Photosynthesis-irradiance relationship for winter phytoplankton in Pacific waters off Mexico

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ABSTRACT
In the winter season, 1981, we generated photosynthesis-irradiance curves for phytoplankton from ten locations of the Pacific region off Mexico (15°-28°N). In general, photosynthetic parameters, phytoplankton abundance and chlorophyll a showed great vertical changes within the euphotic zone, even in cases where thermohaline vertical homogeneity indicated high instability and mixing. The assimilation number \( P^{\alpha} \) had a two to three fold variation with depth within the mixed layer. Where the bottom of the euphotic zone was within the thermocline, \( P^{\alpha} \) was 5 to 25% of the values for the surface and near surface waters. There was no particular geographic trend of photosynthetic parameters. Relatively high \( P^{\alpha} \)'s for surface and subsurface waters of the tropical region, with low or undetectable nutrient concentrations, indicated use of regenerated nutrient made available through grazing, or nutrient flux through the thermocline by turbulence, or both.


INTRODUCTION
Two important parameters of the photosynthesis-irradiance (P-I) curve of phytoplankton are \( \alpha \), the initial slope, and \( P^{\alpha} \), the assimilation ratio at saturating light, or assimilation number (Platt et al., 1976). Marra (1980) has shown that the photosynthetic parameters are variable in time and such phenomena can only be analyzed by time series analysis. Due to the cost, it is very difficult to produce this kind of time series for oceanic waters; but it is desirable to have at least some data to compare relatively large regions of the ocean. We used the Varifront-II cruise of the US Navy's "DeSteiguer" as an opportunity to generate P-I curves for ten sites from 28°N to 15°N off Mexico, in winter 1981. Our objectives were to describe the vertical variation of photosynthetic parameters, and to compare their values from the California current system and from the tropical region off Mexico.
METHODS AND MATERIALS

At ten hydrographic stations (Fig. 1; during 8-26 January 1981) we took phytoplankton samples from five depths corresponding to 100, 50, 25, 10 and 1% of the irradiance measured just below the sea surface ($I_0$). Irradiance was measured with a photometer, Kahlsico No. 268WA310, with cosine corrector, filtered to give only the photosynthetic active radiation. The total length of the photometer cable was only 15 m; we thus measured irradiance at different depths up to 12 m, and estimated an average attenuation coefficient which was assumed to be constant—throughout the euphotic zone. Lambert-Beer's law was used to estimate depths corresponding to different percentages of $I_0$.

Sampling was done with 7-litre Niskin bottles. Ten 125 ml clear glass bottles were filled with water from each sampled depth; each glass bottle was inoculated with 5 $\mu$Ci of $^{14}$C, basically following Steemann-Nielsen (1952). Two replicate samples from each depth were incubated on board, in sunlight, at each of five irradiances: 86, 32, 14, 7 and 1% of solar irradiance measured on deck. The incubator consisted of acrylic tubes with black plastic filter screens to control irradiances. Incubation irradiances were measured inside empty bottles and tubes. Incubations were done between 11:00 and 14:00 hrs. After ~2 hr incubation, samples were filtered with 0.45 $\mu$m pore membrane filters. The filters were put into liquid scintillation vials with 15 ml of Aquasol. $\beta$ counting was done in the Naval Ocean System Center laboratory at San Diego, California, with a Nuclear Chicago unilux III counter. Calculations of assimilated carbon were done following Strickland and Parsons (1972). For each sampled depth we also measured temperature ($T^\circ\mathrm{C}$), salinity, chlorophyll $a$ (Chl $a$), nutrients (NO$_2$, NO$_3$, PO$_4$, and SiO$_2$) and phytoplankton abundance. Chl $a$ samples were obtained using 0.45 $\mu$m Millipore filters, and analysis were performed basically by the SCOR-UNESCO (1966) spectrophotometric method, with second readings after acidification following Lorenzen (1967). Phytoplankton abundance was determined by the Utermöhl (1958) inverted microscope technique. Values of $\alpha$ were calculated with simple linear regression of $I$ and $P^\beta$, with data of the two lowest irradiances of each curve, and assuming $P^\beta=0$ at $I=0$. When the correlation coefficient of this regression ($r^2$) was lower than 0.7, we considered the data to be too scattered and did not use that $\alpha$. Values of $P^\beta$ were taken from the graphs, and values of $I_m$ are the corresponding optimum irradiances. These $P^\beta$'s should be taken as minimum estimates because we have very few data points at high irradiances.

