



Spatial and temporal variation of photosynthetic parameters of phytoplankton in a subtropical coastal lagoon

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Abstract

We generated photosynthesis–irradiance ($P-E$) and phytoplankton absorption data for a coastal lagoon of northwestern Baja California. This was done for different seasons and tidal conditions. Using the vertical attenuation coefficient of light we partitioned the lagoon into two regions to run the ^{14}C incubation experiments: an outer and an inner region. Since there is substantial variability within data sets, we conclude that it is not possible at this time to predict fine time-and-space scale variations in photosynthetic parameters. For simple primary production models, we recommend working averages for each of the two regions. There were no significant differences of the photosynthetic parameters average values for the same region and for different tidal conditions or seasons. The mean and standard error for the assimilation number were 14.6 and 2.6 mg C mg Chl $^{-1}$ h $^{-1}$, for the outer region, and 7.7 and 1.8 for the inner region, respectively. The mean and standard error for the initial slope were 0.036 and 0.008 mg C mg Chl $^{-1}$ h $^{-1}$ ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) $^{-1}$, for the outer region, and 0.019 and 0.005 for the inner region, respectively. Average values of maximum photosynthetic quantum yield were 0.082 and 0.053 mol C (mol quanta) $^{-1}$, for the outer and inner regions, respectively. Its standard error was the same for both regions (0.012). These average values should be used only for non-El Niño years.

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1. Introduction

Empirical and semianalytical algorithms to estimate primary production for open ocean waters from satellite-derived photosynthetic pigments have been developed (e.g. Behrenfeld et al., 1998; Sathyendranath, Longhurst, Caverhill, & Platt, 1995). The parameters used in these algorithms belong to three categories: environmental (e.g. geographic location, atmospheric conditions, the irradiance profile), ecological (e.g. the chlorophyll concentration), and physiological (e.g. the phytoplankton photosynthesis–irradiance ($P-E$) curve parameters, the chlorophyll-specific absorption coefficient of phytoplankton, photosynthetic quantum efficiency) (Morel, 1991). Similar algorithms could be developed to estimate production of phytoplankton in

coastal lagoons. Satellite ocean colour data are not yet appropriate for these small coastal environments. Nevertheless, irradiance (E_0) and chlorophyll concentration (chl) time series data from coastal lagoons may be generated with automated equipment or discrete sampling. However, the generation of data on the physiological parameters of phytoplankton requires experiments that are time consuming.

Linked physical and biological frameworks are applied to assess biogeochemical dynamics in shallow estuarine and lagoonal ecosystems. Often, this kind of modelling is done estimating primary production with the assumption of space and temporal invariance of the physiological parameters of phytoplankton (e.g. Buzzelli et al., 1999). In other cases the phytoplankton production is estimated with the oxygen evolution of discrete samples incubated in light and dark bottles (e.g. Lin et al., 1999; Revilla, Iriarte, Madariaga, & Orive, 2000), or using the ^{14}C method (Sorokin, Sorokin, & Ravagnan, 1999). Nevertheless, coastal lagoons are

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characterized by high spatial and temporal variability of phytoplankton abundance and production. In coastal lagoons of northwestern Baja California, alternation of upwelling events in the adjacent ocean is the main cause of phytoplankton production variability, followed by semi-diurnal tides (Lara-Lara, Alvarez-Borrego, & Small, 1980; Millán-Núñez, Alvarez-Borrego, & Nelson, 1982). Thus, estimates of phytoplankton production with incubation of few discrete samples may not be representative, and a quasi-continuous sampling and incubating program would be very expensive and time consuming. Therefore, we need to consider the application of E_0 -chl algorithms that could be run with working averages of the physiological parameters for certain time and space scales.

At latitudes of $\sim 32^\circ\text{N}$, near surface phytoplankton is conditioned to relatively high irradiance during the whole year, and their P - E curves do not show photo-inhibition at the highest incubation light levels (e.g. Valdez-Holguín, Alvarez-Borrego, & Mitchell, 1998; and results from this work). In this case, the parameters of P - E curves are the assimilation number (P^*_m) or the maximum photosynthesis at optimum irradiance, and the initial slope at low irradiance (a^*). To compare samples with different phytoplankton biomass, both parameters are normalized to chl. They show great day-to-day variability in coastal waters (Côte & Platt, 1983; Gonzalez-Morales, Gaxiola-Castro, & Lara-Lara, 1993; Silva-Cota & Alvarez-Borrego, 1988; Valdez-Holguín et al., 1998). Ecological and physiological models are not yet capable of predicting the short-term P - E parameters. Nevertheless, it is possible to estimate mean values of the P - E parameters to calculate primary production for large time scales to which the data apply (Sathyendranath et al., 1995). Gaxiola-Castro and Alvarez-Borrego (1984) and Silva-Cota and Alvarez-Borrego (1988) reported on summer values of phytoplankton photosynthetic parameters for lagoons of the Baja California coast, but no description has been given of the spatial and temporal variation during a complete annual cycle. It would be desirable to have representative working averages of the P - E parameters for different seasons, and regions within the lagoons, and to explore the possibility of significant differences with changing tidal conditions (spring and neap tides).

