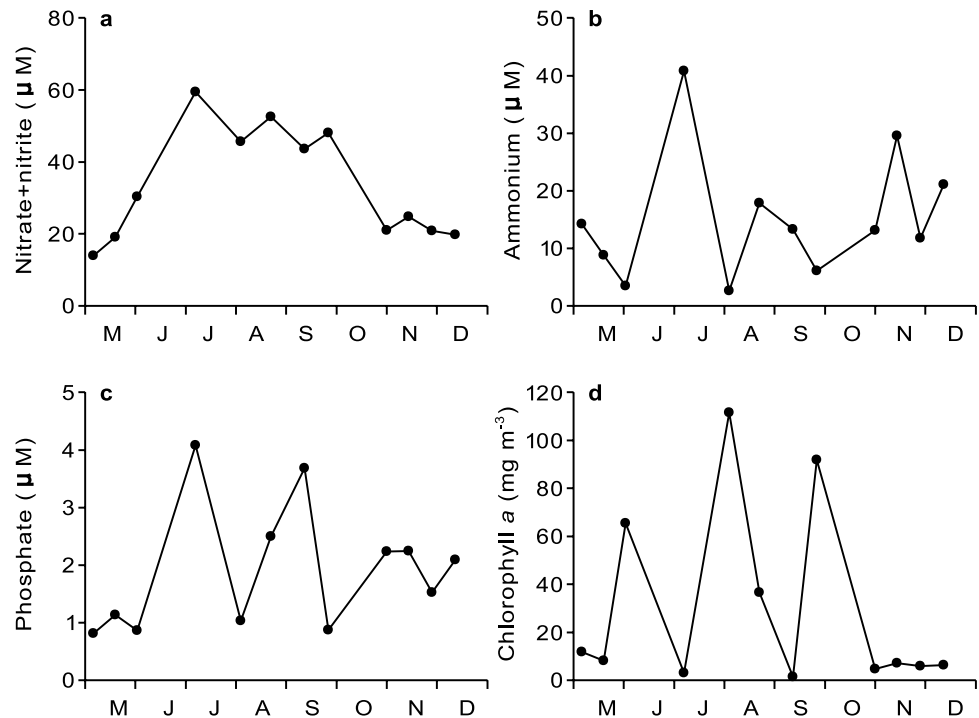


**Fig. 3** Temporal variations in water temperature (a), salinity (b), (●) dissolved oxygen and (○) dissolved oxygen saturation (c), and saturation rate of oxygen (d) in the surface layer in the inner part of Tokyo Bay during the study period

### 3.3 Nutrients

The nitrate + nitrite concentrations during the observation period varied in the range of  $13.9$ – $59.5 \text{ } \mu\text{M}$  ( $33.3 \pm 4.3 \text{ } \mu\text{M}$ ) (Fig. 4a). Nitrate + nitrite concentrations were above  $30 \text{ } \mu\text{M}$  from June to October with a maximum on 6 July. The ammonium concentrations were in the range of  $2.6$ – $40.8 \text{ } \mu\text{M}$  ( $15.2 \pm 3.1 \text{ } \mu\text{M}$ ) (Fig. 4b).

**Fig. 4** Temporal variations in nitrate + nitrite (a), ammonium (b), phosphate (c), and chlorophyll *a* concentration (d) in the surface layer in the inner part of Tokyo Bay during the study period



Ammonium concentrations reached a maximum on 6 July and tended to increase from late September (6.1  $\mu\text{M}$ ) to December (21.1  $\mu\text{M}$ ). The phosphate concentrations varied in the range of 0.8–4.1  $\mu\text{M}$  ( $1.9 \pm 0.3 \mu\text{M}$ ) (Fig. 4c). Phosphate concentrations were higher than other survey dates, exceeding 3  $\mu\text{M}$  on 6 July and 11 September, when DO was relatively low. Similar to ammonium concentrations, phosphate concentrations tended to increase from late September (0.9  $\mu\text{M}$ ) to December (2.1  $\mu\text{M}$ ). We found a significant positive correlation between ammonium and phosphate levels ( $p < 0.01$ ,  $r = 0.74$ ).

