

Satellite derived photosynthetic pigment surveys: A review of marine phytoplankton biomass and productivity

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RESUMEN

El sensor Coastal Zone Color Scanner (CZCS) que voló a bordo del satélite Nimbus-7 proveyó datos de pigmentos fotosintéticos del océano entre 1978 y 1986. El procesado de los datos se terminó en 1990 y nos permitió apreciar la distribución global de la concentración de pigmentos y del coeficiente de atenuación vertical de luz, aunque su cobertura fue escasa. Los datos del CZCS representan una serie de tiempo única, y durante varios años serán la fuente principal para el estudio de la distribución de pigmentos en el océano y su variación interanual. Con el lanzamiento del SeaWiFS hacia el final de 1995, la comunidad de ciencias de la Tierra podrá contar con una serie de tiempo ininterrumpida de color del océano. Estos datos de satélite son la única forma de monitorear la productividad marina total y nueva en la escala de cuencas oceánicas. La productividad nueva es el componente crítico que limita el transporte de CO₂ de la superficie a las aguas profundas por la biota. Esto abre una nueva posibilidad para el estudio de los flujos de carbono en las escalas regional y global, y de días a años. Además, la variabilidad espacio/temporal de los pigmentos fotosintéticos que se aprecia en las imágenes del CZCS, también se ha usado como trazador superficial para describir fenomenología física, especialmente en áreas donde la temperatura superficial es homogénea. De la revisión presente es claro que aún hay mucho por hacer con la base de datos del CZCS.

PALABRAS CLAVE: Datos de satélite, pigmentos fotosintéticos, productividad primaria marina.

ABSTRACT

The Coastal Zone Color Scanner (CZCS) flying on board the Nimbus-7 satellite provided oceanic photosynthetic pigment data during 1978-86. The CZCS data processing completed in 1990 furnished data on the global distribution of total pigment concentration and the vertical attenuation coefficient of diffuse light, even though coverage was sparse. Beginning with the launch of SeaWiFS at the end of 1995, we may look forward to a long-term ocean color time series. New primary productivity is the critical component limiting the transport of CO₂ by marine biota from the surface to deeper waters. The new data open possibilities for the study of carbon fluxes at regional and global scales, on time scales from days to years. Space/time variability of photosynthetic pigments, as obtained from CZCS images, has also been used as a surface tracer to describe physical phenomena where the surface temperature is homogeneous.

KEY WORDS: Satellite data, photosynthetic pigments, marine primary productivity.

1. INTRODUCTION

In physical and biological oceanography, satellite data collection is limited to electromagnetic radiation. Thus the oceanographic information is restricted to the immediate surface layers of the ocean (La Violette, 1974). Only a narrow spectral region, from about 400 to 600 nm, provides data for water depths greater than a few meters. At longer wavelengths, water absorption quickly attenuates the signal generated by bottom or water reflectance. At shorter wavelengths, water absorption also increases rapidly in all but very clear oceanic water. Perhaps even more significantly, at the shorter wavelengths there is a rapid increase of the veiling effects of the atmosphere (Austin, 1974).

In October 1978 the Nimbus-7 satellite was launched, carrying the Coastal Zone Color Scanner (CZCS) designed specifically for remote sensing of photosynthetic pigments in the aquatic environment. The mission was designed as a proof-of-concept experiment with limited objectives, namely, two hours of coverage per day and a one-year demonstration lifetime. The CZCS generated data until June 1986. It had four 20 nm-wide bands in the visible re-

gion, centered at 443, 520, 550 and 670 nm, plus one band in the near infrared (700-800 nm), and another in the infrared (10.5-12.5 μ m) (for details of the optical system see Hovis, 1978). Its telescope had an instantaneous field of view of 865 μ radians. At the satellite altitude of 955 km, this yields a pixel 825 m square of the sea surface. The craft surveyed a continuous swath 1636 km wide; individual sections were typically 700 km along the track. The high reflectance of clouds and land in the 700-800 nm wave band was used to distinguish these areas from open water.

The CZCS represented a major advance in the technology of remote sensing of aquatic environment. However, the resolution was rather low for inland water bodies or coastal features such as estuaries and small bays (Kirk, 1983). Another limitation shared with other remote sensors was that 90% of the upwelling light from the water column originates within the upper optical depth within which the incident light falls to 1/e of the value at the surface. Thus the euphotic zone in which light falls to 1% of the subsurface value equals 4.6 optical depths. Therefore, remote sensors provide information on optical properties of the seawater for the upper 22% of the euphotic zone.

About 80-90% of the radiance received by a satellite-borne meter, outside the sun glitter, originates in scattering of atmospheric Rayleigh (airmolecule) and aerosol particles (dust, water droplets, salt, etc.). This is known as the path radiance, which must be removed, and the attenuation of the atmosphere allowed for (Kirk, 1983).

Bio-optical and atmospheric correction algorithms for the CZCS were developed after launch (Clark, 1981; Austin and Petzold, 1981; Gordon *et al.*, 1983a, 1983b, 1988a). Water quality products derived from the CZCS data included pigment concentration and diffuse light attenuation coefficients at 490 nm (K_{490}). Both were based on ratios of emergent radiances. The NASA Goddard Space Flight Center completed processing the global CZCS data in March 1990. These data survey the global distribution of total pigment concentration and K_{490} even though coverage is sparse. While the CZCS mission exceeded the original goals the data set does not fully resolve the seasonal cycle and interannual variability (McClain *et al.*, 1991).

