Biogeochemical Conditions in the Equatorial Pacific in Late 1994

New Production, Oct 15, 1994 (mmol m\(^{-2}\) d\(^{-1}\))

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Picophytoplankton dynamics in the equatorial Pacific:
Growth and grazing rates from cytometric counts

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Abstract. During a 7 day time series in the central equatorial Pacific (0°, 150°W, October 1994) flow cytometry measurements were performed four times per day throughout the surface layer. Cell abundance of the major algal groups, Prochlorococcus, picoeukaryotes, and Synechococcus, exhibited a well-marked diel rhythm within the mixed layer (50-60 m deep) whereas the signal became unclear below. Cell numbers were minimum at the midday or dusk stations and maximum in the middle of the night. The amplitude of the diel variations in the mixed layer, as observed, was of the order of 40% of the daily minimum and varied significantly during the time series. For each cell group the abundance variations implied that each day, cell division was rather tightly synchronized and that grazing was efficiently competing growth. Assuming that abundance variations were only due to these two processes, a simple model was designed to estimate their rates. The division rates averaged 0.53 (±0.18) d⁻¹ for Prochlorococcus, 0.42 (±0.13) d⁻¹ for the picoeukaryotes, and 0.56 (±0.21) d⁻¹ for Synechococcus in the mixed layer and decreased rapidly below. The rates varied significantly along the time series for all groups whereas growth and grazing closely balanced at the day scale. The estimates compared well with those obtained using various methods during the time series and previously in the equatorial Pacific. Primary production was tentatively predicted from the growth rates. Prochlorococcus, the picoeukaryotes, and Synechococcus contributed 57%, 33%, and 10% of the picoplankton total, and the predictions were consistent with the ¹⁴C measurements during the time series.

1. Introduction

Marine primary production is a key process for the understanding and the prediction of the biogeochemical fluxes exchanged within the surface layer, with the atmosphere, and with the deep ocean. It involves a diversity of processes, which vary over a huge range of timescales and space scales, from minute changes in local physiological rates to interannual variations at the basin scale. Its assessment, which is at the core of Joint Global Ocean Flux Study (JGOFS), involves therefore numerous methods. Ocean color (Coastal Zone Color Scanner (CZCS)) has supported global-scale estimates [Longhurst et al., 1995; Antoine et al., 1996], and coupled dynamical/biological models allowed its prediction at the basin scale [Sarmiento et al., 1993; Stoens et al., this issue] or addressed its response to mesoscale dynamics [e.g., Levy et al., 1998]. High-frequency variability (from hours to days) has to be studied at the laboratory or during in situ time series. Daily primary production was recently estimated from diel variations in optical properties [Gardner et al., 1993; Stramska and Dickey, 1992; Clairet et al., this issue] and from flow cytometry diel data (cell abundance and DNA cycle measurements) [Vaulot et al., 1995; Liu et al., 1997]. These are promising approaches, as alternatives to the sometimes confusing ¹⁴C incubations [e.g., Maestrini et al., 1993]. In the equatorial Pacific, diel variations are significant [e.g., Cullen et al., 1992]. Another typical feature there is the close coupling between primary production and its consumption by grazing [Cullen et al., 1992; Landry et al., 1997]. Short-term variability is all the more relevant in this region since the variations at longer timescales, e.g. seasonal, are weak. The variation range of the growth and grazing budget, as settled at the scale of 1 to a few days, would hold for long periods over large areas. In October 1994, the Flux dans l'ouest du Pacifique équatorial (FLUPAC) cruise was performed in the western half of the Pacific as part of the JGOFS-France program Elude de processus dans l'Océan Pacifique équatorial (EPGE). During a 7 day equatorial time series (ETS) at 150°W, diel variations in the algal cell abundance were studied by flow cytometry. The present study aims at inferring picoplankton dynamics from these variations. It is as follows. Section 2 is dedicated to the in situ observations. The general conditions in the region at the time of the ETS are briefly recalled. Then the vertical structure of the surface layer and the diel rhythm in the vertical mixing at the ETS are briefly described. Finally, the diel variations in the cell abundances are analyzed and interpreted in terms of cell division and grazing. Section 3 is dedicated to an estimate of growth and grazing rates based on this interpretation. A simple model is designed and applied to the abundance data at the ETS, and the results are compared to the literature. In section 4, methods and results are discussed, and using the model results, primary production is tentatively assessed. The paper ends with a few concluding remarks.

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2. Observations at 0°, 150°W

2.1. Measurement Sampling and Techniques

During the ETS, hydrocasts were carried out six times a day at 0300, 0700, 1100, 1500, 1900, and 2300 LT. Temperature, salinity, and density were obtained using a Sea-Bird SBE 911+ Conductivity temperature depth (CTD) and the companion software. Niskin bottles (12 L) were used for nutrient and pigment analysis at 12 depths between 0 and 150 m. Nitrate was measured according to Oudot and Montel [1988], and pigments were measured according to Neveux and Lantoine [1993]. Flow cytometry was operated four times a day on the 0300, 1100, 1900 and 2300 LT stations every 10 m from the surface (excepted at 10 and 90 m). The measurements were performed within 2 hours after sampling on 0.1 mL water volumes with a fluorescence activated cell sorter scan (FACScan) flow cytometer (Becton-Dickinson) as described by Blanchot and Rodier [1996]. The apparatus was installed in a dark temperature-controlled laboratory. GF/F-filtered deep water (1000 m) was used as a sheath fluid, and 2 µm beads were used as internal standard. The data were treated with the Becton-Dickinson LYSYS-II software and analyzed with the Cytowin software [Vaulot, 1989]. Only the cytometric counts (cells mL⁻¹) are used for the present study. Light scattering and fluorescence measurements, partly presented by Blanchot et al. [1997], will not be considered here.

