Preliminary estimate of primary production by phytoplankton in Marennes-Oléron Bay, France

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Abstract:

The macrotidal bay of Marennes-Oléron is the most important French site for shellfish production (oysters and mussels); yet the primary productivity of the phytoplankton compartment in this system is not well known. In this study, photosynthetic parameters were determined using 14C incubations of bottom and surface water samples, during fall, winter and summer (2001–2002), along a north–south transect in the bay. Estimates of primary productivity showed that water column primary production is light-limited in the bay and that a BZpI0 type model can be applied. Spatial differences existed in the bay, with a more productive northern zone and less productive river area. With a water column primary production of 185 g C m−2 yr−1, Marennes-Oléron Bay lies in the mean range for phytoplankton primary production capacity among European and North American estuaries.

Keywords: photosynthesis parameters; phytoplankton; turbidity; light limitation; tidal bay; $BZ_p I_0$ model

1. Introduction

The macrotidal bay of Marennes-Oléron on the French Atlantic coast (Figure 1) is the most important site for commercial shellfish production in France, with a stock of 81,000 tons of oysters and mussels and an annual production of 40,000 tons,. The large scale of shellfish culture in the bay has led to studies on the carrying capacity of the ecosystem (Bacher, 1989; Bacher et al., 2000). However, as is the case for many intertidal estuaries, the factors controlling primary production in the bay are not well known. The Charente River represents the major source of nutrients entering the system (Ravail et al., 1988) but Marennes-Oléron Bay is also influenced by the Gironde plume (Boutier et al., 2000), which enters through the northern strait of the basin. The bay waters are often turbid because of sediment resuspension from extensive intertidal mudflats that make up half of the total surface area (180 km^2).

Phytoplankton in the bay waters are both of pelagic and benthic origin. Oceanic waters transport pelagic phytoplankton to the bay, and microphytobenthos can become resuspended from the intertidal mudflats (Riera and Richard, 1996). Physical forcing, exchanges and mixing between water masses could create variability in photosynthetic parameters on a time scale of hours (Lucas et al., 1999; MacIntyre et al., 2000), days (due either to circadian or tidal variation) (Sournia, 1974, Demers and Legendre, 1979; Fréchette and Legendre, 1982; Brunet and Lizon, 2003), and/or seasons (Harrison and Platt, 1980). Spatial and temporal heterogeneities could also contribute to variability in parameter estimates (Platt, 1975; MacCaull and Platt, 1977; Forbes et al., 1986). Previous studies in Marennes-Oléron Bay have measured the variability of photosynthetic parameters for the microphytobenthos on the mudflats (Blanchard and Cariou-Le Gall, 1994) and for phytoplankton in the mouth of the Charente River (Ravail, 1993), but not throughout the bay. As a consequence, model estimates of primary production for Marennes-Oléron Bay have relied on literature values for calibration (Raillard and Ménesguen, 1994; Bacher et al., 1998).

The objectives of the present study were: (1) to calibrate a model of primary production in the water column by measuring photosynthetic parameters along a north-south transect in the bay during fall, winter and summer, (2) to determine which factor(s) limit primary production, and (3a) to compare the water column primary production with microphytobenthic primary production in Marennes-Oléron Bay and (3b) with other intertidal ecosystems.

2. Materials and methods

2.1. Site description and water sampling

Roughly triangular in form, the broad northern end of Marennes-Oléron Bay, which is open to the French Atlantic Ocean, tapers down to a narrow channel in the south. There is a residual current between the northern and southern portions of the bay (Dechambenoy et al., 1977). Two rivers discharge into the bay, the Charente River in the north (mean annual input: 100 m^3 s^{-1}), and the Seudre River in the south (mean annual input: 10 m^3 s^{-1}, (data from Direction Départementale de l'Environnement, http://www.equipement.gouv.fr)).

A water quality monitoring network was established in 1977 for the bay (the RAZLEC database, Soletchnik et al., 1998). Five points in this network, sites 1, 2, 3', 5 and 6 (Figure 1), were selected for this study as being representative of different hydrological conditions (Héral et al., 1983, 1984). Site 1 is located in the north of the bay and is influenced by oceanic water. Sites 2 and 5 are located in the mouths of the Charente and Seudre rivers, respectively. Site 3' is located in the centre of the bay where waters from the northern and southern portions of the bay mix. Site 6, in the south of the bay, can be influenced by oceanic waters depending on the tidal regime. This study was based on the sites 1, 2, 5 and 6, with two additional sites in the central channel, 3 and 4, replacing site 3'.

In October 2001 and in March and June 2002, fall, winter and summer respectively, water sample were collected during spring tides from the six sites, providing an approximately

north-south transect of Marennes-Oléron Bay (Figure 1). The six sites were sampled at 2 hours intervals during daylight hours, for diel production experiments and for environmental parameter measurements. For primary production estimates, two types of water samples were collected at each site using Niskin bottles: (1) near-surface, at less than 1 meter deep, and (2) near-bottom, at less than one meter above the bottom. All water samples were filtered onboard with Whatman GF/F glass-fibre filters. Other survey cruises were conducted to measure light attenuation profiles at the sites, within 15 days of the water sampling cruises.

2.2. Field Measurements

Salinity and temperature were measured with a LF196 conductivity meter (WTW, USA), while photosynthetically available radiation (PAR) was measured simultaneously in the water column and onboard the boat, using a PNF-300A profiler (Biospherical Instruments, USA) to determine light attenuation. An exponential model was adjusted based on the relative available light recorded in the water column (PARwater/PARsurface, %). Water samples were collected to measure total particulate matter (TPM, mg L^{-1}) and the power relationship between the attenuation coefficent (k, m^{-1}) and TPM was corrected accordingly. A power function was used to fit relation between the coefficient of light attenuation (k, m^{-1}) and TPM.

2.3. Laboratory Analyses

Chlorophyll a (Chl a, μg L^{-1}) and pheophytin (Pheo, μg L^{-1}) were measured on triplicate water samples that had been filtered through Whatman GF/F glass-fibre filters and stored frozen until analysis. The samples were extracted in 90 % acetone for 24h, and then analysed fluorometrically (Model 10-AU fluorimeter, Turner Designs, USA) both before and after addition of 80 μL of 1N HCl (Aminot and Chaussepied, 1983).

Subsamples of the filtered seawater were also stored frozen and later used for nutrient analysis. Dissolved nutrients concentrations (urea, ammonium, nitrite, nitrate, phosphate and silicate, μM) were determined using an autoanalyser (Skalar, Netherlands) according to the protocols of Strickland and Parsons (1972).

