



Review

Phytoplankton functional type modelling: Running before we can walk? A critical evaluation of the current state of knowledge



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ARTICLE INFO

Article history:

Received 16 May 2015

Received in revised form 23 August 2015

Accepted 24 August 2015

Keywords:

Mathematical models

Resource competition

Phytoplankton functional grouping

Ecological diversity

Cyanobacteria

ABSTRACT

In the context of aquatic biogeochemical modelling, there is an increasing pressure to explicitly treat multiple biogeochemical cycles and to increase the functional diversity of biotic communities. In this study, we evaluate the capacity of 124 aquatic biogeochemical models to reproduce the dynamics of phytoplankton functional groups. Our analysis reinforces earlier findings that aquatic ecosystem modellers do not seem to consistently apply conventional methodological steps during the development of their models. Although there is an improvement relative to earlier critiques, significant portion of published studies did not properly assess model sensitivity to input vectors; aquatic ecosystem modellers are still reluctant to embrace optimization techniques during model calibration; and assess the ability of their models to support predictions in the extrapolation domain. We also found significant variability with respect to the mathematical representation of key physiological processes (e.g., growth strategies, nutrient kinetics, settling velocities) as well as group-specific characterizations typically considered in the pertinent literature. Cyanobacteria blooms are a major concern for water industries as they represent high risk for human health and economic costs for drinking water treatment, and thus one of the outstanding challenges is to offer credible modelling tools that can serve as early warning systems to assist with the operational control of cyanobacteria blooms. Our study suggests that the derivation of distinct functional groups from fairly heterogeneous planktonic assemblages poses challenging problems. Because of the still poorly understood ecology, we do not have robust group-specific parameterizations that can support predictions in a wide array of spatiotemporal domains. In this context, we argue that the most prudent strategies are the gradual incorporation of complexity, where possible and relevant, along with an open dialogue on how we can mathematically depict the interconnections among different phytoplankton subunits or even how we can frame the suitable data collection efforts.

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“. . . Inadequacies and dysfunctionalities in models are not compensated for by the collection and use of data describing only part of the story. The devil is indeed in the details; nutrient-phytoplankton-zooplankton (NPZ) models get away with an awful lot by not exploring the details. If we are going to open Pandora's box to explore the details, then we had better be ready to handle the demons that escape from it. . .”

Flynn, 2006, J. Plankton Res. 28, p. 875.

1. Introduction

It is more than 40 years ago, when Chen (1970) proposed a general set of differential equations for describing key physical, chemical, and biological processes of aquatic ecosystems with site-specific parameters, initial conditions, and forcing functions, which were then used to address water quality problems (Fulton et al., 2004; Friedrichs et al., 2006). The philosophy and basic set of equations originally proposed remain the core of the current generation of mechanistic aquatic biogeochemical models, although advances in scientific understanding and improvements in methods of numerical analysis have brought significant progress in regard to the accuracy and sophistication (Ward et al., 2013). Early models were simple mathematical descriptions of aquatic systems that accounted for the interplay among nutrients, organic matter and aggregated biotic compartments, such as the generic “phytoplankton” and “zooplankton” state variables (Anderson, 2005). At higher aggregation levels, plankton communities exhibit satisfactory predictability and are often proposed as a paradigm for shedding light on the spatiotemporal patterns of complex natural systems (McCauley and Murdoch, 1987; Scheffer et al., 2003). Nonetheless, the aggregate plankton properties (total biomass, productivity) are also characterized by lower sensitivity to external perturbations (episodic meteorological events, invasion of exotic species, excessive nutrient enrichment) and may be unreliable indicators of structural ecosystem shifts (Schindler, 1990; Frost et al., 1995). Further, in the context of water quality management, one of the central issues revolves around the elucidation of the mechanisms that shape the composition of phytoplankton assemblages and the capacity to predict the occurrence of harmful algal blooms, such as toxin-producing cyanobacteria. Thus, it is not surprising that simple models are frequently perceived as inadequate (or even obsolete) management tools (Flynn, 2005, 2006; Le Quere, 2006), and modellers increasingly opt for more sophisticated constructs designed to explicitly represent multiple biogeochemical cycles, to accommodate the functional diversity of biotic communities, and to depict the interactions of plankton communities with the higher food web (Van Nes and Scheffer, 2005).