The California Current System (CCS) has a pronounced influence on the structure and function of lagoons on the Pacific coast of Baja California. The coastal ocean off Baja California is a classic wind-driven coastal upwelling system. Tidal currents propagate upwelled waters into the lagoons (Millán-Núñez et al., 1982). The Mediterranean-type climate of the region is hot and dry with prevalence of desert conditions, though considerable local variations may occur. Since land-to-ocean stream flux is limited, the advected nutrient-rich waters of the ocean directly affect most biogeochemical

processes in the lagoons. Most of these coastal lagoons are pristine or are barely modified and they represent highly productive and diverse environments (Ibarra-Obando, Camacho-Ibar, Carriquiry, & Smith, 2000).

The objective of this work was to characterize the parameters of the P - E curve of phytoplankton in Estero de Punta Banda, a northwestern Baja California coastal lagoon. We also estimated $a^*_{\text{ph}(\lambda)}$, the specific absorption coefficient of phytoplankton, which allowed us to derive maximum photosynthetic quantum efficiency (φ_{max}) from a^* and the spectral distribution of light in our incubator. The purpose was to obtain working averages of the physiological parameters for seasons and for regions within the lagoon, or preferably for the whole lagoon and the whole year. The intention is to support the use of light-chlorophyll algorithms to estimate this lagoon's primary production for large temporal scales, not to estimate the instantaneous local primary productivity.

1.1. Study area

Estero de Punta Banda (EPB) is located between $31^\circ 41' - 31^\circ 48' \text{N}$ and $116^\circ 37' - 116^\circ 40' \text{W}$, 123 km south of the Mexico-USA border (San Diego), 12 km south of Ensenada, Baja California. The lagoon is at the southeastern extreme of Todos Santos Bay, its mouth is at ≈ 13 km from the open ocean, the upwelling area off Punta Banda. The lagoon is L shaped, with a short arm of ≈ 3 km, and a long arm of ≈ 7.5 km (Fig. 1). It has a single entrance at the extreme of the long arm. It has an area of $\approx 3.6 \text{ km}^2$ at low tide and 11.6 km^2 at high tide. The average width of the lagoon is ≈ 345 m at low tide and ≈ 1100 m at high tide (Pritchard, De-la-Paz-Vela, Cabrera-Muro, Ferreras-Sanz, & Morales, 1978). Its importance as a spawning, nursery, and feeding zone for fishes has been documented, and it is also important as bird habitat (Ibarra-Obando & Escofet, 1987). There are only four coastal lagoons along the northern Baja California coastline, and Punta Banda is a relatively isolated estuary, the nearest to it being located 180 km to the south (San Quintín Bay).

In general the lagoon behaves as a negative estuary, with salinity and temperature increasing from the mouth to the internal extreme (Acosta-Ruiz & Alvarez-Borrego, 1974; Pritchard et al., 1978), due to excess of evaporation in the lagoon. During 'El Niño' events higher winter precipitation causes estuarine conditions in the lagoon (Galindo-Bect, Galindo-Bect, Hernández Ayón, Ley-Lou, & Alvarez-Borrego, 1999). Freshwater is input mainly through two streams, San Carlos near the mouth and La Grulla at the internal extreme. Range of spring tides is > 2 m and tidal mixing is strong. Maximum depth (~ 8 m) is at the mouth of the lagoon and it decreases toward the head. Circulation in EPB is dominated by tidal currents, which can renew up to 60% of

