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Photosynthetic Characteristics and Estimated Growth Rates Indicate Grazing Is the Proximate Control of Primary Production in the Equatorial Pacific

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Macronutrients persist in the surface layer of the equatorial Pacific Ocean because the production of phytoplankton is limited; the nature of this limitation has yet to be resolved. Measurements of photosynthesis as a function of irradiance (P-I) provide information on the control of primary productivity, a question of great biogeochemical importance. Accordingly, P-I was measured in the equatorial Pacific along 150°W, during February-March 1988. Diel variability of P-I showed a pattern consistent with nocturnal vertical mixing in the upper 20 m followed by diurnal stratification, causing photoinhibition near the surface at midday. Otherwise, the distribution of photosynthetic parameters with depth and the stability of P-I during simulated in situ incubations over 2 days demonstrated that photoadaptation was nearly complete at the time of sampling: photoadaptation had not been effectively countered by upwelling or vertical mixing. Measurements of P-I and chlorophyll during manipulations of trace elements showed that simple precautions to minimize contamination were sufficient to obtain valid rate measurements and that the specific growth rates of phytoplankton were fairly high in situ, a minimum of 0.6 d^{-1}. Diel variability of beam attenuation also indicated high specific growth rates of phytoplankton and a strong coupling of production with grazing. It appears that grazing is the proximate control on the standing crop of phytoplankton. Nonetheless, the supply of a trace nutrient such as iron might ultimately regulate productivity by influencing species composition and food-web structure.

1. INTRODUCTION

Concentrations of chlorophyll *a* and rates of primary production are elevated along the equator, where the vertical flux of nutrients is enhanced by upwelling at the equatorial divergence [*Chavez and Barber*, 1987; *Berger*, 1989]. Primary productivity and phytoplankton biomass are not as high as the flux of macronutrients could support, however: near-surface concentrations of nitrate are elevated over a broad expanse of the equatorial ocean and this unexploited nutrient is thought to indicate limitation of the yield of phytoplankton biomass. This condition has been labeled a high-nutrient, low-chlorophyll situation (HNLC [*Minas et al.*, 1986]). Thus, the question confronting oceanographers is not "Why is the tropical region so rich?," but rather "Why isn't the equator greener?"

Incomplete utilization of nitrate at the equator might be due to physiological impairment of phytoplankton. For example, *Barber and Ryther* [1969] found a local minimum in productivity index (g C g Chl^{-1} d^{-1}) at the equator in the eastern Pacific Ocean. Their experimental results indicated that specific growth rates of phytoplankton were depressed because the waters were low in the natural organic chelators which facilitate trace element nutrition [*Huntsman and Sunda*, 1980]. More recently, *Martin et al.* [1989] supported the concept that iron can limit the production of open-ocean phytoplankton. They suggested that the potential for growth of phytoplankton in the eastern equatorial Pacific might be limited by the supply of iron, which in the open ocean comes principally from atmospheric sources. The conclusions of Martin and colleagues have been questioned [*Banse*, 1990] and the concept of iron-limitation has become the subject of active debate.

The perspective of *Dugdale and Wilkerson* [1989; *Dugdale et al.*, this issue] is somewhat different: they suggest that phytoplankton in upwelling systems such as at the equator fail to exploit supplies of nitrate because initial concentrations of nitrate are too low to support a rapid "shift-up" of assimilatory pathways. Suboptimal nitrate assimilation is therefore seen as the result of physical forcing (rate of upwelling coupled with nitrate concentration in the source water) rather than nutritional limitation per se. Incomplete shift-up is regarded here as a type of physiological impairment, i.e., suboptimal adaptation of phytoplankton to ambient conditions.

A different explanation for the apparent impairment of nitrate assimilation in equatorial upwelling is that the neritic bloom-forming diatoms which characterize coastal upwelling systems [*Smetacek*, 1985] are absent from the offshore regions, possibly because of inadequate seed-stocks [*Chavez*, 1989]. The small oceanic species that dominate may be genetically incapable of the shift-up response described by *Dugdale et al.* [this issue].

Nutritional limitation of phytoplankton need not be invoked to explain persistence of macronutrients in surface waters at the equator. *Walsh* [1976] asserted that rates of productivity normalized to chlorophyll were similar over much of the ocean, including the equatorial divergence. He suggested that growth rates of phytoplankton at the equator are unimpaired but that a lack of significant environmental variability on the scale of 5 - 10 days allows persistence of a coupled phytoplankton-herbivore system so that herbivory limits the standing crop of phytoplankton. *Minas et al.* [1986] also felt that grazing was the most plausible explanation of the HNLC situation in open-ocean upwelling. The small

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phytoplankton that dominate the equatorial phytoplankton [*Chavez*, 1989; *Chavez et al.*, 1990; *Peña et al.*, 1990] are especially susceptible to control by small grazers with short generation times.

Questions about limitation of primary production at the equator can be partially resolved by looking at the physiology of phytoplankton. One approach, described here, is to examine their photosynthetic characteristics. Because photosynthetic performance is extremely adaptable to growth conditions [*Falkowski*, 1980; *Osborne and Geider*, 1986; *Harding et al.*, 1987; *Cullen and Lewis*, 1988; *Cullen*, 1990], we expect that hindrances to the growth of phytoplankton, whether due to nutritional deficiencies or to inadequate time to adapt to physical forcing, can be detected in measurements of photosynthesis as a function of irradiance. Here we describe such measurements. We show that the photosynthetic systems of phytoplankton in much of the euphotic zone were well adapted to ambient conditions, indicating that neither upwelling nor vertical mixing impaired the growth of phytoplankton. Different measures of primary productivity are compared and several estimates of phytoplankton growth rates are examined. All of these estimates indicate fairly rapid growth of phytoplankton, balanced by grazing. We conclude that specific growth rates of phytoplankton in the equatorial Pacific were fairly high and that grazing was an important factor controlling the standing crop of phytoplankton.

2. METHODS

Basic Measurements

Observations were made during cruise WEC88 on the R/V *Wecoma*, February-March 1988, extending from 15°N to 15°S along 150°W. This analysis focuses on the equatorial station, occupied from March 2 to 7, 1988.

Seawater was obtained with 5-L Niskin bottles attached to a rosette sampler. Silicone rubber tubing was used for o-rings and for securing the closures [*Chavez and Barber*, 1987; *Price et al.*, 1986; *Williams and Robertson*, 1989]. Samples were drawn into clean polycarbonate containers, shielded from direct sunlight. Cleaning procedures are described below. Temperature, conductivity and pressure (depth) (CTD) were measured with a Neil Brown Mark III CTD. The sampling rosette was also equipped with a fluorometer, but it failed early in the cruise. Solar irradiance at the sea surface (photosynthetically available radiation (PAR), 400-700 nm, μmol m^{-2} s^{-1}) was recorded continuously with a Biospherical Instruments QSR-240 hemispherical quantum irradiance reference sensor.

Optical data were collected with a Bio-Optical Profiling System (BOPS), an updated version of the package developed by *R. C. Smith et al.* [1984]. Central to the system is a Biospherical Instruments MER-1048 spectroradiometer which measures upwelling and downwelling spectral irradiance, upwelling spectral radiance, and quantum scalar irradiance (PAR). The MER-1048 also has sensors for pressure (depth), tilt and roll. The BOPS measures conductivity and temperature (Sea-Bird CTD), chlorophyll fluorescence (Sea Tech fluorometer) and beam attenuation (Sea Tech 25-cm transmissometer, 660 nm). Deck sensors record downwelling spectral irradiance in four channels. Data are acquired at 16 Hz, averaged to 4 Hz, then sent to a Compaq-286 computer, where they are stored on a hard disk. Data from the BOPS were filtered to remove obvious spikes and then averaged over 1-m intervals.

Photosynthesis Versus Irradiance

The method of *Lewis and Smith* [1983] was used to measure photosynthesis as a function of irradiance (P-I) on samples obtained from four depths at dawn, midday and dusk. Samples were inoculated with ^{14}C-bicarbonate (final activity, about 10 μCi mL^{-1}) and aliquots of 1 mL were dispensed into glass scintillation vials (7-mL capacity, not specially cleaned) in a temperature-controlled aluminum block. The exact amount of label added was determined by subsampling into a scintillation vial nearly filled with the non-acidic fluor, Aquasol II, thereby avoiding the problem of losing labeled inorganic C from acidic fluor [*Iverson et al.*, 1976]. A range of irradiance was provided from below with 2 ENH-type tungsten-halogen projection lamps directed through a heat filter of circulating water, and attenuated with neutral density screens. Quantum scalar irradiance in each position was measured with a Biospherical Instruments QSL-100 4π sensor with a modified collector, small enough to fit in the bottom half of a scintillation vial for the measurements. Incubations began within 30 min of sampling and were terminated after 1 hour. Inorganic carbon was expelled by adding 0.5 mL 6N HCl and agitating the open vials for at least 1 hour in a hood. Aquasol II fluor was added and the vials were agitated again before counting with a Beckman LS1800 scintillation counter. Counts were corrected for quench with the H# method. No correction for isotope discrimination was made. Total CO_2 was assumed to be 2.1 mM.

The P-I equation of *Platt et al.* [1980] was used to model the results:

$$P_i^B = P_S (1 - e^{(-\alpha I / P_S)})(e^{(-\beta I / P_S)}) \quad (1)$$

where P_i^B (g C (g Chl)$^{-1}$ h^{-1}) is the instantaneous rate of photosynthesis normalized to Chl at irradiance I (μmol m^{-2} s^{-1}, PAR); P_S (g C (g Chl)$^{-1}$ h^{-1}) is the maximum rate of photosynthesis in the absence of photoinhibition; α (g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$) is the initial slope of the P-I curve, and β (g C (g Chl)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$) is a parameter to characterize photoinhibition.

Parameters were fit simultaneously using the multivariate secant method [*Ralston and Jennrich*, 1978] of the NLIN procedure of SAS [*SAS Institute*, 1985]. An intercept, P_o, (g C (g Chl)$^{-1}$ h^{-1}) was included as a parameter and subsequently subtracted from estimates of P_i^B as one would do with a dark bottle value. The parameter P_o is not a reliable measure of respiration because of limitations of tracer methodology [*Jassby and Platt*, 1976; *Peterson*, 1980]. Rather, the inclusion of P_o increases the amount of variability explained and improves the distribution of residuals. By subtracting P_o from estimates of P_i^B rather than including it, the modeled photosynthesis in the dark is always zero. The realized maximum rate of photosynthesis, P_{max} (g C (g Chl)$^{-1}$ h^{-1}), was calculated according to *Platt et al.* [1980] and its error was determined according to the principles described by *Zimmerman et al.* [1987].

For many of the P-I experiments, one or more of the 24 values for carbon assimilation deviated quite substantially from a continuous function of irradiance. These were high values, possibly due to large, rare cells or to aggregates of cells, but conceivably the result of inadequate purging of inorganic ^{14}C. The points were excluded from the analysis at an early stage in

data reduction, when samples were identified only by sequence numbers. Decisions to omit points were therefore not influenced by expected results for any particular sample.

Concentrations of chlorophyll *a* (Chl), corrected for pheopigment, were determined fluorometrically using a Turner Designs 10-005R fluorometer fitted with a Corning 5-60 excitation filter and a 2-64 emission filter and calibrated with purified Chl. Samples were collected in triplicate on Whatman GF/F filters and extracted in 10 mL of 90% acetone in the dark for at least 24 hours at - 4°C.