There are plans to launch two more sensors of the color of the ocean. NASA has purchased data from the commercial SeaWiFS (Sea-Viewing Wide Field Sensor) on board the SEASTAR satellite scheduled for launch at the end of 1995; and Japan's NASDA has scheduled the OCTS (Ocean Color and Temperature Sensor) for mid-1996. A high priority of these future missions is the rapid distribution of data to the oceanographic community in a form which will permit ready integration of satellite data into field and modelling efforts. The SeaWiFS will have six bands in the visible region, each 20 nm wide, centered on 412, 443, 490, 510, 555 and 670 nm, plus two bands in the near infrared (745-785 and 845-885 nm). SeaWiFS will be a precursor of NASA's EOS (Earth Observing System) program to be implemented towards the end of the 1990's as a contribution to the U. S. Global Change Program.

The purpose of this review is to summarize the applications of the ocean color data obtained from remote sensors. An important application is to estimate total primary productivity and the "new" productivity component related to the flux of carbon and associated biogenic elements below the euphotic zone to the bottom of the ocean. On a more regional and local scale, long time series of primary productivity data, with large synoptic spatial coverage should provide us with a capability for improving fishery management and a better understanding of the impact of natural phenomena such as "El Niño" events.

2. ESTIMATING PIGMENT CONCENTRATIONS FROM SATELLITE DATA

The CZCS "universal" bio-optical algorithm adopted by NASA to calculate pigment concentration (chlorophyll a and phaeopigments) from the corrected water radiance (L_w) was developed by Gordon *et al.* (1983a). The algorithm is empirical and applies to Case I waters ($C_{sat} < 1.5 \text{ mg} \cdot \text{m}^{-3}$) and a mixture of Case I and Case II waters ($C_{sat} > 1.5 \text{ mg} \cdot \text{m}^{-3}$), where C_{sat} is the satellite-derived pig-

ment concentration. Where phytoplankton and their covarying detrital material and colored dissolved organic material (CDOM) play a dominant role in determining the optical properties of seawater we speak of Case I waters; when the suspended material mostly does not covary with phytoplankton, we have Case II waters (Morel and Prieur, 1977). Most of the open ocean approaches Case I. To develop the algorithm, pigment fluorometric analyses were performed on water samples from over sixty locations off Mexico and the east coast of U. S. A.

The pigment algorithm relates C_{sat} to the ratio of the water-leaving radiance at two different wavelengths. If C_{sat} is low $L_{w(443)}$ and $L_{w(520)}$ are relatively large with respect to $L_{w(550)}$, and vice versa. The algorithm switches band ratios: for Case I

$$\log C_{sat} = 0.053 - 1.71 \log \left[\frac{L_{w(443)}}{L_{w(550)}} \right];$$

if $C_{sat} > 1.5 \text{ mg} \cdot \text{m}^{-3}$ then C_{sat} is recomputed using the green bands (Case I and Case II together):

$$\log C_{sat} = 0.522 - 2.44 \log \left[\frac{L_{w(520)}}{L_{w(550)}} \right];$$

Over the 0.08 - 1.5 $\text{mg} \cdot \text{m}^{-3}$ range, the error in the retrieved pigment concentration was of the order of 30-40% for a range of atmospheric turbidities (Gordon *et al.*, 1983a).

The algorithm has been used for all portions of the world ocean, but its performance outside the region of calibration is unknown. After SeaWiFS is launched, more in-situ calibrations will be required to produce regional bio-optical algorithms.

3. QUALITY OF PIGMENT DATA

Comparing ship data and satellite imagery may present difficult problems. For low pigment concentrations and the associated weak horizontal gradients this poses no problem, since the precise position of the ship is irrelevant. However, for high pigment concentrations and associated strong horizontal gradients, it is necessary to know the exact pixel in which the ship is located. We cannot navigate CZCS imagery to better than about 3 pixels; i.e., we can only locate a pixel to within a 3 by 3 box. Even with more precise navigation, gradients on the subpixel scale (825 by 825 m) would cause differences between the ship-board and pixel-averaged values of C_{sat} (Gordon *et al.*, 1983a). Furthermore, satellite data averaged over larger pixels are often used; e. g., Balch *et al.* (1992) used the CZCS 20 km daily resolution.

Yet, comparisons between both sets of data must be made. Balch *et al.* (1992) ran a regression of satellite-derived pigment versus ship-derived pigment, mostly for the northern hemisphere, and obtained a coefficient of determination (r^2) of 0.40 ($n=731$ stations). The satellite underestimated the "true" pigment concentration in mesotrophic

