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ORIGINAL ARTICLE

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Photosynthetic property and primary production of phytoplankton in sublittoral sand bank area in the Seto Inland Sea, Japan

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Abstract We investigated the photosynthesis–light intensity (P–I) relationships of phytoplankton collected from a sublittoral sand bank in the Seto Inland Sea, Japan, under different temperature conditions. In spite of low chlorophyll *a* concentration (<3 mg m^{-3}), phytoplankton had considerably high photosynthetic potential (>10 mg C (mg chl $a)^{-1}$ h^{-1}) in the study area. Based on the P–I relationships, we conducted numerical simulation of areal primary production using published data on water temperature, chlorophyll *a* concentration, and irradiance. The areal primary production ranged between 159 and 187 g C m^{-2} year^{-1}. This production was within the range of typical values reported previously in deeper areas of the Seto Inland Sea. The productivity in the sand bank area was discussed in relation to water current, allochthonous resource input, and fisheries.

Keywords Phytoplankton · Photosynthesis · Primary production · Sand bank · Seto Inland Sea

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Introduction

Primary production of phytoplankton is the foundation of the marine food chain. Quantitative measurements of primary production help understand ecological processes of production from low to higher trophic levels in marine ecosystems (Nixon 1988). In addition, such measurements are important for the management of fishery resources. The Seto Inland Sea is the largest semi-enclosed coastal sea in Japan and is known as a treasury of fishery resources (Hashimoto and Takeoka 1998). There are a number of sand banks in the Seto Inland Sea, making patchy shallow zones less than 10 m deep (Yoshino et al. 2006). Sand banks have long been viewed as important fishery grounds (e.g. Daan et al. 1990). This may be related to the occurrence of fronts with enhanced production in the region (Munk 1993). Three large sand banks off Hojo, Ehime prefecture, are among the most important fishery grounds for sand lance (*Ammodytes personatus*) and juvenile anchovy (*Engraulis japonicus*) in Japan. These fishes, especially collected in the Hojo area, are served as the highest grade of boiled-dried fish to make Japanese soup stock, being a daily essential in the food culture of Japan.

In the Seto Inland Sea, primary production, along with standing stocks of phytoplankton, in the entire region of the sea has been studied (Uye et al. 1987; Hashimoto et al. 1997; Tada et al. 1998). On a smaller scale, little is known for production in specific topographic structures such as sand banks. Stable isotope analyses by Yoshino et al. (2006) showed that benthic algae attached on sand banks can contribute considerably to the coastal production. In this study, we estimated primary production of phytoplankton in a sand bank area by measuring the photosynthetic–light intensity (P–I) relationships of phytoplankton. The P–I relationships have been often used for measuring, modeling and predicting primary production (e.g. Furuya et al. 1998). The results of the present study were discussed in the light of typical primary production values previously reported in the Seto Inland Sea and the fishery yield in the Hojo area.