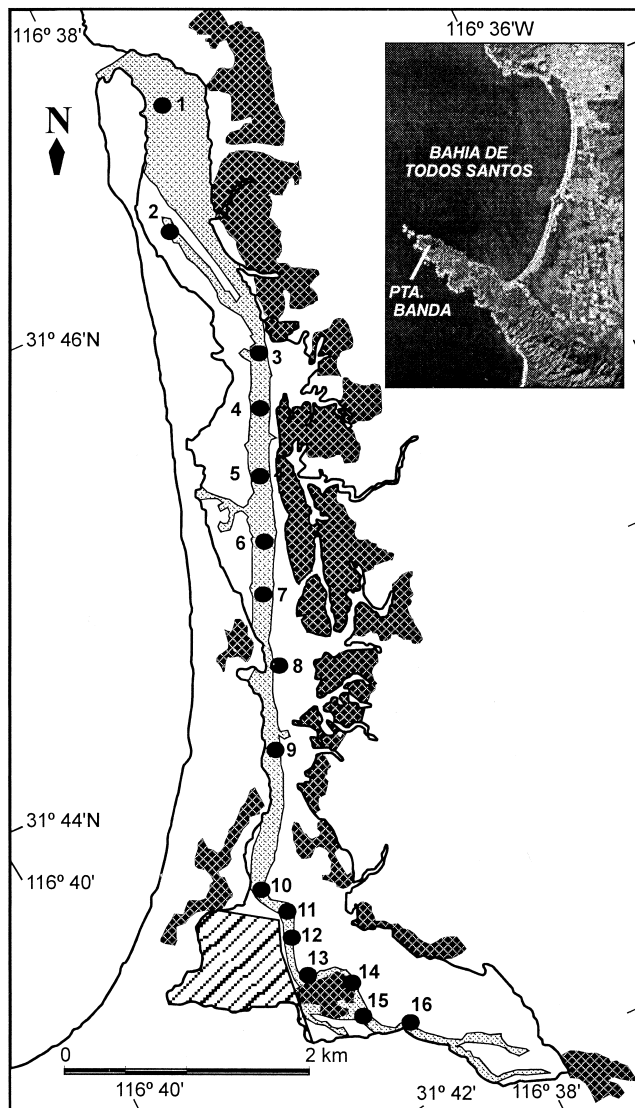


Fig. 1. Sampling locations in Estero de Punta Banda. The light gray area is the channel, and the dark gray area is the mudflats and marshes. On the southern-left corner (dashed area) there is a zone affected by an artificial dike built in the early 1980s. The construction planned for the area inside the dike was not done. The insertion is a Landsat image showing Todos Santos Bay and Punta Banda. A high turbidity plume from the Estero can be seen extending into Todos Santos Bay.

the lagoon water during a tidal cycle (Pritchard et al., 1978). In coastal lagoons of northwestern Baja California mixing by tidal currents is strong, even with neap tides, and it tends to homogenize the water column (Lara-Lara et al., 1980). Alvarez-Borrego and Alvarez-Borrego (1982) indicated that upwelled water, from off Punta Banda, is transported by coastal currents to the area off the mouth of Estero de Punta Banda, and then it is transported to its interior by tidal currents.

About 60% of the gross primary production in the coastal lagoons of northwestern Baja California depends on the phytoplankton contribution while benthic primary producers contribute the rest (Ibarra-Obando

et al., 2000). Extensive salt marshes, mud-flats, and beds of *Zostera marina*, are the main ecological sub-systems of Estero de Punta Banda. The most extensive salt marshes are located in tidal creeks, and are particularly well developed at the head of the lagoon (Ibarra-Obando & Poumian-Tapia, 1991). Seawater properties have a very patchy distribution (Acosta-Ruiz & Alvarez-Borrego, 1974; Galindo-Bect et al., 1999). Nutrient concentrations in pore waters of the low salt marshes of Estero de Punta Banda's inner region are very high. Pore waters of surface intertidal sediments have PO_4^{-3} and NH_4^{-1} concentrations in the ranges 2–30 and 15–95 μm , respectively, with great temporal and spatial variability. The flux of these nutrients to the water column is high due to strong tidal stirring (Camacho-Ibar & Alvarez-Borrego, 1988).

2. Materials and methods

Sampling and experiments were done in August, September, and November, 1998, and in January, March, May, and June, 1999. To test the hypothesis of different $P-E$ parameters with different tidal conditions, sampling and ^{14}C incubations were done twice in August, September and November, with neap and spring tides. Water samples were obtained from depths of 1–2 m with a 2.5 l Niskin bottle. We measured profiles of temperature, salinity (CTD, Sea-Bird Inc.), photosynthetically available scalar irradiance ($E_{o(z)}$) (PNF-300, Biospherical Instr.) and spectral irradiance ($E_{d(\lambda)}$) (PRR-600, Biospherical Instr.). The light meters were calibrated at San Diego State University's Center for Hydro-Optics and Remote Sensing. The vertical attenuation coefficient for $E_{o(z)}$ (K_o) was calculated with the Lambert-Beer equation (Kirk, 1994). In general, K_o increased from the mouth to the head of the lagoon, and most of the time it had a clear relationship with salinity and temperature. Using K_o we partitioned the EPB into two regions to run the ^{14}C incubation experiments to estimate the $P-E$ parameters. The outer region extends from stations 1–9. The inner region extends from station 10 to the head and in general it had larger mean K_o values than those for the outer region.

Nutrient samples (PO_4^{-3} , NO_2^- , NO_3^- , and SiO_4^{-4}) were kept in dry ice in the field, in a freezer at Ensenada, and transported in dry ice to Santa Barbara to be processed at the Marine Sciences Institute, University of California. Nutrient analysis was done basically following Strickland and Parsons (1972). Water samples for phytoplankton cells identification and counting were preserved with Lugol's solution and examined by the inverted microscope technique (Utermöhl, 1958). Chlorophyll *a* and particle absorption samples were filtered in the field through Whatman GF/F glass-fibre filters and frozen in liquid nitrogen. Chlorophyll samples were

extracted in 90% acetone for 48 h, and analysed fluorometrically (Venrick & Hayward, 1984). Particle absorption was measured by the method originally described by Yentsch (1962) and modified by Kishino, Okami, Takahashi, and Ichimura (1985), with an ELYPTICA spectrophotometer. Optical densities of phytoplankton (OD_{ph}) were calculated subtracting the non-pigmented particle densities (OD_d) from the total particle densities (OD_p). Since our samples had a high content of detritus, it was very difficult to correct raw optical densities for the path-length amplification effect. Thus, the OD_{ph} spectra were normalized dividing $OD_{ph(\lambda)}$ by $OD_{ph(440)}$. The absorption coefficient of phytoplankton ($a_{ph(\lambda)}$) was obtained scaling the normalized $OD_{ph(\lambda)}$ with the expression of Bricaud, Babin, Morel, and Claustre (1995) for $a_{ph(440)}$ [$a_{ph(440)} = 0.0403(\text{chl})^{0.668}$]. The specific absorption coefficient of phytoplankton was then calculated ($a^*_{ph(\lambda)} = a_{ph(\lambda)} \text{Chl}^{-1}$).

