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Prochlorococcus growth rates in the central equatorial Pacific: An application of the f_{max} approach

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Abstract. Minimum daily growth rates of ***Prochforococcus*** were estimated for the central equatorial Pacific (12°S–12°N, 140°W) during El Niño (February-March 1992) and normal upwelling (August-September 1992) conditions. Growth rate estimates were based on the percentages of cells in the S and G_2 division phases at dawn (-0700 LT) and dusk (-1800 LT) as approximate values for f_{min} and f_{max}, respectively. During both environmental conditions, depth-integrated growth rates of ***Prochlorococcus*** were higher in oligotrophic waters at the northern end of the transect (0.36-0.52 d^{-1}) and decreased to a minimum at the equator. The lowest growth rates were found at the equator during El Niño and at 2°N during normal upwelling, where a large biomass of buoyant diatoms had accumulated in the vicinity of a convergent front. ***Prochlorococcus*** growth rate reached a high of 0.64 d^{-1} at 1°S and maintained a moderate rate (0.36-0.49 d^{-1}) throughout the southern end of the transect. An inverse relationship was found between the contribution of ***Prochlorococcus*** to the total primary production and nitrate concentration as well as total primary production measured by the ^{14}C method. While ***Prochlorococcus*** is a dominant primary producer in tropical and subtropical open-ocean ecosystems generally, it is relatively more important in oligotrophic waters than in the nutrient rich equatorial upwelling zone.

1. Introduction

Despite its relatively recent discovery in the mid-1980s [*Chisholm* ***et al.,*** 1988] the prokaryotic picoplankter *Prochlorococcus* is now recognized as a major component of photosynthetic biomass throughout tropical and subtropical regions of the open oceans. Interest in understanding the factors that influence its rates of growth and contributions to primary production is thus considerable. Pigment labeling [e.g., ***Gieskes and Kraay,*** 1989], ***flow*** cytometric sorting [e.g., *Li*, 1994], and dilution [*Landry* ***et al.,*** 1995a, b] techniques have all been applied with varying degrees of success to these growth and production rate measurements; however, cell cycle analysis is particularly well suited for this organism because of its bimodal DNA distribution and synchronous cell division ***[Vaulot et al.,*** 1995]. The cell cycle approach derives growth rate estimates from the fractions and durations of S (DNA synthesis) and G_2 (DNA replication complete but not yet divided) phases of the ambient population over a diel cycle and thus avoids incubation artifacts [*Vaulot* ***et al., 1995;*** *Liu* ***et al.,*** 1997]. However, the approach requires frequent sampling over a 24 hour cycle, which limits its use to situations where a station will be occupied for a day or more and where the time demands of other sampling activities do not conflict. Such conditions are rarely met in major oceanographic research programs with multiple investigators and scientific agendas.

Such was the case for survey cruises of the U.S. Joint Global Ocean Flux Study (JGOFS) Equatorial Pacific (EqPac) Program in 1992 which sampled along a transect of stations from 12°S to 12°N, 140°W during both El Niño and normal upwelling conditions. Routine dawn and dusk water column samples during these cruises were not sufficient for standard cell cycle analysis, but they lend themselves to a modified f_{max} approach [*Vaulot*, 1992] which uses the percentages of $S + G_2$ cells at dawn and dusk to approximate values for f_{min} and f_{max}, respectively. In the present study we use this approach to examine variations in ***Prochlorococcus*** growth rates and contributions to total primary production across the environmental gradient from oligotrophic to high-nutrient equatorial waters and during El Niiio and normal upwelling conditions.

2. Materials and Methods

2.1. Growth Rate Estimates From Cell Cycle Analyses

There are two main ways to compute in situ growth rates from cell cycle analysis: (1) from the total number of cells in a

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cell cycle terminal event (duration = t_d) over the 24 hour period and (2) from the daily maximum fraction of cells in the terminal event. The first category is illustrated by the *Carpenter and Chang* [1988] model, which is based on the derivation by *McDuff and Chisholm* [1982]. The most recent version of this model using S + G_2 phases as the terminal event was presented by *Liu et al.* [1997] as

$$\mu_p(\mathrm{h}^{-1}) = \frac{1}{t_{S+G_2}} \int_0^{24} \ln[1 + f_{S+G_2}(t)]\, dt \qquad (1)$$

where μ_p is the average specific growth rate over the photoperiod t_p (usually 24 hours), $f_{S+G_2}(t)$ is the fraction of cells in the S + G_2 phases of cell division at time point t in the 24 hour sampling period, and t_{S+G_2} is the duration of S + G_2 computed as twice the time between the peak fraction of cells in S and the peak fraction of cells in G_2 (see notation section) *[Carpenter and Chang,* 1988]. This equation is based on the assumption that all cells within the population have the same t_d (in our case, t_{S+G_2}); thus it is not accurate if part of the population becomes dark-arrested in the terminal event. Moreover, since t_{S+G} is determined from the time interval between observed peaks of cells in the S and G_2 phases the quality of this estimate is strongly dependent on the frequency of population sampling.

In contrast to the time-integrated μ_p calculation, the "f_{max} approach" does not require knowledge of t_d. *McDuff and Chisholm* [1982] concluded that when the terminal phase t_d is long compared to the cytokinesis, then

$$\mu_{f_{max}} = 1/t_p \ln(1 + f_{max}) \qquad (2)$$

wherein f_{max} is the maximal fraction of cells in the terminal phase of the cell cycle (see notation section). Growth rate estimates from (2) give a lower bound to the daily division rate because f_{max} decreases when phasing becomes less tight [see *McDuff and Chisholm, 1982,* Figure 1; *Antia et al.,* 1990].