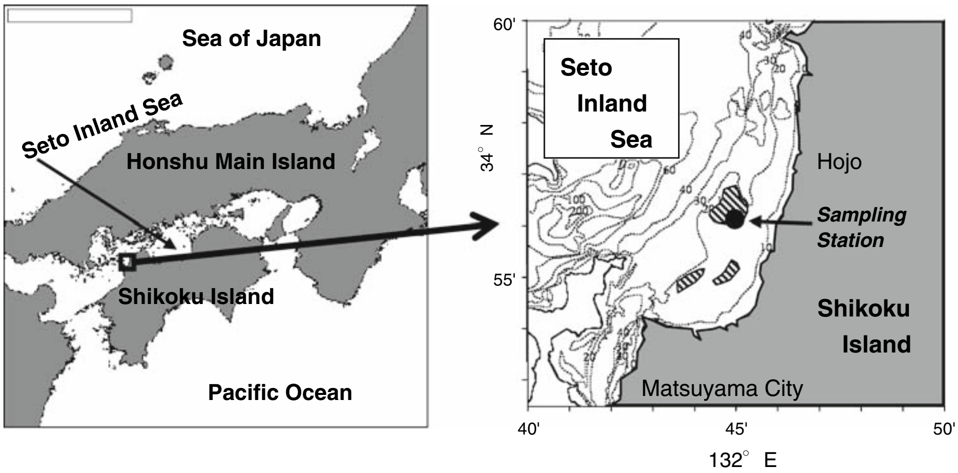

Fig. 1 Study area and sampling station on the sand bank "Ozu" off Hojo. *Dotted lines* indicate depth contour. Sand banks are indicated by *shaded areas* in the right panel (Ozu, Tsugai East and Tsugai West)

Methods

Study area and sampling

Surveys were conducted on board R/V Tobiuo at the sampling station (33°56′N, 132°45′E; 11 m deep; Fig. 1) on one of the three large sand banks in the sublittoral zone off Hojo district of Matsuyama city, Ehime prefecture, Japan, on 27 September and 4 November 2005. Water samples were collected using a 10 l Van-Dorn water sampler. Sampling depths were 0, 1, 2.5, 5, 7.5 and 10 m. At the same time as water samples were collected, water temperature was measured vertically with a temperature data logger (Compact-CLW, Alec electronics) and underwater light intensity was measured as photon flux density (μmol m^{-2} s^{-1}) using a quanta-meter (LI-1400, LiCor) at depths of 0, 1, 2.5, 5, 7.5 and 10 m.

Processing of water samples

Water samples for determination of chlorophyll *a* concentration were filtered onto Whatman GF/F glass-fiber filters. Chlorophyll *a* concentration was measured fluorometrically by the method of Parsons et al. (1984). Concentrations of nitrate and phosphate were determined by the hydrazine reduction method (Mullin and Riley 1955) and the molybdate method (Murphy and Riley 1962), respectively. Water samples for determination of phytoplankton species were fixed with Lugol's solution at a final concentration of 1%. Phytoplankton species were identified and counted under a microscope with magnifications of ×200 and ×400.

Photosynthetic activity measurement

Photosynthesis of phytoplankton was measured with the ^{13}C method (Hama et al. 1983) under laboratory conditions. Since Nakanishi (1976) showed that a specific phytoplankton sample from one depth can be used for the estimation of primary production within the whole water column, water samples for measurement of photosynthetic activity were collected from a depth of 5 m in this study. Collected water samples were transported to the laboratory within 2 h after sampling under a dark, cool condition. Polycarbonate bottles of 500 ml were filled with the water samples in the laboratory. Then, we added $NaH^{13}CO_3$ (10% of the total inorganic carbon of the sea) to the bottles. The bottles were incubated in water baths at three different water temperatures (15, 20 and 25°C on 27 September, and 10, 15 and 20°C on 4 November) and exposed to the natural solar radiation. Water temperature was checked with a thermometer every 15 min and regulated manually by addition of ice cubes. Five gradients of the light condition were made by covering the polycarbonate bottles with polyester bags (Nelnet 18 Black, Isshiki Honten): polycarbonate bottles with no bag (100% of the air light intensity), one bag (58%), two bags (26%) and three bags (6%), and a dark polypropylene bottle (0%). The incubation was made from 11:35 to 16:15 on 27 September and 11:45 to 16:00 on 4 November. The air light intensity (photon flux density) was measured every 15 min next to the water baths using the quanta-meter.

After incubation, the waters in the bottles were filtered onto precombusted (550°C for 3 h) Whatman GF/F glass-fiber filters. The filters were treated with HCl fumes to remove carbonate and then dried in a desiccator. The concentrations of organic carbon and the isotope ratios of ^{13}C and ^{12}C in the samples were determined with a mass spectrometer (Integra-CN, Sercon). The concentration of inorganic carbon was determined with a total organic carbon analyzer (TOC-V CSH, Shimadzu).