Water samples for particulate matter analyses were filtered through pre-combusted (500 °C for 3 h) and pre-weighed Whatman GF/C glass-fibre filters and then rinsed with distilled water to remove the salts. The filters were dried for 24h at 60 °C and re-weighed for the determination of TPM. Particulate inorganic matter (PIM, mg L^{-1}) was calculated from the mass of ash remaining after combustion of the filter at 500 °C for 3 h. The particulate organic matter fraction (POM, mg L^{-1}) was estimated from the difference between TPM and PIM.

Primary production measurements were made using the incubation system described in Lewis and Smith (1983), with 24 individual incubators. Scalar irradiance in each incubator was measured with a QSL-100 irradiance sensor (Biospherical Instrument, USA) connected to a 4π quantum sensor. During the incubation, seawater samples were exposed to a range of PAR (wavelength range from about 400-700 nm) from 0 to about 1300 μE m^{-2} s^{-1}. Each incubator chamber contained one five-mL aliquot of the light-exposed seawater in a 20 mL scintillation vial which was inoculated with 100 μL of ^{14}C-bicarbonate solution (20 μCi mL^{-1} specific activity) and then incubated for 20 min. The incubation temperature was maintained using a circulating water bath at the ambient water temperature of each sample site and date (range: 8 to 20 °C).

After incubation was complete, all biological reactions were stopped by the addition of 250 μL of buffered formalin. Two dark and two time-zero formalin-killed controls were processed using the same procedures. The total added activity was measured by dispensing 100 μL of ^{14}C-bicarbonate solution into 10 mL of scintillation cocktail (Insta-Gel Plus, Packard Bioscience, France) containing 250 μL phenyl-ethylamine. The total dissolved CO_2 was estimated by measuring the carbonate alkalinity (Parsons et al., 1984). Excess ^{14}C-

bicarbonate was removed by adding 1 mL of 6 N HCl and shaking for 2 h, then adding 10 mL of scintillation cocktail to each vial. Radioactivity (in dpm) was measured using a Packard Tri-carb 2100 liquid scintillation counter with the quenching correction applied. All photosynthetic rates were normalized to Chl a.

The hyperbolic tangent function (Eq. 1) of Jassby and Platt (1976) was used to fit the experimental data:

$$P^B = P_{max}^B \cdot \tanh\left(\frac{\alpha^B \cdot E}{P_m^B}\right) \qquad (1)$$

where P^B (mgC mgChla^{-1} h^{-1}) is the photosynthetic rate normalized to Chl a at the scalar irradiance E (μE m^{-2} s^{-1}), P_{max}^B (mgC mgChla^{-1} h^{-1}) is the maximum photosynthetic rate at saturating irradiance, and α^B (mgC mgChla^{-1} h^{-1} (μE m^{-2} s^{-1})$^{-1}$) is the initial slope of the P-E curve at sub-saturating irradiance. Superscript ^{B} indicates photosynthetic rates that are normalized to Chl a. The photoacclimation index E_k (ratio P_{max}^B/α^B, μE m^{-2} s^{-1}) is then calculated. The mean irradiance in the water column E_m is calculated from:

$$E_m = \frac{E_0}{k \cdot z_m} \cdot \left(1 - e^{-k \cdot z_m}\right) \qquad (2)$$

where E_0 is the incident irradiance, k is the attenuation coefficient (m^{-1}) and z_m is the depth of the water column. Hourly data for E_0 were obtained from a Météo France weather monitoring station (http://www.meteofrance.com), located north of the bay, which can be reasonably assumed to represent conditions in the Marennes-Oléron Bay.

For photosynthetic parameters, ANOVAs were performed to compare sites and compare surface and bottom water type samples for each survey.

Models of primary production in the water column developed for Marennes-Oléron Bay were based on nutrient limitations (Raillard and Ménesguen, 1994). The definitions of nutrient limitations of Dortch and Whitledge (1992) were applied (DIN-limitation: DIN<1 μM and DIN/PO$_4^{3-}$<10; P-limitation: PO$_4^{3-}$<0.2 μM and DIN /PO$_4^{3-}$>30; Si-limitation: Si<2 μM, Si/DIN<1 and Si/PO$_4^{3-}$<3). For uptake by phytoplankton in the turbid estuarine zone, the threshold of Fisher et al. (1988) could be also be applied. These authors considered that limiting nutrient conditions may exist when the *in situ* concentration of a nutrient is less than half the saturation constant (DIN: 2 μM; PO$_4^{3-}$: 0.5 μM; Si: 5 μM). Nutrients limit primary production in the absence of light limitation defined by the E_m/E_k ratio (Sakshaug et al., 1997; Tillmann et al., 2000).

2.4. Primary production estimates

For each sampling site and time, the local productivity in the water column was calculated by integrating photosynthetic rates over the water depth. The productivity at depth z, (P(z,t); mgC m^{-2} h^{-1}), was calculated from the mean of the measured bottom and surface water photosynthetic parameters, Chl a concentration and the attenuation coefficient (k):

$$P(z, t) = Chla(t) \cdot P_m^B(t) \cdot \tanh\left(\frac{\alpha^B(t) \cdot E(z, t)}{P_m^B(t)}\right) \qquad (3)$$

where the irradiance at depth z is:

$$E(z, t) = E_0(t) \cdot e^{-k(t) \cdot z} \qquad (4)$$

The profile P(z,t) was then integrated over depth to estimate the productivity per unit area, P(t) (mgC m^{-2} h^{-1}):

$$P(t) = \sum_{z=0}^{z=z_{max}} P(z,t) \cdot \Delta z \qquad (5)$$

with integration step of $\Delta z = 0.05$ m.

Using the RAZLEC database, the monthly means of TPM and Chl a were calculated for sites 1, 2, 5 and 6 in 2001 and 2002. Sampling sites 3 and 4 were not part of the RAZLEC database therefore an intermediate site was substituted, site 3' (Fig. 1). Using the mean P_{max}^{B} and α^{B} values, hourly data for E_0 during 2001 and 2002, and calculated water depths based on the tide equation, estimates of daily, monthly and annual production were made for these 5 sites in 2001 and 2002.

Using the site estimates, primary production of the entire bay was computed based on a 200 m x 200 m bathymetric grid. Eq. (3) was spatialized (becoming P(x,y,z,t)) and was then integrated over depth to estimate the productivity of the bay per unit area, P(x,y,t). Daily and annual estimates of total production were calculated by integrating successive values of hourly productivity per unit area.

A sensitivity analysis was done using the minimum and maximum values of the photosynthetic parameters.

Using data from the RAZLEC database for site 3', all the monthly minima and maxima for TPM and Chl a were used to construct a series of hypothetical extreme conditions. New estimates for primary production were then calculated based on these scenarios.

