What Minimal Models Cannot Tell: A Comment on "A Model of Phytoplankton Blooms"

Egbert H. van Nes* **and Marten Scheffer**

Department of Aquatic Ecology and Water Quality Management, Wageningen University, P.O. Box 8080, NL-6700 DD Wageningen, The Netherlands

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In a recent contribution, Huppert et al. (2002, p. 167) analyze a simple model of bottom-up controlled phytoplankton blooms to conclude that "although zooplankton have often been implicated as the agents responsible for crashes in many spring and summer phytoplankton blooms, the model shows that the key factor is more likely to be the large-scale reduction of nutrients used up in supporting the phytoplankton bloom." Although we agree that bottom-up control could be a key factor in some lakes, we feel that the cited conclusion is too general and is not justified by the analyses and data presented.

To illustrate that their model is correct, Huppert et al. (2002) used data from only one arbitrary year from a large time series of phytoplankton of Lake Kinneret and compared total phytoplankton biomass in the model with the biomass of only one species, the dinoflagellate *Peridinium gatunense*. In addition to the arbitrary selection of data, there seems to have been a scaling procedure that was not reported in the text. We could not reproduce the surprisingly good fit to the data that they presented using their model and parameter settings, and we came to the conclusion that the time must have been scaled by a factor of approximately $10/16.5t + 25$ to obtain the fit (fig. 1*a*). We acknowledge that minimal models are hard to compare with real systems because many processes are left out. Usually, it is only possible to compare with data qualitatively. However, we feel that any uncommon scaling procedure should at least be reported, as the figure alone suggests a too optimistic good fit. Indeed, when calibrating the initial conditions of the model with the same data set using standard methods (Nelder-Mead simplex method without changing the timescale), we could not obtain a very good fit ($R^2 = 0.48$; fig. 1*b*).

Of importance, the authors do not provide information about observed nutrients patterns or about other phytoplankton species in the lake. Both are essential for a judgement of whether the fit is indeed caused by the nutrient dynamics. Therefore, the presented results do not convince us that the model gives a good fit for the correct reason. After the *Peridinium* bloom, usually various other phytoplankton species take over in Lake Kinneret (Stone et al. 1993; Hambright et al. 2001). An obvious alternative explanation for the *Peridinium* crash is that these other species are better competitors, for instance, because they are more shade tolerant but slower growers. This and other alternative hypotheses should be tested.

While Huppert et al. (2002) do not show nutrient data from Lake Kinneret, they present a time series of chlorophyll and nutrient data from a very different system, the Danube River. The authors suggest that the striking inverse correlation between algae and nutrients in these data supports the idea that bottom-up control of algal biomass is dominant. Again alternative hypotheses are not mentioned here. Causation could as well be opposite: when other factors (e.g., grazing) reduce algal biomass, reduced algal uptake could allow free nutrient concentrations to rise. Alternatively (as a time lag seems absent), the correlation could be caused by an unknown factor affecting both phytoplankton and nutrients simultaneously. Note also that the Danube pattern cannot be reproduced by the presented model because the latter only shows slow damped oscillations and no fast cycles as observed in the data.

Indeed, the phytoplankton bloom in Lake Kinneret is exceptionally long (from the beginning of April to mid-July). Most lakes in the classic literature have quite different dynamics with much shorter spring phytoplankton blooms, typically of 1 mo, often followed by a clear-water phase (Lampert et al. 1986; Sommer et al. 1986; Luecke et al. 1990). Therefore, even if the model would reproduce

* Corresponding author; e-mail: egbert.vannes@wur.nl.