Vaulot [1992] developed a more general form of (2) for phased cell division, including the possibility that slow growing cells spend more than 1 day in the terminal phase:

$$\mu_{fmin,fmax}(\mathrm{h}^{-1}) = \frac{1}{t_p} \ln\left(\frac{1 + f_{max}}{1 + f_{min}}\right) \qquad (3)$$

where f_{max} and f_{min} are the daily maximal and minimal fractions of cells in the terminal phase of the cell cycle (e.g., S + G_2) (see notation section). When $t_d < t_p$, f_{min} is equal to zero, and (3) reduces to (2). In the present study we used the fraction of *Prochlorococcus cells* in the S + G_2 phases from the samples taken at 0700 (f_{0700}) and 1800 (f_{1800}) LT as proxies for f_{min} and f_{max}, respectively.

Prochlorococcus has been shown to have a tightly phased cell cycle beginning with DNA replication in late afternoon followed by cell division in the evening *[Vaulot et al.,* 1995; *Partensky et al., 1996;* Liu *et al.*, 1997, 1998]. The exact timing for the time of maximum f_{S+G_2} is generally only known within an hour or two because of coarse sampling over the diel cycle. Nonetheless, it is apparent that cells near the surface usually begin DNA synthesis and cell division later than the cells deeper in the euphotic zone (Figure 1). Interregional comparisons suggest that *Prochlorococcus* enters S and G_2 phases slightly later in oligotrophic regions, such as Station ALOHA in the subtropical North Pacific (Figure 1). Because the time of maximum f_{S+G_2} varies within the water column and among different regions, depth-profile samples from ~1800 LT will likely capture only part of the population at maximum S + G_2, leading to underestimates in the growth rates at other depths and the depth-integrated average rate.

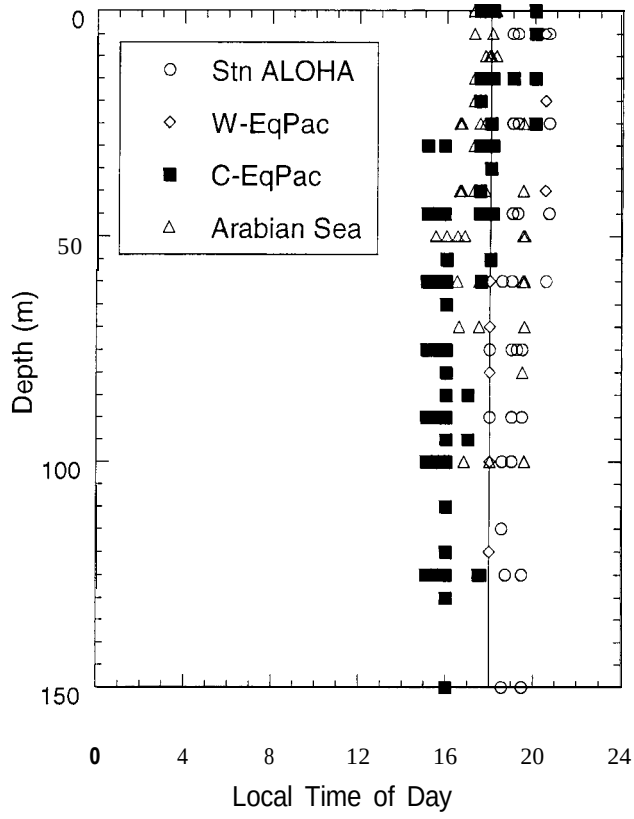

Figure 1. Depth profiles of the time at which the maximum fraction of *Prochlorococcus cells* in S + G_2 phases were observed during diel sampling in different oceanic regions: Central Equatorial Pacific (C-Eqpac), including data from 0°, 150°W (Flux dans lòuest du Pacifique Equatorial (FLUPAC), October 1994) [Liu *et al.,* 1997], 0°,140°W (EqPac TT008 and TT012, April and October 1992) *[Vaulot et al.,* 1995], and 5°, 150°W (Oligotrophie en Pacifique (OLIPAC), November 1994) *[Vaulot and Marie,* this issue]; Station ALOHA, U.S. Joint Global Ocean Flux Study (JGOFS) Hawaiian Ocean Time Series (HOT) Station ALOHA (22°45′N,158°W), during HOT 55 (July 1994), 64 (July 1995), 65 (August 1995), and 70 (March 1996); Arabian Sea, 5 stations in the Arabian Sea, ranging from oligotrophic open ocean to mesotrophic coastal waters, during U.S. JGOFS Arabian Sea process cruises TN050 (August 1995) and TN054 (December 1995) *[Liu et al.,* 1998]; and Western Equatorial Pacific (W-EqPac), including the oligotrophic western equatorial Pacific (0°,166°E) during French JGOFS FLUPAC cruise in October 1994 *[Liu et al.,* 1997]. The solid vertical line shows the time of 1800 LT.