RESULTS AND DISCUSSION

Results are summarized in the Table; and illustrations are provided for stations D, F (California Current), J, K (entrance to the Gulf of California), L and O (tropical region off Acapulco; Fig. 2). There was no particular geographic trend of euphotic zone depth variation. The euphotic zone was within the mixed layer at stations F, H and L; and the bottom of the euphotic zone (1% $I_0$ depth) of stations G, J, K, KP, N and O was within the thermocline and nutricline. At station D we had a vertical $T^\circ\mathrm{C}$ gradient from the sea surface, with a difference of ~3.5$^\circ\mathrm{C}$ between the surface and the 1% $I_0$ depth (Tab.). With the exception of nutrients,
in general there were great vertical changes of variables controlling primary productivity, even where thermona
tive vertical homogeneity indicated high instability and mixing of the euphotic zone. Nutrients were in general
low for surface and near surface waters; although they were high in the deepest sections of the euphotic zone when these were within the thermocline. Chl a showed subsurface maxima at stations D, K, L, N and O, and presented highest measured values at the bottom of the euphotic zone at stations F, G, H, J and N (Tab.). Phytoplankton abundance changed irregularly with depth and with no correlation with Chl a. Nannoplankton
dominated the phytoplankton with relatively few diatom and dinoflagellate cells. In some cases, Chl a was high and nannoplankton abundance was relatively low (e.g.: station O), possibly indicating high abun-
dance of picoplankton (size <2.5 μm) not detected with the Utermöhl technique. PPHY did not reach light photoinhibiting values in incubation experiments for stations F and G, with exception of those for samples from the 1% I0 depth; also, the surface sample of station J did not show clear sensitivity to photoinhibition. In all other cases, phytoplankton showed clear sensitivity to photoinhibition, even surface samples. The initial slope, a, varied quite irregularly with depth, with a range of 0.06 to 0.95 (Tab.). PPHY clearly changed with depth, very often presenting subsurface maxima. PPHY had a two to three fold variation within the mixed layer. In general, PPHY of the 1% I0 depth was relatively low. When phytoplankton become conditioned to lower irradiances PPHY decreases (Prézelin, Matlick, 1980; Falkowski, Owens, 1980). Where the 1% I0 depth was
within the thermocline, its $P_m$ and $I_m$ were lower than where it was within the mixed layer (Tab.). This was due to greater residence time of phytoplankton at depth in the first case. The very high $P_m$ value of the 1% $I_m$ depth of station KP was an anomalous exception, and our data are not sufficient to provide an explanation. Our data indicate that phytoplankton were not conditioned to the irradiances at the depths sampled. Phytoplankton from the bottom of the euphotic zone presented $I_m$'s much higher than 1% $I_m$ phytoplankton from the surface often presented $I_m$'s lower than $I_m$, perhaps because turbulence moves phytoplankton up and down the water column. The subsurface $P_m$ maximum found for most of our stations is a striking feature. One possible explanation for this maximum is that subsurface waters were brought to the surface by turbulence very shortly before sampling and the rapid change to strong irradiance depressed $P_m$. According to Steemann-Nielsen (1962), when changing from a weak irradiance to a strong one, some temporary changes may take place in some species of phytoplankton; in Chlorella, after 3 hours at strong irradiance a substantial part of the photochemical mechanism is inactivated and $P_m$ decreases to about 50% of the initial value. Marra (1978) showed that at high irradiance, photosynthetic rate of a diatom (Lauderia borealis) decreased after ~2 hrs, and after seven hours it was about 50% of the initial value, with a very slight increase of Chl a content per cell. The mechanism producing inactivation of the photochemical reaction in photosynthesis has the effect that, in the sea, curves showing the rate of photosynthesis versus depth on bright days usually have the maximum not at the very surface, but at 30-50% $I_m$ depth (Steemann-Nielsen, 1975). Thomas (1970) estimated $P_m$'s for phytoplankton from 10 m depth, from a series of stations in the Eastern Tropical Pacific. His stations with undetectable NO$_3$ had ammonium and amino nitrogen concentrations of only ~0.5 $\mu$M and had a somewhat lower mean $P_m$ (mean=3.15; range: 1.15 to 5.18) than those stations with nitrogen-rich waters (NO$_3$ up to 7.8 $\mu$M) (mean=4.95; range: 3.53 to 6.19). His nutrient-poor water stations were north of the Equator, in the region where our L, N and O stations are. Our $P_m$ values for stations L, N and O, at depths close to 10 m, had a range of 1.6 to 8.2, with a mean of 4.6 (Tab.). Malone (1971a and b) estimated $P_m$'s for phytoplankton samples collected from 2 m depth and incubated at 42 W.m$^{-2}$. His $P_m$'s for Tropical surface waters with undetectable NO$_3$ had a range of 1.1 to 3.6. Our $P_m$ surface value for station O was 2.0, but those for stations L and N were ~6.0. Malone's (1971a) $P_m$'s for the Peru Current region are in general higher than our surface values, with a range of 5.7 to 20, and with a mean of NO$_3$ of 5.3 $\mu$M. Station K had the highest surface NO$_3$ and $P_m$ (9.6) of our data set (Tab.) and NO$_3$ was only ~0.8 $\mu$M. Malone's (1971b) $P_m$'s for the California Current region (36°-45°N) fluctuated around a mean of 7.7±1.1 and did not vary with NO$_3$. Our results corroborate those of Thomas (1970) and Malone (1971a and b) and indicate that low nutrient concentrations are not a sufficient index of "water poorness". It is interesting to notice that with undetectable NO$_3$ values and very low PO$_4$ values (~0.1 $\mu$M) in the mixed layer, stations L and N had relatively high $P_m$ values, while station O had relative low values (Tab.). $P_m$ values of stations L and N indicate the possibility of two mechanisms: "regenerated" nitrogen (and other nutrients) was being made available through grazing pathways (Dugdale, 1985); and b) some nutrient flux was occurring through the thermocline, as suggested by Klein and Coste (1984). We have to consider that low oxygen and high nutrient waters are close to the sea surface in this region of the Pacific (~100 m; Alvarez-Borrego et al., 1978), and it does not take much energy to mix them with surface waters in winter (notice, for example, that at 77 m PO$_4$ was 1.4 $\mu$M and NO$_3$ was 17 $\mu$M, at station O). Grouping stations D, F, G and H (California Current Region) and KP, L, N and O (Tropical Region), we tested the hypothesis that the mean $P_m$ of surface and near surface waters (first 10 m) of one region was different from that of the other, and also for the waters at the bottom of the euphotic zone. In both cases the result was that differences are not significant even at the 60% confidence level.

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