2.2. General Conditions and Mean Vertical Structures

The general situation of the western and central tropical Pacific at the time of the FLUPAC cruise is described by Stoens et al. [this issue]. The equatorial time series station at 150°W (7 days, from October 19 to 25) followed the equatorial transect described by Eldin et al. [1997], and the general conditions at this station were similar to those in the eastern end of the transect. At 150°W the superimposed effects of a declining downwelling Kelvin wave and of moderate tropical instability waves had been altering the "typical" equatorial upwelling efficiency. The meridional component controlled the surface velocity with slow northward (days 1 and 2) and then southward flows. The surface zonal flow associated with the Kelvin wave, weakly eastward, extended to the Equatorial Undercurrent so that the vertical shear was unusually low for the region. During the ETS, moderate winds (about 6 m s⁻¹) blew from the SE with a maximum on day 1 (9 m s⁻¹) and a minimum between days 3 and 4 (<4 m s⁻¹). Nebulosity was low (3/8 on average) with a maximum on day 1 (6/8 at noon) and a minimum on day 4 (<2/8). The main thermocline was centered at 70 m, and the overlaying layer temperature was higher than 27°C and the salinity was higher than 35.1 practical salinity units (psu). The density was on average homogeneous down to 50-60 m (Figure 1) with a significant variability near the surface resulting from the convective cycle (see below). The nitracline was situated between 60 and 70 m, and the NO₃

![Figure 1](image-url)
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Figure 2. Evolution of the water density at selected depths (0, 20, 40 and 60 m) during the 7 days of the ETS (conductivity-temperature-depth (CTD)) profiles at 0300, 0700, 1100, 1500, 1900, 2300 LT. The shaded areas mark the night periods (from 1800 to 0600 LT).

concentration above was about 3 μM (Figure 1). More precisely, the concentration was a little over 3 μM until day 5 when it started to decrease and was of 2.5 by the end of day 7 (not shown). Chlorophyll concentration was ~0.35 mg m⁻³ near the surface and decreased rapidly below a smooth maximum (Figure 1). As occurred for NO₃, the concentration decreased from day 5 and was of 0.28 by the end of day 7 (not shown). As observed by flow cytometry, the picophytoplankton consisted of three main groups, *Prochlorococcus* sp., *Synechococcus* sp., and picoeukaryotes. Cell abundances were high and rather homogeneous down to 50-60 m and rapidly decreased below, leveling at 100 m for 10% of the surface values (Figure 1). These vertical distributions are similar to recent observations in the equatorial upwelling [e.g. DuRand and Olson, 1996; Binder et al., 1996] and are intermediate between typical mesotrophic and oligotrophic distributions [Partensky et al., 1996].

2.3. Diel Rhythm of the Vertical Mixing Along the Time Series

The evolution of the water density during the ETS is presented in Figure 2 for selected depths. Each day, a diurnal stratification began from the surface with sunrise (at 0600 LT). The maximum density gradient was observed at 1500 LT between 0 and 25 m. A weak delayed signal is still visible in the 40 m curve of Figure 2. Destratification closely followed, and nocturnal convection (buoyancy frequency was minimum between 2300 and 0300 LT) was always intense enough to rehomogenize the water before the next dawn (the density was constant down to 50-60 m at the 0700 LT hydrocast). Such a deep nocturnal mixed layer has been previously observed in the central Pacific [e.g. Peters et al., 1994; Lien et al., 1995]. The diurnal stratification was variable from day to day: the daily maximum density difference between 0 and 25 m was weakest on days 1 and 2 (0.05 units) and strongest on day 3 (0.13 units). This variability should be a direct response to the meteorological forcing as minimum and maximum stratification corresponded to the minimum and to the maximum in both wind and cloud cover, respectively. Below the mixed layer, on entering the main thermocline, the density varied irregularly with time (not shown in Figure 2), likely

Figure 3. Diel variations in the cell abundance of *Prochlorococcus* ((a) 10⁶ cells mL⁻¹) of the picoeukaryotes ((b) 10⁵ cells mL⁻¹), and of *Synechococcus* ((c) 10⁴ cells mL⁻¹) at selected depths (0, 40, and 80 m) during the 7 days of the ETS (cytometric measurements at 0300, 1100, 1900, and 2300 LT). The shaded areas mark the night periods (from 1800 to 0600 LT).
because of internal waves. On day 5 the mixed layer maximum density began to decrease (0.06 units at 60 m over the last 3 days). This was because of a salinity decrease (from 35.28 to 35.10). The variations in salinity, nitrate, and chlorophyll from day 5 consistently suggest that a slightly different water mass was then sampled.

2.4. Diel Variations of the Algal Abundances Along the Time Series

Figure 3 presents the evolution of the cell abundances at selected depths over the 7 days of the time series. The most striking feature is a well-marked and generally regular diel cycling within the mixed layer. For Prochlorococcus the maximum values (up to $2 \times 10^5$ cells mL$^{-1}$) were generally measured at 2300 LT and the minimum values (down to $1 \times 10^3$ cells mL$^{-1}$) were measured at 1100 LT, except at the surface where it was usually at 1900 LT. For the eukaryotes our measurements do not indicate that the timing varied with depth in the mixed layer, as the maximal values (up to $7 \times 10^6$ cells mL$^{-1}$) occurred almost always at 0300 LT and the minimum values (down to $4.10^4$ cell mL$^{-1}$) occurred almost always at 1900 LT. For Synechococcus the daily increase always occurred between the 1100 and 1900 LT measurements. The diel signal disappeared below the mixed layer (as shown at 80 m in Figure 3) as its amplitude became rather weak and as it was very likely perturbed by the water vertical movements. For the three algal groups the maximum variations occurred near the surface and averaged 51% (±13) of the daily minimum for Prochlorococcus, 37% (±12) for the eukaryotes, and 50% (±28) for Synechococcus. These amplitudes varied significantly from day to day. They increased from day 1 to 4 (down to 40 m) and were strongly reduced for all groups on days 5 and 6 when the daily mean abundances were also the lower.