### 3.4 Chl *a*

Chl *a* concentrations during the study period varied in the range of 1.4–111.6  $\text{mg m}^{-3}$  ( $29.5 \pm 10.7 \text{ mg m}^{-3}$ ) (Fig. 4d). Although Chl *a* concentrations were highly variable, they tended to be higher from June to October, which is similar to previously reported seasonal variations (Shibata and Aruga 1982; Yamaguchi et al. 1991; Nakane et al. 2008). Chl *a* concentrations were above 50  $\text{mg m}^{-3}$  on 1 June, 3 August and 25 September, and they were below 5  $\text{mg m}^{-3}$  on 6 July and 11 September when DO was relatively low. They showed large fluctuations from June to October, but ranged between 5 and 10  $\text{mg m}^{-3}$  in May, November and December (Fig. 4d).

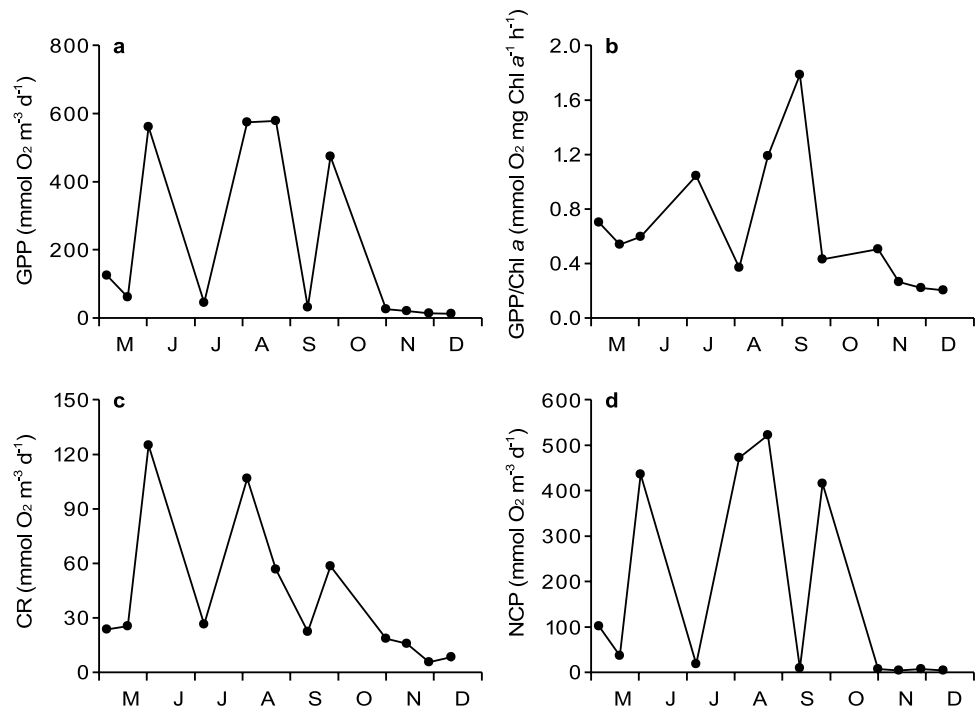
### 3.5 GPP, CR and NCP

GPP ranged from 12.5 to 579.1  $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  ( $210.6 \pm 69.8 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ) during the observation period (Fig. 5a). Although the variation in GPP was very variable, similar to Chl *a* concentrations, it tended to be higher from June to September (Figs. 4d and 5a). GPP on 6 July and 11 September, when Chl *a* was relatively low, was less than 50  $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ . GPP showed a significantly positive correlation with Chl *a* ( $p < 0.001$ ,  $r = 0.88$ ). GPP per unit Chl *a* (GPP/Chl *a*) ranged from 0.20 to 1.79  $\text{mmol O}_2 \text{ mg Chl a}^{-1} \text{ h}^{-1}$  (Fig. 5b). GPP/Chl *a* showed values above 1.0  $\text{mmol O}_2 \text{ mg Chl a}^{-1} \text{ h}^{-1}$  on 6 July, 21 August and 11 September, with a trend toward higher values from spring to fall and lower values in winter. GPP/Chl *a* showed a significant positive correlation with phosphate concentration ( $p < 0.05$ ,  $r = 0.62$ ), but not with water temperature or other nutrients (temperature;  $p > 0.1$ ,  $r = 0.47$ , nitrate + nitrite;  $p > 0.05$ ,  $r = 0.51$ , ammonium;  $p > 0.1$ ,  $r = 0.17$ ).