To generate the P – E curves ^{14}C incubations were performed in miniaturized incubators similar to the one designed by Talbot, Thoreson, and Perry (1985). Incubations in the outer region were done on the first and second sampling days of each field trip, and those of the inner region were done on the third and fourth days, under the same tidal conditions (spring or neap tides). An exception to this was the first November sampling when incubations for the inner region were done prior to those of the outer region. A volume of 840 ml from each water sample were passed through a 390 μm mesh to remove large herbivores, then ^{14}C was added to a final concentration of 0.05 $\mu\text{Ci ml}^{-1}$. A 20 ml aliquot was pipetted into each of 36 scintillation vials, and then incubated for an hour. Incubation was done under a light gradient in the range 0–1500 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$. Temperature was maintained close to in situ values by pumping surface seawater through the incubators. Two additional aliquots were taken for dark incubation, and two more for a time-zero control; the latter were immediately acidified after filtration. After incubation, samples were filtered through 0.45 μm cellulose ether filters (GN-6, 25 mm diameter, Metrical, Gelman Sciences). Filters were acidified for 8 h with HCl vapour and disposed in glass vials with 10 ml of scintillation cocktail. Radioactivity was counted with a liquid scintillation counter (Beckman LS-100C) and the calculation of carbon uptake was done following Strickland and Parsons (1972). To construct the P – E curves, carbon uptake values (P) were normalized to chl ($P^* = P \text{Chl}^{-1}$).

The initial slope, a^* ($\text{mg C mg Chl}^{-1} \text{h}^{-1}$ ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) $^{-1}$), was estimated with a linear regression of the low irradiance points. This a^* corresponds to the spectral distribution of light in the incubator (a^*_{inc}). Only significant linear regression slopes were chosen (93% of the data set). To estimate the maximum P^* or assimilation number, P^*_m ($\text{mg C mg Chl}^{-1} \text{h}^{-1}$), the data were

fitted to the equation: $P^* = (P^*_m a^*_{inc} E_o) [(P^*_m)^2 + (a^*_{inc} E_o)^2]^{-1/2}$ (Smith, 1936), using commercially available software. The coefficient of determination (r^2) varied in the range 0.70–0.99.

Maximum photosynthetic quantum yield (φ_{max} , $\text{mol C (mol quanta)}^{-1}$) was calculated by dividing a^*_{inc} by the average $a^*_{ph(\lambda)}$ weighted by the incubator's light spectral distribution ($E_{(\lambda)inc}$, 400–700 nm) (Sosik, 1996). Thus, $\varphi_{max} = 0.02315 a^*_{inc} [a^*_{ph(PARinc)}]^{-1}$, where 0.02315 is a factor to convert $\mu\text{mol quanta}$ to mol quanta , hours to seconds, and mg C to mol C . In the latter expression $a^*_{ph(PARinc)}$ is equal to $\sum(a^*_{ph(\lambda)} E_{(\lambda)inc}) / \sum E_{(\lambda)inc}$. In order to simplify calculations, as a first approximation a normalized $a_{ph(\lambda)}$ spectrum with an average shape may be used ($a_{ph(\lambda)norm} = a_{ph(\lambda)} / a_{ph(440)}$). With our incubator's light spectrum $\sum(a_{ph(\lambda)norm} - E_{(\lambda)inc}) / \sum E_{(\lambda)inc} = 0.396$. Thus:

$$\begin{aligned} \varphi_{max} &= 0.02315 a^*_{inc} [0.396 a^*_{ph(440)}]^{-1} \\ &= 0.02315 a^*_{inc} [0.396(\text{chl})^{-1} (0.0403)(\text{chl})^{0.668}]^{-1} \\ &= 1.451 a^*_{inc} (\text{chl})^{0.332}. \end{aligned}$$

And the value of the initial slope corresponding to the spectral distribution of in situ irradiance ($E_{d(z)}$) is $a^*_{(in situ)} = 43.2 \varphi_{max} a^*_{ph(PARin situ)}$, where $a^*_{ph(PARin situ)} = \sum(a^*_{ph(\lambda)} E_{d(z,\lambda)}) / \sum E_{d(z,\lambda)}$.

Means of the physiological parameters were compared at the 95% confidence level to test the following hypotheses: there is no significant difference between neap and spring tides for the same region and season; there is no significant seasonal difference in each region; there is no significant difference between regions. One-way ANOVA was used to test differences between tidal conditions, for the same region and season. Differences between regions and seasons were tested using two-way ANOVA. Differences in a^* were analysed by comparison of regression lines (Sokal & Rohlf, 1995).

