THE EFFECTS OF LIGHT ON PRIMARY PRODUCTIVITY IN SOUTH KANEOHE BAY

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We certify that we have read this thesis and that in our opinion it is satisfactory in scope and quality as a thesis for the degree of Master of Science in oceanography.

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ABSTRACT

Primary production at a single station in Kaneohe Bay, Oahu, Hawaii was studied over a six-month period. Vertical profiles of production, plant biomass, light, and temperature were obtained and the data applied to a production model. The diel changes in surface production were measured and used to estimate daily production.

Primary production per unit surface area was found to average 1.5 grams carbon per square meter per day and was higher on days with little vertical stratification and with lower incident radiation. Light appeared to limit production below .12 langleys per minute which occurred below about five meters depth.

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INTRODUCTION

This investigation examines sunlight as a potentially limiting resource to phytoplankton in the southern end of Kaneohe Bay, a semi-enclosed marine inlet on the northeast coast of Oahu. Surface primary productivity in the south sector of the bay is not nutrient-limited (Caperon et al., 1971) and total primary productivity per unit area of sea surface was unexamined prior to this work. It was postulated that light limits total primary productivity and that a production model based upon light could be used to predict total productivity if the algal biomass were known.

The above hypothesis is based on the assumptions that (1) high nutrient input provides unlimited nutrients at all depths and (2) light is reduced to a limiting level in a major portion of the water column. Nutrient concentrations at 10 meters depth on each of six weekly preliminary samples of four stations in the south bay in the fall of 1972 always exceeded concentrations at 1 meter, and subsequent analyses have revealed minima of 0.5 µg-at ammonium- plus nitrate-nitrogen per liter in subsurface samples (D. Schell, personal communication), a non-limiting amount (Caperon and Meyer, 1972). Light extinction coefficients of .32 m^{-1} (Clutter, 1969), .47 m^{-1} (Gundersen, 1973), and .48 m^{-1} (Krasnick, 1973) in south Kaneohe Bay reduce photosynthetically active light at 6 meters depth to about .05 $ly(min)^{-1}$, which would appear to be limiting to most marine phytoplankton (Strickland, 1960).

Photosynthetic index (PI equals unit carbon fixed per unit chlorophyll *a* per hour) is a well established parameter for evaluating phytoplankton growth and its relationship to light intensity (Strickland, 1960; Platt, 1973). A hyperbolic relationship of PI versus light is found up to some optimal light intensity above which a decrease in PI occurs due to photoinhibition of photosynthesis. Variations in maximum PI may result from adaptation to ambient illumination (Steemann-Nielsen, 1968) which may be controlled in nature by the stability of the water column. An experimental design incorporating vertical profiles of algal biomass and productivity, bioassay of light effects, observation of diel changes in productivity rate, and consideration of wind effects was required in order to understand the dependence of productivity on light.

MATERIALS AND METHODS

Sampling

Field samples for productivity-depth profiles were collected at a station having a depth of 14 meters one km southeast of Coconut Island near the center of the southern sector of Kaneohe Bay. Sea water was pumped on board an anchored launch with an electric positive displacement pump drawing through a one-half inch diameter garden hose at a rate of 6.7 liters per minute. The transit time through the hose was about twenty seconds. A Turner fluorometer was mounted on the suction side of the pump and water was collected from the pump discharge in a 20 liter carboy. Water from a single depth was mixed in the carboy and dispensed through 333-μ mesh screening into replicate BOD bottles and opaque plastic storage bottles for pigment analysis. Water temperature was measured in the carboy and the pigment bottles. Productivity bottles were suspended from an anchored buoy at the sampling location from 0930-1230 Hawaiian standard time. Replicates of some samples were incubated at various depths to test the effects of illumination and were termed "transplant" samples.

Water samples for time-course productivity estimates were collected before sunrise from a depth of one meter with a Van Dorn bottle, mixed in a carboy, and dispensed into BOD bottles. The bottles were suspended at a depth of one meter from a floating beam and collected serially at two hour intervals.

Productivity

The methods used for productivity measurement were those of Strickland and Parsons (1968) with the following specific techniques: a. Duplicate light and single dark 300 ml BOD bottles were incubated for each sample. b. The sodium bicarbonate inoculant was from either 1μCi sealed ampules from New England Nuclear or from a $1\mu Ci(ml)^{-1}$ stock solution (Strickland and Parsons, 1968) which was added to the bottles by means of a Cornwall repeating syringe. c. All bottles were stored in the dark without poisoning after collection and the contents filtered within three hours. d. Millipore HAWP .45-μ filters were sucked dry, rinsed three times with ten ml of Whatman GF/C filtered bay water, fumed one minute in HCl vapor and placed in scintillation vials containing ten ml Aquasol scintillation fluid. e. Activity of filters was determined by counting in a Beckman Model 230 liquid scintillation counter. Counting efficiency was determined by the channels ratio method. A quench curve obtained by counts of ^{14}C toluene standard in Aquasol with acetone added as the quenching agent gave efficiencies of 82 to 90%. Efficiency of counting of filters with activities less than 500 counts per minute was assumed to be 86%.

Pigment Analysis

Chlorophyll and carotenoid pigments were determined by the spectrophotometric method of Strickland and Parsons (1968) on samples from all depths at which productivity estimates were made. One-to-two liters were filtered on

Whatman 2.4-cm GF/C filters, the filters stored overnight in 90% acetone, ground in a tissue grinder, and refiltered. The extinction of the resulting 12-15 ml extract was determined in a 4-cm cell in a Beckman DB-G spectrophotometer. Phaeo-pigments and the abbreviated chlorophyll _a_ estimate were also determined on samples taken after September 9, 1973.

In vivo fluorescence of chlorophyll _a_ (Strickland and Parsons, 1968) was measured with a Turner fluorometer fitted with a large-volume flow-through door at one meter depth intervals during sampling. The fluorometer was operated in the "door 10" position after zeroing with GF/C filtered sea water.

Light

Light extinction was measured with a GM Manufacturing Co. submersible light meter and a Secchi disk near local apparent noon each day. Total surface light during incubations was measured by an Eppley pyrheliometer located at Coconut Island. The radiation recorded on the pyrheliometer digital integrator was corrected to photosynthetically active radiation by multiplying by 0.5 (Strickland, 1958). The average illumination at each depth during incubation was calculated by multiplying the percent of surface light found at each depth by the photosynthetically active radiation at the surface. This method underestimates the light available to organisms in a BOD bottle since only light striking the horizontal surface of the light meter is measured. Horizontal light (measured with the face of the meter in a vertical plane) at 10 meters depth at noon on May 4, 1973 was 35% of vertical light. Jerlov (1968) stated that horizontal light varies from 75-85% of vertical light but Atkins and Poole (1958) stated that horizontal light averages only 25% of vertical. As it is probable that this ratio changes with depth and meteorological conditions, its effect is uncertain.

Wind

Wind data was obtained from the aerology office at Kaneohe Marine Corps Air Station and was recorded at a point 2 km from the sampling site and 5 meters above sea level.

RESULTS

Vertical Profiles

Productivity index decreased significantly ($P<.01$) with increasing depth on every sampling day, and PI's of transplanted samples responded directly to imposed light changes in 24 of 25 cases. Detailed results of vertical profiles of plant pigments, productivity, light, and productivity index on sixteen days are presented in table 1. Samples transplanted to non-source depths are identified in column 2 with the depth at which they originated followed by the depth at which they were incubated. Total chlorophyll a and total hourly production in the water column are given in the "total" line for each day.

Chlorophyll a concentration and temperature were more nearly constant with increasing depth when winds were steady in direction and at speeds over 10 knots, but complete mixing from a stratified condition appeared to take more than one day. Light trade winds September 9-13 did not mix the bay vertically. Maximum chlorophyll a concentrations usually occurred either near the surface or near the bottom.

Plots of chlorophyll a, productivity, and temperature versus depth for the days studied appear in figure 1. Vertical stability is indicated by a temperature gradient greater than $.04^{\circ}C(m)^{-1}$ in the absence of a salinity gradient (Strickland, 1960; Harvey, 1960). Such stable conditions occurred on June 25 and 29, July 12, August 31 and

September 11, 13, and 20. These days also exhibited vertical gradients in chlorophyll a greater than 0.1 $mg(m)^{-1}$. The absence of vertical stability is indicated by temperature gradients of less than $.04^{\circ}C(m)^{-1}$ and mixing was considered complete if the chlorophyll a gradient was similarly small ($<.07$ $mg(m)^{-1}$). Well-mixed days occurred on May 15 and 21, September 7, and October 9, 12, and 25. The remaining three days had small temperature gradients but large chlorophyll a gradients and were considered transitional in terms of stability. The existence of stability during the summer months followed by mixed conditions in the fall was reported by Bathen (1968) and is a function of wind as well as the vertical density gradient. A wind summary consisting of percent of time wind was from each quadrant and average speed in that quadrant during the 24 hours preceding sampling is included in figure 1.

Production per square meter per hour on the days studied was negatively correlated with surface light intensity ($r=-.61$, $P<.05$) and was not well correlated with total chlorophyll a ($r=.48$, $P>.05$) nor with wind speed. The total production on mixed days averaged 145 $mgC(m)^{-3}hr^{-1}$ and was significantly greater ($P<.001$) than the 102 $mgC(m)^{-3}hr^{-1}$ produced on stratified days. Differences in total production were more closely correlated with temperature gradients than with surface light.

The regression of extracted chlorophyll a on *in vivo* fluorescence is shown in figure 2. The regression chl *a* = .0494 x fluorescence + .717 is significant at the .001 probability level and the error of prediction of a single Y-value is ± 1 mg chl *a*$(m)^{-3}$.

The inclusion of phaeopigments in the tri-chromatic chlorophyll *a* determinations probably results in over-estimates of chlorophyll *a* and consequently underestimates of productivity index. Preliminary phaeopigment measurements in the fall of 1972 often yielded negative values of phaeo-pigment but phaeopigments as a percent of chlorophyll *a* (+ phaecpigment) never exceeded 38%. Similar comparisons in October 1973 yielded percentages as high as 74%. The high phaeopigments found on days with strong winds suggests lifting of bottom deposits containing phaeopigments (Strickland, 1968). The scatter in the chlorophyll *a* versus *in vivo* fluorescence regression (figure 2) is likely due to variations in accessory pigments as well as phaeopigments and other degradation products. The lack of data on inactive chloro-phyll pigments between May and October constitutes a regrettable void and may contribute to the variation in maximum PI's observed.