3. Results

3.1. Environmental parameters

Water temperatures were warmer in fall and summer, from 17 °C up to 20 °C, compared to 8 °C during the winter sampling. Freshwater inflow, from the Charente River to the northern portion of Marennes-Oléron Bay near site 2, varied (in approximate figures) from 25 m³ s⁻¹ during October 2001, to around 40 m³ s⁻¹ in early February 2001, peaking at 100 m³ s⁻¹ at the beginning of March, then decreasing to 50 m³ s⁻¹ in mid-June and continuing down to 15 m³ s⁻¹ at the beginning of July. The salinity was about 33 at all sites, except in site 2 where it ranged from 9 and 33.

At site 2, Chl a ranged between 2 and 6 μg L⁻¹ in fall, while in winter and summer varied from 2 to 14 μg L⁻¹. The concentration range for Pheo at this site was between 5 and 30 μg L⁻¹ (maximum of 100 μg L⁻¹ near low tide at 11:00 UT during the fall sampling). For the other sites, the concentration range of Chl a was lower, around 1 to 3 μg L⁻¹, in fall and winter, increasing to 3 to 6 μg L⁻¹ in summer (Fig. 2A). The concentration of Pheo ranged between 1 and 8 μg L⁻¹ over the whole studied period. Pheopigments are stable relative to Chl a (data not shown) and therefore the Chl a/(Pheo+Chl a) ratio depended on variations in Chl a.

TPM ranged between 50 and 1500 mg L⁻¹ at site 2, with an absolut maximum of 3500 mg L⁻¹ near low tide in fall (data not shown). For all other sites, TPM varied between 20 and 110 mg L⁻¹ in fall, between 25 and 225 mg L⁻¹ in winter and between 10 and 80 mg L⁻¹ in summer. There was a large difference between surface water samples and bottom water samples for some sites, such as sites 2 and 5. Variations in PIM were similar to those of TPM. PIM/TPM ratio ranged between 85 % and 95 % in fall, between 90 % and 95 % in winter and between 70 % and 95 % in summer. Differences between sites were larger in winter.

In fall, except for sites 2 and 4, the dissolved inorganic nitrogen (DIN) ranged between 8 and 17 μM; values for sites 2 and 4 ranged between 10 and 110 μM and there were significant differences between surface and bottom water samples (data not shown). In

winter, again with the exception of site 2, DIN increased to between 17 and 40 μM, with a maximum of 90 μM at site 3. In winter at site 2, DIN ranged between 35 and 120 μM. During summer, DIN ranged between 5 and 25 μM and lower values were measured at site 1. The maximum concentration of 78 μM was determined at low tide at site 2 in summer.

Silicate ($Si(OH)_4$) concentrations ranged from 8 to 95 μM. Most $Si(OH)_4$/DIN ratios were close to 1 during fall and winter, and around 0.6 in summer at all the sites (data not shown).

Dissolved phosphate (PO^{3-}_4) concentrations ranged between 0.2 and 0.8 μM in fall with the maximum, 1.6 μM, recorded at site 2 at low tide. In winter, PO^{3-}_4 increased between 10 and 25 μM, except for site 2 which reached 100 μM around low tide. In summer, PO^{3-}_4 decreased to between 0.01 and 0.5 μM, again with the maximum value, 2 μM, being measured at site 2 during low tide (Fig. 2B).

Positive and significant correlations (Spearman's test $p<0.05$) were found between Pheo/TPM/POM and PO_4/$Si(OH)_4$. Negative and significant ($p<0.05$) correlations existed between Chl a/PO_4 and Chl a/$Si(OH)_4$.

3.2. Photosynthetic parameters

Only good fits of Eq. 1 (Fig. 3) on experimental data were kept (F-test, $p < 0.005$, n=123). Comparison of the non-linear curves showed differences between surface and bottom water photosynthetic parameters for some samples, for example, at site 6 (Fig. 4A and B).

The maximum photosynthetic rate, P_{max}^B (Fig. 4A), ranged between 5.12 and 13.53 mgC mgChla^{-1} h^{-1} (mean: 9.07 ± 1.58 mgC mgChla^{-1} h^{-1}). The value for α^B (Fig. 4B) ranged between 0.011 and 0.066 mgC mgChla^{-1} h^{-1} (μE m^{-2} s^{-1})$^{-1}$ (mean: 0.025 ± 0.008 mgC mgChla^{-1} h^{-1} (μE m^{-2} s^{-1})$^{-1}$). P_{max}^B and α^B were significantly correlated ($p<0.05$). The photoacclimation index, E_k, ranged between 181.68 and 772.66 μE m^{-2} s^{-1} (mean: 390.38 ± 106.12 μE m^{-2} s^{-1}).

While some significant differences (one-way ANOVA, $p<0.05$) existed between surface-bottom pairs at each site, there were no sites or sample types that were characterised as significantly different under all conditions.

3.3. Relationship between k and TPM

The regression equation was ($R^2 = 0.73$, n=114), therefore

$$k = 0.154 \cdot TPM^{0.66} \tag{6}$$

Using Eq. 6 with TPM values recorded during the surveys, k ranged between 0.6 and 36.1 m^{-1}. The maximum value corresponded to a light level of 1 % at 0.12 m. Values of k were highest at site 2 and in bottom samples. Lowest values for k were estimated from surface water samples collected at sites 1 and 6 (Fig. 2C).

3.4. Limitation of primary production in the bay

Applying the definitions of Dortch and Whitledge (1992), neither DIN or Si were limiting factors for primary production during the sampling periods. However, in summer, phosphorus was limiting. While considering the thresholds defined by to Fisher et al. (1988), there was also no limitation for DIN, but phosphate was limiting in summer at all the sites and occasionally in fall. Silica was only limiting in summer in site 1.

