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Top-Down Control of Cyanobacteria: A Theoretical Analysis

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ABSTRACT: Field patterns and experimental results suggest that the effect of zooplankton grazing on the abundance of large colonial cyanobacteria may differ strongly from case to case. In this article we present an extensive analysis of a model that describes the competition between cyanobacteria of the *Oscillatoria* group and green algae exploited by *Daphnia*. In particular, we study the response of the model to changes in the nutrient concentration and predation by zooplanktivorous fish. The analysis is repeated for an array of different assumptions on the nutritional value of cyanobacteria and selectivity of zooplankton grazing. When fish predation pressure is so high that *Daphnia* density is negligible, there is competitive exclusion between the two primary producers, and over a range of nutrient levels, there are two alternative attractors: one with only cyanobacteria and one with only green algae. When fish predation pressure is lower, zooplankton becomes important, and if grazing by these animals is sufficiently selective, this may cause a third attractor on which *Daphnia*, cyanobacteria, and algae coexist. This "mixed" attractor may be stationary, oscillatory, or chaotic. Depending on the nutrient level, the nutritional value of cyanobacteria, and the selectivity of zooplankton, cyanobacterial dominance may be either induced or eliminated in response to reduced fish predation. This is well in line with the confusing array of field studies and experimental results.

Keywords: plankton dynamics, cyanobacteria, top-down control, chaos.

Blooms of large colony-forming cyanobacteria such as *Microcystis*, *Oscillatoria*, *Anabaena*, and *Aphanizomenon* often

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dominate the plankton in eutrophic lakes (Berger 1975; Schindler 1975; Reynolds 1984; Smith 1986; Trimbee and Prepas 1987; Sas 1989). In eutrophic shallow lakes, dominance of the filamentous cyanobacteria of the *Oscillatoria* group is a particularly important water quality problem. *Planktothrix agardhii* (formerly *Oscillatoria agardhii*) is especially notorious for forming blooms that can persist even throughout the year (Berger 1975; Sas 1989). Although eutrophication is seen as a main reason for these blooms, attempts to restore the original phytoplankton community in shallow lakes by means of reduction of the nutrient loading are often unsuccessful (Sas 1989). This may be explained by the fact that *Oscillatoria* dominance is likely to represent an alternative stable state of the plankton community of shallow lakes (Scheffer et al. 1997a). A plausible underlying mechanism is that these cyanobacteria are able to cause a higher turbidity than other algae at a given nutrient concentration, while they are also the superior competitors at high turbidity when the underwater light levels are low. As a result, dominance by filamentous cyanobacteria is highly resilient.

An often mentioned explanation for the success of large colony-forming cyanobacteria is the fact that they seem less susceptible to zooplankton grazing than other algae. There are different reasons for this. Several experiments suggest that the nutritional value of many cyanobacteria for zooplankton is low (Arnold 1971; Hawkins and Lampert 1989; De Bernardi and Giussani 1990) and that some can even be lethally toxic (Reinikainen et al. 1994; Codd 1995) or release substances that inhibit feeding activity of zooplankton (Haney et al. 1994). Also, many colonies are simply too large to be ingested by most zooplankters, and filamentous colonies may clog the filtration apparatus of the animals, reducing the feeding efficiency of especially the larger *Daphnia* species (Hawkins and Lampert 1989; Gliwicz 1990; Gliwicz and Lampert 1990).

The relative inedibility of cyanobacteria suggests that they may be favored by the presence of zooplankton because these will tend to eliminate competing algae that are more susceptible to grazing. Such selective grazing is often mentioned as an explanation for a shift to cyanobacterial dominance following the spring peak of zooplankton (Sommer et al. 1986; Sarnelle 1993), and enclosure studies

have confirmed that inedible algae tend to become more abundant at higher zooplankton grazing pressure (McCaughey and Briand 1979). Inedibility is also thought to make biomanipulation (fish stock reduction allowing zooplankton development) unlikely to work as a way to eliminate dense blooms of cyanobacteria (Gliwicz 1990; Hosper and Meijer 1993; Boon et al. 1994). However, other work suggests that colonial cyanobacteria can well be eliminated by zooplankton grazing (Matveev et al. 1994), and reduction of the fish stock has been observed to result in the disappearance of cyanobacterial dominance in several instances (Rose and Moen 1952; Scavia et al. 1988; Sarnelle 1993). Thus, there is evidence that grazing may either favor cyanobacterial dominance or eliminate cyanobacteria. This ambiguity is well illustrated by a case study in a eutrophic lake (Sarnelle 1993). Algal dominance in the lake usually shifted to "inedible" filamentous cyanobacteria in summer, and selective grazing by zooplankton was thought to be an important mechanism involved in causing this shift. However, *Daphnia* manipulation in enclosures, and whole-lake observations before and after a fish kill, showed that intense *Daphnia* grazing could retard succession to grazing-resistant, filamentous cyanobacteria in summer.

In summary, the field observations and experimental work show a large variation in edibility and nutritional value of colonial cyanobacteria and suggest that depending on the situation, grazing may either favor or eliminate cyanobacteria. In this article, we explore the spectrum of patterns that may theoretically be expected using a model of competition between filamentous cyanobacteria and edible green algae with zooplankton as a third state variable. We analyze the response of the system to fish predation and nutrient concentration for different assumptions on edibility and nutritional value of cyanobacteria.

Our effort should be seen in the context of the long history of analyzing the role of top-down versus bottom-up control in food webs by means of simple models. The potential for top-down control was already a hot item more than a century ago. An impression of this debate is given by the Italian scientist Lorenzo Camerano (1880). He presents a theoretical framework for understanding food chain dynamics that contains many of the key concepts of later ecological theory and explains in detail how the effect of disturbances on one trophic level will cascade through the food chain. Camerano's work was ignored until recently, but independently the same ideas provoked much debate almost a century later. An important focus of this debate was a paper in which Hairston, Smith, and Slobodkin present the so-called HSS hypothesis, named after the first letters of the last names of the authors (Hairston et al. 1960). In short, the idea is that in a world without consumers plants will be abundant. Introduction of herbivores would lead to a repression of plants resulting

in a desertlike world. Subsequent introduction of carnivores would, in turn, control the herbivores, releasing the plants from exploitation, resulting in a green world again.

Although, obviously, these ideas are somewhat simplistic, the theoretical consequences of complete top-down control have been explored further in various model analyses over the subsequent decades. An important prediction of various basic models is that in food chains with an odd number of trophic levels producers should increase in response to an increase in the nutrient concentration, whereas in food chains with an even length, the abundance of the highest trophic level, but not that of producers, should increase in response to enrichment (Rosenzweig 1971, 1973; Oksanen et al. 1981). In practice, such a straightforward top-down control is usually not observed. Rather, the tendency seems to be that enrichment results in an increase of consumer and producer biomass alike, as shown for lake plankton by various authors (Canfield and Watkins 1984; Sarnelle 1992; Watson et al. 1992). Various explanations for this deviation from predictions by simple models have been analyzed. In the case of plankton, spatial heterogeneity is likely to be an important factor smoothing the response to enrichment (and preventing unrealistically wild oscillations; Scheffer and De Boer 1995). Also, low nutrient availability may affect the quality of algal food for zooplankton, complicating the trophic cascade in lakes (Sterner et al. 1997; Elser et al. 1998).

Perhaps the most obvious oversimplification in classical food chain models, however, is that in real biological communities trophic levels consist of many competing species that differ in their ability to use resources and in their vulnerability to predation. Indeed, models accounting for this complication show patterns that may deviate widely from those predicted by the simple food chain models (Abrams 1993). An often observed phenomenon is that the availability of alternative prey leads to an increase in predator numbers and, therefore, indirectly, to a suppression of the preferred prey of these predators (Holt 1977, 1984). Also, various authors discuss the important consequences of the fact that increase of predation pressure and/or nutrient enrichment tends to lead to change in the community composition due to a replacement of species with higher growth rates and/or a higher resistance to predation (Armstrong 1979; Leibold 1989, 1996; Holt et al. 1994).

