

Elements of support to estimate total and new primary production in the Gulf of California based on satellite data

Elementos de apoyo para estimar la producción primaria total y nueva del Golfo de California basada en datos de satélite

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ABSTRACT

High rates of primary production support the great animal biodiversity of the Gulf of California. One of the main limitations to estimate total (P_T) and new (P_{NEW}) primary production by ^{14}C and ^{15}N bottle incubations, respectively, is the small number of point samples generated for a particular area, and with very poor time coverage. Satellite ocean color sensors offer an alternative to estimate phytoplankton production rates in the oceans with an ample spatial-temporal variability that is not possible to cover with research vessels. With ocean color sensors in orbit, scientific expectations remain to improve ocean primary production models. Parameters used by these algorithms fall into three categories: environmental, ecological, and physiological. A review is given on studies that have generated information on these parameters for Gulf of California waters, and opportunities for new research are highlighted. Satellite surface pigment (Chl_s) and irradiance data (PAR_{sat}) need to be associated to vertical profiles (Chl_z and PAR_z) generated with a Gaussian distribution function and Lambert-Beer's law, respectively. A detailed description is given of the parameters that characterize this Gaussian function and a vertical attenuation coefficient of PAR variable with z , for different seasons and regions within the Gulf of California. The weakest part of modeling primary production are the photosynthesis-irradiance (P-E) curve parameters: the initial slope, assimilation number, and quantum efficiency, and these give us an opportunity for new research. Summer data to characterize all the set of parameters needed for modeling primary production based on satellite data are the scarcest.

Key words: Gulf of California, satellite ocean color sensors, modeled primary production, pigment and irradiance profiles parameters, photosynthesis-irradiance parameters.

RESUMEN

La gran biodiversidad animal del Golfo de California es producto de su elevada producción primaria. Una de las principales limitaciones para estimar la producción primaria total (P_T) y nueva (P_{NUEVA}) mediante incubaciones con ^{14}C y ^{15}N , respectivamente, es el pequeño número de muestras puntuales generadas para un área en particular, y con cobertura temporal muy pobre. Los datos de satélite ofrecen una alternativa para estimar la producción fitoplanctónica del océano con una variabilidad espacio-temporal grande que no es posible cubrir con barcos oceanográficos. Con sensores de color del océano en órbita, se tienen altas expectativas científicas de mejorar los modelos de producción primaria oceánica. Los parámetros usados por estos algoritmos son de tres tipos: ambientales, ecológicos y fisiológicos. Se

hizo una revisión de los estudios que han generado información sobre estos parámetros para las aguas del Golfo de California, y se indican las oportunidades de nuevos proyectos de investigación. Se requiere asociar los datos superficiales de satélite de pigmentos (Chl_s) e irradiancia (PAR_{sat}) con los perfiles verticales (Chl_z y PAR_z) generados con una distribución Gaussiana y la ley de Lambert-Beer, respectivamente. Se da una descripción detallada de los parámetros que caracterizan esta función Gaussiana y de un coeficiente de atenuación vertical de PAR variable con z , para diferentes estaciones y regiones del Golfo de California. La parte más débil del modelado de la producción primaria son los parámetros de la curva fotosíntesis-irradiancia (P-E): la pendiente inicial, el número de asimilación y la eficiencia cuántica, lo cual representa una oportunidad para nuevos proyectos de investigación. Los datos más escasos son los que caracterizan todo el conjunto de parámetros para modelar la producción primaria basada en las imágenes de satélite de verano.

Palabras clave: Golfo de California, imágenes satelitales de color, producción primaria modelada, parámetros de los perfiles de pigmentos e irradiancia, parámetros de la curva fotosíntesis-irradiancia.

INTRODUCTION

Few places in the world can claim such a diversity of species as the Gulf of California, with its 6,000 recorded animal species estimated to be half the number actually living in its waters. Over half-million tons of seafood is taken from it annually. The accumulation of species diversity, since the Gulf's opening ~5.6 million years ago, has produced one of the biologically richest marine regions on earth (Brusca, 2010). This great biodiversity is supported by high rates of primary production. The Gulf of California has three main natural fertilization mechanisms: net water exchange with the Pacific, upwelling, and mixing by winds and by phenomena associated with tides (Álvarez-Borrego, 2010). Upwelling occurs off the eastern coast with northwesterly winds ("winter" conditions from December through May), and off the Baja California coast with southeasterly winds ("summer" conditions from July through October), with June and November as transition periods (Álvarez-Borrego & Lara-Lara, 1991). With northwesterly winds upwelling is strong, it has a marked effect on phytoplankton communities (surface chlorophyll a concentration, Chl_s , values up to $>10 \text{ mg m}^{-3}$), and due to eddy circulation it increases the phytoplankton biomass across the Gulf (Santamaría-Del-Angel *et al.*, 1994). However, because of strong stratification during summer, upwelling with southeasterly winds has a very weak effect on phytoplankton biomass (Santamaría-Del-Angel *et al.*, 1999).

New primary production (P_{NEW}) is the fraction of primary production (P_T) supported by the input of nitrate from outside the euphotic zone (Dugdale & Goering, 1967), mainly from below the thermocline by vertical eddy diffusion (Eppley, 1992). It is an estimate of oceanic particle flux in the global carbon cycle (Eppley & Peterson, 1979). Phytoplankton cells use nutrients recycled within the euphotic zone for regenerated production (P_r). Total production is equal to the sum of both new and regenerated production ($P_T = P_{\text{NEW}} + P_r$). Eppley & Peterson (1979) defined the ratio of P_{NEW} to P_T as the f -ratio ($f = P_{\text{NEW}}/P_T$) and showed that f is an asymptotic function of the magnitude of P_T . The description of the temporal and spatial variability of P_{NEW} may give us an idea of the variability of the flux of organic matter out of the surface layer. However,

one of the main limitations to estimate P_T and P_{NEW} by ^{14}C and ^{15}N bottle incubations, respectively, is the small number of point samples generated for a particular area, and with very poor time coverage. Thus, satellite ocean color sensors offer an alternative to estimate the phytoplankton primary production rates in the oceans with an ample spatial-temporal variability that is not possible to cover with research vessels.

The processes of fixation of inorganic carbon in organic matter during photosynthesis, its trophodynamic transformation, physical mixing, transport and gravitational settling are referred to collectively as the "biological pump" (Ducklow *et al.*, 2001). The ratio of sinking flux to primary production (e -ratio) and the f -ratio depend on the pathways by which nitrogen flows among different organisms (phytoplankton, large and small grazers and bacteria), but the only way to change the absolute amount of export is to change P_{NEW} , which is usually controlled by physical factors (Frost, 1984).