Apart from summer 2002 at sites 3, 4 and 5, the ratio E_m/E_k were always less than 1 (Fig 4C). If the maximum photosynthetic rate, P_{max}^B, is never reached, then Equation (1) is reduced to a linear relationship. Equation (3) then becomes:

$$P(z,t) \approx Chla(t) \cdot \alpha^B(t) \cdot E_0(t) \cdot \int_{z=0}^{z=z_{max}} e^{-k \cdot z} .dz \qquad (7)$$

$$P(z,t) \approx Chla(t) \cdot \alpha^B(t) \cdot E_0(t) \cdot \left[-\frac{e-k}{k} \right]_0^{z_{max}} \qquad (8)$$

$$P(z,t) \approx Chla(t) \cdot \alpha^B(t) \cdot E_0(t) \cdot \frac{1}{k} \cdot \left(-e^{-k \cdot z_{max}} +1 \right) \qquad (9)$$

The expression $e^{-k \cdot z_{max}}$ is equivalent to $e^{-\frac{4.61}{Z_p} \cdot z_{max}}$, where Z_p is the photic depth (m). Since z_{max} was greater than Z_p in most cases, the exponential expression was very small with respect to 1. Expression (9) becomes:

$$P(t) \approx Chla(t) \cdot \alpha^B(t) \cdot E_0(t) \cdot \frac{1}{k} = Chla(t) \cdot \alpha^B(t) \cdot E_0(t) \cdot \frac{Z_p}{4.61} \qquad (10)$$

A significant correlation ($R^2 = 0.92$, $p < 0.001$) was found for the dataset:

$$Prod = 0.005 \cdot Chla \cdot E_0 \cdot Z_p \qquad (11)$$

where 'Prod' is in mgC m^{-2} h^{-1} and the algal biomass, Chl a, is in mg Chl a m^{-3}.

The value for α^B calculated from this slope (Eq. 11) was 0.023 mgC mgChla^{-1} h^{-1} (μE m^{-2} s^{-1})$^{-1}$, close to the previously estimated mean α^B (0.025 ± 0.008 mgC mgChla^{-1} h^{-1}).

3.5. *Measured primary productivity and estimate of annual production*

The hourly productivity per unit area (Fig. 5) was less than 10 mgC m^{-2} h^{-1} in fall and winter at all sites. In summer, this productivity increased to a range between 10 and 50 mgC m^{-2} h^{-1}. A maximum of 120 mgC m^{-2} h^{-1} was estimated for site 6. Excluding this value, the pattern of productivity was sinusoidal and the maximum was reached near midday. The daily coefficient of variation on hourly productivity estimates ranged between 11 % and 119 %. Site coefficient of variation (CV) ranged between 38 % and 62 %. The seasonal CV ranged between 52 % and 126 % and the overall CV was 140 % (Table 1).

The different TPM and Chl a concentrations for the sites, as well as the variation in irradiance during 2001 and 2002, resulted in spatial and temporal variability in production estimates (Fig. 6A). The daily production estimates varied between 0.006 gC m^{-2} d^{-1} (site 2) and 3.6 gC m^{-2} d^{-1} (site 6). The monthly production (Fig. 6B) estimates were maximal between May and August, and could be as high as 62 gC m^{-2} month^{-1} (site 1, summer 2002). In site 2, production was always the lowest with a maximum of 18 gC m^{-2} month^{-1} in summer. During winter, all sites had lower production, between 0.5 and 0.8 gC m^{-2} month^{-1}. The annual production varied between 64 (site 2, 2001) and 301 gC m^{-2} yr^{-1} (site 1, 2002).

The annual production in Marennes-Oléron Bay was estimated at 185 gC m^{-2} yr^{-1}. Using minimum and maximum values of P_{max}^B and α^B, the annual production was calculated as ranging between 11.5 and 55.6 gC m^{-2} yr^{-1}. Using the mean α^B, 50 % of the variation in the

mean P^B_{max} created a variance of 21.4 % in the mean production. Using the mean value for P^B_{max}, 50 % of the variation in the mean α^B produced a variance of 29.5 %. Assuming that the photosynthetic parameters were the same for site 3', scenarios for maximum and minimum conditions (Chl a minimum and TPM maximum, and the inverse) were created and produced an estimate of between 65 and 330 gC m^{-2} yr^{-1} for this site

4. Discussion

4.1. Site comparisons

Marennes-Oléron Bay is directly influenced by Charente River freshwater discharge. Thus, site 2, which was situated at the mouth of Charente River, shows the effect of river discharges on dissolved nutrients, such as orthophosphates, in this part of the bay. Apart from the high phosphate values (>10 µM) measured in winter at site 1, the pigment, TPM and nutrient values were within the range of values typically recorded in Marennes-Oléron Bay (RAZLEC database, Soletchnik et al., 1988). Changes in freshwater inputs, wind-driven mixing, and different tidal coefficients (110, 110 and 85, in the fall, winter and summer surveys respectively) could explain some of the observed variability. Low ratios of Chl a/(Pheo+Chl a) (< 1) calculated in fall and winter suggested that a large part of the micro-algal pigments were detritus.

There were differences in the production estimates between 2001 and 2002. For the most oceanic site (site 1), the water was less turbid and richer in Chl a and production estimates were higher. In the mouth of the Charente River, despite the source of nutrients, light limitation was more important and the estimated production was low relative to other locations. The spatial-temporal variability of primary productivity of different parts of Marennes-Oléron Bay shows its heterogeneity, between 30 % and 130 %, suggesting that sites for shellfish culture could be re-evaluated in light of their proximity to areas of high primary production in the bay.

4.2. Photosynthetic parameters and relationship between k and TPM

Photosynthetic parameters are correlated with temperature, light or nutrients (Geider et al., 1997) and sometimes with cell size and species composition (Harrison and Platt, 1980). Variability is circadian, with minima at dawn and sunset and the maximum at noon (Sournia, 1974); moreover, tides can interfere with these circadian rhythms (Demers and Legendre, 1979). The values determined for phytoplanktonic photosynthetic parameters, P_{max}^B and α^B are within the range of those reported for other estuarine and littoral systems (Côté and Platt, 1983; Pennock and Sharp, 1986; Ravail-Legrand, 1993; Kromkamp and Peene, 1995; Cabeçadas, 1999; Tillmann et al., 2000; Shaw and Purdie, 2001).

E_k is a convenient indicator of phytoplankton photoacclimation state (Sakshaug et al., 1997); thus, the high E_k values found for the Marennes-Oléron Bay phytoplankton community suggests its acclimation to high light intensities, in spite of the mean low irradiance levels prevailing in the turbid water column. High E_k values are associated with phytoplankton adapted to surface or near-surface conditions (Gallegos and Platt, 1985; Mallin and Pearl, 1992) and may be linked, in these samples, to the presence of recently resuspended microphytobenthos not yet adapted to the lower light conditions of the water column. E_k values for microphytobenthos typically ranges between 150 and 900 µE m^{-2} s^{-1} (Blanchard and Montagna, 1992; Barranguet et al., 1998; Hartig et al., 1998; Wolfstein et al., 2000) and values between 370 and 650 µE m^{-2} s^{-1} have been reported for microphytobenthos Marennes-Oléron Bay intertidal mudflats (Blanchard and Cariou-Le Gall, 1994). The high E_k indicates that the microphytobenthos on emerged intertidal mudflats are adapted to high light conditions. Shade adaptation occurs only after low light conditions become stable.