2.2. **Sample and Data Analysis**

During EqPac cruises TT007 (El Niño conditions; February–March 1992) and TT011 (normal upwelling conditions: August-September 1992), seawater samples were collected at 10 m depth intervals to 120 m and at 150 and 200 m from early morning (between 0600 and 0800 LT) and late afternoon (between 1730 and 1830 LT) hydrocasts at each of 15 stations along a transect from 12°N to 12°S,140°W. These samples were previously analyzed by dual-beam flow cytometry for abundances and distributions of picoplankton populations

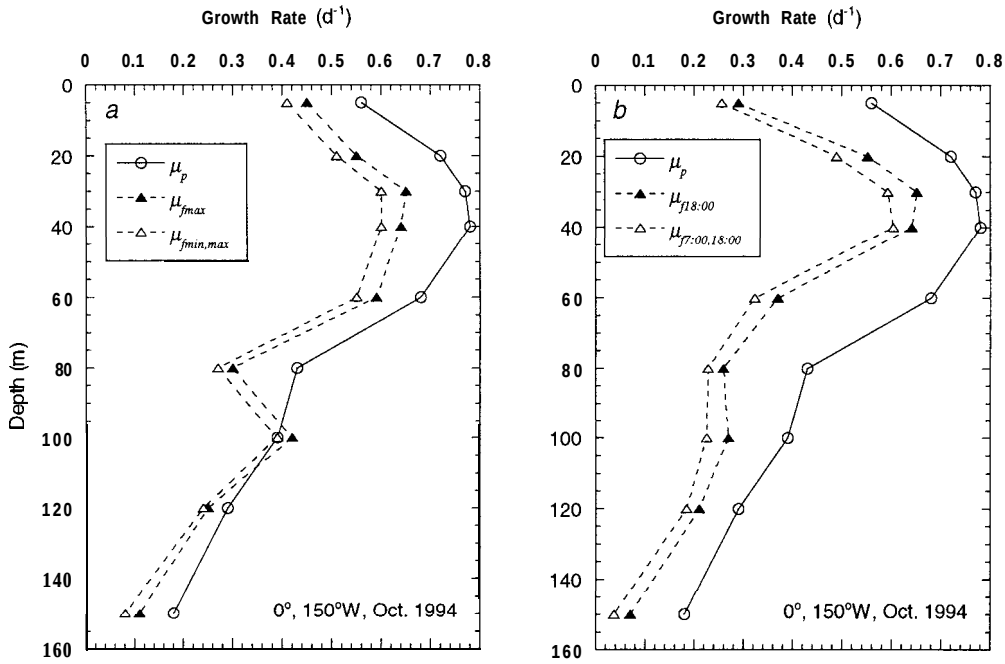

Figure 2. Comparison of (a) $\mu_{f\max}, \mu_{f\min,\max}$, and μ_p and (b) $\mu_{f1800}, \mu_{f0700,1800}$, and μ_p of *Prochlorococcus* from a diel sampling collected from the central equatorial Pacific (150°W) during the FLUPAC cruise in October 1994 [*Liu*, 1995]. The $\mu_p, \mu_{f\max}, \mu_{f\min,\max}, \mu_{f1800}$, and $\mu_{f0700,1800}$ terms are defined in the notation section.

(DNA staining with Hoechst 33342 after ***Monger and Landry*** [1993]; ***see Landry et al.*** [1996] for detailed descriptions of sample collection and analytical protocols). For the present study we reanalyzed the listmode files by first projecting the data for the ***Prochlorococcus*** population to a set of single-parameter histograms and converting the histograms of log-blue (DNA) fluorescence to ASCII format using CYTOPC software [*Vaulot*, 1989]. The integrated log-blue fluorescence data were then converted to a linear scale using the following equation

$$X_{\mathrm{Lin}} = \mathrm{A} \times 10^{B} \times X_{\mathrm{Log}}/\text{total channels} \qquad (4)$$

where X_{Lin} and X_{Log} are the signal channels in linear and log scale and A and B are coefficients for the logarithmic decadal scale (e.g., A = 1 and $B = 3$ corresponds to a 3 decade logarithmic scale). For the photomultiplier tube (PMT) amplifier of log-blue fluorescence in our flow cytometer, A and B were 0.18 and 3.16, respectively. The rebuilt, linear blue fluorescence histograms were analyzed with MCYCLE (Phoenix Flow Systems, San Diego, California) to compute the percentage of ***Prochlorococcus*** cells in the S and G_2 phases.

Growth rates of ***Prochlorococcus***, μ_{f1800} and $\mu_{f0700,1800}$ were computed using (2) and (3), respectively. Growth rates were integrated throughout the depth range of positive growth using the formula described by *Vaulot* ***et al.*** [1995] that weights division rates by cell concentrations at each depth:

$$\mu_{\mathrm{int}} = \ln \left[\int N_{1800}(z) e^{\mu(z)}\, dz \Big/ \int N_{1800}(z)\, dz \right] \qquad (5)$$

where z is the water depth, $\mu(z)$ is the growth rate estimate at depth z, and $N_{1800}(z)$ is the cell concentration of *Prochlorococcus* at depth z at ~1800 LT.

Depth-integrated rates of daily carbon production of *Prochlorococcus* were estimated from cell concentrations in dusk samples and cell division rates according to

$$P = C_{\mathrm{cell}} \int N_{1800}(z)[e^{\mu(z)} - 1]\, dz \qquad (6)$$

where C_{cell} is the intracellular carbon content of *Prochlorococcus*, estimated as 53 fg C cell^{-1} ***[Campbell et al.,*** 1994]. In (5) and (6) we used cell concentrations from the 1800 LT sampling as approximations of the minimum cell concentrations just before division. Primary production estimates from the ^{14}C assimilation method and nutrient data were obtained from JGOFS data system available at http://www1.whoi.edu/eqpac.html [see also ***Barber et al., 1996; Archer et al.,*** 1996].