Satellite-derived estimates of basin-scale and global-scale primary production have been performed (i.e., Sathyendranath *et al.*, 1991; Longhurst *et al.*, 1995). The approach used is based on partition of the ocean into a suite of domains and provinces within which physical forcing, and the algal response to it, are distinct (Platt *et al.*, 1991). Empirical and semianalytical algorithms to estimate primary production from photosynthetic pigment concentration have been developed (i.e., Behrenfeld & Falkowski, 1997). Usually the objective is not to obtain instantaneous local rates of production, but rather to calculate primary production for relatively large geographic areas and for periods of months. With ocean color sensors in orbit, high expectations remain to improve ocean primary production models (Behrenfeld *et al.*, 1998; Hidalgo-González & Álvarez-Borrego, 2004). Parameters used by these algorithms fall into three categories: environmental (e.g., location, atmospheric conditions, the irradiance vertical profile); ecological (e.g., the chlorophyll a concentration (Chl_z) vertical profile); and physiological (e.g., the photosynthesis-irradiancia (P-E) curve parameters, the chlorophyll-specific absorption coefficient of phytoplankton ($a_{\text{ph}(\lambda)}^*$), photosynthetic quantum yields (Φ_{PSII}) (Morel, 1991).

A primary goal of a production algorithm is to observe variability in oceanic values occurring on time scales up to interannual-to-decadal and regional-to-global space scales. It is impossible to observe variability at these scales by any means other than by satellite (Behrenfeld *et al.*, 1998). We are interested in improving the precision of primary production estimates at the global scale, and also in generating primary production time series for particular regions of the ocean that could be applied to, for example, oceanographic fisheries studies. Studies to generate information on the parameters involved in the calculations of primary production in Gulf of California waters have been performed (Álvarez-Borrego & Gaxiola-Castro, 1988; Valdez-Holguín *et al.*, 1999; Gaxiola-Castro *et al.*, 1999; Giles-Guzmán & Álvarez-Borrego, 2000; Cervantes-Duarte *et al.*, 2000; Hidalgo-González & Álvarez-Borrego, 2001), but more data are needed to improve the characterization of parameters involved in estimating primary production for the Gulf based on ocean color. Opportunities for new research will be highlighted.

GENERAL CONSIDERATIONS

Early models to estimate primary production in the ocean were based on laboratory experiments to characterize the photosynthesis-light relationship (Ryther, 1956; Ryther & Yentsch, 1957). They offered the basis for models that make use of variables measured from remote sensors (e.g., pigments, irradiance, etc.) (Platt & Sathyendranath, 1988; Longhurst *et al.*, 1995; Behrenfeld & Falkowski, 1997; Hidalgo-González *et al.*, 2005). P_T is given pixel-by-pixel as a standard product in the NASA web page (<http://oceancolor.gsfc.nasa.gov/>) calculated from satellite chlorophyll *a* concentration (Chl_{sat}), sea surface temperature (SST), and scalar photosynthetically active radiation, 400-700 nm, ($PAR_{o(sat)}$) using Behrenfeld and Falkowsky's (1997) vertically generalized production model (VGPM) (Behrenfeld *et al.*, 1998). The VGPM is a non-spectral, homogeneous-biomass vertical distribution, vertically integrated, production model. This means that chlorophyll and the quality of light are not allowed to change with depth, and this causes inaccuracy. Furthermore, there are no data for the Gulf of California on the parameters used by this model: P_{opt}^b (the photosynthetic ratio or photosynthesis per unit Chl at the optimum light level in the water column) ($mgC\ mgChl^{-1}\ h^{-1}$), and $f(PAR_o)$ (a function that represents the effect of light in the whole euphotic zone and throughout the whole day). As a first approximation, representative values for these parameters are used for large oceanic provinces and for the whole year. A better approximation to reality is to generate the P_{Tz} ($mg\ C\ m^{-3}\ h^{-1}$) vertical profile (with a P_{Tz} value for each meter) with the model proposed by Platt *et al.* (1991), or its modification proposed by Hidalgo-González & Álvarez-Borrego (2004). Platt *et al.*'s (1991) model is a non-homogeneous, non-spectral model, and this means that Chl is allowed to change with depth (Chl_z) by means of a Gaussian curve that reproduces the deep chlorophyll maximum, but the change of the

spectral distribution of PAR_z with depth is not taken into consideration. Hidalgo-González & Álvarez-Borrego's (2004) modification is a non-homogeneous, spectral model that allows for the change of the spectral distribution of irradiance with depth, based on the method proposed by Giles-Guzmán & Álvarez-Borrego (2000).

In the context of remote sensing, a classification which has been found useful divides oceanic waters into "Case I" and "Case II" waters (Morel & Prieur, 1977; Gordon & Morel, 1983). Case I waters are those for which phytoplankton and their derivative products (organic detritus and colored dissolved organic matter (CDOM), arising by zooplankton grazing, or natural decay of algal cells) co-vary and play a dominant role in determining the optical properties of seawater. Case I waters have $Chl_z < 1.5\ mg\ m^{-3}$. Case II waters are those for which the above mentioned optical components of seawater do not co-vary, and also an important or dominant contribution to the optical properties of seawater may come from inorganic suspended matter or material carried by river runoff. Case II waters have $Chl_z > 1.5\ mg\ m^{-3}$.

Platt *et al.*'s (1991) model has been used for Gulf of California case II waters:

$$P_{Tz} = [P_m^* Chl_{sat(z)} \alpha_{PAR}^* PAR_z] \times [(P_m^*)^2 + (PAR_z \alpha_{PAR}^*)^2]^{-0.5} mg\ C\ m^{-3}\ h^{-1},$$

where: the asterisk means that the value is normalized per unit of chlorophyll *a* concentration; P_m^* ($mg\ C\ (mg\ Chl)^{-1}\ h^{-1}$) is the photosynthetic rate at saturating irradiance or assimilation number; $Chl_{sat(z)}$ is the average Chl for depth *z* for a whole season and region within the Gulf, derived from the satellite data (Chl_{sat}) and a model for the Chl vertical distribution; α_{PAR}^* ($mg\ C\ (mg\ Chl)^{-1}\ h^{-1}$) ($\mu mol\ quanta\ m^{-2}\ s^{-1}$) is the initial slope of the photosynthesis-irradiance (P-E) curve; and PAR_z ($\mu mol\ quanta\ m^{-2}\ s^{-1}$) is PAR for depth *z*, derived from the satellite data ($PAR_{o(sat)}$) and Lambert-Beer's law with a constant vertical attenuation coefficient of diffuse light (K_{PAR}).

