

## PHOTOSYNTHETIC PARAMETERS OF PHYTOPLANKTON IN THE CALIFORNIA CURRENT SYSTEM

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### ABSTRACT

We analyzed photosynthesis-irradiance (P-E) and phytoplankton absorption data from the coastal waters of the Southern California Bight (SCB) as well as data in the literature for other coastal and oceanic regions of the California Current system (CCS). 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 the CCS between northern California and Bahía de San Quintín (300 km south of San Diego) based on data we summarized from coastal and oceanic waters. For the upper half of the euphotic zone we propose to use the following averages:  $\alpha^B = 0.047 \pm 0.004$  mg C (mg chl)<sup>-1</sup> h<sup>-1</sup> ( $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ )<sup>-1</sup> (the initial slope of the photosynthesis-irradiance curve); and  $P_{\text{max}}^B = 8.60 \pm 0.060$  mg C (mg chl)<sup>-1</sup> h<sup>-1</sup> (assimilation number). A linear interpolation for the gradient of  $\alpha^B$  and  $P_{\text{max}}^B$  is recommended for the lower half of the euphotic zone (10%–1%  $E_0$  depths), with values for the 1%  $E_0$  depth equal to 25% of the values of the upper euphotic zone:  $\alpha^B = 0.012$ , and  $P_{\text{max}}^B = 2.15$ .

### INTRODUCTION

The advent of remotely sensed ocean color data has made the synoptic estimation of primary productivity for large geographic areas an attainable goal. Empirical and semianalytical algorithms to estimate primary productivity from satellite-derived photosynthetic pigments have been compared (e.g., Balch et al. 1989; Platt et al. 1995; Sathyendranath et al. 1995). The parameters used in these algorithms belong to three categories (Morel 1991): environmental (e.g., location, atmospheric conditions); ecological (e.g., the chlorophyll vertical profile); and physiological (e.g., the photosynthesis-irradiance curve parameters, the chlorophyll-specific absorption coefficient of phytoplankton, photosynthetic quantum yields).

Given a set of ecological and physiological parameters, the evolution of productivity in response to environmental changes is unambiguously derived, since the physics involved are rather accurately modeled (Morel

1991). On the basis of the CalCOFI data set, Millán-Núñez et al. (1996, 1997) proposed regression models to predict the vertical profiles of chlorophyll (chl) from surface values for the California Current system (CCS). Fewer data exist, however, on the physiological parameters of phytoplankton.

The Southern California Bight (SCB) constitutes a unique physical environment within the CCS. A dramatic change in the angle of the coastline, coupled with the topography of the southern California offshore coastal area results in circulation patterns that differ significantly from other locations of the west coast of the United States and northern Baja California. During summer, the CCS bends shoreward south of San Diego, then poleward, recycling water through the SCB in the large-scale Southern California Countercurrent (Hickey 1993). The growth and productivity of SCB phytoplankton is intermediate when compared to other areas of the world's ocean. It is greater than the growth and productivity in the North Pacific Central Gyre, but less than that in nutrient-rich upwelling regions (Hardy 1993).

Peláez and McGowan (1986) analyzed satellite color imagery and found a sharp zonal boundary just south of San Diego—the Ensenada Front. It coincides with the CCS onshore component and is best defined from about 100 km to 500 km offshore. It is an abrupt transition between two large and different biological water masses, with a threefold change in phytoplankton pigment content over a distance of a few kilometers, with very low surface-pigment concentrations in the southern, warmer, water mass. From June through winter the oligotrophic water mass intrudes into the Southern California Bight. This low-pigment area is located immediately offshore of the narrow coastal band of higher pigment, and it is continuous with the low-pigment region south and west of the Ensenada Front (Peláez and McGowan 1986).

The objective of this work was to characterize the parameters of the P-E curve: its initial slope ( $\alpha^B$ ), and the maximum rate ( $P_{\text{max}}^B$ ), both normalized to chl, for the coastal region of the Southern California Bight. We also estimated  $a_{ph}^*(\lambda)$ , the specific absorption coefficient of phytoplankton, which allowed us to derive maximum photosynthetic quantum efficiency ( $\phi_{\text{max}}$ ) from  $\alpha^B$  and the spectral distribution of irradiance in our incubator. We analyze here the variability of these parameters at a

station off Bahía de Todos Santos (100 km south of San Diego) for a period of 20 days, and compare our values with those in the literature for other coastal and oceanic regions of the CCS. Finally, we propose a set of working averages of the physiological parameters to be used in primary-productivity algorithms for the CCS region represented by the various data sets.

## METHODS AND MATERIALS

From 20 July to 8 August 1994, daily samples were taken at a station 7 km west of Isla Todos Santos within the CCS (31°50'N, 116°53'W; fig. 1). Bahía de Todos Santos is near the southernmost extreme of the Southern California Bight (fig. 1.5 in Dailey et al. 1993). Sampling was done around noon. Wind speed and direction, and atmospheric temperature were measured at Punta Morro (fig. 1). Once each day we measured profiles of temperature and salinity (CTD; SeaBird Inc.), natural (daylight-induced) fluorescence, and photosynthetically available scalar irradiance (PNF-300, Biospherical Instr.).

We also took water samples from two depths, corresponding to 100% and 10% of the irradiance incident just below the sea surface ( $E_0^-$ ). Water samples were transported to the laboratory on land, in 20 L glass bottles covered with dark cloth and placed in insulated boxes filled with seawater to maintain constant temperature. We assume that transportation time from the field to the laboratory (maximum, 2 hrs) did not affect the P-E relation of our samples since changes from high to low irradiance result in negligible photoacclimation (change of chlorophyll cell<sup>-1</sup>) at time scales less than 5 hours (Post et al. 1984).

Upon arrival in the laboratory, chl samples were filtered through Whatman GF/F glass-fiber filters. The samples were later extracted in 90% acetone for 24 hours, and analyzed fluorometrically (Yentsch and Menzel 1963; Holm-Hansen et al. 1965; Venrick and Hayward 1984). Water samples were filtered through GF/F filters for particle absorption, which was measured with a Perkin-Elmer Lambda 6 spectrophotometer. Raw absorbances were corrected for the path-length amplification effect according to Mitchell (1990). Estimates of total particle absorption ( $a_p$ ) were corrected for detrital absorption ( $a_d$ ) following Kishino et al. (1985), to obtain an estimate of phytoplankton absorption ( $a_{ph}$ ). Spectrophotometric phosphate concentration ( $PO_4$ ) analyses were done following Strickland and Parsons (1972).