2.5. Interpretation of the Algal-Abundance Diel Variations

During the ETS the ship was drifting under the parallel actions of weak winds and weak currents in the surface layer. Horizontal advection is therefore not able to explain many of the features in Figure 3. The currents, however, changed on day 5, and the changes previously reported in all the observed parameters including the cell abundances (see sections 2.2 and 2.3) can only be explained by the advection of a different water mass. In this new water mass the diel rhythm was nevertheless present. Sedimentation is believed to be negligible for algal cells of a few micrometers or less. As reported above (section 2.3 and Figure 2), vertical mixing also obeyed a marked diel rhythm, but this process cannot explain more than the homogeneity of the cell distribution observed down to 50 m in the middle of the night (see also the mean profiles in Figure 1). The diel variations in the abundance therefore must be essentially due to biological processes. The succession of sharp increases within the mixed layer (Figure 3) implies that cell division occurred each day in a rather narrow time interval. Cytometer light scattering measurements (a proxy for the mean cell size of an algal group) were also performed at the ETS and support this interpretation [Blanchot et al., 1997], as shown by DuRand and Olson [1996]. In pelagic waters, viral lysis would be responsible for the daily disappearance of only a few percent of the algae [Suttle, 1994]. The decrease in the abundance that followed the division bursts at the ETS very likely occurred as the result of an active grazing. Several recent studies in the equatorial Pacific [Vaulot et al., 1995; Binder et al., 1996; Liu et al., 1997] based on flow cytometry and DNA cycle analysis show that the division of Prochlorococcus is tightly synchronized. Cells divide once a day within a period beginning between dusk (at the surface, when solar illumination has been high) or midafternoon (at depth) and ending in the middle of the night. The DNA data of Liu et al. [1997] obtained on the last day of the ETS indicate that the division of this algal group began ~1600 LT at 40 m and below and ~1800 LT at 0 m and that the process was completed in the middle of the night. As far as we know, no similar DNA analysis has been performed in situ for the other algal groups. What we know, or believe, about the in situ dynamics of their cell division thus solely relies upon the interpretation of abundance diel variations. Blanchot et al. [1997] and Vaulot and Marie [this issue] were able to follow such variations thanks to hourly measurements on day 5 of the ETS and 3 weeks later at 5°S, 150°W (respectively). Both studies concluded that the algae were dividing daily during a period of a few hours. The surface data of Blanchot et al. [1997] indicated that picoeukaryote division began shortly after the sunset (~1900 LT), and the data of Vaulot and Marie [this issue] indicated that it was somewhat later in the night (~2200 LT). The recent measurements of DuRand and Olson [1996] at 0°, 140°W also suggest such a synchrony and that the division began with nightfall (~1800 LT; DuRand and Olson [1996, Figure 2] for the "ultraplankton" data). The data given by Landry et al. [1996, Figure 2] at 1°N, 140°W indicate only that these cells did not divide during the day. As

| Table 1. Division Timing As a Function of Depth for the Three Algal Groups. |
|---------------------|---------------------|---------------------|---------------------|---------------------|
|                     | Prochlorococcus     | Picoeukaryotes      | Synechococcus       |
|                     | Observed Ranges     | Averaged Estimates  | Observed Ranges     | Averaged Estimates  |
|                     | (1-7)               | (3,4,6, and 7)      | (3,4, and 7)        | (3,4, and 7)        |
| 0, m                |                     |                     |                     |                     |
| t_d             | 16-18               | 16.4 ± 0.8          | 19-22               | 18.3 ± 0.7          |
| t_c             | 24-27               | 23.7 ± 0.8          | 25-30               | 25.1 ± 0.9          |
| ≥40, m            | 16                  | 15.2 ± 0.3          | 19-22               | 17.9 ± 0.5          |
| t_d             | 24-27               | 23.4 ± 0.6          | 25-30               | 25.4 ± 0.7          |
| t_c             | 12-14               | 11.5 ± 0.5          | 19-24               | 22.7 ± 0.9          |
| ≥40, m            | 12-14               | 11.1 ± 0.6          | 19-24               | 22.0 ± 0.6          |

The averaged estimates are at the equatorial time series (present study). The observed ranges in the equatorial Pacific were set up according to the results by 1, Vaulot et al. [1995]; 2, Binder et al. [1996]; 3, DuRand and Olson [1996]; 4, Landry et al. [1996]; 5, Liu et al. [1997]; 6, Blanchot et al. [1997]; 7, Vaulot and Marie [this issue].
regards *Synechococcus*, the daily increase began ~1400 LT for Vaulot and Marie [this issue] and around ~1200 LT for DuRand and Olson [1996], while the data given by Landry et al. [1996] indicate only that it began before 1800 LT. On the basis of these repeated observations it appears reasonable to assume that the sharp daily increase in the abundance of the picoeukaryotes and of *Synechococcus* at the ETS (Figure 3), was due (as for *Prochlorococcus*) to highly synchronized cell division. The division timings observed in the equatorial Pacific are summarized in Table 1. It is worth noting that *Synechococcus* division, as it began in early afternoon, fell into the 8 hour gap between our 1100 and 1900 LT measurements and was less well observed than for the two other algal groups.

3. Model-Based Estimates of Growth and Grazing Rates

3.1. Model and Method

On the basis of the previous interpretation (section 2.5) it was assumed that the cell abundance at the ETS varied only because of the processes of cell division and mortality (grazing). Under this assumption a simple model was designed to estimate the rates of both processes for each algal group. In the model the cell number \( N(t) \), varies over a time step \( dt \) by \( dN(t) \), according to

\[
dN(t) = [\mu(t) + g(t)]N(t)\ dt
\]

Grazing was assumed to proceed at a constant rate \( g \) (% h\(^{-1}\) or % d\(^{-1}\); this assumption will be discussed in section 4.2) whereas the instantaneous division rate, \( \mu \) (% h\(^{-1}\)) was assigned a Gaussian shape:

\[
\mu(t) = \mu_{\text{max}} \exp \left[-\frac{(t-t_{\text{di}})^2}{2\sigma^2}\right]
\]

with \( t_{\text{di}} = (t_{\text{d}} + t_{\text{gi}})/2 \), where \( t_{\text{d}} \) and \( t_{\text{gi}} \) are the division period beginning and ending times, respectively, and \( \sigma = (t_{\text{d}} - t_{\text{gi}})/2 e \), so that 99% of the divisions occur between \( t_{\text{d}} \) and \( t_{\text{gi}} \). The selected Gaussian shape accounts for the natural dispersion in the cell cycle period and is well suited for the case of tightly synchronized cell divisions [McDuff and Chisholm, 1982; Vaulot, 1992]. The aim was to estimate the four parameters \( \mu_{\text{max}} \), \( g \), \( t_{\text{d}} \) and \( t_{\text{gi}} \) for a given diel cycle. Diel cycles were defined as 1100-1100 LT periods, as beginning largely after the end of the division of the previous day and finishing before that of the next day. A diel cycle thus corresponds to five measurements (this will be discussed in section 4.1). Equation (1) was integrated over each cycle, and the parameter values that minimize the Rms distance between predicted and measured abundances were computed.

