

The Relationship between Photosynthesis and Irradiance for Gulf of California Phytoplankton¹

SAÚL ALVAREZ-BORRERO, GILBERTO GAXIOLA-CASTRO, AND DAVID U. HERNÁNDEZ-BECERRIL²

ABSTRACT: During June 17-28, 1982, we carried on experiments to generate photosynthesis-irradiance curves for phytoplankton from five locations of the central and northern Gulf of California. Using natural sunlight, on board ¹⁴C incubations were done with samples collected from five different depths within the euphotic zone. In general there were great vertical changes of variables controlling primary productivity, even in cases where weak vertical T°C gradients indicated high instability and mixing of the euphotic zone. The assimilation number (P_m^B) had a two fold variation within the mixed layer. In general P_m^B decreased monotonically with depth due to phytoplankton conditioning to lower irradiances. Surface P_m^B values had a range of 8 to 15 mg C · mg Chl a⁻¹ · h⁻¹. When a thermocline was present, P_m^B for the bottom of the euphotic zone was about 4 to 10% of that for surface waters. But, without a thermocline, P_m^B for the bottom of the euphotic zone was ~60% of that for surface waters, due to turbulence moving phytoplankton up and down the water column. Diatoms were abundant in three stations near Angel de la Guarda and Tiburon islands. For the station at the central gulf and the one at the very northern gulf, very few nano and microplankton were found with the inverted scope technique, but high chlorophyll concentrations and primary productivity indicated a high abundance of picoplankton. This difference in plankton size composition was not reflected in P_m^B values. Nutrient concentrations were high and did not limit P_m^B values. Our P_m^B values are higher than those reported for the gulf's winter phytoplankton; and they are about two times higher than those for winter phytoplankton of the oceanic region between San Diego and Acapulco. Our Gulf of California integrated primary productivity values had a range of 1.3 to 4.4 g C · m⁻² · d⁻¹.

PRIMARY PRODUCTIVITY in the Gulf of California is comparable to the productivity in areas such as the Bay of Bengal and the upwelling areas off the west coasts of Baja California and North Africa. It is about two to three times greater than that in the open Atlantic or the open Pacific at similar latitudes (Zeitzschel, 1969). Lara-Lara et al. (1984) estimated very high average integrated primary productivity values in the gulf, during

an "El Niño" event (3.1 g C · m⁻² · d⁻¹ in March, and 1.8 g C · m⁻² · d⁻¹ in October, during 1983). Highest value reported by Zeitzschel (1969) was 0.8 g C · m⁻² · d⁻¹.

Platt and Jassby (1976) proposed a new approach to study the environmental control of primary productivity based on the fundamental relationship between photosynthesis and irradiance under different environmental conditions. We can relate changes of the photosynthesis-irradiance curve parameters of natural phytoplankton assemblages with changes in the environmental variables (light, nutrients, temperature, turbulence, etc.); and this covariance can be used to establish the relative importance of the environmental

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² Departamento de Ecología Marina, División de Oceanología, Centro de Investigación Científica y de Educación Superior de Ensenada, B.C., Espinoza 843, Ensenada, Baja California, Mexico.

variables in the control of photosynthesis. The photosynthesis-irradiance (P-I) curve relates the photosynthesis per unit chlorophyll biomass P^B (in $\text{mg C} \cdot \text{mg Chl a}^{-1} \cdot \text{h}^{-1}$), or assimilation ratio, to the irradiance I (in $\text{W} \cdot \text{m}^{-2}$) (Platt and Jassby, 1976). Two important parameters of this curve are α^B , the initial slope of the curve, and P_m^B , the specific productivity at saturating light, or assimilation number (Platt et al., 1976). Marra (1980) has shown that the photosynthetic parameters of phytoplankton are variable in time and such phenomena can only be analyzed by time series analysis so that both the magnitude and the time history of the irradiance regime are required. For example, Côté and Platt (1983) generated 70-day time series for phytoplankton of Bedford Basin and found a three fold variation of α^B and P_m^B ; and Torres-Moye and Alvarez-Borrego (subm. for publ.) generated 20-day time series for coastal Baja California phytoplankton and also found a three fold variation of these photosynthetic parameters.

Due to the problem of time, distance and cost, it is very difficult to produce this kind of time series data for oceanic waters; and yet it is desirable to have at least some preliminary data that could allow us to compare relatively big regions of the ocean. We decided to use the CONACYT-I cruise of the R/V "El Puma" to the Gulf of California, between spring and summer of 1982, as a "cruise of opportunity" to carry on experiments to generate P-I curves for five different hydrographic stations. These stations were chosen to represent, as much as possible, different hydrographic conditions in the central and northern Gulf (Figure 1). We can compare these data with those from the California Current System and the Tropical region off Mexico (Gaxiola-Castro and Alvarez-Borrego, subm. for publ.), and with those from a winter cruise to the Gulf of California (Gaxiola-Castro et al., in prep.). Differences in the values of photosynthetic parameters may then be related to differences in environmental conditions. On board, ^{14}C incubation experiments were carried on only once per hydrographic station. In general, we found P_m^B and I_m , the optimum or saturating irradiance, for the Gulf of California spring-summer phytoplankton greater than those for

the Gulf's winter phytoplankton. Our Gulf's spring-summer P_m^B 's were about two times higher than those for winter phytoplankton of the oceanic region between San Diego and Acapulco.