In this article, rather than explore the consequences of the interaction of predators with prey of different edibility in a general sense, we study a particular case in greater depth. Our model describes zooplankton grazing on two competing types of phytoplankton: filamentous cyanobacteria of the *Oscillatoria* type and green algae. The model takes two separate aspects of edibility into account: selectivity of zooplankton and nutritional value of different

types of phytoplankton. It appears that these two aspects have quite different implications for the response of the system to nutrient enrichment and predation pressure on zooplankton from fish.

Model Formulation

The model we analyze is composed of three differential equations representing the growth of green algae (g); filamentous cyanobacteria (c), sometimes called blue-green algae; and *Daphnia*, called also zooplankton (z):

$$\begin{aligned} \frac{dg}{dt} &= g \left(r_g \frac{n}{h_g + n} \frac{1}{1 + q_g E} - d_g - f - r_z \frac{z}{h_z + g + \alpha c} \right); \\ \frac{dc}{dt} &= c \left(r_c \frac{n}{h_c + n} \frac{1}{1 + q_c E} - d_c - f - r_z \frac{\alpha z}{h_z + g + \alpha c} \right); \\ \frac{dz}{dt} &= z \left(-d_z - f - F \frac{z}{z^2 + s^2} + r_z \frac{e_{zg}g + e_{zc}\alpha c}{h_z + g + \alpha c} \right). \end{aligned} \quad (1)$$

All parameter values and dimensions are listed in table 1 (note that we consistently used units of phosphorus rather than dry weight or total carbon). Growth of both algal groups depends in a simple Monod fashion on light and nutrients. The light conditions are represented by E , which stands for the Lambert-Beer vertical light-extinction coefficient. This shade factor depends on the biomass of both algal groups and their specific light-attenuation coefficients (k_g and k_c):

$$E = k_g g + k_c c. \quad (2)$$

Obviously, this treatment of shade effects is rather crude. Light intensity varies in the course of the day and decreases also with depth. For an idealized well-mixed system of homogeneous depth, the integration of photosynthesis over the light gradient can be treated elegantly (Huisman and Weissing 1994). However, in real lakes, the situation is always much more complex. Since it is, nonetheless, obvious that available light and, therefore, relative productivity in the lake declines with turbidity, we directly describe this in the employed pragmatic way.

Free available nutrients (n) depend on the total available pool (P) and the amount contained in the two algal groups and zooplankton:

$$n = P - g - c - z. \quad (3)$$

Grazing by zooplankton is represented by a simple sigmoidal response depending on the maximum grazing rate

Table 1: The parameters of the model, their values, and their units

Parameter	Value	Units	Source
r_g	1.2	1/d	1
r_c	.6	1/d	1
r_z	.6	1/d	2
d_g	.09	1/d	3
d_c	.06	1/d	3
d_z	.175	1/d	4
r_g	.003	mg P/L	5
h_c	.003	mg P/L	5
h_z	.0009	mg P/L	2
k_g	5	m ² /g P	6
k_c	10	m ² /g P	6
q_g	2	m	7
q_c	1	m	7
s	.01	mg P/L	4
e_{zg}	.6	...	4
e_{zc}	.1	...	8
f	.02	1/d	2
α	.5	...	9

Note: The sources used to estimate the parameter values are (1) Mur et al. 1977b; (2) Matsamura and Sakawa 1980; (3) Van Liere and Mur 1979; (4) Scheffer 1991; (5) Riegman and Mur 1984; (6) based on a k value of 0.1 m²/g cell biomass (Kirk 1983) and P concentrations in phytoplankton compiled in Reynolds 1984, table 14; (7) estimated using equation 5 in Scheffer et al. (1997a) for a temperate lake with a depth of 3 m from laboratory experiments (Mur et al. 1977a) in mixed water columns with varying turbidity; (8) several experiments suggest that the nutritional value of many cyanobacteria for zooplankton is lower than that of other algae (Arnold 1971; Hawkins and Lampert 1989; De Bernardi and Giussani 1990); (9) selectivity against cyanobacteria by *Daphnia* varies strongly (Hawkins and Lampert 1989; Gliwicz 1990; Gliwicz and Lampert 1990; Epp 1996). The default value used is arbitrarily chosen and the effect of different values is analyzed (see fig. 6).

of zooplankton (r_z) and a half-saturation constant (h_z) that represents the density of algae at which zooplankton reaches 50% of its maximum consumption rate in a case where all algae are perfectly edible. The selectivity factor (α) represents the proportion of encountered cyanobacteria that are ingested relative to the encountered green algae that are ingested. Higher selectivities imply lower values of α . Zooplankton growth is positively correlated to the weighted sum of the amount of green algae and cyanobacteria ingested and their nutritional values (e_{zg} and e_{zc}). When the nutritional value of cyanobacteria chosen is sufficiently low, this formulation is sufficient to generate the phenomenon, observed by Gliwicz and others (Gliwicz 1990; Gliwicz and Lampert 1990), that zooplankton growth becomes negative when the density of cyanobacteria in the mixed algal culture that serves as food becomes too high.

Losses due to fish predation are represented through a sigmoidal functional response depending on the maximum consumption rate of the fish community in the lake (F)

and a half saturation constant (s). The rationale behind this formulation is that the predation loss term should represent the impact of the fish community as a whole. In reality, different groups of fish forage on *Daphnia* with different functional responses. Therefore, this term is really just a pragmatic solution to mimic the effect of many different animals switching to forage on *Daphnia* at different moments with different efficiencies. Since most of the larger individuals usually switch to *Daphnia* only when it is not too scarce (Mills and Forney 1983; Lammens 1985; Lammens et al. 1985), the predation pressure is likely to increase more than linearly with *Daphnia* density over this initial range. Because of this prey-switching behavior of fish, the overall functional response is likely to be sigmoidal. The maximum consumption rate (F) is set directly rather than as the product of the fish biomass and their weight-specific maximum intake. The latter is not easily defined for a whole community, since large animals consume less per gram of body weight than small ones.

Zooplankton and algae also have loss factors due to outflow from the lake (f , for flushing) and specific loss rates (d) representing respiration and other factors not accounted for explicitly in the model.

In earlier papers, we analyzed the competition between filamentous cyanobacteria and green algae (Scheffer et al. 1997a) and the effect of zooplankton grazing on a single population of edible algae (Scheffer 1991; Scheffer et al. 1997b; M. Scheffer, S. Rinaldi, and Y. A. Kuznetsov, unpublished manuscript). The model we analyze here is a combination of the models presented earlier, and an extensive discussion of the choices made in formulating the model can be found in these papers. The new aspect is that, depending on the selectivity of zooplankton, consumption is now divided over two different algae with different nutritional values. As explained in the introduction, experimental results and field studies suggest a large variation in selectivity and nutritional value, and therefore, the effects of the parameters that represent these aspects (α and e) are explored extensively in the following analysis.

Analysis and Results

The aim of this section is to identify all possible asymptotic modes of behavior (for $t \rightarrow \infty$ or $t \rightarrow -\infty$) of the model (eqq. [1–3]) in a suitable range of two control parameters, namely, total nutrient concentration P and fish predation pressure F . Since the model has three differential equations (it is a “third order” model), its attractors, saddles, and repellers can be equilibria and limit cycles, as in second order systems, but also chaotic attractors (as well as chaotic saddles and chaotic repellers). Each point (P, F) of the two-dimensional parameter space corresponds to one model of our family (eqq. [1–3]) and, therefore, to one

specific set of attractors, saddles, and repellers. If point (P, F) is slightly changed, that is, if at least one of the two control parameters is slightly perturbed, by continuity the position and the form of the attractors, saddles, and repellers in state space will vary smoothly (e.g., a cycle might become slightly bigger and faster), but all trajectories will remain topologically the same (e.g., an attracting cycle will remain an attracting cycle). Only at some particular points in parameter space, the above continuity argument will fail. At these points, called “bifurcation points,” small variations of the parameters entail significant changes in the model behavior. Bifurcation points are located on curves, called “bifurcation curves,” in the parameter space (P, F) , and these curves partition the parameter space into subregions. All the models corresponding to the same subregion have qualitatively the same behavior. Thus, by determining all bifurcation curves, we can produce a complete map showing where the different modes of behavior of a system occur in the parameter space. We produced a map of the bifurcation curves of the model by using specialized software for carrying out the computations (Khibnik et al. 1993). We show the results of this analysis in figure 1 for the following values of selectivity and nutritional value of cyanobacteria: $\alpha = 0.5$; $e_c = 0.1$.