To generate the photosynthesis-irradiance (P-E) curves, 420 ml from each water sample were passed through a 333  $\mu$ m mesh to remove large herbivores, then <sup>14</sup>C was added to a final concentration of 0.5  $\mu$ Ci ml<sup>-1</sup>. A 10 ml aliquot was pipetted into each of 36 scintillation vials, which were incubated for an hour in an incubator similar to the one designed by Talbot et al. (1985). Tem-

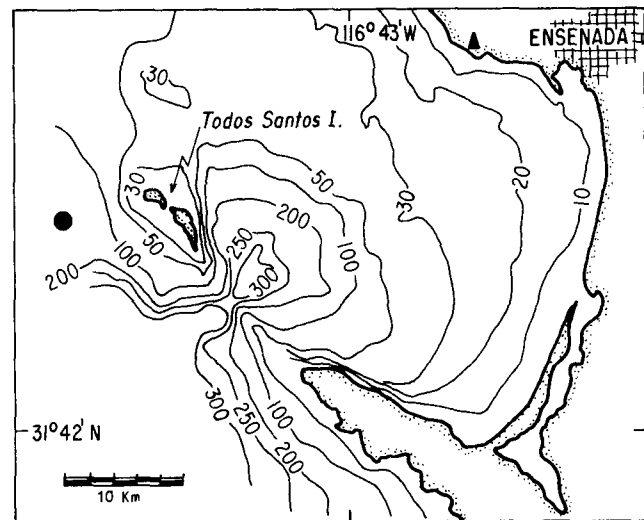


Figure 1. Study area. Sampling site (●) and Punta Morro meteorological station (▲).

perature was maintained at 16°C ± 2° for all samples. Three additional samples were taken for dark incubation, and three more for a time-zero control; the latter were immediately acidified after filtration. After incubation, each sample was filtered through a 0.45  $\mu$ m Gelman membrane filter, after which 0.2 ml of 1.2 N HCl was added to each filter. Radioactivity was determined with a Beckman LS5000 scintillation counter. Carbon assimilation was estimated according to Strickland and Parsons (1972).

The initial slope,  $\alpha^B$ , was estimated with a linear regression of the low irradiance points. To estimate  $P_{max}^B$ , we fit the data points to Smith's (1936) equation

$$P^B = (P_{max}^B \alpha^B E) [(P_{max}^B)^2 + (\alpha^B E)^2]^{-1/2},$$

using the STATISTICA software package. Maximum photosynthetic quantum efficiency ( $\phi_{max}$ ) was calculated by dividing  $\alpha^B$  by the  $a_{ph}^*(\lambda)$  weighted by the spectral irradiance of the P-E incubator (Schofield et al. 1993; Sosik 1996).

## RESULTS

Dominant winds were from the northwest, with large diurnal variations. During the first five days, maximum wind speeds were as high as 9 m s<sup>-1</sup> (not illustrated). Sea-surface temperature (T °C) was 16.5°–17° the first four days and decreased to 15° the following two days; then, as the winds relaxed to 3 m s<sup>-1</sup> on the tenth day, T increased to 20°. Thereafter, winds increased without reaching the intensities of the first days, and surface T decreased again to 16.5° on the thirteenth day. Finally, winds decreased toward the end of the sampling period, and surface T increased to 20.6° (fig. 2a). At the 10%

$E_0$  depth  $T$  behaved in a similar manner as at the surface. These temperature fluctuations are believed to be caused partly by local upwelling, as indicated by changes in isopycnal depths (fig. 3). Temperature differences from  $1.5^\circ$  to  $5^\circ$  between the surface and the 10%  $E_0$  depth suggest strong stratification (fig. 2a).

Very clear skies during the first two days and on day 18 of our sampling period produced high incident scalar irradiance ( $E_0^-$ ). But on the other sampling days, variable cloudiness caused  $E_0^-$  values lower than  $500 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$  (fig. 2b). The density field indicates vertical mixing up to 15 m on some dates (fig. 3). The  $24.5 \sigma_t$  isopycnal fluctuated between 10 m and the surface up to day 18, then subsided deeper than 25 m after day 18. The 10%  $E_0$  depth behaved similarly to the  $24.5 \sigma_t$  isopycnal. Its minimum was near 10 m on the twelfth day, and its maximum was almost 30 m toward the end of our sampling period (fig. 3).

Phosphate concentration ( $\text{PO}_4$ ) varied irregularly with time and was not correlated with  $T$   $^\circ\text{C}$ . In general, there were slightly higher  $\text{PO}_4$  values at the 10%  $E_0$  depth than at the surface (fig. 4). For our data set,  $\text{PO}_4$  concentration and standard error ( $s/n^{1/2}$ ) were  $0.26$  and  $0.013 \mu\text{M}$ , respectively. We have used CalCOFI data from the upper 50 m for 1993–97 to derive empirical regressions of

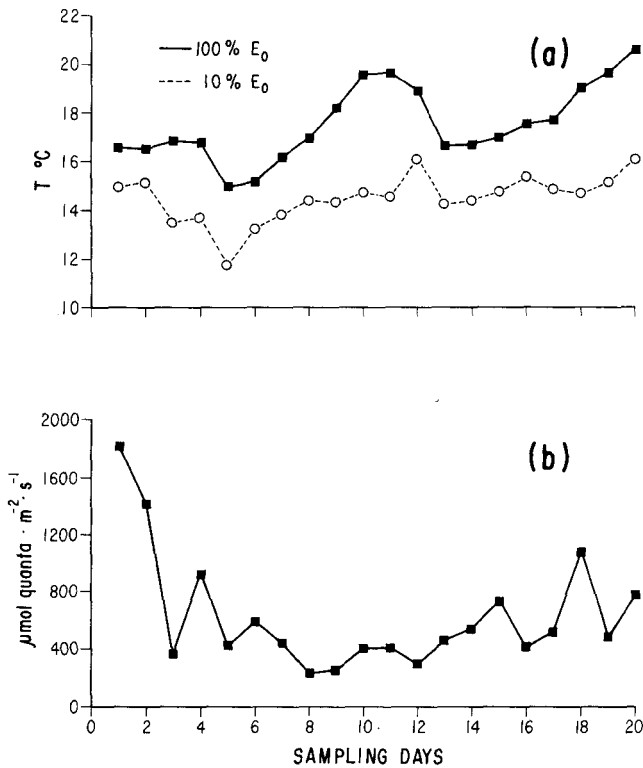


Figure 2. a, Temperature time series (surface and 10%  $E_0$  depth); b, incident irradiance ( $E_0^-$ ) time series.