When $E_k >> E_m$ the photosynthetic capacity of phytoplankton to use light is greater than the available light in the water column and the ratio Em/Ek<1 then there are light limiting conditions. As it was observed on many occasions during this study, the Em/Ek (Fig. 4C) was usually less than 1. Light saturating conditions (Em/Ek≥1) were occasionally recorded in summer in the center (sites 3 and 4) and in the south of the bay (site 6).

The relationship between k and TPM was close to that established by Ménesguen (1995) for the Seine Estuary, but lower than that reported by Cloern (1987) for San Francisco Bay.

4.3. Light limitation and the BZ_pI_0 model

The coefficient of attenuation in Marennes-Oléron Bay was highly variable, which is typical of estuarine waters. With a photic depth varying from 0.12 to 7.6 m, Marennes-Oléron Bay is among the 26 most turbid estuaries (Cloern, 1987).

Since Cole and Cloern (1984, 1987) published their regressions, models of production as a function of phytoplankton biomass and light availability have been applied to nutrient-rich estuaries. Converting regression Eq.11 to the units (mgC m^{-2} d^{-1}) used in the compilation dataset from Brush et al. (2002) yielded a $P_d = 0.08 \cdot BZ_PI_0 + 23.3$ (R^2=0.90). As this y-intercept value suggested that there may be net production in the absence of Chl a and/or light, the regression was forced through the origin (Brush et al., 2002), giving: $P_d = 0.10 \cdot BZ_PI_0$ (R^2=0.72). The determined slope is thus within the low range of their dataset which included small slopes for Delaware Bay (0.07 in non-summer and 0.23 in summer) and the Westerschelde Estuary (0.22), which are both very turbid systems. The steepest slope was reported for San Francisco Bay (0.82).

4.4. Estimate of primary production

The water column primary production in the Marennes-Oléron Bay of 185 gC m^{-2} yr^{-1} is close to the mean of other primary production capacity estimates for European estuaries (Table 2). Annual phytoplankton primary production estimates of European estuaries and coastal areas (*see* compilation in Tillmann et al. 2000 and Table 2), ranged between 7 gC m^{-2} yr^{-1} (Inner Bristol Channel) and 550 gC m^{-2} yr^{-1} (Oosterschelde) with a mean of 180 gC m^{-2} yr^{-1} (Tillmann et al., 2000). Low estimates of water column primary production in eutrophic estuaries are common. Kocum et al. (2002) estimated water column primary production in the Colne Estuary at 8.9 gC m^{-2} yr^{-1}, but this low water column primary production did not affect secondary production of the ecosystem because the microphytobenthos primary production contributed between 25 and 1,200 gC m^{-2} yr^{-1} (Thornton et al., 2002). For example, through resuspension, the microphytobenthos of the Ems Estuary which represented 22 % to 60 % of the total phytoplankton in the water column and 50 % of the food available to filter feeders living on the tidal flats (De Jonge and van Beusekom, 1992, 1995). Average relative contributions of benthic microalgae were around 20 % in Marennes-Oléron Bay (Guarini et al., 2004). The annual microphytobenthic production in Marennes-Oléron Bay has been estimated between 178 (Guarini, pers. comm.) and 372 gC m^{-2} yr^{-1} (Leguerrier et al., 2003) and could be available to suspension feeders in the bay (Riera and Richard, 1996).

5. Conclusion

The present study allowed a BZI_0 model of primary production to be calibrated and showed that water column primary production is light limited in Marennes-Oléron Bay. Using monthly means for TPM and Chl a, the day-to-day variability in production estimates was caused by variability in irradiance, while seasonal variability in production was attributed to seasonal variations in irradiance, TPM and Chl a. Differences in the TPM between sites affected the estimates of primary production. On a tidal time scale of hours, variations in TPM could also be reasonably assumed to affect production. Water column

primary production in the Marennes-Oléron Bay was estimated at 185 gC m^{-2} yr^{-1} using the same mean TPM value applied over the entire bay. This value is in the low range of microphytobenthic production (372 gC m^{-2} yr^{-1}, Leguerrier *et al.,* 2003) and close to the mean of other primary production in intertidal ecosystems (180 gC m^{-2} yr^{-1}, Tillman et al., 2000). However, important changes of TPM (eg over the intertidal mudflats during flood and ebb tides) and associated changes in turbidity and thus light conditions in the water column, interacted to create spatial and temporal heterogeneity in production estimates for different areas of the Marennes-Oléron Bay. Water in the north and south of the bay are more productive and could become areas for offshore shellfish production.

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Tables

Table 1. Coefficient of variation (%) for productivity estimates for each sampling date and the spatial, seasonal and total variation.

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Spatial
Fall	24	119	44	31	59	40	38
Winter	57	64	34	62	57	34	36
Summer	40	11	39	50	62	69	62
Seasonal	54	52	64	81	81	126	**total:140**

Table 2. Estimates of annual primary production (gC m^{-2} yr^{-1}) for various estuaries and bays worldwide (adapted from Tillmann et al., 2000 and Heip et al., 1995)

Type	Region	Annual production	Reference
phytoplankton	*Europe*		
	Marennes-Oléron Bay, France	185	This study
	Estuarine part of Northfrisian Wadden Sea, Germany	127 - 177	Tillmann et al., 2000
	Tagus estuary, Portugal	26	Cabeçadas, 1999
	Bristol Channel, UK	7 -165	Joint and Pomroy, 1981
	Westerschelde, Netherlands	100 - 300	Kromkamp and Peene, 1995
	Colne Estuary, UK	8.9	Kocum et al., 2002
	USA		
	Delaware Estuary	307	Pennock and Sharp, 1986
	Narragansett Bay	323	Oviatt et al., 2002
	San Francisco Bay	6 - 418	Cole and Cloern, 1984
	Hudson River	70 - 240	Cole et al., 1992
	Chesapeake Bay	324 - 569	Malone et al., 1988
	Chesapeake Bay	570	Harding et al., 2000
microphytobenthos	Marennes-Oléron Bay,France[a]	372	Leguerrier et al., 2003
	Marennes-Oléron Bay,France[a]	178	Guarini, unpubl data
	Bay of Somme, France[b]	147	Migné et al., 2004
	European estuaries	60 - 314	Heip et al., 1995
	Intertidal flats of Westerschelde, Netherlands[b]	7 - 53	Barranguet et al., 1998
	Colne Estuary, UK	25 – 1 199	Thornton et al., 2002
	North American estuaries	29 - 226	Heip et al., 1995
	Estuarine flat of Seto Inland Sea, Japan[c]	434	Montani et al., 2003

[a]: Brouage mudflat – [b]: sand and muddy-sand – [c]: sand

Figure legends

Figure 1. Sampling site locations in Marennes-Oléron Bay, France. Sites 1, 2, 3', 4 and 6 (●) were sampled during 2001 and 2002 for this study. Sites 1, 2, 5, 6 (●) and 3' (▲) were also sampled bi-monthly for the RAZLEC water quality database. Light gray areas indicate the intertidal mudflat areas. The black rectangle indicates the zone of primary production estimation.