In order to interpret the bifurcation diagram of figure 1 biologically, we should first specify the set of attractors, saddles, and repellers characterizing each region of figure 1. These regions are so many (50) that it would be boring for the reader to follow a complete discussion. For this reason, we present only a small sample of this discussion by looking at the three subregions [a], [b], and [c] in figure 1 and showing their attractors, saddles, and repellers in the corresponding figure 2.

In region [a] there are only equilibria: one is an attractor characterized by absence of cyanobacteria and the three others are saddles (see fig. 2A). Thus, in region [a], the system can only settle to a stationary green monoculture $(g, 0, z)$.

In region [b], there are two extra unstable equilibria in the (g, z) plane that collide and disappear crossing the fold bifurcation curve FE from the right to the left. Thus, in region [b], there is still a unique attractor, namely, a stationary green monoculture, as in region [a]. This means that if we limit our discussion to the attractors, as we should if we like to extract meaningful biological messages from figure 1, the fold bifurcation curve FE that separates regions [a] and [b] must be erased, and the two regions must be considered as a single region. For similar reasons, many other bifurcation curves can be eliminated from figure 1, thus reducing the number of significant subregions.

Finally, in region [c], we still have the three saddle equi-

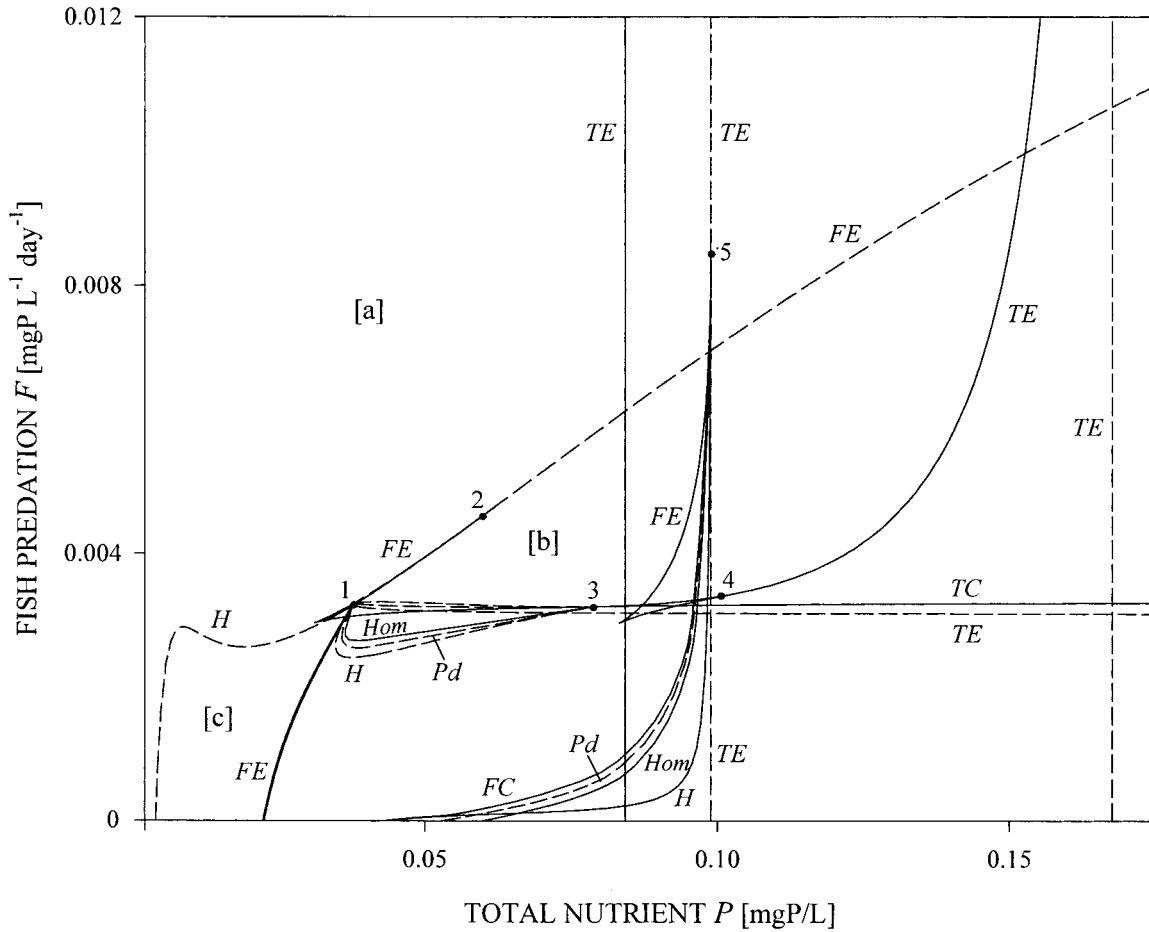


Figure 1: Bifurcation diagram of the model (eq. [1–3]) in the parameter space (P, F). All other parameters are at their reference values (see table 1). Points 1–5 are the so-called organizing centers, namely, the points where many bifurcation curves are rooted. Dashed curves are noncatastrophic bifurcation curves, while the others are catastrophic. The nature of each bifurcation curve is identified by a symbol: TE , transcritical bifurcation of equilibria; FE , fold bifurcation of equilibria; H , Hopf bifurcation; TC , transcritical bifurcation of cycles; FC , fold bifurcation of cycles; Pd , period doubling bifurcation; Hom , homoclinic bifurcation.

libria present in region [a], but the equilibrium in the (g, z) space is now a saddle surrounded by a stable limit cycle in the (g, z) plane. This means that the Hopf bifurcation curve H separating regions [a] and [c] is a “planar Hopf” bifurcation curve, concerning only the (g, z) space. Crossing curve H from region [a] to region [c], the stable equilibrium ($g, 0, z$) becomes a saddle because it remains stable in the [c] direction but becomes unstable in the (g, z) space. At the same time, a stable cycle appears in the plane (g, z). Going in the other direction, namely, from [c] to [a], the stable cycle shrinks and disappears by colliding with the saddle equilibrium ($g, 0, z$) that becomes stable. This means that in region [c] the system has only

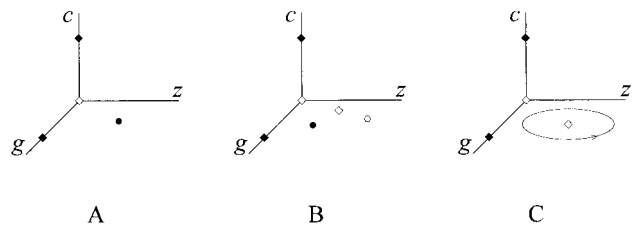


Figure 2: Attractors (black circles, limit cycles), saddles (black squares, white squares), and repellers (white circles) in the state space. A, B, and C refer to subregions [a], [b], and [c] of figure 1.

one attractor, which is still a green monoculture. Nevertheless, in region [c], the monoculture is cyclic and not stationary as in regions [a] and [b]. Thus, the Hopf bifurcation curve H can be eliminated, and region [c] can be lumped together with regions [a] and [b], if we are interested in pointing out the region where the system can only settle to a green monoculture. By contrast, if we like to distinguish between stationary and cyclic monocultures, regions [a] \cup [b] and [c] must be kept separated.

