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Estimating ocean production from satellite-derived chlorophyll : insights from the Eastropac data set Télédétection de la chlorophylle Photo-adaptation

Primary production Satellite images of chlorophvll Photoadaptation (of photosynthesis) Mixing layer depth Phytoplankton

Couche de mélange Phytoplancton

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ABSTRACT

The Eastropac expedition took place in 1967-1968 in the Eastern tropical Pacific Ocean. Primary production was related to near-surface chlorophyll in these data. Much of the variability in the relation was due to the light-history of the phytoplankton and its photoadaptive state. This was due to changes in the depth of mixing of the surface waters more than changes in insolation. Accurate estimates of production from satellite chlorophyll measurements may require knowledge of the temporal and spatial variation in mixing of this region.

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RÉSUMÉ

Estimation de la production océanique par télédetection de la chlorophylle : un aperçu des données « Eastropac »

Dans les données de la campagne Eastropac, qui s'est déroulée en 1967-1968 dans l'Est du Pacifique tropical, la production primaire est reliée aux concentrations superficielles en chlorophylle. Une grande partie de la variabilité de cette relation est le fait de l'exposition antérieure du phytoplancton à la lumière et de sa photoadaptation, et ce conditionnement dépend davantage de la profondeur de la couche de mélange que des variations de l'insolation. L'estimation précise de la production primaire à partir de mesures satellitaires de la chlorophylle peut donc requérir, dans une telle région, la connaissance des variations spatio-temporelles de l'intensité du mélange vertical.

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INTRODUCTION

The coastal Zone Color Scanner (CZCS) aboard the Nimbus 7 satellite has for the first time provided large-scale views of near-surface chlorophyll-like pigments (Gordon et al., 1983 : Hovis et al., 1980),

particularly of the coastal regions of North America. Within a few years satellite images of chlorophyll may be available for many regions of the ocean and hopefully for the global ocean (National Academy of Sciences, 1984). A second generation instrument to replace the CZCS is not yet funded as of this writing.

Characteristically these images have a large spatial scale. Potentially these images can also provide temporal coverage adequate to describe event scale and longer term phenomena. For example pigment changes near the Galapagos Islands were noted during the recent El Niño events (Feldman *et al.*, 1984). Satellite images were used also to study other interannual changes in pigments and primary production in the eastern equatorial Pacific (Feldman, 1986). Because of these prospects it is useful to ask whether primary productivity can be quantitatively reconstructed from the chlorophyll images in order to provide information relevant to biological resources of the ocean and to global biogeochemical cycles. Needed is a relationship of the form

Production (mgC $m^{-2} d^{-1}$) =

= $\dot{F} \times Pigment (mg m^{-3}), (1)$

where Pigment is the near-surface, chlorophyll-like pigment and F is either a constant or a variable that can be constrained by environmental parameters.

Direct comparisons of ocean production with satellitederived chlorophyll are few (Smith *et al.*, 1982). As an indirect approach to evaluating F we can compare primary production and chlorophyll in historical data from oceanographic cruises to examine the relations between primary production and near-surface chlorophyll and the temporal and spatial variations in such relationships. This report considers the Eastropac data collected in 1967-68 on chlorophyll and primary production in the eastern tropical Pacific, including the equatorial upwelling area (Owen, Zeitzschel, 1970 a).

Previous comparisons of primary production and near-surface chlorophyll have shown clear regional differences that may determine the choice among alternative strategies of estimating primary production from space. For example, in the central gyre of the North Pacific, near-surface chlorophyll is not correlated with primary production in the historical ship data (Hayward, Venrick, 1982). Production there varies by only a factor of two between stations, seasons and years, and a mean value, either of F or of primary production, might be adequate for most models of carbon flux. On the other hand, production is related to near-surface chlorophyll and to certain environmental variables in southern California coastal waters and the historical ship data suggest satellite chlorophyll data can be used effectively to estimate primary production (Eppley et al., 1985), a conclusion reached also by comparing satellite chlorophyll with concurrent measures of chlorophyll and production (Smith et al., 1982). Significant correlations have been found between primary production and surface chlorophyll in several studies (Lorenzen, 1970; Taniguchi, 1972; Smith. Baker, 1978; Eppley et al., 1985) when data from disparate ocean regions were included in the correlations, but the predictive value of such coarse relations may not be great.

