

Satellite-derived total and new phytoplankton production in the Gulf of Mexico

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Integrated total (P_{Tint}) and new production (P_{newint}) ($gC\ m^{-2}\ d^{-1}$) were calculated for the Gulf of Mexico with semi-analytical models from the literature, using chlorophyll *a* concentrations (Chl_{sat}) and the vertical attenuation coefficients of light (K_{490}) from monthly composites of the satellite sensor SeaWiFS (1997–2004). The phytoplankton biomass vertical distribution associated with Chl_{sat} , and the vertical distribution of the *f*-ratio [$f_z = P_{new(z)}/P_{T(z)}$], were deduced from historic oceanographic data. Based on bathymetry, surface $T\ ^\circ C$, Chl and nutrients, the Gulf was partitioned into three regions: Yucatan, Deep-waters, and Mississippi. The year was divided into two periods for the Deep-waters region, “cool” and “warm.” The whole year was treated as a single period for the Yucatan and Mississippi regions. Average values for P_{Tint} had a significant seasonal variation for the Deep-waters region (0.37–0.44 and 0.22–0.24 $gC\ m^{-2}\ d^{-1}$, for the “cool” and “warm” periods, respectively), and similarly for P_{newint} (0.023–0.026 and 0.013–0.014 $gC\ m^{-2}\ d^{-1}$). Ranges for the average P_{Tint} values were 1.18 – 1.22, and 1.60 – 1.68 $gC\ m^{-2}\ d^{-1}$, for the Yucatan and Mississippi regions, respectively. Ranges for P_{newint} were 0.97 – 1.05, and 1.38 – 1.44 $gC\ m^{-2}\ d^{-1}$. The present, limited data, do not show a significant interannual P_{Tint} and P_{newint} variability in any region of the Gulf. Longer satellite time series for more complete future work may lead to the description of significant interannual primary production variability in the Gulf.

[**Key words:** Gulf of Mexico, chlorophyll, remote sensing, primary production, *f*-ratio]

Introduction

Satellite radiometer data have been used with semi-analytical models to estimate global primary production in the ocean¹. However, it is interesting to perform this kind of estimate for particular regions of the ocean where there is more detailed knowledge of the parameters used in the models, so that a better approximation to reality can be attained. Also, it is of interest to explore possible seasonal and interannual variations of primary production that may be relevant to CO_2 flux, fisheries, or other type of studies. Oceanic total primary production (P_T) has two components: new and regenerated production ($P_T = P_{new} + P_r$). New production (P_{new}) is the fraction of total primary production that is supported by external or “new” input of nutrients². Phytoplankton cells use nutrients recycled within the euphotic zone for regenerated production (P_r). Eppley & Peterson³ assumed that P_{new} is quantitatively equivalent to the organic matter that can be exported from the total production in the euphotic zone without the

production system running down. These latter authors defined the ratio of P_{new} to P_T as the *f*-ratio ($f = P_{new}/P_T$) and showed that *f* was an asymptotic function of the magnitude of total production.

Oceanic new production is a potential avenue for the removal of atmospheric carbon dioxide to the deep abyss⁴. The processes of fixation of inorganic carbon in organic matter during photosynthesis, its transformation by trophodynamics, physical mixing, transport and gravitational settling are referred to collectively as the “biological pump”⁵. The ratio of sinking flux to primary production (*e*-ratio) and the *f*-ratio vary as functions of 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 factors⁶. Thus, 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. Measuring P_T and P_{new} with bottle

incubation experiments using compounds labelled with ^{14}C and ^{15}N respectively, has been the basic method to generate direct estimates. But it is very time consuming and yields very limited data with low temporal and spatial coverage. The alternative is to make indirect estimates of P_T and P_{new} , by using remotely sensed temperature and color to estimate P_T and P_{new} ⁷⁻⁹.

The Gulf of Mexico chlorophyll and ^{14}C data collected by expeditions in the 1960s and 1970s remain the basis for the general paradigm that standing stocks and productivity of phytoplankton are both quite low seaward of the shelf-slope break ($< 0.1 \text{ mg Chl m}^{-3}$; $< 0.15 \text{ gC m}^{-2} \text{ d}^{-1}$)¹⁰. Biggs & Ressler¹⁰ support that description of the mean state but they also showed that “hot spots” in primary production ($>2 \text{ gC m}^{-2} \text{ d}^{-1}$) occur when/where nutrient availability is locally enhanced, even in deep-waters ($>300 \text{ m}$). Most of the reported Gulf’s ^{14}C -incubation productivity data are for the continental shelf. More recently (1987-1999), data for deep-waters have been generated¹¹. These data have provided a very limited view of the temporal and spatial variation of the Gulf’s total primary production, and there are no reports on P_{new} for the Gulf of Mexico. Satellite ocean color data give us the opportunity to generate a more complete description of the Gulf’s P_T and P_{new} spatial and temporal variability.