and oligotrophic waters ($< 1 \text{ mg m}^{-3}$) and overestimated the pigment concentration in eutrophic waters ($> 1 \text{ mg m}^{-3}$). The error in the satellite estimate showed no trends with time between 1978 and 1985. In general the variability of the satellite retrievals increased with pigment concentration. The deviation of the satellite retrievals from the ship data in eutrophic shelf waters was typically from -50% to 400%. Müller-Karger *et al.* (1990) compared ship and CZCS pigment distributions in the southeastern Bering Sea, and found that CZCS values underestimated the ship data by a factor of at least 2 during spring 1979. During the spring of 1980 both sets of data were similar. Santamaria-Del-Angel *et al.* (1994a) found good agreement between CZCS and ship pigment values generated in 1981-1984 for the Gulf of California. Strub *et al.* (1990) studied seasonality of satellite-derived surface pigment concentration over a large area of the California Current and concluded that the single-scattering Rayleigh algorithm produced too high winter values. Symptoms for this error would be a uniformly increasing pigment concentration with latitude, and a seasonal maximum in winter. Gordon *et al.* (1988b) suggested that the algorithm used to correct the satellite radiance values is valid for solar zenith angles less than $50^\circ - 55^\circ$, which corresponds to latitudes of $26.5^\circ - 31.5^\circ$ in late December. Thomas and Strub (1990) confirmed that CZCS pigment estimates for high latitudes and winter cannot be trusted. Martin and Perry (1994) pointed out that Rayleigh-aerosol multiple scattering must be taken into account when using their atmospheric correction algorithm. Fargion *et al.* (1993) compared seasonal variations in pigment concentrations in the California Current from in situ measurements and from the CZCS-West Coast Time Series in its original version, based on a single-scattering Rayleigh algorithm. They found substantial differences between the two methods. The WCTS-CZCS data showed peak pigment concentration in winter, but the in-situ data did not. The in-situ data provided no convincing evidence for a seasonal cycle, with exception of some coastal data that did show a spring maximum.

The deviation of satellite data from ground truth estimates may be attributed to errors such as: ship-satellite collocation error, shipboard error in pigment determination, error due to the calculation of C_{sat} from satellite-derived L_w 's, errors in L_w determinations, error due to different sampling times of the ship and satellite sensors, error due to the presence of different phytoplankton taxa (containing various accessory pigments), the presence of coccolithophorids whose coccoliths reflect light very strongly (e.g., Balch *et al.*, 1989), and error due to absorption of upwelling light by non-chlorophyllous compounds that either do not covary with chlorophyll or covary in a different way from waters sampled for the bio-optical algorithm of Gordon *et al.* (1983a) (e.g., detritus, CDOM, sediments). The smallest error for spectral estimates of chlorophyll averages about 15% (Yentsch and Phinney, 1982). In order to develop improved algorithms taking into account the absorption of inert suspended particles and CDOM, the SeaWiFS will have a band at 412 nm. The absorption of these optical components increases exponentially with decreasing wavelength (Kirk, 1980; Bricaud *et al.*, 1981).

In addition to the long-term degradation of CZCS sensitivity, short-term (2 weeks to 1 month) variations in the radiometric sensitivity of the red and shorter-wavelength bands started in early fall 1981 and continued during the rest of the mission (Evans and Gordon, 1994). According to these authors, after these fluctuations began the actual values of CZCS-estimated pigment concentrations at a given location should be viewed with skepticism; however, the global spatial patterns of pigment distribution should be valid.

4. SPATIAL VARIABILITY OF MARINE PHYTOPLANKTON BIOMASS

The abundance and distribution of phytoplankton biomass vary over a wide range of space and time scales, of which only a fraction can be resolved by any single observational platform (Esaias, 1981). Satellite data provide an opportunity to resolve the large space scales and long time scales. Pigments may also be used as surface tracers to describe physical phenomena, to improve management of fisheries, and to improve the design of sampling schemes, including studies of benthic communities.

The space/time variability of phytoplankton is central to dynamical biological oceanography for characterizing scales under different environmental conditions, for identifying the mechanisms of persistence of space/time heterogeneity in phytoplankton populations, and for understanding stability of ecosystems, phytoplankton growth and its linkages to higher trophic levels, and the fundamental variability of the ocean environment in order to improve the reliability of sampling (Legendre and Demers, 1984; Smith *et al.*, 1988). Some applications of CZCS imagery to space/time variability of phytoplankton biomass and physical dynamics of the environment are mentioned below.

For the California Current, Peláez and McGowan (1986) described a latitudinally oriented sharp front off Ensenada (32°N). This front starts about 160 km off the coast and extends some 500 km offshore. Phytoplankton pigment concentration across the front varies by a factor of three over a distance of some 50 km. The front retains its identity throughout the year, though it may wobble, tilt, or change position. It coincides with meanders of the geostrophic flow, which at this latitude has a strong on-shore component. The vertical structure and dynamics associated with this front were described by Haury *et al.* (1986, 1993), and Gaxiola-Castro and Alvarez-Borrego (1991).

Smith *et al.* (1988) compared the CZCS satellite imagery for the California Current with CalCOFI chlorophyll distributions by Owen (1974). The observed large scale patterns included a shore-to-offshore chlorophyll gradient throughout the year, as well as centers of upwelling near the coast in spring and early summer. The satellite data show that the distributions of pigment biomass are more complex and variable than might have been concluded from shipboard data alone.

Smith *et al.* (1988) showed that biological processes dominate the smaller scales of pigment variance, while mesoscale eddies and geostrophic currents dominate the larger scales. There is general agreement on the spectral shape between temperature and pigment for wavelengths longer than 10 km, but there are differences at wavelengths less than 10 km. At larger scales the biological factors are overcome by physical processes; but for wavelengths less than 10 km growth rate, dispersion, grazing, and other biological factors begin to play a greater role in influencing chlorophyll distribution in space. At such scales both biological and physical mechanisms are responsible for the observed variability of pigment concentrations. Smith *et al.* (1988) and Denman and Abbott (1994) agree that phytoplankton cells (identified by CZCS patterns) behave largely as passive scalars at the mesoscale.