3. Results

Sampling for this work was done during non-El Niño years. It was a very dry period. In general, water temperature and salinity increased from the outer to the inner region (Fig. 2a,b), as reported in the literature. In general, our temperature and salinity data show homogeneity of the water column (not illustrated) due to strong tidal mixing, even with neap tides. Average temperature was highest during summer, up to $>27^\circ\text{C}$ in the inner region. But lowest salinities of our data set were recorded in August, with means of 33.04 and 33.26 for the outer and inner regions, respectively, with spring tides. In November there were also relatively low salinity values in the outer region, with a mean of 33.10. Salinity was highest at the end of spring, up to >34.91 in the in-

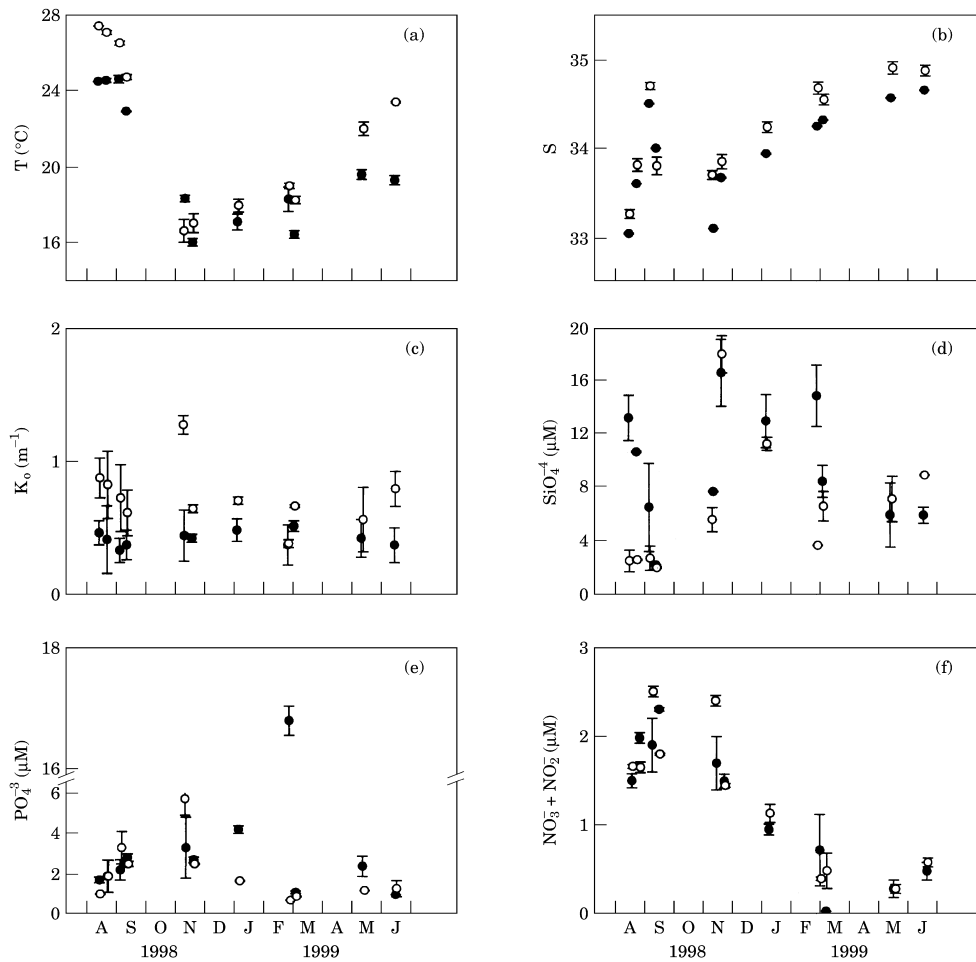


Fig. 2. Means of the environmental variables time series. Dark circles represent the outer region of Estero de Punta Banda, and clear circles represent the inner region. Bars are the standard errors. In each case, for August, September and November, the first couple of dark and clear circles correspond to spring tides, and the second to neap tides.

ner region. In general, the coefficient of vertical attenuation of diffused light, K_0 , had lower averages for the outer than for the inner region (Fig. 2c). In general, lowest average K_0 value was 0.36 m^{-1} , for the outer region, and the highest was 0.87 m^{-1} , for the inner region, with an exceptionally high average value of 1.27 m^{-1} for November.

There was not a clear nutrient temporal or spatial pattern of change, with the exception of $\text{NO}_3^- + \text{NO}_2^-$. Highest and lowest SiO_4^{4-} average values were 18 and $2 \mu\text{M}$, respectively, both for the inner region, and they were not significantly different from those of the outer region (Fig. 2d). Phosphate had an exceptionally high average value of $16.8 \mu\text{M}$ for the outer region, possibly due to flux of pore waters into the water column. The rest of the PO_4^{3-} means fluctuated between 0.8 and $5.7 \mu\text{M}$ (Fig. 2e). The oxidized nitrogen forms, $\text{NO}_3^- + \text{NO}_2^-$, had relatively high average values during summer–fall (up to $2.5 \mu\text{M}$ for the inner region), and low values during winter–spring ($<1 \mu\text{M}$). The lowest $\text{NO}_3^- + \text{NO}_2^-$ average value was recorded in winter for the outer region ($<0.1 \mu\text{M}$) (Fig. 2f).

Average chl values did not show significant differences between regions or seasons. They were within the range reported in the literature. In general, standard errors for chl were high due to its very patchy distribution with extreme fluctuations (Fig. 3a). Highest chl average value was $\sim 12 \text{ mg m}^{-3}$ for the outer region, and it was not significantly different from the highest value for the inner region. Chlorophyll concentrations were often $>4 \text{ mg m}^{-3}$ throughout the lagoon. In general, diatom and dino-flagellate abundance was higher at the outer than at the inner region, while the nanoplankton fraction was sometimes more abundant in the inner region (Table 1). According to reports in the literature, this seems to be common in northwestern Baja California coastal lagoons (Abraján-Villaseñor & Alvarez-Borrego, 1987; Millán-Núñez et al., 1982). In Table 1, the nanophytoplankton fraction ($<10 \mu\text{m}$) was underestimated because only phytoplankton cells $>5 \mu\text{m}$ can be counted with the inverted microscope technique.