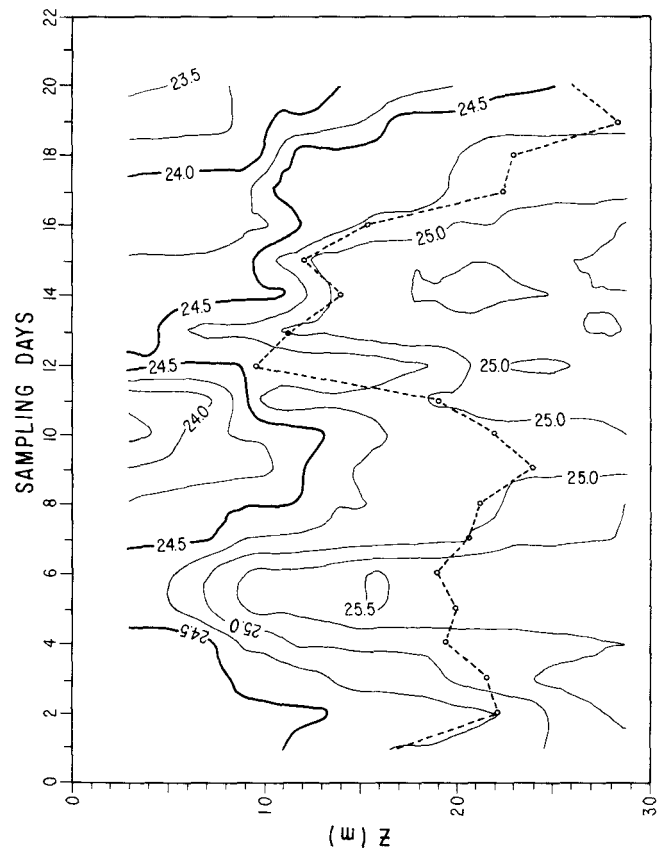


Figure 3. Vertical distribution of density, the 10%  $E_0$  depth (dashed line), and the  $24.5 \sigma_t$  isopycnal (bold line).

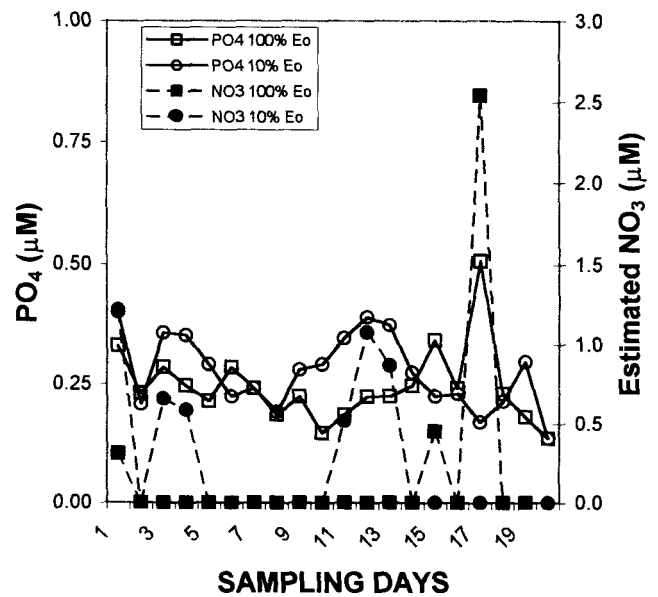


Figure 4. Phosphate concentration (open symbols,  $\mu\text{M}$ ) for surface and the 10%  $E_0$  depth. Nitrate values (closed symbols,  $\mu\text{M}$ ) are based on regression estimates from CalCOFI data.

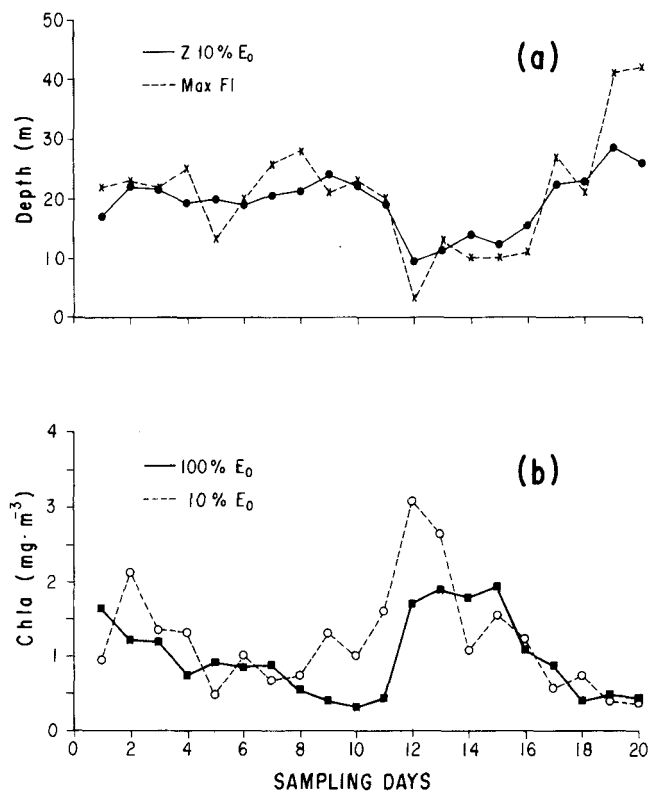


Figure 5. a, Fluorescence maximum and the 10%  $E_0$  depths; b, chlorophyll a time-series (surface and 10%  $E_0$  depth).

phosphate vs. nitrate ( $\text{NO}_3$ ) that were used to estimate  $\text{NO}_3$  in figure 4. Analysis of the CalCOFI data showed that there is residual  $\text{PO}_4$  after  $\text{NO}_3$  depletion, thus accounting for the poor correlation of  $\text{PO}_4$  with temperatures over this narrow temperature range. In the CalCOFI data set,  $\text{PO}_4$  is well correlated with temperatures lower than  $15^\circ$ .

Depth of the fluorescence maximum was not significantly different from the 10%  $E_0$  depth ( $p \leq 0.10$ ; fig. 5a). In general, there was no significant difference between surface chl and that at the 10%  $E_0$  depth (fig. 5b). However, during sampling days 8–13, chl was higher at the 10%  $E_0$  depth than at the surface ( $p \leq 0.005$ ). The minimum and maximum chl values, respectively, for the 10%  $E_0$  depth were 0.42 and 3.1  $\text{mg m}^{-3}$ ; for the surface they were 0.36 and 1.95  $\text{mg m}^{-3}$ . We had lowest chl values and highest temperatures in the middle and at the end of the sampling period (figs. 2a and 5b).

The chlorophyll-specific phytoplankton absorption spectra are shown in figure 6. Variations in the spectral shape are represented by changes in the ratios of the blue (440 nm) to red (675 nm) peaks. This ratio differed significantly between the 100% and 10% depths only on day 1 (fig. 6c).