Müller-Karger *et al.* (1988) used CZCS imagery and drifting buoys to study the dispersal of Amazon river water. The discharge is carried offshore around a retroflection of the North Brazil Current and into the North Equatorial Countercurrent towards Africa between June and January each year. From about February to May the countercurrent and the retroflection weaken or vanish, and Amazon water flows northwestward towards the Caribbean Sea. Satellite-derived pigment concentration is a useful tracer of Amazon water advection. Spatial variability is so large that samplings from ships may lead to misconceptions about the circulation. The greater flux of organic particulates to the bottom of the tropical Atlantic as compared to the tropical central Pacific may be due to the phytoplankton in the Amazon plume. Muller-Karger *et al.* (1989) and Hochman *et al.* (1994) studied CZCS pigment distribution in the Caribbean Sea. The Orinoco River plume extends from Venezuela to Puerto Rico shortly after maximum discharge and remains the most important freshwater source of CDOM affecting "apparent" CZCS pigment distributions (Muller-Karger *et al.*, 1989). As much as 50% of the remotely sensed pigment biomass within the plume is an artifact due to the presence of CDOM.

Barale *et al.* (1986) used CZCS time series for 1979 and 1980 to study the surface color field and circulation patterns in the northern Adriatic Sea. Kuzmic (1991) used CZCS imagery of the northern Adriatic to corroborate mathematical model findings. During winter the "bura" wind induces a pronounced transient component of the northern Adriatic currents on a scale of several days. Kuzmic and Orlic (1987) showed that the vorticity of the bura wind induces a double-gyre response in the sea, with the large cyclonic gyre covering most of the basin, plus a smaller anticyclonic gyre covering the lower, smaller part of the modelled area. The strong upwind flow predicted for the middle of the basin carries turbid and nutrient-rich waters of the Po river and is very well detected by CZCS imagery (Kuzmic, 1991).

Sturm *et al.* (1992) investigated further the influence of the Po river and found two types of CZCS-derived patterns. They concluded that during summer, the Po waters spread to the surface into the interior, or along a narrow coastal

band. In winter, when the northern Adriatic is vertically mixed, the river waters remain confined to the Italian coast all the way down to the southern Adriatic.

The Journal of Geophysical Research has published a retrospect of scientific studies using CZCS (Mitchell, 1994). The numerous contributions to this special issue suggest that much work remains to be done to fully take advantage of the CZCS data base. Most areas of study are located in the north Atlantic and north Pacific, with very few examples from other areas.

Brown and Yoder (1994) used a multispectral classification scheme of CZCS global composites to separate pixels into coccolithophorid bloom and nonbloom classes. Classified blooms were more extensive in the Subarctic north Atlantic. Large expanses of bloom were also detected in the North Pacific, off Argentina, and in lower latitude marginal seas and shelf regions. Standing stock estimates suggest that the blooms may be a significant source of calcite and DMS sulfur on a regional scale, though they play a minor role on the global scale.

Santamaría-Del-Angel *et al.* (1994a) applied principal-component analysis to pigment concentration time series in the Gulf of California. They defined 14 biogeographic regions. There are pigment maxima in winter and spring, during the upwelling period on the eastern coast of the Gulf, and minima in summer. Strong tidal mixing and upwelling in the interior of the Gulf of California masked the effect of El Niño 1982-84, that showed up clearly in other coastal ecosystems of the eastern north Pacific (Santamaría-Del-Angel *et al.*, 1994b).

Müller-Karger *et al.* (1991) and Biggs and Muller-Karger (1994) studied the seasonal phytoplankton concentration and the effect of interacting cyclone-anticyclone eddy pairs on chlorophyll stocks in the Gulf of Mexico. The seasonal variation seaward of the shelf is synchronous throughout the Gulf of Mexico, with highest values in December to February and lowest values in May to July. The seasonal cycle in surface pigment concentration is controlled largely by the depth of the mixed layer. Between May and October, sea surface temperature fields are uniform but the Loop Current and large anticyclonic eddies could be traced with the CZCS (Muller-Karger *et al.*, 1991). In the western Gulf of Mexico, CZCS pigment concentrations were locally high in the flow confluence of cyclone-anticyclone pairs, and these eddy pairs were shown to transport high-chlorophyll shelf water seaward at least 100-200 km off-shelf (Biggs and Muller-Karger, 1994).

Yentsch *et al.* (1994) speculated that CZCS bandlike patterns observed on Georges Bank, in the western Atlantic, may be related to alternating zones of convergence and divergence created by tidal currents, as the water flows over large sand dunes and ridges which dominate the bottom topography. This banding appears to be seasonal, following the sequence of primary productivity in the Gulf of Maine.

CZCS images have proven to be useful for detecting oceanic features and describing oceanic phenomena that could not be studied from remotely sensed sea surface temperature alone. Such studies remain to be done for many regions of the world ocean.