Model of Primary Production

Photosynthesis was modeled as a function of depth and time for a representative day at the equatorial station using estimates of solar irradiance, light penetration, in situ fluorescence, Chl, and P-I. Profiles of photosynthesis were constructed with 1-m resolution for 30-min intervals from dawn until dusk. The approach was much like several Chl-light models [e.g., *Jitts et al.*, 1976; *Harrison et al.*, 1985] except that the temporal and spatial resolution was substantially enhanced and the P-I relationship was modeled as a function of depth and time.

Each estimate of photosynthesis required a value for Chl, I, and P_i^B. These values were obtained as follows.

Chlorophyll. A calibration of fluorescence profiles with contemporaneous measurements of Chl was not possible because the in situ fluorometer on the CTD rosette failed, so detailed profiles of Chl were obtained by calibrating average profiles of fluorescence from the optical casts with averages of Chl from the hydrocasts. Fluorescence from the in situ fluorometer [Fl_{iS}] was averaged at 1 m intervals of depth (z) for the 13 daytime optical casts at the equatorial station. The concentration of Chl was averaged at the four hydrocast sampling depths (0, 20, 40, 60 m) for which P-I was determined. From these averaged data, the fluorescence yield [Fl_{iS}/Chl(z)], was calculated at the four depths. Fluorescence yield increased with depth. To construct a vertical profile of chlorophyll with 1-m resolution, Fl_{iS}/Chl(z) was estimated by linear interpolation between depths, maintaining the 60-m value for greater depths. The estimate of chlorophyll, Chl(z) was obtained by dividing $Fl_{iS}(z)$ by Fl_{iS}/Chl(z).

Irradiance. Irradiance at the sea surface throughout the day ($I_o(t)$, where the subscript indicates irradiance just above the surface) was obtained by choosing from the 6-day record of on-deck PAR the 75th percentile value for each 10-min interval. These points represented irradiance under clear skies. A four-parameter model was chosen to describe irradiance at depth ($I(z)$):

$$\frac{I(z)}{I_o} = T\left[(R\, e^{(-k_1 z)}) + ((1-R)\, e^{(-k_2 z)})\right] \qquad (2)$$

The parameter T (dimensionless) accounts for reflection at the surface. The attenuation of irradiance with depth follows the model of *Simpson and Dickey* [1981], accounting for the rapid attenuation of longer wavelengths near the surface. The two attenuation coefficients are k_1 and k_2 (m^{-1}) and R is a dimensionless parameter which determines what proportion of the irradiance is attenuated rapidly. Only PAR is considered here. Values for $I(z)/I_o$ were averages for daytime profiles: $I(z)$ came from the PAR sensor on the profiler and I_o was calculated from the on-deck spectral irradiance data recorded by the BOPS. Values for T, R, k_1 and k_2 were obtained by a nonlinear curve-fit of equation (2) to a profile of $I(z)/I_o$ versus depth (6-day average, 1-100 m, 1-m intervals). Irradiance as a function of depth and time (I(z,t)) is the product of $I_o(t)$ and $I(z)/I_o$.

Photosynthesis normalized to chlorophyll. The photosynthetic parameters α, P_S, and β were averaged over the 6 days for each of the four depths and three time periods. From these parameters and the appropriate irradiance, $P^B(z,t)$ was calculated (1) for each of 12 primary coordinates in depth and time. To estimate $P^B(z,t)$ at the other (secondary) depth-time coordinates, four values of P_i^B were calculated using P-I parameters from each of closest primary coordinates and I(z,t) from the secondary coordinate. The four estimates of P_i^B were weighted linearly as a function of their relative proximity to the secondary coordinate in depth and time, and averaged.

Profiles of photosynthesis. Modeled photosynthesis, $P(z,t)$ is the product of $P^B(z,t)$ and Chl(z). Vertical profiles were constructed for 30-min intervals and integrated over time to obtain a vertical profile of daily photosynthesis at 1-m intervals. To estimate daily photosynthesis in the water column, this vertical profile was integrated to 100 m.

Conventional Measurement of Primary Production

Primary productivity was measured directly as the uptake of ^{14}C-bicarbonate during 24-hour simulated in situ (SIS) incubations [*Chavez et al.*, 1990]. Measurements presented here were made on samples collected between 0830 and 0930 hours from depths corresponding to $I(z)/I_o$ = 100, 50, 30,15, 5, and 1% as estimated from optical profiles. Water was drawn into screw-capped "Vitro" glass 150-ml bottles (Wheaton Corporation) encased in nickel screens (Perforated Products) that act as neutral density filters, reducing the light intensity to the appropriate relative irradiance. Each bottle was inoculated with 10 μCi of $NaH^{14}CO_3$ and incubated for 24 hours on deck under natural sunlight in open, seawater-cooled Plexiglas incubators. A time-zero sample was inoculated with radioactive tracer and filtered immediately to determine abiotic particulate ^{14}C incorporation. For determination of particulate carbon fixation during the incubations, samples were filtered onto Whatman GF/F filters, rinsed with 0.01 N HCl, and counted in 10 mL of Aquasol II. The total inorganic ^{14}C-activity in each sample was determined by adding 1.0 mL of water from the bottle to a scintillation vial containing 20 mL of Aquasol II. A sample for fluorometric determination of Chl [cf. *Chavez et al.*, 1990] was taken from each depth in the productivity cast and from the other hydrocasts (F. Chavez and R. Barber).

Productivity From Changes in Beam Attenuation

Morning (about 0830 hours) and afternoon (about 1330 hours) profiles of beam attenuation were compared to examine diel changes of attenuation at 660 nm and their relation to primary productivity. The analysis was very similar to that presented by *Siegel et al.* [1989]. Attenuation is presented as beam $c - c_w$, where c (m^{-1}) is total attenuation and c_w, the attenuation due to water, is taken as 0.364 m^{-1}, as specified by the manufacturer. The carbon-specific beam attenuation coefficient (c_C^*) to convert variations of c to variations of particulate organic carbon (POC) was taken from *Siegel et al.* [1989]: 3.92 x 10^{-3} m^2 mg C^{-1} (255 (mg C m^{-3}) m). The validity of this assumption will be discussed below.

Experimental Manipulations

For experiments on photoadaptation and the influence of trace metals on phytoplankton, a combined sample of water

from 30 and 40 m (about 5% - 15% I_0) was collected at the equatorial station at midday on March 2. Samples were dispensed into 265-ml polycarbonate bottles and placed in Plexiglas SIS incubators cooled by surface water [*Eppley and Holm-Hansen*, 1986]. Light was attenuated by perforated nickel screen. The bottles were incubated on deck at 11% relative irradiance and one from each treatment was analyzed for Chl and P-I on subsequent days at 1400 h. Irradiance in the incubator was measured with a Biospherical Instruments QSL-100 4π sensor on a sunny day while the cooling water was running. Percent transmittance is reported relative to irradiance recorded by the deck sensor.

Collecting bottles and the incubations bottles were initially prepared by rinsing with deionized water, soaking in 2% Micro detergent for at least 2 days, thorough rinsing with Nanopure (reagent-grade) water, a soaking of at least 2 days in 2% HCl, and thorough rinsing with Nanopure water. At sea, the bottles were rinsed with Milli-Q (reagent-grade) water between uses and well rinsed with sample water prior to filling.

The concentrations and availability of trace elements were manipulated experimentally. The three treatments and final concentrations were: EDTA (Na_2EDTA, 400 nM), copper ($CuNO_3$, 5 nm) and iron ($Fe(NO_3)_3$, 10 nM). Stock solutions were kindly provided by John Martin. Controls were not modified, but we recognize that some trace-element contamination is likely to have occurred. Thus, toxic trace elements such as copper and zinc might have influenced results [*Fitzwater et al.*, 1982], and iron, a trace nutrient, would likely have been enriched even in the controls. These possibilities are considered in our analysis.

Similar, but less comprehensive experiments were performed at stations between 6°N and 2°S. Treatments included: "NH_4" (0.8 μM NH_4Cl in one experiment; 5 μM in another); "NH_4 + EDTA" (0.8 μM NH_4Cl + 0.4 μM Na_2EDTA); and one experiment in 2-L polycarbonate bottles, which were held in an on-deck incubator and subsampled during the time-course.

3. RESULTS

Vertical Structure

Hydrography, the distributions of nutrients, and vertical mixing are discussed elsewhere in this volume [*Carr et al.*, this issue]. We present here some vertical profiles that describe mean conditions over six days at the equator and some of the changes that occurred between the morning and afternoon optical profiles and bottle casts (Figure 1).

Profiles of temperature (Figures 1*a* and 1*b*) reflect stratification in the upper 100 m, which was disrupted to at least 20 m by nocturnal mixing and reestablished by solar heating during the day [*Carr et al.*, this issue]. In situ fluorescence shows a broad subsurface maximum centered at about 50 m (Figures 1*c* and 1*d*), where $I(z)$ was about 2.5% I_0. Of the profiles considered here, beam attenuation displays the most pronounced diurnal variation (Figures 1*e* and 1*f*), with greater attenuation in the afternoon, especially at depths of 20-40 m, where the relative increase over 5 hours was as much as 53%. The concentration of Chl also increased during the day in much of the euphotic zone, an average of 17% between the

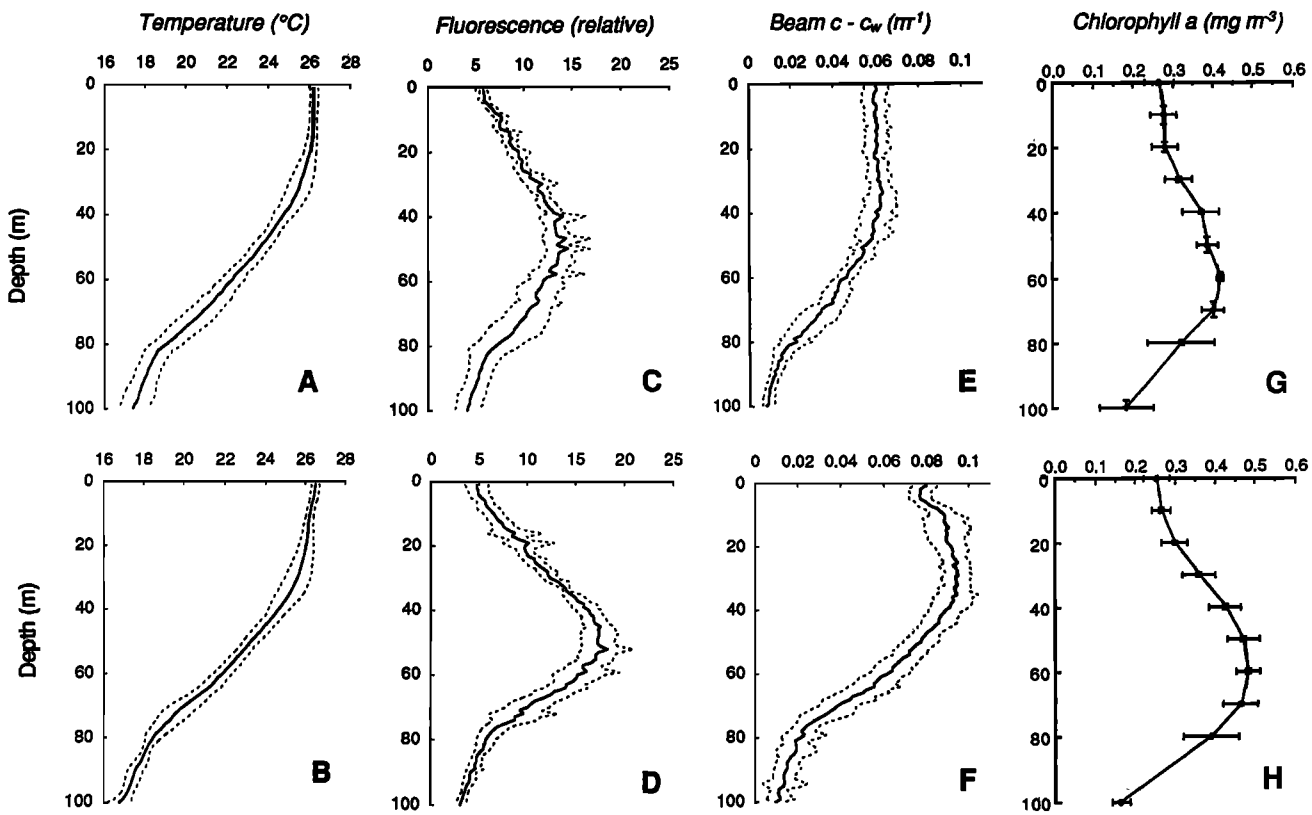


Fig. 1. Mean vertical profiles (± s.d.) from the equatorial station at 150°W, March 2-7, 1988. Data from the biooptical profiling system: (*a*) temperature (morning profiles, 0830 hours); (*b*) temperature (afternoon profiles, 1330 hours); (*c*) in situ fluorescence (morning profiles); (*d*) in situ fluorescence (afternoon profiles); (*e*) beam attenuation (c - c_w, morning profiles); (*f*) beam attenuation (c - c_w, afternoon profiles). Data from bottle casts: (*g*) Chl (morning profiles, 0600 hours); (*h*) Chl (afternoon profiles, 1200 hours).