3.2. Results

3.2.1. A detailed example. In order to show in detail how the method copes with the data the diel cycle of *Prochlorococcus* at 0 m on day 1 of the ETS was selected as an example. The results of the computations are given in Figure 4. The relative Rms distance between predicted and measured cell numbers, \( \Delta \), is <1%, and the deviation in \( \mu_{\text{max}} \) or \( g \) is rather small (2% and 4% of their respective value). The daily division rate corresponding to the results in Figure 4 is \( \mu = 0.65 \text{ d}^{-1} \) and does not significantly differ from the estimated mortality (\( g = 0.66 \text{ d}^{-1} \)), as expected from the periodicity in the measured abundance for the selected example. The reconstructed diel cycle is compared to the data in Figure 4 (lower curve). As shown, the sampling missed the minimum abundance, estimated to occur at 1630 LT (1 hour after the beginning of the division), and the predicted minimum is ~20% lower than the measured one (at 1100 LT). In contrast, the 2300 LT measurement was close to the maximum abundance. If grazing had not proceeded during the division period (middle curve), the abundance would have increased (because of cell replication) by 92% (corresponding to \( \mu = 0.65 \text{ d}^{-1} \)). As the maximum relative variation in the data is 42% (between 1100 and 2300 LT), the "correction" achieved by the method is very significant. If no grazing had occurred from dawn (upper curve), the abundance would have been higher by ~30% at the beginning of the division, and the maximum would have been 1.5% higher than observed.

3.2.2. General results. The method was applied to the data at each depth from days 1 to 6 (on day 7 our measurements stopped at 2300 LT so that the last diel cycle is incomplete). For each algal group, 42 diel cycles were analyzed, 24 above 40 m and 18 below. For the 0-40 m layer the rates and the division times could be estimated in all cases. Below 40 m, only 20% of the cycles were amenable to the modeling, as was to be expected from the irregular variations at these depths (Figure 3). On the whole the agreement between the reconstructed cycles and the data was rather good. The \( \Delta \) values ranged between 0.2% and 14.8%.
rates averaged over the 0-40 m layer. For the three groups the rate variations reflect those reported in the abundance cycles (section 2.4 and Figure 3). For Prochlorococcus (Figure 5a), the growth rate increased during the first 4 days (by 35%), and grazing closely balanced division. Both the computed rates changed suddenly on day 5, with g twice higher than \( \mu \). As discussed further (section 4.5), the estimates for this day were probably biased because of an advective event and should be taken with caution. The rate values were closer again on day 6. The rates varied less with depth at the beginning of the ETS (±15% around the mean until day 4) than on the last 2 days (±50%). The estimated division times averaged 1554 LT (±0.8 hours) and 2330 LT (±0.6 hours) over the 6 days, with \( t_d \approx 1530\) LT on days 1-3 (see the results for day 1 in Figure 4) and ~1630 LT on days 4-6. For the eukaryotes (Figure 5), growth and mortality fluctuated in parallel during the 6 days. Although less regularly than for Prochlorococcus, their growth rate tended to increase during the first 4 days (by 60%) and the changes in both rates on day 5 are weaker. The vertical variability was also the highest on days 5-6. During the first 4 days their growth rates were significantly lower than those of Prochlorococcus (by up to a factor 2) and then became higher (by 30%-50%). The picoeukaryotes divided slightly later than Prochlorococciis at the ETS. Their estimated times averaged 1800 LT (±0.8 hours) and 2512 LT (±0.7 hours) over the 6 days (without significant tendencies). The results for Synechococcus (Figure 5) are very similar to those for Prochlorococcus, with average rates 10%-15% higher. Their division rate also increased from day 1 to 4 (by 60%), and both \( g \) and \( \mu \) were also probably misestimated on day 5 (these features are discussed in 4.5). The division times differed, however, as they averaged 1118 LT (±0.6 hours) and 2212 LT (±0.6 hours) over the 6 days, without significant day to day variations.

Figure 5. Depth averages (0-40 m) for the growth rate (solid symbols, left ordinate, \( d^{-1} \)) and for the mortality to growth rate ratio (open symbols, right ordinate, no units) during the ETS for (a) Prochlorococcus, (b) the picoeukaryotes, and (c) Synechococcus. The small symbols are the present study estimates. The larger symbols are the selective inhibitor technique (days 2 and 4) and relative grazing technique (day 6) results of H. B. Liu [Le Borgne and Gesbert, 1995] (see text). The bars are at plus or minus the standard deviation around the average.

and averaged 5% (±3%), and a typical dispersion of 10% in the rates was obtained. The values for Synechococcus were a few percent higher than for the other groups, probably because their afternoon division was less well resolved by the sampling. For Prochlorococcus and Synechococcus the estimated division and mortality rates were both in the range 0.2-0.9 \( d^{-1} \), and in most cases the two rates were similar. In the case of the picoeukaryotes the growth rates ranged between 0.2 and 0.7 \( d^{-1} \), the mortality ranged rates between 0.1 and 0.9 \( d^{-1} \), and as for the other groups, the corresponding values of the two rates were similar in most cases. The main features of the results are presented in Figures 5 and 6. Figure 5 compares the evolution throughout the ETS of the estimated

Figure 6. Vertical profiles of (a) the growth rate and (b) the grazing rate at the ETS. Solid symbols are the averages of the present study estimates for days 1-6 (solid circles, Prochlorococcus; solid triangles, picoeukaryotes; and solid squares, Synechococcus; the bars are at plus or minus the standard deviation). The open circles are from Liu et al. [1997] (from DNA analysis for Prochlorococcus on day 7).
The mean vertical profiles are presented in Figure 6. As shown, the mean growth rates did not vary greatly between 0 and 40 m except that the rate of *Prochlorococcus* was somewhat higher at 0 m (the influence of vertical mixing will be discussed in section 4.4). The relatively high standard deviations (15% to 40% of the averages) reflect the significant variations of the rates throughout the ETS (Figure 5). Below 40 m the averages are based on very few values (1-3) and are thus less reliable but indicate a decrease with depth. On average the rates were similar for *Prochlorococcus* and for *Synechococcus* and were higher than for the eukaryotes (by 20% to 45%). The estimated division timings are given in Table 1. *Prochlorococcus* began to divide around 1500 LT at 40 m and more than 1 hour later at the surface and had finished around midnight at all depths. The division timing of the eukaryotes and of *Synechococcus* did not show significant variations with depth (no more than with time, as previously noted). The grazing rates (Figure 6b) were close to the growth rates at all depths and their variability was similar (the standard deviations have not been reported).

