

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

Phytoplankton
Photosynthesis-irradiance
Assimilation number
Eastern Pacific
Winter

Phytoplankton
Photosynthèse-irradiance
Quotient d'assimilation
Pacifique oriental
Hiver

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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_m^B) 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_m^B 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_m^B '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.

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RÉSUMÉ

Relation entre la photosynthèse et l'irradiance pour le phytoplancton d'hiver dans les eaux du Pacifique au large du Mexique

Nous avons obtenu les courbes de photosynthèse contre irradiance pour le phytoplancton de dix endroits au large du Mexique (15° - 28° N), pendant l'hiver 1981. Les paramètres photosynthétiques, l'abondance du phytoplancton et de la chlorophylle présentaient de fortes variations verticales dans la zone euphotique, y compris dans les cas où l'homogénéité thermohaline verticale indiquait une grande instabilité et un mélange prononcé. Le nombre d'assimilation (P_m^B) varie d'un facteur deux ou trois avec la profondeur dans la couche de mélange. Quand le bas de la zone euphotique se trouve dans la thermocline, P_m^B varie entre 5 et 25% de sa valeur à la surface. Nous n'avons pas trouvé de répartition géographique particulière des paramètres photosynthétiques. Des valeurs relativement élevées de P_m^B dans les eaux tropicales de surface, accompagnées de valeurs faibles ou indétectables des sels nutritifs, traduisent l'utilisation de sels nutritifs régénérés par le broutage, ou le flux de sels à travers la thermocline, ou les deux.

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INTRODUCTION

Two important parameters of the photosynthesis-irradiance (P-I) curve of phytoplankton are α^B , the initial slope, and P_m^B , 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 μ Ci of 14 C, basically following Steemann-

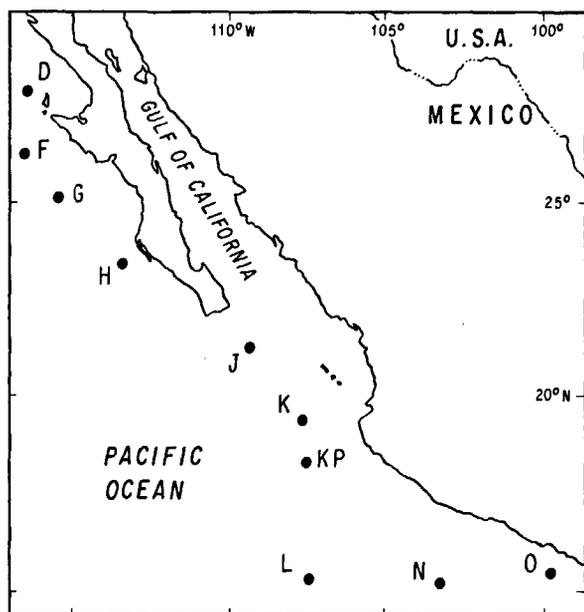


Figure 1
Station locations.

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 \sim 2 hr incubation, samples were filtered with 0.45 μ m pore membrane filters. The filters were put into liquid scintillation vials with 15 ml of Aquasol. β 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° 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 μ 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 α^B were calculated with simple linear regression of I and P^B , with data of the two lowest irradiances of each curve, and assuming $P^B=0$ 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 α^B . Values of P_m^B were taken from the graphs, and values of I_m are the corresponding optimum irradiances. These P_m^B '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° C gradient from the sea surface, with a difference of \sim 3.5 $^\circ$ C between the surface and the 1% I_0 depth (Tab.). With the exception of nutrients,