CR ranged from 5.5 to 125.0  $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  ( $41.0 \pm 10.7 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ) (Fig. 5c). The CR showed a seasonal pattern similar to the variability of Chl *a* and GPP, with a maximum on 1 June (Figs. 4d and 5a, c). However, the maximum CR value was less than one-quarter of the maximum GPP value.

NCP varied between 4.1 and 522.3  $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  ( $169.5 \pm 60.5 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ) (Fig. 5d). NCPs were all

**Fig. 5** Temporal variations in gross primary production (GPP) (a), GPP per unit Chl *a* (GPP/Chl *a*) (b), community respiration (CR) (c), and net community production (NCP) (d) in the surface layer in the inner part of Tokyo Bay during the study period



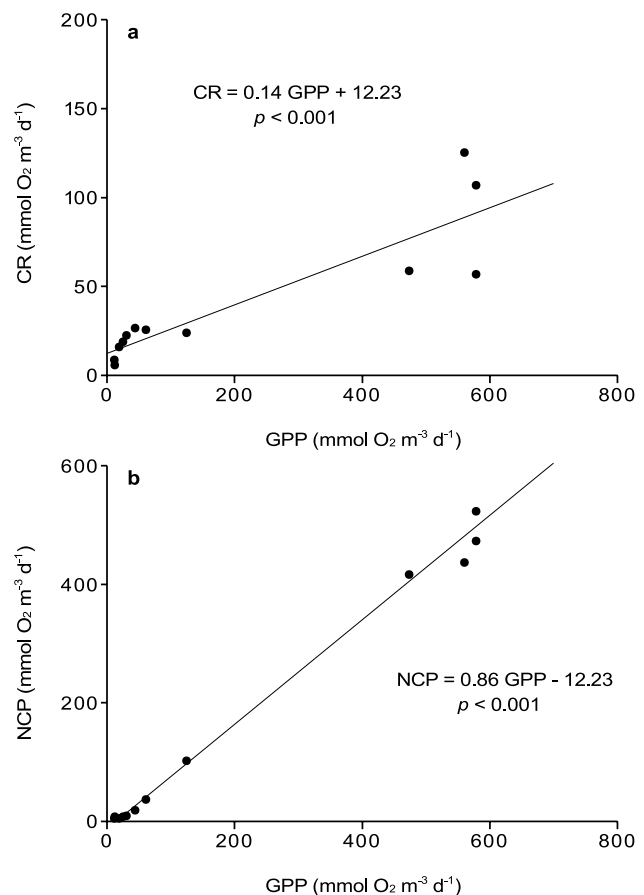
positive (GPP/CR ratio:  $3.80 \pm 0.82$ ) throughout the study period, which indicates that the study area was dominant in the autotrophic community. The NCP exhibited a seasonal variation similar to that of Chl *a* with a significantly positive correlation ( $p < 0.001$ ,  $r = 0.86$ ).

There was a significant positive correlation among CR, NCP and GPP (Fig. 6a, b; CR:  $p < 0.001$ ,  $r = 0.93$ ; NCP:  $p < 0.001$ ,  $r = 0.99$ ). Based on the functional relationships between GPP and NCP, we calculated the threshold of GPP for metabolic equilibrium in the region. Using the slope and intercept for NCP = 0 in Fig. 6b, the threshold GPP that separates the planktonic communities of the autotrophs and heterotrophs in the inner part of Tokyo Bay was determined to be  $14.2 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  in the surface layer.

## 4 Discussion

### 4.1 Physicochemical environment and the response of phytoplankton communities

Previous studies have shown that surface water temperatures in the coastal areas of Tokyo Bay reach a maximum of approximately 30 °C in August, followed by a decrease to below 10 °C by February of the following year (Nakane et al. 2008). The present study showed results similar to those previously reported values. Surface salinity in the northwestern coastal area of Tokyo Bay fluctuates widely from June to October, often reaching a minimum of 10 due to run-off from the Ara, Edo and Tama Rivers (Nakane et al.