The effect of phytoplankton on the extinction of sunlight is significant ($P<.001$) and is depicted in figure 3. The coefficient of determination (r^2) for total water column chlorophyll *a* and extinction coefficient at 13 meters is 60% (n=16). Krasnick (1973) reported a more significant but similar correlation for data from one meter depths. The present data support Steinhelper's (1970) report that living plant carbon in the bay was 57% of particulate organic carbon.

A comparison of light extinction coefficients and observed Secchi depths yields the factor f=1.26 (n=9, S.D.=.16) for estimating extinction from Secchi depths by means of the equation $k=f(z)^{-1}$. This is a reasonable reduction of the usual factor f=1.7 as suggested by Holmes (1970) for turbid water.

Time-course Productivity

Time-course surface productivity experiments conducted on September 27, October 3, and November 13 revealed a pattern of productivity generally conforming to the pattern of illumination. Productivity during each of six two-hour periods from sunrise to sunset was determined by difference between adjacent 2, 4, 6, 8, 10, and 12 hour incubations. The light, productivity and productivity index data are listed in table 2. In calculating PI, the chlorophyll a concentration was assumed constant throughout the day even though slight changes occurred. On September 27 chlorophyll was measured only at 0630. On October 3 chlorophyll a rose slightly from 2.10 $mg(m)^{-3}$ at 0630 to 2.71 $mg(m)^{-3}$ at 1830. On November 13 chlorophyll a ranged from 3.35 $mg(m)^{-3}$ at 0630 to 2.36 $mg(m)^{-3}$ at 1430 and averaged 2.94 $mg(m)^{-3}$. Hourly productivity and average illumination at one meter during each period are plotted in figure 4. October 3 was a calm, unusually clear day which appears to have resulted in light inhibition of photosynthesis near midday. The apparent recovery later in the day suggests physiological adaptation within a few hours which conflicts with adaptation times greater than a day suggested by Jorgensen (1969) but is supported by a recent report on fresh water algae (Harris, 1973).

The temporal pattern of percent total light per day and percent total production per day throughout the day are very similar as is shown by figure 5. Production prior to 0930 averages 13% of the total, and prior to 1230 40% of the total, so that 27% apparently occurs between these two times. An excess of afternoon over morning production was reported by Doty (1964) as the norm in inshore waters, however almost all evidence from oceanic locations is toward greater production in the morning than in the afternoon (Doty, 1964; Eppley and Strickland, 1968; Malone, 1971c).

DISCUSSION

The results of this study indicate that light is usually limiting to phytoplankton growth below about 5 meters depth in South Kaneohe Bay. Phytoplankton concentration is often the controlling factor for production near the surface and largely determines the pattern of illumination below the surface. The relationships between light, pigment concentration, and productivity are the subject of the following discussion.

There is considerable precedence for describing phytoplankton growth rate as a hyperbolic function of a limiting substrate and in particular as a function of light intensity (Strickland, 1960; Eppley, 1972), at least for cultured populations. If mixing is adequate to homogenize the population in a shallow body of water such as Kaneohe Bay, then it seems reasonable to apply the same treatment to natural populations. Growth rate is equated herein with productivity index, as determined in 3-hour incubations. Values are *in situ* or transplanted sample values at the incubation illumination and do not represent maximum PI under "optimum" illumination (Platt and Subba Rao, 1973) except in the case of maxima on well mixed days.

Both temperature and chlorophyll *a* concentration were nearly constant with depth on May 15 and 21, September 7, and October 9, 12, and 25 (see figure 1) indicating that thoroughly mixed conditions occurred on these days. Graphs of *in situ*

PI versus light intensity for these days appear as figure 6. The curves are least squares fit of the rectangular hyperbola $PI_z = PI_{max} \cdot I_z \cdot (k_i + I_z)^{-1}$ where PI_z and I_z are respectively photosynthetic index and light at depth z; and PI_{max} and k_i are respectively maximum projected PI and the half-saturation constant for light.

The above equation provides a good fit to the daily data as can be seen in table 3, which lists calculated PI_{max}, k_i, and sample standard deviations $(\Sigma(Y-\hat{Y})^2(n-1))^{1/2}$ from the curves for each of the days, which are grouped according to their degree of vertical stability. The high PI_{max} of the fitted curves for May 15 and 21 is partly due to lack of sampling shallower than three meters on those days. A decline in PI above 3 meters depth on October 12 and 25 is evident in figure 6 and a similar decline occurred on October 17 and 23. This decline may indicate light inhibition of photosynthesis (Steemann-Nielsen, 1952), however Harris and Lott (1973) stated that moored bottles tend to underestimate surface productivity on days when vertical mixing is significant due to photoinhibition in bottles which is not present _in situ_. During seven of the ten days when there was clear chlorophyll _a_ stratification, the productivity index-light relationship is also well described by a hyperbola. Although PI_{max} was lowest on well mixed days as expected, four stratified days also have low PI_{max}, indicating that light inhibition or lowered nutrients near the surface may limit PI after a few days without mixing. The extremely high PI_{max} values for June 25, August 31, and September 13 are not ecologically realistic and simply reflect the lack of a light-saturation plateau in the data for those days. The days studied cannot be separated into mixed and stratified days on the basis of PI_{max} and k_i.

The purpose of transplanting samples for incubation at altered light intensities was twofold: first, to test whether or not light was limiting production, and second, to compare PI's of samples from different depths incubated at equal light intensities in order to examine effects of light adaptation on productivity index. In the first case, confirmation of light limitation is unequivocal, since 21 of 25 transplanted sample PI's closely match the in situ PI at the incubation depth. Transplanted PI's averaged 102% (S.D.=29%, n=25) of in situ PI's. In the second case, the results are inconclusive due to a change from generally stratified conditions to generally mixed conditions coincidental with a change in the depth at which samples were obtained and incubated. From June 25 to September 20 transplants were made from 13 to 11 and 11 to 9 meters and increases in PI confirmed that productivity was limited by light at those depths. After September 20 transplants were made from 3 to 9 and 9 to 3 meters in an attempt to bracket the depth at which light became limiting. The absence of stratification during sampling after September 20 prevented examination of light adaptation.

Some other variables, a consideration of which follows, have the potential to alter results of ^{14}C productivity or pigment estimates and consequently PI's.

Prefiltering samples through 333-μ mesh is ineffective in removing predominant herbivores. Maximum micro-copepod densities in Kaneohe Bay of 30 $mg(m)^{-3}$ could consume about 0.7 $mgC(m)^{-3}hr^{-1}$ (Bartholomew, 1973). Some of this loss might be eliminated by using finer mesh, especially if primary producers are predominantly in the nanno size range. Pigment measurements on five paired samples were done on October 10 and 25 to examine this possibility. Bay water which had been passed through 35 or 20-μ mesh contained 80% of both chlorophyll a and phaeopigments. This may be compared with about 60% of chlorophyll a through 22-μ mesh for neritic areas reported by Malone (1971a). The proportion of net versus nanno plankton in sea water is affected by water column stability (Malone, 1971b) and "benthic" diatoms have been observed in surface water of Kaneohe Bay during strong winds (D. Redalje, personal communication). It appears that grazing effects, while small, could be reduced by selection of a prefiltering mesh between 35 and 333-μ pore size but that temporal variations in phytoplankton size hinder the selection.

Pigment increases during ^{14}C incubations could result in decreases in PI from those reported here. Chlorophyll a in four test samples incubated three hours, however, increased an average of only 3% and the error so induced is considered minimal.

An understanding of the general effect of light on productivity may be gained by fitting a hyperbola to the combined light and PI data. Figure 7 presents the resulting curve $PI_z=8.33 \cdot I_z \cdot (.058+I_z)^{-1}$. The values of PI_{max} and k_i are similar to parameters of hyperbolae for mixed days, which seem to be most representative of average conditions in the bay. Since production above .116 $ly(min)^{-1}$ ($=2k_i$) is independent of light intensity, the question may be asked "what limits production above .116 $ly(min)^{-1}$?" The regression of productivity on chlorophyll a concentration for samples above this intensity has a coefficient of determination of 81% ($r=.90$, $P<.001$) indicating that no photosynthetic substrate is limiting and that productivity is mainly a function of plant biomass. Below .116 $ly(min)^{-1}$ there is no correlation between productivity and chlorophyll a ($r=.13$, $P>.05$) but a fair correlation of PI with light ($r=.68$, $P<.001$), indicating that light controls productivity below about 5 meters depth.

If the values of k_i in table 3 are taken as half the intensity at which light saturation occurs (Vollenwieder, 1965), then saturation generally occurs at .06 to .4 $ly(min)^{-1}$. This range of saturation intensities compares well with Quasim's (1972) report of .1 to .2 $ly(min)^{-1}$ for tropical diatoms and .1 to .3 $ly(min)^{-1}$ for tropical dinoflagellates. The above values are slightly higher than Ryther's (1956) range of .03 to .16 ly(min)$^{-1}$ for temperate species and Dunstan's (1973) report of .09 ly(min)$^{-1}$ for a variety of microalgae. The differences could be due to differences in preconditioning light or could be inherent in the latitudinal adaptation of phytoplankton populations (Steemann-Nielsen and Hanson, 1959).

The mean PI at light saturation in figure 7 is 6.9 mgC(mg chl a)$^{-1}$hr^{-1} (S.D.=2.1, n=47) and considering the possible effects of auxiliary pigments and phaeopigment, this is a minimal estimate. A PI of 7 is lower than reported surface values for the same area of 11.2 (S.D.=6.8, n=115) (Caperon et al., 1971) which may be a result of differing ^{14}C counting procedures. The present results are similar to tropical values of Steemann-Nielsen and Hanson (1959) but less than apparently maximal rates (see Eppley, 1972) of 12 to 16 in a shallower local estuary (Harris, 1972).