Remote sensors provide information on the average photosynthetic pigment concentration for the upper 22% of the euphotic zone¹². Empirical and semi-analytical algorithms to estimate primary production ($P_{T(z)}$) from satellite-derived photosynthetic pigments have been compared^{13, 14}. These models apply to the entire euphotic zone, and ideally, they should use the vertical profile of pigment biomass as input¹⁵. Therefore a gap exists between the limited satellite pigment 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 production¹⁶. The deep chlorophyll maximum (DCM) is a consistent feature in the ocean^{17, 18}. Since the early studies on the DCM an emphasis has been placed on understanding these features¹⁹. Generally, accounting for its presence increases estimates of integrated production (P_{Tint}), and since the DCM often appears below the mixed layer, it would be likely that most of its production is P_{new} ²⁰. Chlorophyll concentration ($\text{Chl}_{(z)}$) historical data can be used to fit a Gaussian distribution function to represent the pigment vertical

profile for different seasons and regions of the ocean^{21, 22}. Hidalgo-González & Alvarez-Borrego²³ used this method to represent the pigment vertical profile for the Gulf of Mexico. A difficulty in estimating oceanic production from surface measurements arises from the regional differences in the vertical distribution of chlorophyll. The underlying assumption of a Gaussian distribution function is that for a given region of the ocean, in a given season, the typical shape of the chlorophyll profile is stable.

The objective of this work is to quantify the spatial and temporal variation of P_T and P_{new} for the Gulf of Mexico. To accomplish this, we used Sea-viewing Wide Field-of-view Sensor imagery, the Gaussian vertical distribution of $\text{Chl}_{(z)}$ as proposed by Hidalgo-González & Alvarez-Borrego²³ for the Gulf, and average photosynthetic parameters from the literature.

Materials and Methods

The Gulf of Mexico is a deep marginal sea located between 18° and 31° N , and 81° and 98° W (Fig. 1). The Gulf is connected to the Caribbean Sea through the Yucatan Channel and to the North Atlantic Ocean through the Straits of Florida. The main oceanographic feature of the Gulf is the Loop Current. It is part of the Gulf Stream system²⁴. It enters the Gulf through the Yucatan Channel (sill depth $\sim 1850 \text{ m}$), turns anti-cyclonically, and exits through the Straits of Florida (sill depth $\sim 800 \text{ m}$). Upwelling along the edge of the Loop Current is a major source of nutrients to the euphotic zone. Increased near-surface chlorophyll along the edge of the Loop Current attests to the significance of this process²⁵. Along the Florida Escarpment (northeastern Gulf) and the Campeche Banks (adjacent to the Yucatan peninsula), frictional interaction of the current and the bottom appear to be important²⁶, upwelling is produced and brings denser water close to the sea surface reducing vertical stratification²⁷.

The Gulf of Mexico ecosystem encompasses a broad spectrum of phytoplankton productivity from eutrophic coastal waters to oligotrophic deep ocean conditions²⁸. Major chemical and physical processes affecting productivity include the influences of a major river system and the Loop Current with high variable penetration into the northern and eastern Gulf of Mexico²⁷. In general, data support the findings of El-Sayed & Turner²⁹ that pico + nanoplankton make up more than three quarters of deep water cell counts and account for more than two thirds of the primary

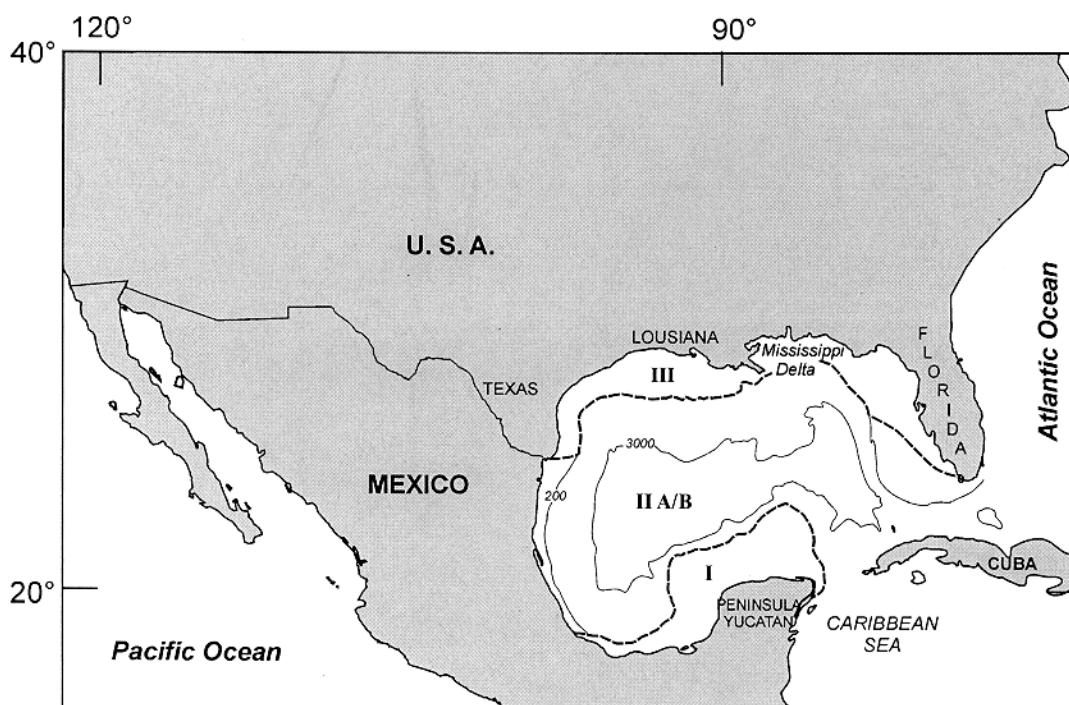


Fig. 1—Regions of the Gulf of Mexico. The Mississippi region is I, the Deep-waters region is II, and the Yucatan region is III. For the Deep-waters region, II A refers to the “cool” period and II B to the “warm” period. Bathymetry is in meters.