### 3.3. Comparison With Other Estimates

Picophytoplankton dynamics have been studied on several occasions in the Pacific. The measurements of Vaulot et al. [1995] showed that *Prochlorococcus* division rates were maximal (0.73-0.93 d\(^{-1}\)) at 30 m and averaged 0.58 d\(^{-1}\) in the 0-150 m layer (DNA analysis at 0°-140°W). Liu et al. [1995] found that *Prochlorococcus* growth rates were 0.4-0.6 in near-surface waters and decreased to 0.1-0.2 at the 1% light level with a mortality of 20% to more than 100% of growth, while for *Synechococcus*, \( \mu = 1.06-0.17 \), and mortality was 43% to 87% of growth (selective inhibitor technique at station ALOHA). Landry et al. [1995a] obtained average rates at the surface of \( \mu = 0.24 \) and \( g = 0.70 \) for *Prochlorococcus*, \( \mu = 0.77 \) and \( g = 0.60 \) for the eukaryotes, \( \mu = 0.5 \) and \( g = 0.74 \) for *Synechococcus*, and \( \mu = 0.87 \) and \( g = 0.53 \) for total chlorophyll (dilution and relative grazing techniques at 1°N-1°S, 140°W in normal upwelling conditions). Landry et al. [1995b] found that picophytoplankton grew with \( \mu = 0.83 \) at 10-20 m and 0.34 at the basis of the mixed layer and that \( g \) was lower than \( \mu \) by 15% (chlorophyll dilution technique at 2°N-2°S, 140°W, in weak El Niño conditions, with N\(_0\), and chlorophyll levels similar to those at the ETS). Binder et al. [1996] obtained *Prochlorococcus* division rates of 0.28-0.52 d\(^{-1}\) at the surface and 0.49-0.64 between 15 and 30 m (DNA analysis, 0°, 140°W). Verity et al. [1996] observed that growth and grazing were maximum at 15 m and that growth was lower in El Niño conditions, with \( \mu = 0.4-0.6 \) in the mixed layer, than in normal conditions, with \( \mu = 0.8-1.1 \) (chlorophyll dilution technique at 0°, 140°W). Vaulot and Marie [this issue] measured a maximum rate of 0.8 at 35 m for *Prochlorococcus* (DNA analysis at 5°S, 150°W, 3 weeks after the ETS). Because of both natural and methodological causes, growth and mortality exhibit therefore a significant variability, and the estimates of the present study appear to be reasonable.

### 4. Discussion

#### 4.1. Data Frequency

The cytometric measurements at the ETS were made at a relatively low frequency (four per day) and were nevertheless used to resolve diel variations. The influence of the data frequency on the results has to be assessed. For that a high-frequency cycle measured by Vaulot and Marie [this issue] at 5°S, 150°W was used to generate a set of subsampled cycles. Their data for *Prochlorococcus* on November 19 at 0 m (their Figure 2) was selected because a parallel DNA experiment was performed and provides an independent estimate of \( \mu \). The method was applied to the various cycles, and the results are presented in Table 2. With the initial 1 hour-cycle (case 1), \( \mu \) was estimated to be 0.7 d\(^{-1}\), a value rather close to the 0.62 d\(^{-1}\) given by the DNA analysis [Vaulot and Marie, this issue, Figure 8a]. The grazing rate (not considered by Vaulot and Marie [this issue]) was estimated to be 0.55, and this result is coherent with the higher level of abundance at the end of the 24 hour period compared to that at the beginning [Vaulot and Marie, this issue, Figure 2]. The estimate of 1600 and 2754 LT for \( t_d \) and \( t_g \) is consistent with the indication by the authors that the division generally began in late afternoon and ended ~0200 LT the next morning (timing estimates are specifically discussed in section 4.3). For a data subsampling of 1/3, three 1/3 hour cycles were obtained (beginning at 1100
LT ±1 hour) and six cycles for a subsampling period of 6 hours (from 1100 LT ±3 hours) were obtained. As shown in Table 2 (cases 2 and 3), the estimated rates compare very well on average with those for the high-frequency data with typical differences of ±10% between cycles. The division timings for the three cases are consistent, with typical differences of ±0.5 hours in \( t_d \) and \( t_a \). The fourth case in Table 2 was that of a FLUPAC cycle (subsampling at 1100, 1900, 2300, 0300, and 1100 LT), and the same remarks can be made. It is also worth noting that the RMS dispersion \( \Delta \) remains in a range of 5%-8% for the three data frequencies. Subsampled cycles at 1/2 and 1/4 hours were also considered and led to similar results (not shown). For subsampled cycles at 1/8 data points (eight cycles of four data points) the averaged results (\( \mu = 0.71, g = 0.59, t_d = 16.5, \) and \( t_a = 27.8 \)) compared well with those for the other cases, but the standard deviations increased to 25% in the rates and to 1 hour in the times (not reported in Table 2). Frequencies lower than four per cycle are unable to support the estimate of the four parameters and were not considered. These results indicate that the abundance sampling at the ETS was frequent enough to support the growth and grazing rate estimates (and that a lower-frequency sampling would have not be sufficient). The differences in the rates and timing from one cycle to another occurred very likely in response to some noise in the data, probably because of small-scale patchiness in the cell distributions. Part of the dispersion around the averages reported in Figure 5 would also be due to such an effect.