Analysis of P-E response indicated slight photoinhibition with irradiances higher than 600  $\mu\text{mol quanta}$

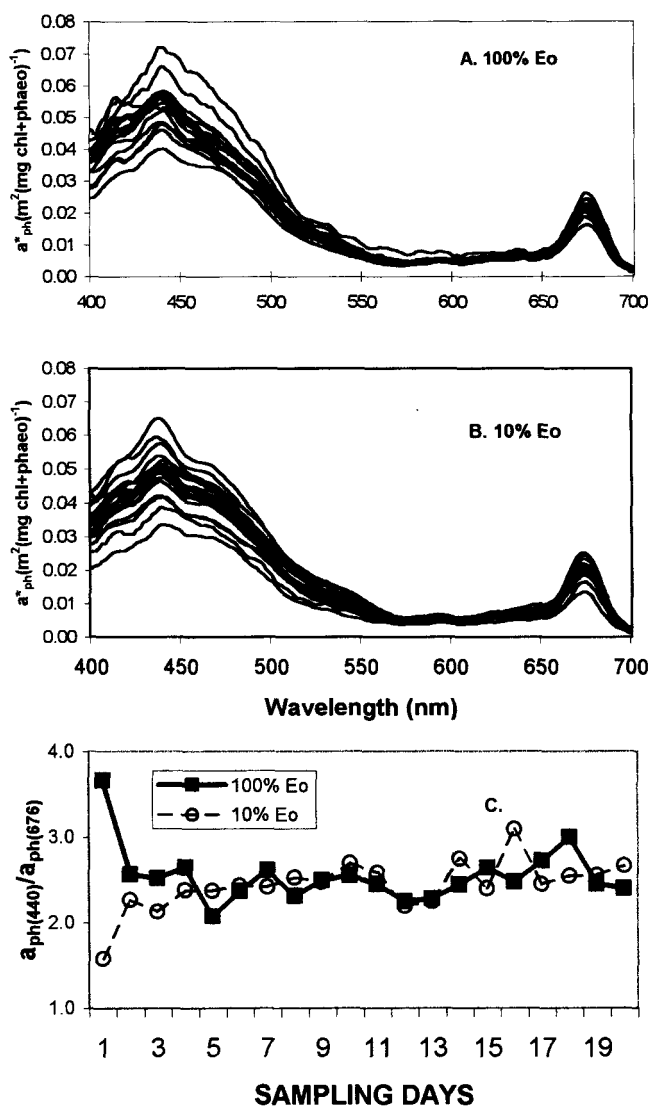


Figure 6. Phytoplankton pigment-specific absorption spectra ( $a_{ph}^*$ ) for (A) 100%  $E_0$  depth, and (B) 10%  $E_0$  depth. C, Absorption ratio (440/676) time series.

$\text{m}^{-2} \text{s}^{-1}$  (for example, surface samples on day 6 and day 8; fig. 7), but in general there was no photoinhibition up to 1,400  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ . The average saturation parameter of photosynthesis ( $E_k = P_{\text{max}}/\alpha$ ) was 246  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  for the surface and 255 for the 10%  $E_0$  depth, with a standard error of 14 and 21  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ , respectively. These  $E_k$  values are not statistically different, and the overall average of 250  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  can be adopted.

The initial slope,  $\alpha^B$ , was variable; its mean and standard error for our whole data set were 0.039 and 0.005  $\text{mgC}(\text{mg chl})^{-1} \text{h}^{-1}(\mu\text{mol quanta m}^{-2} \text{s}^{-1})^{-1}$ , respectively. Except for days 6, 8, 9, and 19,  $\alpha^B$  values for both depths were very similar (fig. 8a). The maximum  $\alpha^B$  value was estimated for sampling day 8 [0.153  $\text{mg C}$

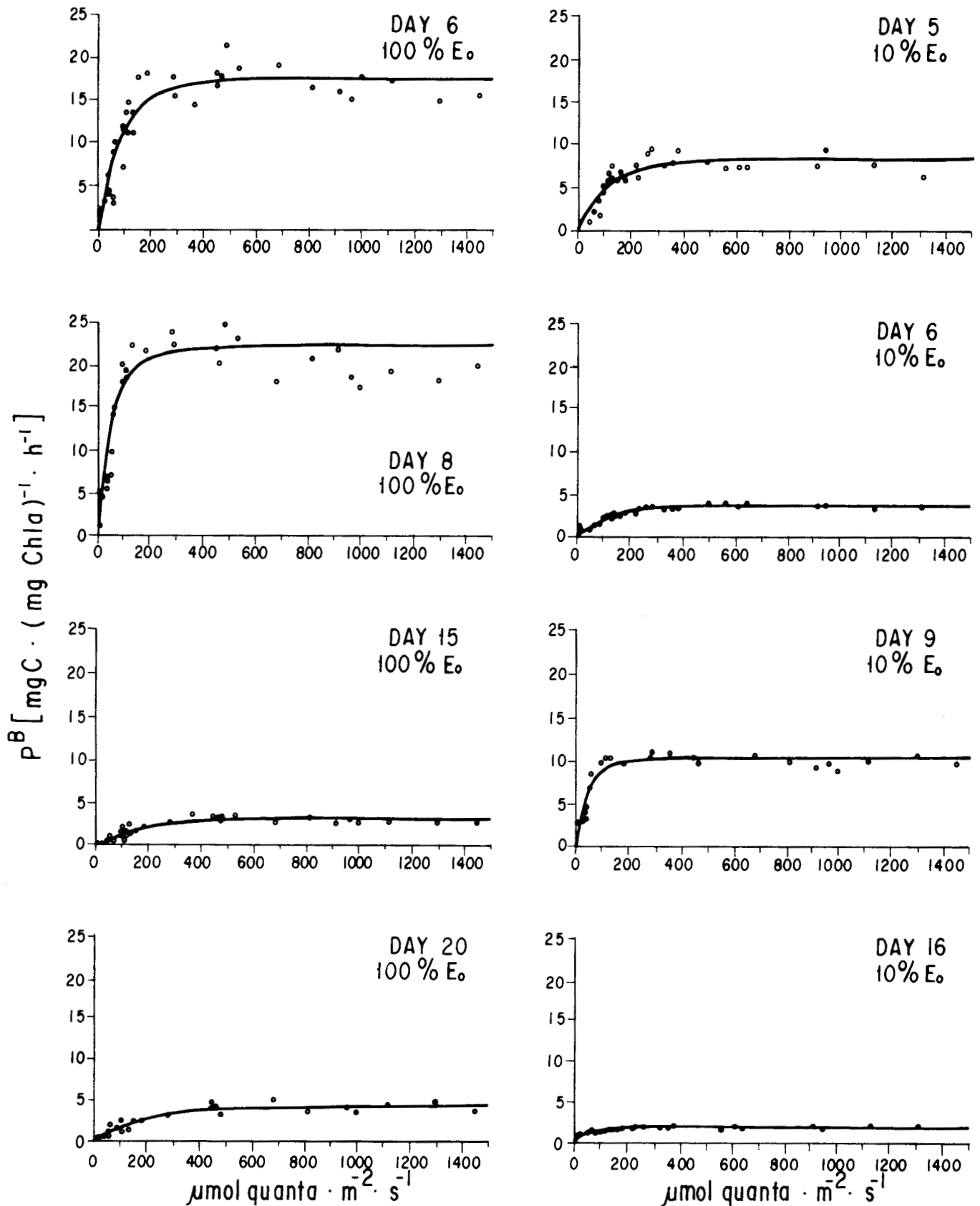


Figure 7. Examples of photosynthesis-irradiance (P-E) curves at 100% and 10%  $E_0$  depths for different sampling dates.