Based on Platt et al. (1980), the P–I curves were fitted by a modified minimal model that can express the photoinhibition effect under high light intensities:

$$P = aIe^{-bI}, \qquad (1)$$

where P represents the photosynthetic rate at a give light intensity (I), and a and b are constants. These constants were obtained by non-linear curve-fitting using STATISTICA (StatSoft Inc.).

Calculation for seasonal change in the areal primary production

Areal monthly primary production of phytoplankton on the sand bank was calculated based on the P–I curves obtained in this study, solar irradiance data (Matsuyama Local Weather Station 2006), and water temperature and chlorophyll *a* data (Seto Inland Sea Water Quality 2000–2005). We derived the relationship between photosynthetic rate and light intensity at a given temperature (i.e. P–I curve at T°C) using the P–I curves at 20–25°C obtained on 27 September and at 10–20°C obtained on 4 November. We assumed that the photosynthetic rate P at T°C was given by linearly interpolating the rates at 10 and 15°C when $10 < T < 15$°C, the rates at 15 and 20°C when $15 < T < 20$, and the rates at 20 and 25°C when $20 < T < 25$. Because the sea temperature in the study area was still higher than 20°C on 4 November, we used the P–I curve at 20°C by averaging the equations at this temperature obtained on 27 September and 4 November. The photosynthetic rate at light intensity I and T°C, $P(I, T)$, was given by

$$P(I,T) = P(I,10)\cdot(15-T)/5 + P(I,15)\cdot(T-10)/5 \quad \text{for } 10 < T < 15 \tag{2}$$

$$P(I,T) = P(I,15)\cdot(20-T)/5 + P(I,20)\cdot(T-15)/5 \quad \text{for } 15 < T < 20 \tag{3}$$

$$P(I,T) = P(I,20)\cdot(25-T)/5 + P(I,25)\cdot(T-20)/5 \quad \text{for } 20 < T < 25. \tag{4}$$

Underwater light intensity measured as photon flux density in units of μmol $\mathrm{m^{-2}\,s^{-1}}$ was calculated based on the relationships between photon flux densities in the air (I_0) and under the water at a depth of z m ($I(z)$) and between photon flux density (I_0) and solar irradiance in units of MJ $\mathrm{m^{-2}\,h^{-1}}$ (L). Taking into consideration the effect of chlorophyll on light attenuation, the relationship between underwater photon flux density at a depth of z m ($I(z)$) and photon flux density in the air (I_0) measured on 27 September and 4 November was fitted using a Lambert–Beer equation:

$$I(z) = I_0 \exp[-s_0 - (s_1 + s_2 A)z], \tag{5}$$

where A was the chlorophyll *a* concentration; s_0 was the air–water surface light attenuation coefficient; s_1 was the phytoplankton-independent background light attenuation coefficient; and s_2 was the specific light attenuation coefficient per unit chlorophyll *a* concentration. Based on our photon flux density data measured with the quanta-meter every 15 min (averaged over the hour) on 27 September and 4 November and solar irradiance data at Matsuyama on these days (Matsuyama Local Weather Station 2006), the relationship between photon flux density (I_0) and solar irradiance (L) was fitted by linear regression. We referred to the mean daily solar irradiance (L_{day}, MJ $\mathrm{m^{-2}\,d^{-1}}$) of each month in Matsuyama city to estimate the hourly change of solar irradiance (L, MJ $\mathrm{m^{-2}\,h^{-1}}$). The hourly solar irradiance at a given time (t) was assumed to be given approximately by the following formula (Ikusima 1967; Nozaki 2001):

$$L(t) = L_0 \sin^2 \frac{\pi t}{D}, \tag{6}$$

where L_0 and D were the maximum solar irradiance (MJ $\mathrm{m^{-2}\,h^{-1}}$) and daytime length (h) in each month, respectively. The daytime length (D) in each month was defined by the difference between the hours just after sunrise and just before sunset on the 15th day of the month in Matsuyama city (National Astronomical Observatory of Japan 2006). The parameter L_0 was calculated using the following relationship:

$$L_{\mathrm{day}} = \int_0^D L_0 \sin^2 \frac{\pi t}{D}\,\mathrm{d}t, \tag{7}$$

(i.e. $L_0 = 2\,L_{\mathrm{day}}/D$). Using Eqs. (5)–(7), we converted the solar irradiance data (L_{day}) to underwater light intensity ($I(z)$).