METHODS AND MATERIALS

During 17-28 June, 1982, the R/V "El Puma's" CONACYT-I cruise covered the central and northern Gulf of California. At five hydrographic stations (Figure 1), phytoplankton samples were taken 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 to give only the photosynthetic active radiation. The irradiance attenuation coefficient and depths corresponding to different percentages of I_0 were calculated with Lambert-Beer's law: $I_z = I_0 \exp(-kz)$, where I_z is irradiance at depth z in watts per square meter ($\text{W} \cdot \text{m}^{-2}$), and k is the attenuation coefficient, assumed to be constant with depth. Sampling was done with 7 liter Niskin bottles. Ten 125 ml clear glass bottles were filled with water from each sampled depth; each glass bottle was inoculated with $5 \mu\text{Ci}$ of ^{14}C , basically following Steemann-Nielsen (1952); and they were put into an incubator on board. This incubator consisted of five acrylic tubes, 7 cm diameter and 150 cm length, with neutral black plastic filter nets, to allow for different irradiances. Incubation irradiances were measured inside empty bottles and tubes. Samples were incubated at irradiances equal to 86, 32, 14, 7 and 1% of solar irradiance measured on deck. For incubations we used sunlight. To avoid heating of samples, surface water was pumped through the incubation tubes. Two replicate samples from each depth were put at each incubation irradiance. To obtain maximum incident irradiance, incubations were done at noon, between 11:00 and 14:00 hrs. After ~ 2 hr incubation, samples were filtered with $0.45 \mu\text{m}$ pore and 47 mm diameter membrane filters. The filters were put into liquid scintillation vials with 15 ml of aquasol. β counting was done in the Scripps Institution

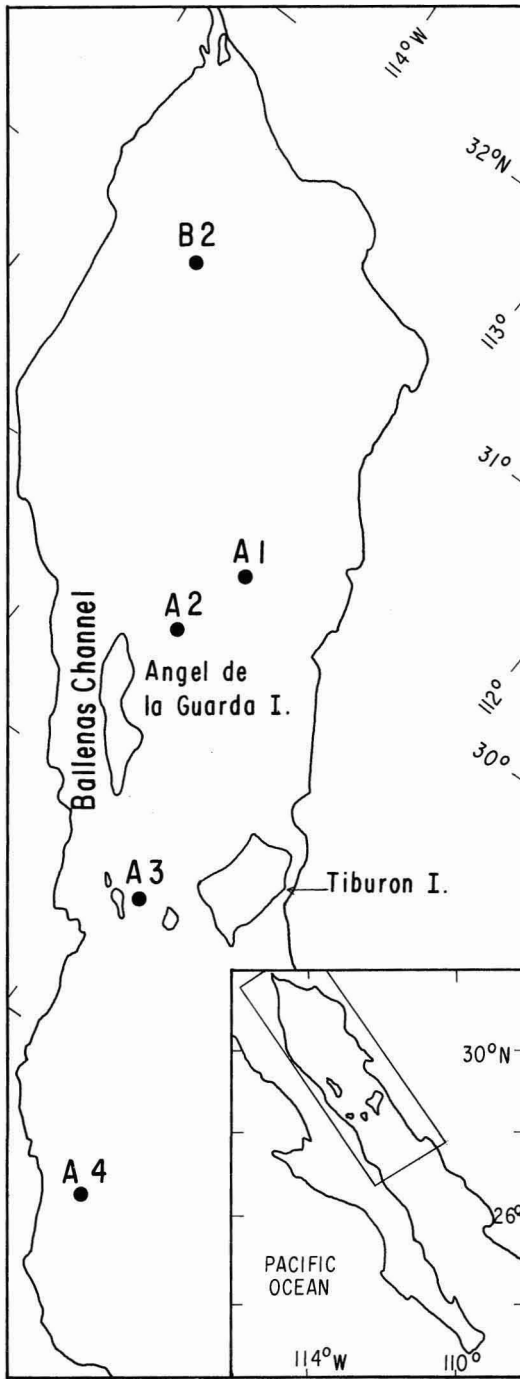


FIGURE 1. Location of stations.

of Oceanography laboratory at La Jolla, California, with a Beckman LSC100 counter. Calculations of assimilated carbon was done following Strickland and Parsons (1972).

For each sampled depth we also measured $T^{\circ}\text{C}$, and analyzed for $S\text{‰}$, chlorophyll a, nutrients (NO_2 , NO_3 , PO_4 and SiO_2) and phytoplankton abundance. $S\text{‰}$ was analyzed with a Kahlisico 118 WA200 salinometer. Chlorophyll a samples were obtained using $0.45\ \mu\text{m}$ pore-size Millipore filters, and analyses were performed basically by the SCOR-UNESCO (1966) method, with second readings after acidification following Lorezen (1967). Nutrients were analyzed for with a Scientific Instruments autoanalyzer. Phytoplankton abundance was determined by the Utermöhl (1958) inverted scope technique.