5. PHOTOSYNTHESIS-IRRADIANCE RELATIONSHIP FOR PHYTOPLANKTON

Platt and Gallegos (1981) reviewed observations on the relationship between photosynthesis and available light, commonly known as the photosynthesis-irradiance ($P-E$) curves. To compare samples with different phytoplankton biomass, the productivity values (P) are normalized by the concentration of chlorophyll (Chl). The dependent variable is $P^B = P/Chl$, the assimilation ratio. For low values of scalar irradiance (E_o), the relationship is linear and may be characterized by the initial slope α^B (Figure 1). For higher values of E_o , the slope decays and P^B eventually attains an upper bound. Further increases in E_o may cause the slope to become negative (in the photoinhibited range). If there is no apparent photoinhibition the curve approaches an asymptote. The magnitude of the upper bound (P_m^B , the assimilation number) provides one way to characterize the curve. Another parameter is a combination of α^B and P_m^B called the conditioning factor $E_k = P_m^B / \alpha^B$. It is the irradiance such that P_m^B would be attained if the linear relationship between P^B and E_o were maintained (Figure 1).

^{14}C incubations are often done in the field to generate $P-E$ curves. Replicate samples are incubated for relatively long times under constant light. Under natural conditions, due to turbulence, phytoplankton cells stay a short time near the surface where E_o is high. Hence the photoinhibition effect may not be common in the ocean, and many researchers do not take into account the photoinhibition range of $P-E$ curves as in the equation originally proposed by Smith (1936):

$$P^B = \frac{P_m^B \alpha^B E_o}{(P_m^{B2} + \alpha^{B2} E_o^2)^{1/2}}$$

Another expression is by Jassby and Platt (1976):

$$P^B = P_m^B \tanh(\alpha^B E_o / P_m^B)$$

6. SATELLITE PIGMENT DATA IN ESTIMATING PHYTOPLANKTON PRODUCTIVITY

Three types of models are used to estimate primary productivity from satellite pigment data: by $P-E$ curves; by the quantum yield of photosynthesis; and by empirical models that estimate integrated photosynthesis for the entire euphotic zone.

Based on Smith's (1936) equation, Sathyendranath *et al.* (1989) proposed the model

$$P_{(z)} = \frac{P_m^B(z) B_{(z)} \{E_{(z)} / E_{k(z)}\}}{\left[1 + \{E_{(z)} / E_{k(z)}\}^2\right]^{1/2}}$$

where $P_{(z)}$ is primary productivity at depth z ($mgC\ m^{-3}\ h^{-1}$) and $B_{(z)}$ is the phytoplankton biomass represented by the satellite pigment concentration ($mgChl\ m^{-3}$) at depth z . This model implies knowledge of the photosynthetic parameters P_m^B and α^B for each depth z , and of the vertical profiles of $B_{(z)}$ and $E_{(z)}$, as they evolve in time. Also, the change of the spectrum and the angular distribution of light with depth must be considered (Sathyendranath and Platt, 1989). When scalar irradiance is used, there is no need to correct for the angular distribution of light.

Kiefer and Mitchell (1983) proposed a relatively simple mechanistic model:

$$P_{(z)} = \phi_{(z)} \bar{\alpha}_{ph(z)}^* B_{(z)} E_{o(z)}$$

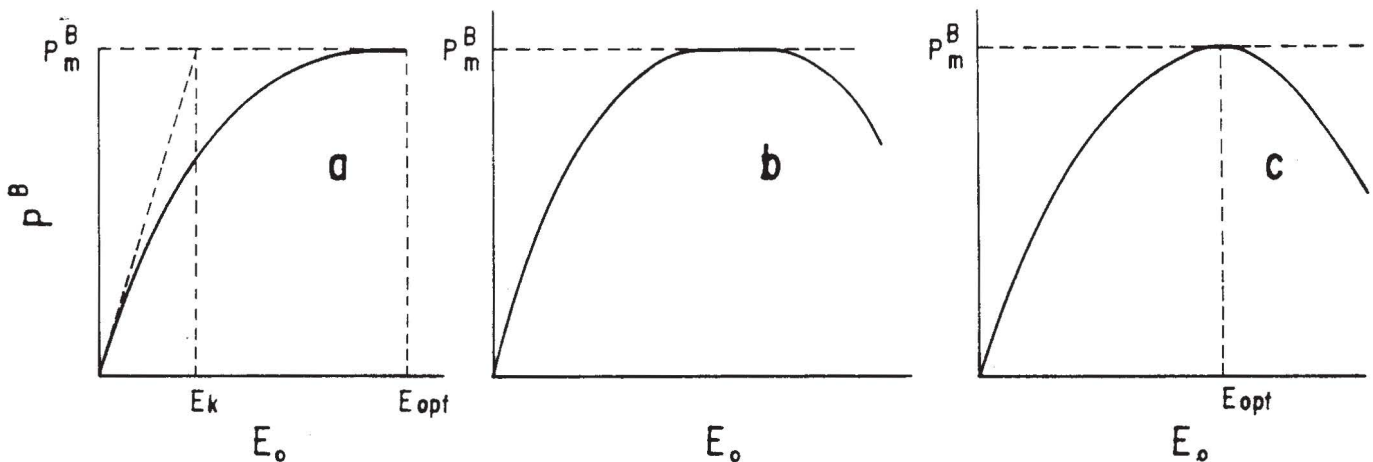


Fig. 1. Photosynthesis-Irradiance relationship. a) Case with no photoinhibition; b) Case where the productivity maximum is maintained for a relatively large irradiance range and then photoinhibition shows at high irradiance; c) Case where the productivity maximum is clearly present at an optimum irradiance.

where $\phi_{(z)}$, the quantum yield of phytoplankton at in-situ irradiance, is the ratio of number of moles of carbon photosynthesized to number of moles of photons absorbed; and $\bar{\alpha}_{ph(z)}^*$ is the average specific absorption coefficient of phytoplankton per unit of chlorophyll concentration. The spectrum of light changes with depth because the absorption spectra of the optical components of sea water are not flat. Thus, when using total $E_{o(z)}$ for the visible spectrum we have to introduce the average value $\bar{\alpha}_{ph(z)}^*$ weighted by the light available at each wavelength.