3. Results and Discussion

3.1. Comparison of Computational Methods

To assess differences in growth rate estimates among computational methods, we compared $\mu_p, \mu_{f\max}, \mu_{f\min,\max}, \mu_{f1800}$ and $\mu_{f0700,1800}$ for ***Prochlorococcus*** using depth profiles collected over a diel cycle in the central equatorial Pacific in October 1994 ***[Liu,*** 1995; ***Liu et al.,*** 1997]. The $\mu_{f\max}$ and $\mu_{f\min,\max}$ values were calculated from (2) and (3), respectively, using the observed maximum f_{S+G_2} during diel sampling. The results show that μ_p estimates exceed $\mu_{f\max}$ by ~0.1 d^{-1} throughout the upper 80 m of the water column (Figure 2). It was anticipated that $\mu_{f\max}$ would underestimate μ_p because of imperfect synchrony in the natural dividing population ***[Vaulot,*** 1992] and that the discrepancy would be exaggerated if limited sampling failed to hit the real peak of cells in the $S + G_2$ phases. On the other hand, inaccuracies in the estimate of t_{S+G_2} due to sampling frequency and high "background" f_{S+G_2} during the nondivision period could also have caused μ_p to

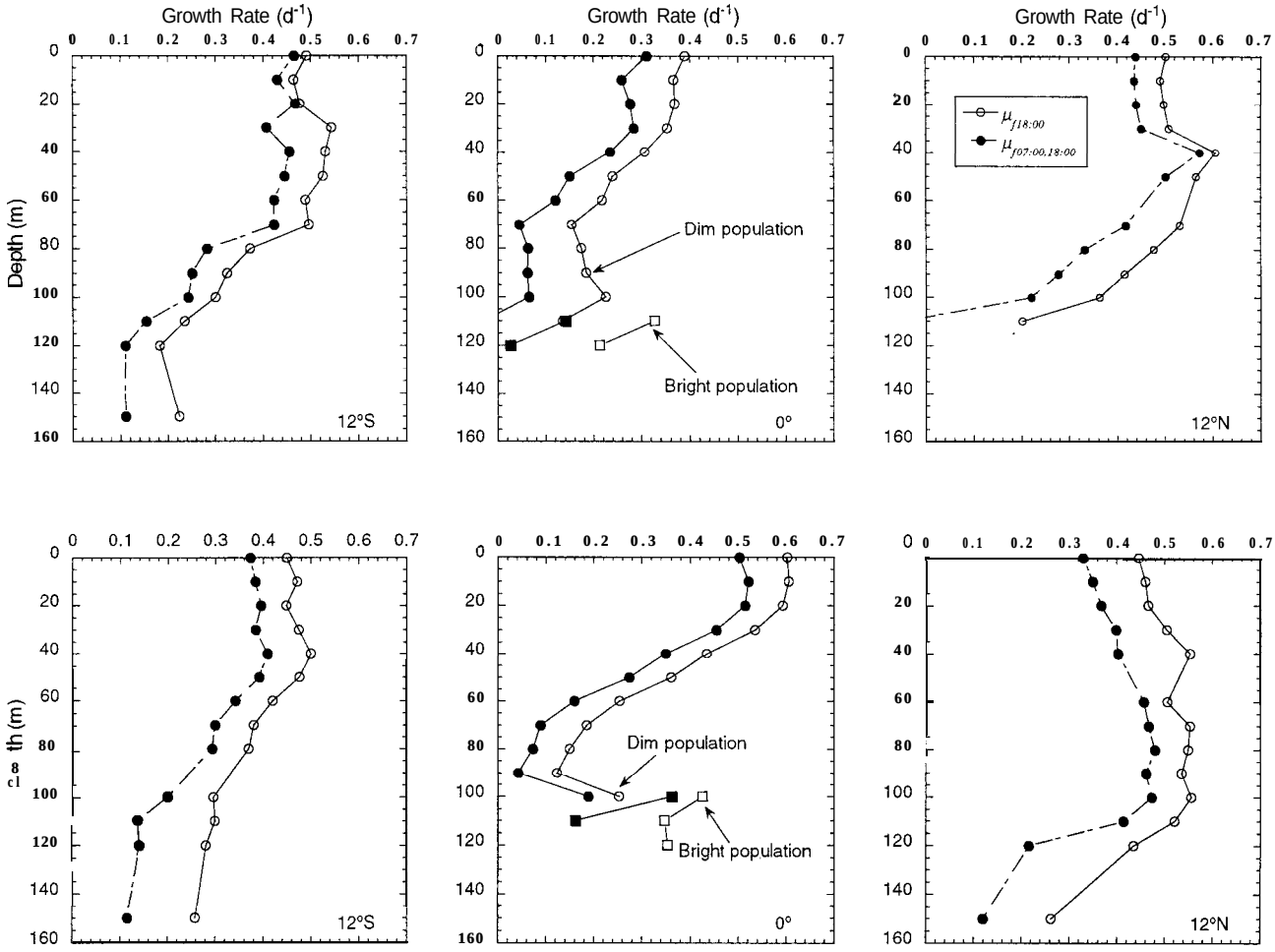

Figure 3. Examples of depth profiles of ***Prochlorococcus*** growth rate calculated with $\mu_{f,800}$ and $\mu_{f0700,1800}$ approaches from three stations on the 140°W transect during (top) El Niño and (bottom) normal upwelling conditions, the TT007 and TT011 cruises, respectively.

overestimate the true growth rates of ***Prochlorococcus*** [*Liu et al.,* 1997]. In comparing the $\mu_{f\max}$ method with its μ_{f1800} proxy for this data set the latter calculation underestimated $\mu_{f\max}$ by as much as 37% at the surface and below 60 m (Figure 2b). The differences between the growth rate estimates from (2) and (3) were generally smaller, implying that only a minor fraction of the cells were still dividing in the dawn samples.