We assumed a water column from the surface to the bottom (11 m deep) with a unit area (i.e. 1 × 1 × 11 m) on the sand bank in the study area. The water column was divided vertically into subcolumns at intervals of 0.1 m (i.e. 1 × 1 × 0.1 m). We first calculated the hourly production within each subcolumn using the corresponding light intensity (Eqs. (5)–(7), Matsuyama Local Weather Station 2006) and chlorophyll *a* concentration data (Seto Inland Sea Water Quality 2000–2005) to the depth. The mean light intensity in a subcolumn with its upper surface at a depth of z_1 m and lower surface at a depth of $z_1 + 0.1$ m was calculated as

$$\bar{I}(z_1) = \int_{z_1}^{z_1+0.1} I(z)\,\mathrm{d}z \bigg/ 0.1. \tag{8}$$

The hourly primary production within the subcolumn with its upper surface at z m and lower surface at $z + 0.1$ m at time t, $PP_t(z)$, is given by

$$PP_t(z) = P(\bar{I}_t(z), T) \times A \times 0.1, \tag{9}$$

where A is the chlorophyll *a* concentration available at Seto Inland Sea Water Quality (2000–2005). The daily primary production within the subcolumn, $PP(z)$, is given by

$$PP(z) = \sum_{t=0}^{D} PP_t(z). \tag{10}$$

The daily primary production within the entire water column from the surface ($z = 0$) to the bottom

(z = 11 − 0.1 = 10.9, the depth at this point (11 m) subtracted by the thickness of the subcolumn (0.1 m)), PP, is given by

$$PP = \sum_{z=0}^{10.9} PP(z). \tag{11}$$

For water temperature and chlorophyll *a* concentration, we referred to the Seto Inland Sea Water Quality (2000–2005) data at the closest sites to the study area (IY2MY30: 33°56′N, 132°39′E and AKIHS15: 34°00′N, 132°34′E; sampling depth was 2 m deep for both sites) available since May 2000. We used the averaged data from these two sites (IY2MY30 and AKIHS15) for water temperature and chlorophyll *a* concentration and they were assumed uniform in the water column from the surface to the bottom (11 m deep).

Carbon mass of *Ammodytes personatus* and juvenile *Engraulis japonicus*

For the catches of *A. personatus* and juvenile *E. japonicus* in the Hojo area, we referred to Agriculture, Forestry and Fisheries Resources Annual Report of Ehime (2001–2004). The wet weight and carbon content of these species collected in the area were measured with an electronic balance (AB 135-S, Mettler Toledo) and a mass spectrometer (ANCA-SL, Sercon), respectively.

Results

Water temperature was uniform throughout the water column from the surface to the bottom during the investigated periods and was 24.1 and 21.9°C on 27 September and 4 November, respectively (Fig. 2). The chlorophyll *a* concentration was almost uniform from the surface to the bottom on 27 September (2.2–2.7 mg m^{-3}), and there was slightly higher chlorophyll *a* near the surface on 4 November (0.5–0.9) (Fig. 2). The nitrate (NO_3–N) concentration was 2.4–3.1 and 4.2–4.8 mmol m^{-3} on 27 September and 4 November, respectively. The phosphate (PO_4–P) concentration was 0.4–0.5 mmol m^{-3}. The concentration of inorganic carbon was 25 g C m^{-3}. The phytoplankton community in this area was dominated by planktonic diatoms (Table 1).