### 4.2. Grazing Variations Along a Diel Cycle

Protists would be the main consumers of picoplankton [e.g., Hansen et al., 1994], and this was confirmed on a few occasions in the equatorial Pacific [Vors, 1995; Verrity et al., 1996]. The statistics of Peters [1994] predict that protists would graze more in presence of more abundant and/or smaller preys. When an algal population divides at 100%, the prey abundance doubles, and the prey volume halves (roughly). The predicted response is a 70% increase in the ingestion rate. The time-scales of the grazer responses to changing prey size and density, however, probably differ [e.g., Strom and Loukos, 1998]. Turbulence development, as may be due to nocturnal convection, would increase the contact rates between protozoa and their preys [Hill et al., 1992] with variable (species dependent) impacts on the ingestion rates [e.g., Shimeta et al., 1995; Peters and Gross, 1994]. This is still an open field for research [Browman et al., 1996]. Nanoplankton grazers also obey specific dynamics. Sherr et al. [1992] observed a preferential grazing on dividing bacteria whereas feeding rates were considerably lower at night in the experiments of Christoffersen [1994]. In situ observations also show varying features. Liu et al. [1997] found that in three of their four studies in the Pacific, Prochlorococcus mortality was higher (by 50% to 100%) during the division. On day 7 of the ETS, however, it halved during the division period. Claustre et al. [this issue] estimated that grazing might be twice as high during the night (Oligotrophie en Pacifique (OLIPAC) time series). Vaulot and Marie [this issue], and Blanchot et al. [1997] observed that the algal abundance decreased faster after sunrise. In the present study, as only five measurements per day were available, no attempt was made to resolve grazing variations along a diel cycle. As the constant-grazing assumption has every chance to be violated, its impact on the estimated parameters must be assessed. For this, grazing-variation scenarios were simulated, and the method was applied to the generated data. On the basis of the above review of grazing variations, three cases have been selected (Table 3). The first case is consistent with the findings of Liu et al. [1997] at the ETS (and of Christoffersen [1994]): the grazing is lower during the division period, and we chose the extreme case of an abrupt variation of a factor 2 (\( g_{div} = 0.5 g_{div} \)). The second case is consistent with the findings of Liu et al. [1997] at three other Pacific sites and of Claustre et al. [this issue]: the grazing is higher during the division period, and here also the rate jumps by a factor of 2 at \( t = t_d \) and \( t = t_a (g_{div} = 2 g_{div}) \). The third case resembles case 2 except that the rate \( g(t) \) varies continuously with the cell number \( N \) and the mean cell volume \( V \) according to Peters [1994]. \( V \) is assumed to vary linearly with time, and \( F \) being the fraction of dividing cells at the end of the day, \( V \) increases by a factor \( 1 + F \) during the photoperiod and decreases by the same factor as the cells divide. With a selected value of 0.69 \( d^4 \) for \( \mu, F = 1 \) so that \( g \) is slowly decreasing during the photoperiod, increases by a factor of 1.7 from \( t = t_d \) to \( t = t_a \) and then smoothly returns toward its minimum. In order to make comparisons easier the three cases have the same division rate, the same 24 hour average for \( g \), and the same division timing (1800-2400 LT). To enhance the expected effects, a relatively high value is given to \( \mu (0.69 d^4) \), and grazing balances growth over the diel cycle. The retrieved parameters are compared to the inputs in Table 3. As shown, \( \mu \) differs from its initial value, and \( g \) differs from the 24 hour average of the initial rate by 20% at the most, and both rates undergo parallel underestimations or overestimations. The departures are higher in cases 1 and 2 where the initial grazing varies

<table>
<thead>
<tr>
<th>Case</th>
<th>Sampling</th>
<th>Data Per Cycle</th>
<th>Cycles</th>
<th>( \mu, d^{-1} )</th>
<th>( g, d^{-4} )</th>
<th>( t_d - t_a ) hours</th>
<th>( \Delta %, )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>every 1 hour</td>
<td>25</td>
<td>1</td>
<td>0.70</td>
<td>0.55</td>
<td>16.0 - 27.9</td>
<td>6.5</td>
</tr>
<tr>
<td>2</td>
<td>every 3 hours</td>
<td>9</td>
<td>3</td>
<td>0.69 ± 0.08</td>
<td>0.51 ± 0.06</td>
<td>15.5 ± 0.5 - 28.2 ± 0.3</td>
<td>5.9 ± 1.6</td>
</tr>
<tr>
<td>3</td>
<td>every 6 hours</td>
<td>5</td>
<td>6</td>
<td>0.67 ± 0.07</td>
<td>0.50 ± 0.08</td>
<td>15.4 ± 0.6 - 27.5 ± 0.7</td>
<td>7.3 ± 1.1</td>
</tr>
<tr>
<td>4</td>
<td>1100, 1900, 2300, 0300, 1100 LT</td>
<td>5</td>
<td>1</td>
<td>0.69</td>
<td>0.56</td>
<td>15.4 - 27.8</td>
<td>5.5</td>
</tr>
</tbody>
</table>

The high-frequency measurements were effected for Prochlorococcus, at 5°S, 150°W, 0 m, on November 19, 1994, by Vaulot and Marie [this issue], and a parallel DNA analysis gave \( \mu = 0.62 d^4 \).

<table>
<thead>
<tr>
<th>Case</th>
<th>( \mu, d^{-1} )</th>
<th>( g, d^{-1} )</th>
<th>( t_{di} - t_{df}, \text{hours} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simulated Cycles</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Case 1 (( g_{div} = 0.78 ) and ( g_{ndiv} = 0.39 ))</td>
<td>0.69</td>
<td>0.69</td>
<td>18.0-24.0</td>
</tr>
<tr>
<td>Case 2 (( g_{div} = 0.53 ) and ( g_{ndiv} = 1.10 ))</td>
<td>0.81</td>
<td>0.83</td>
<td>17.6-24.5</td>
</tr>
<tr>
<td>Case 3 (( g(t) = N(t)^{1.17} P(t)^{-2.2} ), ( 0.52-0.86 ))</td>
<td>0.58</td>
<td>0.61</td>
<td>18.0-24.1</td>
</tr>
</tbody>
</table>

The 3 cases have the same value for \( \mu \), the same 24 hour average for \( g \), and the same division timing. In cases 1 and 2, \( g \) is given the values \( g_{div} \) and \( g_{ndiv} \) during and outside the division period (respectively). In case 3, \( g \) is continuously varying with the cell number \( N \) and with the mean cell volume \( V \) according to Peters [1994] (see text), and the reported values are its minimum and maximum (occurring at approximately \( t = t_{di} \) and \( t = t_{df} \), respectively).

*The 24 hour average

abruptly at the ends of the division periods. For the probably more realistic case of a continuous time variation of \( g \) the impact on the estimated rates is unsignificant (case 3). It is worth noting that in all cases the estimated timing does not differ from the initial one by more than 0.5 hours in \( t_{di} \) and \( t_{df} \). The simulations were repeated for various values of the control parameters, and the results were similar to those presented in Table 3 (not shown). At the end of this section it is thus possible to consider that the probable in situ variations of the grazing along a diel cycle do not prevent the method from providing reliable estimates of the division rate and timing and of the mean diel grazing rate. It is very likely that the high-frequency measurements recently performed in the equatorial Pacific by Vaulot and Marie [this issue] and during the EBENE cruise in November 1996, at 3°S, 180° could provide some information about grazing diel variations.