A model based upon PI as a function of light was not entirely satisfactory in predicting production. From figure 7, $PI_z=8.33\cdot I_z\cdot(.058+I_z)^{-1}$, and given also that $I_z=I_o e^{-kz}$, total production per square meter per hour can be calculated as $\Sigma P=\int_0^z chl_z\cdot PI_z dz$. For the present data the predicted hourly production rates for each day are given in table 4. The error of the prediction for each day as a percent of the measured production ranges from -52% to +82% (mean 28%, S.D.=25%) and is given in column 4. Since total production on mixed days (mean 145 mgC(m)$^{-2}$hr^{-1}) exceeded total production on stratified days (mean 102 $mgC(m)^{-2}hr^{-1}$) this method underestimates production on mixed days and over-estimates production on stratified days. Separate models could be used for mixed and stratified days, but attempting this without more data was considered unwarranted. Simplification of the present model by using mean chlorophyll a concentration for each day increases the average error from 28% to 37% (S.D.=32%, table 4 columns 5 and 6).

Total production over a twelve hour light day may be calculated by assuming that 27% of the daily production is measured during the 0930-1230 incubation as determined during the time-course experiments. Multiplying the hourly rates in table 1 by 11.1 (3 hours/27%) results in total production ranging from 0.92 to 2.07 $gC(m)^{-2}day^{-1}$ (mean 1.58, S.D.=0.3). This exceeds the production of 1.0 $gC(m)^{-2}day^{-1}$ in fertile sea areas (Strickland, 1965) but is well below the rate in a turbid local estuary (Harris, 1972) and other tropical inshore areas (Platt and Subba Rao, 1973).

SUMMARY

1. Primary production in south Kaneohe Bay was usually limited by light at depths greater than five meters.

2. Primary production near the surface was primarily a function of algal biomass.

3. Total production per unit surface area was higher when the water column was mixed than when hydrographic conditions were stable.

4. Total production during a twelve hour light day averaged 1.6 grams carbon per square meter.

TABLE 1
Plant pigments, productivity, and light.

Date	Depth meters	Chl *a* mg/m^3	Chl *b* mg/m^3	Chl *c* mg/m^3	Carot mg/m^3	Ab Chl mg/m^3	Phaeo mg/m^3	Prod $\frac{mgC}{m^3 hr}$	Light ly/min	PI $\frac{mgC}{chla \cdot hr}$
5/15/73	3	.73	.22	.91	.14			7.4*	.22	10.1
	5	.77	.14	.95	.27			7.3*	.20	9.5
	7	.84	.29	1.13	.07			7.1*	.14	8.5
	9	1.30	.40	1.62	.16			11.5*	.09	8.8
	11	1.25						7.7*	.07	6.2
	13	1.37	.42	1.72	.11			6.9*	.03	5.0
	total	13.98						110.3		
5/21/73	3	2.05	.22	1.58	.63			17.2	.12+	8.4
	5	1.77	.38	1.81	.52			12.1	.08+	6.8
	7	1.86	.23	.94	.49			13.0	.04	7.0
	9	1.83	.81	4.11	.57			7.9	.03+	4.3
	11	2.20	.72	3.25	.07			4.2	.02	1.9
	13	1.99	.76	3.43	.50			2.8	.01+	1.4
	total	27.50						148.8		
6/25/73	1	2.40	.10	1.59	2.82			21.6	.42	9.0
	3	1.29	.23	1.40	1.19			5.4	.28	4.2
	5	1.13	.17	1.05	1.38			4.8	.19	4.3
	7	1.07	.17	.94	1.17			3.5	.14	3.2
	9	1.42	.11	.85	.86			3.7	.10	2.6
	11-9							1.6		1.3
	11	1.28	.22	1.05	1.13			2.7	.08	2.1
	13-11							8.8		2.0
	13	4.48	.21	2.52	5.22			8.5	.03	1.9
	total	26.14						100.4		

* activity determined by GM counter
\+ estimated from extinction coefficient

TABLE 1 (continued)
Plant pigments, productivity, and light.

Date	Depth	Chl *a*	Chl *b*	Chl *c*	Carot	Ab Chl	Phaeo	Prod	Light	PI
	meters	mg/m^3	mg/m^3	mg/m^3	mg/m^3	mg/m^3	mg/m^3	$\frac{mgC}{m^3 hr}$	ly/min	$\frac{mgC}{chl a \cdot hr}$
6/29/73	1	.82	1.73	.38	1.13			6.5	.41	7.9
	3	.82	neg	neg	.20			5.5	.30	7.7
	5	.87	neg	.14	.10			6.5	.20	7.5
	7	.93	neg	.01	.98			4.7	.13	5.2
	9	1.03	.03	.44	1.39			5.5	.08	5.3
	11-9							8.0		5.0
	11	1.59	.00	.52	1.62			5.5	.06	5.3
	13-11							12.3		3.6
	13	3.40	.15	1.93	3.36			9.9	.03	2.9
	total	18.96						88.4		
7/12/73	1	1.01	.13	.66	.96			5.4	.42	5.3
	3	1.01	.11	.10	.75			5.4	.29	5.3
	5	1.16	.16	.77	1.83			4.2	.19	3.6
	7	1.49	.12	.94	1.53			4.0	.12	2.7
	9	1.93*	.33*	1.19*	1.70*			4.3	.08	2.2
	11-9							3.9		2.0
	11	1.97*	.34*	1.26*	1.45*			3.5	.05	1.8
	13-11							4.8		1.6
	13	3.10*	.49*	1.01*	3.50*			3.6	.03	1.2
	total	23.34						61.0		
8/31/73	1	3.21*	.03*	1.51*	1.26*			37.5+	.16	11.7
	3	2.77	neg	1.04	1.92			28.5	.13	9.8
	5	1.39	.11	.66	1.13			6.3	.10	4.5
	7	1.33	.07	.49	1.32			6.5	.04	4.9
	9	1.34	.10	.46	1.28			5.4	.03	4.0

* mean of two replicates   + slipped to three meters during incubation

TABLE 1 (continued)
Plant pigments, productivity, and light.

Date	Depth meters	Chl *a* mg/m^3	Chl *b* mg/m^3	Chl *c* mg/m^3	Carot mg/m^3	Ab Chl mg/m^3	Phaeo mg/m^3	Prod $\frac{mgC}{m^3 hr}$	Light ly/min	PI $\frac{mgC}{chl\,a \cdot hr}$
8/31/73	11-9							6.3		3.7
cont'd	11	1.69	.11	.75	1.51			3.9	.02	2.3
	13-11							5.1		2.8
	13	1.80	.05	.55	1.45			2.1	.01	1.2
	total	27.11						180.4		
9/7/73	1	1.68*	.24*	.60*	2.39*			19.5	.39	11.6
	3	1.88	.06	.91	2.37			18.3	.12	9.7
	5	1.94	.09	1.00	2.64			14.9	.07	7.7
	7	1.88	.11	.42	2.49			10.0	.03	5.3
	9	2.38	.17	.62	2.82			5.4	.02	2.3
	11-9							7.4		3.2
	11	2.33	.14	1.32	2.81			5.4	.01	2.3
	13-11							3.5		1.5
	13	2.38	.14	.95	2.82			2.5	.00	1.1
	total	28.94						152.0		
9/11/73	1	2.40	.23	.70	3.41			10.0	.28	4.2
	3	1.50	.07	.63	2.25			10.8	.17	7.2
	5	1.60	.07	.79	2.15			7.4	.11	4.6
	7	1.55	.17	.60	2.24			3.7	.07	2.4
	9	2.01	.45	.81	2.75			3.4	.04	1.7
	11-9							8.1		1.4
	11	5.62	.06	1.91	6.35			5.0	.02	.9
	13-11							3.2		.7
	13	4.80	neg	2.10	5.41			1.2	.01	.3
	total	38.08						83.0		

* mean of two replicates

TABLE 1 (continued)
Plant pigments, productivity, and light.

Date	Depth meters	Chl *a* mg/m^3	Chl *b* mg/m^3	Chl *c* mg/m^3	Carot mg/m^3	Ab Chl mg/m^3	Phaeo mg/m^3	Prod $\frac{mgC}{m^3 hr}$	Light ly/min	PI $\frac{mgC}{chla \cdot hr}$
9/13/73	0.2	2.18	.18	.91	3.00					
	1	2.95	.08	.13	3.64			27.8	.36	9.4
	3	1.05	.17	.65	1.87			5.2	.22	5.0
	5	1.00	.17	.53	1.66			4.0	.13	4.0
	7	3.04	.45	1.22	4.10			8.4	.08	2.8
	9	2.96	.42	1.14	3.84			5.6	.05	1.9
	11-9							6.4		1.9
	11	3.40	.43	1.37	4.40			3.9	.03	1.1
	13	4.38	.07	1.25	4.75			1.9	.01	.4
	total	37.50						113.6		
9/18/73	0.2	5.16	.07	1.95	6.20			54.2	.32	10.5
	1	5.86	.49	3.95	7.39			49.4	.25	8.4
	3	3.27	.34	1.52	4.58			23.4	.12	7.2
	5	2.01	.58	.89	3.40			5.8	.05	2.9
	7	2.04	.38	.73	3.19			3.9	.03	1.9
	9	2.48	.41	.71	3.50			3.1	.02	1.3
	11-9							3.9		1.5
	11	2.67	.37	.59	3.24			2.0	.01	.7
	13	2.25	.37	.49	2.96			.7	.00	.2
	total	40.57						181.4		
9/20/73	0.2	1.87	.25	.63	3.11			11.7	.42	6.3
	1	1.92	.21	.60	3.10			11.7	.35	6.1
	3	1.96	.21	.78	3.08			9.1	.19	4.6
	5	2.10	.37	.43	3.28			6.3	.11	3.0
	7	2.36	.54	.64	3.44			5.2	.05	2.2
	9	3.43	.61	.86	4.74			6.4	.02	1.9

TABLE 1 (continued)
Plant pigments, productivity, and light

Date	Depth meters	Chl *a* mg/m³	Chl *b* mg/m³	Chl *c* mg/m³	Carot mg/m³	Ab Chl mg/m³	Phaeo mg/m³	Prod mgC/m³hr	Light ly/min	PI mgC/chl*a*·hr
9/20/73	13-9							3.6		2.4
cont'd	11	2.87	.51	.86	3.75			3.3	.01	1.1
	13	1.51	.26	.40	1.92			1.2	.00	.8
	total	33.55						86.4		
10/9/73	0.2	3.10	.59	1.16	2.43	1.97	1.89	21.7	.39+	7.0
	1	3.25	.50	1.10	2.34	1.91	2.22	18.8	.31+	5.7
	3	3.36	.55	1.07	2.87	2.16	1.99	23.5	.14+	7.0
	9-3							21.7		6.9
	5	3.42	.58	1.74	2.67	2.22	1.99	17.8	.06+	5.2
	7	3.33	.50	1.13	2.55	2.12	2.00	9.0	.03+	2.7
	9	3.15	.45	1.00	2.52	2.00	1.89	4.0	.01+	1.3
	3-9							4.0		1.2
	11	3.44	.48	.90	2.71	2.16	2.12	2.1	.00+	.6
	13	2.59	.36	.64	2.04	1.28	2.16	.9	.00+	.3
	total	44.93						155.1		
10/12/73	.2	3.19	.58	1.24	1.37	2.00	1.98	15.7	.40	4.9
	1	3.10	.46	1.10	1.11	1.44	2.76	19.9	.35	6.4
	3	3.34	.40	1.28	1.44	2.16	1.93	22.0	.20	6.6
	9-3							23.4		7.1
	5	3.29	.48	.85	2.19	2.08	1.99	21.8	.10	6.6
	7	3.40	.36	1.19	1.40	2.04	2.23	14.6	.06	4.3
	9	3.28	.46	.79	2.19	2.05	2.02	8.9	.03	2.7
	3-9							9.0		2.7
	11	3.41	.40	1.24	2.17	2.88	.82	5.0	.02	1.5
	13	3.14*						3.0	.01	.9*
	total	39.71						186.2		

+ estimated from chart record   * estimated from fluorescence

TABLE 1 (continued)
Plant pigments, productivity, and light.