depths of 30 and 80 m (Figures 1*g* and 1*h*). However, near the surface the afternoon mean was slightly lower than the morning mean.

Photosynthesis Versus Irradiance

Measurements of P-I at the equatorial station (Figure 2) show strong patterns with depth and time of day. Good fits to the P-I model (equation (1)) were obtained so that the photosynthetic parameters P_{max}, α, and β describe photosynthetic performance well. Three patterns are particularly clear (Figure 3).

1. Diurnal variation of maximum photosynthesis, P_{max} [*Harding et al.*, 1982*a*], is clearly evident at each depth, with the highest rates near midday.

2. Vertical patterns of α and P_{max} are characteristic of photoadaptation: P_{max} decreases with depth (irradiance) [*Falkowski*, 1980, 1983; *Cullen and Lewis*, 1988] and α is lower near the surface, where irradiance is high [*Cullen and*

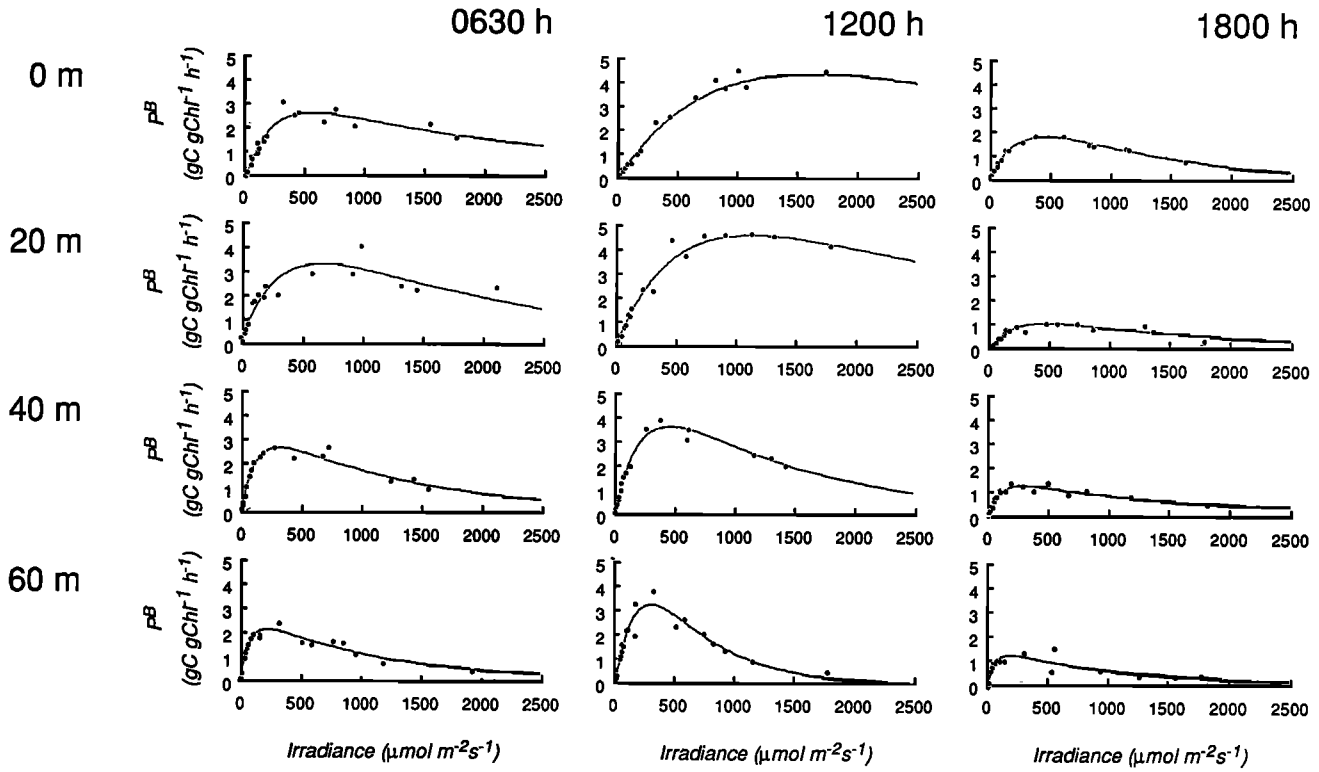


Fig. 2. Measurements of photosynthesis versus irradiance at the equator, 150°W, March 4, 1988. Lines are best fits to equation (1).

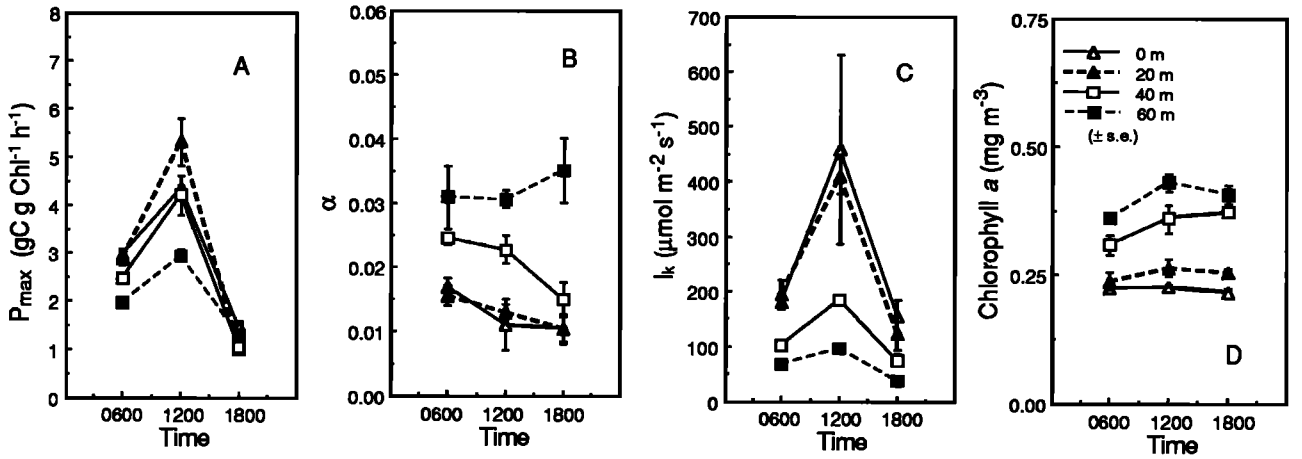


Fig. 3. Photosynthetic parameters and Chl at the equatorial station, March 2-7, 1988. Averages and standard errors at each of four depths, three times per day: (*a*) P_{max} (g C g Chl^{-1} h^{-1}); (b) α (g C g Chl^{-1} h^{-1})(µmol m^{-2} s^{-1})$^{-1}$); (*c*) I_k (µmol m^{-2} s^{-1}); *d*) Chl (mg m^{-3}).

Lewis, 1988]. Also consistent with photoadaptation to ambient irradiance, the saturation parameter I_k (P_{max}/α [*Talling*, 1957; *Platt et al.*, 1980]) decreases with depth.

3. Nocturnal mixing [Carr *et al.*, this issue] homogenized the phytoplankton assemblage in the upper 20 m, eliminating to a great extent the differentiation of chlorophyll concentration and photosynthetic parameters that occurred between 0 and 20 m during the day (Figure 3; see also *Vincent et al.* [1984]). Diurnal stratification [*Vincent et al., 1984*] led to a response characteristic of photoinhibition near the sea surface [*Vincent et al.*, 1984; *Neale and Richerson*, 1987; *Cullen and Lewis*, 1988]: compared to the assemblage at 20 m, phytoplankton at the surface at midday had lower P_{max} and α, and showed less net synthesis of Chl.

Model of Productivity

The model of productivity yields a vertical profile with 1 m resolution (Figure 4*a*). Integral primary productivity was 469 mg C m^{-2} d^{-1}. Maximum productivity was at 10-15 m and photoinhibition of photosynthesis near the surface had only a minor effect on integrated water column production. A composite P-I curve for the water column is obtained by plotting the daily mean values of $P^B(z)$ against average $I(z)$ (Figure 4*b*). The curve is similar to a simple exponential model of productivity [see *Ryther and Yentsch*, 1957; *Cullen*, 1990], with about the same initial slope, but the maximum average daily rate (3.3 g C g Chl^{-1} h^{-1}) is lower than in other general models of P^B versus I.

Conventional Measurement of Primary Productivity

The 24-hour SIS incubations yielded estimates of primary productivity that were higher than those from the productivity model (Figure 5*a*). Daily productivity from the morning casts,

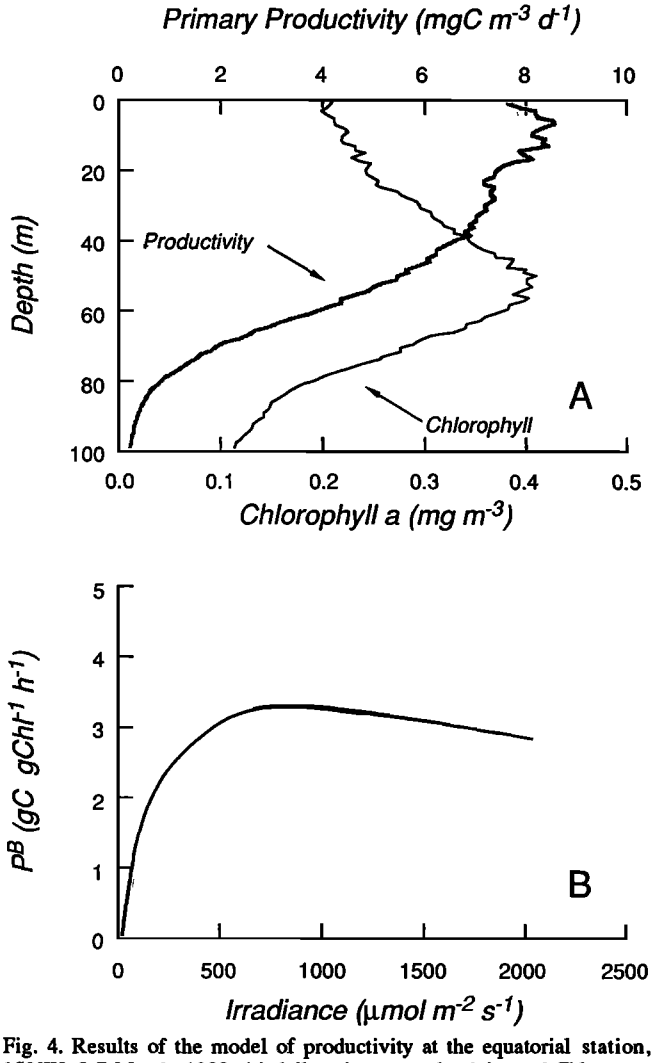


Fig. 4. Results of the model of productivity at the equatorial station, 150°W, 2-7 March, 1988: (a) daily primary productivity and Chl versus depth; (b) productivity normalized to biomass (P^B_i; average hourly rate over the day) as a function of average irradiance over the day.