A fruitful approach would be to assimilate the cytometric counts in a predator-prey model.

4.3. Division Timing

Although the estimated timings at the ETS appeared to be reasonable when compared to the observations in the equatorial Pacific (Table 1), it is worth assessing the uncertainties and limitations in the estimates. The sensitivity of the present study method was examined as follows. For a given diel cycle, once the rates and times were estimated, \( t_{di} \) and \( t_{df} \) were changed from their estimated values and the least squares procedure was reapplied for the estimate of \( \mu \) and \( g \) only. For independent changes of ±0.5 hours in \( t_{di} \) and \( t_{df} \) \( \Delta \) increased from its initial value by a few percent, and the retrieved rates differed by <10% from their initial estimates. For ±1 hour variations the response increased to 20%-30% in the rates with \( \Delta \) up to 10%, whereas the response became insignificant when \( t_{di} \) and \( t_{df} \) were changed by <±0.5 hours. As the measurement accuracy is of a few percent, the sensitivity of the method cannot be better than, approximately, half an hour in the division times and 10% in the rates. When the impacts of the data frequency were examined (section 4.1), it was shown that typical "errors" in the division hours were also of ±0.5 hours. When the impacts of grazing variations were examined (section 4.2), it was also shown that an error of ±0.5 hours could occur. Otherwise, \( t_{di} \) and \( t_{df} \) were defined according to a selected mathematical representation (equation 2). Predicted cell numbers do not vary by more than 5% during the first and last hours of the division period (Figure 4), and such a variation is of the same order as the counting accuracy. Our estimates for \( t_{di} \) and \( t_{df} \) would therefore be validated with still an uncertainty of ~1 hour, even by using continuous measurements. In the case of DNA cycle experiments the estimate of \( t_{di} \) and \( t_{df} \) relies on the proper observation of the peaks in the successive phases [Carpenter and Chang, 1988]. Setting aside the specific uncertainty in their estimates [Vaulot, 1992; Liu et al., 1997], these times are not expected to match exactly the period during which the number of cells is increasing, and 1 hour differences between the methods are likely. Finally, the measurement times themselves are not perfectly reliable. There is a gap of 1 hour or more between the underwater sampling time and the moment when a subsample enters the cytometer on board or is preserved for delayed analysis. Division and grazing processes are likely to go on during this variable gap, and their rates are likely to be perturbed by the handling. As a consequence, neither the sampling time nor the cytometer (or preservation) time is perfectly adequate, and here also differences of 1 hour or more between division-timing estimates can occur. Taking into account all these uncertainties and taking also into account a significant natural variability, our estimated timings should be therefore considered as consistent with the observations effected in the equatorial Pacific (Table 1).

4.4. Vertical Mixing

Our estimates relied on the assumption that mortality (grazing) and cell division were the sole causes of the abundance variations at the ETS. Convective mixing was neglected, although the abundance measured at night near the surface must have been under its influence. If the division rates were actually greater at 30 m than at 0 m, as is the case with the DNA results of Liu et al. [1997] on day 7 of the ETS (see Figure 6) and as previously observed in the Pacific [e.g., Vaulot et al., 1995; Binder et al., 1996], the nocturnal mixing would decrease the cell numbers at 30 m and increase them at 0 m. As a consequence, our 0 m and 30 m rates would be overestimated and underestimated, respectively. This impact would vary from day to day with the variable strength of diurnal stratification and nocturnal convection (see section 2.3) and cannot be further quantified (part of the dispersion around the 0-40 m averages reported in Figure 5 is likely due to this variable impact). DNA rates are also probably influenced by nocturnal mixing. However, as far as they rely...
on a larger number of daytime samples, they may be less sensitive. We therefore consider the gradient in our results near the surface (Figure 6) with caution.

4.5. Rate Variations During the Time Series

As previously reported (sections 2.2 and 2.3), all the measured parameters changed after day 4 with the arrival of a different water mass. The drop in the estimated growth rates on day 5 is thus very likely an artefact due to the transition toward lower levels of cell abundance (in parallel, mortality is overestimated). In contrast, horizontal advection is believed to have been negligible at the beginning of the ETS. The day-to-day increase in the amplitude of the abundance diel variations (Figure 3) and, consequently, the increase in the computed growth rates (Figure 5) should thus correspond to actual increases in the number of cells dividing daily. From day 1 to 4, as nebulosity decreased, the incoming daily photosynthetically available radiation (PAR) increased by 25% and the diurnal stratification strengthened (Figure 2). As no significant day-to-day variations occurred with the in situ 14C production (A. Le Bouteiller, personal communication, 1998), the increase in the growth rates may therefore have been a response to a stabilization of the cells in the light field. That this increase was generally not paralleled by an increase in the daily minimum abundance supports our result that mortality (grazing) was responding to growth variations at the day scale for the three algal groups (the \( \mu/g \) ratios remained close to 1).

4.6. Primary Production Estimates

As the cells must have doubled their carbon content \( C_c \) during daytime in order to divide, primary production \( P \) can be estimated according to [e.g., Vaulot et al., 1995]:

\[
P = C_c N [\exp(\mu) - 1]
\]