production. As the Loop Current penetrates northward into the Gulf, its path becomes unstable and large rings are shed³⁰. These rings are as much as 400 km or more in diameter, and they slowly propagate westward. When these rings collide with the western coast they form triads (cyclone-anticyclone-cyclone), parallel to the coast³¹. Between the northern cyclone and the anticyclone there is a current that transports water from the continental shelf seaward. These currents have been detected with satellite color imagery as plumes of relatively high Chl that extend tens to hundreds of kilometers seaward of the continental shelf-slope break³².

Based on temperature and $Chl_{(z)}$ data and for the purpose of characterizing the average shape of the $Chl_{(z)}$ vertical profile, Hidalgo-González & Alvarez-Borrego²³ divided the Gulf of Mexico into three regions: Yucatan (I), Deep-waters (II), and Mississippi (III) (Fig. 1). Surface temperature data from 1946-1998 suggest that interannual variation is small in the whole Gulf. The Mississippi River is the largest river in North America, and some local high rates of primary production measured with the ^{14}C method in this region (sometimes up to $5 \text{ g C m}^{-2} \text{ d}^{-1}$) can be attributed to nutrient loading from the Mississippi and Atchafalaya rivers³³. Divergence associated with the Loop Current may be a factor

producing upwelling on the Campeche bank (off the Yucatan peninsula), and off the southwestern tip of Florida, and it occurs through most of the year²⁸. Zavala-Hidalgo *et al.*³⁴ studied the seasonal circulation on the western shelf of the Gulf and found three distinct portions. The Louisiana-Texas shelf has a cyclonic circulation, except during summer months when the flow is eastward. On the narrow Tamaulipas-Veracruz shelf (westernmost Gulf) there is a swift reversal of the along-shelf current, down-coast from September to March and up-coast from May to August when there is upwelling due to offshore Ekman transport. Circulation on the western Campeche Bank is down-coast, off the western coast of the Yucatan peninsula, throughout the year³⁴.

Data and methods

Platt *et al.*'s¹⁶ non-spectral model with inhomogeneous biomass profile was used to estimate total primary production for the Mississippi region (case II waters)

$$P_{T(z)} = [P_{m(z)}^{*} Chl_{(z)} \alpha_{PAR(z)}^{*} PAR_{(z)}] [(P_{m(z)}^{*})^2 + (PAR_{(z)} \alpha_{PAR(z)}^{*})^2]^{-0.5} (\text{mg C m}^{-3} \text{ h}^{-1}),$$

where PAR is the photosynthetically active radiation, P_m^{*} is the assimilation number ($\text{mg C mg Chl}^{-1} \text{ h}^{-1}$),

and α_{PAR}^* is the initial slope [$\text{mg C mg Chl}^{-1} \text{ h}^{-1}$ ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) $^{-1}$] of the photosynthesis-irradiance relationship (P-E curves). A modification to this model proposed by Giles-Guzmán & Alvarez-Borrego³⁵ was used for the Yucatan and Deep-waters regions (case 1 waters, $\text{Chl} < 1.5 \text{ mg m}^{-3}$)

$$P_{T(z)} = [P_{m(z)}^* \phi_{\max} \text{Chl}(z) \bar{a}_{\text{phyto}(z, \text{Chl})}^* PAR(z)] / [(0.02315 P_{m(z)}^*)^2 + (PAR(z) \bar{a}_{\text{phyto}(z, \text{Chl})}^* \phi_{\max})^2]^{1/2}.$$

This modification is a spectral model with inhomogeneous biomass profile and corrects the initial slope (α_{PAR}^*) of the P-E curves by the *in situ* spectral distribution of scalar *PAR*. Instead of α_{PAR}^* in Platt *et al.*'s¹⁶ expression, we used $43.2 \phi_{\max} \bar{a}_{\text{phyto}(z, \text{Chl})}^*$ ³⁵. The maximum photosynthetic quantum yield at low irradiance [$\text{mol C (mol quanta)}^{-1}$] is $\phi_{\max}$. The average specific absorption coefficient of phytoplankton is $\bar{a}_{\text{phyto}(z, \text{Chl})}^*$ ($\text{m}^2 \text{ mg Chl}^{-1}$), weighted by the *in situ* spectral distribution of *PAR*, it is a function of depth and chlorophyll concentration and it is calculated following Giles-Guzmán & Alvarez-Borrego³⁵. The factor 43.2 converts mol C to mg C, s to hours, and mol quanta to $\mu\text{mol quanta}$. These expressions show that to estimate primary production we need not only Chl_{sat} but also the vertical profiles of *Chl* and *PAR*. For the purpose of defining the chlorophyll vertical profile, Hidalgo-González & Alvarez-Borrego²³ proposed to divide the year into two periods for the Deep-waters region, the “cool” period is winter and spring, and the rest of the year is the “warm” period. The average shape of the $\text{Chl}(z)$ profile does not change significantly throughout the year for the Yucatan and Mississippi regions, thus the whole year is a single period for these regions.