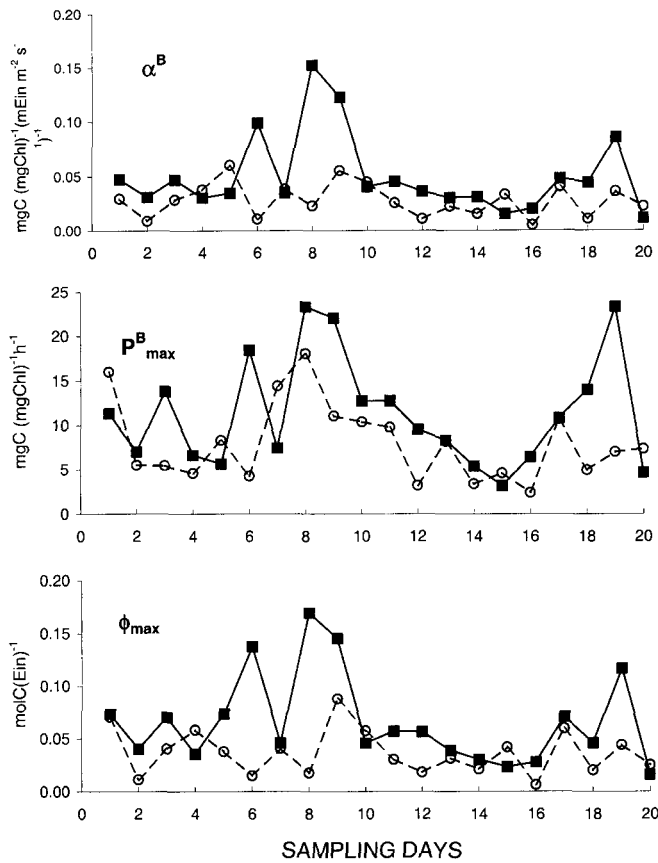


Figure 8. Time series of initial slope ( $\alpha^B$ ), maximum photosynthetic rate ( $P_{max}^B$ ), and maximum quantum efficiency ( $\phi_{max}$ ).

( $\text{mg chl}^{-1} \text{ h}^{-1} (\mu\text{mol quanta m}^{-2} \text{ s}^{-1})^{-1}$ ) for the surface. On the other hand,  $\alpha^B$  values as low as 0.01 were estimated for the 10%  $E_0$  depth.

Like  $\alpha^B$ ,  $P_{max}^B$  varied over time but with a greater similarity between the two sampled depths (fig. 8b). For the entire data set,  $P_{max}^B$  ranged from 2.5 to 23. The mean and standard error for  $P_{max}^B$  were 9.6 and 0.9  $\text{mg C mg chl}^{-1} \text{ h}^{-1}$ , for all P-E data.

Because of its dependence on  $\alpha^B$ , and relatively little variability in  $a_{ph}^*$ ,  $\phi_{max}$  showed the same pattern of variation as  $\alpha^B$  (fig. 8c). Minimum  $\phi_{max}$  values for both sampled depths were about 0.01  $\text{mol C (mol quanta)}^{-1}$ , and maximum estimates were 0.088 for the 10%  $E_0$  depth and up to 0.169 for surface waters. The mean and standard error for  $\phi_{max}$  were 0.051 and 0.006  $\text{mol C (mol quanta)}^{-1}$  for our whole data set. However, error of individual samples was greater, and the highest  $\phi_{max}$  values were not significantly different from the theoretical maximum of 0.125. None of the three parameters ( $\alpha^B$ ,  $P_{max}^B$ , and  $\phi_{max}$ ) were correlated with either chl or T °C.

The phytoplankton absorption was well correlated

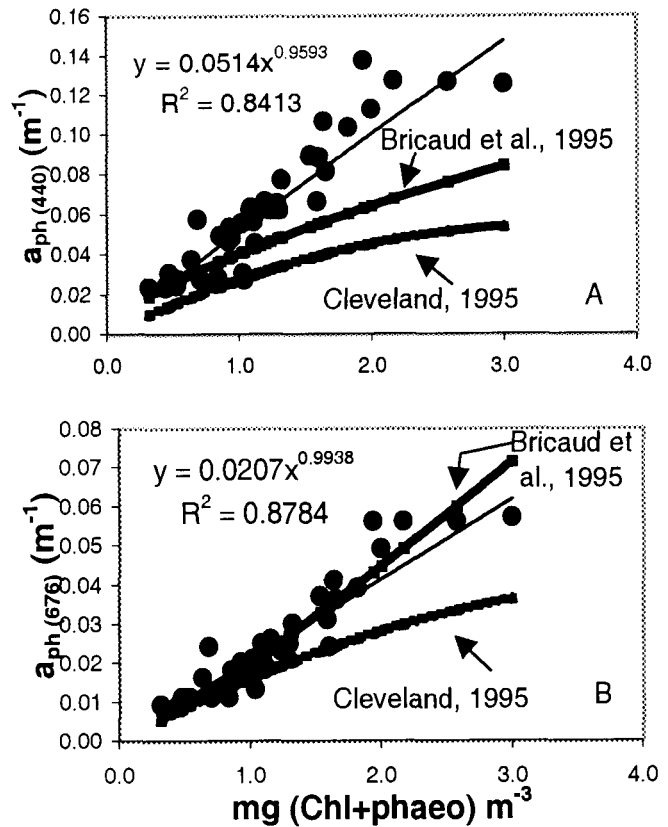


Figure 9. Best fits with a power function model for the phytoplankton absorption coefficients versus chlorophyll a concentration for 440 nm (A) and 676 nm (B) for our entire data set. The thick lines represent prediction of the models of Cleveland (1995) and Bricaud et al. (1995).

with pigment (chl + phaeo) concentrations (fig. 9), as found by other investigators (Mitchell and Kiefer 1988; Bricaud et al. 1995; Cleveland 1995; Sosik and Mitchell 1995). But unlike the modeling parameterizations of Cleveland (1995) or Bricaud et al. (1995), our study showed little nonlinearity in the  $a_{ph}$  versus chlorophyll relation at 440 or 675 nm, as shown by the exponent of the power fit, which is not significantly different from 1.0 (fig. 9). This may be caused by the relatively narrow range of pigment concentration in our data set. Our data at 675 nm agree well with the Bricaud et al. (1995) model, but both our data and the Bricaud et al. model are higher than the Cleveland (1995) model at this wavelength. At 440 nm our data are greater than either of the previous model predictions.

