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Commentary

Response to "Model assumptions limit implications for nitrogen and phosphorus management": The need to move beyond the phosphorus = biomass = toxin doctrine

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ABSTRACT

In commentary about our recent model of microcystin production by *Microcystis*, Stow and colleagues argued our efforts ignored the ecology of the lake system and did not result in identical biomass predictions made by existing models. We provide below responses to their statements and show that their commentary does not refute our model. While all models require assumptions to be made, we reiterate the reproducibility of our model and its potential future value in Adaptive Management.

COMMENT

Stow et al. (this issue) ("*Model assumptions limit implications for nitrogen and phosphorus management*") are critical of our recent publication of an agent-based, mechanistic model of microcystin production by *Microcystis* (Hellweger et al., 2022) that was used to predict toxin concentration in response to the planned reduction in P-loading in Lake Erie. They argue that the model ignores lake level processes, uses inherently limited assumptions, and that an adaptive management program should dictate recommendations on future nutrient loads. Alternatively, they advocate for a continued focus on existing models that are based primarily on correlations between spring P-loads and accumulation of biomass in summer, and on predictions of hydrodynamic movement of biomass around the lake. We recognize the limitations of our model and in fact acknowledged them in our paper. However, we feel that Stow et al. have: 1) dismissed the separate and differing objectives of our model *vs* existing models and 2) obscured the fact that our model, though using simpler hydrodynamic assumptions, predicts similar biomass trends in response to reduced P-loading as do existing models. While we agree that ecosystem and lake-wide processes should be considered in setting policy and management, we advocate for coupling mechanistic models such as ours to ecosystem models that simulate nutrient loads and broader phytoplankton community dynamics. Only by leveraging our growing understanding of the biology of the system can we hope to accurately predict complex biological responses to management and climate scenarios. Our agent-based model is an essential step towards that goal.

Existing lake-wide ecosystem and hydrodynamic models are valuable tools for understanding and predicting biomass, and they have been highly useful to the regional community. But these models do not mechanistically address microcystin production. To make any projection about microcystin concentration, they rely on the implicit but flawed assumption that phosphorus = biomass = toxin. Numerous studies have demonstrated that this assumption is wrong. A logical step forward is to develop approaches that specifically address mechanisms of toxin production based on knowledge that the scientific community has developed over the last two decades.

The model Stow et al. (this issue) call into question (Hellweger et al., 2022) incorporates current-state-of-knowledge on the regulation of biosynthetic pathways at the cellular level to predict the production of microcystin by a cyanobacterium (*Microcystis* spp.) that has been abundant and dominant in Lake Erie for ~ 2 decades (Steffen et al., 2017). Additionally, our model incorporates differences in competitive advantage between toxigenic and non-toxigenic strains of *Microcystis* to estimate changes in the toxigenic fraction of a bloom. The model has been validated against 708 experiments with 87 % reproducibility. Microcystin can render potable water supplies unusable and recreational and fisheries

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resources potentially dangerous; to this end, understanding and developing long-term predictions for toxin production represents a substantial leap forward.

Despite their critical approach, Stow et al. never call into question the mechanistic validity of our model (nor directly address its predictions). They instead lay out a series of arguments (Electronic Supplementary Material (ESM) Appendix S1) designed to refute the model's applicability to a natural system. Yet a key component of their argument is that our new model does not function the same, or make precisely the same biomass predictions, as existing models. Conceptually and logically, this is a weak argument. If the standard by which new models are judged is agreement with existing models, then we may as well stop new model development altogether. Stow et al. highlight differences in biomass predictions due to P reduction between our model and existing models, while glossing over the fact that both predict similar trends. Moreover they ignore the fact that existing models periodically miss their mark and need midseason corrections (*e.g.,* DuPont, 2022). More important, however, is the fact that existing models are not designed to predict microcystin production. To make any suggestion or prediction of toxin concentration, they must rely on the failed equivalency of P = biomass = toxin. Our model attempts to move beyond this flawed assumption.

The mechanisms incorporated into our model originate largely from lab-based experiments. Questions rightfully arise as to whether lab-based observations are applicable and scalable to ecosystem-wide predictions. Yet all mechanistic ecosystem models, including those cited by Stow et al., use observations from lab studies as components, *e.g.*, the Monod function (Verhamme et al., 2016). Stow et al. suggest our effort is untenable without consideration of a wide host of lake function parameters, including biological diversity, Fe dissolution from the sediments, the addition of oxidizing agents, and colonization by dreissenid mussels. However, we note that few if any existing models incorporate all these parameters. It is possible that future changes, including management, climate change, and others (*e.g.,* invasive species) will result in a shift of the phytoplankton community away from *Microcystis*. Our present understanding of the lake ecosystem is insufficient to predict such a change. In the meantime, a prediction of how *Microcystis* might change is possible and useful information for the management community.

Our long-term goal is to incorporate our model as a component into a larger model on lake biogeochemistry and ecology to provide a sorely needed update to existing approaches that use the flawed P = biomass = toxin assumption. As noted by a companion piece in *Science* (Ofiţeru and Picioreanu, 2022), "*No model is perfect, but some are useful*". That piece correctly notes (as did we) that many assumptions are needed in the early days of developing a complex and completely new approach to predict biological function (which, as noted, the model does quite accurately). Indeed, assumptions are in place because of the complexity that has hindered others from moving beyond P = biomass = toxin. We agree with Stow et al. that the Adaptive Management principle should guide long-term lake management. But it can take decades to decide on management plans, decades to implement these plans, and decades for lakes to respond. In the meantime, resource managers make decisions today, and they can benefit from insight and guidance offered by the predictions of models incorporating the best current understanding of the mechanisms at play. We think there is incredible value in knowing *a priori* the possible toxin outcomes of P-only reductions and that insight into the possible will serve the adaptive management approach well. Our new model can contribute to this endeavor.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2022.10.001.

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