

ESTIMATING THE GROWTH RATES OF *PROCHLOROCOCCUS* AND
SYNECHOCOCCUS IN THE SEA FROM DIEL CELL CYCLE ANALYSIS

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ABSTRACT

Photosynthetic bacteria -- *Prochlorococcus* and *Synechococcus* -- are important components of phytoplankton biomass and primary production in the most warm open ocean. To determine the relative importance of *Prochlorococcus* and *Synechococcus* to primary production in various oceanic ecosystems, appropriate growth rate methods were required to permit species-specific estimates. Cell cycle analysis has been proven a reliable tool for estimating growth rates of *Prochlorococcus* spp. Applying a modified model to *Prochlorococcus* in the equatorial and subtropical North Pacific Ocean revealed that *Prochlorococcus* grew equally well in oligotrophic and mesotrophic conditions at about one doubling per day in the surface mixed layer. However, the contribution by *Prochlorococcus* to primary production was significantly higher in the oligotrophic subtropical North Pacific than in the mesotrophic central equatorial Pacific.

Further, I tested the application of the $f_{\min,\max}$ approach to a transect across central equatorial Pacific (12°S-12°N, 140°W) during El Niño and normal upwelling conditions and demonstrated that this approach yields comparable growth rate estimates to diel cell cycle analysis for *Prochlorococcus* but with the advantage that the sampling requirement is reduced significantly. During both periods, water-column integrated growth rates of *Prochlorococcus* were higher within the oligotrophic waters at the northern end of the transect and decreased toward a minimum at the equator. The lowest growth rates occurred at the equator during the spring El Niño cruise and at 2°N during the normal

upwelling cruise where a large biomass of buoyant diatoms had accumulated in the vicinity of a convergent front. *Prochlorococcus* growth rate reached a peak of 0.52 d^{-1} at 1°S and maintained a moderate rate ($0.35 - 0.48 \text{ d}^{-1}$) to the southern end of the transect. An inverse relationship was found between the contribution of *Prochlorococcus* to total primary production and primary production measured by the ^{14}C method, again implying that *Prochlorococcus* is more important in oligotrophic waters than the nutrient-rich equatorial upwelling region.

Attempts to estimate the growth rate of *Synechococcus* from cell cycle analyses were negatively impacted by preliminary results which showed that natural *Synechococcus* populations are less tightly synchronized to the daily photocycle and some populations possess irregular cell cycle patterns, such as multiple DNA replication peaks, large fraction of dark arrested cells, and cells with high DNA copies. All of the above observations make the determination of $t_{\text{S}+\text{G}2}$ difficult for *Synechococcus*. Chemostat cultures were conducted with the aim of finding a constant $t_{\text{S}+\text{G}2}$ or to establish a relationship between $t_{\text{S}+\text{G}2}$ and measured growth rate. However, applying the relationship between $t_{\text{S}+\text{G}2}$ and chemostat growth rate of *Synechococcus* WH7803 to field samples collected from the Arabian Sea provided unrealistic results. Therefore, an alternative method was developed in which *Synechococcus* growth rate could be calculated from diel variations in population abundances based on the fact that *Synechococcus* cell division occurred mostly during daytime. The approach was validated by good agreement between growth rates estimated from diel changes in cell abundance and the cell cycle model for *Prochlorococcus*.

Using this approach for *Synechococcus* and the diel cell cycle analysis for *Prochlorococcus*, I estimated their growth and mortality rates in Arabian Sea during SW and NE Monsoons. *Prochlorococcus* growth rates were typically less than 1 doubling per day, although growth rate in excess of one doubling per day were observed. *Synechococcus* spp. grew much faster than *Prochlorococcus* in the upper water column at almost every station during both seasons, but the depth range of its maximum growth rate was shallower and its growth and abundance decreased sharply in deeper waters. Maximum growth rates $> 2 \text{ d}^{-1}$ were observed at onshore stations during both seasons. *Synechococcus* growth rate increased with nutrient availability whereas *Prochlorococcus* growth rates did not vary dramatically with nutrient conditions. Although there was no significant difference in *Synechococcus* growth rates between the late SW and early NE Monsoon seasons, the estimated carbon production and relative contribution to primary production was greater during the early NE Monsoon owing to the larger biomass of *Synechococcus* and lower total primary production. Maximum *Prochlorococcus* production was found only in the most oligotrophic regions and *Prochlorococcus* was not a major contributor of primary production for the most part of the Arabian Sea during the SW and NE Monsoons. Maximum *Synechococcus* production occurred in mesotrophic (nitrate concentration $0.1\text{-}3 \mu\text{M}$) areas during both SW and NE Monsoon, but decreased at offshore and coastal stations. Overall, I have demonstrated that an inverse relationship between the importance of *Prochlorococcus* and *Synechococcus* to primary production exist. This relationship holds among all studied oceanic regions with nutrient conditions ranging from oligotrophic open ocean to nutrient-rich coastal upwelling water.