According to Navarenne [1998], the mean size of Prochlorococcus in the relatively rich surface waters of the ETS was of \( -0.7 \mu \text{m} (0.6-0.8 \text{ for Chisholm et al. [1988] and 0.54-0.67 for Morel et al. [1993]) } \). The mean size of the picoeukaryotes was \( -2 \mu \text{m} (2.3 \text{ for Campbell et al. [1994], 1-2 for Chaves et al. [1990], and DuRand and Olson [1996]). According to Verity et al. [1992] the corresponding carbon contents would have been 84 and 1490 \( \text{fg cell}^{-1} \). For Prochlorococcus, our conversion factor is significantly higher (by 60%) than the 53 \( \text{fg cell}^{-1} \) value used by Campbell et al. [1994] in more oligotrophic conditions. For Synechococcus, the 250 \( \text{fg cell}^{-1} \) value of Verity et al. [1992] was used. Accordingly, the average carbon biomass at the ETS would have been of 0.95, 0.16, and 0.74 \( \text{g m}^{-2} \) for Prochlorococcus, Synechococcus, and the picoeukaryotes, respectively (52%, 8%, and 40% of the picophytoplankton biomass, respectively). As the production predicted with equation 3 does not take into account the additional carbon that must have been fixed by photosynthesis to compensate dissolved organic carbon (DOC) release and \( \text{CO}_2 \) expiration, it tends toward a net production. With \( N = N_{net} \) in equation 3, the losses due to grazing from dawn to the beginning of the division are accounted for (Figure 4), so that \( P \) approximates the daytime net community production. With \( N = N_{net} \) in equation 3 grazing is corrected for (Figure 4), and multiplying the resulting \( P \) by \( (1+R) \), where \( R \) is the metabolic loss fraction, will approximate gross production. Nocturnal losses amounted to 20% of the 24 hour \( \text{C} \) production at the ETS (A. Le Bouteiller, personal communication, 1998). Assuming that this value held true for the daytime [but see Bender et al., 1992], \( R \) was 40% for the 24 hour period. Net and gross productions were computed for each algal groups and for the whole picophytoplankton as the sum of the three contributions. The mean integral values at the ETS are given in Table 4. At the end of daytime, Prochlorococcus, the picoeukaryotes, and Synechococcus would have retained 0.43, 0.25, and 0.08 \( \text{gC m}^{-2} \), respectively, that is to say 57%, 33%, and 10% of the picophytoplankton total. The 0.43 \( \text{gC m}^{-2} \) value we computed for Prochlorococcus is higher than the value of 0.183 \( \text{gC m}^{-2} \) estimated in a similar way by Liu et al. [1997]. The difference is partly due to the carbon content of 84 \( \text{fg} \) we adopted for these cells whereas Liu et al adopted 53 \( \text{fg} \) (after Campbell et al. [1994]). The remaining difference is likely due to the low abundance values Liu et al. [1997, Figure 2] found on day 7 (their Fig. 2) and this might be explained by their sample preservation procedure. Vaulot et al. [1995] estimated this production at 0°, 140°W in contrasted El Niño Southern Oscillation (ENSO) conditions and their results ranged between 0.174 and 0.498 (also using a conversion factor of 53 \( \text{fg} \)). As far as we know, no equivalent estimates have been published for the other picoplankton groups. The gross to net production ratio, as computed here, was 1.75, which agrees with the 1.55 value used by Liu et al. [1997] (following Bender et al. [1992]) but is lower than the 1.04 (=2.5) value used by Vaulot et al. [1995] (following Bender et al. [1994]). The picophytoplankton \( \text{C} \) assimilation was estimated by subtracting 20% from the average of 17 in situ incubations (data provided by Y. Dandonneau and A. Le Bouteiller, personal communication, 1998), in order to correct for the contribution of the \( >3 \mu \text{ size fraction (A. Le Bouteiller, personal communication, 1998). The resulting value (1.1 \( \text{gC m}^{-2} \text{d}^{-1} \) ) falls between the net and gross productions (Table 4), as they were estimated here, as should more generally be expected from this incubation technique [e.g., Langdon et al., 1995]. It is lower than our gross production by 22%, which is not an unreasonable value (e.g., 17%-32% in Kidson et al. [1995]). Because of the numerous uncertainties in the various estimates and corrections that led to the results, this comparison does not warrant further discussion, and we must be satisfied with the consistency between the estimates and the measurements of the picophytoplankton production at the ETS.

| Table 4. Daytime Net Community Production and Daily Gross Production for the Three Algal Groups and Picophytoplankton \( ^{14} \text{C} \) Assimilation. |
|-----------------|---|---|
|                | Net | \( ^{14} \text{C}) |
| Prochlorococcus | 0.43 | 0.78 |
| Picoeukaryotes  | 0.25 | 0.44 |
| Synechococcus   | 0.08 | 0.13 |
| Total picophytoplankton | 0.76 | 1.34 |
| Picophytoplankton \( ^{14} \text{C} \) | 1.1 |

Values are average integrals (0-100 m) for the equatorial time series (ETS), in \( \text{gC m}^{-2} \text{d}^{-1} \) (see text).  

a From present study.  

5. Summary and Concluding Remarks

During a time series in the equatorial Pacific at 150°W flow cytometry measurements were carried out four times per day at discrete depths. The sampling frequency was sufficient to resolve the diel variations in the cell abundance of the three major components of the picophytoplankton over six days. Each day, the abundances exhibited a well-marked periodicity near the surface whereas the signal was generally unclear below the mixed layer. The diel periodicity was attributed to highly synchronized cell division and to cell mortality (by grazing). In the equatorial ocean such a synchrony has been proved through proper analysis of the cell cycle only in the case of Prochlorococcus. For the two other groups, such a synchrony was only a (very) reasonable interpretation which remains to be ascertained. For the three groups, mortality (by grazing) was also an assumption, as grazing was not studied per se during the ETS. Cell division and mortality were then simply modeled in order to estimate their rates from the observed abundance variations. Measured abundances were reproduced with an accuracy of a few per cent, which was consistent with the typical accuracy of cytometric measurements. Division and mortality rates and division times were typically estimated within ±10% and 1 hour, respectively, and such an accuracy was consistent with the uncertainties due to the measurement protocol and with other method accuracies. The estimated rates were in good agreement with previously published results based on the various techniques, including during the ETS. Our method, however, as it did not explicitly take vertical mixing into account, probably failed in assessing the vertical profile of growth and grazing rates near the surface. The mean rates in the mixed layer significantly increased during 4 days for the three algal groups, and this increase was attributed to a variation in the light forcing. Such variations indicate that extrapolating the results of short-term observations at larger timescales might be dangerous. Our results otherwise confirmed that growth and grazing are in close balance at the day scale in the equatorial Pacific. Using the model, both net and gross productions could be predicted for each algal group, and the results were consistent with 14C assimilation measurements during the ETS. At the date, and because of the large uncertainties at various stages in the prediction, this is only an encouraging result. As soon as the cell carbon content can be reliably estimated from in situ observations, as it might be thanks to a cell-size calibration of light scattering measurements, flow cytometry will be instrumental in assessing primary production in those oceanic regimes, like the equatorial Pacific, where synchronized cell division is the rule.

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