SeaWiFS monthly composites of Chl_{sat} and K_{490} with a spatial resolution of $\sim 9 \text{ km}$ for the period October 1997 - August 2004 were used to obtain representative averages for the periods and regions of the Gulf. The Chl_{sat} means were obtained from each period composite and for each Gulf region using the program WIM (Windows Image Manager, developed by M. Kahru, Scripps Institution of Oceanography, La Jolla). K_{490} means were obtained from each yearly composite for the Mississippi region.

Surface scalar *PAR* ($\text{PAR}_{z=0+}$) was estimated with the Bedford Institute of Oceanography (Halifax, Canada) program [available at <http://www.amigo.bio.dfo.ca>]. This program uses latitude, longitude, year, and Julian day. A representative mean geographic location was chosen for each region

within the Gulf, and *PAR* was obtained for each Julian day, and an average *PAR* was calculated for each region and period. Following Morel & Maritorena³⁶, this value was multiplied by 0.965 to estimate *PAR* immediately under the sea surface ($\text{PAR}_{z=0-}$). For the Yucatan and Deep-waters regions, the *PAR* profile ($\text{PAR}_{(z)}$) was calculated following Giles-Guzmán & Alvarez-Borrego³⁵, with a variable K_{PAR} ($K_{\text{PAR}(z)}$) calculated with the *Chl* profile and taking into account the variation of the spectral distribution of light with depth. For the Mississippi region, the *PAR* profile was calculated with a vertical attenuation coefficient constant with depth, K_{PAR} , deduced from the satellite K_{490} average values. As a first approximation, the regression model proposed by Cervantes-Duarte *et al.*³⁷ for the most turbid waters of the Gulf of California (its northern part) ($Z_{\text{PAR}1\%} = A + B/K_{490}$, where $A = 3.76$, and $B = 2.27$) was used to estimate the mean euphotic zone depth ($Z_{\text{PAR}1\%}$) of the Mississippi region as a function of the K_{490} mean for each year, and an average K_{PAR} was estimated for each year ($K_{PAR} = 4.6/Z_{\text{PAR}1\%}$). Cervantes-Duarte *et al.*'s³⁷ regression models for different water types in the Gulf of California differ by the values of the parameters A and B, and most of the variation of $Z_{\text{PAR}1\%}$, depends on the values of K_{490} (the greatest difference in $Z_{\text{PAR}1\%}$ for different values of A and B and the same value of K_{490} is ~ 4 meters). The K_{490} yearly mean range for the Mississippi region ($0.12 - 0.21 \text{ m}^{-1}$) is the same as that for the Gulf of California northern waters reported by Hidalgo-González & Alvarez-Borrego³⁸.

There are no data for the photosynthetic parameters of the Gulf of Mexico phytoplankton. As a first approximation to reality, we used Malone's³⁹ assimilation ratios for Caribbean surface waters ($z = \sim 2 \text{ m}$) and for Atlantic waters near Cuba. His assimilation ratios were estimated with incubations under the equivalent of $\sim 210 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$, which may have been below saturation level. Thus, his assimilation ratios may be lower than P_m^* . He generated data for micro-phytoplankton ($> 20 \mu\text{m}$) and nanno-phytoplankton ($< 20 \mu\text{m}$), and the range of the weighted mean was $6.3 \pm 2 \text{ mg C mg Chl}^{-1} \text{ h}^{-1}$, at the 95 % confidence level. Taking into consideration that the mean Gulf's surface T °C changes within a narrow range ($24 - 28^\circ\text{C}$), from region to region, and from season to season, an assimilation number $P_m^* = 7 \pm 2 \text{ mg C mg Chl}^{-1} \text{ h}^{-1}$ was chosen as representative of the whole Gulf and for the whole year, to compensate for the light under-saturation in Malone's³⁹ experiments.

Assuming an average P_m^* vertical profile shape for the Gulf of Mexico similar to that reported by Valdez-Holguín *et al.*⁴⁰ for the Gulf of California, P_m^* values of 2.8 ± 0.4 and 0.8 ± 0.2 mg C mg Chl⁻¹ h⁻¹ were used for the middle and the bottom of the euphotic zone, respectively, with linear variations between them (surface-middle, and middle-bottom of the euphotic zone). Also, assuming an average value of the saturation parameter (E_k) for the Gulf of Mexico's surface phytoplankton, for the whole year, equal to that reported by Valdez-Holguín *et al.*⁴⁰ for the Gulf of California ($E_k = P_m^* / \alpha_{PAR}^* = 285 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$), the α_{PAR}^* surface average value for the Gulf of Mexico, for the whole year, is 0.025 ± 0.002 mg C mg Chl⁻¹ h⁻¹ ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$)⁻¹. In a similar manner, α_{PAR}^* for the bottom of the euphotic zone is 0.002 with a linear variation between this and the surface value; and a single value $\phi_{\max} = 0.027 \pm 0.004$ mols C mol quanta⁻¹.

