Ecological Modelling 385 (2018) 197–212

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Optimality-based approach for computationally efficient modeling of phytoplankton growth, chlorophyll-to-carbon, and nitrogen-to-carbon ratios

Bingzhang Chen*, S. Lan Smith

Research Center for Global Change Research, JAMSTEC (Japan Agency for Marine-Earth Science and Technology), 3173-25 Showa-machi, Kanazawa-ku, Yokohama 236-0001, Japan

ARTICLE INFO

Keywords:
Ocean model
North Pacific
Light
Nutrient
Metraopolis-Hastings Monte Carlo

ABSTRACT

To increase the efficiency of computing phytoplankton growth rate (μ), chlorophyll-to-carbon (θ) and nitrogen-to-carbon ratios (Q^N) in three-dimensional ocean circulation models, it is preferable to directly calculate θ and Q^N from ambient environmental factors instead of treating them as independent tracers. Optimality-based modeling has emerged as a novel and efficient approach to fulfill this task. However, it is still unclear precisely how the response of optimality-based models differs from conventional models. We compare a recent optimality-based phytoplankton model (PAHLOW model), based on which the familiar Droop function can be derived, to a commonly used Monod-type (MONOD) model. The two models generate similar patterns of μ with some important differences. Compared to the MONOD model, the PAHLOW model predicts higher μ under light limitation. The PAHLOW model also predicts that θ decreases with decreasing light under dim light and predicts decreasing Q^N with increasing light even at constant nutrient levels. Compared to the MONOD model, these features of the PAHLOW model qualitatively agree better with laboratory data. The PAHLOW model also suffers from a few shortcomings including the underestimation of θ under very low light and two times of computation time compared to the MONOD model. The two models generate striking differences of Q^N and θ in a one-dimensional implementation. Validation of such patterns will require more direct in situ measurements of μ, θ and Q^N.

1. Introduction

Functional relationships for phytoplankton properties such as the growth rate (μ), chlorophyll-to-carbon (θ), and nitrogen-to-carbon ratios (Q^N) in terms of abiotic environmental factors such as nutrient and light are essential to any plankton model and have been studied extensively (Droop, 1974; Jassby and Platt, 1976; Cloern et al., 1995; Litchman et al., 2007; Edwards et al., 2012, 2015, 2016). A widely-adopted approach is to treat phytoplankton carbon, nitrogen, and chlorophyll as independent tracers and make μ dependent on Q^N such as the Droop function (Droop, 1974) and also dependent on θ and light as in Geider et al. (1997, 1998). This approach has been implemented in some three-dimensional ocean general circulation models (GCMs) such as ERSEM (Butenschön et al., 2016) and a global size-structured plankton model (Ward et al., 2012). Although sound, this approach requires a great many calculations, particularly when a large number of phytoplankton species are included in a 3D GCM (Follows et al., 2007; Barton et al., 2010; Ward et al., 2012). Another drawback is that for tracers having spatial gradients of opposite sign (e.g., phytoplankton carbon concentrations are typically higher near the sea surface while chlorophyll concentrations are higher at depth due to photo-acclimation), their corresponding diffusive fluxes will be in opposite directions, which is unrealistic. It is therefore preferable not to have multiple tracers for components of the same phytoplankton biomass. On the other hand, fixed θ or Q^N based on the Redfield ratio are unrealistic and should be avoided to the extent possible (Geider and La Roche, 2002; Flynn, 2003; Christian, 2005).

One approach to this dilemma is provided by optimality-based models, which can be viewed as intermediate between the two extremes considered above (Flynn, 2003). The principle of the optimality concept is that all organisms that face physiological tradeoffs can be assumed to attain maximal fitness by adjusting trait values (Sutherland, 2005; Armstrong, 2006; Smith et al., 2011). Mathematically, the optimal trait value can be computed by solving the fitness gradient function by assuming instantaneous acclimation (Smith et al., 2011) and μ, θ, and Q^N can be directly calculated based on external environmental conditions such as temperature, light, and nutrient concentrations. This speeds up computation because otherwise two or more independent tracers

---

* Corresponding author.
E-mail address: 13512928@qq.com (B. Chen).

https://doi.org/10.1016/j.ecolmodel.2018.08.001
Received 1 April 2018; Received in revised form 1 August 2018; Accepted 1 August 2018
0304-3800/

