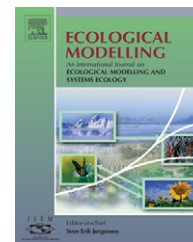


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Short communication

Quantitative comparison of photoacclimation models for marine phytoplankton

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ABSTRACT

Photoacclimation models for marine phytoplankton describe the changes in their composition (typically C, N and chlorophyll) and growth in response to changing light and nutrient environment. We compared two such models: that of Geider et al. (Geider, R.J., MacIntyre, H.L., Kana, T.M., 1998. A dynamic regulatory model of phytoplankton acclimation to light, nutrients, and temperature. *Limnol. Oceanogr.* 43, 679–694), hereafter the G model, and that of Pahlow (Pahlow, M., 2005. Linking chlorophyll-nutrient dynamics to the redfield N:C ratio with a model of optimal phytoplankton growth. *Mar. Ecol. Prog. Ser.* 287, 33–43), hereafter the P model. Using the Monte Carlo Markov Chain method, we fitted both models to the data set from an incubation experiment by Flynn et al. (Flynn, K.J., Davidson, K., Leftley, J.W., 1994. Carbon–nitrogen relations at whole-cell and free amino-acid levels, during batch growth of *isochrysis galbana* (prymnesiophyceae) under conditions of alternating light and dark. *Mar. Biol.* 118, 229–237). Data consisted of measured concentrations for particulate organic N, particulate organic C, chlorophyll and ammonium. The authors of the G model began their simulation from day 5 for this experiment, claiming that their model could not reproduce the initial lag phase (slow growth during the first few days of the experiment). The author of the P model claimed that its ability to reproduce this initial lag phase (starting from the beginning of the experiment) was a significant improvement over previous models.

Our fitting revealed that the G model can reproduce this initial lag phase as well as the P model, and that both models simulate the data set well. In the best-fits of both models, chlorophyll synthesis during the initial lag phase was limited by the rate of carbon assimilation, even though the G model was designed to have chlorophyll synthesis limited only by the rate of N assimilation. The requirement of organic carbon for energy to assimilate nitrogen results in this indirect limitation of chlorophyll synthesis by C assimilation in the G model, whereas chlorophyll synthesis is explicitly limited by the rate of C assimilation in the P model. This suggests that chlorophyll synthesis is in fact limited by the rate of C assimilation during the initial lag phase. As in the hand-tuned simulations previously published, the P model simulated the initial decrease in Chl:N ratio (as observed) whereas the G model simulated an initial increase in this ratio (contrary to the observations). We also discuss the relative merits of the two models for applications at large scales. Although data

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assimilation is not perfectly objective, because it requires certain choices such as weights for various data types and which data to include when fitting, our results show the advantage of mathematically rigorous fitting as opposed to hand-tuning of models. Our best-fits were significantly better than the hand-tuned fits originally published, especially for the G model, and this yielded insight into the mechanism responsible for the initial lag in phytoplankton growth.

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1. Introduction

Phytoplankton change their composition in response to changes in light and nutrient availability. Such changes are important to marine ecosystems because phytoplankton are the primary producers of organic matter and energy. These variations in composition are also key to interpreting observations of phytoplankton chlorophyll (Chl) in terms of N or C biomass.

To describe such changes, Geider et al. (1998) developed a model (hereafter the G model) of phytoplankton acclimation to light and nutrients, a Photoacclimation model. It describes how the C, N and Chl content of phytoplankton change in response to changes in light and nutrient availability. Recently Pahlow (2005) developed a different photoacclimation model (hereafter the P model) based on the principle of optimizing the daily mean net growth of phytoplankton.

Both studies simulated an experiment by Flynn et al. (1994), in which *Isochrysis galbana* was incubated under alternating light–dark conditions. Both obtained generally good simulations of the experiment, without using any mathematically rigorous fitting algorithm. Pahlow (2005) began the simulation from the start of the experiment, whereas Geider et al. (1998) began from the 5th day because, they reported, their model could not simulate the initial lag phase (a period of slow growth during the first few days of the incubation). Pahlow (2005) claimed that a key advantage of his formulation was that it allowed realistic simulation of this initial lag.

However, in both studies the “hand-tuned” fits of model to data were subjective. Geider et al. (1998)’s decision to begin their simulation from day 5 of the incubation was apparently based only on such “hand-tuning”. Without applying a mathematically rigorous algorithm, one cannot say that the G model cannot simulate the initial lag or that the P model can better simulate it. We sought to quantitatively compare these two models’ abilities to simulate this experiment, using data assimilation.

Flynn et al. (2001) compared various photoacclimation models, by fitting them to data from an experiment in which plankton were incubated under nutrient-replete conditions with step changes in irradiance (Anning et al., 2000). However, that experiment did not include exponential phase growth of phytoplankton followed by depletion of nutrients, as did that of Flynn et al. (1994). Such growth with nutrient depletion approximates an oceanic bloom, and the mechanisms underlying the initial lag phase are likely important to the development of oceanic blooms. Accurate simulations of such blooms are a major goal of large scale marine ecosystem models. Part of the motivation for this study was to evaluate which

of the models considered would be better suited for large scale simulations.

2. Experiment

Flynn et al. (1994) incubated *Isochrysis galbana* under alternating light–dark conditions (an idealized daily cycle) for 26 days. Ammonium was the only form of inorganic nitrogen supplied, and the incubations were conducted in batch mode so that it was depleted as phytoplankton grew. Concentrations of particulate organic carbon, particulate organic nitrogen, chlorophyll and ammonium were measured at 12 h intervals (Fig. 1). They observed an initial lag phase (slow growth) lasting about 5 days, followed by exponential growth, then a stationary phase (with no net C fixation). The initially N-starved cells first took up ammonium, raising their N:C ratio. They then synthesized chlorophyll, which allowed them to grow faster, terminating the lag phase. After nutrient depletion, the phytoplankton continued to assimilate carbon in excess of nitrogen, lowering their N:C ratio until it leveled off around day 20.

There was an imbalance in the total observed nitrogen concentration ($\text{NH}_4 + \text{N}$) of as much as 15% in the experiment. These errors in the data would adversely affect the data assimilation, because the model can not accurately simulate such an imbalance. We therefore excluded observations of organic nitrogen for any time at which this nitrogen imbalance was greater than twice the standard deviation of the nitrogen imbalance for all remaining observations. Thus the observed N was excluded for time = 2.5, 3, 3.5, 4, 4.5 and 6 days.

3. Models

Both models simulate the concentrations of C, N and Chl in phytoplankton, and account for changes in cellular composition in response to light and nutrient environment. Both are quota models, meaning that they are formulated in terms of the intracellular quota of N, expressed as the ratio of N:C.

3.1. G model

Geider et al. (1998) developed the first dynamic model of phytoplankton acclimation to variations in light, inorganic nitrogen availability and temperature. In addition to those environmental variables, rates of assimilation of C and N and of Chl synthesis depend on intracellular N:C and Chl:C ratios. The model was based on a mechanistic understanding of these processes and was formulated to consistently simulate general observations about variations in phytoplankton composition and growth. Chl synthesis depends directly on N assimilation, based on the requirement of N for protein synthesis. Exclud-

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