METHODS

The Eastropac expedition consisted of seven 2-month cruise periods from February, 1967 through April, 1968. The cruises covered an area between 20N and 20S and from the coast of America to 119W. We have limited our analysis to the offshore area bounded by 93W on the east, 119W on the west, and 300 km offshore on the north in order to emphasize the equatorial upwelling region (Fig. 1). The Eastropac







data have been published in the form of atlases (Love, 1970-1977) which contain detailed cruise tracks and data in chart form. Primary production was measured with the ¹⁴C method in noon to sunset, simulated in situ incubations (Owen, Zeitzschel, 1970 b). Samples from each of seven depths in the euphotic zone were incubated under neutral density screens at the temperature of surface seawater. The resulting rates were integrated over depth to express water column pri-mary production mgC $m^{-2} d^{-1}$. This quantity is hereafter called Pi (Bannister, 1974). Chlorophyll and phaeopigments were measured using a fluorometer (Owen, Zeitzschel, 1970 a). Insolation was measured on the ships with pyrheliometers (Owen, unpublished). The stepwise linear regression program we used, number P2R, is from BMDP-83 (Dixon, 1983). To estimate the chlorophyll-like pigments expected to be registered by the Coastal Zone Color Scanner and its successors, we calculated the average value of chlorophyll *a* plus phaeopigment for the upper two sampling depths, mg m⁻³. This value is called Ck (Smith, Baker, 1978). We calculated the diffuse attenuation coefficient for light, Kt, by assuming the irradiance at the bottom of the euphotic zone equaled one percent of the surface value.

It is assumed that the 14C method of measuring primary production, as used in the Eastropac expeditions and elsewhere since 1952, provides an accurate measure of primary production during the incubation period. Thus the discrepancies between results with this method and those that integrate over larger space and time scales are due to an inadequate scale of sampling, a problem that may be overcome using satellite information.

RESULTS

Multiple regression model

Since present or future satellite data may include sea surface temperature, insolation, and winds from which the depth of mixing might be estimated, we used these variables (except winds) in stepwise multiple linear regression models of Pi. In the absence of wind data we used mixed layer depth, inferred from temperature profiles. The results were not impressive and at most only 34 % of the variability in Pi could be explained (Tab. 1). The second equation of Table 1 includes a parameter, Ic (a concept introduced by Myers and Graham, 1959), an estimate of the average irradiance experienced by a phytoplankter in the euphotic zone. Ic combines insolation, Kt and mixed layer depth in an analytical expression that has proved useful in studies of photosynthesis and growth of algal cultures (Tab. 1).

Table 1

Stepwise multiple linear regression equations for Pi (primary production, mg C m⁻²d⁻¹), Ck (near-surface chlorophyll-like pigments, mg m⁻³), lo (irradiance, watt m⁻²), Kt (diffuse attenuation coefficient, m⁻¹), MLD (mixed layer depth, m), and Ic (mean irradiance experienced by the phytoplankton : $I_c = (I/KLMLD)$ (1exp-KLMLD). Values in parenthesis represent the variance explained by the parameter.

$\ln Pi = 6.90 + 0.722 \ln Ck (0.269) -$	+ 0.0010 Io (0.033) - 8.50 Kt
(0.019) - 0.0043 MLD (0.016)	Total $r^2 = 0.336$
$\ln Pi = 5.07 + 0.580 \ln Ck (0.269)$	$+ 0.245 \ln I_{c} (0.047)$
	Total $r^2 = 0.316$

The Ck was the most important variable in these equations (Tab. 1). Ic explained about 5% of the variability, only a bit more that insolation alone. Regression equations without the log transformation of variables explained less of the variability in Pi than those shown.

Analytical model

Bannister (1974) and Smith and Baker (1978) developed a simple model relating Pi and Ck to the photoadaptive state of nutrient-sufficient phytoplankton:

Pi = 2.3 Pmax (Ck/Kt), (2) where Pmax is the highest rate of photosynthesis per weight of chlorophyll observed at some discrete depth in the water column. Figure 2 shows the result in the form of the identity Pi/Ck = F = 2.3 Pmax/Kt. The slope of the least squares regression line is 2.3, as predicted, and about 70 % of the variation in Pi is accounted for in the regression. We can draw two conclusions from Figure 2. First, variations in F are probably due to photoadaptation. The photoadaptive state of the plankton reflects its recent light history, that is whether the plankton grew in bright or dim light. Photoadaptation depends upon irradiance, daylength and the depth of mixing of the surface waters as those are the factors which determine the parameters of the photosynthesis-light curves of the plankton. They are expected to be correlated with F (Smith,



Figure 2

Inglie 2 Variation in the ratio Pi/Ck (primary production/near surface chlorophyll-like pigments = F of equation 1) with the ratio Pmax Kt (see text). Units of Pi are mgC m⁻²d⁻¹, Ck mg m⁻³, Pmax mgC (mg pigment)⁻¹d⁻¹, and Kt m⁻¹. Each point represents a station. The regression line slope was 2.3. The regression explained 71 % of the variation.