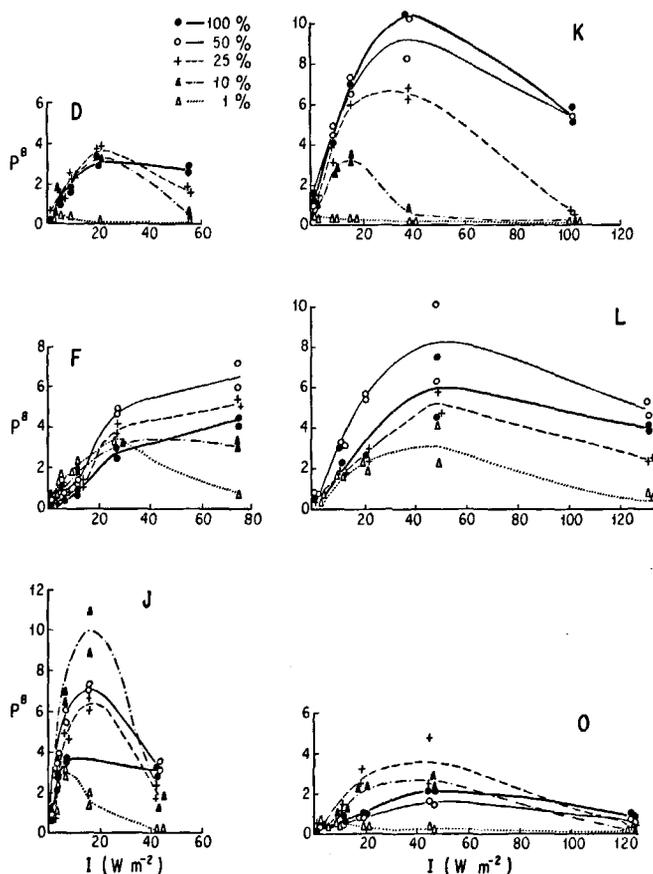


Figure 2
Photosynthesis-irradiance curves for phytoplankton samples collected from irradiance levels as indicated by symbols. P^B in $\text{mgC}(\text{mg Chl } a)^{-1} \text{h}^{-1}$.

Table

Environmental variables, phytoplankton abundance by major taxa and photosynthetic parameters for the stations sampled. PO_4 , NO_2+NO_3 and SiO_2 in μM . $Chl a$ in $mg \cdot m^{-3}$. Diatoms, dinoflagellates and nanoplankton in $cells \cdot ml^{-1}$. P_m^B in $mgC \cdot (mg Chl a)^{-1} \cdot h^{-1}$; I_m in $W \cdot m^{-2}$, and α^B in $mgC \cdot (mg Chl a)^{-1} \cdot h^{-1} \cdot W^{-1} \cdot m^2$.

Sta.	Z(m)	T°C	S	PO_4	NO_2+NO_3	SiO_2	$Chl a$	Diatoms	Dinoflagellates	Nannoplankton	P_m^B	I_m	α^B
D	0	18.69	33.56				0.54	1	2	227	3.0,3.4	20	0.24
	7	17.50	33.55					5	5	164			
	14	17.38	33.54				0.42	10	7	150	3.7,3.7	20	0.28
	23	16.99	33.51	0.30	0.1	2.7	0.86	2	8	214	3.4,3.4	20	0.31
	46	14.97	33.48	0.55	3.0	5.3	0.55	3	2	220	0.3,0.3	5	0.29
F	0	18.40	33.74		0.2	3.5	0.38	2	2	1327	4.5,4.0	72	0.07
	6	18.30	33.75		1.1	3.0	0.27	2	1	744	7.3,6.1	72	0.12
	13	18.26	33.74		0.1	3.0	0.33	1	2	953	5.4,5.2	72	0.17
	21	18.27	33.79		0.1	3.1	0.28	1	2	1693	3.4,3.1	72	0.16
	42	17.53	33.63		0.2	4.0	0.77	1	0	1440	3.3,3.3	26	0.26
G	0	19.50	33.74	0.21	0.1	2.8	0.34	21	1	1082	3.5,4.4	34	0.32
	9	19.33	33.74	0.22	0.1	2.7		1	4	319			
	18	19.17	33.73	0.22	0.1	2.7	0.17	12	4	393	7.6,8.2	34	0.70
	29	18.89	33.65	0.20	0.5	2.7		1	8	823			
	58	13.12	33.46	0.48	4.6	7.2	1.25	2	1	1092	0.8,0.9	5	0.19
H	0	22.00	34.07	0.20	0.1	1.6		1	1	3083			
	5	21.93	34.08	0.20	0.1	1.6	0.11	1	1	1718	5.3,4.2	36	0.32
	10	21.86	34.08	0.20	0.1	1.6	0.21	0	1	550	3.0,3.2	36	0.18
	17	21.76	34.09	0.18	0.2	1.6	0.21	1	1	764	3.6,2.2	36	0.15
	34	21.22	33.99	0.16	0.0	1.6	0.22	1	19	739	2.4,1.8	36	0.13
J	0	23.58	34.41	0.23	0.1	2.3	0.15	1	1	851			0.60
	6	23.61	34.41	0.23	0.1	1.9	0.10	1	1	639	7.0,7.3	16	0.95
	13	23.60	34.41	0.23	0.1	1.9	0.16	5	2	519	6.1,6.7	16	0.75
	21	23.55	34.41	0.24	0.5	1.9	0.11	1	1	794	11.0,8.9	16	0.95
	42	23.20	34.35	0.81	5.2	6.2	0.60	9	3	202	3.1,3.0	7	0.58
K	0	23.85	34.29	0.36	0.9	1.7	0.67	6	3	997	10.4,10.4	38	0.41
	9	23.82	34.30	0.34	0.9	1.3	0.60	4	3	1180	8.2, 10.4	38	0.44
	18	23.64	34.30	0.36	1.0	1.6	0.76	8	6	288	6.7,6.3	38	0.33
	31	18.80	34.12	1.17	12.3	7.6	0.88	2	3	901	3.4,3.2	16	0.26
	61	15.83	34.34	1.80	23.1	15.6	0.53	0	1	1685	0.5,0.4	1	0.40
KP	0	24.05	34.46	0.33	0.1	1.3	0.52	7	9	412	3.6,5.1	42	0.17
	6	24.08	34.46	0.32	0.1	1.3	0.30	2	5	361	6.1, 5.0	42	0.22
	11	23.94	34.46	0.33	0.1	1.3	0.32	5	8	612	8.0,8.7	42	0.18
	19	23.90	34.46	0.32	0.2	1.6	0.31	4	2	1668	5.0,9.0	42	0.32
	38	21.56	34.52	0.78	4.8	7.3	0.22	1	5	351	9.4,6.7	18	0.48
L	0	26.95	33.49	0.10	0.0	0.30	0.21	1	2	2656	7.6,4.6	49	0.22
	6	27.15	33.50	0.10	0.0	0.30	0.16	0	2	845	6.3,10.1	49	0.27
	12	26.70	33.57	0.09	0.0	0.30	0.32	0	1	1954	4.6,5.9	49	0.15
	21	26.06	33.82	0.09	0.0	0.30		0	2	927			
	41	26.07	34.30	0.08	0.0	0.30	0.21	0	0	1390	4.1,2.2	49	0.13
N	0	27.95	33.71	0.13	0.1	1.3	0.37	1	5	534	5.8,5.9	29	0.35
	7	27.86	33.70	0.13	0.1	1.1	0.52	0	1	335	4.4,2.8	29	0.25
	14	27.71	33.70	0.13	0.1	1.1	0.52	0	2	657	4.8,4.6	29	0.31
	23	27.70	33.71	0.12	0.2	1.1	0.18	1	1	830	9.8,8.1	29	0.68
	45	24.56	33.61	0.78	10.2	4.2	1.05	1	2	851	2.5,2.4	13	0.13
O	0	27.90	33.71	0.12	0.0	1.3	0.69	0	1	551	2.0,2.0	46	0.07
	11	27.72	33.70	0.10	0.0	1.1	0.86	0	1	224	1.5,1.6	46	0.06
	23	27.69	33.71	0.10	0.1	1.0	0.35	1	2	780	2.5,4.7	46	0.10
	38	27.71	33.75	0.10	0.2	1.0	0.42	0	1	463	2.3,2.7	46	0.10
	77	18.84	34.23	1.44	17.3	8.7	0.32	0	1	404	0.3,0.4	1	0.38

