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Photoacclimation and nutrient-based model of light-saturated photosynthesis for quantifying oceanic primary production

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ABSTRACT: Availability of remotely sensed phytoplankton biomass fields has greatly advanced primary production modeling efforts. However, conversion of near-surface chlorophyll concentrations to carbon fixation rates has been hindered by uncertainties in modeling light-saturated photosynthesis ($P^b{}_{max}$). Here, we introduce a physiologically-based model for $P^b{}_{max}$ that focuses on the effects of photoacclimation and nutrient limitation on relative changes in cellular chlorophyll and CO_2 fixation capacities. This 'PhotoAcc' model describes $P^b{}_{max}$ as a function of light level at the bottom of the mixed layer or at the depth of interest below the mixed layer. Nutrient status is assessed from the relationship between mixed layer and nutricline depths. Temperature is assumed to have no direct influence on $P^b{}_{max}$ above 5°C. The PhotoAcc model was parameterized using photosynthesis-irradiance observations made from extended transects across the Atlantic Ocean. Model performance was validated independently using time-series observations from the Sargasso Sea. The PhotoAcc model accounted for 70 to 80% of the variance in light-saturated photosynthesis. Previously described temperature-dependent models did not account for a significant fraction of the variance in $P^b{}_{max}$ for our test data sets.

KEY WORDS: Photosynthesis · Modeling · Primary production

INTRODUCTION

Photosynthesis is a fundamental process of nearly all known ecosystems, such that the level of photoautotrophic carbon fixation supported by a given environment broadly dictates the local biomass of subsequent trophic levels and the biogeochemical exchange of elements between systems. Models of biospheric primary production have been greatly aided by global-scale satellite observations (Field et al. 1998), but conversion of measured plant biomass to net photosynthesis has remained problematic. Whereas terrestrial productivity models suffer from a lack of observational data for parameterization and testing (Field et al. 1998), high-sensitivity measurements of net primary production in aquatic systems have been routine since the introduction of the ^{14}C method by Steemann Nielsen (1952).

Analyses of vertical profiles of phytoplankton photosynthesis revealed early on that, when normalized to depth-specific chlorophyll concentrations, primary production can be modeled to first order simply as a function of subsurface irradiance (Ryther 1956, Ryther & Yentsch 1957, Talling 1957). A variety of analytical expressions have consequently been developed describing this relationship between vertical light attenuation and chlorophyll-normalized carbon fixation (reviewed by Platt & Sathyendranath 1993, Behrenfeld & Falkowski 1997b). Such models can account for most of the observed variance in depth-integrated photosynthesis (ΣPP), particularly when measurements encompass a wide phytoplankton biomass range, provided model input includes measured values for: (1) the vertical distribution of chlorophyll, (2) the downwelling attenuation coefficient (K_d) for photosynthetically active radiation (PAR), and (3) the maximum carbon fixation rate per unit of chlorophyll (P^b_{opt}) (Behrenfeld & Falkowski 1997a,b).

For over 40 yr, developments in phytoplankton primary production models have focused on refining characterizations of the above 3 critical water-column features, with clearly the greatest achievements realized in the description of the underwater light field (e.g. Platt & Sathyendranath 1988, Morel 1991, Antoine et al. 1996). Progress has also been made in predicting vertical profiles of chlorophyll (Platt & Sathyendranath 1988, Morel & Berthon 1989), but models of P^b_{opt} have remained rudimentary and inconsistent (Behrenfeld & Falkowski 1997b). The importance of accurate P^b_{opt} estimates cannot be overstated, especially when model performance is evaluated by comparison with point-source field observations. For globally representative data sets, phytoplankton biomass alone accounts for <40% of ΣPP variability, while inclusion of measured P^b_{opt} values can account for >80% of the variance in ΣPP (Balch & Byrne 1994, Behrenfeld & Falkowski 1997a). In oligotrophic regions where the range in chlorophyll concentration is further constrained, accurate estimates of P^b_{opt} are even more critical (Banse & Yong 1990, Siegel et al. 2000).

The function of P^b_{opt} models is to capture spatial and temporal changes in assimilation efficiencies (i.e. carbon fixed per unit of chlorophyll) resulting from physiological acclimation to environmental variability. Currently, the 2 principal approaches for estimating P^b_{opt} in regional- to global-scale models are: (1) to assign fixed, climatological values to biogeographical provinces (Longhurst 1995, Longhurst et al. 1995), and (2) to define predictive relationships between P^b_{opt} and 1 or more environmental variables (e.g. temperature, nutrient concentration) (Megard 1972, Balch et al. 1992, Antoine et al. 1996, Behrenfeld & Falkowski 1997a). Both techniques have advantages, but differ in their intended application. For example, the first approach furnishes broad-scale average values for designated regions and is not intended to accurately reproduce the much finer scale physiological variability in ^{14}C-uptake rates corresponding to a given day, depth and location. As for the second approach, an effective model should, ideally, provide P^b_{opt} estimates comparable at this point-source scale of field measurements, but a successful model of this genre has not yet been described.

Here we introduce a model, belonging to this second category, that captures P^b_{opt} variability in natural phytoplankton assemblages. The model largely focuses on changes in P^b_{opt} resulting from photoacclimation and is thus referred to as the 'PhotoAcc Model', although a nutrient-dependence is also prescribed. In the following section, we describe the conceptual basis and underlying equations of the PhotoAcc model, the field data used for model parameterization and testing, and our approach to assessing nutrient status and photoacclimation irradiances. Model limitations, directions for expansion, and potential avenues for global implementation are addressed in the section 'Discussion'.

DISCUSSION

The importance of effectively modeling light-saturated photosynthesis at the difficult local scale of daily primary production measurements has been recognized for over 40 yr (Ryther 1956, Ryther & Yentsch 1957). The most common approach to this problem has been to describe P^b_{opt} as a function of temperature. Such models capture only a fraction of the observed variability in P^b_{opt}, because temperature is weakly correlated with causative environmental forcing factors. In contrast, the PhotoAcc model attempts to explicitly describe primary causative relationships at the level of chlorophyll synthesis and changes in the Calvin cycle capacity. With this approach, the model effectively reproduced spatial and temporal variability in light-saturated photosynthesis for the AMT and BATS studies. These field programs do not, however, fully encompass global nutrient, light, and temperature conditions. In the following sections, we evaluate the predictions and hypotheses of the PhotoAcc model, discuss potential alterations to account for additional growth constraints, and propose avenues for global implementation.