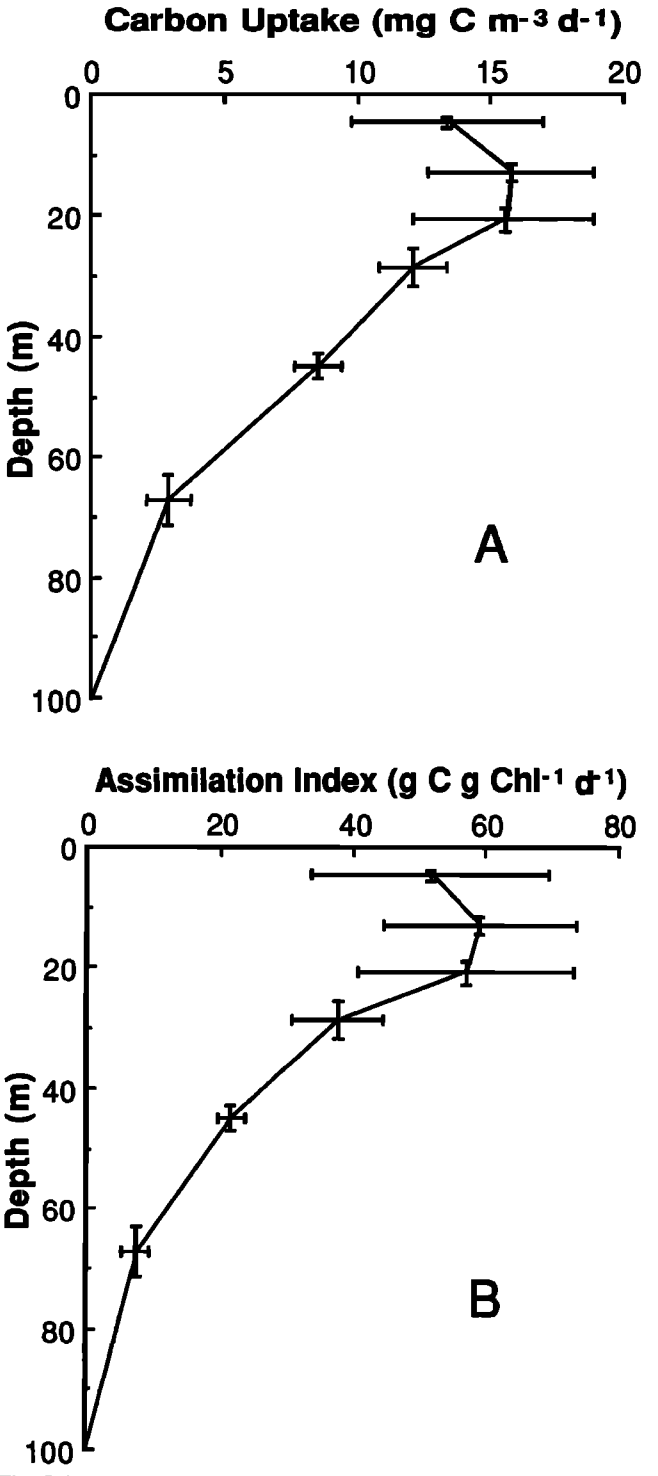


Fig. 5. Results of SIS incubations to determine primary productivity at the equatorial station. Mean ± s.d. for 6 days, morning stations only. (*a*) Daily productivity. Integral productivity to 100 m was 710 mg C m^{-2} d^{-1}. (*b*) Assimilation index (g C g Chl^{-1} d^{-1}).

integrated to an assumed zero point at 100 m, was 710 mg C m^{-2} d^{-1}, higher than all other stations along the transect from 15°N to 15°S on 150°W and consistent with several other estimates of equatorial productivity [*Chavez et al.*, 1990; *Peña et al.*, 1990]. Inhibition at the surface was observed, and maximum rates averaging 16 mg C m^{-3} d^{-1} were measured at 10-25 m.

The mean rate of photosynthesis normalized to initial chlorophyll (assimilation index, g C g Chl^{-1} d^{-1}; Figure 5*b*) was 59 g C g Chl^{-1} d^{-1} in the productivity maximum. Assuming a C:Chl ratio of 58 by weight [*Eppley et al.*, this issue], this assimilation index corresponds to a phytoplankton growth rate of 0.7 d^{-1} (1 doubling d^{-1}). Photoinhibition of photosynthesis was evident near the surface, as was light-dependence at depth. Integrated production normalized to biomass (IP/IB: 0-100 m) was 31.2 g C g Chl^{-1} d^{-1}. Some general models of productivity predict that IP/IB is a positive function of surface irradiance [e.g., *Falkowski*, 1983; *Platt et al.*, 1988; *Cullen*, 1990]. Considering that daily insolation at the equator was near maximum for the world oceans, our measured value for IP/IB is on the low end of what would be expected.

Productivity From Changes in Beam Attenuation

A vertical profile of estimated primary productivity was constructed from daily measurements of the change of beam attenuation [*Siegel et al.*, 1989] over the 5-hour interval between morning and afternoon optical casts (Figure 6). For lack of a robust method of describing optical changes near dawn and dusk and during the late afternoon, hourly rates were multiplied by 10 to obtain rough estimates of daily productivity. The calculated rate was depressed near the surface and was maximal at about 15 mg C m^{-3} d^{-1} between 25 and 30 m. Estimated productivity declined with depth to 0 at the 1% light level, 65 - 70 m. Daily productivity integrated to 100 m was 702 mg C m^{-2} d^{-1}, quite similar to the estimate from SIS incubations. Later, we will discuss why these estimates should be interpreted cautiously.

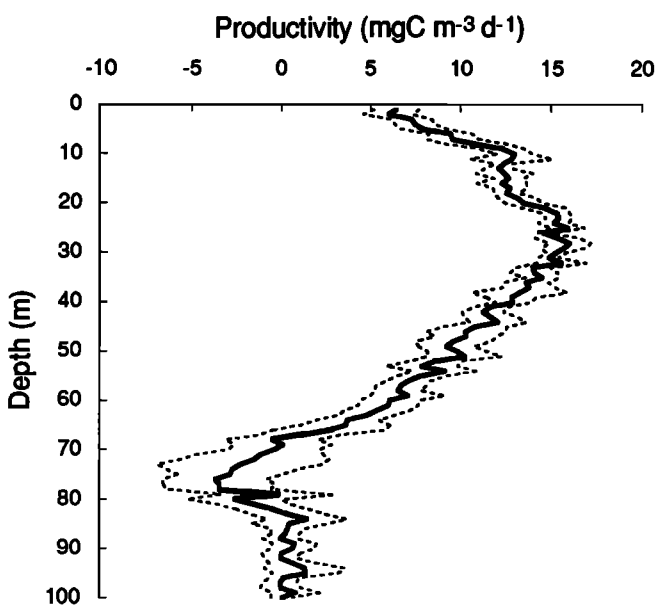


Fig. 6. Primary productivity at the equatorial station (mean ± s.d.), estimated from the average hourly change in beam attenuation between morning (about 0830 hours) and afternoon (about 1330 hours) optical casts over 6 days at the equatorial station. The conversion from attenuation to POC was taken from Siegel *et al.* [1989]: 3.92 x 10^{-3} m^2 mg C^{-1}.

Experimental Manipulations

Measurements of P-I on fresh samples are informative, but more can be learned by measuring changes in the P-I relationship and the increase of Chl during experimental SIS incubations. Accordingly, we incubated samples for 1-4 days to examine the extent of photoadaptation in situ and the possibility that the specific growth rates of the dominant equatorial phytoplankton were regulated by trace metals such as copper and iron. The principal experiment was performed at the equatorial station on March 2 to 6, using a combined sample from 30 and 40 m (see methods section).

Possible artifacts. The results from such incubations should be evaluated with care, so we designed the experiments to assess possible biases associated with SIS incubations. Specifically, if contamination with toxic divalent cations during sampling and containment were severe enough to inhibit photosynthesis [*Carpenter and Lively*, 1980; *Fitzwater et al.*, 1982], the toxicity could be countered by treatment with the chelator EDTA and growth and photosynthetic rates would be higher in EDTA-treated samples than in controls [*Sharp et al.*, 1980; *Cullen et al.*, 1986]. Instead, we found that Chl increased in controls (Figure 7), P-I did not change from time zero (Figures 8 and 9), and that there was no consistent enhancement of apparent growth rate with EDTA (Figure 7*b*), nor was there an effect on P_{max} (Figure 9). There was only the suggestion of consistent effects on the initial slope of the P-I curve, α (Figure 9).

Depletion of nitrate would confound results by curtailing growth that would otherwise have been stimulated by an experimental treatment. We saw no evidence of this curtailment in the experiments reported here. Also, several measurements of nitrate, plus mass-balance calculations show that nitrate depletion would not have seriously influenced the accumulation of chlorophyll.

The extent of photoadaptation in situ. If the phytoplankton assemblage, transported by upwelling, had not yet fully adapted to the irradiance regime at the depth of sampling, characteristic photosynthetic responses to increased irradiance would be observed during the SIS incubations over hours to days [cf. *Cullen and Lewis*, 1988]: photosynthetic capacity (P_{max}) and I_k would increase and susceptibility to photoinhibition (β) would decrease. Instead, during SIS incubation of 2 days, P-I for the control sample was indistinguishable from time-zero (Figures 8 *a* and 8*b*), even though the concentration of Chl increased by a factor of 2.9 (Figure 7), as would be expected if the dominant phytoplankton in situ were fully adapted to the photic environment at the depth of sampling.

The constancy of the P-I relationship over incubations of up to 2 days is strongly consistent with balanced growth, whereby all cellular constituents increase at the same rates over 24 hours [*Eppley*, 1981]. Accordingly, this is one of a restricted set of situations in which changes of Chl can be interpreted as changes in phytoplankton biomass [cf. *Eppley*, 1968; *Cullen*, 1982].