Date	Depth meters	Chl *a* mg/m^3	Chl *b* mg/m^3	Chl *c* mg/m^3	Carot mg/m^3	Ab Chl mg/m^3	Phaeo mg/m^3	Prod $\frac{mgC}{m^3hr}$	Light ly/min	PI $\frac{mgC}{chl a \cdot hr}$
10/17/73	0.2	2.81	.29	.94	2.05	.69	3.53	18.5	.36	6.6
	1	2.79	.28	.86	1.99	1.51	2.11	19.3	.29	6.9
	3	2.44	.35	1.04	1.90	1.50	1.57	19.5	.20	8.0
	9-3							17.8		4.4
	5	2.80	.36	.98	1.92	1.55	2.08	16.6	.13	5.9
	7	2.72	.33	.86	1.89	1.44	2.11	13.1	.07	4.8
	9	4.04	.45	1.16	2.52	2.46	2.59	7.8	.04	1.9
	3-9							6.9		2.8
	11	3.58	.21	1.27	1.88	2.30	2.08	2.9	.03	.8
	13	2.83	.35	.97	1.65	1.66	1.93	2.0	.01	.7
	total	43.26						161.6		
10/23/73	0.2	3.47	.52	1.30	2.39	2.72	1.20	21.5	.42	6.2
	1	3.48	.43	.95	2.42	2.08	2.29	19.4	.32	5.6
	3	3.65	.50	1.09	2.48	2.40	2.05	24.6	.16	6.7
	3L*	3.67	.55	.82	2.66	2.51	1.90			
	9-3							6.4		2.9
	5	3.70	.44	1.10	2.43	2.24	2.39	19.7	.08	5.3
	7	3.41	.46	.99	2.14	2.30	1.82	10.8	.04	3.2
	9	2.20	.33	.61	1.42	1.44	1.25	4.0	.02	1.8
	9L*	2.45	.27	.59	1.40	1.87	.93			
	3-9							7.1		2.0
	11	1.85	.38	.37	1.63	.84	1.68	1.6	.01	.9
	13	1.93	.32	.30	1.17	1.39	.89	.8	.00	.4
	total	40.44						163.9		

* translucent polyethylene bottle incubated three hours

TABLE 1 (continued)
Plant pigments, productivity, and light.

Date	Depth meters	Chl *a* mg/m^3	Chl *b* mg/m^3	Chl *c* mg/m^3	Carot mg/m^3	Ab Chl mg/m^3	Phaeo mg/m^3	Prod $\frac{mgC}{m^3 hr}$	Light ly/min	PI $\frac{mgC}{chl\,a \cdot hr}$
10/25/73	0.2	2.14	.27	.64	1.88	1.32	1.34	11.0	.42	5.1
	1	2.19	.24	.70	1.90	1.40	1.29	13.2	.34	6.0
	3	2.27	.33	.57	1.93	1.56	1.16	11.0	.17	4.8
	3L*	2.69	.23	1.12	2.50	1.80	1.45			
	3<35μ	2.10	.25	.65	1.55	1.59	.83			
	9-3							14.4	0.35	6.3
	5	2.27	.29	.76	1.90	1.68	.95	12.3	.12	5.4
	7	2.19	.21	.64	1.93	1.28	1.49	8.2	.04	3.7
	9	2.29	.24	.47	1.95	1.72	.91	5.1	.02	2.2
	9L*	3.01	.33	1.04	2.45	2.24	1.23			
	9<35μ	2.14	.29	.70	1.89	1.60	.87			
	3-9							6.2		2.7
	11	2.33	.37	.80	1.97	1.80	.86	2.6	.01	1.1
	13	2.19	.24	.70	1.80	1.60	.95	1.5	.00	.7
	total	35.42						118.0		

* translucent polyethylene bottle incubated three hours

TABLE 2
Time-course productivity data.

Date	Time	Total I_o ly	Period I_z ly/min	Total Prod $\frac{mgC}{m^3}$	Period Prod $\frac{mgC}{m^3 hr}$	Period PI $\frac{mgC}{chla \cdot hr}$
9/27	0830	19.0	.03	17.9	9.0	2.3
	1030	41.8	.05	49.5	15.8	4.0
	1230	81.4	.08	87.6	19.1	4.9
	1430	154.2	.16	149.5	31.0	7.9
	1630	210.0	.11	178.2	14.3	3.6
	1830	213.2	.01	192.0	6.9	1.8
10/13	0830	2.0	.00	18.2	9.1	3.8
	1030	113.8	.25	55.2	18.5	7.8
	1230	269.6	.38	105.8	25.1	10.5
	1430	419.4	.39	147.8	21.2	8.9
	1630	509.6	.22	233.0	42.5	17.8
	1830	525.2	.04	301.3	34.2	14.4
11/13	0830	26.8	.07	11.6	5.8	2.0
	1030	81.0	.15	29.8	9.0	3.1
	1230	164.0	.22	60.7	15.5	5.3
	1430	250.0	.22	92.1	15.6	5.3
	1630	334.2	.20	129.0	18.5	6.3
	1830	339.6	.01	155.3	13.2	4.5

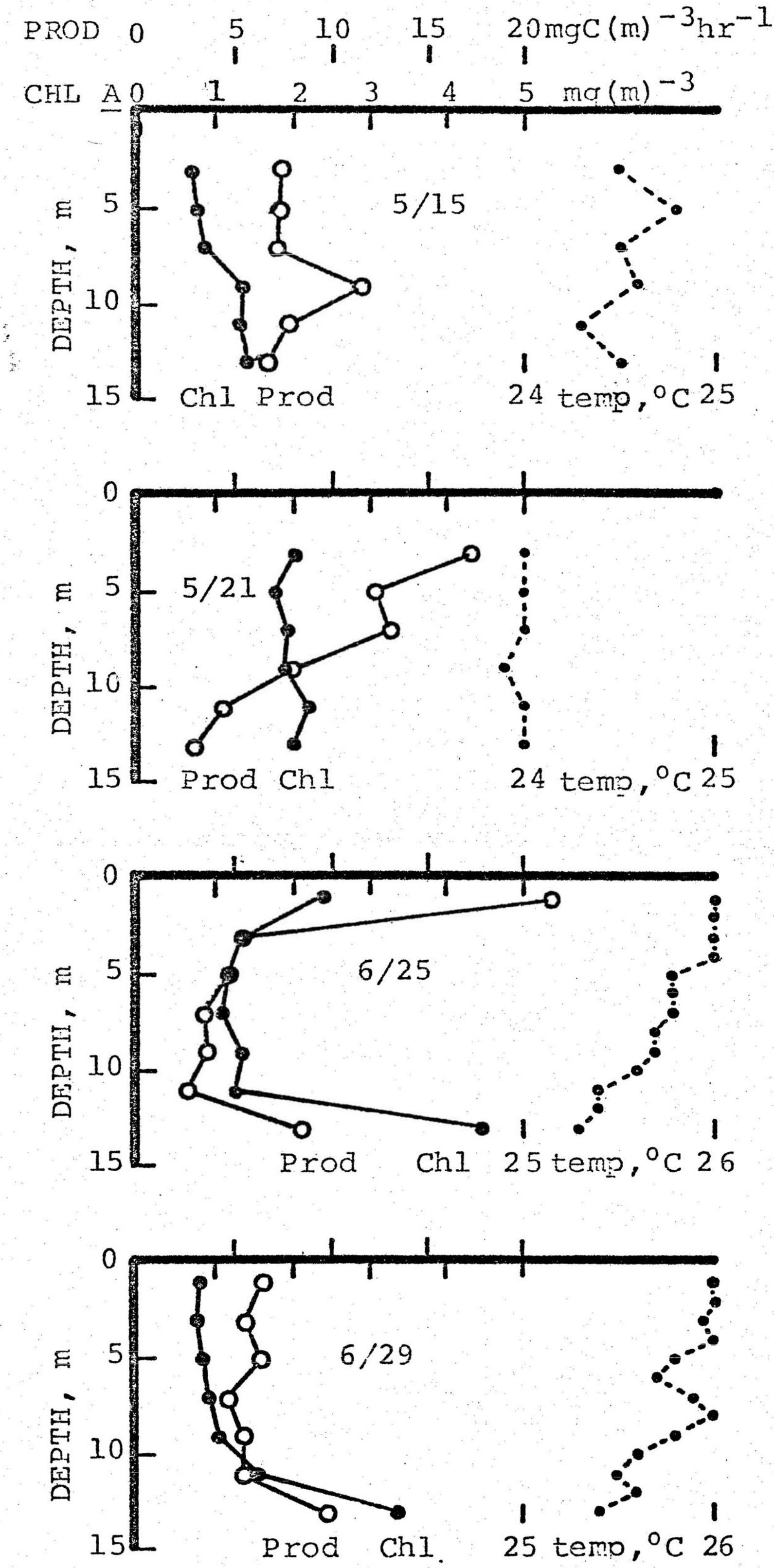
TABLE 3
Parameters of hyperbolae fit to daily PI and light data.