In the EqPac data set we observed few, if any, G_2 cells in 1800 LT samples from the upper layers of oligotrophic regions, indicating that cell division had not yet occurred. In mesotrophic equatorial waters, however, a significant fraction of the near-surface cells were already in the G_2 phase at 1800 LT. This difference in timing may explain the inconsistent pattern of ***Prochlorococcus*** abundance between morning and evening samplings noted in the equatorial Pacific [*Landry et al.*, 1996]. ***Prochlorococcus*** were less abundant in the evening (~1800 LT) than in the morning (~0700 LT) in oligotrophic regions at both ends of the transect, and the reverse was true near the equator.

Light-dependent dephasing of the cell cycle may be a strategy to avoid damage from high irradiance, including UV penetration [*Vaulot et al.,* 1995]. The depth of the surface layer that shows the delay of S and G_2 phases extends deeper in oligotrophic regions as the result of deeper light penetration in the clearer water (Figure 1), and we have noticed that the S phase starts later in oligotrophic compared to mesotrophic waters [*Liu et al.,* 1997]. In addition to environmental conditions the difference in timing of the maximum S + G_2 among geographic locations may also be related to strain variations. Laboratory experiments have shown that different strains react differently in photosynthetic performance and growth kinetics to light intensity and quality [*Partensky et al., 1993; Moore et al.,* 1995]. Experiments have also demonstrated that *Synechococcus*, a close relative of ***Prochlorococcus,*** entered the S phase earlier when phosphorus was added to a P-limited natural population [*Vaulot et al.,* 1996]. In addition, diel samples from on-deck incubations in oligotrophic waters of the Arabian Sea revealed that ***Prochlorococcus cells*** enter S phase earlier in shipboard bottle incubations compared to parallel conductivity-temperature-depth (CTD) sampling (H. Liu, unpublished data, 1997). This implies that the vertical mixing within the surface mixed layer may play a role in regulating the cell cycle timing of ***Prochlorococcus.*** If the ***Prochlorococcus cell*** cycle follows the block point model proposed by *Spudich* ***and Sager*** [1980], regional and seasonal variations in day length should also affect dephasing. Because of the complex dephasing of the ***Prochlorococcus cell cycle,*** it is impossible for a single time point sample to catch the maximum of S + G_2 phases at all

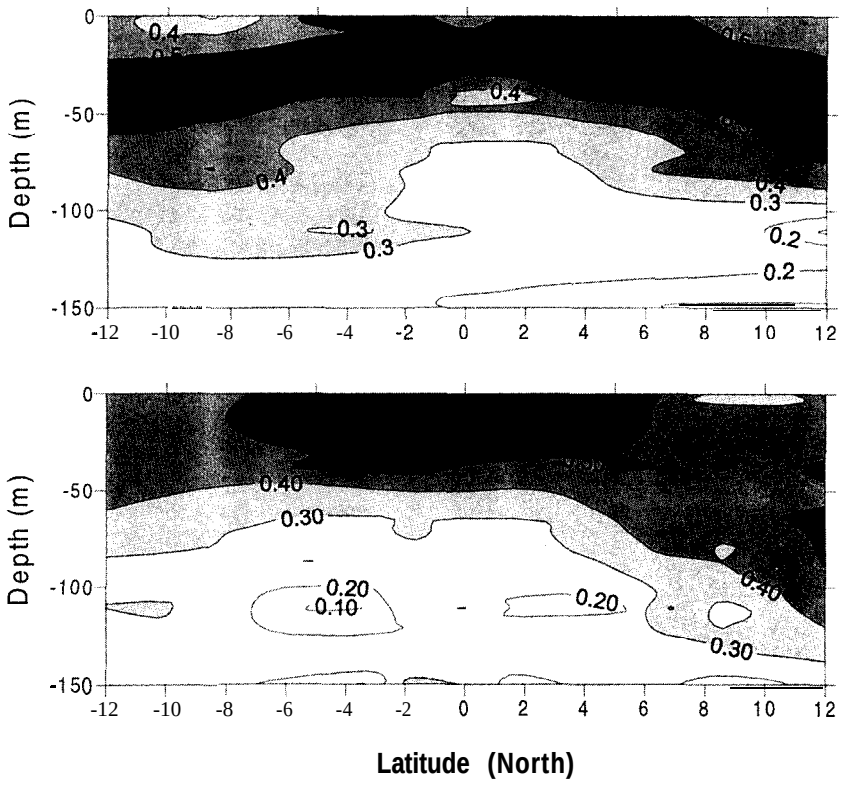

Figure 4. Contour plots of μ_{f1800} for ***Prochlorococcus*** along the 140°W cross-equatorial transect from 12°N to 12°S during (top) February-March and (bottom) August-September 1992.

depths at a given station. Repeated sampling around the expected peak time would enhance the probability of catching the real peak of f_{S+G_2} at different depths.

3.2. Seasonal and Spatial Variations in *Prochlorococcus* Growth Rates

Growth rate estimates increased slightly with depth to a deep maximum at stations from 7" to 12°N (Figure 3). The subsurface peak was better developed during the upwelling cruise around 40-100 m. From 5°S to 5°N the maximum growth rates of ***Prochlorococcus*** occurred in the 10–30 m depth range. Growth rates decreased sharply with depth below the maximum, except at 0" and 1°S during El Niño, where the decrease below 30 m was more gradual. At the southern end of the transect (12°S) the depth profile of the ***Prochlorococcus*** growth rate was similar to that at the northern end, except that the depth of the maximum growth rate was shallower (-50 m) during normal upwelling. One common feature on both cruises was an apparent secondary maximum in ***Prochlorococcus*** growth rate between 90 and 120 m. At stations near the equator we observed two well-separated populations of *Prochlorococcus* around 100 m. The dim (low-chlorophyll) population had a lower growth rate and disappeared below 100 m, whereas the bright (high-chlorophyll) population grew faster and extended deeper (Figure 3). These and similar observations [e.g., ***Campbell and*** *Vaulot*, ***1993; Reckermann and*** *Veldhuis*, 1997] suggest that multiple ***Prochlorococcus*** populations in the deep chlorophyll maximum layer may be a common feature of tropical and subtropical oceans.