Morel (1978) showed that $\phi_{(z)}$ is a function of irradiance: it increases as $E_{o(z)}$ decreases for a given phytoplankton community. At low $E_{o(z)}$'s, $\phi_{(z)}$ tends to $\phi_{(z) \max}$. However, $\phi_{(z) \max}$ is not constant: it is equal to $\alpha_{(z)}^B / \bar{\alpha}_{ph(z)}^*$ where $\alpha_{(z)}^B$ is in moles of carbon instead of milligrams, and in moles of photons (Kirk, 1983). $\phi_{(z) \max}$ is also a function of the pigment composition of phytoplankton which controls $\bar{\alpha}_{ph(z)}^*$. We may define a parameter $G_{(z)}$ such that $\phi_{(z)} = G_{(z)} \phi_{(z) \max} = G_{(z)} (P_m^B / E_k \bar{\alpha}_{ph(z)}^*)$. $G_{(z)}$ is equal to unity at low $E_{o(z)}$'s, and it decreases with the increase of $E_{o(z)}$.

Alvarez-Borrego (1995) suggested that since $P_{(z)}$ is the same irrespective of the model used to estimate it, Sathyendranath *et al.*'s (1989) and Kiefer and Mitchell's (1983) models are equivalent. Thus:

$$\frac{P_{m(z)}^B B_{(z)} \left\{ E_{o(z)} / E_{k(z)} \right\}}{\left[1 + \left\{ E_{o(z)} / E_{k(z)} \right\}^2 \right]^{1/2}} = G_{(z)} (P_{m(z)}^B / E_{k(z)}) B_{(z)} E_{o(z)},$$

$$G_{(z)} = \frac{1}{\left[1 + \left\{ E_{o(z)} / E_{k(z)} \right\}^2 \right]^{1/2}}.$$

As $E_{o(z)}$ tends to zero, $G_{(z)}$ tends to unity; and as $E_{o(z)}$ attains very high values $G_{(z)} (E_{o(z)} / E_{k(z)})$ tends to unity and $P_{(z)}$ tends to $P_{m(z)}$. Other authors have derived similar expressions for $G_{(z)}$ with different equations for the P - E curve. Thus, Bidigare *et al.* (1992) used the hyperbolic tangent expression to derive the expression

$$\phi_{(z)} = \phi_{(z) \max} (E_k / E_{o(z)}) \tanh(E_{o(z)} / E_k).$$

Hence, it is possible to estimate values of $\phi_{(z)}$ from P - E curves and $\bar{\alpha}_{ph(z)}^*$.

To estimate the net integrated primary productivity for the entire euphotic zone ($\text{gC m}^{-2} \text{d}^{-1}$), Morel (1991) proposed the model

$$P = PAR_{(0+)} Chl_{TOT} \Psi,$$

where $PAR_{(0+)}$ stands for the photosynthetically active radiation just above the surface, Chl_{TOT} is the integrated

chlorophyll for the whole euphotic zone (g m^{-2}), and Ψ is the light utilization index ($\text{gC gChl}^{-1} \text{Einstein}^{-1} \text{m}^2$) (Falkowski, 1981).

Estimation of marine primary productivity from photosynthetic pigment data derived from satellites requires a proper characterization of the physiological parameters of phytoplankton communities for different oceanic areas. According to Morel (1991), the physics involved is rather accurately modelled but the choice of physiological parameters may be less well documented.

It is reasonable to expect that photosynthetic performance will reflect the nutritional status of phytoplankton. Should nutrients be incorporated into models of oceanic photosynthesis as a function of chlorophyll and light (Cullen *et al.*, 1992)? Over the past few decades P_m^B values have been interpreted as indicative of nutritional status (i. e., Small *et al.*, 1972). However, Cullen *et al.* (1992) concluded that P^B at ambient irradiance appears to be only weakly influenced by nutrient supply; the effect of nutrient variability is mostly taken into account by pigment concentration variability. Nutrients control the phytoplankton biomass. The physiological parameters are mostly controlled by the irradiance regime, which is controlled by turbulence.

Prézelin *et al.* (1991) reviewed the effect of physical structure of the aquatic environment on phytoplankton photosynthesis. Periodicity in production parameters can be linked to intrinsic and largely environmentally-independent biological clocks and/or environmentally-mediated cell cycle events. Alvarez-Borrego and Gaxiola-Castro (1988) studied the effect of water stratification on photosynthesis of phytoplankton communities in the Gulf of California. They calculated ϕ , the potential energy relative to the mixed state, as defined by Simpson and Hunter (1974), plotted versus the average P_m^B and α^B values for the euphotic zone of each station. In general, the average P_m^B and α^B values increased when ϕ decreased down to a certain value (Figure 2); at very low values ($< 2 \text{ J m}^{-3}$), both P_m^B and α^B decreased. This suggests that in the Gulf of California moderate turbulence causes higher P_m^B and α^B values than does strong turbulence or stratification.