There were no significant differences of the photosynthetic parameters average values for the same region and for different tidal conditions or different seasons. Both

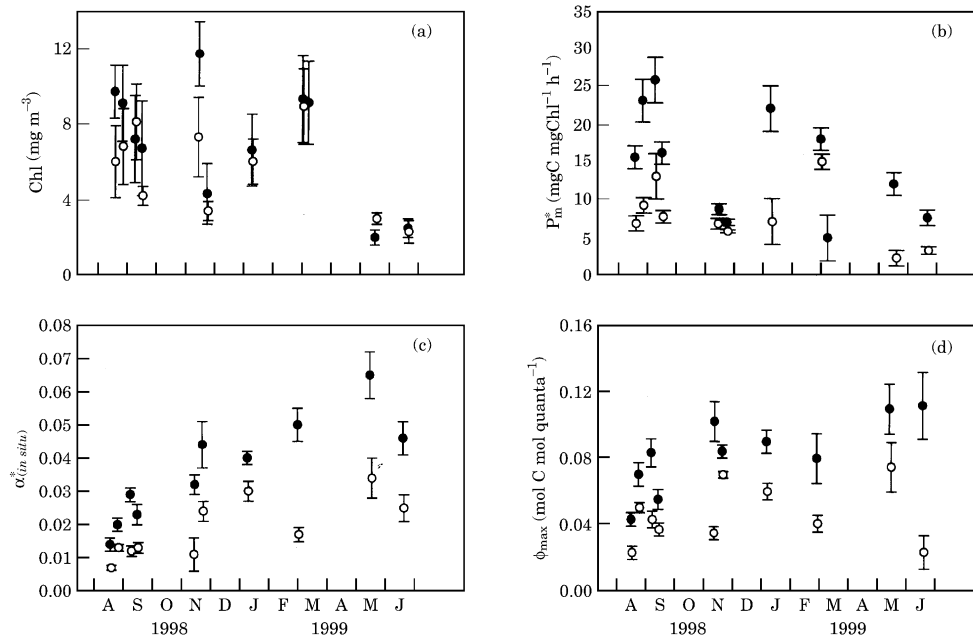


Fig. 3. Same as in Fig. 2, for means of chlorophyll *a* concentration and the phytoplankton photosynthetic parameters.

P_m^* and $a_{(in\ situ)}$ values were significantly higher for the outer than for the inner region (Fig. 3b,c). For our whole data set, the mean and standard error for the assimilation number were 14.6 and 2.6 mg C mg Chl⁻¹ h⁻¹, for the outer region, and 7.7 and 1.8 for the inner region, respectively. The mean and standard error for the initial slope were 0.036 and 0.008 mg C mg Chl⁻¹ h⁻¹ (μmol quanta m⁻² s⁻¹)⁻¹, for the outer region, and 0.019 and 0.005 for the inner region, respectively. The mean of

the photo-acclimation parameter ($E_k = \text{mean of } P_m^* / \text{mean of } a_{(in\ situ)}$) was 405 μmol quanta m⁻² s⁻¹ for both regions. The behaviour of the maximum photosynthetic quantum efficiency (ϕ_{max}) was similar to that of the initial slope (Fig. 3c,d). Average values of ϕ_{max} were 0.082 and 0.053 mol C (mol quanta)⁻¹, for the outer and inner regions, respectively. Its standard error was the same for both regions (0.012). The range for individual values of ϕ_{max} was 0.012–0.156, with the lowest value for the inner region and the highest value for the outer region. This highest ϕ_{max} individual value was not significantly different from the theoretical maximum of 0.125. None of the photosynthetic parameters were correlated with either chl or $T^\circ\text{C}$.

Table 1

Phytoplankton abundance means (10³ cells l⁻¹)

Season	Diatom	Dinoflagellate	Nannoplankton
<i>Outer region</i>			
Summer	79 (7)	17 (2)	5 (3)
	98 (18)	19 (4)	4 (1)
Autumn	39 (9)	84 (18)	11 (1)
	30 (25)	34 (29)	3 (2)
Winter	1 (1)	10 (2)	4 (1)
	145 (38)	182 (47)	253 (95)
Spring	19 (6)	2 (1)	9 (1)
	155 (85)	21 (12)	287 (194)
<i>Inner region</i>			
Summer	37 (29)	5 (4)	2 (1)
	45 (42)	5 (4)	1 (1)
Autumn	8 (7)	22 (19)	1 (1)
	3 (1)	1 (1)	2 (2)
Winter	5 (4)	45 (33)	14 (1)
	28 (18)	21 (14)	139 (86)
Spring	16 (7)	1 (1)	8 (5)
	13 (4)	2 (1)	786 (507)

Numbers in parenthesis are the standard errors. For each season, the upper line corresponds to spring tides, and the lower line to neap tides. Nannoplankton abundances are underestimated because very small cells could not be counted.