Seasonal and spatial differences in ***Prochlorococcus*** growth rates were observed between cruises. Contour plots reveal higher rate estimates in the surface water around the equator and during normal upwelling conditions (Figure 4). Maximum growth rates in the oligotrophic waters generally occurred at a deeper depth, with higher rates during El Niiio conditions. Depth-averaged growth rates of ***Prochlorococcus*** along the 140°W transect displayed similar patterns for both cruises (Figure 5). Maximum depth-integrated rates were observed at 1°S, in what is typically the Equatorial Divergence. The maximum growth rate at 1°S matched the highest measured rate of primary production during the 1992 El Niiio-Southern Oscillation (ENSO), but not later during normal upwelling conditions, when larger phytoplankton increased in relative importance [*Bidigare* ***and Ondrusek, 19963.*** ***Prochlorococcus*** growth rates were usually high at the northern end of the transect (7°–12°N), where population abundances were highest [*Landry* ***et al.,*** 1996], and they decreased toward the equator as the distribution of ***Prochlorococcus*** shifted closer to the surface. Unlike the El Niño cruise, when the minimum in *Prochlorococcus* growth rate occurred at the equator, the lowest growth during the normal upwelling cruise was in the vicinity of a convergent front at 2°N where a large biomass of buoyant diatoms had accumulated ***[Yoder et al.,*** 1994; ***Barber et al.,*** 1994]. As noted by *Landry* ***et al.*** [1996], ***Prochlorococcus*** abundance was also markedly depressed at that front.

The percentage of S and G_2 cells in the 0700 LT samplings were low in the surface waters but increased with depth. This trend may reflect an increasing proportion of cells unable to finish their S or G_2 phases before dawn, especially in deeper waters below the 0.1% light level. For both seasonal transects the percentages of ***Prochlorococcus*** cells in the S + G_2 phases in the dawn samples (f_{0700}) were ~5%–10% at most stations and as high as 20% at a few stations. These percentages were

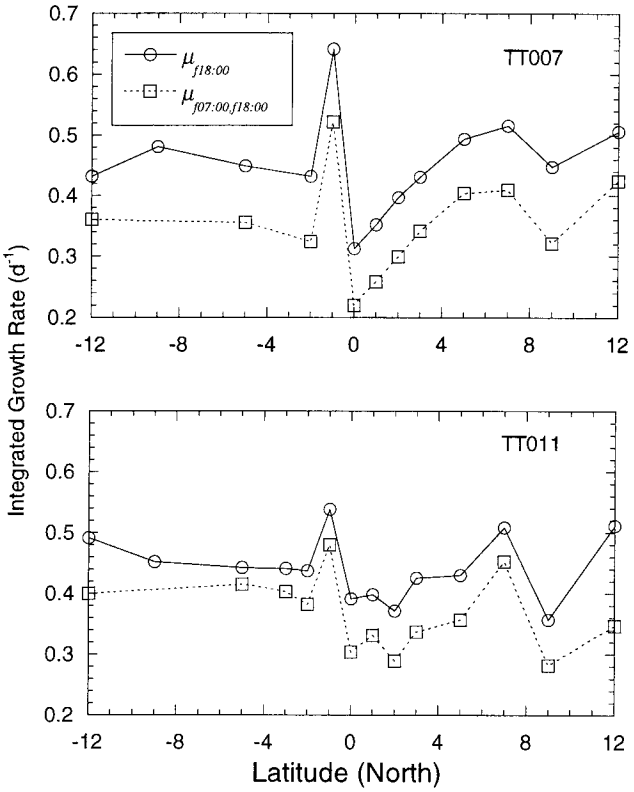

Figure 5. Depth-integrated growth rates of *Prochlorococcus* along the 140°W transect during EqPac El Niño (February–March 1992) and normal upwelling conditions (August–September 1992). Growth rates were integrated according to (5) weight division rates by cell concentrations just before division (here we used the cell concentrations of *Prochlorococcus* from the 1800 LT samples to approximate the minimum).

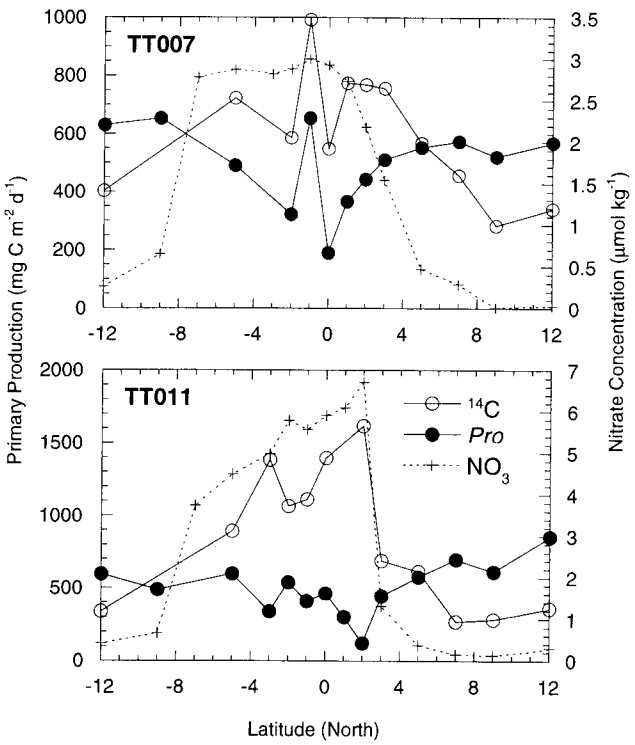

Figure 6. Nitrate concentration in surface water and total primary production and production of *Prochlorococcus* in the upper 150 m water column along the 140°W cross-equatorial transect during February–March (TT007) and August–September (TT011) cruises. Primary production was measured by the ^{14}C method and integrated to 0.1% light level (JGOFS data system at http://www1.whoi.edu/eqpac.html [*Barber et al.*, 1996]). Carbon production of *Prochlorococcus* was calculated from μ_{f1800}.