Hidalgo-González & Álvarez-Borrego (2004) used a modification of Platt *et al.*'s (1991) model for Gulf of California case I waters:

$$P_{Tz} = [P_m^* \phi_{max} Chl_{sat(z)} a_{ph(z,chl)}^* PAR_z] \times [(0.02315 P_m^*)^2 + (PAR_z \phi_{max} a_{ph(z,chl)}^*)^2]^{-0.5} mg\ C\ m^{-3}\ h^{-1}.$$

In this equation ϕ_{max} is the maximum quantum yield ($mol\ C\ (mol\ quanta)^{-1}$), and $a_{ph(z,chl)}^*$ ($m^2\ (mg\ Chl)^{-1}$) is the phytoplankton specific absorption coefficient of light averaged for the spectral distribution of PAR at depth *z*. This corrects the initial slope α_{PAR}^* for the spectral distribution of the *in situ* scalar PAR. In place of α_{PAR}^* the product $43.2 \phi_{max} a_{ph(z,chl)}^*$ was used (Giles-Guzmán & Álvarez-Borrego, 2000). The factor 43.2 converts mol C to mg C, seconds to hours, and mol quanta to μmol quanta. These expressions show that to estimate P_{Tz} , not only the surface Chl value is needed, but also the vertical profiles of Chl and PAR. In this

case PAR_z is derived from the satellite data ($PAR_{o(sat)}$) and Lambert-Beer's law with a variable vertical attenuation coefficient of diffuse light ($K_{PAR(chl, z)}$) as a function of Chl_z and depth.

Algorithms to transform the optical satellite data into products like Chl_{sat} need "ground truth" data from oceanographic cruises. There is the perception that instantaneous point P_T estimates based on satellite data are very imprecise and inaccurate because the development of satellite algorithms are based on calibration cruises that cover limited portions of the ocean. But when the average of satellite data are used for whole oceanic regions, and for relatively large time scales, such as months or seasons, the estimated P_T values can very well represent the biological dynamics of those regions (Hidalgo-González & Álvarez-Borrego, 2004). The large number (n) of pixels within our region of interest, and for whole months, allows for very precise pigment (Chl_{sat}) and PAR_{sat} averages with relatively small standard errors ($s/n^{0.5}$) (Hidalgo-González & Álvarez-Borrego, 2004). Morel & Berthon (1989) indicated that it is unreasonable and probably superfluous to envisage the use of a light-production model on a pixel-by-pixel basis when interpreting satellite imagery. Furthermore, some of the satellite calibration cruises have been carried out in the Gulf of California where personnel from CICESE and the Autonomous University of Baja California have participated on board UNAM's R/V El Puma (1993) and SIO-UC's R/V Melville (1999). The Gulf of California provides with cloudless skies needed for calibration cruises, and this results in relatively accurate satellite products for the gulf.

The vertical distribution of chlorophyll. Satellite data collection is limited to electromagnetic radiation. Thus the oceanographic information is restricted to the immediate surface layer of the ocean. Remotely sensed ocean color is limited to a depth at which 90% of the backscattered solar irradiance from the water column originates. Remote sensors provide information on the *sui generis* average photosynthetic pigment concentration for the upper 22% of the euphotic zone (Kirk, 1993). Primary production models apply to the entire euphotic zone, and ideally, they should use the vertical profile of pigment biomass as input. Therefore a gap exists between the limited satellite information and what is needed when modeling.

The assumption of a mixed layer with a homogeneous pigment distribution could lead to inaccurate estimates of integrated primary production (Platt *et al.*, 1991). The deep chlorophyll maximum (DCM) is a consistent feature in the ocean. Generally, accounting for its presence increases estimates of integrated primary production, and since the DCM often appears below the mixed layer it would be likely that most of its primary production is new production (Sathyendranath *et al.*, 1995). In the Gulf of California the DCM coincides with the upper part of the nitracline, where nitrate concentration is $>1.0 \mu M$ (Cortés-Lara *et al.*, 1999). Lewis *et al.* (1983) proposed a Gaussian distribution function to represent the vertical profile of chlorophyll concentration (Chl_z)

(Fig. 1). A difficulty in estimating oceanic primary production from surface measurements arises from the regional differences in the vertical distribution of Chl_z . Therefore it is necessary to use Chl_z historical data to characterize the parameters of this Gaussian function for each oceanic province or region.

Following Lewis *et al.* (1983), Hidalgo-González & Álvarez-Borrego (2001) used chlorophyll concentration (Chl_z) historical data to fit a Gaussian distribution function to represent the pigment vertical profile for different seasons and regions within the Gulf of California. As a first approximation, we can represent Chl_{sat} by the Chl_z average for the first optical depth, weighted by the irradiance attenuated twice (when the light is going down and when it is backscattered up) (Kirk, 1993). For the available Gulf of California in situ Chl_z data, the Chl_z weighted average for the first optical depth is about 10% higher than the surface Chl (Chl_s), thus $Chl_s = 0.9Chl_{sat}$ (Hidalgo-González & Álvarez-Borrego, 2001). Gulf of California Chl_z profiles were fitted to Lewis *et al.* (1983) equation: $Chl_z = Chl_0 + [h/(\sigma(2\pi)^{0.5})]\exp[-1/2(Z - Z_m)^2/\sigma^2]$, where Chl_0 is the background chlorophyll concentration ($mg\ m^{-3}$), h is the total chlorophyll ($mg\ m^{-2}$) above the baseline Chl_0 , σ controls the thickness of the DCM layer (m), and Z_m is the depth of the maximum (Fig. 1). Hidalgo-González & Álvarez-Borrego (2001) used 268 chlorophyll concentration profiles to estimate these parameters. These latter authors used cluster analysis of surface temperature to define the cool season for the Gulf of California as the period between end of November-end of June, and the rest of the year is considered the warm season. However, to be consistent with