We used NO₃ data from 355 hydrographic stations sampled from 1980 through 1995 (National Oceanographic Data Center, www.nodc.noaa.gov) to generate average NO₃ profiles for each period and region of the Gulf. In all cases NO₃ was determined by the spectrophotometric method following Strickland & Parsons⁴¹. Then, Harrison *et al.*'s⁴² expression was used to calculate the f -ratio for each depth $\{f_{(z)} = f_{\max} [1 - \exp(-m\text{NO}_{3(z)} / f_{\max})]\}$. Unfortunately, there are no reports on the $f_{(z)}$ - NO_{3(z)} relationship for the Gulf of Mexico. Thus, we chose the parameters m and $f_{\max}$ as reported by Harrison *et al.*⁴² and Eppley & Peterson³ for oceanographic conditions similar to those found in the Gulf. For the Yucatan and Mississippi regions we chose $m = 5.84$ and $f_{\max} = 0.86$, which correspond to the Mid Atlantic Bight⁴², and for the Deep-waters region we chose $m = 6.21$ and $f_{\max} = 0.06$ which correspond to oligotrophic waters³.

A sensitivity analysis was performed 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}) (g C m⁻² d⁻¹ or ton C km⁻² d⁻¹). One standard error (s n^{-0.5}) was added and subtracted to each input variable and parameter, one at a time, to assess the effect on P_{Tint} , and the difference was expressed as percentage. Due to the covariation of the photosynthetic parameters ($P_{m(z)}^*$, $\alpha_{PAR(z)}^*$, and $\phi_{\max}$)^{40, 43}, when adding or subtracting one standard error we did it for all of them at the same time. It was not possible to do a sensitivity analysis with the uncertainties associated with $K_{PAR(z)}$ calculated for case I waters

following Giles-Guzmán & Alvarez-Borrego³⁵ because these latter authors did not provide values for the standard errors associated with their equations. They only mentioned that when comparing thirty 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 they 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 due to errors in the measured PAR values. Also, a sensitivity analysis was done to assess the effect of the f -ratio uncertainties on estimates of integrated new production (P_{newint}) (g C m⁻² d⁻¹ or ton C km⁻² d⁻¹).

Results

The high number of pixels allowed for a relatively small standard error for Chl_{sat} and K_{490} , about ± 0.9 % in both cases. Average Chl_{sat} values had no clear interannual variation in any region of the Gulf (Table 1). There was some significant interannual variability of Chl_{sat} , but with no clear trends. The largest Chl_{sat} average values were for 1998 for the Yucatan and Mississippi regions, but not for the Deep-waters region; and the lowest values were for 1999 for the Yucatan and Deep-waters regions, but not for the Mississippi region. There was a clear average Chl_{sat} spatial variation with the lowest values for the Deep-waters region and the highest for the Mississippi region. Also, Chl_{sat} values for the "warm" period of the Deep-waters region was ~75% of those for the "cool" period (Table 1). The absolute values of the standard

Table 1 — Satellite-derived average values for periods and regions (I, II, III) in the Gulf of Mexico of surface chlorophyll (Chl_{sat}) mg m⁻³ (II A and II B are the "cool" and "warm" periods, respectively). The standard error (s n^{-0.5}) is ~ 0.9 % in all cases. Data are from October 1997 to August 2004.

Year	I	II		III
		A	B	
1997			0.16	0.95
1998	0.49	0.23	0.18	1.14
1999	0.45	0.21	0.16	0.95
2000	0.48	0.28	0.16	0.98
2001	0.47	0.24	0.18	0.99
2002	0.47	0.26	0.18	0.96
2003	0.48	0.29	0.19	0.97
2004	0.49	0.24	0.17	0.92

error for NO_3 were similar for different depths, regions and periods (most of them between 0.2 and 0.4 μM), but the relative values changed from $\sim 20\%$ at low NO_3 values to $\sim 3\%$ at high values (not illustrated). Average surface and near surface NO_3 values were lowest for the Deep-waters region and highest for the Mississippi region (Fig. 2). Surface average NO_3 value for the Mississippi region was an order of magnitude larger than those for the other two regions.

Total production, $P_{T(z)}$, had maxima at shallower depths than those of the $\text{Chl}_{(z)}$ maxima (Fig. 3) due to greater $\text{PAR}_{(z)}$ near the surface. Average $P_{T(z)}$ maxima were at the surface in most of the cases, but sometimes they were in subsurface waters due to the relatively low surface $\text{Chl}_{(z)}$ values (Fig. 3). P_{new} maxima had the same depths as those of $P_{T(z)}$ maxima. Production of the deep Chl maximum, both P_T and P_{new} , was relatively low compared to that of near surface waters due to low light levels at the former (Fig. 3).