These differences are partly due to the fact that the earlier models were based on data processed with algorithms dependent on the Mitchell and Kiefer (1988) report, which results in  $a_{ph}$  values about 30% lower than the algorithm we used (Mitchell 1990). There is large variance in the source data sets of the previous models, and our data are within the range of those data.

## DISCUSSION

Segovia-Zavala et al. (in press) reported maximum  $\text{PO}_4$  values of  $0.75 \mu\text{M}$ , and  $\text{NO}_3$  values of  $1.0 \mu\text{M}$  for coastal surface waters between San Diego and Bahía de Todos Santos during an intense upwelling event with minimum surface temperatures under  $13^\circ$ . These are relatively low nutrient values for CCS upwelling at this temperature. Our nutrient values are lower because we did not have an upwelling event as intense as theirs (our lowest surface T was  $15^\circ$ ). Our higher T's and lower nutrients also indicate that there was not a significant "island mass effect" (Doty and Oguri 1956) due to Isla Todos Santos. Smith et al. (1987) also reported relatively low near-surface nutrients for a transect through the northern extreme of the SCB. Nutrient and surface temperature values from  $15^\circ$  to  $20^\circ$ , similar to our observations, are typical of the SCB region (Sosik and Mitchell 1995; Hayward et al. 1996).

Bahía de San Quintín, 200 km south of Bahía de Todos Santos, is about 100 km south of the point where the oligotrophic intrusion turns back offshore (surface geostrophic flow shown in fig. 27 of Reid 1988). During non-El Niño years, strong upwelling events occur in the area off Bahía de San Quintín, with minimum surface T of  $11^\circ$  in July (Alvarez-Borrego and Alvarez-Borrego 1982), more than  $4^\circ$  lower than our minimum surface T. In Bahía de San Quintín the maximum reported surface  $\text{PO}_4$  and  $\text{NO}_3$  values for summer are 2.5 and  $12 \mu\text{M}$  (Millán-Núñez et al. 1982). North of the SCB, off Point Sur (35 km south of Monterey Bay), maximum surface  $\text{NO}_3$  values reported for an upwelling event in June were around  $24 \mu\text{M}$  (Traganza 1985). Thus, north and south of the bight, nutrients are much higher than inside the bight. Our relatively low nutrient concentrations, and also those of Segovia-Zavala et al. (in press) and Smith et al. (1987), are consistent with the concept that our site was only slightly influenced by coastal upwelling and was dominated by the well-described oligotrophic north-flowing currents (Hickey 1993; Hayward et al. 1996).

In the coastal waters of the bight, chl values are also lower than in the coastal waters off Bahía de San Quintín and off Point Sur. Our maximum surface chl values were near  $2 \text{ mg m}^{-3}$ , often in the range  $0.5\text{--}1.5 \text{ mg m}^{-3}$  (fig. 5b). Our data are in agreement with the chl time series at Scripps Pier—where chl values are typically in the range  $0.5\text{--}1.5 \text{ mg m}^{-3}$ , with some relatively isolated peaks greater than  $5 \text{ mg m}^{-3}$ —and with CalCOFI cruise data for within the bight (Sosik and Mitchell 1995; Hayward et al. 1996). Chl values reported for waters off Bahía de San Quintín are often larger than  $5 \text{ mg m}^{-3}$ , with peaks larger than  $15 \text{ mg m}^{-3}$  in summer (Millán-Núñez et al. 1982). Similar high chlorophyll concentrations are observed in northern California waters in the upwelling plumes (Hood et al. 1991).

Both photosynthetic parameters,  $\alpha^B$  and  $P_{\text{max}}^B$ , showed great variability over the sampling period. This agrees with a 70-day time series reported by Coté and Platt (1983) for Bedford Basin, and with other reports for the CCS (Harding et al. 1982; Prézélin et al. 1987; Schofield et al. 1991). According to Coté and Platt, phytoplankton cells respond fairly rapidly to changing environmental conditions, close to the order of a generation time. Harding et al. (1982) demonstrated large diel variability in  $\alpha^B$  and  $P_{\text{max}}^B$ . Hood et al. (1991) and Schofield et al. (1991) also found relatively large variability for these two parameters in northern California and at the northern end of the Southern California Bight, respectively.

These reports for the CCS region place considerable doubt on our ability to predict instantaneous primary production rates by using satellite estimates of chl and irradiance. 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 productivity for large time and space scales to which the data apply (Sathyendranath et al. 1995).

Millán-Núñez et al.'s (1997) algorithms cannot predict the instantaneous chl profiles for a particular geographic location in the CCS, but they are appropriate at regional and seasonal space and time scales. In a similar manner, we might be able to find acceptable averages of the photosynthetic parameters for the CCS region, in order to apply algorithms to estimate primary productivity from chl and light data. Although there is evident short-term variability in P-E relationships, it has still been proposed by Platt and Sathyendranath (1988) that larger-scale biogeographic provinces can be represented by mean parameters. This approach has been applied to provinces of the Atlantic (Sathyendranath et al. 1995) and to northern California waters by Moisan and Hofmann (1996), who proposed using a regional mean set of P-E parameters based on Hood et al. (1991), with diel variability specified as in MacCaull and Platt (1997).

Two relevant questions are: How large is the region within the CCS biogeographic domain for which our data apply? and, What seasonal and interannual time scales can be represented? Taking into consideration that photosynthetic parameters depend mainly on the phytoplankton light regime, we may explore the possibility that the average values of our photosynthetic parameters are representative of a much larger area than just the southern extreme of the SCB and are also representative of different seasons and years.

Malone (1971) reported phytoplankton assimilation ratios for coastal waters off Monterey and for an offshore area as far as  $130^\circ\text{W}$  (about 500 km offshore) and reported a mean assimilation ratio of  $7.4 \pm 1.0$  (95% confidence limits) for coastal phytoplankton and  $7.7 \pm 1.1$

for offshore phytoplankton with no significant difference. Malone (1971) estimated assimilation ratios with incubations under fluorescent light with  $0.06 \text{ langley s min}^{-1}$ , which corresponds to about  $210 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ . This value is lower than our mean  $E_k$  of 250. Thus his "assimilation ratios" may not have been at saturating irradiance like the  $P_{\text{max}}^B$  values we report.