Date	n	PI_{max} mgC/chla·hr	k_i ly/min	S.D. mgC/chla·hr	Comments
6/25	7	76.18	3.401	0.9	stratified
6/29	7	9.04	.057	0.7	''
7/12	7	8.33	.217	0.3	''
8/31	7	23.52	.186	1.5	''
9/11	7	7.87	.162	1.2	''
9/13	7	46.60	1.492	0.5	''
9/20	8	8.15	.134	0.4	''
5/15	6	11.81	.045	0.7	mixed
5/21	6	12.72	.060	1.5	''
9/7	7	13.39	.052	0.6	''
10/9	8	7.57	.039	0.7	''
10/12	8	6.97	.038	0.8	''
10/25	8	6.11	.032	0.6	''
9/18	8	16.55	.200	0.5	transitional
10/17	8	9.86	.105	0.8	''
10/23	8	7.22	.045	0.6	''

mean chl = 32.46 mg/m²

TABLE 4
Measured and predicted hourly production rates

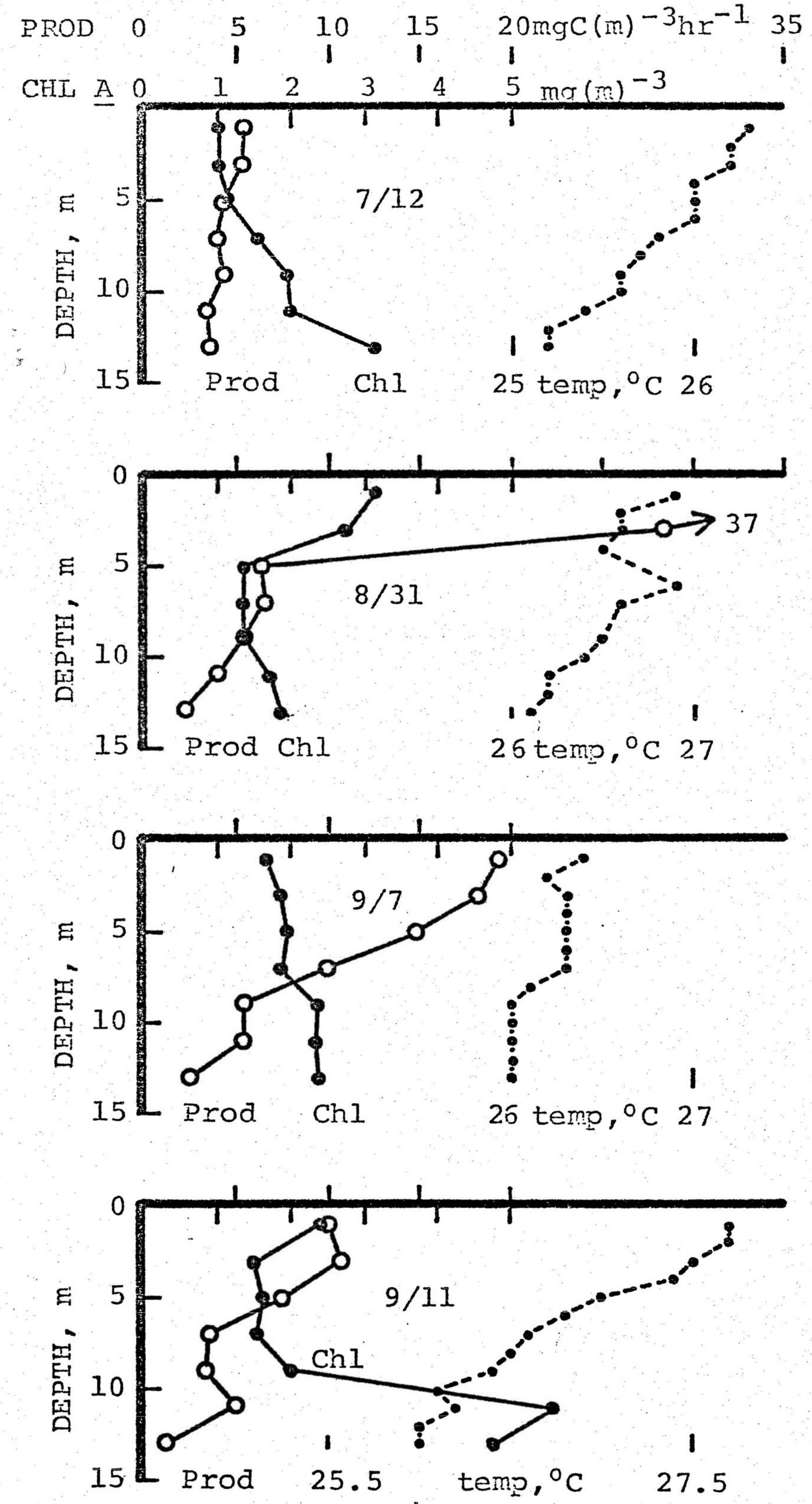
Date	Measured	Predicted using actual (Chl a)$_z$		Predicted using mean Chl a	
	$\frac{mgC}{m^2 hr}$	$\frac{mgC}{m^2 hr}$	% error	$\frac{mgC}{m^2 hr}$	% error
5/15	110.3	52.4	-52	66.6	-39
5/21	148.8	124.9	16	125.4	-16
6/25	100.4	137.6	38	148.2	48
6/29	88.4	94.1	7	108.3	23
7/12	61.0	111.0	82	125.5	106
8/31	180.4	124.0	-31	113.7	-37
9/7	152.0	99.0	-35	107.5	-29
9/11	83.0	144.6	74	173.4	109
9/13	113.6	152.5	34	175.2	54
9/18	181.4	172.8	-5	143.8	-21
9/20	86.4	122.2	42	132.9	55
10/9	155.1	153.8	-1	149.1	4
10/12	186.2	175.5	-6	152.3	-18
10/17	161.6	185.3	14	196.7	21
10/23	163.9	163.4	0	139.8	-15
10/25	118.0	110.0	-7	124.3	5
$\Sigma\|\chi\|/n$	130.6	132.7	28	136.4	37



WIND SUMMARY

quad-rant	per-cent	spd, kts
NE	100	5
SE	0	-
SW	0	-
NW	0	-
NE	100	6
SE	0	-
SW	0	-
NW	0	-
NE	100	11
SE	0	-
SW	0	-
NW	0	-
NE	100	8
SE	0	-
SW	0	-
NW	0	-

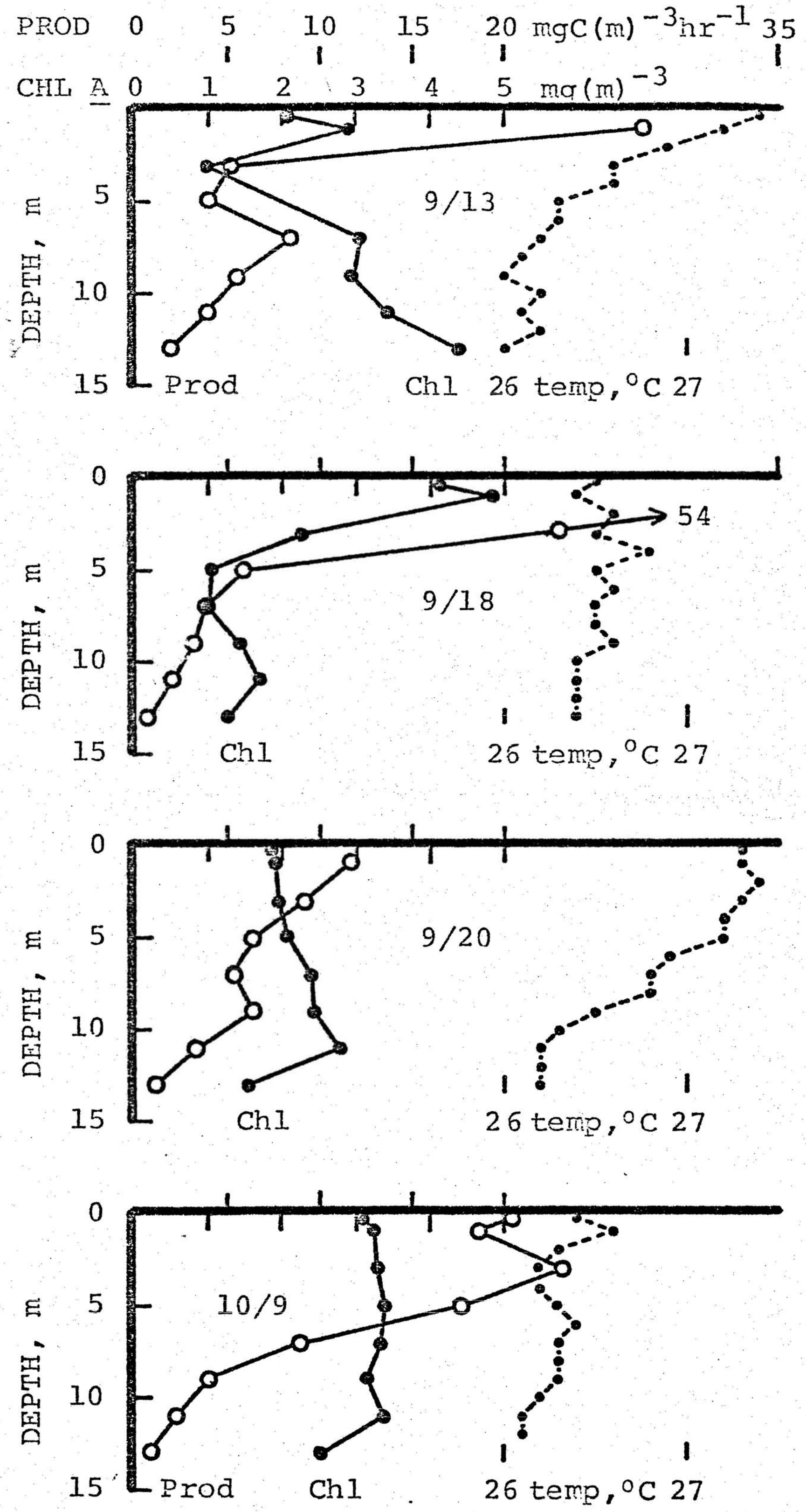
FIGURE 1. Vertical profiles of chlorophyll a, productivity, and temperature and average wind over preceeding 24 hours.