Our P-I data points, in each graph, are too few to try fitting a P-I model to them. Values of α^{B} , the initial slope of the curve at low irradiances ($\text{mg C} \cdot \text{mg Chl a}^{-1} \cdot \text{h}^{-1} \cdot \text{W}^{-1} \cdot \text{m}^2$), were calculated with simple linear regression of I and P^{B} , with data of the two lowest irradiances of each curve, and assuming $\text{P}^{\text{B}} = 0$ when $I = 0$, that is including the intersection (0, 0). When the correlation coefficient of this regression (r^2) was lower than 0.7, we considered the data were too scattered and we did not use that α^{B} . Values of P_m^{B} were taken, in each case, as the maximum P^{B} , from the graphs; values of I_m are the corresponding optimum irradiances. These P_m^{B} 's and I_m 's should be taken as minimum estimates because we have very few data points at high irradiances. We also estimated P_z^{B} directly from the graphs, using I_z . To estimate integrated primary productivity, P_i ($\text{g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$), we first generated the P_z versus z curves for every hour ($\text{P}_z = \text{P}_z^{\text{B}} \cdot \text{Chl a}_z$), from the P-I graphs and with I_0 as a function of time using the cosine equation proposed by Vollenweider (1965); this implies assuming constancy during the whole solar day of all variables and parameters controlling primary productivity, with the exception of light.

RESULTS

At stations A1, A4 and B2 there were thermoclines, without a well defined mixed layer near the surface; at stations A2 and A3, the

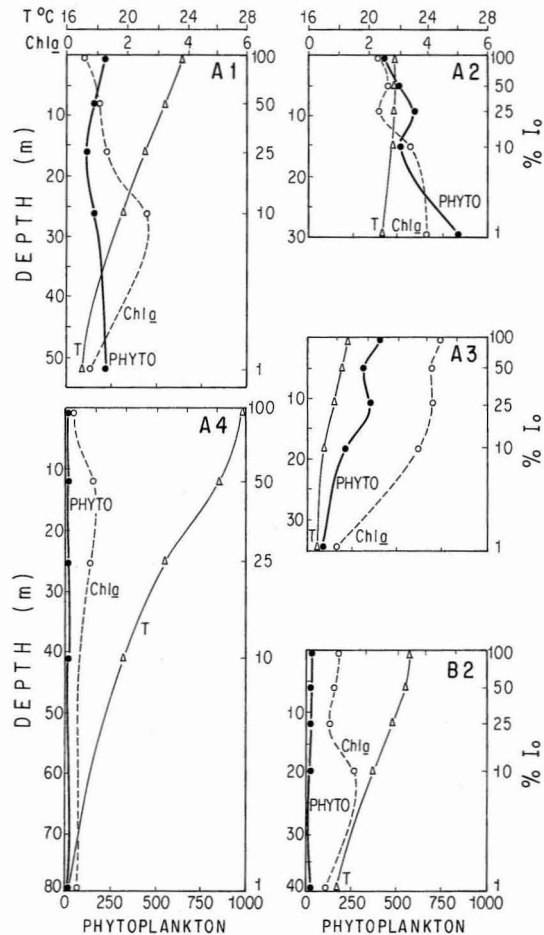


FIGURE 2. Vertical distributions of: $T^{\circ}\text{C}$, phytoplankton abundance ($\text{cells} \cdot \text{ml}^{-1}$), chlorophyll a concentration ($\text{mg} \cdot \text{m}^{-3}$). I_0 is the irradiance measured just below the sea surface.

euphotic zone was within the mixed layer, with a $T^{\circ}\text{C}$ decrease from the surface to the $1\% I_0$ depth of only 0.8°C at station A2 and of $\sim 2^{\circ}\text{C}$ at station A3 (Figure 2, Table 1). Within the euphotic zone, salinity was very homogeneous at stations A2 and A3; and it decreased $\sim 0.3\text{‰}$ from the surface to the $1\% I_0$ depth at the other stations (Table 1). In spite of thermohaline homogeneity at stations A2 and A3, variables controlling primary productivity changed with depth (Figure 2). At station A2, chlorophyll a had the highest measured value at the bottom of the euphotic zone; and it presented the opposite situation for station A3, with the highest measured

TABLE 1

ENVIRONMENTAL VARIABLES AND PHOTOSYNTHETIC PARAMETERS FOR THE STATIONS SAMPLED. P_z in $\text{mg C} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$; P_z^B and P_m^B in $\text{mg C} \cdot (\text{mg Chl } a)^{-1} \cdot \text{h}^{-1}$; I_m in $\text{W} \cdot \text{m}^{-2}$; α^B in $\text{mg C} \cdot (\text{mg Chl } a)^{-1} \cdot \text{h}^{-1} \cdot \text{W}^{-1} \cdot \text{m}^2$