Gaxiola-Castro and Alvarez-Borrego (1991) tested the hypothesis that greater primary productivity on the cold side of the Ensenada Front is due to higher assimilation numbers. They rejected the hypothesis, finding no significant difference between relative  $P_{\text{max}}^B$  values from both sides of the front. They attributed the higher primary productivity values on the cold side to the shallower subsurface chl maximum, which causes less limitation of light for the phytoplankton. Unfortunately, the absolute value of the  $^{14}\text{C}$  activity added by Gaxiola-Castro and Alvarez-Borrego (1991) to their incubation samples was uncertain (but constant), which is why they used relative assimilation numbers instead of absolute values.

Lara-Lara et al. (1980) and Millán-Núñez et al. (1982) reported phytoplankton assimilation ratios for surface waters off San Quintín, derived from summer in situ  $^{14}\text{C}$  incubations carried out in the morning, noon, and afternoon. Possibly at noon they had saturating irradiances, so their noon assimilation ratios should be close to  $P_{\text{max}}^B$  values. The mean  $\pm$  standard error of Lara-Lara et al.'s (1980) noon values are  $7.0 \pm 0.57 \text{ mg C mg chl}^{-1} \text{ h}^{-1}$ ; Millán-Núñez et al.'s (1982) noon values are  $6.2 \pm 0.66 \text{ mg C mg chl}^{-1} \text{ h}^{-1}$ .

We could compare Malone's (1971), Lara-Lara et al.'s (1980), and Millán-Núñez et al.'s (1982) assimilation ratios with our  $P_{\text{max}}^B$  values to test the hypothesis that lower surface chl values in the coastal waters of the SCB, with respect to those of coastal waters to the north and south, may be associated with lower photosynthetic parameters of phytoplankton. The alternative hypothesis is that photosynthetic parameters are not related to phytoplankton biomass, and their values in the SCB waters are not significantly lower than those of waters farther north and farther south, off San Quintín and off Monterey.

*Strictu sensu*, we cannot run a proper statistical test, because assimilation ratios for San Quintín and off Monterey may not correspond to optimum irradiances and thus may be lower than  $P_{\text{max}}^B$  values. Furthermore, when different laboratories generate P-E curves, the reported P-E parameters differ significantly, even when the same water sample is used (Richardson 1991). Nevertheless, we note that with lower nutrient concentrations and phytoplankton biomass values, our mean  $P_{\text{max}}^B$  values are not lower than assimilation ratios of Malone (1971), Lara-Lara et al. (1980), and Millán-

Núñez et al. (1982). At the 95% confidence level our  $P_{\text{max}}^B$  mean overlaps theirs.

In table 1, we have assembled P-E,  $a_{\text{ph}}^*$  (440), and  $\phi_{\text{max}}$  data that have been reported for the CCS from northern and southern California, including coastal waters and open-ocean waters up to 500 km offshore. Phytoplankton assemblages in coastal California waters seem to behave similarly to those of oceanic waters across the Ensenada Front with respect to photosynthetic parameters. In other words, lower nutrients and chl in the SCB are not associated with lower photosynthetic parameters. This agrees with the conclusion of Cullen et al. (1992) that phytoplankton are acclimated to their irradiance regimes and that nutrition has a small influence on assimilation ratios and P-E parameters. Nutrients appear to be a major factor regulating the standing stock of phytoplankton (Eppley et al. 1979). Thus seasonal and interannual variations in the relative distributions of colder high-nutrient water and warmer low-nutrient water may not strongly influence the P-E parameters.

For our data,  $P_{\text{max}}^B$  and  $\alpha^B$  for surface waters are not significantly different ( $P > 0.05$ ) from those of the 10%  $E_0$  depth (fig. 8b, table 1). This agrees with Prézelin et al. (1987), who found similar values for  $P_{\text{max}}^B$  for the water column between the surface and the 10%  $E_0$  depth, at the northern extreme of the SCB. Also, Gaxiola-Castro and Alvarez-Borrego (1991) reported similar relative  $P_{\text{max}}^B$  values for the water column between the surface and the 10%  $E_0$  depth on both sides of the Ensenada Front. Prézelin et al. (1987) and Gaxiola-Castro and Alvarez-Borrego (1991) reported much lower values for the 1%  $E_0$  depth—about 25% of the surface values. For the upper half of the euphotic zone (10%–100%  $E_0$ ), the mean  $P_{\text{max}}^B$  [ $8.6 \pm 0.60 \text{ mg C (mg chl)}^{-1} \text{ h}^{-1}$ ] and  $\alpha^B$  [ $0.047 \pm 0.004 \text{ mg C (mg chl)}^{-1} \text{ h}^{-1} (\mu\text{mol quanta m}^{-2} \text{ s}^{-1})^{-1}$ ] values in table 1 are proposed for all the region between San Quintín and Point Sur (near Monterey Bay). Also, the results of others (Malone 1971; Gaxiola-Castro 1991; Hood et al. 1991; Sosik 1996) make it possible for us to extend this region offshore to include the oceanic area of the CCS.

We propose a linear variation of  $\alpha^B$  and  $P_{\text{max}}^B$  for the lower half (10%–1%  $E_0$  depths), with values for the 1%  $E_0$  depth of  $\alpha^B = 0.012$  and  $P_{\text{max}}^B = 2.15$  where the 1% irradiance depth values are 25% of the values recommended for the upper euphotic zone (Gaxiola-Castro and Alvarez-Borrego 1991). We have few data in table 1 for the 1% light level or the deep chl maximum. Prézelin et al. (1987) and Schofield et al. (1991) tended to have estimates lower than other reports for the 10%–100% depths, so we believe their deeper data may be an underestimate. When estimating integrated primary productivity, errors for the lower half of the euphotic zone due to errors in P-E parameters will be