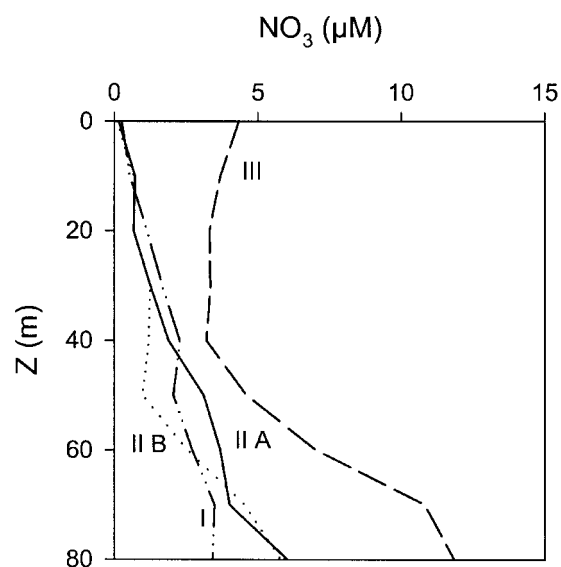


Fig. 2—Average NO_3 profiles for the periods and regions in the Gulf of Mexico as shown in Fig. 1.

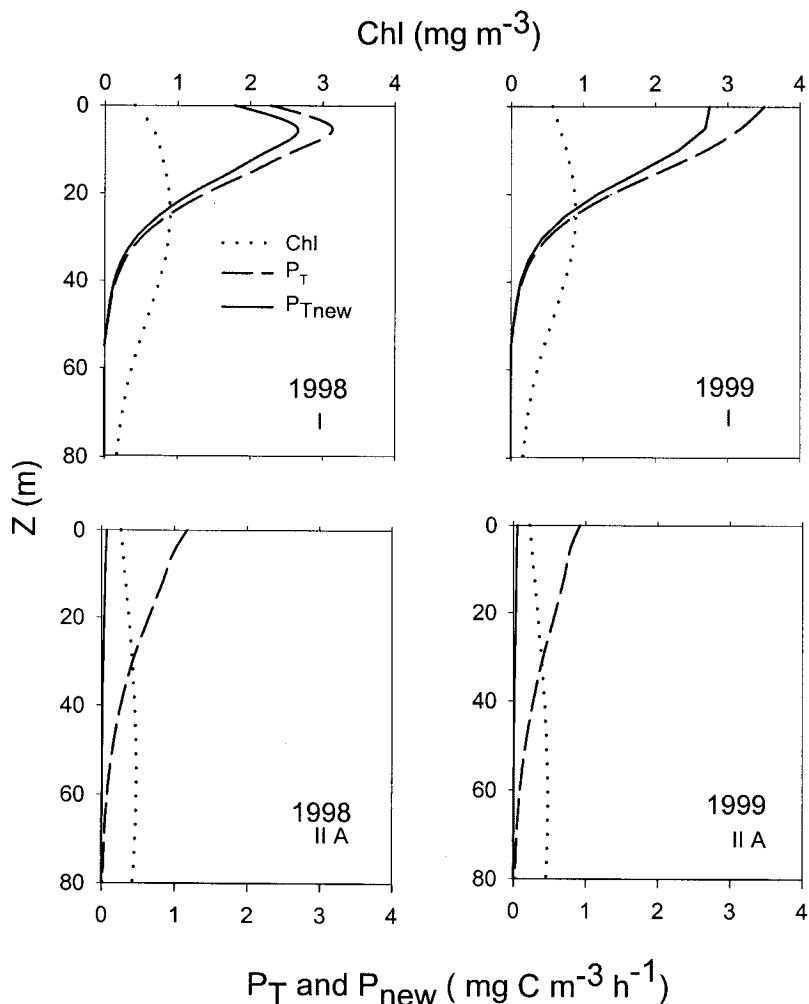


Fig. 3—Examples of the average chlorophyll, total primary production, and new production profiles for regions I and II in the Gulf of Mexico.

Greatest uncertainties of the estimates for average integrated total production for the whole euphotic zone and for the whole day (P_{Tint}) ($\text{g C m}^{-2} \text{d}^{-1}$ or $\text{ton C km}^{-2} \text{d}^{-1}$) are due to uncertainties in the photosynthetic parameters. When augmenting or diminishing the photosynthetic parameters by one standard error, P_{Tint} changed as much as 18%. This is due to the few degrees of freedom in the P-E parameters. Since we are using single average values for the whole Gulf, these large intervals do not affect the comparisons of P_{Tint} between regions. When changing Chl_s by one standard error, P_{Tint} changed only ≤ 0.2 of one percent, and when changing K_{490} by one standard error P_{Tint} changed $\sim 0.3\%$. The probability of having all these errors added together simultaneously is low due to the multiplication rule.

Average integrated total production for the Deep-waters region, for the whole euphotic zone and for the whole day (P_{Tint}) ($\text{gC m}^{-2} \text{d}^{-1}$ or $\text{tonC km}^{-2} \text{d}^{-1}$) shows a regular annual cycle as the dominant feature of this time series. Taking into consideration the uncertainties due mainly to the photosynthetic parameters, there was no significant interannual change in any region of the Gulf (Table 2). The average P_{Tint} range for the whole Gulf was from $0.22 \text{ g C m}^{-2} \text{d}^{-1}$ for the “warm” period of the Deep-waters region to 1.68 for the Mississippi region.