4. Discussion

Comparing our data with that of the literature from the 1970s, the hydrographic behaviour of Estero de Punta Banda persists essentially the same at present, during non-El Niño years. During El Niño events, fresh-water input may significantly reduce the salinity, mainly at the inner region. During the winter of 1983, an El Niño year, salinity was as low as 14.3 in the outer region and 6.1 in the inner region, (Alvarez-Borrego, Granados-Guzmán, & Beltrán-Félix, 1984). During the winter of 1993, it was as low as 28 and 21 in the outer and inner regions, respectively (Galindo-Bect et al., 1999). Flushing of phytoplankton communities caused by fresh-water input during El Niño events possibly results in physiological parameters that are significantly

different from those reported in this study. Thus, our conclusions on photosynthetic parameters of phytoplankton may not apply to El Niño years.

During our study period, salinity was lowest during summer–fall (as low as 33.04). Lowest surface oceanic salinity of the California Current System in this geographic area is about 33.3 (Hayward et al., 1999). Thus, these low salinity values in EPB do not originate from Todos Santos Bay. Green-Ruiz, Caschetto, and Alvarez-Borrego (1983) sampled pore waters from sediments at the mouth of EPB, in July 1981 (a non-El Niño year), and their lowest salinity value was <31 at 4–18 cm depth into the sediment. They explained these low salinity values as a result of flux of the San Carlos brook underground water. The agricultural valley of Maneadero is near EPB, and water is pumped from wells to irrigate crops. The volume flow of these wells is high showing a high flow of underground water. Camacho-Ibar and Alvarez-Borrego (1988) reported that the vertical variation of salinity in pore waters of sediments at the head of EPB for summer 1986, with values as low as 32.5, was partially the result of underground fresh-water input from the La Grulla brook. There are no reports in the literature on the annual cycle of salinity in pore waters of EPB. Nevertheless, our water column salinity data indicate the effect of higher fresh-water input during summer–autumn than during winter–spring during non-El Niño years. A possibility is that agricultural drainage from Maneadero is reaching EPB with higher volumes during summer–autumn than during the rest of the year. Fertilizers in these drainage waters would explain the higher $\text{NO}_3^- + \text{NO}_2^-$ values in EPB during summer–fall (up to $2.5 \mu\text{m}$). Hernández-Ayón, Galindo-Bect, Flores-Báez, and Alvarez-Borrego (1993) reported high NO_3^- and relatively low salinity values at the internal extreme of the Colorado River inverse estuary as the result of input of agricultural runoff from adjacent farmland. A similar phenomenon may be occurring at EPB.

Strong remineralization of nutrients through bacterial degradation of organic matter in the sediments and the flux of pore waters into the water column are important mechanisms for enrichment of coastal lagoons of northwestern Baja California. These phenomena produce relatively high NH_4^+ values in the water column (Camacho-Ibar & Alvarez-Borrego, 1988). Coastal lagoons of northwestern Baja California export significant amounts of ammonium to the adjacent ocean (Farfan & Alvarez-Borrego, 1983). These latter authors reported ammonium concentrations as high as $3 \mu\text{m}$ for the mouth of San Quintín Bay (300 km south of San Diego). It has long been known that when ammonium concentrations are higher than $0.5\text{--}1.0 \mu\text{m}$, phytoplankton rely solely upon the reduced form of nitrogen for nutrition even when nitrate is present in excess (Eppley, Coatsworth, & Solorzano, 1969). According to Silva-Cota and Alvarez-Borrego (1988), light is controlling photo-

synthesis in lagoons of northwestern Baja California, not nutrients. Since bacterial degradation of organic matter in the sediments produces reduced nitrogen forms (such as ammonium), agricultural drainage is the most important source of oxidized forms of nitrogen in Estero de Punta Banda.

We did not find significant differences for the average values of the photosynthetic parameters of phytoplankton when comparing different seasons or different tidal conditions. There is great day-to-day variability of photosynthetic parameters in coastal waters (Côte & Platt, 1983; Valdez-Holguín et al., 1998; this work), but we were not able to detect significant differences between seasons in EPB. Thus, the high temporal variability of phytoplankton production in EPB is mainly caused by variations of chl. Valdez-Holguín et al. (1998) analysed the $P\text{--}E$ relationship of phytoplankton in coastal and oceanic waters of the California Current System. They proposed a single set of working averages for the assimilation number, the initial slope and the maximum photosynthetic quantum yield for the CCS between northern California and San Quintín Bay, for the whole year. On the other hand, Valdez-Holguín, Alvarez-Borrego, and Trees (1999) proposed two sets of working averages of these parameters for the Gulf of California, one for the ‘cool’ season and another for the ‘warm’ season. Extremely high temperatures during summer ($>29^\circ\text{C}$) throughout most of the Gulf of California cause lower photosynthetic parameters than during winter. According to Behrenfeld and Falkowski (1997), with high summer surface $T^\circ\text{C}$, relatively low values of both P_m^* and a^* (in situ) are to be expected. Due to the effect of summer upwelling, water temperature is not very high on the northwestern Baja California coast. Our highest $T^\circ\text{C}$ average value was a little more than 27°C , and it was for the inner region. However, our data do not show a relationship between $T^\circ\text{C}$ and the photosynthetic parameters in EPB.