Primary productivity on the cold side of a seasonally recurring front in the California Current may not be due to higher P_m^B 's than on the warm side. Gaxiola-Castro and Alvarez-Borrego (1991) generated P - E curves for whole communities sampled across the front and showed that higher primary productivity values on the cold side appear to be due to a shallower subsurface chlorophyll maximum, which causes less limitation of light for phytoplankton.

The sensor in the satellite only generates single estimates of photosynthetic pigments at a time for each location (C_{sat}). There is no information on the vertical structure of phytoplankton biomass $B_{(z)}$. Vertical homogeneity is often assumed, i. e., a well-mixed euphotic zone. This

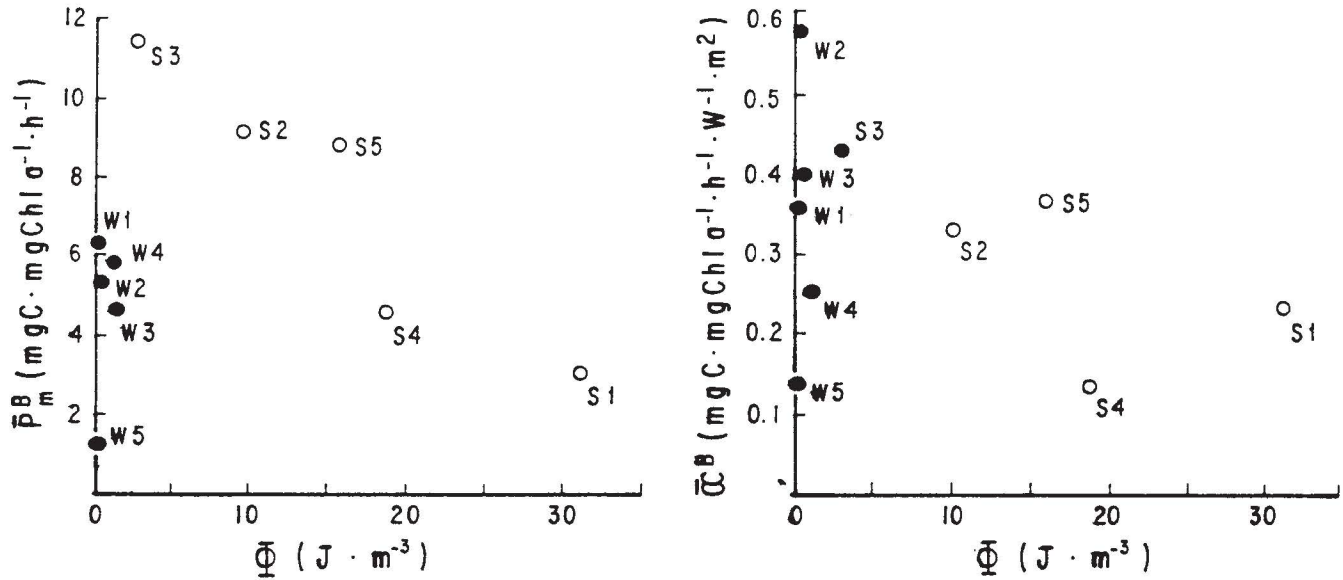


Fig. 2. Average assimilation number (\bar{P}_m^B) for the euphotic zone, and average initial slope ($\bar{\alpha}^B$), of each station, versus the stratification index (ϕ) (after Alvarez-Borrego and Gaxiola-Castro, 1988).

may either over- or underestimate primary productivity. Errors depend on where the deep Chl maximum (DCM) is.

Platt *et al.* (1988) proposed the following model of the vertical profile of $B_{(z)}$:

$$B_{(z)} = B_o + [h / (\sigma(2\pi)^{1/2})] \exp[-(z - z_m)^2 / 2\sigma^2] .$$

This is a Gaussian curve representing the DCM over a constant background B_o (mg · m⁻³) (Figure 3). The three parameters may be fitted to the shapes of the DCM likely to be encountered in the field. Thus, h (mgChl · m⁻²) controls the total biomass above the baseline B_o ; z_m (m) is the depth of the maximum; and σ (m) defines the thickness of the DCM layer.

Morel and Berthon (1989) processed about 4,000 vertical profiles of pigment (*Chl+Phaeo*) in oceanic Case I waters. They categorized the profiles into seven trophic situations and computed a mean vertical profile for each. These situations fall between a quasi-uniform profile in eutrophic waters, and a strong deep maximum in oligotrophic waters.

Primary productivity may be either "new" or "regenerated" productivity. When light is available, the vertical flux of nutrients (NO_3) from below the euphotic zone defines the maximum rate of absorption of these new nutrients, and the ensuing primary productivity is considered to be new productivity (Dugdale and Goering, 1967). In contrast, the regenerated productivity is based on recycled nutrients (NH_3). New productivity (P_n) is the part of total primary productivity (P_t) in excess of local community metabolism. The ratio of P_n to P_t is called the f -ratio. This

fraction of the primary productivity can be removed without destroying the long-term integrity of the pelagic ecosystem (Eppley and Peterson, 1979).