We obtained the relationship between the solar irradiance (L, MJ m^{-2} h^{-1}) and photon flux density (I_0, µmol m^{-2} s^{-1}):

$$I_0 = 488.3L \tag{12}$$

(n = 10, r^2 = 0.98). For the relationship between air light intensity (I_0) and underwater light intensity ($I(z)$), we obtained s_0 = 0.39, s_1 = 0.50, and s_2 = 0.08 in Eq. (5). The light intensity at 10 m depth was 4 and 11% of the light intensity just below the sea surface on 27 September and 4 November, respectively. The entire column in the study area can be considered a euphotic layer (> 1% of the surface light intensity, Strickland 1958). The conversion of underwater light intensity (dependent on depth, chlorophyll *a* concentration, and time) from solar irradiance was given by

$$I(z,A,t) = 488.3\frac{2L_{\mathrm{day}}}{D}\sin^2\frac{\pi t}{D}e^{-0.39-(0.5+0.08A)z}. \tag{13}$$

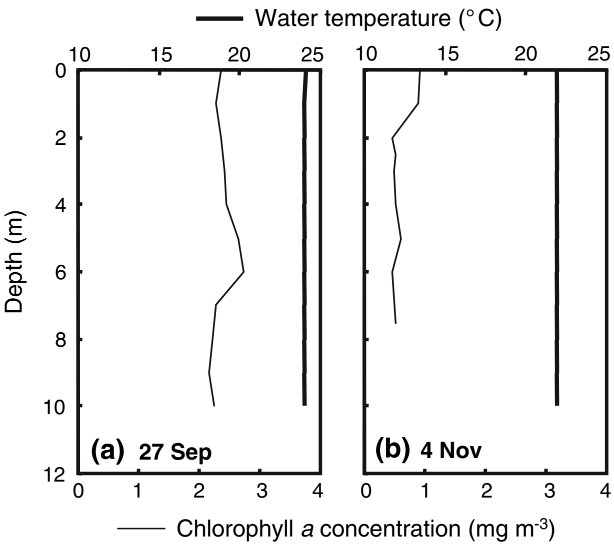

Fig. 2 Vertical profiles of water temperature and chlorophyll *a* concentration at the sampling station on 27 September 2005 (**a**), and 4 November 2005 (**b**)

Table 1 Dominant phytoplankton taxa and their dominance calculated based on counts of cell number

Date	Taxon	Dominance (%)
27 September 2005	*Chaetoceros* spp.	53.4
	Skeletonema spp.	23.8
	Melosira spp.	11.4
	Asterionella spp.	11.4
4 November 2005	*Navicula* spp.	35.8
	Thalassiothrix sp.	34.3
	Nitzschia spp.	29.9

The P–I relationship curves of phytoplankton on the sand bank are shown in Fig. 3 (Table 2). Photosynthetic activity of phytoplankton was inhibited by photoinhibition under high light intensities. The maximum photosynthetic rates increased with water temperature.

Using the solar irradiance data Matsuyama Local Weather Station (2006) and water temperature and chlorophyll *a* concentration data Seto Inland Sea Water Quality (2000–2005), we conducted numerical simulation of seasonal change in areal primary production in the study area based on the P–I curves obtained in this study (Fig. 4). The primary production changed seasonally, being the highest in summer (August and