Regulation of photosynthesis by copper. Manipulations of trace elements were used to assess the influence of trace elements on photosynthesis in situ. Consider the regulation of equatorial primary productivity by copper toxicity: if the chelation capacity of the water were so low that free copper was toxic to phytoplankton in situ [cf. *Huntsman and Sunda*, 1980], an experimental addition of Cu would further inhibit growth (increase of Chl) or photosynthetic capacity relative to

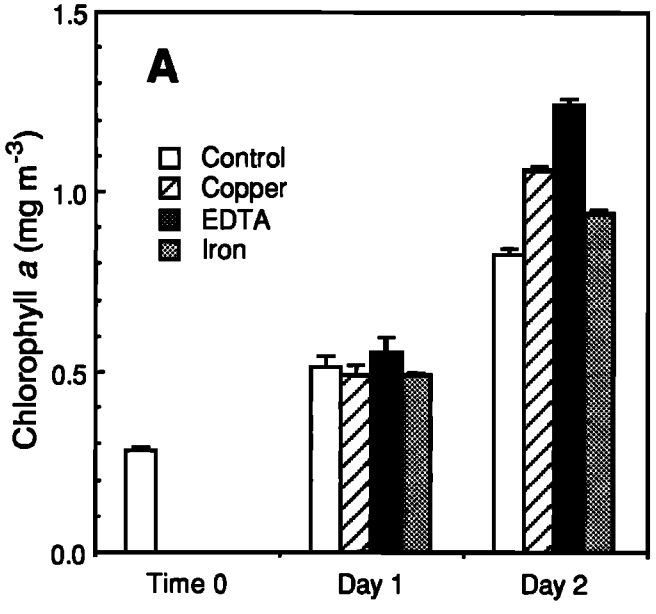
a control, and a sample treated with the chelator EDTA would show better growth and photosynthesis than a control. Conversely, if natural chelation were more than enough to bind free copper in situ, an addition of Cu sufficient to limit growth only in unchelated water would alter neither the rate of increase of Chl nor photosynthetic performance relative to an untreated sample. To test this, we used a treatment with Cu at 5 x 10^{-9} M. Calculations show that 93% of that copper would be complexed by inorganic ions [*Morel*, 1983], so the activity of added copper, in the absence of chelation from organics, would be 3.5 x 10^{-10} M. This activity of Cu^{++} inhibits growth of many clones of phytoplankton [*Gavis et al.*, 1981] and would likely have influenced equatorial phytoplankton if their rate of photosynthesis had been regulated by the activity of Cu^{++} at the time of sampling. Apparently, it was not: copper had little effect on the increase of Chl (Figure 7) or on P-I (Figures 8*c* and 9). Also, treatment with EDTA did not influence results (Figures 7 and 9).

Regulation of photosynthesis by iron. Our samples were probably contaminated with iron, so all of our incubated samples, including controls, should be considered enriched with iron. We therefore cannot determine if the availability of iron in situ limits the terminal yield of equatorial phytoplankton [cf. *Martin et al.*, 1989], but we can assess the degree to which enrichment with iron influences the specific growth rates and photosynthetic characteristics of the dominant phytoplankton. Copper and EDTA had no significant influence on our measurements during the incubations, so we can include them in this analysis.

Measurable responses to iron enrichment seem to require at least one and usually several days [*Martin et al.*, 1989], so if iron regulated the specific growth rates of phytoplankton in situ, we would expect initial rates to reflect those in nature and the rates after several days to reflect any stimulation attributable to iron. In other words, we can discount the influence of iron contamination over the first 24 hours, and compare early changes in growth and P-I to those observed over days 2-4.

The concentration of Chl increased over 48 hours in each of the four treatments on the sample from the equatorial station (Figure 7*a*), averaging an increase of 83% between time zero and day 1, 96% between days 1 and 2 (exponential rates of increase are 0.60 d^{-1} and 0.67 d^{-1}, respectively). The differences between treatments were not large and not the same on consecutive days. The average change of Chl during this experiment was consistent with other experiments in equatorial waters: for all available data from incubations, the increase of chlorophyll was roughly exponential over the first two days, with a specific rate of increase of 0.59 d^{-1} (Figure 7*b*). Between days 2 and 4, when effects of iron enrichment might be expected, the specific rate of increase was 0.89 d^{-1}. For all data combined, there were no consistent effects of treatments on the increase of chlorophyll during SIS incubations.

The apparent acceleration of growth rate over 4 days (Figure 7*b*) could have been due to a number of factors, but it may well



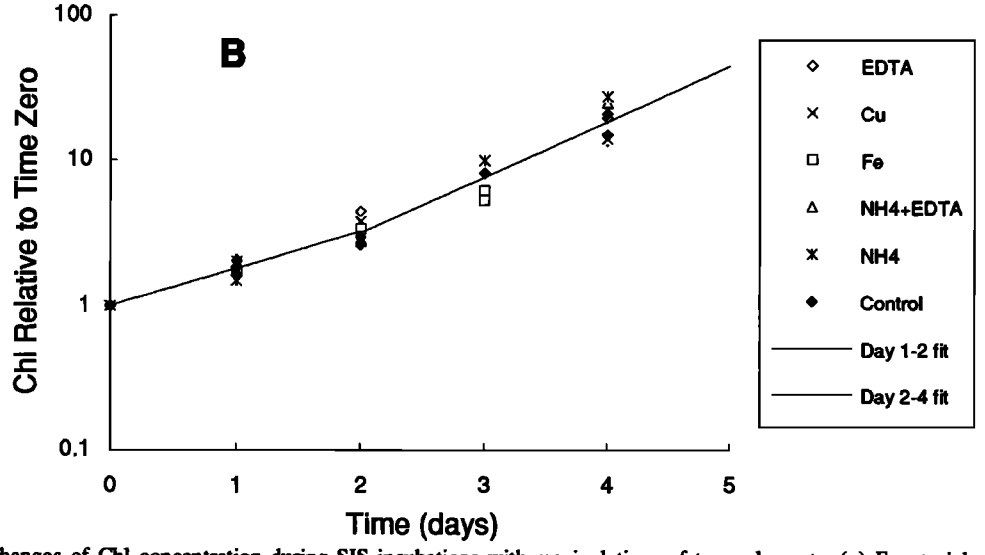


Fig. 7. Changes of Chl concentration during SIS incubations with manipulations of trace elements. (*a*) Equatorial station, 11% I_0, March 2-4, 1988, treatments described in text. Error bars are standard errors of triplicates from one bottle. (*b*) Results from all SIS incubations between 2°S and 6°N, >10% I_0; treatments described in section 2. Results normalized to Chl concentration at time zero. There were no consistent differences between treatments, so all were combined to calculate specific rates of increase. The lines are best fits for days 1-2 (regression forced through 0, on log-transformed data: slope=0.59 d^{-1}, n=21, r^2=0.82) and days 2-4 (regression on log-transformed data, slope=0.89, n=21, r^2=0.92).

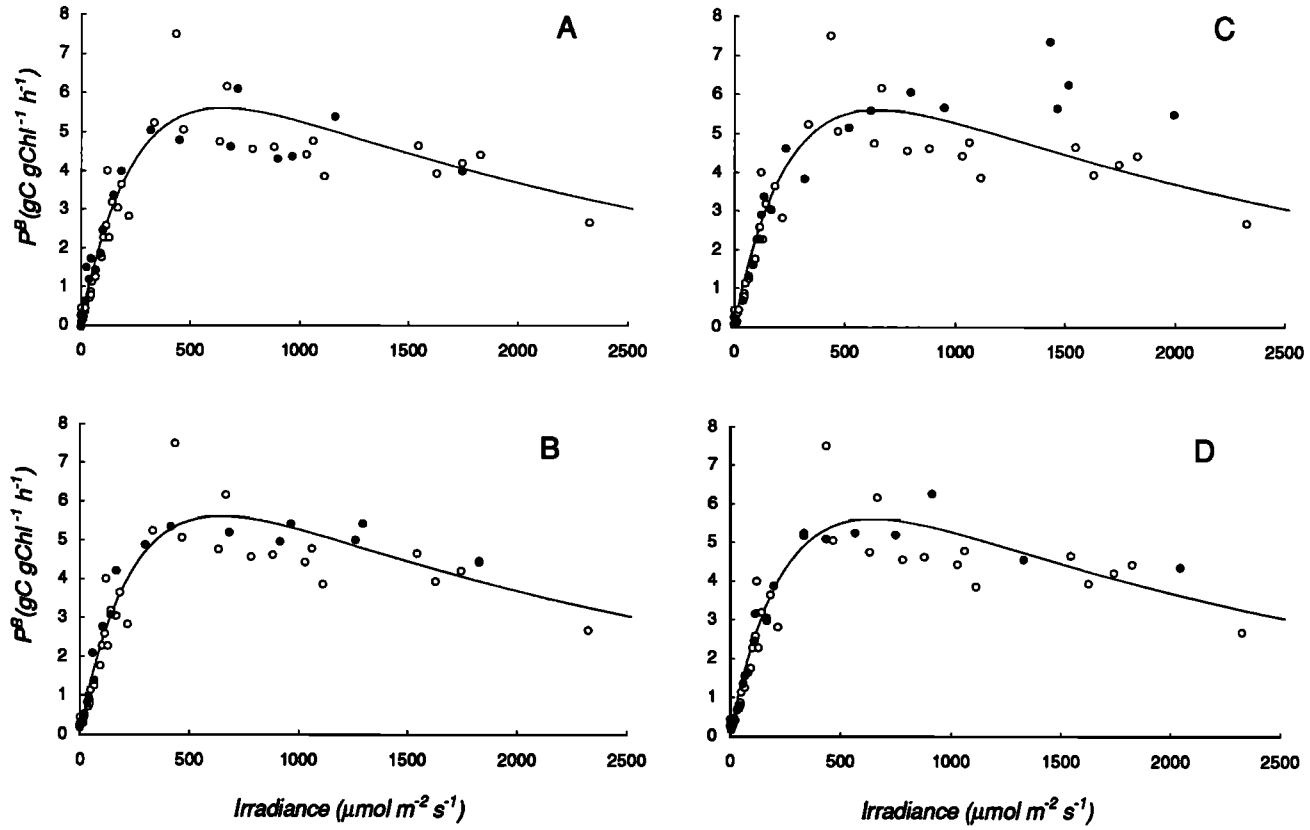


Fig. 8. Effects of experimental treatments during SIS incubations at 11% I_0 over two days. Measurements of photosynthesis (g C g Chl^{-1} h^{-1}) versus irradiance (µmol m^{-2} s^{-1}) during an experiment at the equatorial station, March 2-4 ,1988. In each plot, results from an experimental treatment (solid circles) are plotted with the time-zero (T_0: open circles) measurements. The curve is the best fit to equation (1) for T_0 P-I: (*a*) control sample after 24 h; (*b*) control sample after 48 h; (*c*) Cu-treated sample after 48 h; (*d*) Fe-treated sample after 48 h.

have reflected enhanced growth of large cells stimulated by iron or released from grazing pressure [*Banse*, 1991]. Species composition was not determined, but visual inspection of the bottles showed that after incubations of 4 days, many aggregates had formed.

4. DISCUSSION

Influence of Physical Forcing on Photosynthetic Performance

In equatorial upwelling systems, physical forcing influences primary productivity on a number of spatial and temporal scales. Wind-induced turbulent mixing, when suppressed during the day by solar heating [*Moum and Caldwell*, 1985; *Carr et al.*, this issue], can produce a diel cycle of mixing and stratification that disrupts the adaptation of phytoplankton to their photic regime [cf. *Vincent et al.*, 1984]. Upwelling at the equatorial divergence can replace surface waters on the time scale of several days: if growth and adaptation of phytoplankton keep pace, the upwelling will enhance local productivity, but if vertical advection moves phytoplankton through the light gradient faster than they can adapt and grow, primary productivity and enrichment of higher trophic levels will be displaced laterally [*Walsh*, 1976; *Minas et al.*, 1986; *Dugdale and Wilkerson*, 1989]. The El Niño Southern Oscillation (ENSO) cycle, an aperiodic perturbation of the ocean/atmosphere system, strongly modifies the heat content and productivity of the Pacific Basin on an annual time scale, acting as a major determinant of the ecological character of the low-latitude Pacific Ocean [*Barber and Kogelschatz*, 1988]. In the central equatorial Pacific, proximate effects of ENSO include warmer surface temperatures, a deeper thermocline and lower near-surface nutrient concentrations as compared to the climatological mean. These changes in thermal structure and nutrient concentrations must influence the effects of vertical mixing and upwelling on phytoplankton so that physical forcing mechanisms interact on several scales. Here, we examined responses of phytoplankton to physical forcing on time scales from hours to days.