STA.	Z(m)	T°C	S‰	P_z	P_z^B	P_m^B	I_m	α^B
A1	0	23.55	35.58	3.8	7.2	9.7, 6.7	149	0.21
	8	22.60	35.56	4.4	4.2	4.7, 3.7	55	0.12
	16	21.30	35.51	5.0	3.8	4.8, 5.1	55	0.16
	26	19.80	35.44	5.9	2.2	4.9, 4.5	24	0.12
	52	17.10	35.30	0.2	0.3	0.9, 0.9	24	0.04
A2	0	21.88	35.52	29.3	12.2	12.5, 13.8	53	0.57
	5	21.80	35.52	27.5	10.3	10.5, 10.5	53	0.38
	9	21.80	35.52	20.4	8.5	12.6, 12.6	53	0.48
	15	21.70	35.52	17.7	5.1	13.6, 13.4	53	0.36
	30	21.10	35.52	2.8	0.7	7.7, 7.0	53	0.37
A3	0	18.69	35.13	35.0	10.1	11.4, 11.1	53	0.40
	5	18.40	35.08	36.5	11.4	12.1, 11.4	53	0.50
	11	17.95	35.12	19.5	6.1	8.6, 8.4	53	0.30
	18	17.10	35.09	8.3	3.1	6.4, 6.6	53	0.31
	35	16.65	35.08	0.8	0.8	8.0, 7.8	53	0.14
A4	0	28.54	35.24	2.1	8.3	11.4, 11.7	52	0.35
	12	26.40	35.31	3.4	3.7	3.9, 3.7	52	0.13
	25	22.85	34.94	3.0	3.8	4.3, 4.2	52	0.22
	41	19.85	35.06					
	82	15.70	34.98	0.1	0.2	0.4, 0.4	23	
B2	0	22.97	35.41	6.0	5.7	17.6, 13.3	47	0.45
	6	22.55	35.40	8.5	9.2	8.9, 9.5	47	0.36
	12	21.85	35.40	7.4	9.3	10.7, 10.1	47	0.51
	20	20.60	35.32	6.4	4.0	6.9, 6.9	21	0.41
	40	18.00	35.16	0.2	0.3	2.0, 2.2	21	0.14

value at the surface and decreasing monotonically with depth (Figure 2, Table 2). These two stations, A2 and A3, presented the highest chlorophyll a concentrations, and phytoplankton abundance, of our data set. Chlorophyll a showed subsurface maxima at the other stations: at the 10% I_0 depth at stations A1 and B2; and at the 50% I_0 depth at station A4. Lowest chlorophyll a concentrations and phytoplankton abundance values were found for station A4, which had the deepest euphotic layer (Figure 2, Table 2).

Nutrient concentrations were very high in all stations, with relatively lower values in station A4 (Table 2). Two exceptionally high PO_4 values of more than $4 \mu\text{M}$ were found, one for station A4 at the 1% I_0 depth, and another for station B2 at the surface. Highest surface and near surface nutrient values were found for station A3.

Diatoms were abundant in stations A1, A2 and A3, with dominant numbers in A3 (Table 2). In these stations they were an order of magnitude more abundant than dinoflagel-

lates. Station A3 had the highest abundance of dinoflagellates. Nanoplankton was most abundant in station A2. For stations A4 and B2, phytoplankton numbers were two orders of magnitude lower than those for the other stations, while chlorophyll a was only about one third (Table 2); this may indicate the presence of abundant picoplankton in stations A4 and B2 not counted with the inverted scope technique. Primary productivity, P_z , and integrated primary productivity, P_i , were very high in all of our stations (Tables 1 and 2). Highest values were estimated for stations A2 and A3. At the bottom of the euphotic zone of station A2 there was high productivity in spite of low light, $2.8 \text{ mg C} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ (Table 1); at that depth, chlorophyll a was the highest of our data set (Figure 2). In spite of low phytoplankton abundance, stations A4 and B2 also had very high productivity estimates; values for B2 were higher than those for A1.

With the exception of the station A1 surface sample, all of our incubated samples clearly showed sensitivity to photoinhibition at the

TABLE 2

ENVIRONMENTAL VARIABLES, PHYTOPLANKTON ABUNDANCE BY MAJOR TAXA AND INTEGRATED PRIMARY PRODUCTIVITY FOR THE STATIONS SAMPLED. Chl *a* in $\text{mg} \cdot \text{m}^{-3}$; Diat., Dino., and Nano. in $\text{no. cells} \cdot \text{ml}^{-1}$; PO_4 , NO_2 , NO_3 and SiO_2 in μM . The numbers below each station letter are from top to bottom in each case: I_0 = irradiance measured just below sea surface ($\text{W} \cdot \text{m}^{-2}$); k = attenuation coefficient (m^{-1}); P_i = integrated primary productivity ($\text{g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$)