Figure 2. Evolution of Chl *a* (A) and phosphate concentrations (B) (note scale change for winter data) and light attenuation coefficient k (C), in surface (solid lines) and bottom water (dashed lines) samples, during each survey.

Figure 3. Example of a P-E curve. Sample data are plotted with the adjusted model of Jassby and Platt (1976) for surface water (model S), bottom water (model B) and the adjusted model for all data (model S+B).

Figure 4. Change in the photosynthetic parameters P^B_m (A), α^B (B) and in the Em/Ek ratio (C) in surface water (solid lines) and bottom water (dashed lines) samples, during each survey. Error bars for (A) and (B) are for model estimates.

Figure 5. Estimated change in primary production per unit area of surface water (solid lines) or bottom water (dashed lines) samples, during each survey.

Figure 6. The estimated daily (A, at sites 1 and 2) and monthly (B, at sites 1, 2, 3', 5 and 6) primary production per unit area in 2001 and 2002.

Figure 1. Sampling site locations in Marennes-Oléron Bay, France. Sites 1, 2, 3', 4 and 6 (●) were sampled during 2001 and 2002 for this study. Sites 1, 2, 5, 6 (●) and 3' (▲) were also sampled bi-monthly for the RAZLEC water quality database. Light gray areas indicate the intertidal mudflat areas. The black rectangle indicates the zone of primary production estimation.
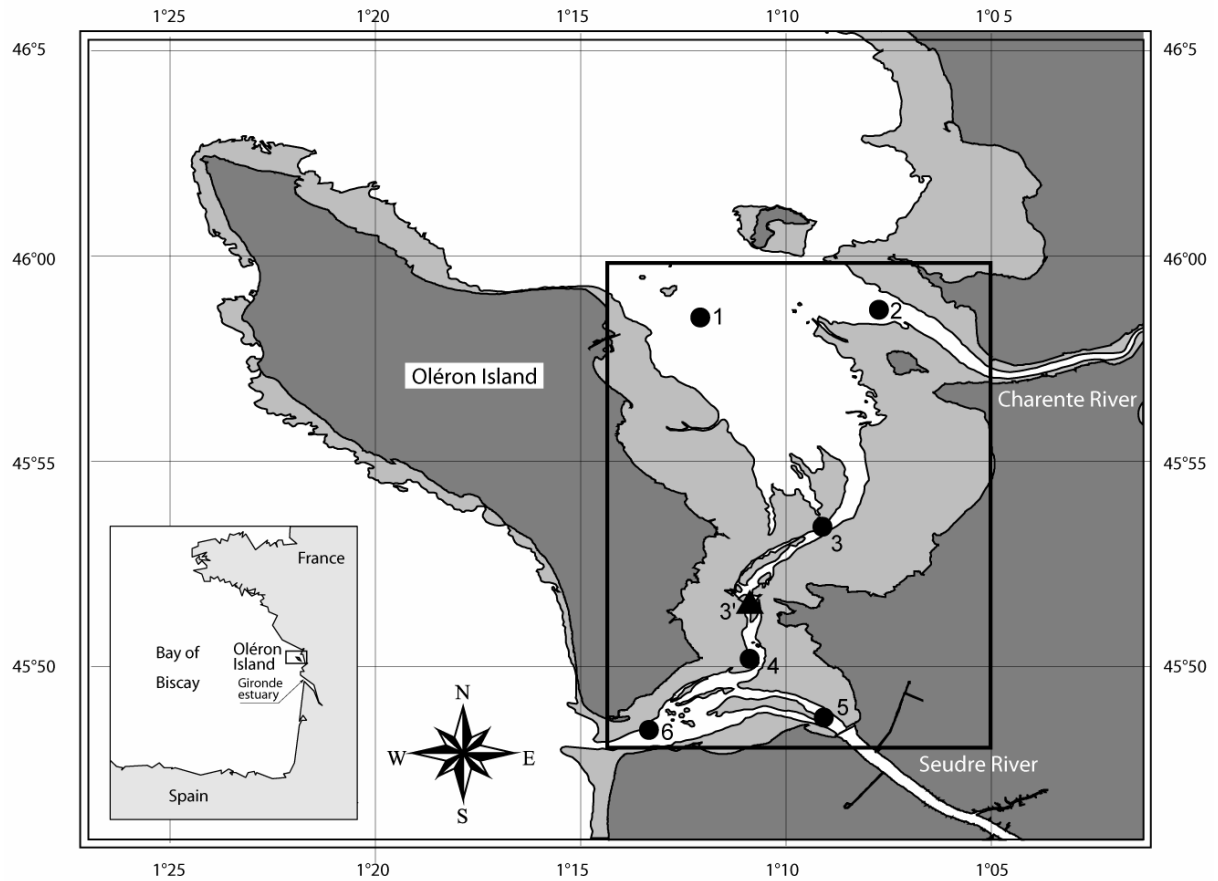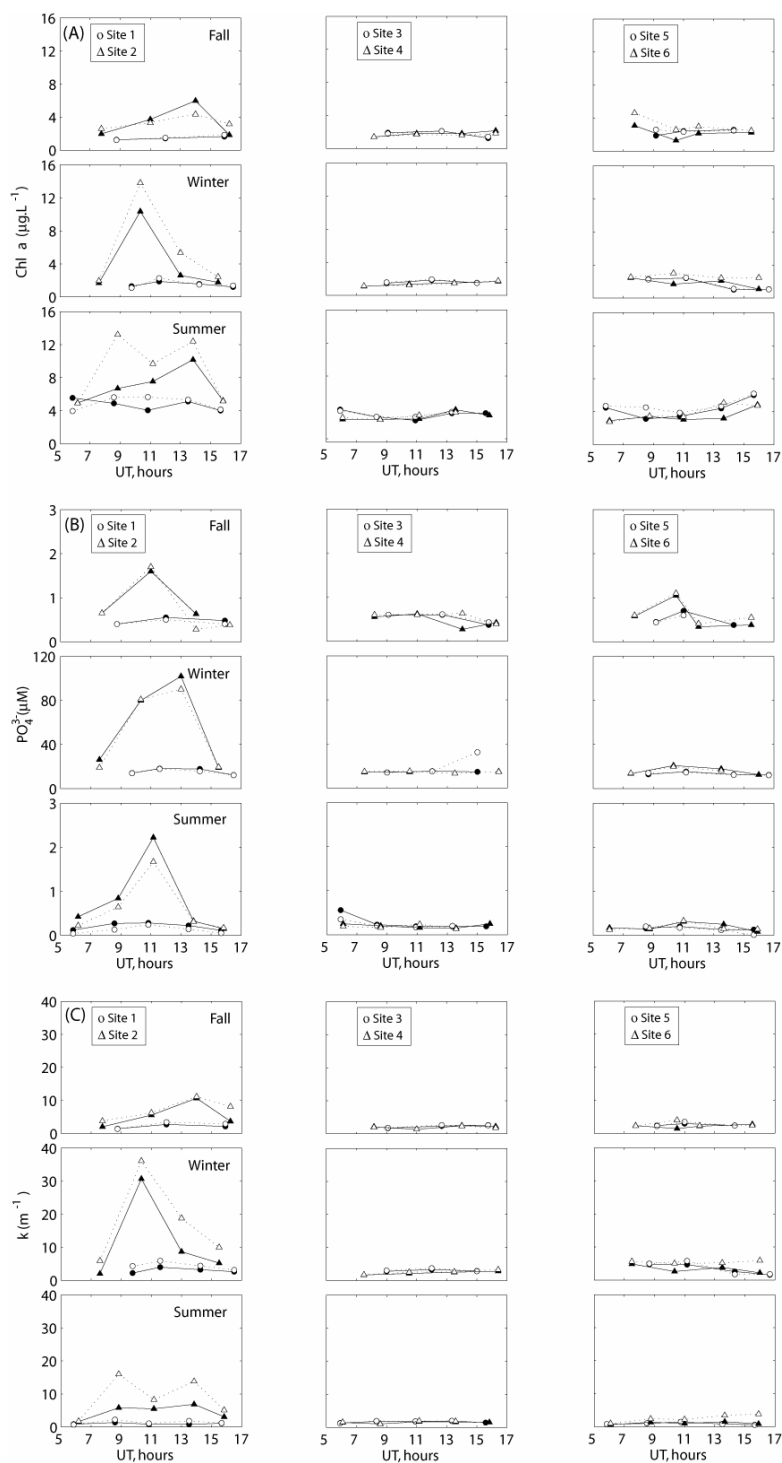
Figure 2. Evolution of Chl *a* (A) and phosphate concentrations (B) (note scale change for winter data) and light attenuation coefficient k (C), in surface (solid lines) and bottom water (dashed lines) samples, during each survey.