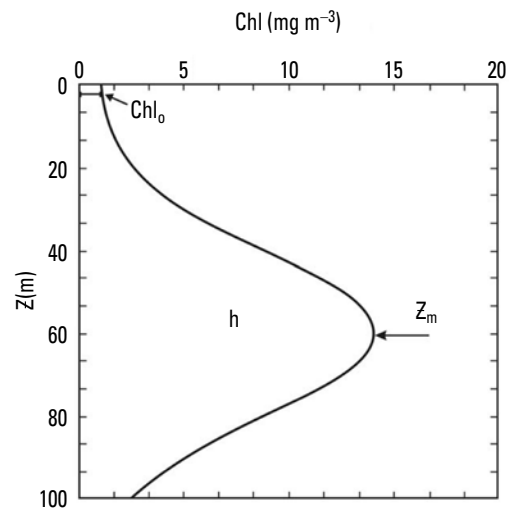


Figure 1. Example of a Gaussian curve with the parameters that characterize the vertical distribution of chlorophyll concentration. The parameter σ (m) characterizes the curve width in a similar manner as the standard deviation characterizes the width of the normal distribution. The parameter h ($mg\ Chl\ m^{-2}$) is the integral under the whole curve (even in the air) and above Chl_0 . Adapted from Hidalgo-González & Álvarez-Borrego (2001).

the previously defined “winter” and “summer” conditions, with November and June as transition periods, and recognizing inter-annual variability, Hidalgo-González & Álvarez-Borrego (2001) followed Valdez-Holguín *et al.*'s (1999) criteria and considered mean surface temperatures of $<24^{\circ}\text{C}$ as indicative of cool sea-

son. Surface temperatures $<24^{\circ}\text{C}$ indicate either strong mixing or the start of upwelling events off the east coast. Cluster analysis of surface temperature and chlorophyll data grouped the stations into four regions for the cool season and into two regions for the warm season (Fig. 2). The warm season data are less abundant

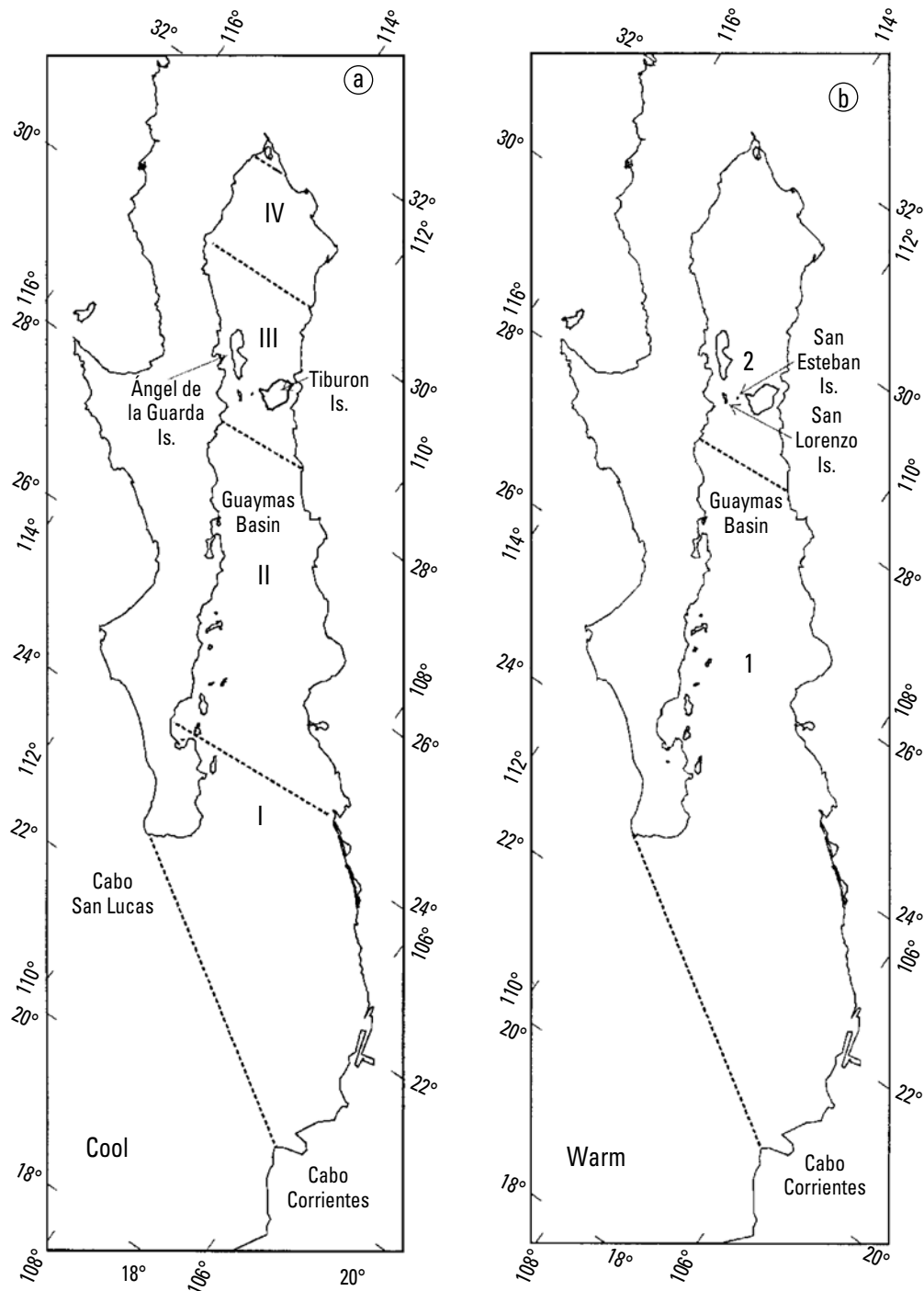


Figure 2. Regions of the Gulf of California: (a) for the cool season; and (b) for the warm season. Adapted from Hidalgo-González & Álvarez-Borrego (2004).

(only 48 profiles) and show less horizontal structure in the Gulf. The four regions for the cool season coincide very closely with those proposed by Gilbert & Allen (1943) based on the abundance of phytoplankton during winter-spring.

During both seasons, h significantly increased from south to north (Table 1). Lowest h mean value was 30 mg m^{-2} , for region I, and highest value was 236 mg m^{-2} , for region IV (Table 1). Values for the parameter h are higher than integrated chlorophyll for the euphotic zone because h values include the whole area under the Gaussian curve. Regions II and IV had very different h values with very similar σ and Chl_0 values because of different average Chl values at the DCM (Chl_m). In the cool season, Chl_0 increased slightly from region I to region II (0.07 to 0.11 mg m^{-3}), then it had a relatively high value in region III (0.39 mg m^{-3}) and decreased in region IV to a value similar to that of region II (0.14 mg m^{-3}). In the warm season, Chl_0 increased northward (Table 1). The mean of σ did not have a monotonic pattern of geographic change in the cool season. Its range was 14.6 - 34.4 m . During the warm season, σ had values similar to the one for region I, with no significant difference between regions 1 and 2 (Table 1). Relatively few of the profiles ($\sim 15\%$) had surface maxima ($Z_m = 0 \text{ m}$), and none of these were in regions I and 1. The mean depth of the DCM, Z_m , showed a clear tendency to decrease from south to north in the cool season (from 36.6 to 11.3 m), but this tendency was not as strong in the warm season (28.3 to 19.8 m) (Table 1). Due to the scarcity of data from the Gulf of California, Hidalgo-González & Álvarez-Borrego (2001) were not able to build regression models to predict the parameters h , Chl_0 , σ , and Z_m as functions of remotely sensed variables such as Chl_{sat} and SST. Thus, they proposed to use means of Chl_0 , h , and σ , for each region and season (Table 1), to calculate the representative Chl_z profile. There are two alternatives to estimate Z_m . One is to use the mean of Z_m for each region and season, but this leaves no degrees of freedom for the use of satellite imagery. Thus, a better alternative to estimate Z_m is to use the Gaussian equation and the mean value of Chl_{sat} for the chosen region and season of the particular year. Thus:

$$\text{Chl}_s = 0.9\text{Chl}_{\text{sat}} = \text{Chl}_0 + [h/(\sigma(2\pi)^{0.5})\exp\{-Z_m^2/2\sigma^2\}], \\ Z_m = \sigma\{2\ln[h/(\sigma(2\pi)^{0.5}(0.9\text{Chl}_{\text{sat}} - \text{Chl}_0))]\}^{0.5}.$$

The Z_m values derived from this latter equation are practically the same as those derived directly from the chlorophyll profiles (Hidalgo-González & Álvarez-Borrego, 2001). It is important to notice that a single Chl_s value produces different Chl_z profiles for the different regions and seasons. However, there is an opportunity for new research because more Chl_z profiles are needed to better characterize the Gaussian parameters for the "summer" season. With only 48 "summer" profiles the spatial coverage is very poor.

The vertical attenuation coefficient of PAR (K_{PAR}). Bio-optical models to estimate primary production in the ocean, based on analysis of P-E curves, are mathematically tedious but give predictive

Table 1. Means (\pm one standard error = $s/n^{0.5}$) of the Gaussian parameters, for seasons (winter is the roman numbers, and summer is the Arabic numbers) and regions within the Gulf according to Figure 2 (taken from Hidalgo-González & Álvarez-Borrego, 2001).

Region	h (mg m^{-2})	Chl_0 (mg m^{-3})	σ (m)	Z_m (m)
I	30.2 ± 0.3	0.07 ± 0.002	25.2 ± 0.7	36.6 ± 4.4
II	85.4 ± 0.1	0.1 ± 0.01	14.6 ± 0.2	18.7 ± 1.6
III	227.4 ± 3.9	0.4 ± 0.01	34.4 ± 0.3	14.1 ± 1.6
IV	236.0 ± 1.0	0.1 ± 0.03	17.5 ± 0.2	11.3 ± 1.0
1	79.4 ± 5.5	0.1 ± 0.02	27.4 ± 1.2	28.3 ± 2.5
2	167.1 ± 12.4	0.3 ± 0.03	24.2 ± 1.9	19.8 ± 3.2

capability by permitting continuous calculation of primary production based on the rate of light absorbed (Falkowski & Raven, 1997). Part of the tediousness arises from the decomposition of parameters and variables into spectral components, and from their variation with the composition of seawater (e.g., $\text{PAR}_{(\lambda, z)}$, $a_{\text{ph}(\lambda, z)}$, $K_{\text{PAR}(\lambda, z)}$). It would be much better if biological oceanographers could do the computations using single values for *in situ* scalar PAR (PAR_z), and for an average of $a_{\text{ph}(\lambda, z)}$ ($a_{\text{ph}(\text{PAR}_z)}$). This average should be weighted by the shape of the *in situ* spectrum of PAR.

The universal bio-optical algorithm of the Coastal Zone Color Scanner (CZCS) for case I waters (Gordon *et al.*, 1983) implicitly contains an average covariance of the absorption by phytoplankton and CDOM and detritus in surface and near surface waters. That covariance was made explicit by combining the CZCS algorithm with an expression for reflectance. Case I waters are more than 95% of the ocean. The spectral variation of absorption by CDOM plus detritus for case I waters may be estimated by the expression: $a_{\text{gd}} = 2a_{\text{ph}(440)}^* \text{Chl}\{\exp[-0.013(\lambda-440)]\}$ (Giles-Guzmán & Álvarez-Borrego, 1996). Based on this expression, and data and empirical models found in the literature for the absorption of phytoplankton and pure seawater (Cleveland, 1995; Pope, 1993), Giles-Guzmán & Álvarez-Borrego (2000) deduced an expression to estimate the average coefficient of total absorption for case I waters, for the whole visible range, weighted by the spectral distribution of PAR at depth, as a function of Chl and L (length of the mean trajectory of light):

$$a_{\text{TPAR}(\text{Chl}, L)} = 0.0221 + 0.0466\text{Chl} + (0.1378 - 0.0141\text{Chl})[\exp(-mL)], \\ \text{where } L = Z/0.72, \text{ and}$$

$$m = 0.28 - 18.319(10^{-2})\text{Chl} - 70.9(10^{-4})L + 41.8(10^{-6})\text{Chl}L \\ + 16.604(10^{-2})\text{Chl}^2 + 99.2(10^{-6})L^2 + 19(10^{-5})\text{Chl}^2L - 29(10^{-7})\text{Chl}L^2 \\ - 46.4(10^{-3})\text{Chl}^3 - 4(10^{-7})L^3.$$

Giles-Guzmán & Álvarez-Borrego (2000) also used an empirical expression for the scattering coefficient (Gordon & Morel, 1983) and data on the volume scattering function (Petzold, 1972) to deduce an expression for the average backscattering coeffi-

cient and for the visible range, weighted by the *in situ* spectral distribution of PAR, as a function of Chl: $b_{\text{PAR(Chl)}} = 0.019[0.0015 + 0.3(\text{Chl})^{0.62}]$. Preisendorfer's (1961) expression can be used with $a_{\text{TPAR(Chl, L)}}$ and $b_{\text{PAR(Chl)}}$ to estimate $K_{\text{PAR(Chl, L)}}$, the vertical attenuation coefficient of PAR for case I waters ($K_{\text{PAR(Chl, L)}} = (a_{\text{TPAR(Chl, L)}} + b_{\text{PAR(Chl)}})/\mu_d$). Giles-Guzmán (1998) showed that a satisfactory choice for μ_d , the average cosine for downwelling light, is to follow Zaneveld *et al.*'s (1997) suggestion and set μ_d invariable with depth and equal to the value for the asymptotic region, $\mu_{d(\alpha)} = 0.72$. If we know the Chl vertical profile and the irradiance incident at the surface (PAR_{sat}), the vertical profile of scalar irradiance (PAR_z) may be calculated. Following Morel & Maritorena (2001), PAR_{sat} is multiplied by 0.965 to estimate PAR immediately under the sea surface ($\text{PAR}_{z=0}$), and then Lambert-Beer's law is applied with a variable $K_{\text{PAR(Chl, L)}}$ to generate the PAR_z profile.