**Fig. 6** Relationship between community respiration (CR) (a) and net community production (NCP) (b) and gross primary production (GPP). The solid lines show the fitted regression equations

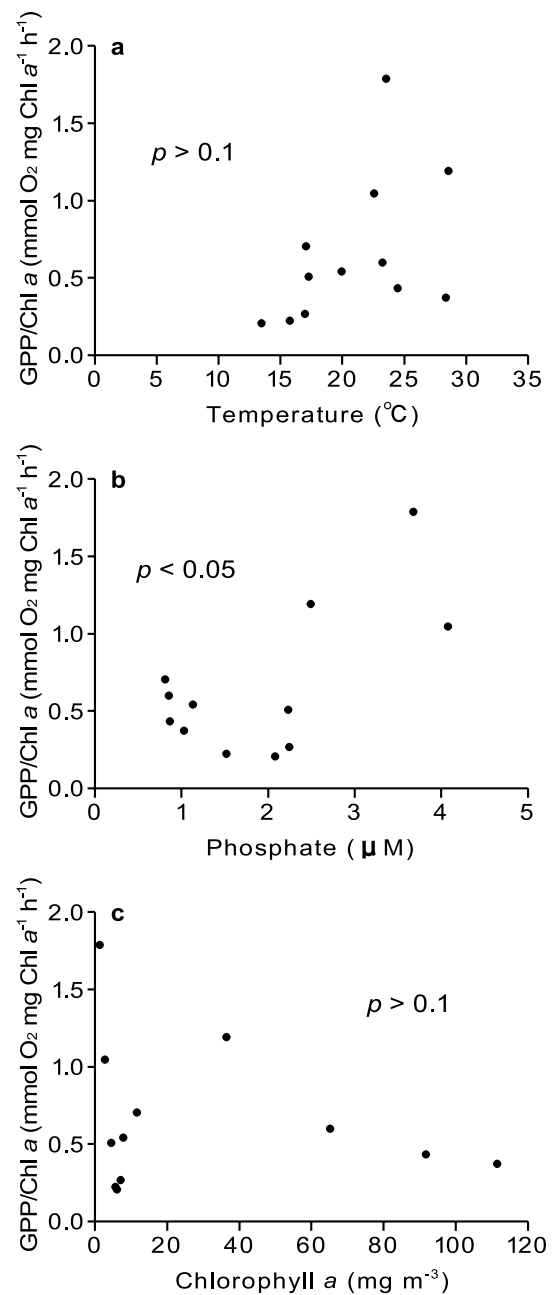
2008). During the study period, 206 mm of precipitation was recorded between 1 and 5 July (Fig. 2b), suggesting that salinity reached a minimum of 15 on 6 July due to run-off from the river.

Each nutrient concentration measured in this study was within the range of values previously reported (nitrate + nitrite:  $< 0.5$ – $131 \mu\text{M}$ , ammonium:  $0.5$ – $130 \mu\text{M}$ , phosphate:  $0.1$ – $4.7 \mu\text{M}$ ; Nomura 1995; Matsumura et al. 2001; Nakane et al. 2008; Kubo et al. 2019). Nitrate + nitrite tended to increase from June to October (Fig. 4a). Nitrate concentrations previously measured near the station in this study also showed a trend toward higher concentrations from spring to fall (Koibuchi et al. 2000a; Nakane et al. 2008). Increased precipitation has increased freshwater inflow into the inner part of Tokyo Bay from, for example, the Arakawa and Sumida Rivers, and increased nutrient concentrations (Koibuchi et al. 2000a; Matsumura and Ishimaru 2004; Nakane et al. 2008). Nutrient concentrations showed seasonal variations similar to those reported in previous studies.

Seasonal variations in DO showed that there were survey days from June–September when oxygen saturation exceeded 100%. Notably, Chl *a* concentrations and GPP were higher on those days than on other survey days, with the concentration of Chl *a* reaching  $> 30 \text{ mg m}^{-3}$  and GPP reaching  $> 450 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ . Therefore, the high phytoplankton biomass and primary production likely result in oxygen saturation levels greater than 100%.