The effects of diel variation in irradiance and vertical mixing were measured directly: photosynthetic parameters varied with time of day and showed vertical patterns reflecting nocturnal mixing, diurnal stratification, and near-surface photoinhibition. Photoinhibition was observed in conventional incubations, but such static incubations over 24 hours at surface irradiance are unnatural because vertical movements are not simulated [*Marra*, 1978; *Gallegos and Platt*, 1985]. Short-term measurements of P-I showed depressed photosynthetic capacity at the surface, a direct manifestation of photoinhibition in situ, independent of incubation artifacts. The diurnal increase of beam attenuation was also depressed near the surface. It seems clear, therefore, that nocturnal mixing and diurnal stratification promoted photoinhibition in the equatorial Pacific, much as it does in the tropical alpine Lake Titicaca [*Vincent et al.*, 1984; *Neale and Richerson*, 1987]. Nocturnal mixing at the equatorial station was relatively weak during March 1988 [*Carr et al.*, this issue], so

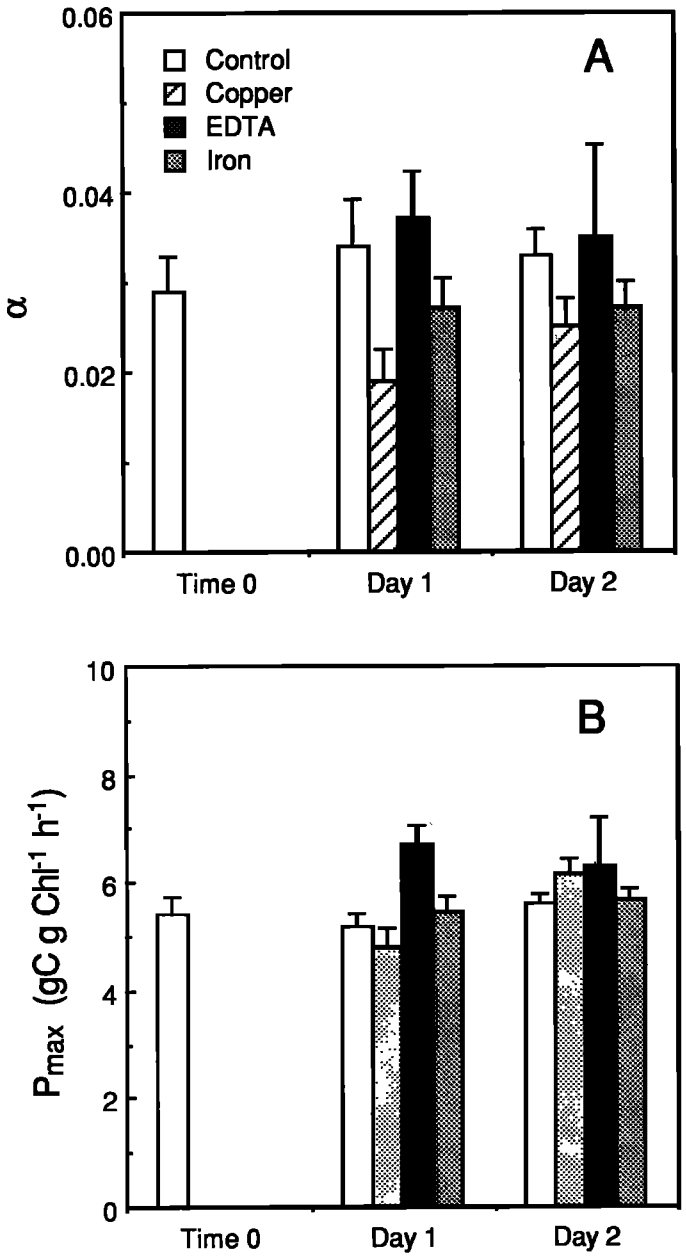


Fig. 9. Photosynthetic parameters (best fit to equation (1) ± s.e.) during an experiment at the equatorial station, March 2-4, 1988. Treatments described in the text: (*a*) α (g C g Chl^{-1} h^{-1})(μmol m^{-2} s^{-1})$^{-1}$); (*b*) P_{max} (g C g Chl^{-1} h^{-1}).

photoinhibition at the surface might be more severe at other times of year.

Responses of phytoplankton to physical forcing on the time scale of days can be inferred from direct measurements and experimental results. Vertical differentiation of photosynthetic characteristics (Figure 3), a process that requires hours to days [*Cullen and Lewis*, 1988], demonstrates that through much of the euphotic zone, the photosynthetic systems of phytoplankton had time to adapt at least partially to ambient irradiance. Measurements of P-I on fresh samples did not reveal the extent to which phytoplankton had adapted, however. We determined the degree of adaptation by incubating samples under SIS conditions to see if the phytoplankton would adapt further. For the assemblage sampled at the equator, there was little or no indication of photoadaptive changes of P-I during SIS incubations. We conclude that with respect to photosynthetic characteristics, the dominant phytoplankton assemblage at 30-40 m on the equator was well adapted to ambient irradiance. Neither upwelling nor vertical mixing was sufficiently intense to overwhelm photoadaptation [cf. *Lewis et al.*, 1984]. This conclusion is consistent with estimates of mixing and upwelling that indicate a minimum residence time of 20 days for passive particles in the upper 30 m at the equator (M.E. Carr, personal communication, 1991).

This study was concerned primarily with photosynthesis. *Dugdale et al.* [this issue], studying the uptake of nitrate and ammonium, concluded that the equatorial phytoplankton assemblage was not well adapted to ambient conditions, particularly the nutritional environment. In their words, the assemblage was not "shifted-up." Could the assemblage be "photoadapted" but not shifted-up? The question can not be answered at this time because too. little is known about the relationships between carbon and nitrogen assimilation in these phytoplankton: uptake of nitrogen can be substantially uncoupled from photosynthesis [*Morris*, 1981; *Cullen*, 1985], and it is possible that the equatorial phytoplankton assemblage is physiologically distinct from the cultured phytoplankton on which our understanding of phytoplankton physiology is based. More study is clearly warranted.

The Model of Primary Productivity

Our method of modeling productivity from P-I, fluorescence, Chl and irradiance is based on established principles recently applied and evaluated by *Harrison et al.* [1985]. Here, we use more information to improve the vertical and temporal resolution of the estimates: instead of describing photosynthesis in the water column with one P-I relationship, we use 12 (four depths, three times per day) to encompass diel variability [*Harding et al.*, 1982*b*] and photoadaptive differentiation of P-I with depth [*Falkowski*, 1983; *Lewis et al.*, 1984 and references therein]; measurements of Chl at four depths are used to model fluorescence yield as a function of depth [cf. *Cullen*, 1982]; a profile of fluorescence is used to estimate Chl at 1-m intervals; and productivity is estimated from irradiance profiles at 30-min intervals. The result is a detailed depiction of primary productivity at the equatorial station, with superb vertical and temporal resolution. But is the model accurate?

Modeled daily productivity in the water column is 34% lower than that measured by conventional SIS methods (Figure 5). At 10 - 20 m, modeled rates of daily productivity are only about 50% the rates measured by SIS incubations. Several factors could contribute to this discrepancy.

Unnatural accumulation of chlorophyll. The concentration of Chl changed little from day to day in the water column, but during 24-hour SIS incubations, Chl increased by as much as 80% (samples from > 10% I_0; Figure 7). This accumulation was an artifact of containment, so the SIS method overestimated productivity to the extent that Chl in the bottles exceeded natural levels [*Eppley*, 1968]. If the unnatural increase of Chl in bottles were linear, an artifactual 80% increase over 24 hours would lead to a 40% overestimate of primary productivity for SIS incubations. If we assume constant photosynthetic rate in daylight and an artifactual exponential increase in Chl of 0.6 d^{-1} during a 24-hour incubation beginning at 1000 hours, the estimate of bias is 31%. This estimate may be valid for 10 - 30 m, but it overstates

the bias for other depths: increases of Chl during incubation were small or nonexistent at surface irradiance (data not shown) and below about 30 m, changes declined with depth due to light limitation (results from one experiment not shown). Changes of Chl were measured in polycarbonate bottles: increases may have been less during the ^{14}C incubations in glass bottles (F. Chavez, personal communication, 1990).

The unnatural accumulation of chlorophyll was presumably due to disruption of grazing. Sinking is another potential loss that is eliminated in bottles, but it was not important here: the dominant phytoplankton [*Chavez*, 1989; *Peña et al.*, 1990] are small and incapable of rapid sinking; and during the night there was no downward displacement of the beam c maximum, as would be expected had sinking of particles been important.

Diel variability of P-I. Our data (Figures 3*a* and 3*b*) specify the minimum amplitude of diel variability in α and P_{max}. Maximum chlorophyll-specific rates may have occurred before or after midday [*MacCaull and Platt*, 1977; *Harding et al.*, 1982*a*]. If these peaks had been measured, the model estimates of productivity would have been higher. Even if maximum rates had occurred at midday, the linear function used to describe diurnal changes of P-I might have led to underestimation of productivity. In nature, P_{max} can be near maximal for several hours [*MacCaull and Platt*, 1977]. We conclude that the modeled values of $P^B(z,t)$ are underestimates of true rates because diel variability is inadequately described. Data are not sufficient to quantify the error: it might be 10 - 20%, in the light-saturated upper 30 m.

Irradiance spectra in the incubators. The light source in the P-I incubator, qualitatively similar to that used by *Harrison et al.* [1985], has relatively less blue light and more red light than does the attenuated solar spectrum in the SIS incubator, and both incubators have relatively less blue light than what is present in situ [*Herman and Platt*, 1986]. Because the action spectrum of photosynthesis has a major peak in the blue region, red light is inefficiently utilized and the P-I incubator should yield underestimates of photosynthesis at light-limiting irradiance when compared to the same irradiance in a SIS incubator. Both incubation methods should yield underestimates when compared to the same subsaturating irradiance in situ [*Lewis et al.*, 1985]. Spectral quality should have little influence on short-term measurements of light-saturated rates, but I_k will be affected. Calculations show that estimates of light-limited photosynthesis from the P-I model could be about 60% lower, and SIS results might be 40% lower than those from in situ incubations [*Harrison et al.*, 1985]. Thus, spectral quality can account for the observed difference of about 20% between the model and SIS results at depths where SIS photosynthesis was light-limited.

The contribution of large, rare cells or aggregates was excluded from the model. Aliquots for measurement of P-I were only 1 mL, so large cells or aggregates of cells present in concentrations of less than about 10 mL^{-1} would not be evenly distributed between samples. A large amount of the biomass and production of phytoplankton in the central equatorial Pacific can pass a 5 μm filter [*Chavez*, 1989; *Peña et al.*, 1990], so we expected a relatively small contribution by large, rare cells or aggregates. Nonetheless, a few measurements in each set of 24 were substantially higher than the others and were excluded from analysis. If large, rare cells or aggregates had been responsible for these high points, our estimates of $P(z,t)$ would be low. Future studies should assess this potentially serious complication.