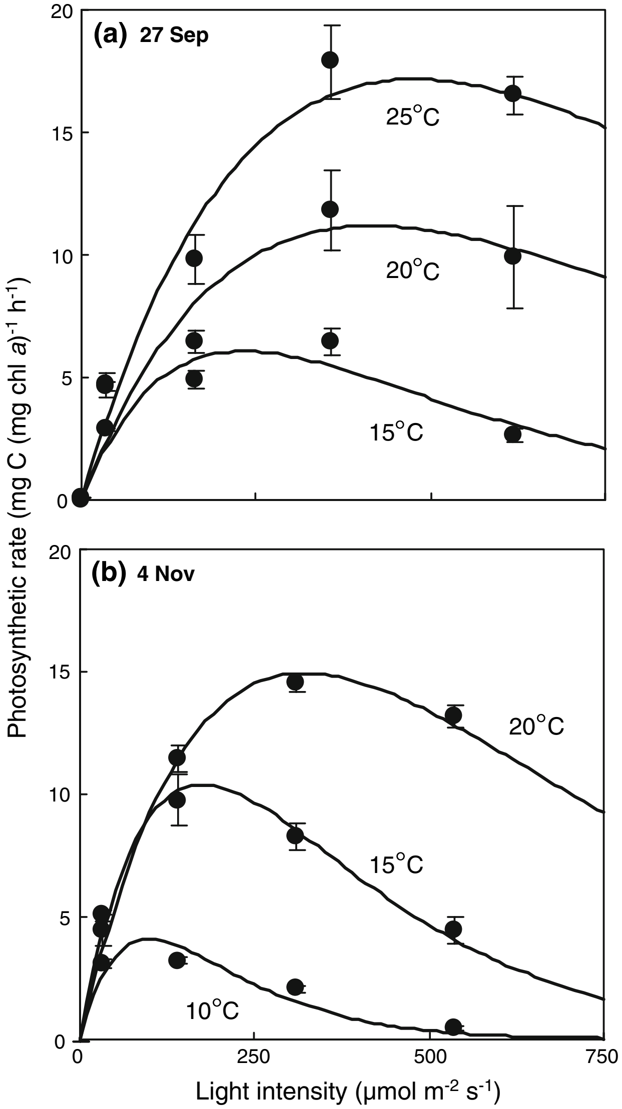

Fig. 3 Photosynthesis–light intensity (P–I) curves of phytoplankton at different water temperatures on 27 September 2005 (**a**), and 4 November 2005 (**b**). Lines were fitted by equations listed in Table 2

Table 2 Relationships between the photosynthetic rate (P) and light intensity (I) approximated to the formula $P = a I e^{-bI}$

Date	Temperature (°C)	a	b
27 September 2005	25	0.098	0.0021
	20	0.073	0.0024
	15	0.071	0.0043
4 November 2005	20	0.126	0.0031
	15	0.161	0.0057
	10	0.112	0.0101

September) and the lowest in winter (February). Based on this simulation, the annual primary production per unit area was estimated at 176, 169, 187 and 159 g C m^{-2} yr^{-1} in 2001, 2002, 2003, and 2004 respectively. The annual primary production in the sand bank area (total area of Ozu, Tsugai East and Tsugai West banks shallower than 13 m: 1.94×10^6 m^2) was estimated at 341, 328, 363 and 309 t C yr^{-1} in 2001, 2002, 2003, and 2004, respectively. The proportion of the total catch of *A. personatus* and juvenile *E. japonicus* to the annual primary production on the sand bank was 3.7, 11.0, 10.3 and 6.6% in 2001, 2002, 2003, and 2004 respectively, where conversion from wet weight to carbon mass was 9 and 9.4% for *A. personatus* and juvenile *E. japonicus*, respectively.

Discussion

The profiles of water temperature and chlorophyll *a* concentration were vertically uniform from the water surface to the bottom (Fig. 2) due to fast current of water in the region (Guo et al. 2004). Data on water temperature and chlorophyll *a* concentration from Seto Inland Sea Water Quality (2000–2005) were also vertically uniform regardless of season or year. The assumption made in our simulation of primary production in the sand bank area that water temperature and chlorophyll *a* concentration were the same within the water column was reasonable.

Photosynthetic property of phytoplankton (P–I curves in Fig. 3) showed photoinhibition at all temperature conditions on both dates. The maximum photosynthetic rates (mean values) ranged from 3.2 mg C (mg chl $a)^{-1}$ h^{-1} at 10°C on 4 November to 17.9 at 25°C on 27 September 2005. The nitrate concentration on 27 September was lower than that on 4 November, whereas the phosphate concentration took similar values on both sampling dates. This indicates that nitrogen could be a limiting nutrient for phytoplankton growth in September (mean N:P ratio by atoms: 6.1 in September and 10.0 in November). In fact the maximum photosynthetic rate at 20°C was higher in November (14.6 mg C (mg chl $a)^{-1}$ h^{-1}) than in September (11.8 mg C (mg chl $a)^{-1}$ h^{-1}) (Fig. 3).