in general there were great vertical changes of variables controlling primary productivity, even where thermohaline 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 $< 2.5 \mu m$) not detected with the Utermöhl technique. P_m^B did not reach light photoinhibiting values in incubation experiments for stations F and G, with exception of those for samples from the 1% I_0 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, α^B , varied quite irregularly with depth, with a range of 0.06 to 0.95 (Tab.). P_m^B clearly changed with depth, very often presenting subsurface maxima. P_m^B had a two to three fold variation within the mixed layer. In general, P_m^B of the 1% I_0 depth was relatively low. When phytoplankton become conditioned to lower irradiances P_m^B decreases (Prézelin, Matlick, 1980; Falkowski, Owens, 1980). Where the 1% I_0 depth was

within the thermocline, its P_m^B 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^B value of the 1% I_0 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_0 , phytoplankton from the surface often presented I_m 's lower than I_0 , perhaps because turbulence moves phytoplankton up and down the water column. The subsurface P_m^B 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^B . 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^B 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_0 depth (Steemann-Nielsen, 1975). Thomas (1970) estimated P_m^B '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 μM and had a somewhat lower mean P_m^B (mean=3.15; range: 1.15 to 5.18) than those stations with nitrogen-rich waters (NO_3 up to 7.8 μM) (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^B 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 (1971 a and b) estimated P_m^B 's for phytoplankton samples collected from 2 m depth and incubated at 42 $W.m^{-2}$. His P_m^B 's for Tropical surface waters with

undetectable NO_3 had a range of 1.1 to 3.6. Our P_m^B surface value for station O was 2.0, but those for stations L and N were ~6.0. Malone's (1971 a) P_m^B '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 μM . Station K had the highest surface NO_3 and P_m^B (9.6) of our data set (Tab.) and NO_3 was only ~0.8 μM . Malone's (1971 b) P_m^B '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 (1971 a 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 μM) in the mixed layer, stations L and N had relatively high P_m^B values, while station O had relative low values (Tab.). P_m^B 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 μM and NO_3 was 17 μM , 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^B 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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