STA.	Z(m)	Chla.	DIAT.	DINO.	NANO.	PO_4	NO_2	NO_3	SiO_2
A1	0	0.53	147	4	44	1.16	0.20	2.54	5.39
	8	1.06	96	5	61	1.32	0.20	2.26	6.23
107	16	1.33	40	2	63	2.80	0.20	2.20	6.79
0.09	26	2.67	7	0	150	3.17	0.33	2.83	10.92
1.8	52	0.80	6	0	15	2.97	0.27	10.47	22.50
A2	0	2.40	96	7	310	1.25	0.21	2.32	6.93
	5	2.67	129	9	358	1.29	0.22	2.26	5.62
117	9	2.40	115	7	469	1.34	0.22	2.26	5.43
0.15	15	3.47	128	7	375	1.38	0.22	2.23	5.62
4.3	30	4.00	182	3	651	1.41	0.26	2.54	6.93
A3	0	3.47	311	21	72	2.14	0.41	13.71	29.7
	5	3.20	252	4	63	2.19	0.40	13.29	30.3
93	11	3.20	245	22	82	2.21	0.43	14.60	30.9
0.13	18	2.67	91	13	116	2.41	0.36	15.33	34.4
4.4	35	1.06	35	20	36	2.57	0.34	18.04	37.7
A4	0	0.26	0	0	2	1.64	0.13	1.05	4.6
	12	0.93	1	1	2	0.89	0.09	1.04	5.2
120	25	0.80	0	1	5	0.81	0.08	1.09	2.9
0.06	41		4	4	0	1.21	0.25	2.73	5.6
1.3	82	0.37	1	0	0	4.36	0.14	24.26	28.8
B2	0	1.06	2	0	25	4.70	0.04	0.97	14.1
	6	0.93	2	1	14	1.73	0.02	0.90	13.9
120	12	0.80	2	1	18	1.71	0.03	0.95	14.2
0.11	20	1.60	2	1	5	1.77	0.04	1.00	13.8
2.3	40	0.56	1	0	0	2.76	0.12	15.06	14.2

highest irradiance (Figure 3). The behavior of P_m^B , the assimilation number, was different from station to station. Stations A1, A4 and B2, which had a thermocline, presented P_m^B values for the 1% I_0 depth of about 4 to 10% of that for surface waters; while stations A2 and A3 had P_m^B values for the bottom of the euphotic zone of ~60% of that for surface waters. In general, P_m^B values were highest at the surface and decreased monotonically with depth (Table 1). Lowest P_m^B values were estimated for station A1, and highest for station B2; with a surface range of about 8 to 15, and a 1% I_0 depth range of about 0.4 to 8. The initial slope, α^B , also had a general tendency to decrease with depth (Table 1). It also presented the lowest values for station A1; but highest values were estimated for station A2. There was a range for α^B surface values of about 0.21 to 0.57; and 0.04 to 0.37 for 1% I_0 depth values.

DISCUSSION

Since we have few degrees of freedom for each P-I curve, and we did not generate time series, our data are very limited; however, some conclusions may be reached on the behavior of the photosynthetic parameters. The assimilation number, P_m^B , clearly changed with depth. Beardall and Morris (1976), and Falkowski and Owens (1980) found that P_m^B decreases as phytoplankton becomes shade adapted. P_m^B changes with depth have been observed for lakes (Gessner, 1949), for summer arctic plankton (Stemann-Nielsen and Hansen, 1959), for coastal waters (Platt and Jassby, 1976; Gaxiola-Castro and Alvarez-Borrego, 1984) and for oceanic Pacific waters (Gaxiola-Castro and Alvarez-Borrego, *subm.* for publ.). Platt and Jassby (1976) indicated that for coastal waters prediction of phytoplankton productivity from chlorophyll and