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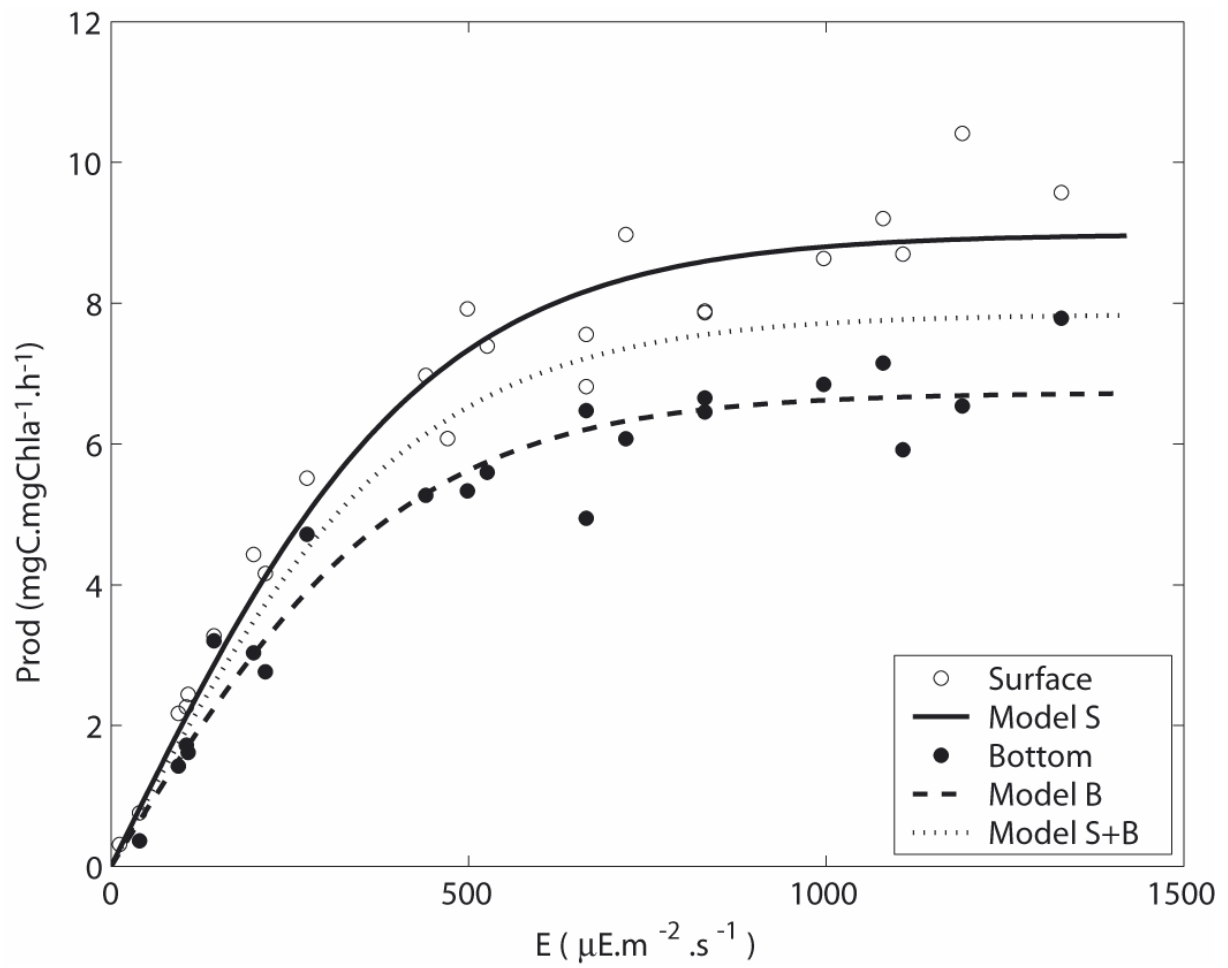
Figure 4. Change in the photosynthetic parameters P^B_m (A), α^B (B) and in the Em/Ek ratio (C) in surface water (solid lines) and bottom water (dashed lines) samples, during each survey. Error bars for (A) and (B) are for model estimates.
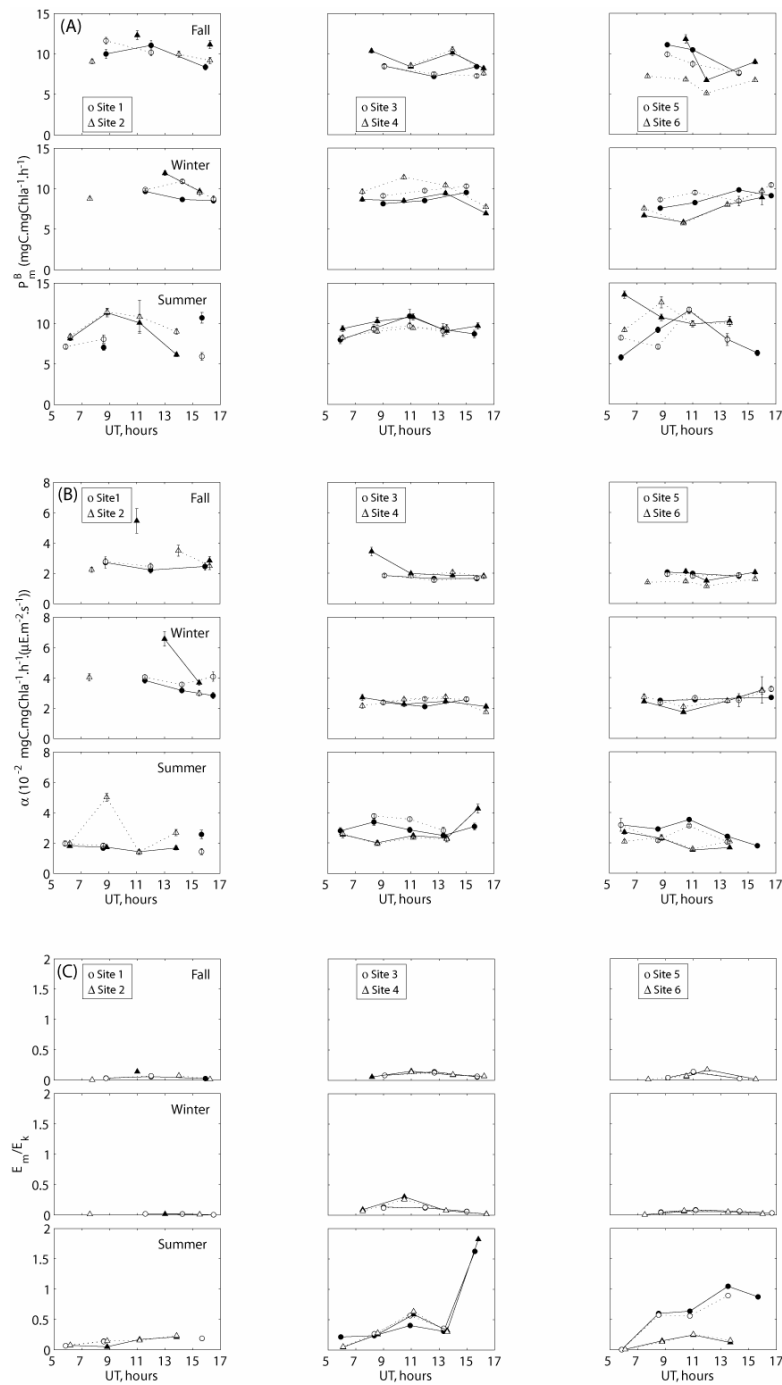