The maximum photosynthetic rates of marine phytoplankton in the temperate zone were in the range of 2–3 mg C (mg chl $a)^{-1}$ h^{-1} (Harrison and Platt 1986; Furuya et al. 1998). In coastal seas, Ichimura and Aruga (1964) reported that they generally ranged from 2 to 6 mg C (mg chl $a)^{-1}$ h^{-1}. However, Hogetsu et al. (1959) reported that the rate could amount to 9.6–16.9 when a bloom of *Skeletonema costatum* occurred at water temperature 20–25°C in Tokyo Bay. Although, our data on chlorophyll were far below the algal bloom level, *Skeletonema* spp. were among the dominant taxa in the study area in September when photosynthetic rates were high (Table 1). The phytoplankton on the sand bank may potentially have high photosynthetic activities comparable to algal communities that cause blooms.

The areal annual primary production on the sand bank (159–187 g C m^{-2} $year^{-1}$) was in good accord with previous estimations reported as averaged values in

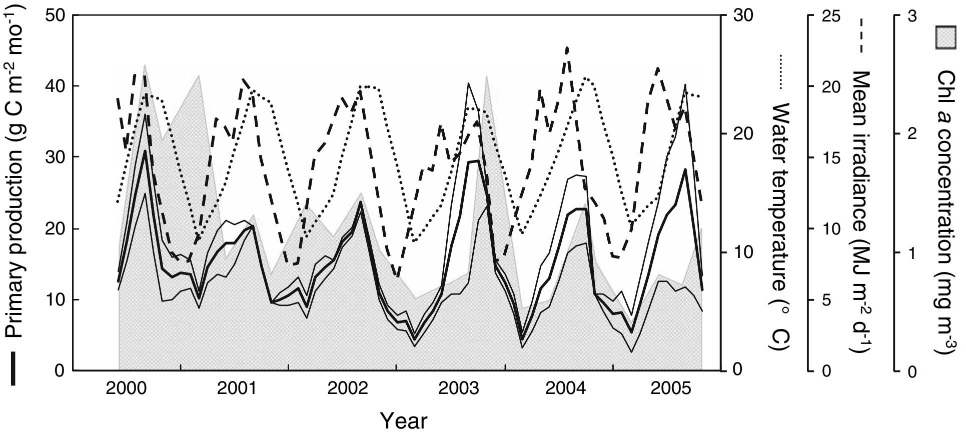

Fig. 4 Monthly changes in water temperature at 2 m deep (*dotted line*), mean irradiance (*broken line*), chlorophyll *a* concentration at 2 m deep (*shaded line*), and calculated areal primary production (*solid lines*) from May 2000 through October 2005. Note that there are three areal primary production lines (*two thin solid lines* and *one thick solid line* in between). The thick line corresponds to the mean areal primary production, calculated using the averaged chlorophyll *a* concentrations at sites IY2MY30 and AKIHS15 of Seto Inland Sea Water Quality (2000–2005). Other *thin lines* correspond to overestimated (*above the thick line*) and underestimated (*below the thick line*) areal primary production, calculated using the maximum and minimum values of chlorophyll *a* concentration at those sites, respectively

the Seto Inland Sea of 122 g C m^{-2} $year^{-1}$ by Uye et al. (1987) and 218 by Tada et al. (1998). High photosynthetic activity (>10 mg C (mg chl *a*)$^{-1}$ h^{-1}) in spite of low chlorophyll *a* concentration (<3 mg m^{-3}) was a characteristic of phytoplankton in the study area.