Phytoplankton growth rates are also affected by water temperature (Parsons et al. 1984a). Previous studies have indicated that the volume-specific carbon fixation rate of phytoplankton communities is strengthened by increasing water temperature when nutrient concentrations do not constrain their growth (Marañón et al. 2014, 2018). Here, the relationship between water temperature, phosphate, and Chl *a* concentrations and GPP/Chl *a* was investigated (Fig. 7). The GPP/Chl *a* ratio showed no significant relationship with water temperature (Fig. 7a,  $p > 0.1$ ). GPP/Chl *a* showed a large range (0.20–1.79) when Chl *a* concentration was  $< 10 \text{ mg m}^{-3}$  and, similar to water temperature, showed no significant relationship with Chl *a* (Fig. 7c,  $p > 0.1$ ). However, GPP/Chl *a* showed a significant positive relationship with the phosphate concentration (Fig. 7b,  $p < 0.05$ ). These results indicated that growth rates were higher when phosphate concentrations were higher. Thus, it is likely that phosphate supply is a more important factor controlling phytoplankton growth than water temperature in the inner part of Tokyo Bay. Marañón et al. (2014) examined the relationship between phytoplankton growth rate and water temperature ( $10$ – $30 \text{ }^\circ\text{C}$ ) in oligotrophic waters ( $\text{NO}_3^- < 10 \mu\text{M}$ ) and found no relationship between the growth rate and water temperature when nutrient concentrations were depleted.

The GPP/Chl *a* on 1 June ( $0.60 \text{ mmol O}_2 \text{ mg Chl } a^{-1} \text{ h}^{-1}$ ), 3 August ( $0.37 \text{ mmol O}_2 \text{ mg Chl } a^{-1} \text{ h}^{-1}$ ) and 25 September



**Fig. 7** Relationship between water temperature (a), phosphate (b) and chlorophyll *a* concentrations (c), and GPP per unit Chl *a* (GPP/Chl *a*)

( $0.43 \text{ mmol O}_2 \text{ mg Chl } a^{-1} \text{ h}^{-1}$ ) was  $< 1.0 \text{ mmol O}_2 \text{ mg Chl } a^{-1} \text{ h}^{-1}$  when Chl *a* concentration was  $> 50 \text{ mg m}^{-3}$  despite the water temperature being  $> 20 \text{ }^\circ\text{C}$ . Therefore, GPP/Chl *a* may not have been significantly correlated with water temperature in the present study. A significant positive correlation between GPP/Chl *a* and water temperature was observed ( $p < 0.01$ ) during the study period, except on 1 June, 3 August and 25 September. Thus, GPP/Chl *a* may not show a significant relationship with water temperature when the Chl *a* concentration is above  $50 \text{ mg m}^{-3}$  even at high

water temperatures ( $> 20$  °C). Notably, the Chl *a* concentrations and GPP were lower in May, 6 July and 11 September, and from October to December than those on other survey dates. Water temperature on all survey dates except 6 July and 11 September was below 20 °C (Fig. 3a), suggesting that the low Chl *a* concentrations and GPP might be a result of low water temperature. Thus, it seems that phytoplankton growth rate is affected by water temperature when nutrient concentration is abundant and Chl *a* concentration is less than  $50 \text{ mg m}^{-3}$ .