Average surface chlorophyll (Chl_s) for whole seasons and regions within the Gulf is usually $<1.5 \text{ mg m}^{-3}$, but due to the DCM in some cases Chl_s is $>1.5 \text{ mg m}^{-3}$. In those cases, the PAR_z profile for the near surface waters (with $\text{Chl}_z <1.5 \text{ mg m}^{-3}$) is calculated following Giles-Guzmán & Álvarez-Borrego (2000), and the PAR_z profile for deeper waters (with $\text{Chl} >1.5 \text{ mg m}^{-3}$) is calculated with Lambert-Beer's law and an average vertical attenuation coefficient, K_{PAR} , deduced from the satellite K_{490} average value (K_{490} is another product deduced from the satellite sensor's data and provided by NASA). The regression models proposed by Cervantes-Duarte *et al.* (2000) ($Z_{\text{PAR1\%}} = A + B/K_{490}$) are used to estimate the euphotic zone depth (Z_{eu}) as a function of K_{490} in each case, and K_{PAR} is estimated ($K_{\text{PAR}} = 4.6/Z_{\text{PAR1\%}}$). The regression parameters A and B have different values for different regions within the Gulf (A = -5.12, B = 5.31 for the northern basin; A = 5.6, B = 4.24 for the midriff islands region; and A = 16.21, B = 3.13 for the southern basins). Data used by Cervantes-Duarte *et al.* (2000) were collected during cruises carried on during autumn and winter only, and hydrostations were occupied mostly at and near the Guaymas basin, with few locations in the northern and southernmost basins, and this gives an opportunity for future research to better characterize this kind of regression parameters (A and B) for all seasons and regions of the Gulf.

THE PHYTOPLANKTON PHYSIOLOGICAL PARAMETERS

At least one liter of water sample is filtered through GF/F glass-fiber filters for $a_{\text{p}(\lambda)}$ measurements. Particle absorption is measured with a spectrophotometer equipped with an integrating sphere to include all scattered light. A second reading is obtained after extraction of pigments with hot methanol following Kishino *et al.* (1985), to determine detrital absorption ($a_{\text{d}(\lambda)}$) and the difference is phytoplankton pigment absorption: $a_{\text{ph}(\lambda)} = a_{\text{p}(\lambda)} - a_{\text{d}(\lambda)}$. Raw absorbances (optical densities, OD) are corrected for the path-length amplification effect (β factor, due to light scattered inside the filter) by using algorithms empirically derived from laboratory cultures (Valdez-Holguín *et al.* 1999).

A photosynthesis-irradiance (P-E) curve is constructed by plotting P_T normalized per unit Chl ($P^* \text{ mg C mg Chl}^{-1} \text{ h}^{-1}$) versus PAR (Fig. 3). To generate the P-E curves phytoplankton samples are taken from a number of predetermined depths, each water sample is passed through a 333- μm mesh to remove large herbivores, and then incubation experiments are run with n aliquots from each sample. Before incubating, ^{14}C is added to each aliquot to a final concentration (usually $0.5 \mu\text{Ci mL}^{-1}$, but it depends on Chl), and then incubated for one or two hours under a light gradient. The latter has been done either with the natural sun light (using neutral screens to simulate the *in situ* light levels) or in incubators with lamps. Generally, temperature is maintained within 3°C of *in situ* temperature. Additional aliquots are used for dark incubation and for a time-zero control; the latter are immediately acidified after filtration. After incubation, the samples are acidified and then filtered. Radioactivity is determined with a scintillation counter and carbon assimilation estimated usually following Strickland & Parsons (1972). Productivities per unit Chl are calculated (P^*) and plotted versus the incubator's irradiances. The initial slope of the P-E curve, α^* , is determined with a linear regression of the low irradiance points (this is α^* for the incubator's light, α_{inc}^*). To estimate the maximum P^* or assimilation number, P_m^* , the data are fitted to Smith's (1936) equation: $P^* = (P_m^* \alpha_{\text{inc}}^* \text{ PAR}_{\text{inc}}) (P_m^* + (\alpha_{\text{inc}}^* \text{ PAR}_{\text{inc}})^2)^{-0.5}$. Maximum photosynthetic quantum yield (ϕ_{max}) is calculated by dividing α_{inc}^* by the mean of $a_{\text{ph}(\lambda)}$ for the photosynthetically active radiation ($a_{\text{ph}(\text{PARinc})}$), weighted by the incubator's light spectral distribution ($\phi_{\text{max}} = 0.02315 \alpha_{\text{inc}}^* / a_{\text{ph}(\text{PARinc})}$) (Sosik, 1996), and the factor 0.02315 converts mg C to mol C, hours to seconds, and μmol quanta to mol quanta.

To have a good understanding of how oceanic photosynthesis evolves with time, long-term time series of climate and biolo-

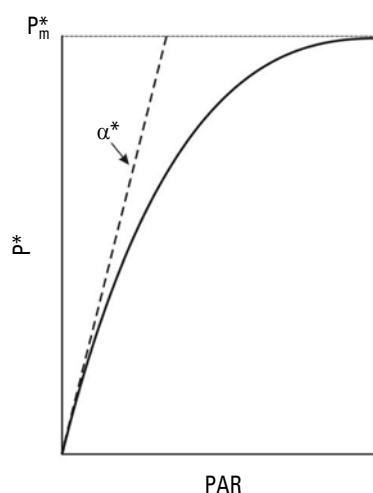


Figure 3. The photosynthesis-irradiance curve showing the parameters P_m^* (the assimilation number or photosynthesis at saturating light level per unit Chl, $\text{mg C (mg Chl)}^{-1} \text{ h}^{-1}$) and α^* (the initial slope per unit Chl, $\text{mg C (mg Chl)}^{-1} \text{ h}^{-1}$ ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) $^{-1}$) (adapted from Valdez-Holguín *et al.*, 1998).

gically relevant variables are needed. However, such records are extremely rare because of the costs and logistics involved. P-E parameters for short time series have been generated for coastal waters such as those of Bedford Bay, Canada (Cote & Platt, 1983) and off the northwestern coast of Baja California (Valdez-Holguín *et al.*, 1998). According to Cote & Platt (1983), the response of phytoplankton cells to changing environmental conditions is fairly rapid, being close to the order of a generation time. These time series show great variability and co-variation of α^* and P_m^* , and they clearly indicate that there is no capacity to predict the P-E parameters from day to day. This places considerable doubt on our ability to predict instantaneous primary production rates using satellite estimates of Chl and PAR. Nevertheless, it is possible to estimate mean values of the P-E parameters to calculate primary production for large time and space scales to which the data apply (Sathyendranath *et al.*, 1995). Thus, it is possible to find acceptable averages of the photosynthetic parameters for seasons and regions within the Gulf of California.