WIND SUMMARY

Date	quad-rant	per-cent	spd kts
7/12	NE	92	12
	SE	8	12
	SW	0	-
	NW	0	-
8/31	NE	0	-
	SE	8	5
	SW	16	4
	NW	67	9
9/7	NE	100	12
	SE	0	-
	SW	0	-
	NW	0	-
9/11	NE	71	6
	SE	8	9
	SW	12	3
	NW	0	-

FIGURE 1 continued. Vertical profiles of chlorophyll a, productivity, and temperature, and average wind over preceeding 24 hours.



WIND SUMMARY

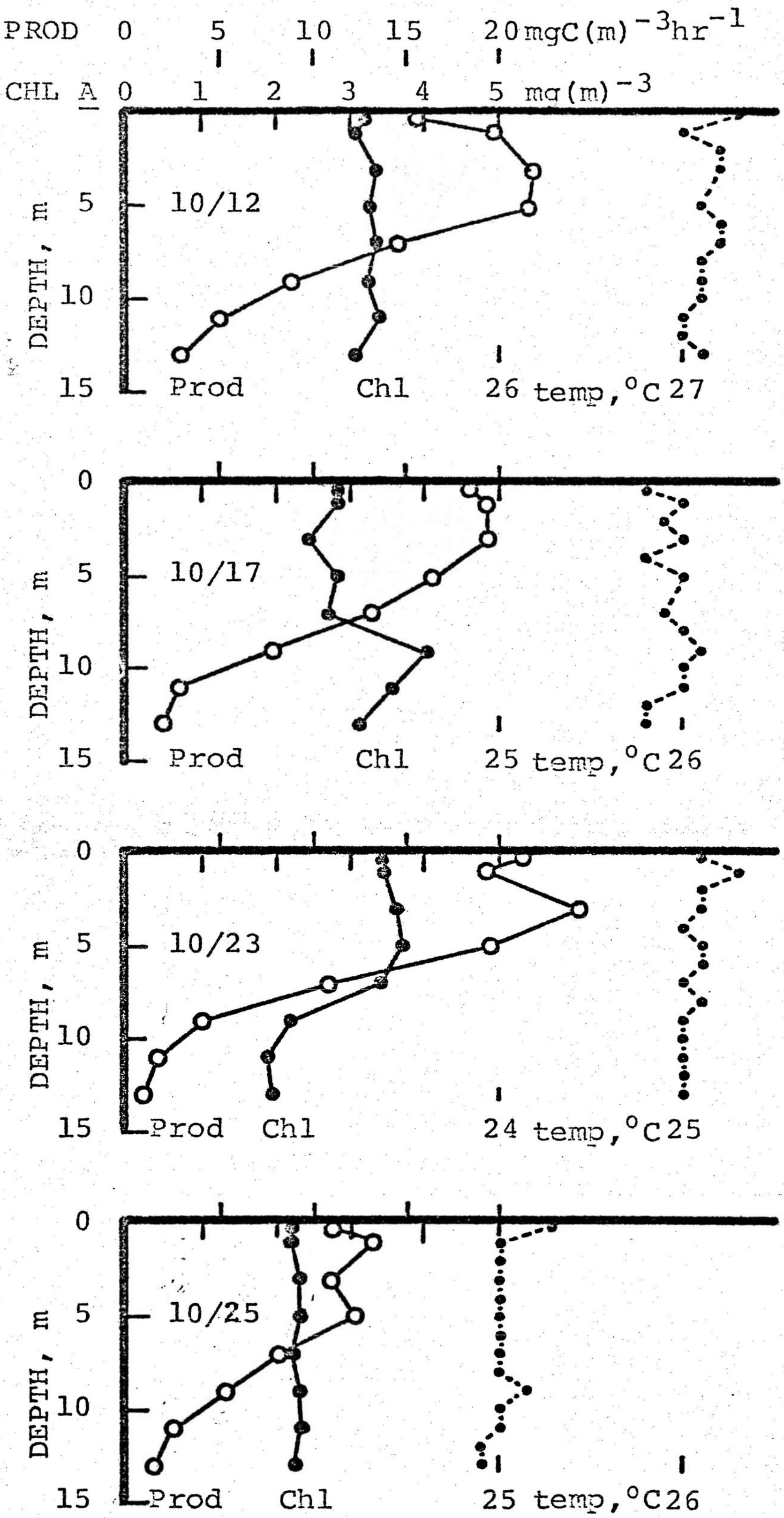
quad-rant	per-cent	spd, kts
NE	75	7
SE	8	9
SW	4	4
NW	0	–
CALM	13	–

quad-rant	per-cent	spd, kts
NE	83	10
SE	13	6
SW	4	6
NW	0	–

quad-rant	per-cent	spd, kts
NE	83	7
SE	13	11
SW	4	2
NW	0	–

quad-rant	per-cent	spd, kts
NE	96	10
SE	4	10
SW	0	–
NW	0	–

FIGURE 1 continued. Vertical profiles of chlorophyll a, productivity, and temperature, and average wind over preceeding 24 hours.



WIND SUMMARY

quad-rant	per-cent	spd, kts
NE	100	8
SE	0	-
SW	0	-
NW	0	-
NE	42	4
SE	8	6
SW	21	4
NW	8	3
CALM	21	-
NE	25	12
SE	75	11
SW	0	-
NW	0	-
NE	50	12
SE	50	11
SW	0	-
NW	0	-

FIGURE 1 continued. Vertical profiles of chlorophyll a, productivity, and temperature, and average wind over preceeding 24 hours.

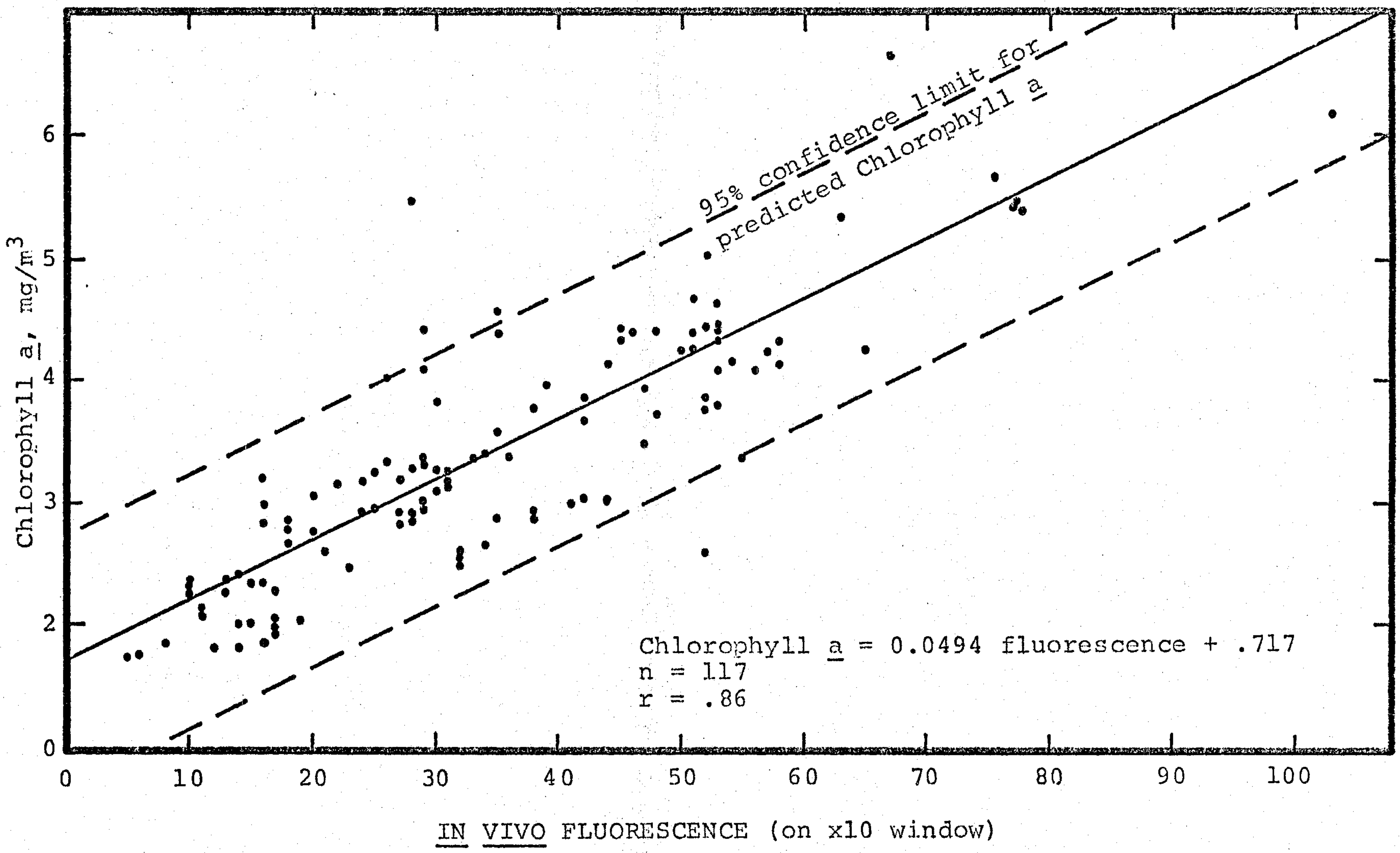


FIGURE 2. The relationship between *in vivo* fluorescence and chlorophyll *a*.