DO, Chl *a*, and GPP in surface water on 6 July and 11 September were lower than on other survey dates (Figs. 3c, 4d and 5a). In contrast, phosphate concentrations were higher (Fig. 4c). In the inner part of Tokyo Bay, stratification intensifies from summer to autumn, and anoxic water masses exist in the bottom layer (Kajiyama and Uto 2016). In 2021, an anoxic water mass formed in the bottom layer of the inner part from June to October (Chiba Prefectural Fisheries Research Center 2021). Under anaerobic conditions, phosphate is released from the bottom sediment (Matsumura et al. 2001; Suzumura et al. 2003). Therefore, it is likely that phosphate was abundant in anoxic water masses in the bottom layer of the inner part from June to October. Miyata and Hattori (1986) reported that de-stratification occurs when the average wind speed is greater than  $3 \text{ m s}^{-1}$ . However, the influence of wind seemed lower, with an average wind speed before 6 July was less than  $3 \text{ m s}^{-1}$  (Fig. 2c). The salinity on 6 July was 15, the lowest during the study period, with a total of 206 mm of precipitation recorded in Tokyo from 1 to 5 July (Fig. 2b). Kaneko and Nihei (2012) reported the large-scale formation of hypoxic water masses in the tidal areas of urban rivers such as the Sumida River due to the decomposition of organic matter contained in sewage overflow during rainfall. Phosphate-rich river water with hypoxia formed by rainfall overflow sewage may have been present at the surface of the survey station on 6 July. In contrast, northerly winds with a maximum speed of approximately  $5 \text{ m s}^{-1}$  blew continuously from 31 August to 9 September before 11 September (Fig. 2c, d). A two-day period of northerly winds of  $5 \text{ m s}^{-1}$  or more causes surface water to move southward along the shore and bottom anoxic water to flow northward, promoting vertical mixing and reducing DO in the surface layer (Nakata and Kuramoto 1992; Watanabe et al. 1998). Therefore, it is likely that the lower DO and phosphate-rich surface water observed on 11 September resulted from wind-driven bottom water. Blue tides have been reported to have occurred on the northern shore of Tokyo Bay from 3 to 10 September (Chiba Prefectural Fisheries Research Center 2021). Anoxic water has high phosphorus concentration, but the Chl *a* concentration and GPP seem low. Similar seasonal variations in DO and Chl *a* in the surface layer have been reported by Uchiyama et al. (1998) in the inner part of Tokyo Bay. Similar vertical changes in DO and Chl *a*

concentrations have also been reported in Osaka Bay and Ise Bay (Nakatsuji et al. 2003; Adachi et al. 2014). The Chl *a* concentration in the inner part of Tokyo Bay from July to August increased after low-DO ( $< 125 \text{ mmol m}^{-3}$ ) in the surface layer (Uchiyama et al. 1998). Chl *a* and GPP showed a significant negative relationship with phosphate in Spearman's rank correlation (Chl *a*:  $p < 0.001$ ,  $r = -0.83$ , GPP:  $p < 0.05$ ,  $r = -0.60$ ). It is possible that phosphate-rich water with low Chl *a* was brought to the surface layer and the conditions before bloom were observed on 6 July and 11 September. Thus, the growth rate of phytoplankton seems to be higher when phosphate concentrations are high in the inner part of Tokyo Bay. In the coastal zone of the inner part of Tokyo Bay from summer to autumn, nutrients (especially phosphate) are sporadically supplied to the surface layer by river water run-off due to rainfall and upwelling from the bottom layer due to wind-induced destruction of stratification, followed by large phytoplankton blooms (Uchiyama et al. 1998; Nakane et al. 2008). Consequently, our results suggest that rising water temperature and increasing nutrient (especially phosphate) concentration in the inner part of Tokyo Bay are important factors regulating the growth rate of the phytoplankton community when Chl *a* concentrations are below  $50 \text{ mg m}^{-3}$ .

The GPPs were incubated at a light intensity of  $350 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ . According to Koibuchi et al. (2000b), when Chl *a* concentration was approximately  $70 \text{ mg m}^{-3}$  in May in the inner part of Tokyo Bay, the PAR at a depth of 0.5 m was about  $400 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$  and approximately  $1300 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$  when Chl *a* concentration was about  $20 \text{ mg m}^{-3}$ . The light level in the incubator used in this study may have been lower than those in the field when Chl *a* concentrations were below  $70 \text{ mg m}^{-3}$ . Consequently, GPP/Chl *a* on 21 August may be underestimated because the Chl *a* concentration ( $36.6 \text{ mg m}^{-3}$ ) was less than  $70 \text{ mg m}^{-3}$ .