Gaxiola-Castro *et al.* (1999) showed that there are no significant differences of P-E parameters for waters within and outside cool filaments and jets in the central Gulf of California. These authors tested the hypothesis that assimilation number values increase from cooler to warmer waters, but their data did not support it. They concluded that the phytoplankton irradiance regime may be the most important factor controlling these parameters. But $T\text{ }^\circ\text{C}$ may not be discarded as a controlling factor because they had few degrees of freedom, and with data from a single cruise (November 1985) their $T\text{ }^\circ\text{C}$ range was relatively small. The irradiance regime depends on the degree of turbulence or stratification which affects the vertical excursion of the phytoplankton cells. Álvarez-Borrego & Gaxiola-Castro (1988) reported a relation between an index of stratification of the water column and the P-E curve parameters of the Gulf's phytoplankton. With very high stratification or mixing, these parameters are low, and with intermediate stratification, they are high. But this kind of relationship has not been found in later studies. Since there is substantial variability within data sets, they concluded that it is not possible at this time to predict fine time-and-space scale variations in photosynthetic parameters. For primary production models, they recommended working averages for the Gulf of California.

In most studies of the P-E relationship in the Gulf of California, few P-E data were generated due to time constraints. With few degrees of freedom often it has not been possible to reject the null hypothesis when comparing different regions of the Gulf or different hydrographic conditions. However, Valdez-Holguín *et al.* (1999) proposed a significant seasonal variation for the Gulf of California, with lower P_m^* and α^* values during "summer" than during "winter". This may be due to very high summer surface temperatures in the Gulf, sometimes $>30\text{ }^\circ\text{C}$, and a very strong thermocline. There are large differences between different sets of "summer" P-E parameters (Álvarez-Borrego & Gaxiola-Castro,

1988; Gaxiola-Castro *et al.*, 1999; Valdez-Holguín *et al.*, 1999), and it is necessary to generate more P-E Gulf of California "summer" data to solve these large discrepancies. Also, all authors have reported P_m^* and α^* decreasing significantly with depth, because of phytoplankton conditioning to a lower irradiance regime at deeper waters (Álvarez-Borrego & Gaxiola-Castro, 1988; Valdez-Holguín *et al.*, 1999; Gaxiola-Castro *et al.*, 1999). It has long been known that when phytoplankton is photo-acclimated to a low irradiance regime, the photosynthetic parameters tend to be low (Falkowski & Owens, 1980). In general, where the 1%PAR depth is within the mixed layer, its P_{max}^* and α^* values are higher than when it is within the thermocline, due to a greater residence time at depth in the latter case (Álvarez-Borrego & Gaxiola-Castro, 1988).

Based on their own data and those of other authors cited by them, Valdez-Holguín *et al.* (1999) proposed the following working averages for the photosynthetic parameters for the whole Gulf of California and for the cool season (\pm one standard error): a surface $P_m^* = 9.67 \pm 2.4\text{ mg C mg Chl}^{-1}\text{ h}^{-1}$ (with a large 95% confidence interval), with a linear variation between this and 3.7 ± 0.3 at the middle of the euphotic zone, and then a constant value for deeper waters; a single value of $\alpha_{inc}^* = 0.029 \pm 0.004\text{ mg C mg Chl}^{-1}\text{ h}^{-1}$ ($\mu\text{mol quanta m}^{-2}\text{ s}^{-1}$)⁻¹ (incubator's initial slope); and $\phi_{max} = 0.06 \pm 0.01\text{ mol C (mol quanta)}^{-1}$. And for the warm season: a surface $P_m^* = 3.7 \pm 0.3$, with a linear variation between this and 1.5 ± 0.2 at the middle of the euphotic zone, and another linear variation between the latter and 0.4 ± 0.1 at the bottom of the euphotic zone; a surface $\alpha_{inc}^* = 0.013 \pm 0.001$, with a linear variation between this and 0.001 at the bottom of the euphotic zone; and a single value $\phi_{max} = 0.014 \pm 0.002$. Taking into consideration the spectral distribution of light in Valdez-Holguín *et al.*'s (1999) incubator and following Giles-Guzmán & Álvarez-Borrego (2000), for surface waters $\alpha_{insitu}^* = 1.2\alpha_{inc}^*$. In case II waters, α_z^* tends to maintain the value that corresponds to the spectral distribution of PAR at the surface. This is due to the strong absorption of both red and short-wavelength light because of the abundance of pigments, detritus and CDOM. Thus, when using Platt *et al.*'s (1991) non-spectral model to estimate primary production for case II waters, it may be done without any correction of α_z^* for the spectral distribution of light at depth.

For case I waters, $a_{ph(z, chl)}^*$ may be estimated with Giles-Guzmán & Álvarez-Borrego's (2000) expression:

$$a_{ph(L, Chl)}^* = 0.0152 - 0.0022Chl + (0.0137 - 0.0074Chl)[1 - \exp(-nL)],$$

where

$$n = 0.0648 + 0.0466Chl - 18.09(10^{-4})L - 38.4(10^{-5})ChlL - 84.6(10^{-3})Chl^2 + 30.33(10^{-6})L^2 - 15.01(10^{-4})Chl^2L + 18.16(10^{-6})ChlL^2 + 77.2(10^{-3})Chl^3 - 18.4(10^{-8})L^3.$$

The f-ratio ($f = P_{NEW}/P_T$). There are no reports on ^{15}N incubations to estimate P_{NEW} for the Gulf of California. Thus, it is not possi-

ble to make a direct estimate of the f -ratio for any region of the Gulf. One alternative is to use empirical algorithms developed for other regions of the world's ocean with similar hydrographic conditions to those found in the Gulf. Hidalgo-González & Álvarez-Borrego (2004) used NO_3 data from 268 hydrographic stations to generate average NO_3 profiles for each season and region of the Gulf, and they used Harrison *et al.*'s (1987) expression ($f_z = f_{\max}[1 - \exp(-m\text{NO}_{3(z)}/f_{\max})]$) to calculate the f -ratio for each depth. Unfortunately, there are no reports on the $f_z - \text{NO}_{3(z)}$ relationship for the Gulf of California. Thus, Hidalgo-González & Álvarez-Borrego (2004) chose the parameters m and f_{\max} as reported by Harrison *et al.* (1987): for the cool season they chose $m = 0.98$ and $f_{\max} = 0.77$, which correspond to the coastal upwelling Peruvian zone; and for the warm season they chose $m = 12.1$ and $f_{\max} = 0.64$, which correspond to the summer oligotrophic intrusion of the Southern California Bight.