New productivity limits the transport of CO_2 by marine biota, from the euphotic layer to deeper waters. If dissolved inorganic carbon moves upward with the vertically transported nitrate, only the sinking flux due to new production associated with nitrogen fixation and nutrient inputs from terrestrial and atmospheric sources can be identified as a biologically-mediated transport of atmospheric carbon to the deep ocean (Eppley and Peterson, 1979). Sathyendranath *et al.* (1991) estimated new productivity for the Georges Bank region in the northwestern Atlantic by compound remote sensing. Sea surface temperature (SST) was estimated by the advanced very-high-resolution radiometer (AVHRR) technique. Nitrate concentration may be estimated from temperature through empirical relations, a method that works particularly well on Georges Bank. In some waters, f is a well-known function of NO_3 . Remotely sensed data on ocean color can be used to estimate P_t , allowing P_n to be found as the product of f and P_t . Such ideas open a new possibility for the study of carbon fluxes at the regional and global scales, and on time scales from days to years.

7. RESEARCH FOR THE NEAR FUTURE

Beginning with the launch of SeaWiFS the earth science community can look forward to what may become a long-term ocean color time series (Mitchell, 1994). Calibration and validation of data generated by SeaWiFS have been under detailed discussion (i.e., Mueller *et al.*, 1991). One lesson learned from CZCS is the need for good radio-

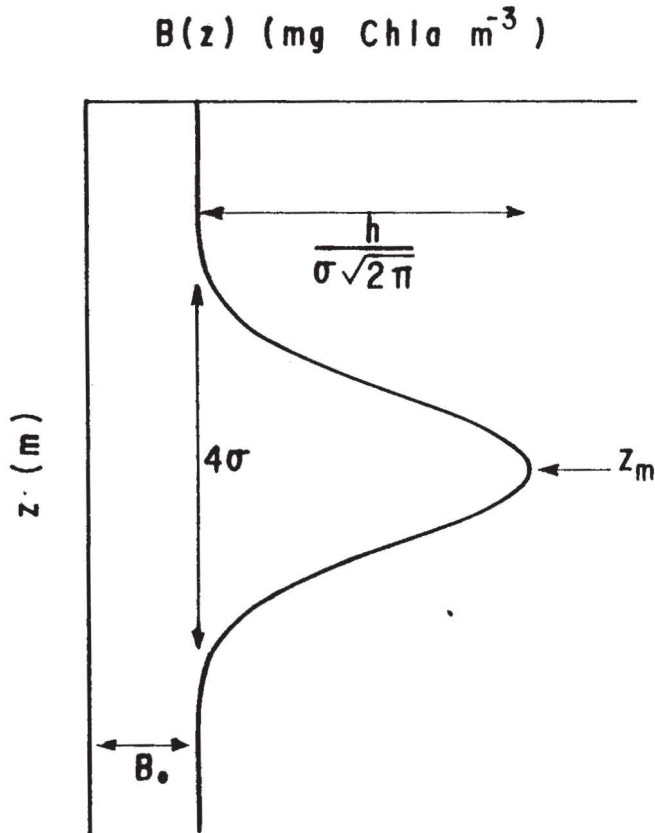


Fig. 3. Idealized deep chlorophyll maximum, represented by a Gaussian curve superimposed on a constant background. Parameters, B_0 = background biomass (mg m^{-3}), z_m = depth of chlorophyll maximum (m), σ = standard deviation (m) and h = total biomass above the background (mg m^{-2}). The peak height above the baseline is given by $h/(\sigma\sqrt{2\pi})$ (after Platt *et al.*, 1988).

metric calibration and stability, and for "sea truth" stations to monitor the performance of the sensor and the algorithms (Evans and Gordon, 1994).

The estimation of pigment concentration from CZCS data failed in areas with high concentration of suspended matter and CDOM (Case II waters) (Doerffer and Fischer, 1994). New algorithms using the SeaWiFS bands must be constructed. Hopefully, with the extra bands the CZCS did not have, the new bio-optical algorithms will be capable of discriminating between these optical components and the photosynthetic pigments to relax the assumption of their covariability.

Once the SeaWiFS is orbiting, models to simulate water-leaving radiance from an ocean containing a bloom of coccolithophorids could be tested with contemporaneous pigment, particulate calcite, and available satellite data (Ackleson *et al.*, 1994).

We want to be able to accurately characterize the phytoplankton biomass patterns and their temporal changes, in order to relate these patterns to the physical phenomena of

each oceanic region and to estimate primary productivity and its role on carbon flux. It is important to learn how to merge bio-optical and other data sources with mathematical models of the components of primary productivity and other processes controlling carbon fluxes in the ocean (Falkowski *et al.*, 1993).

There is a need for more local studies on the effect of different physical phenomena upon the physiological parameters of phytoplankton. The sequence of upwelling, with intensification and relaxation events; the sequence of spring and neap tides; the effect of internal waves; the passage of tropical storms; and other phenomena causing turbulence and/or vertical advection may change the irradiance regime of phytoplankton and its physiological parameters.

In order to properly use the primary productivity models, in situ pigment data need to be used to relate surface values of satellite derived variables, such as pigment and temperature, to the shape of the $B(z)$ vertical profiles, either in a descriptive or analytical manner. Oceanic regions should be characterized in terms of the behavior of the $B(z)$ profiles.

Differences in the temporal patterns of phytoplankton concentrations may be determined from ocean physics or from the zooplankton species. Thus, future attempts of delineating biogeochemical provinces may have to take zoogeography and phytogeography into account (Banse and English, 1994).

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