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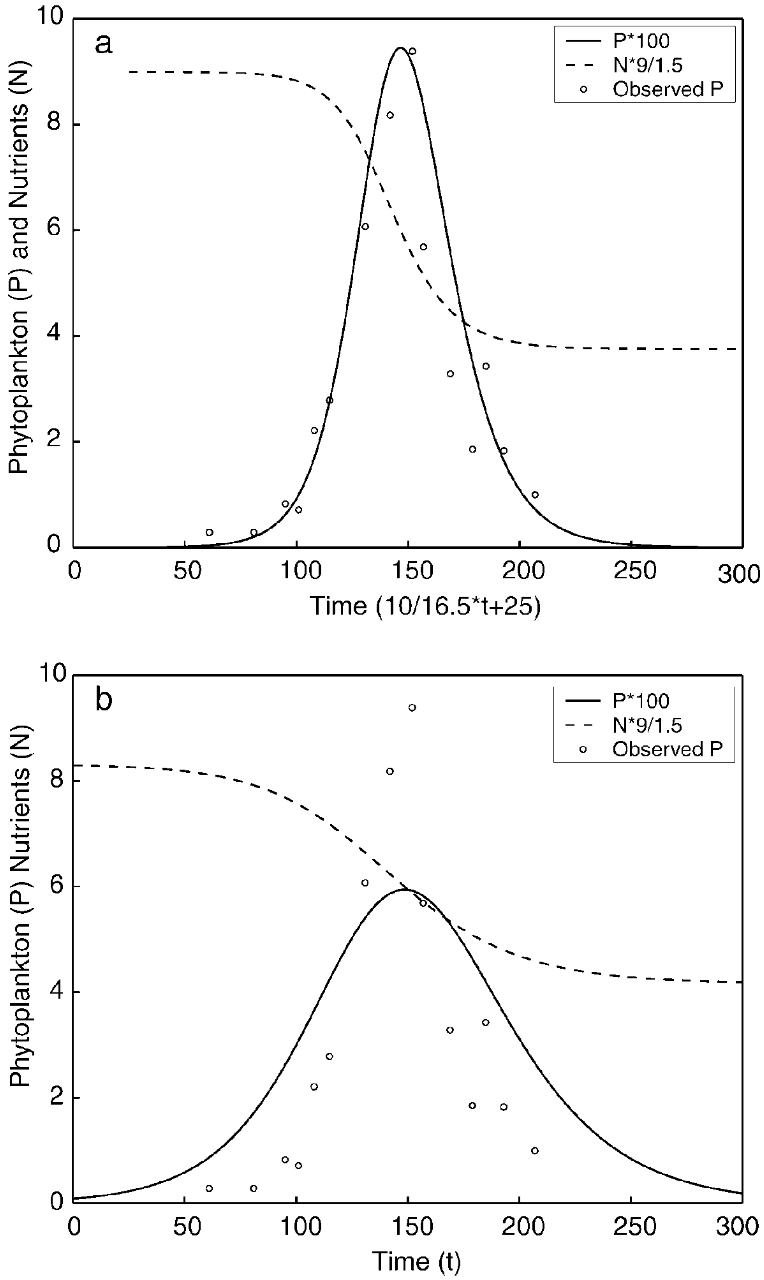

Figure 1: Fitting the theoretical bottom-up model to data from Lake Kinneret (digitized from Huppert et al. 2002, fig. 4). *a*, This reproduction of figure 4 of Huppert et al. could be made only by scaling of the time axis, which was not mentioned in the original figure. *b*, Poor fit obtained by optimization of initial conditions ($N = 1.382$, $P = .000897$) without scaling of the time axis. Optimization was done by the Nelder-Mead simplex method as implemented in MATLAB. Adjusted $R^2 = 0.48$.

a pattern in Lake Kinneret for good reasons, it is questionable whether this particular observation would warrant the rather generic conclusions about the dominant role of nutrient limitation in making phytoplankton blooms crash in other lakes. While it is interesting that a minimal model with only bottom-up control may produce a collapse of phytoplankton blooms in spring, the fit of the model to Lake Kinneret seems to add little to the discussion of whether top-down or bottom-up control is most important in general.

This brings us to another more philosophical objection against the reasoning in the article. As simple minimal models necessarily leave out many potentially important mechanisms, they can be used to point out possible explanations but not to reveal the relative importance of different mechanisms. The latter requires well-pondered evidence from experiments, field situations, and alternative models. The key problem here is that in ecosystems we often face a multiplicity of causality (Scheffer and Beets 1994). One phenomenon can be caused by different mechanisms simultaneously, and the relative importance of each mechanism may differ from case to case. This is certainly true for the regulation of phytoplankton blooms. In the 1960s and 1970s, the prevailing view was that lake food webs are bottom-up controlled (e.g., Vollenweider 1976; Schindler 1978). However, starting in the 1980s, there has been overwhelming experimental evidence that top-down regulation can be very important in lakes (e.g., Shapiro and Wright 1984; Carpenter et al. 1985; Meijer et al. 1999), and zooplankton grazing is in many cases the main cause of the spring phytoplankton crash (Lampert et al. 1986; Luecke et al. 1990). It is now generally accepted that the potentials for top-down control are high in many lakes (Jeppesen 1998; Scheffer 1998). However, the relative importance of top-down versus bottom-up control may differ considerably from case to case, depending, among other things, on the trophic status of lakes (McQueen et al. 1986) and lake depth (Jeppesen et al. 1997). To complicate things more, there are also interactions between both processes because nutrient excretion by zooplankton is an important recycling process (Lehman 1980) and zooplankton growth is reduced when they feed on nutrient deficient algae (Van Donk et al. 1997).

In view of the well-documented complexity of the regulation of algal biomass, it seems premature to draw the generic conclusion that bottom-up regulation is more important than top-down control (Huppert et al. 2002) on the basis of a minimal model.

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