

What Minimal Models Can Tell: A Reply to van Nes and Scheffer

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While criticizing our work and going to considerable effort to preach “what minimal models cannot tell,” van Nes and Scheffer overlooked that our article (Huppert et al. 2002) was intended to convey the opposite, namely, “what minimum models can tell.” Our article reflects a more positive and optimistic philosophy. In their critique, van Nes and Scheffer confuse three different and unrelated problems. The most serious technical point relates to a parameter scaling error of little consequence that had mistakenly crept into our article. The others concern the bottom-up versus top-down controversy in ecology and the role of minimal models. We address these in turn.

The main technical argument of van Nes and Scheffer concerns their failure to reproduce a key figure (fig. 4) in Huppert et al. 2002 (equivalently fig. 1a of van Nes and Scheffer 2004). Their difficulties in fitting the Kinneret bloom data with a suitably parameterized model is partly our fault because a scaling error crept into the text when recasting our model during the referee process. In actual fact, our model fit, as displayed in their figure 1a, is genuine and easily obtained by using the model equations

$$\frac{dN}{dt} = -bNP,$$

$$\frac{dP}{dt} = bNP - dP,$$

where N is nutrient concentration (mg/m^3) and P phytoplankton biomass (kg/m^3). The parameters are $b = 1.7$ ($\text{m}^3/[\text{kg d}]$) and $d = 0.17$ ($1/\text{d}$), with initial conditions $N_0 = 0.15$, $P_0 = 0.0000002$. (For optimal visualization, nutrient levels in fig. 1a are magnified by a factor of 60). The original parameters given in Huppert et al. (2002) were equivalent to those above but (time) rescaled by a factor of 1.7, because this led to the very convenient parameter set $b = 1$, $d = 0.1$. Either way, the fit of figure 1a is extremely good, explaining 88% of the variance ($R^2 = 0.88$) of the phytoplankton data. Remarkably, the fit was obtained with a minimal qualitative “strategic” model that was not really designed for the purpose of matching field data with any precision. Even though figure 1a singles out a particular year from the Kinneret *Peridinium* time series, fits of equal success can be obtained easily for any year of the data set. Therefore, the assertion that our results rely on an arbitrary selection of data is without substance.

Van Nes and Scheffer were unable to obtain a reasonable fit because, after noting the need to rescale time, they neglected to compensate by rescaling their model parameters. By using wrong parameters, it is little wonder they obtained the poor “fit” ($R^2 = 0.48$) seen in their figure 1b. The latter figure certainly makes all our hard work look very silly. Had van Nes and Scheffer contacted us before writing their criticism, this trivial mistake could have been easily clarified, thereby avoiding any further confusion.

Moving now to the second issue of van Nes and Scheffer, we should point out that it was not our intention to suggest that bottom-up regulation is more important than top-down control nor would we want to enter this controversial debate. As the introduction of our article emphasizes, our model is relevant for phytoplankton blooms that are bottom-up or nutrient controlled, for example, many toxic harmful algae blooms. As we wrote (Huppert et al. 2002, p. 156), “top-down control, with zooplankton strongly controlling the initiation of blooms is an unlikely mechanism for the many blooms that are toxic or largely inedible and that can thus hardly be affected by zooplankton grazing.”

Van Nes and Scheffer would be wrong to ignore the

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possibility that some blooms are bottom-up controlled. For instance, with respect to the English lakes, Lund (1950) and Macan (1970) argue similarly that “grazing by animals has no appreciable effects on the fluctuations in [phytoplankton] numbers” (Lund 1950, p. 31). The annual Kinneret *Peridinium* bloom is a good case in point because it is not even grazed by zooplankton. Remarkably, without supporting evidence, van Nes and Scheffer argue that (2004, p. 924) “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.” However, this simply is not the case. The Kinneret’s winter *Aphanizomenon* bloom, which is the main subject of discussion in Hambright et al. (2001), has no impact on the *Peridinium* bloom (occurring well after the triggering of the crash) and is of relatively negligible biomass. In any case, the Kinneret bloom has appeared for centuries, while the *Aphanizomenon* has only been seen in Lake Kinneret over the last 5 yr. So it could hardly be responsible for the Kinneret crash over all this time. And the other summer nanophytoplankton/chlorophytes are too small (in biomass; Stone et al. 1993) to even compete effectively. *Peridinium* dominates the algal biomass, comprising as much as 99% of the total during the bloom and ranging from 80% to 89% of the annual average (for details, see Berman and Pollinger 1974; Pollinger 1981).

We also discussed the oscillatory phytoplankton blooms in the Danube river. The phytoplankton is dominated by diatoms (mainly *Stephanodiscus hantzschii*) that reach up to 80% of the biomass (Bodemer et al. 2000). Van Nes and Scheffer (2004, p. 924) claim that the Danube River chlorophyll oscillations cannot be reproduced by our model (Huppert et al. 2002) “because the latter only shows slow damped oscillations.” Our extension of the article (A. Huppert, B. Blasius, R. Olinky, and L. Stone, unpublished manuscript) shows how the same model, with appropriate seasonal forcing, is easily able to generate realistic oscillations. This is achieved by seasonally modulating phytoplankton growth so that in some periods of the year environmental conditions are more suitable for growth than in others. With this additional component, the model shows rich behavior including limit cycle oscillations, chaos, and fast recurrent algal blooms. Although this is a crude simplification, it serves as a good first approximation for investigating how seasonal factors influence the simple nutrient phytoplankton dynamics.

Further, we would argue that in order to disentangle the different causes that may be involved in the control of an algae bloom, it is absolutely crucial to know what happens under the assumption, even if it is sometimes theoretical, that the bloom is only bottom-up controlled.

Therefore, the general importance of our model relies on the fact that it allows one to clearly analyze the outcome of algae dynamics under the hypothesis of strict bottom-up control. Due to the simplicity of the model, we are even able to understand the (sometimes nonintuitive) model properties because the quantities of interest (bloom height, timing, etc.) not only are simulation results but also can be calculated analytically. In this sense our model serves as a benchmark for other bloom crash explanations.

We are somewhat puzzled as to why van Nes and Scheffer argue so strongly against the use of simple models because this is their own preferred approach, and one that they have championed for years in limnology (for a satirical exposé, see Golterman 2002). We are the first to admit that simple models have their own special problems. Yet in the context we make use of them, they allow us to identify new universal mechanisms that should be inherent in much more complex limnological models. For example, we have identified important threshold effects governing bloom events and made clear why the annual bloom peak itself increases or decreases in a manner that can often be nonintuitive.

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