On the other hand, means of the photosynthetic parameters were higher for the outer than for the inner region of the Estero. Possibly, the higher turbidity at the inner region caused photo-acclimation of phytoplankton to a lower irradiance regime. It has long been known that when phytoplankton cells are photo-acclimated to a low irradiance regime, the photosynthetic parameters tend to be low (Falkowski & Owens, 1980). Valdez-Holguín et al. (1998, 1999) reported lower photosynthetic parameters for the lower than for the upper half of the euphotic zone in the CCS and the Gulf of California, respectively. Valdez-Holguín et al. (1998) reported averages of the assimilation number, initial slope, and photosynthetic quantum yield equal to 11.3 ($SE = 1.4$) $\text{mg C mg Chl}^{-1} \text{h}^{-1}$, 0.050 ($SE = 0.008$) $\text{mg C mg Chl}^{-1} \text{h}^{-1}$ ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) $^{-1}$, and 0.066 ($SE = 0.009$) $\text{mol C (mol quanta)}^{-1}$, respectively, for surface waters off Todos Santos Bay. These values are not

significantly different from our average photosynthetic parameters for the outer region of EPB. Also, Valdez-Holguín et al. (1998) reported means for these parameters equal to 8.0 ($SE = 1.0$) $\text{mg C mg Chl}^{-1} \text{h}^{-1}$, 0.028 ($SE = 0.003$) $\text{mg C mg Chl}^{-1} \text{h}^{-1} (\mu\text{mol quanta m}^{-2} \text{s}^{-1})^{-1}$, and 0.037 ($SE = 0.005$) $\text{mol C (mol quanta)}^{-1}$, for the middle of the euphotic zone in waters off Todos Santos Bay. These latter values are not significantly different from those for the inner region of EPB. Thus, the spatial distribution of turbidity in EPB has a similar effect on the photosynthetic parameters of phytoplankton as that of the difference in light levels between the surface and the middle of the euphotic zone in coastal waters off Todos Santos Bay.

Silva-Cota and Alvarez-Borrego (1988) did not find a significant difference between averages of assimilation numbers for the mouth and the internal extreme of San Quintín Bay, a coastal lagoon 180 km south from EPB, during summer of an El Niño year. They indicated that the relatively low average value for P^*_m ($6.0 \text{ mg C mg Chl}^{-1} \text{h}^{-1}$) was due to the dominance of the phytoplankton assemblages by cyanobacteria throughout the whole bay during 1983–1984. El Niño can cause large perturbations in the CCS, with suppressed upwelling and more extensive intrusion of warm, nutrient-depleted subtropical waters near the coast (Lynn & Simpson, 1987). These perturbations cause changes in the distribution of chl. Sosik (1996) reported phytoplankton assimilation numbers in the range 1.1 – $7.5 \text{ mg C mg Chl}^{-1} \text{h}^{-1}$ for the CCS, for winter and early spring of 1992, an El Niño year. Putt and Prézelin (1985) reported that phytoplankton samples from the Santa Barbara Channel in summer 1983 were dominated by chroococcalean cyanobacteria (0.5 – $1.5 \mu\text{m}$, not visible with the inverted microscope). These latter authors reviewed the literature for assimilation numbers of marine cyanobacteria and found most of the field values falling within the range 0.1 – $6.1 \text{ mg C mg Chl}^{-1} \text{h}^{-1}$ (mainly below 2.5). Again, this indicates that our results may not apply to El Niño years.

Our φ_{max} values ranged from 10% to over 100% of the theoretical maximum of $0.125 \text{ mol C (mol quanta)}^{-1}$, although the largest values are not significantly different from 0.125. Sosik (1996) reported φ_{max} values for the CCS, and for the 1992 El Niño year, in the range 10–85% of the theoretical maximum, and she mentioned that this range is as large as has been reported for phytoplankton cultures and natural assemblages. Values as high as $0.10 \text{ mol C (mol quanta)}^{-1}$ have been reported for a variety of coastal and oceanic waters (Sosik, 1996; and others cited there in). Kiefer and Mitchell (1983) found that $\varphi_{\text{max}} = 0.06 \text{ mol C (mol quanta)}^{-1}$ describes a variety of steady-state growth conditions. This latter value is in between and not significantly different from our two means for the outer and inner regions of EPB. For the purpose of estimating primary

production with absorption-quantum yield algorithms (Kiefer & Mitchell, 1983; Sosik, 1996), we propose using the method of Alvarez-Borrego (1996) to estimate the depth dependence of in situ quantum yield: $\varphi_{(z)} = \varphi_{\text{max}} [1 + (E_{o(z)}/E_k)^2]^{-1/2}$, where $\varphi_{(z)}$ is the actual quantum yield at each depth and $E_{o(z)}$ is the in situ irradiance.

Thus, it seems reasonable to use simplified working means for photosynthetic parameters for large time and space scales within coastal lagoons of northwestern Baja California. This approach may provide reasonable large-scale estimates, but poor small-scale instantaneous estimates of primary production. The averages we propose for Estero de Punta Banda should be used only for non-El Niño years. Data on photosynthetic parameters have to be generated for El Niño years, and since the dilution of oceanic water with freshwater from the streams may differ for different El Niño events it may be necessary to characterize several events.

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