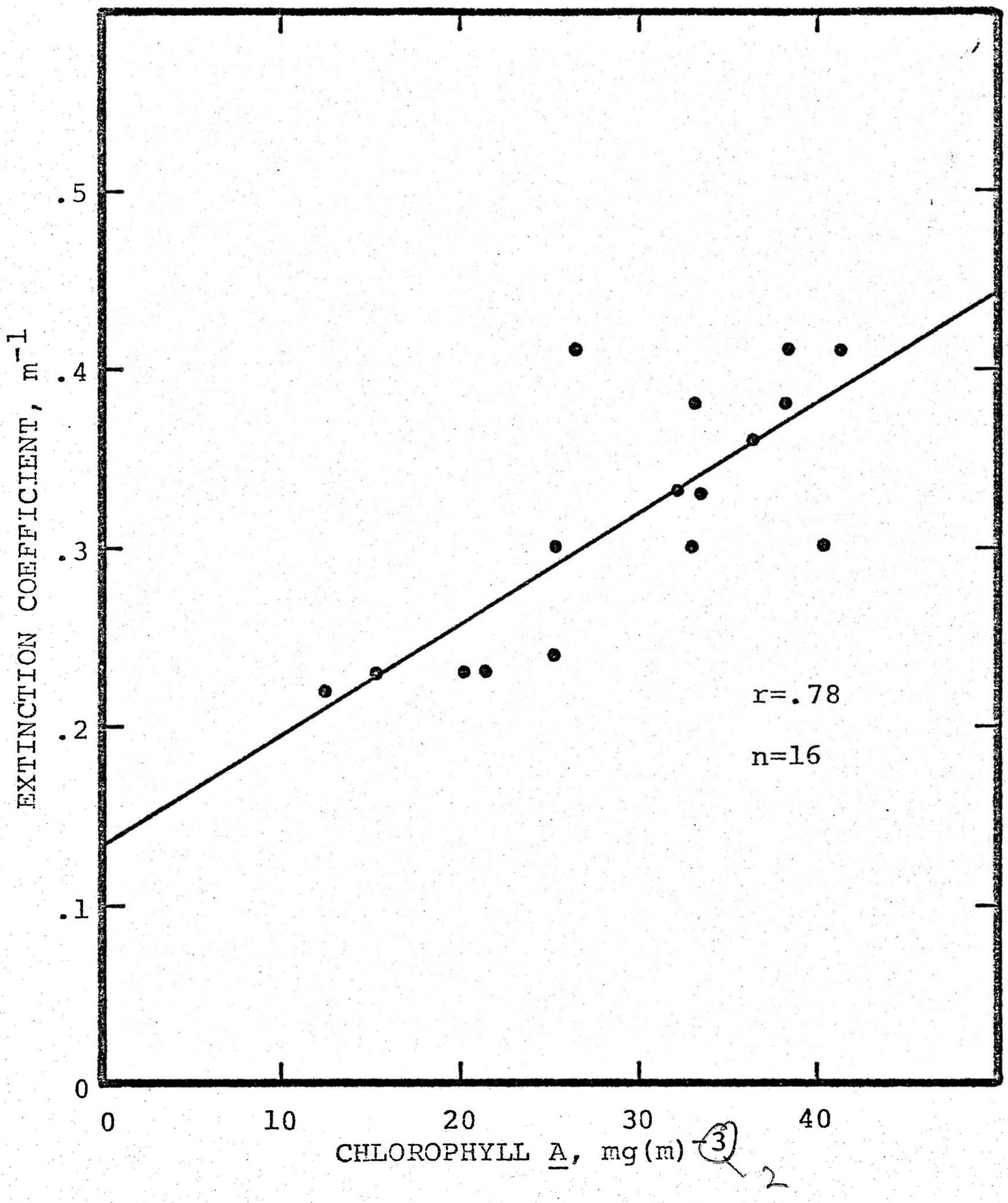


FIGURE 3. The relationship between total chlorophyll a in the water column and light extinction coefficient at 13 meters.

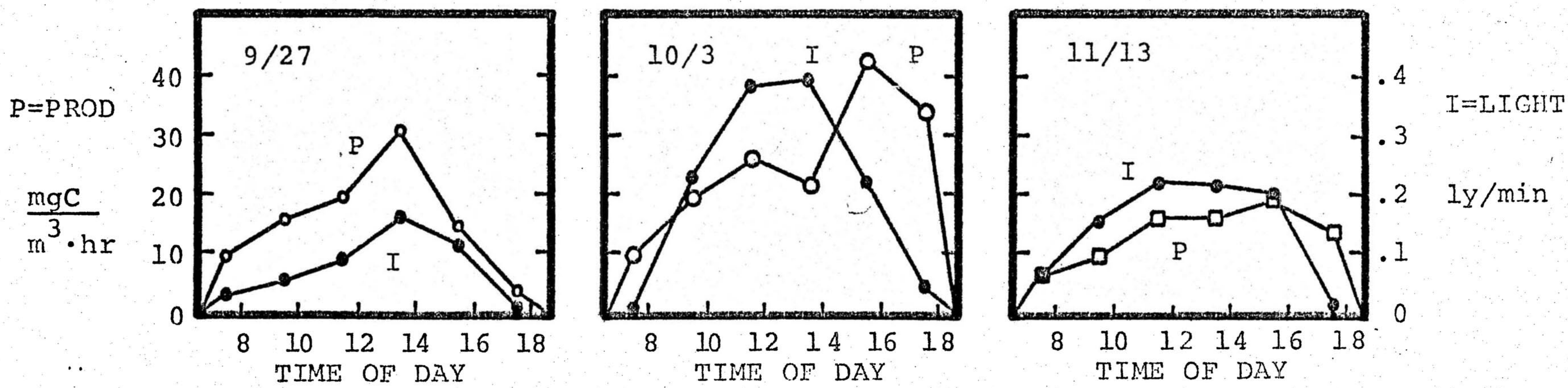


FIGURE 4. Time-course of production rate and light intensity at one meter depth at time intervals of two hours.

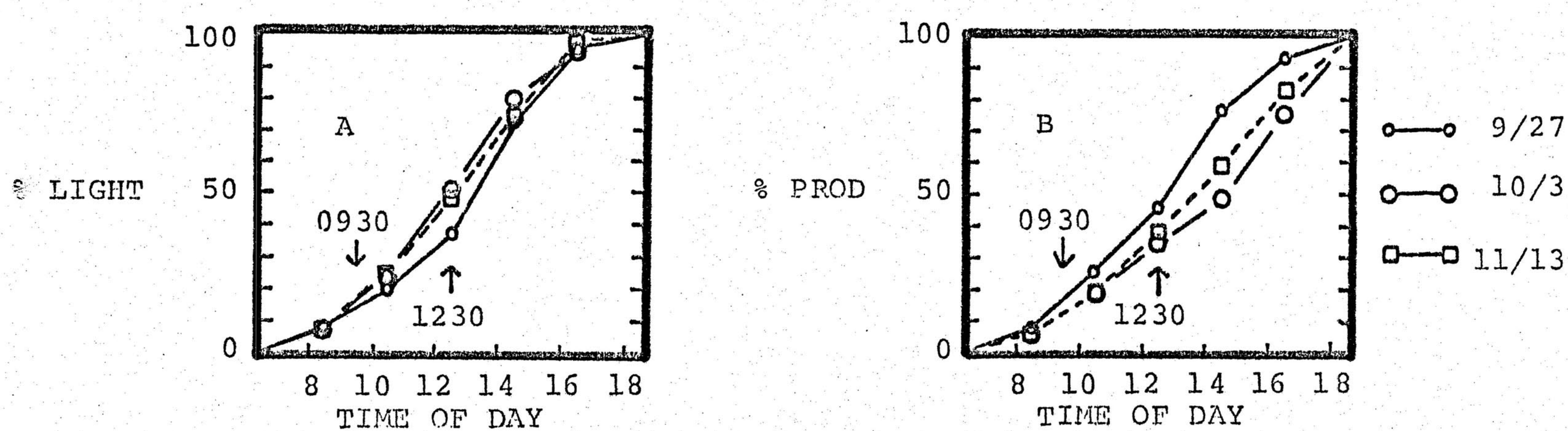


FIGURE 5. Time-course of cumulative percent radiation (A) and cumulative percent production at one meter depth at intervals of two hours.

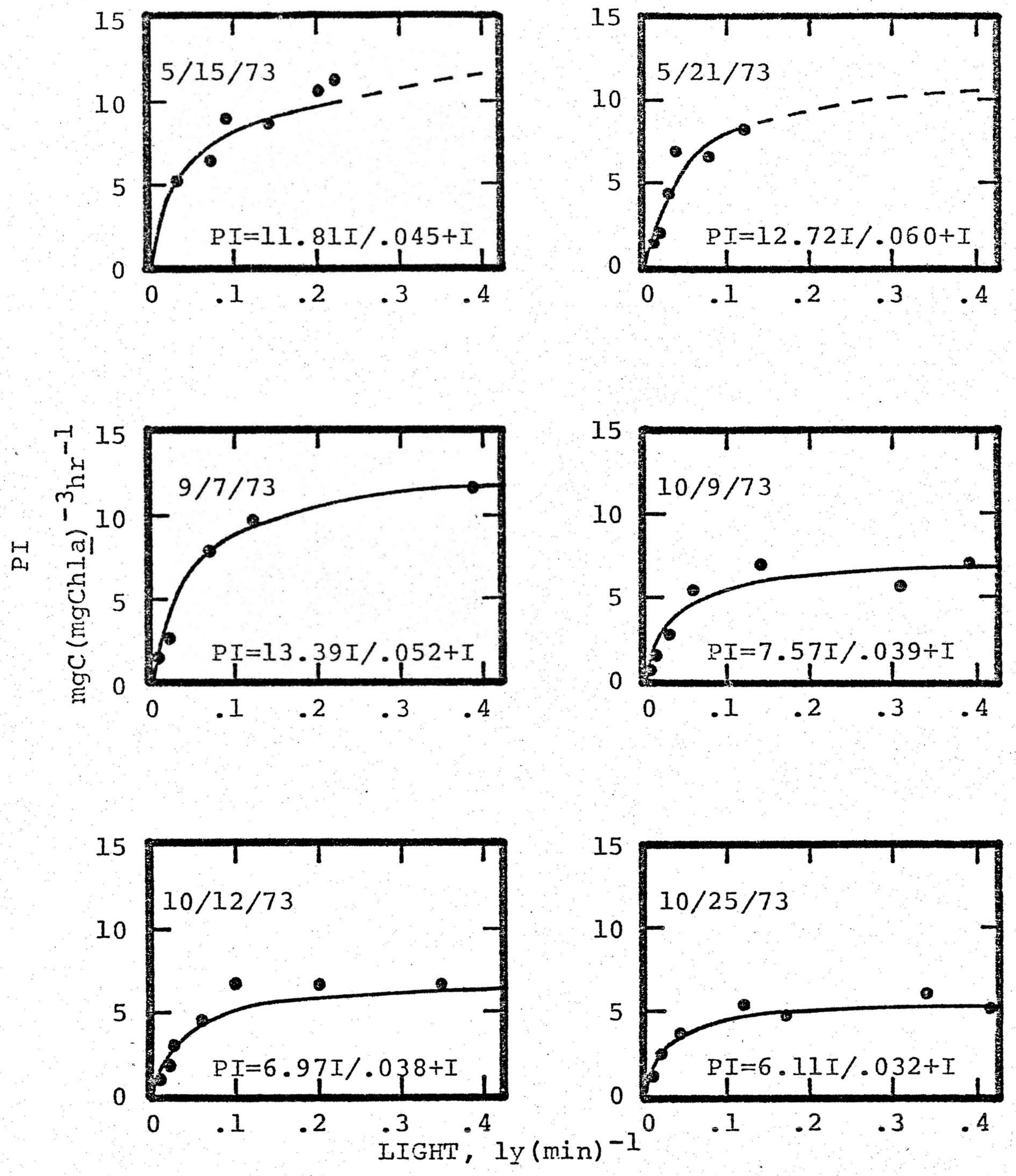


FIGURE 6. The relationship between light and productivity index for the six well mixed days.