Figure 5. Estimated change in primary production per unit area of surface water (solid lines) or bottom water (dashed lines) samples, during each survey.
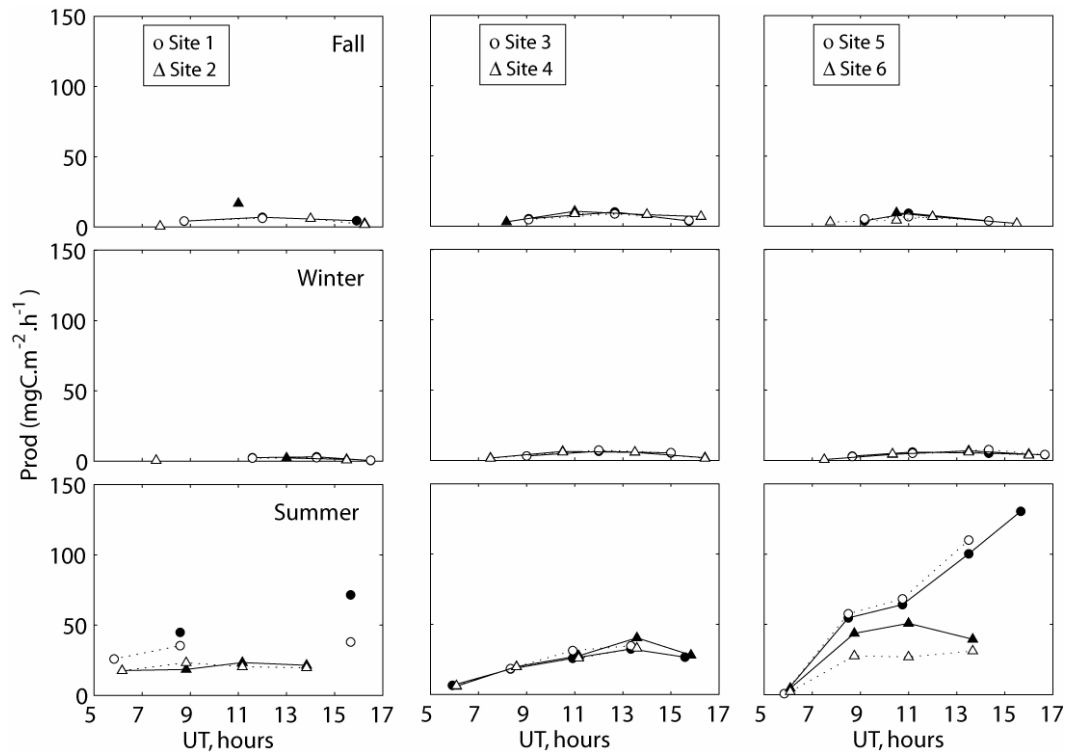
Figure 6. The estimated daily (A, at sites 1 and 2) and monthly (B, at sites 1, 2, 3', 5 and 6) primary production per unit area in 2001 and 2002.