much higher than the f_{min} observed in diel sampling at Station ALOHA (22°45′N, 158°W) in the subtropical North Pacific (2% on average). It is not known whether these cells were arrested or just proceeding slowly through the cell cycle because we do not have midday samples for comparison. On the basis of previous observations from diel sampling at different locations, f_{min} usually occurs around noon right before the start of a new burst of DNA replication and cell division. Since the calculations of μ_{f1800} are already conservative because they generally fail to hit the real f_{max}, including a potentially too high correction for f_{min} only exacerbates the underestimate. Thus, for estimating the carbon production of *Prochlorococcus* according to (6) we used μ_{f1800}.

3.3. Contribution of *Prochlorococcus* to Total Primary Production

Estimated carbon production of *Prochlorococcus* along the 140°W transect was, in general, inversely correlated with nitrate concentration in the surface water and the rate of primary production from ^{14}C uptake (Figure 6). Higher production of *Prochlorococcus* occurred in the less productive oligotrophic areas, while lower *Prochlorococcus* production was observed in high-nutrient/low-chlorophyll (HNLC) equatorial waters where total primary production was higher (Figure 6). One exception was observed at 1°S during El Niño where both *Prochlorococcus* and ^{14}C primary production were highest among all stations and a large fluctuation in primary production between 0° and 2°S appeared to be mostly due to *Prochlorococcus* (Figure 6). As expected from the low abundance and specific growth rate of *Prochlorococcus* at 2°N during TT011, the lowest contribution of *Prochlorococcus* to total primary production was at the diatom-dominated convergent front.

Prochlorococcus production estimates consistently exceeded measured total primary production at the most oligotrophic stations along the 140°W transect (Figure 6). Since the *Prochlorococcus* production estimates were based on presumably conservative calculations of growth rate by the μ_{1800} method we consider below several alternative factors that may have contributed to these discrepancies.

First, calculations of *Prochlorococcus* carbon production by (6) should be based on minimum cell concentrations right before cell division. Mean cell abundances could have been overestimated because neither dawn (0700) nor dusk (1800) sampling times coincided with the minimum [*Vaulot and Marie*, this issue]. Given the lack of a clear pattern in *Prochlorococcus* abundances in dawn and dusk samples [*Landry et al.*, 1996] and the significant fraction of G_2 phase cells in many of our samples, we believe that the minimum concentration of *Prochlorococcus* occurred before the 1800 sampling, especially in the nutrient rich equatorial waters where *Prochlorococcus* entered S and G_2 phases earlier. However, this overestimate of cell abundance was probably not the major cause of the discrepancy between production estimates because it occurred mostly

where the *Prochlorococcus* contribution to primary production was the lowest.

The cellular carbon content of *Prochlorococcus* may be another source of error in our calculations. Our mean carbon estimate (53 fg C cell^{-1}) was derived from a similarly sized culture of *Synechococcus*, but it was very close to the only directly measured value for *Prochlorococcus* of 49 fg C cell^{-1} [*Cailliau et al.*, 1996]. Nonetheless, the appropriate estimate for our rate calculations is not the mean carbon per cell but the carbon content for newly divided cells. Grown under a light-dark cycle, *Synechococcus* displays a two-fold diel variation in cellular carbon content, with the minimum carbon after completion of cell division during the late dark period [*Waterbury et al.*, 1986]. Assuming that a similar diel variation in cell carbon applies to *Prochlorococcus*, the value for newly divided cells should be one third lower than the average, or ~35 fg C cell^{-1}. *Prochlorococcus* production estimates would thus be reduced accordingly.

In addition to the potential measurement problems noted above, growth rate– and ^{14}C-derived estimates of production are inherently difficult to compare directly. For example, our estimates of *Prochlorococcus* production account for the cells that will be lost to grazers over the diel cycle [*Vaulot et al.*, 1995]. In contrast, grazing during the ^{14}C incubation reduces the total particulate carbon fixed by the amount ingested by consumers and subsequently remineralized or excreted as ^{14}C-labeled dissolved organic carbon (DOC). If we assume that grazers in the tightly coupled microbial food webs of open-ocean systems maintain steady state by removing half of the newly fixed phytoplankton production every 24 hours and retain only 30% of that ingested material for their growth, then ^{14}C particulate production will underestimate true phytoplankton net production by ~25%.