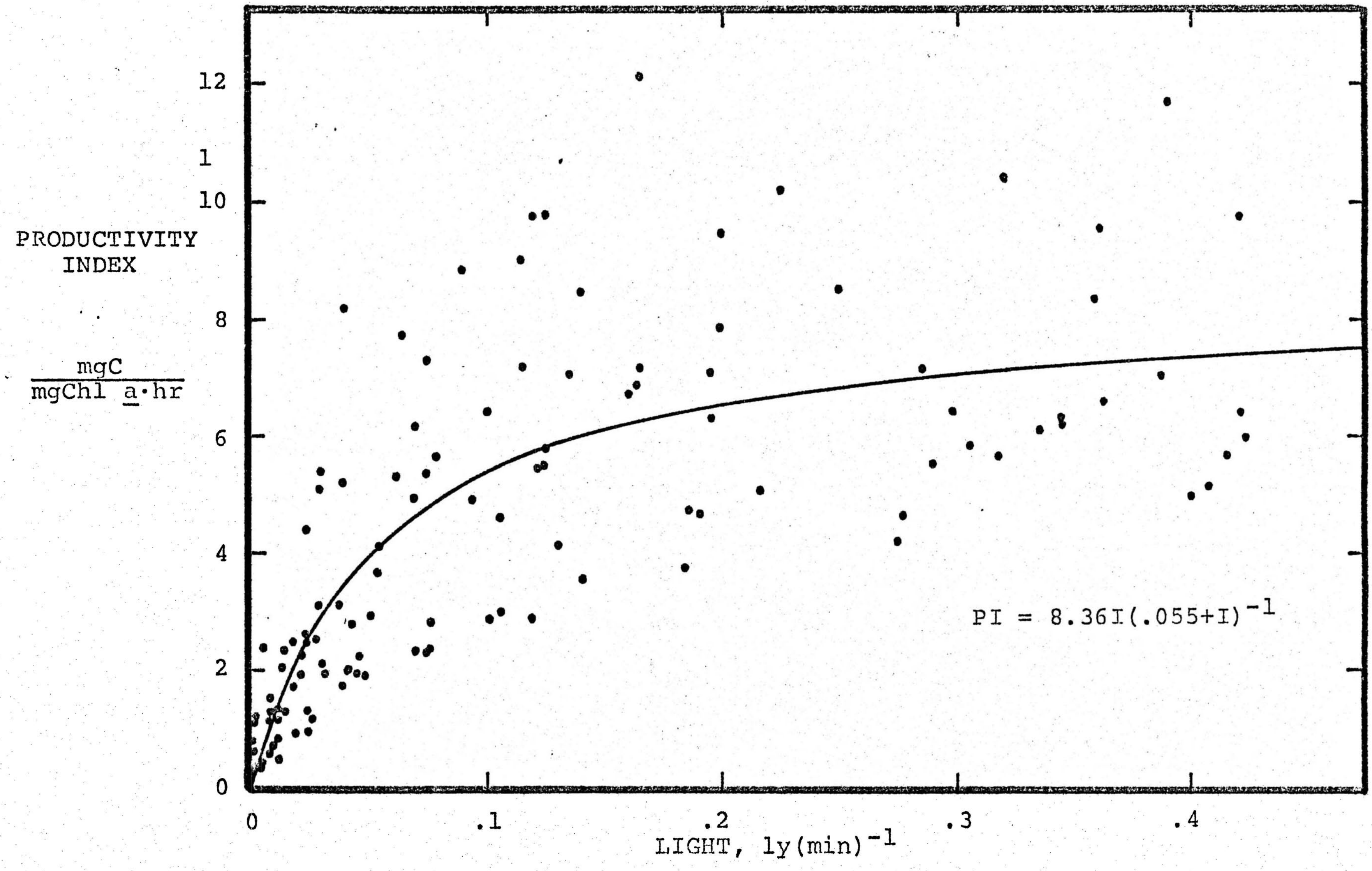


FIGURE 7. The relationship between light and PI during the study period.

LITERATURE CITED

Atkins, W.R.G., and H.H. Poole. 1958. Cube photometer measurements of the angular distribution of submarine daylight and the total submarine illumination. Jour. du Conseil 23:327-336.

Bartholomew, E. 1973. The production of microcopepods in Kaneohe Bay, Oahu, Hawaii. M.S. Thesis, Univ. of Hawaii.

Caperon, J., S.A. Cattell, and G. Krasnick. 1971. Phytoplankton kinetics in a subtropical estuary: Eutrophication. Limnol. Oceanogr. 16:599-607.

Caperon, J., and J. Meyer. 1972. Nitrogen-limited growth of marine phytoplankton-II. Uptake kinetics and their role in nutrient limited growth of phytoplankton. Deep-Sea Res. 19:619-632.

Clutter, R. 1970. Plankton Ecology, p 1-19. In Estuarine pollution in the State of Hawaii. Part II: Kaneohe Bay Study. Water Resources Research Center Tech. Rep. No. 31. Univ. of Hawaii.

Doty, M.S. 1964. Algal productivity of the tropical Pacific as determined by isotope tracer techniques. Haw. Inst. Mar. Biol. Tech. Rep. No. 1. Univ. of Hawaii.

Dunstan, W.M. 1973. A comparison of the photosynthesis-light intensity relationship in phylogenetically different marine microalgae. J. Exp. Biol. 13:181-187.

Eppley, R.W. 1972. Temperature and phytoplankton growth in the sea. Fish Bull. 70:1063-1085.

Eppley, R.W., and J.D.H. Strickland. 1968. Kinetics of marine phytoplankton growth, p 23-61. In E.J.F. Wood and M.R. Droop (eds.) Advances in the Microbiology of the Sea. Academic Press. London.

Gundersen, K. 1973. In situ determination of primary production by means of the new incubator, ISIS. Helgolander Wissenschaftliche Meeresunter Suchungen, 1973. Internation Helgoland Symposium, Sept. 1972.

Harris, C. 1972. Primary production in a small tropical estuary. M.S. Thesis, Univ. of Hawaii.

Harris, G.P. 1973. Diel and annual cycles of net plankton photosynthesis in Lake Ontario. J. Fish. Res. Bd. Can. 30:1779-1787.

Harris, G.P., and N.A. Lott. 1973. Light intensity and photosynthesis rates in phytoplankton. J. Fish. Res. Bd. Can. 30:1771-1778.

Harvey, H.W. 1960. The Chemistry and Fertility of Sea Water. Cambridge. Univ. Press.

Holmes, R.W. 1970. The Secchi disk in turbid water. Limnol. Oceanogr. 15:688-694.

Jerlov, N.G. 1968. Optical Oceanography. Elsevior. New York.

Jorgensen, E.G. 1969. The adaptation of plankton algae. IV. Light adaptation of different algal species. Physiol. Plant. 22:1307-1315.

Krasnick, G.J. 1973. Temporal and spatial variations in phytoplankton productivity and related factors in the surface waters of Kaneohe Bay, Oahu, Hawaii. M.S. Thesis, Univ. of Hawaii.

Malone, T.C. 1971a. The relative importance of nannoplankton and netplankton as primary producers in tropical oceanic and neritic phytoplankton communities. Limnol. Oceanogr. 16:633-639.

Malone, T.C. 1971b. The relative importance of nannoplankton and netplankton as primary producers in the California current system. Fish. Bull. U.S. 69:799-820.

Malone, T.C. 1971c. Diurnal rhythms in netplankton and nannoplankton assimilation ratios. Mar. Biol. 10:285-299.

Platt, T., and D.V. Subba Rao. 1973 Some current problems in marine phytoplankton productivity. Fish. Res. Bd. Can Tech. Rep. No. 370 (manuscript).

Quasim, S.Z., P.M.A. Bhattathiri, and V.P. Devassey. 1972. The effect of intensity and quality of illumination on the photosynthesis of some tropical marine phytoplankton. Mar. Biol. 16:22-27.

Steemann-Nielsen, E. 1952. On the detrimental effect of high light intensities on the photosynthetic mechanism. Physiol. Plant. 5:334-344.

Steemann-Nielsen, E., and V.K. Hanson. 1959. Light adaptation in marine phytoplankton populations and interrelation with temperature. Physiol. Plant. 12:353-

Steemann-Nielsen, E., and E.G. Jorgensen. 1968. The adaptation of plankton algae. III. With special consideration of the importance in nature. Physiol. Plant. 21:647-654.

Steinhelper, F.A. 1970. Particulate organic matter in Kaneohe Bay, Oahu, Hawaii. Haw. Inst. Mar. Biol. Tech. Rep. No. 22. Univ. of Hawaii.

Ryther, J.H. 1956. Photosynthesis in the ocean as a function of light intensity. Limnol. Oceanogr. 1:61-70.

Strickland, J.D.H. 1958. Solar radiation penetrating the ocean. A review of the requirements, data, and methods of measurement, with particular reference to photosynthetic productivity. J. Fish. Res. Bd. Can. 15:453-493.

Strickland, J.D.H. 1960. Measuring the production of marine phytoplankton. Fish. Res. Bd. Can. Bull. 122.

Strickland, J.D.H. 1965. Production of organic matter in the primary stages of the marine food chain. In J.P. Riley and G. Skirrow (eds.) Chemical Oceanography Vol. 1. Academic Press. New York.

Strickland, J.D.H., and T.R. Parsons. 1968. A practical handbook of sea water analysis. Fish. Res. Bd. Can. Bull. 167.

Vollenweider, R.A. 1969. Calculation models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements. In C.R. Goldman (ed.) Primary Production in Aquatic Environments. Blackwell Scientific Publications. Oxford.