Studying the whole bifurcation diagram of figure 1 in the way outlined above, we find that it is possible to extract the basic information concerning green monocultures, cyanobacterial monocultures, and mixed cultures, that is, regions of grazing-mediated coexistence. From now on, the corresponding attractors will be indicated by G , C , and M , respectively. Figure 3A shows the G region, namely, the parameter values for which stable G monocultures exist. For low fish densities ($F < 0.003$), the pressure on zooplankton is not too high, and the attractor is characterized by periodic phytoplankton and zooplankton outbreaks, while for high F , the green monoculture is stationary, as predicted by a simple competition model (Scheffer et al. 1997a). Figure 3B shows, instead, the C region, which is simply delimited by a vertical bifurcation curve. The C attractor is always an equilibrium, characterized by absence of zooplankton. This fact can be immediately de-

duced from the zooplankton equation that shows that for $g = 0$ and very small values of z , the per capita rate of change of zooplankton is approximately given by

$$\frac{\dot{z}}{z} = \frac{e_{zc}r_z\alpha c}{h_z + \alpha c} - d_z - f$$

and is therefore negative even for large values of c since $e_{zc}r_z > d_z + f$. In other words, the nutritional value e_{zc} assigned for the moment to cyanobacteria is too low to allow zooplankton to invade a C monoculture (in the following, it is shown that this is not true for higher nutritional values e_{zc}). Finally, figure 3C shows the M region, where green algae can coexist with cyanobacteria. The region is characterized by intermediate values of nutrients and low values of fish. In one part of the region, the attractor is an equilibrium, that is, we have stationary coexistence, but in other parts, we find cyclic and chaotic coexistence. The fact that grazing-mediated coexistence is possible through a cyclic or even chaotic regime is consistent with previous studies on general two-prey-one-predator models (Vance 1978; Gilpin 1979; Noy-Meir 1981; Takeuchi and Adachi 1984; Klebanoff and Hastings 1994) and with more specific studies on plankton dynamics (Kretzschmar et al. 1993). Figure 4 shows the results of three simulations carried out

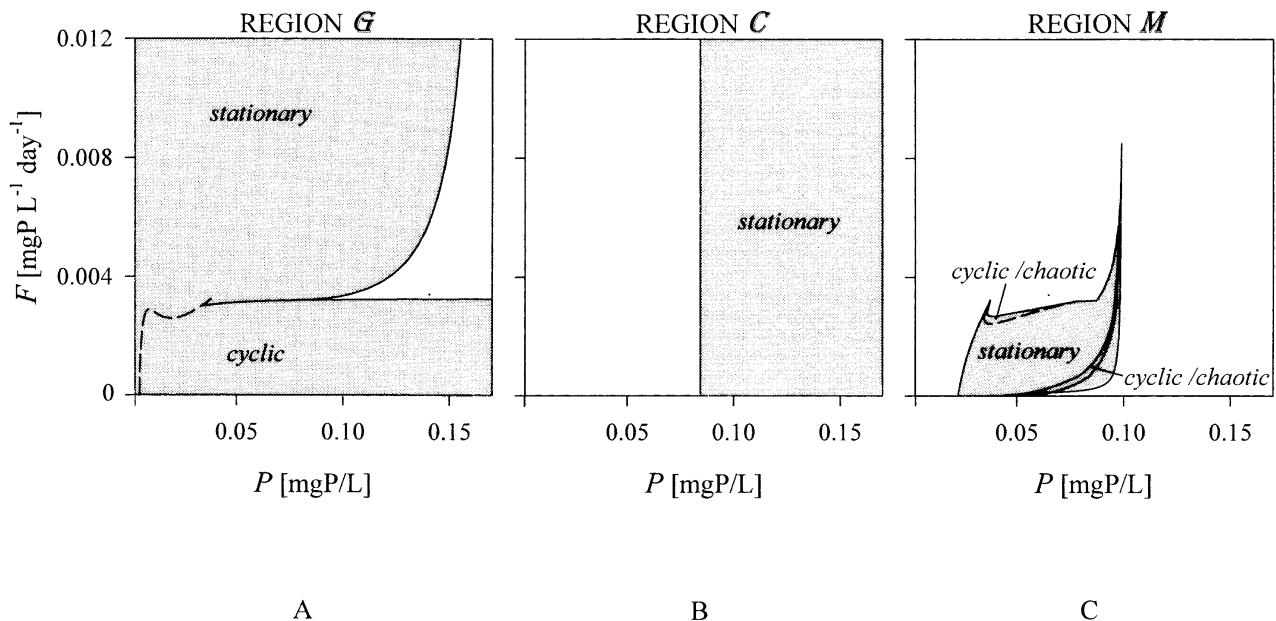


Figure 3: Regions G , C , and M obtained from figure 1. For parameter values in region G , the system can evolve toward a stable green monoculture, and such a monoculture is stationary for high fish predation rate and cyclic for low fish predation rate. For parameter values in region C , stable stationary cyanobacteria monocultures are possible. Finally, for parameter values in region M , mixed cultures are also possible. Notice that grazing-mediated coexistence can be stationary, cyclic, or chaotic.

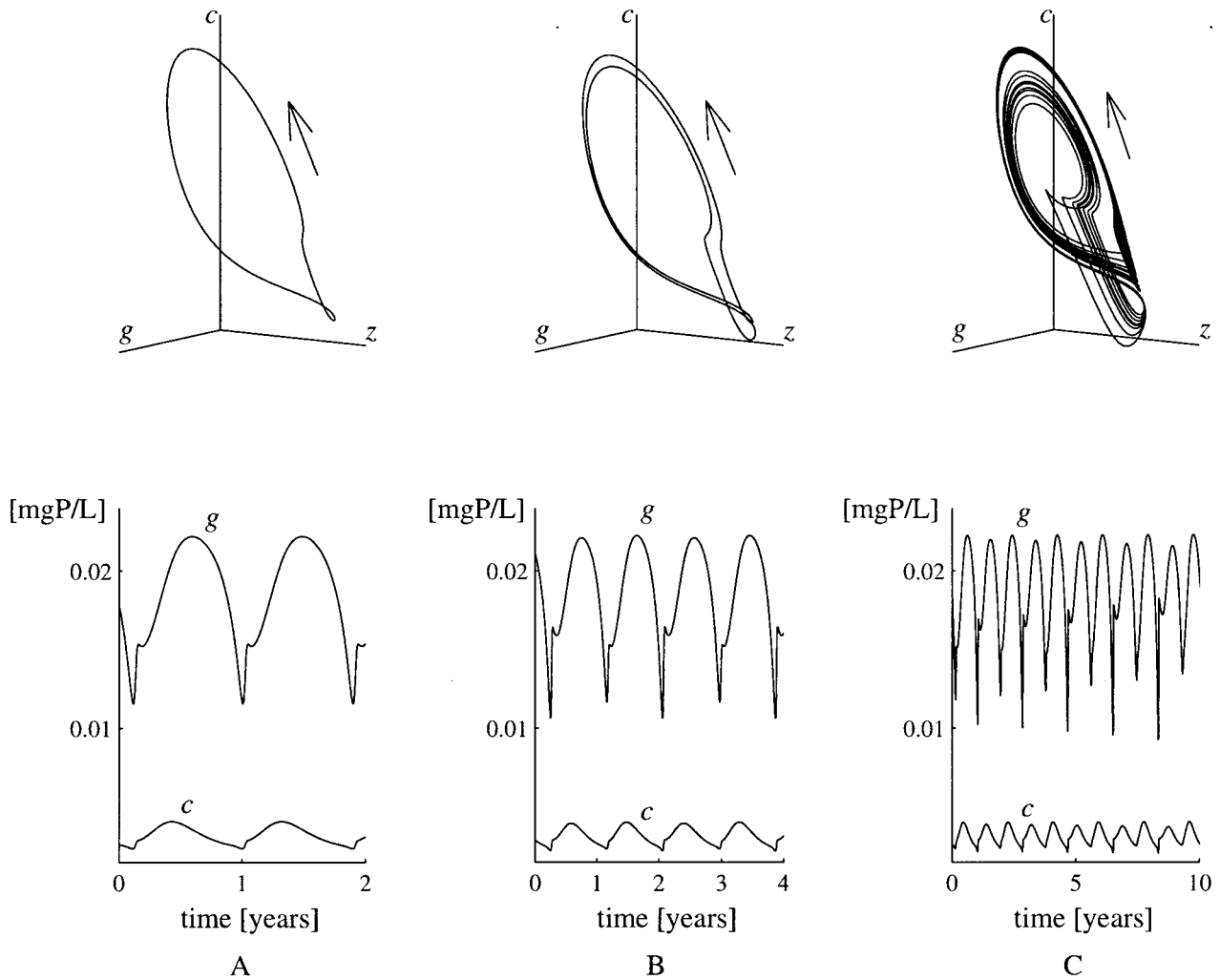


Figure 4: Examples of cyclic (A, B) and chaotic (C) coexistence. The attractors and the time series have been obtained by simulation with $P = 0.037$ and for increasing values of F in the neighborhood of the upper boundary of the M region of figure 3C: (A) $F = 0.259 \cdot 10^{-2}$; (B) $F = 0.2596 \cdot 10^{-2}$; (C) $F = 0.2597 \cdot 10^{-2}$. All other parameters are at their reference values (see table 1).

at constant P for increasing values of F in the neighborhood of the upper boundary of the M region. Figure 4A points out a limit cycle on which green algae and cyanobacteria coexist. This limit cycle has a period of about 1 yr and is therefore much longer than the standard phytoplankton-zooplankton cycles that have periods of about 1 mo. Moreover, green algae and cyanobacteria are slightly out of phase and have one pronounced outbreak per year. Also the two other scenarios reported in figure 4 have approximately one pronounced outbreak per year, but the attractor shown in figure 4B is still a cycle while that in figure 4C is a chaotic attractor.