The f-ratio estimates did not change significantly when changing the NO_3 profiles by one standard error. Thus, uncertainties in the new production estimates are only those associated to uncertainties of total production. Average integrated new production for the euphotic zone (P_{newint} , $\text{g C m}^{-2} \text{d}^{-1}$ or $\text{ton C km}^{-2} \text{d}^{-1}$) was lowest for the Deep-waters region and highest for the Mississippi region (Table 3). Again, the dominant temporal change was the

seasonal cycle for the Deep-waters region. Here, average P_{newint} changed from $0.013\text{--}0.014 \text{ g C m}^{-2} \text{d}^{-1}$ for the “warm” period to $0.022\text{--}0.026$ for the “cool” period. In the Yucatan and Mississippi region, P_{newint} was >1.0 for most of the years (up to $1.44 \text{ g C m}^{-2} \text{d}^{-1}$ for the Mississippi region).

Discussion

Total and new oceanic production calculated from remotely sensed data on ocean color, which depends on parameters developed from ship observations, yield more representative estimates of the large-scale average production than those calculated from ship data alone⁸. Morel & Berthon¹⁵ 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. Our objective was to obtain representative average production values for whole periods and regions within the Gulf of Mexico. Rigorous comparison of the satellite-derived time series of P_{Tint} with results from ^{14}C incubations is difficult due to the very different time and space characteristics of these measurements⁴⁴. Nevertheless, it is interesting to compare both kinds of data. Barreiro-Guemes *et al.*⁴⁵ reported ^{14}C -derived P_{Tint} ranges for coastal regions influenced by estuarine systems in the Gulf of Mexico, with a range of $0.84\text{--}2.11 \text{ g C m}^{-2} \text{d}^{-1}$ for the platform off Yucatan peninsula, compared with our range of $1.12\text{--}1.22$ for the whole Yucatan region; and a range of $0.50\text{--}1.40$ for the Texas Louisiana platform, compared with our range of $1.60\text{--}1.68 \text{ g C m}^{-2} \text{d}^{-1}$ for the whole Mississippi region. Lohrenz *et al.*²⁸ reported mean ^{14}C -derived P_{Tint} values for open Gulf of Mexico waters (a total of 33 point values) with a range of $0.14\text{--}0.48 \text{ g C m}^{-2} \text{d}^{-1}$

Table 2 — Satellite-derived integrated total primary production (P_{Tint}) per unit area ($\text{g C m}^{-2} \text{d}^{-1}$ or $\text{ton C km}^{-2} \text{d}^{-1}$) and for whole regions in the Gulf of Mexico (ton C d^{-1})

Year	I			II				III	
				A		B			
	P_{Tint} $\text{g C m}^{-2} \text{d}^{-1}$	P_{Tint} ton C d^{-1}	P_{Tint} $\text{g C m}^{-2} \text{d}^{-1}$	P_{Tint} ton C d^{-1}	P_{Tint} $\text{g C m}^{-2} \text{d}^{-1}$	P_{Tint} $\text{g C m}^{-2} \text{d}^{-1}$	P_{Tint} ton C d^{-1}	P_{Tint} $\text{g C m}^{-2} \text{d}^{-1}$	P_{Tint} ton C d^{-1}
1997						0.22	2.32×10^5	1.62	4.38×10^5
1998	1.22		2.27×10^5	0.38	4.02×10^5	0.23	2.42×10^5	1.68	4.54×10^5
1999	1.12		2.08×10^5	0.37	3.92×10^5	0.22	2.32×10^5	1.62	4.38×10^5
2000	1.20		2.23×10^5	0.43	4.55×10^5	0.22	2.32×10^5	1.63	4.40×10^5
2001	1.18		2.20×10^5	0.39	4.13×10^5	0.23	2.42×10^5	1.63	4.40×10^5
2002	1.18		2.20×10^5	0.41	4.34×10^5	0.23	2.42×10^5	1.62	4.38×10^5
2003	1.20		2.23×10^5	0.44	4.66×10^5	0.24	2.53×10^5	1.63	4.40×10^5
2004	1.22		2.27×10^5	0.39	4.13×10^5	0.23	2.42×10^5	1.60	4.32×10^5

Table 3 — Satellite-derived integrated new primary production (P_{Newint}) per unit area ($\text{g C m}^{-2} \text{d}^{-1}$ or $\text{ton C km}^{-2} \text{d}^{-1}$) and for whole regions in the Gulf of Mexico (ton C d^{-1})