## 4.2 Metabolic balance in planktonic communities

The GPP, CR, and NCP of plankton are essential factors that regulate the response of the marine carbon cycle to warming and eutrophication. The balance between GPP and CR determines the amount of carbon that can be supplied to the coastal food web and defines the metabolic state of the ecosystem, involving both autotrophic and heterotrophic metabolic activities. The maximum value of CR was less than a quarter of the maximum value of GPP (Figs. 5a, c and 6a). The autotroph community became dominant, with average GPP/CR ratios  $> 3.0$ . This is predictable in productive waters with GPPs much higher than the thresholds determined to distinguish between autotrophic and heterotrophic communities (Duarte and Agustí 1998; Duarte and Regaudie-de Gioux 2009). The mean GPP during the observation period was  $210.6 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ , much higher than the threshold



GPP ( $14.2 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ). GPP and NCP have closely correlated with Chl *a* concentration, with more than 70% of the variance in GPP and NCP explained by Chl *a*. Tokyo Bay is a semi-enclosed system, and the inner part of the bay is one of the highest primary production areas in the world, because more than 70% of the nitrogen and phosphorus in the bay flows in through rivers from spring–autumn (Matsumura and Ishimaru 2004).

A better way to determine trophic status is to use a threshold GPP that separates autotrophic and heterotrophic state (McKinnon et al. 2017). However, the threshold GPPs in oligotrophic areas are lower than those in eutrophic areas (Duarte and Agustí 1998; Duarte and Regaudie-de-Gioux 2009). Duarte and Regaudie-de-Gioux (2009) showed that the average for the global ocean with respect to the threshold GPP is 1.07, the Pacific is 1.33, and the Mediterranean is  $4.16 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ . The threshold GPP in the inner part of Tokyo Bay was much higher than in the open ocean. The threshold GPP in the inner Tokyo Bay exceeded  $10.1 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  in the mangrove channel in Australia, where light disappears at a depth of one meter (McKinnon et al. 2017). The high threshold GPP of mangroves is due to the contribution of organic matter from mangrove forests and tidally induced resuspension of fine sediments, deposited detritus, and microalgae. (McKinnon et al. 2017). The mean values of GPP, CR, and GPP/CR ratio in the mangrove channels were  $19.71 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ,  $10.62 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ , and 1.89, respectively (McKinnon et al. 2017). In comparison, the GPP ( $210.6 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ), CR ( $41.0 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ), and GPP/CR ratio (3.80) in the inner part of Tokyo Bay were several times higher than those in mangrove channels. Therefore, it is thought that the inner part of Tokyo Bay is more eutrophic than mangrove forests. The increased threshold GPP in Tokyo Bay may be due to the abundance of organic matter available to heterotrophic organisms in Tokyo Bay, which has the highest primary production worldwide.

The CR is controlled by many biotic and abiotic ecosystem characteristics, such as water temperature, Chl *a* concentrations, particulate and dissolved organic matter supply, and plankton community composition (Regaudie-de-Gioux and Duarte 2013; Lønborg et al. 2016). The average CR in surface waters of the world is  $3.5 \pm 0.13 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ,  $4.9 \pm 0.23 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  at depths less than 10 m,  $7.4 \pm 0.74 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  in coastal waters, and  $3.3 \pm 0.15 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$  in the open ocean (Robinson and Williams 2005). A few plankton CR measurements are in the inner part of Tokyo Bay. The inner part of Tokyo Bay ( $41.0 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ) is almost six times higher than that of the coastal areas reported by Robinson and Williams (2005). McKinnon et al. (2017) reported that the CR increases with increasing Chl *a* concentration and water temperature. However, the effect of Chl *a* concentration was greater than that of water temperature. Tokyo Bay

is one of the coastal areas with the highest primary production worldwide, where the Chl *a* concentration often reaches  $100 \text{ mg m}^{-3}$  (Cloern et al. 2014). In this study, the Chl *a* concentration measured on 3 August was above  $100 \text{ mg m}^{-3}$ . This implies that primary production is more vigorous in the surface layer of the inner part of Tokyo Bay than in other coastal areas, and that heterotrophs are also more active. As shown in Fig. 6a, the relationship between GPP and CR suggests that heterotrophs were also active during periods when the autotrophs were active. CR could potentially increase not only because of autochthonous organic matter, but also because of allochthonous organic matter ((Regaudie-de-Gioux and Duarte 2013). Therefore, we also need to examine the factors contributing to the high CR in the inner part of Tokyo Bay, including a combined analysis of allochthonous organic matter from rivers, other sources, and bacterial and planktonic communities.

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## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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