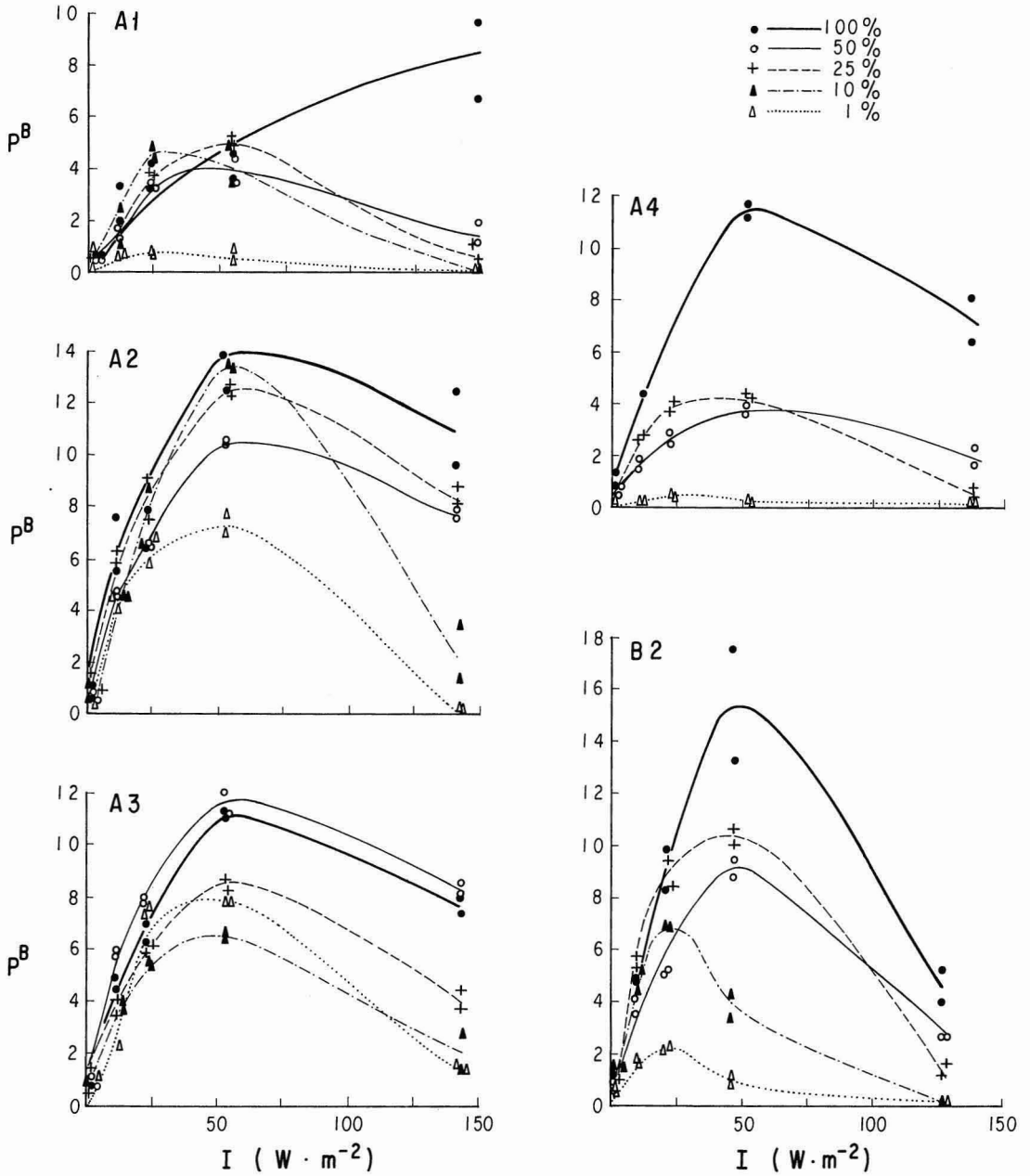


FIGURE 3. Photosynthesis-irradiance (P-I) curves for phytoplankton samples collected from irradiance levels as indicated by symbols.

light data can only result in very rough estimates if the P-I parameters are assumed to be constant. That same limitation exists for the waters of the California Current System and the Eastern Tropical Pacific region (Gaxiola-Castro and Alvarez-Borrego, *subm. for publ.*); and our data show it is also a limitation for the Gulf of California waters. In our data set P_m^B had a two fold variation within the mixed layer; and when a thermocline was present, P_m^B for the bottom of the euphotic zone was about 4 to 10% of that for the surface waters (Table 1). In general, our data show that when phytoplankton is confined to the bottom of the euphotic zone (i.e.: within the thermocline), P_m^B , α^B and I_m for those waters are lower than when phytoplankton can move vertically relatively rapidly within the mixed layer. For example, compare the 1% I_0 depth values of these parameters for stations A1, A4 and B2, versus those for stations A2 and A3 (Table 1).

Most of our surface-incubated samples showed sensitivity to photoinhibition (Figure 3); that is, surface phytoplankton was conditioned to irradiances lower than I_0 . On the other hand, deep samples presented optimum irradiances, I_m 's, higher than the maximum irradiance they could experience in situ, at that depth (Table 1). Particularly for stations A2 and A3, with no thermocline present, all samples showed P_m^B at the same I_m . This was due to turbulence moving phytoplankton up and down. With vertical mixing, conditioning does not seem to occur for average in situ irradiance within the euphotic zone, or within the mixed layer, but it seems to occur for high irradiances, around 50% I_0 (Tables 1 and 2). This indicates a more rapid adaptation to higher than to lower irradiances. Platt et al. (1982) found that in the Arctic, phytoplankton from the 50% I_0 depth was adapted to the maximum irradiance they might be exposed in situ, but that for the populations near the bottom of the euphotic zone optimum irradiance was higher than the populations could experience at that depth. Gallegos et al. (1983) concluded that adaptation to low irradiance is slow, and it requires 2-6 weeks once a population is isolated below a pycnocline. In our Gulf of California stations with a thermocline, phy-

toplankton from the bottom of the euphotic zone were adapted to an optimum irradiance about twenty times the maximum irradiance they were being exposed to at that depth (Table 1). This clearly indicates that, in spite of a thermocline, turbulence is moving these populations up and down, although not as fast as in the case of stations A2 and A3.

Turbulence and solar radiation seem to be more important than nutrient concentrations in controlling P_m^B values. Harrison and Platt (1980) found that for Bedford Basin, minimum assimilation numbers are found in winter when nutrients are at their highest levels for the year. Turbulence may cause nutrient fluxes into the euphotic zone, and adaptation of phytoplankton populations at irradiances different from those they might be exposed to at the depth from which they were collected. The role of turbulence in controlling P_m^B values is not very clear yet; with a strong thermocline, and very low turbulence, phytoplankton is confined to the depths and low P_m^B values may result for the deeper part of the euphotic zone. Stations A1 and A4 had thermoclines and relatively low P_m^B values for the 1% I_0 depth. But, at the other extreme, with very strong turbulence and a very deep mixed layer, relatively low P_m^B values may result for the whole euphotic zone. Gaxiola-Castro et al. (*in prep.*) reported that for a winter P-I experiment in the Northern Gulf of California, after a night storm with up to 40 knot winds, chlorophyll a was two to three times higher and P_m^B values came down to ~25% of those from a P-I experiment the day before. They suggested that possibly this was due to strong turbulence mixing the near surface phytoplankton with a deep chlorophyll maximum with phytoplankton adapted to lower irradiance. We still have very meager P-I data from the Gulf of California (Gaxiola-Castro et al., *in prep.*; and this work); nevertheless, it is interesting to notice that, in general, our summer P_m^B and I_m values are higher than winter values. Gaxiola-Castro et al.'s winter P-I experiments were done for hydrographic stations with much more homogeneous euphotic layers, frequently with no $T^\circ C$ nor $S\text{‰}$ differences from the surface to the 1% I_0 depth. Both data sets show very