The results of the analysis are summarized in figure 5, obtained by superimposing the three bifurcation diagrams

shown in figure 3. In doing this, we have eliminated all bifurcation curves separating stationary from cyclic and cyclic from chaotic regimes. Thus, figure 5 indicates only which attractors (G , C , or M) are present in each subregion but does not say if such attractors are equilibria, cycles, or chaotic attractors.

Region M where green algae and cyanobacteria can coexist is the striped region. Notice that nowhere in such a region is the M attractor a unique attractor because $G \cup C$ covers the entire parameter space (we will see in the following that this property does not hold for higher selectivities and nutritional values of cyanobacteria).

The dotted region in figure 5 is the region $G \cap C$ where both monocultures G and C are possible. If F is high and

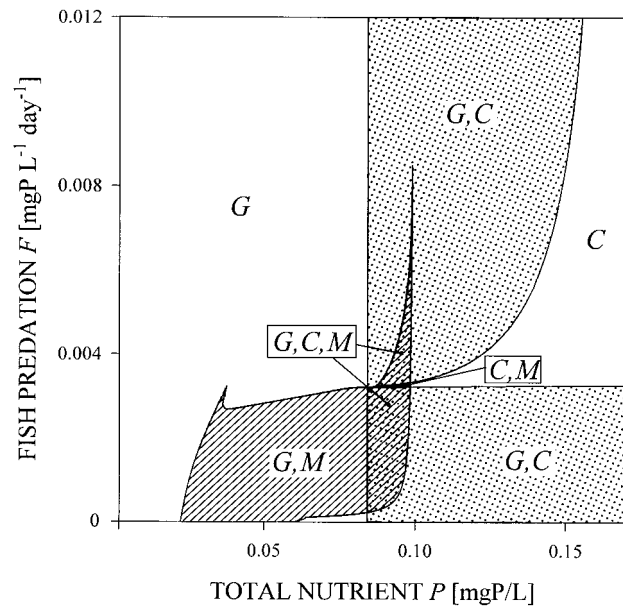


Figure 5: Superposition of the three graphs shown in figure 3. All bifurcation curves separating stationary from cyclic and cyclic from chaotic regimes have been eliminated. The attractors present in each region are identified by *G* (green monoculture), *C* (cyanobacterial monoculture), and *M* (mix of cyanobacteria and green algae). The striped section is region *M*, while the dotted section is region $G \cap C$, where both monocultures *G* and *C* are possible.

nutrients are increased, a *G* monoculture will sooner or later be replaced by a *C* monoculture. The transition from *G* to *C* occurs when the right boundary of the dotted region is crossed from the left. Once the system is settled on the *C* monoculture, the reverse transition can be obtained by reversing the control action, namely, by reducing nutrients, but the effort needed to get rid of cyanobacteria is quite large because the transition from *C* to *G* will occur only when the left boundary of the dotted region is crossed. Such an asymmetric control mechanism is often called "hysteresis" (Scheffer et al. 1997a).

In the regions that are both striped and dotted, there are three attractors: a green algae monoculture *G*, a cyanobacterial monoculture *C*, and a grazing-mediated coexistence *M*. Actually, the nature of these attractors can be different: for example, taking figure 3 into account, the reader can easily verify that *C* can be stationary, *G* cyclic, and *M* chaotic, a rather surprising result. In these regions, the system is particularly sensitive to noise because a shock (a flood, a release of a toxic substance, an epidemic, etc.) can suddenly transfer the state of the system from one basin of attraction into another basin of attraction so that, after a transient, the system will behave in a different way.

Finally, through a careful analysis of figure 1, one can

notice that all bifurcation curves appearing in figure 5 are catastrophic (we will see later that this is often the case). This implies that transitions from one attractor to another, as a result of small variations of the two control parameters, are accompanied by remarkable discontinuities of any water-quality indicator.

The results obtained up to now are all derived from figure 1, which is the bifurcation diagram of the model with respect to the two control parameters *P* and *F* for a given set of biological parameters. As already said, all biological parameters vary from lake to lake, but two of them, namely, selectivity (α) and nutritional value of cyanobacteria (e_{zc}), seem to be characterized by a particularly high variance. We use the model (eqq. [1–3]) to identify the role that these two parameters play. This can be done, once more, through bifurcation analysis, that is, by producing a bifurcation diagram similar to that of figure 1 for different values of the pair (α, e_{zc}) . We have therefore repeated our exercise increasing and decreasing α and e_{zc} with respect to the reference values used up to now, and we have produced, in particular, the diagrams analogous to that shown in figure 5. The result is shown in figure 6, where each diagram refers to a different pair (α, e_{zc}) . Selectivity decreases from left to right because the three columns correspond to increasing values of α (respectively 0.1, 0.5, 1), while nutritional value of cyanobacteria increases from bottom to top ($e_{zc} = 0.1$ in the lower row, and $e_{zc} = 0.5$ in the upper row). Thus, the diagram in figure 6E corresponds to $\alpha = 0.5$, $e_{zc} = 0.1$, and is therefore the bifurcation diagram reported in figure 5. A comparison of all the diagrams shows some interesting patterns.

1. The region of coexistence (striped region) increases with selectivity and decreases with nutritional value of cyanobacteria. Actually, for sufficiently high values of α and e_{zc} (fig. 6B, C, F), coexistence is not even possible and there are, at most, two attractors.

2. At high selectivity (fig. 6A, D), some of the boundaries of the coexistence region (striped region) are noncatastrophic. This implies, in particular, that a green algae monoculture can gradually be invaded by cyanobacteria by increasing nutrients or that a cyanobacterial monoculture can gradually become a mix by decreasing nutrients. Obviously, in this case also, turbidity varies smoothly with respect to nutrients.

3. For sufficiently high nutrients and fish (i.e., in the upper right corner of each diagram), the system settles irreversibly to a cyanobacterial monoculture *C*.

4. For sufficiently low nutrients (i.e., close to the *F*-axis), there is no chance for cyanobacteria to be present and the system settles to a green algae monoculture.