TABLE 1  
 Summary of Photosynthetic Parameters for the California Current System (Standard Error in Parentheses)

| Data source  | Month and year | Sample time    | $\alpha^B$       | $P_{\max}^B$    | $a_{ph(440)}^*$  | $\phi_{\max}$    |
|--|----------------|----------------|------------------|-----------------|------------------|------------------|
| Harding et al. (1982)  | May–Aug. 1980  | 0800–1200      | 0.052<br>(0.014) | 9.41<br>(2.56)  | —                | —                |
|  | May–Aug. 1980  | 1200–1600      | 0.055<br>(0.010) | 8.60<br>(1.81)  | —                | —                |
| Prézelin et al. 1987   | 100% $E_o$     | July 1985      | 0.053<br>(0.011) | 6.06<br>(1.14)  | —                | —                |
|  | 10% $E_o$      | July 1985      | 0.061<br>(0.010) | 6.75<br>(0.68)  | —                | —                |
|  | 1% $E_o$       | July 1985      | 0.035<br>(0.010) | 1.25<br>(0.21)  | —                | —                |
| Hood et al. 1991   | 0–50 m         | June 1987      | 0.092<br>(0.034) | 10.98<br>(4.69) | —                | —                |
| Schofield et al. 1991  | Surface        | July–Aug. 1988 | 0.011<br>(0.003) | 4.14<br>(0.73)  | —                | 0.030<br>(0.005) |
|  | chl max        | July–Aug. 1988 | 0.015<br>(0.008) | 1.00<br>(0.13)  | —                | 0.043<br>(0.005) |
| Sosik 1996   | 100% $E_o$     | Jan.–Apr. 1992 | —                | —               | 0.062<br>(0.002) | 0.025<br>(0.013) |
|  | 4.5% $E_o$     | Jan.–Apr. 1992 | —                | —               | 0.048<br>(0.017) | 0.047<br>(0.003) |
| This report  | 100% $E_o$     | July–Aug. 1994 | 0.050<br>(0.008) | 11.32<br>(1.36) | 0.055<br>(0.002) | 0.066<br>(0.009) |
|  | 10% $E_o$      | July–Aug. 1994 | 0.028<br>(0.003) | 7.95<br>(0.96)  | 0.050<br>(0.002) | 0.037<br>(0.005) |
| Average values for all reports<br>from 100% to 10% $E_o$ depth     |                |                | 0.047<br>(0.004) | 8.60<br>(0.60)  | 0.060<br>(0.031) | 0.040<br>(0.020) |
| Average values for all reports at<br>1% $E_o$ or chl maximum depth |                |                | 0.028<br>(0.007) | 1.17<br>(0.14)  | —                | 0.043<br>(0.005) |

The units for the parameters are:  
 $\alpha^B$  mg C (mg chl)<sup>-1</sup> (mE m<sup>-2</sup> s<sup>-1</sup>)<sup>-1</sup>  
 $P_{\max}^B$  mg C (mg chl)<sup>-1</sup>  
 $a_{ph(440)}^*$  m<sup>2</sup> (mg chl+phaeo)<sup>-1</sup>  
 $\phi_{\max}$  mol C (mol quanta)<sup>-1</sup>

relatively small, because irradiance levels are low (Millán-Núñez et al. 1997). Our proposed averages and the vertical structure of these parameters agree with data reported by others, as summarized in table 1.

For the purpose of estimating primary productivity with absorption-quantum yield algorithms (Kiefer and Mitchell 1983; Smith et al. 1989; Sosik 1996), we propose using the method of Alvarez-Borrego (1996) to estimate the depth dependence of quantum yield:  $\phi_{(z)} = \phi_{\max} [1 + (E_{o(z)}/E_k)^2]^{-1/2}$ , where  $\phi_{(z)}$  is the actual quantum yield at each depth, and  $\phi_{\max}$  is the maximum quantum yield for low-light-adapted phytoplankton. We recommend a  $\phi_{\max}$  of 0.1 mol carbon (mol quanta<sup>-1</sup>), which is slightly lower than the theoretical maximum of 0.125, to account for nitrate-based growth. Sosik (1996) has shown that phytoplankton from the 4.5% light level can have  $\phi_{\max}$  of 0.1, and our data from Bahía de Todos Santos also suggest that  $\phi_{\max}$  values can approach the theoretical maximum. Using our mean  $E_k$  of 250  $\mu$ mol

quanta m<sup>-2</sup> s<sup>-1</sup> results in a  $\phi$  of 0.085 and 0.016 at the 10% and 100% light depths, assuming surface irradiance is 1,500  $\mu$ mol quanta m<sup>-2</sup> s<sup>-1</sup>. For most of our sampling period, we had surface irradiance of approximately 500  $\mu$ mol quanta m<sup>-2</sup> s<sup>-1</sup> (fig. 2b), which results in a  $\phi$  value of 0.045.

For algorithms like Kiefer and Mitchell's (1983), we also require values for the  $a_{ph}^*$  for the 400–700 nm interval, weighted for the spectral distribution of irradiance. One way to estimate the absorption spectra of phytoplankton is to calculate the two absorption peaks and combine them with a normalized shape. Cleveland (1995) proposed empirical models to predict  $a_{ph(440)}^*$  and  $a_{ph(676)}^*$  for tropical and temperate waters. Bricaud et al. (1995) provide tables that allow estimates of  $a_{ph}(\lambda)$  every 2 nm from 400 to 700 nm.

In general, our  $a_{ph(440)}^*$  values are larger than those estimated by Cleveland (1995) or Bricaud et al. (1995; fig. 9). At 676, our data agree well with previous mod-

els and with CalCOFI data (Sosik and Mitchell 1995). Differences between our values and those derived from Cleveland's (1995) model could be due to a lower package effect in the blue peak for our samples. It is important that further work be done to reconcile the variations in  $a_{ph}$  versus chlorophyll models.

Our proposed values for the physiological parameters may be appropriate for the CCS at large time and space scales. Torres-Moye and Alvarez-Borrego (1987) reported surface chl and primary productivity for waters off San Quintín for 1984, an El Niño year, which were an order of magnitude lower than during non-El Niño years. These latter authors reported assimilation numbers in the range of 2.0–5.4 mg C (mg chl)<sup>-1</sup> h<sup>-1</sup>. However, Sosik (1996) reports  $\phi_{max}$  values for a moderate El Niño year that are greater than those of Schofield et al. (1991) for a non-El Niño year. El Niño can cause large perturbation in the CCS, with suppressed upwelling and more extensive intrusion of warm, nutrient-depleted subtropical waters near the coast and in the northern California domain (Lynn and Simpson 1987). These perturbations will cause changes in surface and vertical distributions of chlorophyll biomass. But the data of P-E,  $a_{ph}^*$ , and  $\phi$  parameters from various years, seasons, and distances offshore in the CCS, or previous reports of assimilation numbers off San Quintín, Baja California; Monterey Bay; and the Ensenada Front, do not support the implementation of unique El Niño and non-El Niño photosynthetic parameterizations. And there is no evidence for seasonal differentiation based on the data we summarize in table 1. But since table 1 covers spring and summer seasons primarily, the limited data of Sosik (1996) for winter CalCOFI is not sufficient for making final generalizations about seasonal variability. Still, the variance within data sets at small time and space scales is larger than the variance between means for different regions or seasons. Thus it seems reasonable to use simplified working means for photosynthetic parameters for large time and space scales within the CCS. This approach may provide reasonable large-scale estimates, but poor small-scale instantaneous estimates of primary production.

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