similar chlorophyll *a* and nutrient concentrations, and similar I_0 values. So, it seems that intermediate or less frequent turbulence during spring-summer causes higher P_m^B values than with higher and/or more frequent turbulence during winter, in the Gulf of California. As a result, out spring-summer integrated primary productivity values are higher than their winter values (their range was 0.75 to $1.86 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$).

Gulf of California P_m^B values are higher than those for open ocean Mexican Pacific waters. Gaxiola-Castro and Alvarez-Borrego (subm. for publ.) presented P-I data from a San Diego to Acapulco winter cruise, and in general their P_m^B values were about 30 to 50% of our values. Their nutrient values were much lower than those for the Gulf of California, at times undetectable, i.e., off Acapulco; and their chlorophyll *a* values were in general about 25 to 50% of our values.

With reference to the effect of turbulence on vertical flux of nutrients to the euphotic zone, and primary productivity, in the Eastern Tropical Pacific, we have to consider that here the nutricline coincides with the thermocline; and in the Gulf of California the nutricline is very shallow (Alvarez-Borrego et al., 1978) and there is a lot of energy for mixing from the tides and winds, especially in the Northern Gulf (Alvarez-Borrego, 1983). The Gulf of California, especially the Central and Northern Gulf, is very dynamic. Badán-Dangón et al. (1985), using infrared satellite images, described well defined mesoscale processes resulting from tidal mixing and the changing wind regime. Tidal mixing and upwelling generate plumes of cold water, and thermal frontal structures are developed which very well may also be of chemical and biological character, like those described by Traganza et al. (1980) and Traganza et al. (1981) for the region off the coast of California. Phytoplankton patchiness and great variability with time were recognized as important problems in the early studies of organic productivity of the Gulf (Allen, 1938). Gilbert and Allen (1943) emphasized the need of both continuity of observations and a knowledge of water movements, and indicated that at any one spot both the biomass and the specific com-

position may change completely in a few hours. Because of these dynamics and our limited data, we cannot yet establish differences for the behavior of photosynthetic parameters of different regions within the Gulf. Stations A4 and B2, the southernmost and northernmost stations respectively (Figure 1), had very low phytoplankton abundance (Table 2), possibly with abundant picoplankton, as we indicated in the results section above. This was their main difference with respect to the other three stations, besides station A4 having a much deeper euphotic zone (Figure 2). This difference in microplankton abundance was not reflected in the values of the P-I parameters and cannot be explained in terms of the physical and chemical properties we measured.

Lara-Lara et al. (1984) reported that the Gulf of California was enriched in plankton production and biomass during an "El Niño" event in 1983. However, the average for our June 1982 integrated primary productivity values, $2.8 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, is similar to their March 1983 average of $3.1 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, which was their highest value for 1983. Our average is about three times the highest value reported by Zeitzschel (1969); but some of this difference may be due to the longer incubation time (~ 6 hrs) used by this author. According to Robles-Pacheco and Christensen (1984) the appearance of "El Niño" throughout the Gulf of California was detected at the end of 1982 by positive sea level anomalies. More productivity data covering all seasons of the year and with time and space series, are needed to better characterize the "El Niño" and "normal" conditions in the gulf.