Toxicity associated with P-I incubation technique. Perhaps the simplest explanation for lower rates in the P-I model would be trace element toxicity associated with incubating small samples in borosilicate glass containers (see P-I methods) that are known to harbor contaminants [*Fitzwater et al.*, 1982]. The question here is whether rate measurements were affected during short (1 hour) incubations. If toxicity had been important, measurements of photosynthesis would not only have been low, but also variable [*Fitzwater et al.*, 1982] and sensitive to treatment with the chelator EDTA [*Sharp et al.*, 1980; *Cullen et al.*, 1986]. Results presented here show no indication of trace metal toxicity: most of the data fit modeled P-I curves quite well (Figure 1), and outliers were high, not low as expected from toxicity. Further, in a test for short-term effects of trace elements, rates measured on a sample treated with EDTA were very similar to those measured on a control (Figure 10). We conclude that the time scale of our P-I measurements was too short for toxicity to have had a significant effect.

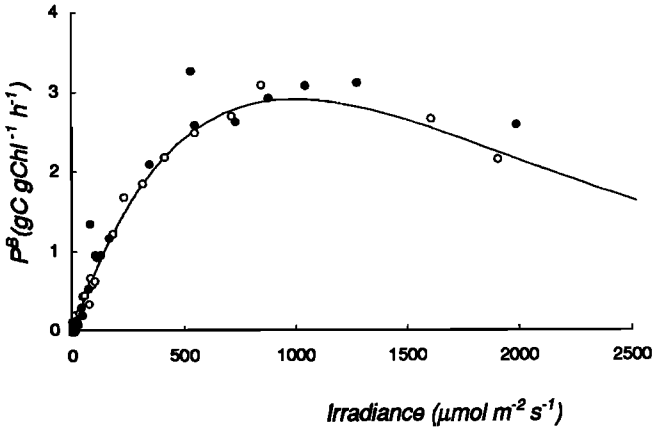


Fig. 10. Assessment of the effects of trace-metal contamination on measurement of P-I. Sample from 18 m at 6°N, 150°W. Control sample, treated as described in section 2 (open circles). Solid line is the best fit to equation (1). Parallel sample treated with 1 μM Na_2EDTA (solid circles). If toxicity from copper or zinc had inhibited photosynthesis in the control, the EDTA treatment would show higher rates [*Cullen et al.*, 1986].

It could nonetheless be argued that substantial and irreversible toxic effects had occurred prior to the first measurements. This daunting criticism was addressed by *Cullen et al.* [1986]. Using the criteria described in that paper, we exclude the possibility of irreversible and catastrophic damage to phytoplankton during sampling. Particularly relevant are our measurements of high in vivo fluorescence normalized to chlorophyll in dark-adapted samples (J. Cullen and C. Davis, unpublished data, 1988), an observation that is inconsistent with toxic contamination.

We conclude that both the P-I method and the SIS method have potentially serious biases that are large enough to account for the discrepancies between methods. These biases should eliminated or better quantified in future studies. The P-I method does not include the contribution of large cells or aggregates, so we must assume that those measurements represent the dominant, small phytoplankton.

Beam Attenuation and Phytoplankton

Primary productivity. Siegel et al. [1989] hypothesized that diel changes of attenuation were due to photosynthetic

production of ultraplankton offset by losses through microzooplankton ingestion. It was assumed that micrograzer abundances were not sampled by the transmissometer. Regardless of the exact nature of growth and loss terms, primary productivity could be estimated from the apparent accumulation of particles during the day. The assumptions implicit in the calculation of productivity from changes in attenuation are (1) the carbon-specific attenuation coefficient (c_C^*; 3.92×10^{-3} m^2 mg C^{-1}) is accurate, and (2) c_C^* is constant throughout the day. To validate the method by direct comparison to conventional measurements, it is also assumed that the accumulation of small particles sensed by the transmissometer represents primary productivity as measured with the ^{14}C method. These assumptions are tenuous at best, so the agreement between productivity calculated from changes in beam c (Figure 6) and SIS estimates (Figure 5) is encouraging.

Let us examine the relationship between the accumulation of ultraplankton and measurements of ^{14}C uptake. *R. E. H. Smith et al.* [1984] modeled productivity and carbon flow using rates of growth and grazing similar to those presented here. In the model of *R. E. H. Smith et al.*, the only losses from the pools of autotrophs and microheterotrophs were to respiration. Here we recognize that grazing by larger organisms should also be considered. For simple models of carbon flow through autotrophs and microheterotrophs, losses from these pools to grazing are equivalent to respiration, so the model of *Smith et al.* should still apply. The pertinent observation is that in a tightly coupled autotroph-microheterotroph system, the accumulation of particulate ^{14}C is nearly equivalent to autotrophic growth plus the autotrophic production assimilated by heterotrophs. During incubations, ^{14}C accumulates in the microheterotrophic pool so that for the systems they modeled, the increase of phytoplankton carbon accounts for only about 50 - 70% of net production in the light. Thus, net accumulation of photosynthetic ultraplankton in the light should be an underestimate of what the ^{14}C method measures. If only phytoplankton contribute to beam attenuation, daytime productivity from beam c should be multiplied by 1.5 to 2 for comparison with ^{14}C uptake. When this correction is applied, productivity from beam c is much higher than measured ^{14}C uptake. This would indicate that either our carbon-specific attenuation coefficient is high or ^{14}C measurements are low. Another possibility is that c_C^* varies during the day, exaggerating the diurnal increase [*Ackleson et al.*, 1990; *Olson et al.*, 1990].

Beam c was measured routinely only twice per day, so the diel variability of attenuation could not be described in detail. To calculate productivity from changes in beam c, we multiplied by 10 the hourly rates determined between 0830 and 1330 hours, implicitly assuming linear accumulation of POC during the day, curtailed near dawn and dusk. Below we describe an exponential model that can be used to estimate productivity, yielding similar results.

Chemical composition of phytoplankton. *Siegel et al.* [1989] clearly recognized that attenuation could not be attributed exclusively to phytoplankton, but it is difficult to quantify the degree to which phytoplankton contribute to the measurement. If we assume that phytoplankton are entirely responsible for beam attenuation, we can calculate the C:Chl ratio (w:w) of phytoplankton from beam c and Chl. This estimate will be too high by an amount corresponding to detrital and heterotrophic attenuation at 660 nm. At the equatorial station, the maximum C:Chl ratio (g:g) of phytoplankton at 30 m, calculated from mean beam c, varied between 50 (morning profiles) and 66 (afternoon profiles) whereas at the chlorophyll maximum (60 m) C:Chl varied between 27 and 33 for morning and afternoon profiles, respectively. These numbers agree with C:Chl ratios calculated by *Eppley et al.* [this issue] on the basis of regressions between POC and Chl, are consistent with other estimates from equatorial waters [*Eppley et al.*, this issue], and have the same vertical pattern as described by *Pak et al.* [1988].

Eppley et al., [this issue] estimated that only about 30% of the POC was phytoplankton carbon. If we assume for discussion that phytoplankton contributed only 30% to attenuation, then calculated C:Chl would be about 10 in the Chl maximum and 20 at 30 m. The latter estimates of C:Chl are low, but it is not possible to determine on the basis of lab studies [*Geider*, 1987] that they are unreasonable.

We do not know the relative contributions of phytoplankton, bacteria, and detritus to beam c, but we can assess absorption by photosynthetic pigments as a component of measured attenuation [*Pak et al.*, 1988]. The concentration of Chl at the equatorial station rarely exceeded 0.5 mg m^{-3}. A typical Chl-specific absorption coefficient for phytoplankton at the red peak (675 nm) is about 0.02 m^2 (mg Chl)$^{-1}$ [*Iturriaga and Siegel*, 1989]. We assume that for the beam transmissometer (peak wavelength in air 660 nm), 0.01 m^2 (mg Chl)$^{-1}$ is an appropriate specific absorption coefficient. Therefore, maximum absorption by phytoplankton was about 0.005 m^{-1}. This is less than 10% of beam c - c_W in the mixed layer, thus attenuation is dominated by scattering.

Specific growth rates of phytoplankton. At the equatorial station, attenuation at 28 m increased 53% over 5 hours between morning and early afternoon (Figures 1*e* and 1*f*). If exponential increase of particles is assumed, these changes in attenuation can be used to estimate growth rates of phytoplankton [*Siegel et al.*, 1989]. The specific particle production rate, r, is estimated from the change in attenuation:

$$r = \frac{1}{t} \ln \left(\frac{c_t}{c_o} \right) \tag{3}$$

where c_t and c_o are beam attenuation at time t (hours) and time zero, respectively. The increase at 28 m corresponds to r = 0.085 h^{-1}. This increase reflects the balance between light-dependent growth (μ) and light-independent grazing (g): $r = \mu - g$. We follow the reasoning of *Siegel et al.* [1989], but for this discussion we assume that (1) the rate of light-dependent growth is constant (μ_{max}) from 0800 until 1600 hours, when irradiance exceeds 200 μmol m^{-2} s^{-1}; (2) the specific rate of particle production (r_{max}) is likewise constant at 0.085 h^{-1} between 0800 and 1400 hours; (3) μ is zero in the dark, increases linearly from 0600 until 0800 hours, and decreases linearly from 1600 until 1800 hours; and (4) a constant grazing rate (g) balances growth over 24 hours (Figure 11*a*). The grazing rate was calculated by iteration (g = 0.061 h^{-1}). The maximum light-dependent growth rate was $r_{max} + g$ (μ_{max} = 0.146 h^{-1}). If only phytoplankton contribute to attenuation, the specific growth rate for phytoplankton over 24 hours is thus 1.46 d^{-1}. Productivity calculated from the model (Figure 11*b*) was only 4% higher than an estimate obtained by multiplying the mean hourly increase by 10 (cf. Figure 6).

Siegel et al. [1989] recognized that if detritus or other particles contributed to beam c, these rates would be

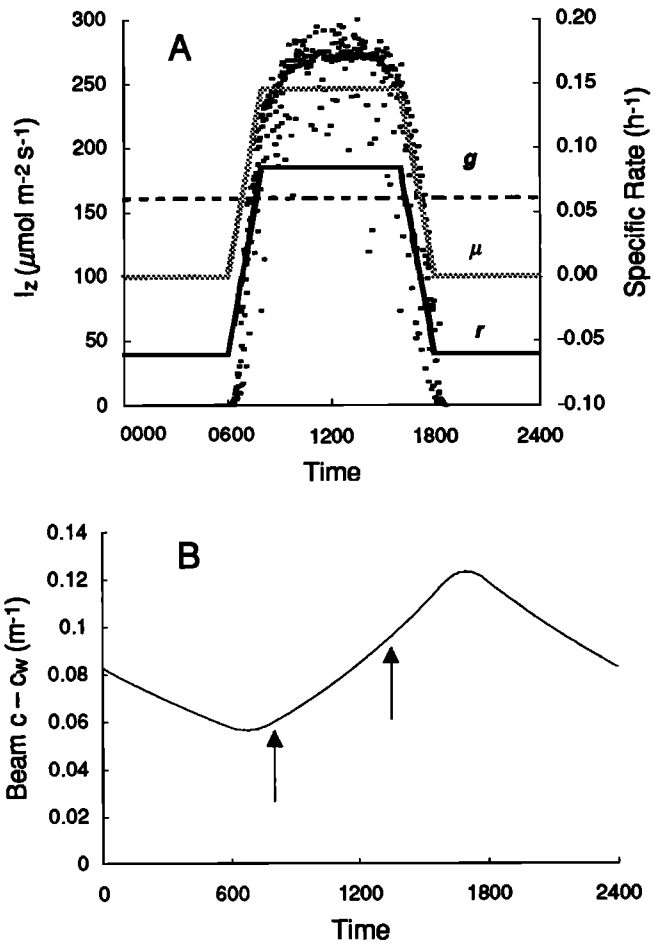


Fig. 11. Model of phytoplankton growth and grazing at the equatorial station, 28 m. (*a*) The three lines represent the constant grazing rate, g (dashed line), the light-dependent growth rate, μ (stippled line), and the specific rate of particle production, r (solid line). Irradiance at 28 m, 10 min averages, observations over 6 days, calculated as 10% I_0 (rectangles). (*b*) Changes of beam attenuation (c - c_w) from the model: the arrows indicate 0830 and 1330 hours, the times at which attenuation was measured. Averages of beam c at these times over 6 days constrained the model.

underestimates. Assume the extreme, that phytoplankton account for only 30% of beam attenuation. The sink for the loss term, g, is still assumed to be unsampled by the transmissometer. In essence, 70% of the attenuation at time zero (the morning observation) is considered as a constant background. Our model shows that autotrophs would have to produce carbon at a high specific rate to support the inferred 53% increase of total particles in 5 hours at 28 m: μ_{max} is 0.349 h^{-1}, and g is 0.145 h^{-1}. The specific growth rate for phytoplankton over 24 hours would be 3.48 d^{-1}. This is extremely high. Results from laboratory cultures indicate that the maximum specific growth rate for phytoplankton at 26°C is about 3.0 d^{-1}, even under continuous light [*Eppley*, 1972].