5. The shape of the left boundary of the dotted region (where both monocultures are possible) shows that one

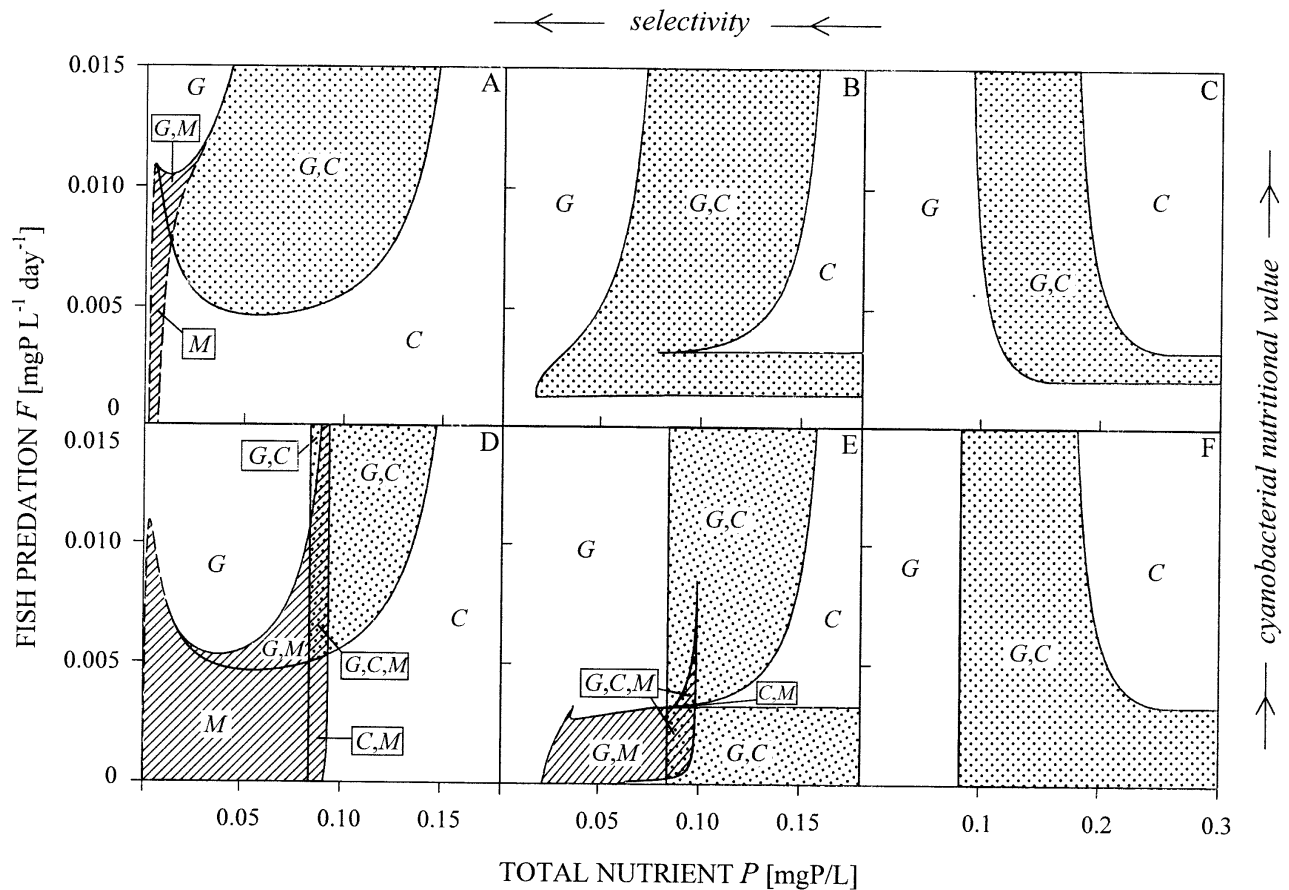


Figure 6: Bifurcation diagrams corresponding to different selectivities and cyanobacterial nutritional values. Selectivity decreases from left to right ($\alpha = 0.1, 0.5$, and 1 , respectively), while cyanobacteria nutritional value increases from bottom to top ($e_{zc} = 0.1$ and $e_{zc} = 0.5$, respectively). All other parameters are at their reference values (see table 1).

can always get rid of cyanobacterial monocultures (in the model) by reducing nutrient load. By contrast, a reduction of fish due to biomanipulation will be successful only if α and e_{zc} are sufficiently high (fig. 6B, C). For high nutritional values of cyanobacteria and high selectivity (fig. 6A, B), also an increase of fish can force the system to switch from a cyanobacterial monoculture to a green monoculture, but this can happen only if nutrients are not too high.

6. The range of nutrients characterizing the hysteresis between the two monocultures at high fish (i.e., the width of the dotted region) increases with selectivity and with nutritional value of cyanobacteria.

Discussion

Probably the most significant result of this article is the finding that edibility (defined as selectivity of the grazer

and nutritional value of the algae) can have widely different effects on community dynamics. Despite the enormous variation in behavior that can arise from the relatively small set of mechanisms represented in the model, some systematic trends can be distinguished. In this section, we highlight the major patterns and discuss their correspondence to field observations and existing theory. The majority of the following comments are extracted from figure 6, which, indeed, summarizes our analysis.

When fish predation pressure (F) is very high, the role of zooplankton is negligible and the model behaves as the simple competition model that we analyzed before (Scheffer et al. 1997a). In that case, there are only two possible attractors: one without green algae and one without cyanobacteria. These two situations are alternative attractors for a certain range of nutrient levels, implying hysteresis in the response to changes in nutrients. In short, this hysteresis is explained by the fact that the modeled filamen-

tous cyanobacteria of the *Oscillatoria* group are better competitors under turbid conditions, but also make the water more turbid, thus, reinforcing their own dominance.

When fish predation is reduced, allowing zooplankton to play a role, coexistence of green algae and cyanobacteria becomes possible (see fig. 6). The fact that grazing can mediate the coexistence of competing species has been noted in various theoretical studies before (Vance 1978; Noy-Meir 1981; Takeuchi and Adachi 1984). Indeed, although filamentous cyanobacteria have a tendency to be either absent or completely dominant in well-mixed lakes, they can also coexist with other algae (Scheffer et al. 1997a). Also, conspicuous coexistence of large-bodied *Daphnia* with large cyanobacterial filaments has been observed in field situations. In fish ponds in Czechoslovakia, for instance, the combination of extremely large (up to 20 mm) filaments of *Aphanizomenon flos-aquae* with large-bodied *Daphnia* was the most common type of summer plankton in the 1950s and 1960s (Pechar 1992). In view of the large filament size, it seems reasonable to assume that *Daphnia* would select strongly against this food. Also, coexistence of *Daphnia pulicaria* with filamentous cyanobacteria in North American lakes has been connected to experimentally demonstrated high selectivity of the feeding (Epp 1996). These observations are well in line with the fact that the model predicts such coexistence to be possible only if cyanobacterial nutritional value is low and/or selectivity of grazers is high (fig. 6).

The attractors of the model can be stationary but also cyclic or even chaotic. Oscillations occur only when fish predation (F) is low enough so that zooplankton can play a major role. At very low nutrient levels, green monocultures are stationary even if there is little fish predation. Enriching the system (increasing P), we find that the stability of the equilibrium soon disappears and the attractor becomes cyclic. This is a well-known phenomenon described in the classical "paradox of enrichment" paper (Rosenzweig 1971). Increasing fish, such cycles inevitably disappear again, and the system shifts to a stable equilibrium with very low zooplankton densities as described in detail elsewhere (Scheffer 1991; M. Scheffer, S. Rinaldi, and Y. A. Kuznetsov, unpublished manuscript) for models with only edible algae. The tendency of the model to oscillate also decreases when cyanobacteria become involved as found in other theoretical analyses (Kretzschmar et al. 1993). Especially the attractor without any green algae is almost always stationary (except for a very narrow range of conditions when cyanobacteria are sufficiently nutritious and consumed by zooplankton). The attractor in which both algal groups coexist tends to be stationary but can also be cyclic. As explained in the previous section, the cycles in this mixed attractor are of a different nature than the classical zooplankton-algae oscillations. They

have a period of about 1 yr (as opposed to about 1 mo for the cycles of the attractors with only one algal type) and can evolve into chaotic dynamics for some conditions, as found for other models of a predator with two competing prey (Vance 1978; Takeuchi and Adachi 1984; Klebanoff and Hastings 1994).

A general point of interest with respect to the response of the system to manipulation of fish and nutrients is that almost all transitions between different attractors of the model are catastrophic. Thus when fish or nutrients are varied, the system tends to stay in the same attractor until a critical point is reached at which that attractor loses stability and a jump to another attractor with a different algal composition and a different turbidity occurs. Reversing the change in fish or nutrients, the system shows hysteresis, that is, it remains in the newly achieved attractor until another critical point is reached where another catastrophic transition occurs. Note that for some parameter settings all three attractors can be simultaneously present, implying that, under the same conditions in terms of fish and nutrients, the system may be characterized by cyanobacteria, green algae, or a mix, depending on the history. Hysteresis between the two monocultures with respect to nutrients can disappear only when grazing is strongly selective and the fish community is relatively low (fig. 6A, D). When in this case cyanobacteria are also nutritious enough to allow zooplankton to develop in a cyanobacterial monoculture (fig. 6A), the transition from green to cyanobacterial monocultures and vice versa is entirely smooth (i.e., noncatastrophic). Obviously, at high fish densities, when zooplankton is repressed, the original hysteresis with respect to nutrients remains.