As we have no data on water temperature or chlorophyll *a* concentration in the study area before the study period, we referred to data from survey stations by Ministry of Land, Infrastructure and Transport of Japan (Seto Inland Sea Water Quality 2000–2005). Because there was little difference in water temperature between sites in the sublittoral area off Hojo district (sites IY2MY30 and AKIHS15, Seto Inland Sea Water Quality 2000–2005), we used water temperatures at IY2MY30 and AKIHS15 in our simulation of primary production. As for chlorophyll, we compared our data and Seto Inland Sea Water Quality data at IY2MY30 and AKIHS15 in 2005. The temporal fluctuation of our data roughly fell in the variation range at these sites. Thus, estimation of primary production in the study area was conducted as the mean areal primary production (thick solid line in Fig. 4) using the averaged chlorophyll *a* concentrations at these sites. We also estimated areal primary production as overestimated and underestimated values using the maximum and minimum values of chlorophyll *a* concentration at these sites, respectively (thin solid lines in Fig. 4). The overestimated (or underestimated) areal primary production was 193, 181, 228 and 192 (or 156, 154, 134 and 124) g C m^{-2} $year^{-1}$ in 2001, 2002, 2003 and 2004, respectively. These overestimate and underestimate did not deviate much from the mean primary production (159–187 g C m^{-2} $year^{-1}$) and was still within the range (122–218) previously reported by Uye et al. (1987) and Tada et al. (1998). The reason why variations in water temperature and chlorophyll *a* concentration between sites and in primary production estimation were small is unknown and an open problem so far, but it could possibly be due to water mixing on a regional scale due to considerably fast current in this region (current velocity was >1 m s^{-1} in strait areas and >0.5 m s^{-1} in sand bank areas and the density of seawater was vertically uniform throughout the water column in the study area; Y. Kawamura and K. Yoshino, unpublished data).

The estimated annual primary production in the whole sand bank area was greater than the annual catch of *A. personatus* and juvenile *E. japonicus*. The ratios of fish catch to primary production calculated for our study area were high compared to other studies such as 1.8% in the Seto Inland Sea (Uye et al. 1987) and 1.2% in the North Sea (Steele 1974), although fish catch is not necessarily equal to fish production. In sublittoral areas, benthic algae attached on the sand banks have been suggested to contribute substantially to the production (Yoshino et al. 2006). Stable isotope analyses by Yoshino et al. (2006) suggested that fishes were sustained by benthic algae through polychaetes in the study area. Benthic algae were observed in the gut contents of many polychaete species in the Hojo area (Fukumoto 2000). Taking into consideration the contribution by benthic algae as well, the areal primary production on the patchy, shallow sand banks should be considerably greater than other deeper pelagic areas in the Seto Inland Sea. Aggregation of the sand lance and juvenile anchovy on the sand banks may be inherent behavior of the native fishes due to the simultaneous productivity by suspended and benthic primary producers. It is likely that high productivity due to suspended and benthic producers sustains the food resource for the fishes such as crustaceans (Takai et al. 2002). So far, ecology of crustaceans (e.g. standing crop and feeding activity) and detailed food chain from algae to fishes are not known in the study area. Inclusion of zooplankton ecology and analysis of food chain from algae to fishes, which was not addressed by this study, will be important future research for fisheries in sublittoral sand bank areas.

The effect of fast current, characteristic of the study area, on the production should be acknowledged. It is likely that primary production of phytoplankton on the sand bank is transported to other pelagic areas due to fast current. Similarly, *A. personatus* and juvenile *E. japonicus* may feed on allochthonous food resources outside the sand bank. This subsidy effect (i.e. autochthonous + allochthonous food supply) is commonly observed in other ecosystems (e.g. stream: Nakano et al. 1999) (lake: Vander Zanden and Vadeboncoeur 2002; Carpenter et al. 2005). However, the subsidy effect due to current is unknown so far. It is likely that high production of commercially important fish species in the sand bank area is sustained in complicated ways by biological factors (high production by phytoplankton and benthic algae), together with physical factors such as topographic structure and fast current (Wieking and Kröncke 2003).

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