Year	I		II				III	
			A		B			
	P_{Newint} $\text{g C m}^{-2} \text{d}^{-1}$	P_{Newint} ton C d^{-1}	P_{Newint} $\text{g C m}^{-2} \text{d}^{-1}$	P_{Newint} ton C d^{-1}	P_{Newint} $\text{g C m}^{-2} \text{d}^{-1}$	P_{Newint} ton C d^{-1}	P_{Newint} $\text{g C m}^{-2} \text{d}^{-1}$	P_{Newint} ton C d^{-1}
1997					0.013	0.14×10^5	1.39	3.77×10^5
1998	1.05	1.95×10^5	0.023	0.24×10^5	0.014	0.15×10^5	1.44	3.90×10^5
1999	0.97	1.80×10^5	0.022	0.24×10^5	0.013	0.14×10^5	1.39	3.77×10^5
2000	1.03	1.92×10^5	0.026	0.27×10^5	0.013	0.14×10^5	1.40	3.78×10^5
2001	1.06	1.98×10^5	0.023	0.25×10^5	0.014	0.15×10^5	1.40	3.78×10^5
2002	0.97	1.81×10^5	0.025	0.26×10^5	0.014	0.15×10^5	1.39	3.77×10^5
2003	1.03	1.92×10^5	0.026	0.28×10^5	0.014	0.15×10^5	1.40	3.78×10^5
2004	1.05	1.96×10^5	0.023	0.25×10^5	0.014	0.15×10^5	1.38	3.72×10^5

compared with our range of 0.22 – 0.44 for the whole Deep-waters region. In spite of great differences in time and space scales, both methods provide average values that are very close. Kahru & Mitchell⁴⁶ compared their satellite-derived primary productions for the California Current with ^{14}C measurements and reported that the first overestimated the second by about 40%. Hidalgo-Gonzalez & Alvarez-Borrego³⁸ used the same methodology that we are using here, and reported that their estimates for the Gulf of California did not systematically overestimated or underestimated P_{Tint} . We can make the same conclusion for the present satellite-based estimates for the Gulf of Mexico.

In spite of possible errors, ocean color satellite imagery are very consistent; the seasonal cycles and the spatial variation within the Gulf of Mexico behave very much as expected according to physical phenomena such as currents, eddies and the occurrence of upwelling. Trees *et al.*⁴⁷ reported that, despite the various sampling periods and numerous geographic locations, there are consistent patterns in the ratios of the log accessory pigments to log total *Chl* (*Chl a*, *Chl a* allomer, *Chl a* epimer, and chlorophyllide *a*), and there is a strong log-linear relationship for these ratios. Trees *et al.*⁴⁷ indicated that this log-linearity largely explains the success in remotely sensed chlorophyll algorithms, even though phytoplankton populations can vary in their composition and suite of pigments.

For the purpose of defining regions to apply primary production models to satellite color data, the larger the regions the better. For example, for the purpose of modeling production, Valdez-Holguín *et al.*⁴⁰ proposed means of photosynthetic parameters

(from P-E curves) for the whole Gulf of California as a single region. Sathyendranath *et al.*²⁰ indicated that most boundaries between biogeochemical regions prove to have some significance for the depth of the chlorophyll maximum. That is the case for the Gulf of Mexico regions also. The effect of nutrient concentration is not explicit in our primary production models because it is implicit in chlorophyll. Nutrients control phytoplankton biomass but have a very weak effect on photosynthetic parameters⁴⁸. Nutrient concentrations have an explicit effect on the estimates of $P_{\text{new}(z)}$ through the f -ratio values.

Present average P_{newint} estimates for the Yucatan and Mississippi regions are very similar to those reported by Hidalgo-González & Alvarez-Borrego³⁸ for the “cool season” of the northern half of the Gulf of California, which is a very rich region. Watts *et al.*⁴ measured P_{new} for the northwestern Indian Ocean using ^{15}N stable-isotope tracer techniques, and found that both the integrated f -ratio ($P_{\text{newint}}/P_{\text{Tint}}$) and P_{newint} were larger during the monsoon, with ranges of 0.10-0.96, and 0.04-3.66 $\text{g C m}^{-2} \text{d}^{-1}$, respectively, and lower during the intermonsoon, with ranges of 0.07-0.52, and 0.05-0.65 $\text{g C m}^{-2} \text{d}^{-1}$, respectively. This was due to upwelling and greater wind-induced vertical mixing during the monsoon. Highest monsoon P_{newint} value reported by Watts *et al.*⁴ for the northwestern Indian Ocean was more than double the highest average value for the Mississippi region, but they reported a great spatial variability for the Indian Ocean.

Karl *et al.*⁴⁹ showed an 11-year time series of the ratio of sinking flux to primary production (e -ratio) for the Bermuda and Hawaii JGOFS sites, and reported a great time variability of the e -ratio with values in the range 0.02-0.21 for Bermuda, and 0.02-

0.15 for Hawaii. The present f -ratio average value for the whole euphotic zone and for the Deep-waters region was only 0.06 (following Eppley & Peterson³). *Strictu sensu*, it is not correct to compare Karl *et al.*'s⁴⁹ e -ratio values with present f -ratios. Since the organic matter is degraded in its way down to the bottom and only the most refractive particles reach the bottom, we expect the e -ratio values to be smaller than the f -ratios. Thus, present f -ratio value of 0.06 is too small, and it should have been > 0.21 . This agrees with Platt & Harrison⁵⁰ that the f value for oligotrophic food webs has been badly underestimated. So, present P_{newint} average values for the Deep-waters region should be multiply by a factor of at least four.

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