One of the most consistent patterns in the analysis is that the upper right-hand corner of the bifurcation diagrams always contains solely the cyanobacterial attractor. This result is in line with the many studies showing that cyanobacteria tend to dominate at eutrophic situations with high fish stocks but often disappear when fish and nutrients are reduced. Note, that it is only the combination of high fish and high nutrients that guarantees cyanobacterial dominance in this model. When nutrients are low enough, cyanobacteria are consistently absent.

Only when zooplankton is not too selective and cyanobacteria are nutritious (fig. 6B, C), the model predicts that a sufficiently strong reduction of fish predation pressure can allow zooplankton to eliminate cyanobacteria, even at high nutrient concentrations. This result is well in line with an analysis of the results of 47 experiments manipulating predation and/or nutrient levels in plankton systems (Leibold 1989), showing that, only when relatively nonselective *Daphnia* dominate the zooplankton, the abundance of "grazing-resistant" algae is significantly related to the presence of fish.

Interestingly, the model suggests that not only a decrease but also an increase in fish may cause a switch from cyanobacteria to other algae in some situations (fig. 6A, B). Thus grazing may favor but also eliminate cyanobacteria, and under some conditions, cyanobacterial dominance is actually limited to situations with intermediate grazing pressure (fig. 6B). The fact that grazing can have opposite effects may be understood from the operation of two different mechanisms in the model. On the one hand, selective grazing may, obviously, shift the competitive balance in favor of cyanobacteria because it affects the other algae relatively more. On the other hand, large cyanobacteria have slow growth rates and are therefore relatively sensitive to increases in the loss rate (grazing, sinking, flushing). The latter is illustrated by the fact that cyanobacteria tend to be replaced by other, faster-growing algae in situations where losses from the lake due to flushing are high (Scheffer et al. 1997a).

Indeed, these two opposite effects of grazing on the competition between cyanobacteria and other algae are also reflected in the results of various field and laboratory studies as explained in the introduction. On the one hand, the shift to cyanobacteria that often occurs after the spring peak of *Daphnia* is usually attributed to the elimination of competing edible algae by selective grazing. On the other hand, *Daphnia* are often observed to eliminate cyanobacteria when fish predation is sufficiently low, and under high zooplankton grazing pressure, the phytoplankton is typically dominated by edible but fast-growing algal species.

Obviously, the overall effect of grazing on the competitive balance depends critically on the selectivity of the grazers. If grazing is entirely nonselective, populations of large cyanobacteria will be more affected than other faster-growing algae, whereas in situations where cyanobacteria are not eaten at all, grazing will merely favor them. Selectivity varies strongly with the individual size of zooplankton. On the one hand, small animals select smaller algae and seem to be relatively little affected by the presence of cyanobacterial filaments. Since the summer zooplankton community is typically dominated by small animals in most lakes, grazing is likely to be strongly selective indeed and thus favor dominance by unpreferred cyanobacteria as suggested by many authors. On the other hand, large *Daphnia* species that usually dominate when fish predation is very low are less selective, and the fact that cyanobacteria are often eliminated in such situations is not surprising in view of the model results. In practice, selectivity of zooplankton grazing will thus be correlated to predation pressure from fish, favoring cyanobacterial dominance in situations with high fish densities when zooplankters are typically small and selective. The model, however, shows that also in the absence of such a corre-

lation between fish predation and zooplankton selectivity there is a tendency for cyanobacteria to be favored by intermediate but not by high grazing pressure.

In our analysis, we distinguished between selectivity and nutritional value as two aspects of inedibility. These two factors imply a negative effect of cyanobacteria on zooplankton only through decreases in the availability of qualitatively good food. As mentioned in the introduction, some cyanobacteria may excrete substances that reduce the filtration rates of zooplankton, and it has also been noted that filamentous cyanobacteria may hinder *Daphnia* by clogging its filtration system. However, in our model, such interference does not affect the range of qualitative results, as we have checked by adding an extra interference term in the model. The main effect of interference on the model results is that it allows the attractor of coexistence of cyanobacteria and other algae to extend up to a higher nutrient concentration.

Several parameters have been kept constant in the current analysis. Earlier work on separate parts of the model may serve to briefly illustrate the robustness to assumptions on the value of various parameters. First, it should be noted that the hysteresis in algal competition is a rather robust property of the model. In the absence of grazers, it can be proven to exist for any set of parameter values satisfying the condition that cyanobacteria have a lower maximum productivity (r), loss rate (d), and sensitivity to turbidity (q) but cause a higher turbidity per unit of nutrients (k) than the other algae (Scheffer et al. 1997a). The collapse of zooplankton in response to increasing fish predation is another relatively robust underlying mechanism discussed extensively in earlier work (Scheffer 1991, 1998). The flush rate (f) is a parameter of special interest as it is quite influential to the balance in the competition between cyanobacteria and other algae. As discussed in our previous analysis of the version of the model without zooplankton (Scheffer et al. 1997a), an increase of the flush rate can be a way to break dominance by relatively slow-growing cyanobacteria. The model without zooplankton predicts that beyond a flush rate of approximately 18% of the lake volume per day, cyanobacteria should be absent irrespective of the nutrient level. This fits well with the observation of Danish workers that large cyanobacteria are not found in lakes with a hydraulic residence time of less than 5 d (E. Jeppesen, personal communication).

In conclusion, the most interesting model parameters from the management point of view are the flush rate, the nutrient level, and the fish density because these can be manipulated in attempts to get rid of nuisance blooms of cyanobacteria. Our analyses suggest that the potential success of fish stock manipulation and nutrient control depends strongly on the selectivity with which cyanobacteria are excluded from the diet of zooplankton and the nu-

tritional value of cyanobacteria. Since in practice selectivity and nutritional value seem to differ strongly from case to case, it is not surprising that field patterns and lab results on the effect of top-down control of cyanobacteria are so variable. Our results suggest that a better analysis of nutritional value and selectivity might help to explain this puzzling variability in future work.

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Literature Cited

- Abrams, P. A. 1993. Effect of increased productivity on the abundances of trophic levels. *American Naturalist* 141: 351–371.
- Armstrong, R. A. 1979. Prey species replacement along a gradient of nutrient enrichment: a graphical approach. *Ecology* 60:76–84.
- Arnold, D. E. 1971. Ingestion, assimilation, survival, and reproduction of *Daphnia pulex* fed seven species of blue-green algae. *Limnology and Oceanography* 16:906–920.
- Berger, C. 1975. Occurrence of *Oscillatoria agardhii* Gom. in some shallow eutrophic lakes. *Verhandlungen Internationale Vereinigung Theoretisch Angewandte Limnologie* 19:2689–2697.
- Boon, P. I., S. E. Bunn, J. D. Green, and R. J. Shiel. 1994. Consumption of cyanobacteria by freshwater zooplankton: implications for the success of “top-down” control of cyanobacterial blooms in Australia. *Australian Journal of Marine and Freshwater Research* 45:875–887.
- Camerano, L. 1880. Dell'equilibrio dei viventi merce la reciproca distruzione. *Accademia delle Scienze di Torino* 15:393–414. (This work was translated into English by C. M. Jacobi and J. E. Cohen, trans., 1994. On the equilibrium of living beings by means of reciprocal destruction. Pages 360–380 in S. A. Levin, ed. *Frontiers in mathematical biology*.)
- Canfield, D. E., Jr., and C. E. I. Watkins. 1984. Relationships between zooplankton abundance and chlorophyll-*a* concentrations in Florida lakes. *Journal of Freshwater Ecology* 2:335–344.
- Codd, G. A. 1995. Cyanobacterial toxins: occurrence, properties and biological significance. *Water Science and Technology* 32:149–156.
- De Bernardi, R., and G. Giussani. 1990. Are blue-green algae a suitable food for zooplankton? an overview. *Hydrobiologia* 200/201:29–41.
- Elser, J., T. H. Chrzanowski, R. W. Sterner, and K. H. Mills. 1998. Stoichiometric constraints on food-web dynamics: a whole-lake experiment on the Canadian shield. *Ecosystems* 1:120–136.
- Epp, G. T. 1996. Grazing on filamentous cyanobacteria by *Daphnia pulicaria*. *Limnology and Oceanography* 41: 560–567.
- Gilpin, M. E. 1979. Spiral chaos in a predator-prey model. *American Naturalist* 113:306–308.
- Gliwicz, Z. M. 1990. Why do cladocerans fail to control algal blooms? *Hydrobiologia* 200/201:83–98.
- Gliwicz, Z. M., and W. Lampert. 1990. Food thresholds in *Daphnia* species in the absence and presence of blue-green filaments. *Ecology* 71:691–702.
- Hairton, N., F. E. Smith, and D. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- Haney, J. F., D. J. Forsyth, and M. R. James. 1994. Inhibition of zooplankton filtering rates by dissolved inhibitors produced by naturally occurring cyanobacteria. *Archiv für Hydrobiologie* 132:1–13.
- Hawkins, P., and W. Lampert. 1989. The effect of *Daphnia* body size on filtering rate inhibition in the presence of a filamentous cyanobacterium. *Limnology and Oceanography* 34:1084–1089.
- Holt, R. D. 1977. Predation apparent competition and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- . 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124:377–406.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* 144: 741–771.
- Hosper, S. H., and M. L. Meijer. 1993. Biomanipulation, will it work for your lake? a simple test for the assessment of chances for clear water, following drastic fish-stock reduction in shallow, eutrophic lakes. *Ecological Engineering* 63–72.
- Huisman, J., and F. J. Weissing. 1994. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. *Ecology* 75:507–520.
- Khibnik, A. I., Y. A. Kuznetsov, V. V. Levitin, and E. V. Nikolaev. 1993. Continuation techniques and interactive software for bifurcation analysis of ODEs and iterated maps. *Physica D* 62:360–370.
- Kirk, J. T. O. 1983. *Light and photosynthesis in aquatic ecosystems*. Cambridge University Press, Cambridge.
- Klebanoff, A., and A. Hastings. 1994. Chaos in one-predator, two prey models: general results from bifurcation theory. *Mathematical Biosciences* 122:221–233.
- Kretzschmar, M., R. M. Nisbet, and E. McCauley. 1993. A predator-prey model for zooplankton grazing on com-