Despite the potential inaccuracies in production estimates which exaggerate the contributions of *Prochlorococcus* to total production we can conclude from Figure 7 and Table 1 that *Prochlorococcus* was relatively more important in oligotrophic areas of the 140°W transect and less important in the HNLC equatorial waters. The ratio of *Prochlorococcus* carbon production from our estimates to total primary production measured by the ^{14}C method decreased with a negative log function as the nitrate concentration in the surface waters increased (Figure 7a). Although a single curve can be imposed to data from both cruises ($y = 0.997 - 0.805 \log(x)$; $R = 0.80$), it is clear that the relationship between nitrate concentration and *Prochlorococcus* contribution varies between normal upwelling and El Niño conditions (Figure 7a). The ratio of *Prochlorococcus* production to total ^{14}C primary production also decreased as a power function with increasing total ^{14}C primary production estimates (Figure 7b). The inverse correlation between nitrate concentration and the percentage of production due to *Prochlorococcus* supports the hypothesis that *Prochlorococcus* increases in relative importance as the euphotic layer of the water column becomes more oligotrophic [*Liu et al.*, 1997]. The lower specific growth rate near the equator could be related to copper toxicity as recently upwelled seawater contains high levels of free Cu [*Coale and Bruland*, 1990] which inhibits *Synechococcus* [*Brand et al.*, 1986; *Moffett et al.*, 1990] and probably *Prochlorococcus* as well [*Mann et al.*, 1997]. It has been generalized that primary production in the eastern tropical Pacific was high during normal upwelling and low during El Niño [*Barber and Chavez*, 1983], whereas the opposite was true for the North Pacific subtropical gyre [*Karl et al.*, 1995]. In the present study, primary productivity increased substantially near the equator and decreased slightly in oligotrophic waters (7°–12°N and 12°S) during normal upwelling in comparison to El Niño conditions, and the opposite trend was observed for the *Prochlorococcus* contribution to production (Table 1). The observed differences in relative importance of *Prochlorococcus* between El Niño and upwelling conditions was primarily driven by variations in ^{14}C primary productivity as neither *Prochlorococcus* abundances [*Landry et al.*, 1996] nor growth rates (Table 1) varied substantially as a function of ecosystem state.

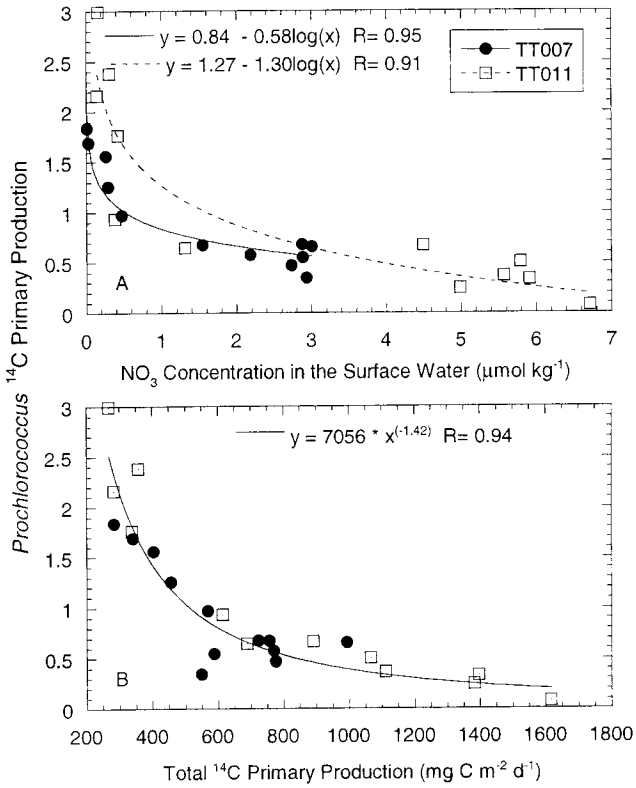

Figure 7. The ratio of *Prochlorococcus* production estimated from f_{1800} to total primary production measured by the ^{14}C technique plotted as a function of (a) NO_3 concentration in surface water and (b) total ^{14}C primary production.

Notation

t_d duration of terminal phase, hours (equivalent to t_{S+G_2} in this paper).
t_p duration of photoperiod (24 hours usually), hours.
S DNA synthesis phase.
G_2 gap at the end of the cell cycle before cytokinesis.
t_{S+G_2} duration of S and G_2 phases, hours.
f_{min} minimal fraction of cells in terminal phase over t_p.
f_{max} maximal fraction of cells in terminal phase over t_p.
f_{0700} fraction of cells in terminal phase at 0700 LT.

Table 1. Contribution of ***Prochlorococcus*** to Total Primary Production in Different Regions Along the 140°W Cross-Equatorial Transect

	Normal Upwelling			El Niiio Condition		
	7°–12°N	5°N–5°S	12"s	7°–12°N	5°N–5°S	12°S
NO, concentration in surface water, μmol kg^{-1}	0.20	4.58	0.42	0.11	2.38	0.26
Prochlorococcus growth rate, d^{-1}	0.46	0.43	0.49	0.49	0.44	0.46
Total ^{14}C primary production, mg C m^{2} d^{-1}	296	1117	373	336	695	403
Prochlorococcus contribution, %	79	16	59	53	21	52

The percentage of ***Prochlorococcus*** contribution has been justified by multiplying ^{14}C primary production values by 2 (D. M. Karl), and ***Prochlorococcus*** production estimates by two thirds (see discussion in text). All rates are integrated to the depth of 0.1% light level.

f_{1800} fraction of cells in terminal phase at 1800 LT.

f_{S+G_2} fraction of cells in S and G_2 phases.

μ_p average growth rate over the photoperiod t_p, h^{-1}.

$\mu_{f\max}$ estimate of growth rate from $f_{\max}$ (equation (2)), h^{-1}.

$\mu_{f\min,f\max}$ estimate of growth rate from $f_{\min}$ and $f_{\max}$ (equation (3)), h^{-1}.

μ_{f1800} estimate of growth rate from f_{1800} (equation (2)), h^{-1}.

$\mu_{f0700,f1800}$ estimate of growth rate from f_{0700} and f_{1800} (equation (3)), h^{-1}.

μ_{int} depth-integrated growth rate, d^{-1}.

$N_{1800}(z)$ cell concentration at depth z at 1800 LT.

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