Baker, 1978). Second, the fit implies that most of the light attenuation is due to plankton.

Variations between current systems

Blackburn *et al.* (1970) described the spatial and temporal variation in chlorophyll and Owen and Zeitzschel (1970 *a*) the corresponding variations in primary production before the stations could be assigned to discrete currents; the geostrophic currents were described later (Tsuchiya, 1974). Table 2 shows

Table 2

Data from the Eastropac expedition, 1967-1968: Pi (primary production mg C $m^{-2}d^{-1}$); Ck (near-surface chlorophyll-like pigments mg m^{-3}) and the ratio PilCk; mean (and standard deviation) for stations in discrete currents.

Current	No. stations	Pi	Ck	F = Pi/Ck
NEC	31	243 (136)	0.16 (.09)	1733 (1134)
NECC	21	194 (133)	0.16 (.07)	1450 (1254)
SEC	54	205 (105)	0.20 (.09)	1160 (638)
Equator	20	307 (159)	0.25 (.07)	1236 (636)

NEC = North Equatorial Current. NECC = North Equatorial Counter current. SEC = South Equatorial Current.

the variation in F between the North Equatorial Current (NEC), North Equatorial Counter Current (NECC), and South Equatorial Current (SEC). The mean value of F was higher and the variability was greatest in the NECC and NEC. Both regions were outside the upwelling area as judged by the absence of nitrate at 10 m depth. Within the SEC, and at stations within about 1.5° latitude of the Equator, where no geostrophic flow could be assigned, F was about 1 200 (Tab. 2), nitrate was present at all these stations.

Equatorial stations with uniform chlorophyll over depth, and therefore with well mixed waters, showed the lowest values of F (about 600 ; the lower limitvalue of F is about 100; Eppley et al., 1985) while higher values, up to 2 400, were found in stratified waters with subsurface chlorophyll maxima. Stations in both the NEC and NECC showed a larger range in the variance of chlorophyll over depth, implying greater chlorophyll stratification, than in the SEC.

DISCUSSION

Highest values of F and greatest variability in Pi and Ck were found in the NEC and NECC where the waters were both oligotrophic, judged by the absence of nitrate at 10 m depth, and stratified. Conversely F was lowest in the nutrient-rich SEC. There, nutrients were in excess and were not likely to limit primary production. Rather, changes in primary production resulted from changes in stability and mixing ; production was reduced by a poverty of light rather than nutrients (Barber *et al.*, 1983; Menshutkin, Finenko, 1975 - cited in Vinogradov, 1981). The reduction in primary production during the 1982 El Niño event was due to a greatly increased mixing depth, rather than a lack of nutrients (Barber et al., 1983).

The variability in the depth distribution of chlorophyll near the Equator and in the SEC generally suggests that even in the nutrient-rich equatorial waters of the eastern Pacific the intensity of vertical mixing must be patchy, as reported earlier from both biological (Vinogradov, 1981) and physical observations (Knox, Anderson, 1985 and references therein).

Improved models for estimating the intensity of mixing using satellite wind data may be possible. At present only about 34 % of the variability in Pi could be explained using our stepwise multiple linear regression model. Better estimates would require either in sing measurements of the intensity of mixing or of photosynthetic parameters such as Pmax. It is interesting that a goal of the TROPIC HEAT program is ... to parameterize the turbulence in terms of larger scale quantities which are both easier to monitor and resolvable in model studies " (Eriksen, 1985). Attainment of this goal would also facilitate estimating primary production from satellite chlorophyll in the eastern tropical Pacific. Also, more extensive studies of primary production and chlorophyll variability in relation to hydrography have taken place in the tropical Atlantic. Variability has been examined on time scales from 24 hour (Le Bouteiller, Herbland, 1982), to several days (Herbland, Le Bouteiller, 1982) and seasons (Herbland et al., 1983). Analysis of this data set is expected to increase significantly our understanding of the use of satellite data to estimate primary productivity in equatorial waters.

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