- peting algal populations. *Theoretical Population Biology* 44:32–66.
- Lammens, E. H. R. R. 1985. A test of a model for planktivorous filter feeding by bream *Abramis brama*. *Environmental Biology of Fishes* 13:289–296.
- Lammens, E. H. R. R., H. W. DeNie, J. Vijverberg, and W. L. T. Densens. 1985. Resource partitioning and niche shifts of bream (*Abramis brama*) and eel (*Anguilla anguilla*) mediated by predation of smelt (*Osmerus eperlanus*) on *Daphnia hyalina*. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1342–1351.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134:922–949.
- . 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* 147:784–812.
- Matsamura, T., and Y. Sakawa. 1980. Non-linear analysis of nitrogen cycle in aquatic ecosystems. *International Journal of Systems Sciences* 7:803–816.
- Matveev, V., L. Matveeva, and G. J. Jones. 1994. Study of the ability of *Daphnia carinata* King to control phytoplankton and resist cyanobacterial toxicity: implications for biomanipulation in Australia. *Australian Journal of Marine and Freshwater Research* 45:889–904.
- McCauley, E., and F. Briand. 1979. Zooplankton grazing and phytoplankton species richness: field tests of the predation hypothesis. *Limnology and Oceanography* 24:243–252.
- Mills, E. L., and J. L. Forney. 1983. Impact on *Daphnia pulex* of predation by young yellow perch *Perca flavescens* in Oneida Lake, New York. *Transactions of the American Fisheries Society* 112:154–161.
- Mur, L. R., H. J. Gons, and L. Van Liere. 1977a. Some experiments on competition between green-algae and blue-green bacteria in light-limited environments. *Fems Microbiology Letters* 1:335–338.
- . 1977b. Licht als regulerende factor bij het optreden van waterbloei van het blauwwier *Oscillatoria agardii*. *H2O* 10:309–313.
- Noy-Meir, I. 1981. Theoretical dynamics of competitors under predation. *Oecologia* 50:277–284.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118:240–261.
- Pechar, L. 1992. Water blooms of *Aphanizomenon flos aquae* an ecological study of fish pond populations. *Archiv für Hydrobiologie Supplementband* 90:339–418.
- Reinikainen, M., M. Ketola, and M. Walls. 1994. Effects of the concentrations of toxic *Microcystis aeruginosa* and an alternative food on the survival of *Daphnia pulex*. *Limnology and Oceanography* 39:424–432.
- Reynolds, C. S. 1984. *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge.
- Riegman, R., and L. R. Mur. 1984. Theoretical considerations on growth kinetics and physiological adaptation of nutrient-limited phytoplankton. *Archiv für Microbiologie* 140:96–100.
- Rose, E. T., and T. Moen. 1952. The increase in game-fish populations in east Okoboji Lake, Iowa, following intensive removal of rough fish. *Transactions of the American Fisheries Society* 82:104–114.
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387.
- . 1973. Exploitation in three trophic levels. *American Naturalist* 107:275–294.
- Sarnelle, O. 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology* 73:551–560.
- . 1993. Herbivore effects on phytoplankton succession in a eutrophic lake. *Ecological Monographs* 63:129–149.
- Sas, H. 1989. *Lake restoration by reduction of nutrient loading: expectations, experiences, extrapolations*. Academia Verlag Richarz, St. Augustin.
- Scavia, D., G. A. Lang, and J. F. Kitchell. 1988. Dynamics of Lake Michigan plankton: a model evaluation of nutrient loading competition and predation. *Canadian Journal of Fisheries and Aquatic Sciences* 45:165–177.
- Scheffer, M. 1991. Fish and nutrients interplay determines algal biomass: a minimal model. *Oikos* 62:271–282.
- . 1998. *Ecology of shallow lakes*. Chapman & Hall, New York.
- Scheffer, M., and R. J. De Boer. 1995. Implications of spatial heterogeneity for the paradox of enrichment. *Ecology* 76:2270–2277.
- Scheffer, M., S. Rinaldi, A. Gragnani, L. R. Mur, and E. H. Van Nes. 1997a. On the dominance of filamentous cyanobacteria in shallow turbid lakes. *Ecology* 78:272–282.
- Scheffer, M., S. Rinaldi, Y. A. Kuznetsov, and E. H. Van Nes. 1997b. Seasonal dynamics of *Daphnia* and algae explained as a periodically forced predator-prey system. *Oikos* 80:519–532.
- Schindler, D. W. 1975. Whole-lake eutrophication experiments with phosphorus, nitrogen and carbon. *Verhandlungen Internationale Vereinigung Theoretisch Angewandte Limnologie* 19:3221–3231.
- Smith, V. H. 1986. Light and nutrient effects on the relative biomass of blue-green algae in lake phytoplankton. *Canadian Journal of Fisheries and Aquatic Sciences* 43:148–153.
- Sommer, U., Z. M. Gliwicz, W. Lampert, and A. Duncan. 1986. The Plankton Ecology Group model of seasonal

- succession of planktonic events in fresh waters. *Archiv für Hydrobiologie* 106:433–472.
- Sterner, R. W., J. J. Elser, E. J. Fee, S. J. Guildford, and T. H. Chrzanowski. 1997. The light : nutrient ratio in lakes: the balance of energy and materials affects ecosystems structure and process. *American Naturalist* 150: 663–684.
- Takeuchi, Y., and N. Adachi. 1984. Existence and bifurcation of stable equilibrium in two prey one predator communities. *Bulletin of Mathematical Biology* 45: 877–900.
- Trimbee, A. M., and E. E. Prepas. 1987. Evaluation of total phosphorus as a predictor of the relative biomass of blue-green algae with emphasis on Alberta lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 1337–1342.
- Van Liere, L., and L. R. Mur. 1979. Growth kinetics of *Oscillatoria agardii* in continuous culture limited in its growth by the light energy supply. *Journal of General Microbiology* 115:153–160.
- Vance, R. R. 1978. Predation and resource partitioning in one predator–two prey model communities. *American Naturalist* 112:797–814.
- Watson, S., E. McCauley, and J. A. Downing. 1992. Sigmoid relationships between phosphorus algal biomass and algal community structure. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2605–2610.

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