DISCUSSION

Rigorous comparison of satellite-derived integrated production values for the whole euphotic zone and for the whole day (P_{Tint}) with results from ^{14}C incubations is difficult due to the different time and spatial characteristics of these measurements (Balch & Byrne, 1994). Nevertheless, it is interesting to compare both kinds of data. Álvarez-Borrego & Lara-Lara (1991) reported 26 ^{14}C -derived P_{Tint} point values for region II of the Gulf of California with an average of $1.43 \text{ g C m}^{-2} \text{ d}^{-1}$, compared with Hidalgo-González & Álvarez-Borrego's (2004) range of 1.52-1.87 for the period 1997-2002; Álvarez-Borrego & Lara-Lara (1991) reported 12 point values for region III with an average of $2.1 \text{ g C m}^{-2} \text{ d}^{-1}$, compared with Hidalgo-González & Álvarez-Borrego's (2004) range of 1.45-1.73; and Álvarez-Borrego & Lara-Lara (1991) reported four point values for region IV with a mean of $1.1 \text{ g C m}^{-2} \text{ d}^{-1}$ compared with Hidalgo-González & Álvarez-Borrego's (2004) range of 1.52-1.68. Álvarez-Borrego & Lara-Lara (1991) only reported five point values for the warm season and for the whole Gulf, which do not allow for comparisons. In spite of great differences in time and spatial scales, both methods provided average values that are very close, and given the uncertainties of Hidalgo-González & Álvarez-Borrego's (2004) satellite-derived estimates, these differences are not significant.

The vertical distribution of model-derived primary production is also very consistent and behaves as expected from ^{14}C experiments. Satellite total production, P_{Tz} , presents maxima at shallower depths than those of the $\text{Chl}_{(z)}$ maxima because of greater PAR_z near the surface. On the other hand, P_{Tz} maxima are often in subsurface waters due to the relatively low surface Chl. With relatively high surface Chl, maximum P_{Tz} is found at the surface. The largest contribution to production is from the surface and near-surface waters (i.e., the upper 15 m), with a relatively small contribution from the DCM because of low-light levels at Z_m .

Hidalgo-González & Álvarez-Borrego (2004) performed a sensitivity analysis to assess the effect of uncertainties of variables and parameters on the estimates of average integrated total production for the whole euphotic zone and for the whole day (P_{Tint}) ($\text{g C m}^{-2} \text{ d}^{-1}$). These latter authors added and subtracted one standard error ($s \text{ n}^{-0.5}$) to each input variable and parameter, one at a time, to assess the effect on P_{Tint} , and they expressed the difference as percentage. When adding or subtracting one standard error to the photosynthetic parameters (P_{m}^* , α_{insitu}^* , and ϕ_{max}), it was done for all of them at the same time because they co-vary according to the results of Cote & Platt (1983), and Valdez-Holguín *et al.* (1999). It was not possible to do a sensitivity analysis with the uncertainties associated with $K_{\text{PAR}(z)}$ calculated for case-I waters following Giles-Guzmán & Alvarez-Borrego (2000) because these latter authors did not provide values for the standard errors associated to their equations. However, when comparing 30 P_{Tint} values estimated with calculated PAR profiles with the corresponding values estimated with measured profiles, the mean of the percent differences was 5.9%. But, as Giles-Guzmán & Alvarez-Borrego (2000) indicated, PAR profiles that resulted from the model were smooth, whereas those that resulted from measurements in some cases had abrupt changes in the PAR vertical variation rate. Thus, possibly, most of the differences between measured and calculated PAR are caused by errors in the measured PAR values. One source of error when measuring PAR with an instrument is the optical effect of gravity waves at the sea surface; these waves focus and disperse the light very much as we can observe in a swimming pool. When lowering the instrument to measure PAR the descent is relatively fast and the instrument may catch a concentrated light beam or a dispersed one. A better way to perform the measurements would be to maintain the instrument at the same depth for few seconds, successively, each meter as it goes down, and then calculate the mean PAR for each depth, but this is usually not the way it is done. When changing K_{490} by one standard error, P_{Tint} changed ~2.7%. But, because of the scarce data used by Cervantes-Duarte *et al.* (2000) the confidence intervals of the parameters A and B are often very large, and they can yield $Z_{\text{PAR}1\%}$ values that differ by as much as 20%. Again, more optical data are needed to better characterize case II waters.

Greatest uncertainties of the estimates for average P_{Tint} are caused by the large confidence intervals of the photosynthetic parameters. When augmenting or diminishing the photosynthetic parameters by one standard error, average P_{Tint} changed as much as 17% with low Chl_s , and as much as 19% with high Chl_s . This is because of the few degrees of freedom in the P-E parameters. The probability of having all these errors added together simultaneously is low due to the multiplication rule.

The vertical profiles of PAR can be relatively well characterized, but those of Chl need more data. Future research should focus

mainly on a better characterization of the average photosynthetic parameters for each season and region within the Gulf, which are the weakest part in modeling primary production for the Gulf of California. The greatest need is for a better characterization of summer average values, both for the photosynthetic parameters and for the Chl profile.

As it was mentioned above, satellite derived estimates of P_{Tint} are in good agreement with results from ^{14}C incubations, but there are no ship ^{15}N data to compare with satellite derived estimates of P_{NEW} . Hidalgo-González & Álvarez-Borrego (2004)'s f -ratio values were particularly high for summer, up to 0.64 compared with the value suggested by Eppley (1992) of 0.1 for oligotrophic waters; but also those for winter might have been high, up to 0.77 compared to 0.4 suggested by Eppley (1992) for rich coastal waters. This is an opportunity for future research in the Gulf. ^{15}N incubations performed in parallel with ^{14}C incubations and nutrient determinations are needed for the whole Gulf to better characterize the parameters used in algorithms like Harrison *et al.*'s (1987) for the calculation of P_{NEW} .

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