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LITERATURE CITED

- ALLEN, W. E. 1938. The Templeton Crocker Expedition to the Gulf of California in 1935. The phytoplankton. Trans. Am. Microsc. Soc., 67:328-335.
- ALVAREZ-BORREGO, S. 1983. Gulf of California, p. 427-449. In: Ketchum, B. H. (ed.), Estuaries and Enclosed Seas, Elsevier, Amsterdam.
- ALVAREZ-BORREGO, S., J. A. RIVERA, G. GAXIOLA-CASTRO, M. J. ACOSTA-RUIZ, and R. A. SCHWARTZLOSE. 1978. Nutrientes en el Golfo de California (in Spanish). Ciencias Marinas, 5(2):53-71.
- BADÁN-DANGÓN, A. F., C. J. KOBLINSKY, and T. BAUMGARTNER. 1985. Spring and summer in the Gulf of California: observations of surface thermal patterns. Oceanologica Acta, 8(1):13-22.
- BEARDALL, J., and I. MORRIS. 1976. The concept of light intensity adaptation in marine phytoplankton: some experiments with *Phaeodactylum tricornotum*. Mar. Biol., 37:377-387.
- CÔTÉ, B., and T. PLATT. 1983. Day to day variations in the spring-summer photosynthetic parameters of coastal marine phytoplankton. Limnol. Oceanogr., 28:320-344.
- FALKOWSKI, P. G., and T. G. OWENS. 1980. Light-shade adaptation: two strategies in marine phytoplankton. Plant. Physiol., 66:592-595.
- GALLEGOS, C. L., T. PLATT, W. G. HARRISON, and B. IRWIN. 1983. Photosynthetic parameters of arctic marine phytoplankton: vertical variations and time scales of adaptation. Limnol. Oceanogr., 28:698-708.
- GAXIOLA-CASTRO, G., and S. ALVAREZ-BORREGO. 1984. Photosynthesis-irradiance relationship for the phytoplankton of coastal waters of northwest Baja California. Ciencias Marinas, 10(3):53-66.
- GAXIOLA-CASTRO, G., and S. ALVAREZ-BORREGO. (subm. for publ.). Photosynthesis-irradiance relationship for winter phytoplankton of Mexican Pacific waters. Oceanologica Acta.
- GAXIOLA-CASTRO, G., S. ALVAREZ-BORREGO, and A. CHAGOYA-GUZMÁN. (in prep.) Photosynthetic parameters and primary productivity of Gulf of California winter phytoplankton.
- GESSNER, F. 1949. Der chlorophyllgehalt im see und seine photosynthetische valenz als geophysikalisches problem. Schweizer, Zeitschr. Hydrol. 9, 378 p.
- GILBERT, J. Y., and W. E. ALLEN. 1943. The phytoplankton of the Gulf of California obtained by the "E.W. Scripps" in 1939 and 1940. J. Mar. Res., 5(2):89-110.
- HARRISON, W. G., and T. PLATT. 1980. Variations in assimilation number of coastal marine phytoplankton: effects of environmental co-variables. J. Plankton Res. 2:249-260.
- LARA-LARA, J. R., J. E. VALDEZ-OLGUIN, and L. C. JIMENEZ-PÉREZ. 1984. Plankton studies in the Gulf of California during the 1982-83 El Niño. Trop. Ocean-Atmosph. Newsletter, 28:16-17.
- LORENZEN, C. J. 1967. Determination of chlorophyll and phaeopigments: spectrophotometric equations. Limnol. Oceanogr., 12:343-346.
- MARRA, J. 1980. Vertical mixing and primary production. p. 121-137. In: Falkowski, P. G. (ed.), Primary Productivity in the Sea, Plenum Press, New York.
- PLATT, T., and A. D. JASSBY. 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J. Phycol., 12:421-430.
- PLATT, T., K. L. DENMAN, and A. D. JASSBY. 1976. Modelling the productivity of phytoplankton. In: Goldberg, E. D. (ed.), The Sea, Interscience, 6:807-856.
- PLATT, T., W. G. HARRISON, B. IRWIN, E. P. HORNE, and C. L. GALLEGOS. 1982. Photosynthesis and photoadaptation of marine phytoplankton in the arctic. Deep-Sea Res., 29(10A):1159-1170.
- ROBLES-PACHECO, J. M., and N. CHRISTENSEN. 1984. Effects of the 1982-83 El Niño on the Gulf of California. Trans. Am. Geophys. Union 52:1039.

- SCOR-UNESCO. 1966. Determination of photosynthetic pigments. Monogr. Oceanogr. Methodol., 18 p.
- STEEMANN-NIELSEN, E. 1952. The use of radioactive carbon (^{14}C) for measuring organic production in the sea. *J. Cons. Explor. Mer.*, 18: 117–140.
- STEEMANN-NIELSEN, E., and V. KR. HANSEN. 1959. Light adaptation in marine phytoplankton populations and its interrelation with temperature. *Physiol. Plant.*, 12: 353–370.
- STRICKLAND, J. D., and T. R. PARSONS. 1972. A practical handbook of seawater analysis. *Bull. Fish. Res. Bd. Canada*, 167 p.
- TORRES-MOYE, G., and S. ALVAREZ-BORREGO. (subm. for publ.). Photosynthetic parameters of phytoplankton from a Baja California upwelling zone: El Niño effect.
- TRAGANZA, E. D., D. A. NESTOR, and A. K. McDONALD. 1980. Satellite observations of a nutrient upwelling off the coast of California. *J. Geophys. Res.* 85(C 7): 4101–4106.
- TRAGANZA, E. D., J. C. CONRAD, and L. C. BRAKER. 1981. Satellite observations of a cyclonic upwelling system and giant plume in the California Current, p. 228–241. *In*: F. R. Richards (ed.), *Coastal Upwelling*, Am. Geophys. Union, Washington, D.C.
- UTERMÖHL, H. 1958. Zur vervollkommnung der quantitativen phytoplankton methodik. *Mitt. Int. Verein Theor. Angew. Limnol.* 9: 1–38.
- VOLLENWEIDER, R. A. 1965. Calculation models of photosynthesis-depth curves and some implications regarding day rate estimate in primary productivity measurements, p. 425–457. *In*: C. R. Goldman (ed.), *Primary productivity in aquatic environments*, Univ. California Press, Berkeley.
- ZEITZSCHEL, B. 1969. Primary productivity in the Gulf of California. *Mar. Biol.*, 3: 201–207.