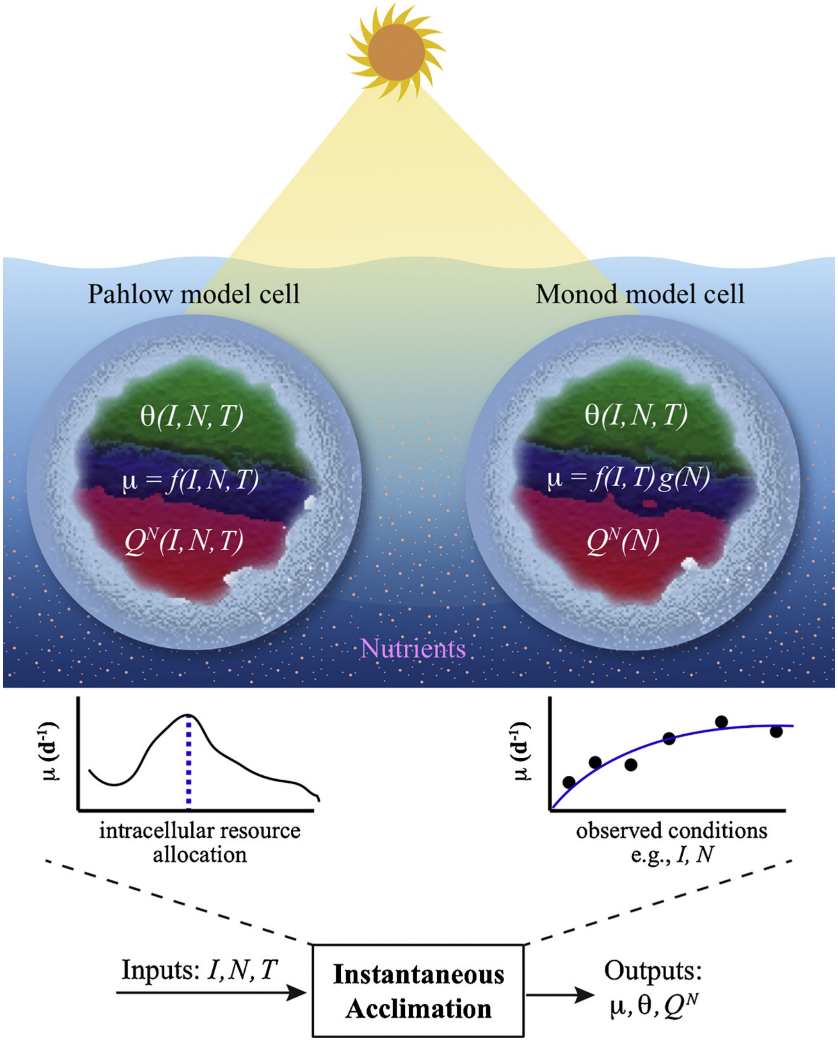

Fig. 1. Conceptual diagram of the two models compared herein. The PAHLOW model (left) calculates the intracellular resource allocation (vertical dashed line in the lower left figure) that optimizes specific growth rate, μ, subject to postulated costs and benefits of carbon and nitrogen assimilation. This gives an inter-dependent functional response to light (I), nutrient (N), and temperature (T). The simpler MONOD model (right) uses empirically based functions (depicted in the lower right figure) for the dependence of μ, θ (Chl:carbon ratio, g:mol), and Q^{N} (cell quota, mol N:mol C). This gives simpler multiplicative dependences. Most notably, Q^{N} depends on I, T, and N in the PAHLOW model, whereas it depends only on N in the MONOD model.

(phytoplankton chlorophyll and carbon) must be added to the model (Geider et al., 1998; Ward et al., 2012). Encouragingly, Ward (2017) recently showed that the instantaneous acclimation of cellular nutrient quota can accurately approximate the simulation outputs of a dynamic quota model, which requires an additional tracer for each nutrient considered, even under dynamic environmental conditions.

In this study, we focus on an optimality-based phytoplankton model developed by Pahlow and coworkers, hereafter PAHLOW model (Fig. 1; Pahlow and Oschlies, 2013; Pahlow et al., 2013; Smith et al., 2016). The success of the PAHLOW model is reflected in that it provided the first theoretical derivation of the well-known Droop quota model (Pahlow and Oschlies, 2013) and has been validated extensively against laboratory datasets (Pahlow et al., 2013) and somewhat against oceanic observations (Arteaga et al., 2014; Fernández-Castro et al., 2016; Smith et al., 2016).

Although elegant, the basic mathematical properties of the PAHLOW model and its coupling to ocean circulation models have not been thoroughly investigated (Smith et al., 2016). In particular, given that the fundamental relationships of μ versus light and nutrient appear similar to the widely used Monod-type model, it remains to be explored to what extent the simpler Monod-type model can, with suitable tuning of parameter values, reproduce the output of the PAHLOW model (Burmaster, 1979; Flynn, 2003). Another consideration is that although the optimality assumptions have simplified much of the computation, the PAHLOW model still requires more calculations compared with the computationally simpler MONOD model. If it can be shown that the two models are mathematically similar and generate similar patterns under realistic ocean conditions, then the use of the MONOD model may be justified in many cases.

Due to the mathematical complexity of the PAHLOW model, its complete algebraic manipulation, as begun by Smith et al. (2016), is beyond the scope of this study. Instead, we tuned the Monod-type models to approximate the output of the mathematically more complex PAHLOW model and compared the resulting growth responses to light and nutrient. We also embedded the two models of phytoplankton in a one-dimensional model set up at two representative time-series observation stations in the subtropical North Pacific (Fig. 2) and compared the performance of the two models against observations.

2. Methods

2.1. Optimality-based phytoplankton model (PAHLOW model)

In the PAHLOW model, phytoplankton cells are assumed to instantaneously optimize their cellular Chl *a* and nitrogen contents to obtain maximal net growth, which is the net outcome of CO_2 fixation minus the energetic costs of photosynthesis and nutrient uptake. Note that although Pahlow et al. (2013) also included phosphorus limitation and nitrogen fixation in their model, for simplicity we here consider only nitrogen as the limiting nutrient.

There are three levels of optimization in the simplified PAHLOW model. The first is the optimization of the Chl:C ratio within the chloroplast ($\hat{\theta}_0$) to maximize net photosynthesis (i.e. gross photosynthesis minus the cost of chlorophyll maintenance). Pahlow et al.