Delineating the optimal resolution level for phytoplankton modelling studies poses significant challenges, and thus far one of the most defensible strategies involves the concept of “functional grouping” relative to strategies that revolve around the specification of size classes, modelling of individual species, or stipulation of goal functions (Jorgensen, 1999; Reynolds et al., 2002). Founded upon the classification of species on the basis of their general morphological, physiological, and ecological characteristics, the functional grouping offers an intuitively plausible approach that accounts for different patterns of adaptive specialism, while accommodating the notion that external (seasonal forcing, resource availability) and internal (inter-specific competition, trophodynamics) factors may profoundly modulate the expected signals of phytoplankton community (Reynolds et al., 2002). In the typical modelling practice, the characterization of each phytoplankton functional group (PFG) postulates different degrees of specialization for limiting resources (nutrients, light) and/or environmental conditions (temperature), while purporting

to reproduce inter-specific competitive interactions which – in reality – are characterized by an inconceivably wide array of physiological adaptations (mixotrophy, life stages) and sustained coexistence (Flynn, 2006; Thingstad et al., 2010). However, because of the poorly understood ecology, the literature debates to what extent we have robust group-specific parameterizations that can support predictions in a variable range of spatiotemporal domains. Modellers often use pre-conceived functional groups with subjective properties that are conveniently derived during the model fitting exercise to observed data (Thingstad et al., 2010). For example, preliminary efforts to incorporate plankton functional types into global biogeochemical models were based on speculative parameterization and – not surprisingly – resulted in unreliable predictions (Anderson, 2005). Likewise, Zhao et al. (2008) showed that the reproduction of seasonal succession plankton patterns in freshwater ecosystems is fairly sensitive and only occurs within a narrow window of the model parameter space. The latter study also pondered if it is “reasonable to expect single-valued data set-specific parameter estimates of artificially defined biotic entities to be extrapolated over wider geographical regions?” Thus, recognizing that the functional group modelling does not necessarily guarantee improved predictability, it is advised that the gradual incorporation of complexity, where possible and relevant, is the most prudent strategy and any such model development should be tightly coupled with rigorous assessment of the underlying uncertainty (Arhonditsis, 2010).

Given the importance of the topic, it is surprising the lack of published work to quantify the ability of PFG models in accurately reproducing the aggregated and compositional phytoplankton variability. In this regard, the present study evaluates the capacity of 124 aquatic biogeochemical models to reproduce the dynamics of phytoplankton functional groups across the range of temporal and spatial scales typically utilized. Following the practices presented in meta-analysis papers (Arhonditsis and Brett, 2004; Arhonditsis et al., 2006; Wellen et al., 2015), we first examine how consistently do modellers follow conventional methodological procedures, such as the quantification of goodness-of-fit, sensitivity analysis, and model validation in its broadest sense (predictive and structural confirmation, model transferability). We then evaluate the capacity of PFG models to reproduce seasonal succession patterns and structural shifts in phytoplankton communities in different geographical locations and environmental conditions. Along with the quantitative information, we also compile the most commonly used mathematical equations, parameter ranges and calibration methods used to reproduce phytoplankton functional groups, with special emphasis on cyanobacteria as one of the major threats to freshwater ecosystem health and integrity. Our intention is not to determine the most reliable way to refine the biotic resolution, but rather to assess the general performance of existing PFG models, to evaluate the methodological consistency during their development, to delve into how autotrophic organisms have been aggregated, and to pinpoint any major issues of model dysfunctionality. Our hypothesis is that the sizable number of modelling studies, which successfully passed the scrutiny of the peer-review process along with the experience gained from addressing a wide range of management problems, can objectively reveal systematic biases, methodological inconsistencies, and common misconceptions characterizing the field of PFG modelling. To the best of our knowledge, this is the first attempt in the literature to present a comprehensive assessment of the current generation of PFG models and examine the potential of improving the representation of phytoplankton adaptive strategies for resource procurement. It is our hope that this study will contribute towards an effective linkage of the variability at the organismal level with ecosystem-scale patterns.

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