If instead we assume that the 70% nonautotrophic particles are heterotrophic, and that they are linked to autotrophic production and increase in concert with phytoplankton (i.e., phytoplankton always contribute 30% of the attenuation), the carbon-specific rates of photosynthesis for phytoplankton from Figure 11*a* would have to be 3.33 times higher (0.49 h^{-1}) to support the observed increase of particle abundance in the light. These examples show that specific growth rates of phytoplankton cannot be accurately estimated from changes in beam attenuation until the relative contributions of phytoplankton, microheterotrophs and detritus are resolved.

In summary, a vertical profile of primary production, calculated from changes in beam c, lends credence to the utility of transmissometry as a tool to examine productivity: calculated production is low close to the surface, where photoinhibition was documented, and it is zero at the 1% light level. High (about 1.5 d^{-1}) to extremely high specific growth rates of phytoplankton are indicated by changes in beam c, suggesting vigorous growth of phytoplankton, effectively controlled by grazing. Even though changes of beam attenuation seem to reflect primary production quite accurately, rigorous interpretations are very difficult because the relative contributions of phytoplankton, microheterotrophs and detritus are not known and the constancy of c_C^* is questionable. These uncertainties are being addressed but they have not yet been resolved [cf. *Morel and Bricaud*, 1986; *Pak et al.*, 1988; *Spinrad et al.*, 1989; *Morel and Ahn*, 1990; *Stramski and Morel*, 1990; *Ackleson et al.*, 1990].

Trace Elements and the Measurement of Primary Productivity

If trace-metal contamination during sampling and incubation [*Carpenter and Lively*, 1980; *Fitzwater et al.*, 1982] had seriously affected photosynthesis or growth, our study would have been greatly compromised. Toxicity would have caused underestimation of productivity; enrichment could have stimulated growth and lead to overestimation. To examine the potential effects of trace elements on the measurement of primary productivity, we measured P-I, a very sensitive indicator of phytoplankton physiology. We added copper, to exacerbate any toxicity, and EDTA, to alleviate toxic contamination [*Sharp et al.*, 1980; *Cullen et al.*, 1986]. Also, we enriched with iron, which conceivably could have stimulated production in the short term. Effects were examined on time scales from 1 hour to 2 days. All results were compared to time-zero controls as well as to other treatments or controls. All results were negative. Changes of P-I over 48 hours at 11% I_0 were negligible (Figure 8). Our conclusion is that with respect to the uptake of bicarbonate, our sampling and SIS incubations did not discernibly perturb the physiology of the dominant phytoplankton. We did not take all possible precautions to prevent trace-metal contamination [*Fitzwater et al.*, 1982], but we were careful and we did eliminate a principal culprit, the black neoprene rubber closures on conventional Niskin samplers [*Chavez and Barber*, 1987; *Williams and Robertson*, 1989]. Our results strongly support the conclusion that legitimate rate measurements can be obtained if simple precautions are observed [*Marra and Heinemann*, 1984; *Cullen et al.*, 1986; *Price et al.*, 1986; *Williams and Robertson*, 1989].

Trace Elements and Limitation of Primary Productivity

When discussing the regulation of primary productivity by nutrients, it is useful to distinguish between regulation of growth rate and limitation of standing crop. If standing crop is kept low by grazing or some other loss process, productivity can be limited even if the specific growth rates of phytoplankton are maximal. Our experiments examine directly the influence of trace elements on the specific growth rates of phytoplankton. We must infer the relationship between trace nutrients and standing crop.

Trace element limitation of specific growth rate. Relatively high specific growth rates of phytoplankton (1.5 d^{-1} or

possibly more) are suggested by diel changes in beam *c*. Experimental incubations also indicated that growth rates in situ were fairly high: during the first two days of incubations, when the P-I relationship, a sensitive indicator of perturbations to growth conditions, showed little change (Figures 8 and 9), the concentration of Chl increased nearly exponentially at a rate of 0.6 d^{-1}. We take this as a minimum estimate of phytoplankton growth rate in situ, given that some grazing was likely in the bottles. These estimated growth rates are not consistent with the notion that the supply of trace elements severely restricted the specific growth rates of phytoplankton at the equatorial station.

Treatments with copper and the chelator EDTA had little effect on the growth of phytoplankton from equatorial waters at 150°W (Figures 7*b*, 8*c*, 9). These results indicate that toxicity from divalent cation contaminants did not compromise our results and that copper toxicity did not regulate the specific growth rates of the dominant phytoplankton in situ. These conclusions do not exclude the possibility that toxic trace elements might influence equatorial phytoplankton assemblages by inhibiting the growth of some species.

Because contamination with iron almost surely occurred during sampling, it can be argued that our experiments are useless for examining the effects of iron on phytoplankton. This would be true except for the observation that the responses of phytoplankton to iron enrichment seem to be slow [cf. *Martin et al.*, 1989]. If growth rates in situ had indeed been limited by Fe, low rates would have been maintained during the first 1-2 days, during which time we might expect to see a change in photosynthetic characteristics, followed by rapid acceleration of growth. We saw no response of P-I over 2 days, but subsequently we did observe an apparent acceleration of growth rate (Figure 7*b*). This more rapid growth may well characterize a distinct assemblage, released from grazing pressures and responding to enhanced availability of iron [*Banse*, 1991]. Even if the abundance of those species in situ had been regulated by the availability of iron, grazing must have been responsible for maintaining the constant standing crop of the dominant equatorial phytoplankton, which was growing at a minimum specific rate of 0.6 d^{-1}.

We cannot assert that the specific growth rates of phytoplankton were maximal for the temperature and irradiance regime at the equator. In fact, some biomass-specific rate estimates were relatively low. Photosynthetic rates were well below those measured in other warm waters: P_{max} was 5-6 g C g Chl^{-1} h^{-1} in surface waters at the equator where the temperature was about 26°C, whereas other studies [*Malone and Neale*, 1981; *Falkowski*, 1983; *Keller*, 1989] indicate that P_{max} can be as high as 20-25 at the same temperature. Accordingly, integrated photosynthesis per unit Chl was lower than predicted from simple models of productivity and insolation [*Platt et al.*, 1988; *Cullen*, 1990]. The relatively low rates of photosynthesis are not necessarily inconsistent with high growth rates. Rapid growth can be supported by relatively low P^B if C:Chl is low.

Trace-element limitation of standing crop. Martin et al. [1989] showed that during incubations of samples from the high-nutrient, low-chlorophyll subarctic North Pacific Ocean, the final yield of chlorophyll was proportional to added iron. This result suggests that iron limits standing crop in those waters. Martin and colleagues have presented independent evidence to suggest that iron limits the growth of phytoplankton not only in the north Pacific, but also in equatorial waters and the Southern Ocean [*Martin*, 1990]. These conclusions have been questioned [*Banse*, 1990; *de Baar et al.*, 1990]. Because we could not prevent iron contamination during sampling, our experiments are not appropriate for examining iron limitation of final yield, so we cannot reject the hypothesis that iron limits the potential standing crop of phytoplankton in the equatorial Pacific. It should be noted, however, that incubations to measure final yield are unnatural: grazing pressure is strong in the equatorial Pacific, and grazing is reduced in incubation procedures. The experiments might therefore show not what limits standing crop in situ, but what limits standing crop when the grazing limitation is relaxed or removed.

5. CONCLUSIONS: WHAT LIMITS PRIMARY PRODUCTIVITY?

The presence of nitrate at relatively high concentrations in equatorial surface waters indicates that the productivity of the system is limited by one or more processes or factors. Simply, assimilation of the excess nitrate would lead to more primary production but something is preventing that from happening.

One possibility is that physical forcing (upwelling and vertical mixing) prevents the phytoplankton assemblage from adapting to ambient conditions so that specific growth rates are low. Our results strongly suggest that phytoplankton are well adapted to ambient conditions through much of the euphotic zone, so physical forcing does not seem to hamper photosynthetic performance. We cannot exclude the possibility that although photosynthetic processes are adapted to ambient conditions, nitrate assimilation is not shifted-up [*Dugdale et al.*, this issue].

Several sets of measurements (^{14}C incubations, increase of Chl during SIS incubations, diel variability of beam *c*) indicate that specific growth rates of phytoplankton are relatively high, about 0.6 d^{-1} or possibly much higher. Nonetheless, Chl was relatively constant day-to-day, indicating that the growth of phytoplankton was closely balanced by losses (e.g., grazing). The pronounced diel variability of beam attenuation, interpreted according to *Siegel et al.* [1989], also suggested tight coupling between autotrophic production and grazing. This is perhaps our best evidence that grazing is the proximate control on standing crop, and thereby productivity, in equatorial waters [cf. *Walsh*, 1976; *Minas et al.*, 1986]. Unfortunately, the temporal change of beam attenuation is a poorly understood (although promising) measure of particle dynamics. The possibility exists that much of the signal is due to diel variability in c_C^*, the carbon-specific attenuation coefficient.

We hypothesize that specific growth rates of phytoplankton were adequate to exploit the excess nitrate in the surface layer at the equator but that standing crop was controlled by grazing. If grazing is the proximate limitation on standing crop and thereby on primary production, the supply of a trace element such as iron might still be the ultimate control. It is conceivable that small oceanic phytoplankton dominate the equatorial upwelling system because they are superior competitors for iron [*Brand et al.*, 1983], effectively excluding phytoplankton such as diatoms that dominate in coastal upwelling. Small phytoplankton are more susceptible than larger diatoms to grazing by microzooplankton, so it is possible that if the supply of iron to the equatorial Pacific were increased substantially, diatoms would bloom, to some extent uncoupled from grazing so that

nitrate would be depleted. Alternatively, large-scale circulation might select against diatoms by isolating surface waters from seed populations [*Chavez*, 1989].

This study and the others in this volume have answered a few questions about planktonic dynamics in the equatorial Pacific, but many have yet to be resolved. Some hypotheses seem mutually exclusive [*Walsh*, 1976; *Martin et al.*, 1989; *Dugdale et al.*, this issue], but we have demonstrated that components of each can be accommodated in a coherent description of the equatorial system. More measurements and continuing debate should answer the question, "Why isn't the equator greener?"

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