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Water Control Policies in Lakes with Vertical Heterogeneity: an Algal Competition Modelling Approach.

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Abstract— **The algal competition between blue-green algae (cyanobacteria) and green algae (chlorophytes) is a topic that is widely treated both from the biological point of view and from that of the ecological modelling. The spread of blue-green algae in fresh waters, in fact, represents a problem of great interest linked to the quality of water and to the production by these organisms of cyanotoxins particularly toxic not only for the flora and fauna but also for humans. Moreover, blue-green algal blooms are associated with high levels of water turbidity and, due to their inedibility, less ecosystem biodiversity. Several models have been proposed to test algal competition and to propose different control strategies on the ecosystem that can lead to the disappearance of blue-green algae with consequent dominance of green algae. However, these models relate to spatially homogeneous lakes. Here, a more realistic algal competition model in a heterogeneous lake is proposed, by introducing a vertical stratification in the water body and assuming that organisms and nutrients can migrate (with mixing rate *D*) from the lower to the upper compartment and vice-versa. The analysis of the model not only shows that small/medium mixing rate *D* can promote algal coexistence, but also provides useful suggestions for the control of water quality that differ to a large extent from what has been achieved in the case of lake homogeneity.**

I. Introduction

THE interest directed towards the problem of algal competition and algal shift between blue-green algae (cyanobacteria) and green algae (chlorophytes) lies in the important environmental implications associated with the prevalence of one or the other species in aquatic ecosystems [1]. In particular, blue-green dominance is considered an important problem by water quality managers: blue-green algae are responsible for high levels of water turbidity (less light is available for aquatic plant growth); they have a low nutritional value and a low edibility for their grazers (typically zooplankton); they produce cyanotoxins particularly toxic also for humans.

In the literature there are several models and several biological studies ([2] and references therein) that try to reproduce the lake ecosystem affected by algal competition, trying to determine what are the control actions to be taken to avoid the dominance of blue-green algae or to limit their proliferation. In most of the models it is supposed that the lake is constituted by a single basin perfectly mixed, without any type of horizontal or vertical stratification. For example, in [3] an algal competition model in a homogenous lake is proposed and its analysis shows that algal community is a hysteretic system with competitive exclusion: only two alternative equilibria are possible, i.e., green dominance and blue-green dominance. Two control parameters, nutrient input P_0 and flush-rate δ determine water quality. In particular, blue-green dominance can be prevented by decreasing P_0 and/or increasing δ.

Nevertheless, the monoculture behaviour is an artefact of the simple proposed model [4]. Several studies have shown that temporal variation in the environment [5,6], increased complexity in the food chain [7] or horizontal/vertical lake heterogeneity [8, 9] help prevent competitive exclusion, and it is reasonable to assume that each of these factors if not all play an important role in algal communities. Through a modelling approach, the role of zooplankton species grazing on algal communities [10] and the effects of horizontal heterogeneity on water quality shifts [11] have been already investigated, while seasonality and vertical heterogeneity of the fate of lake ecosystems are still missing.

Therefore, a more realistic algal competition model in a lake is here proposed, by introducing a vertical stratification in the water body and assuming that organisms and nutrients can migrate (with mixing rate D) from the lower to the upper compartment and vice-versa.

The aim of the paper is not only to show that small/medium mixing D can promote algal coexistence, but also to provide useful suggestions for the control of water quality that differ to a large extent from what has been achieved in the case of spatial lake homogeneity.

The proposed model can then be used for further analysis on the role of seasonality in water quality.

The paper is organized as follows: in the next section the algal competition model with spatial heterogeneity is formulated; then, by a complete bifurcation analysis, its behaviour is classified with respect to parameters useful to control water quality: input nutrient intake P_0, flush-rate δ and mixing rate D. Obtained results will allow in the Conclusions to derive the guidelines to be followed to better manage the ecosystem ensuring the best water quality: green dominance or, if not possible, low turbidity conditions).

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I. Model Formulation

Consider a lake stratified in two different compartments: shallow (or superior *S*) and deep (or inferior *I*). In each compartment only green (*G*) and blue-green (*B*) algae are present [3] but only *S* compartment is subject to flush-rate (δ) and nutrient input P_0 (typically phosphorus *P*). A continuous slight mixing (*D*) between the two compartments is also present causing a small input/output of *G*, *B* and available (free) nutrient P_f between each region (see Fig. 1).

State variables are the following:

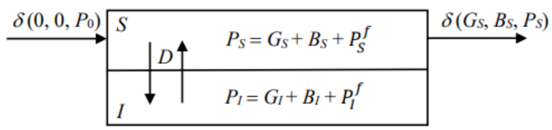

Fig. 1. A schematic representation of a stratified lake

P_S (P_I) = total nutrient concentration in *S* (*I*) compartment [mgP/L]

G_S (G_I) = green algal concentration in *S* (*I*) compartment [mgP/L]

B_S (B_I) = blue-green algal concentration in *S* (*I*) compartment [mgP/L]

Equations describing the variations in time of the state variables are written as mass balance equations. In particular, algal equations are written considering algal productivity due to nutrients and light availability and losses due to mortality, respiration, and flushing. As for the dependence of the productivity upon the available (free) nutrient concentrations (P_S^f or P_I^f, in *S* or *I* compartment) we take the classical Monod form with a half-saturation concentration (*h*). The dependence of productivity on light conditions is more complicated to write. Nevertheless, it is obvious that in a lake the availability of light and, therefore, the relative algal productivity decreases with turbidity *E* (which in turns depends on the material presents in the suspension of the water body).

The complete model then becomes:

$$\dot{P}_S = \delta P_0 - \delta P_S + D(G_I - G_S) + D(B_I - B_S) + \\ +D\left(P_I^f - P_S^f\right) = \delta P_0 - \delta P_S + D(P_I - P_S)$$

$$\dot{P}_I = D(G_S - G_I) + D(B_S - B_I) + D\left(P_S^f - P_I^f\right) = \\ = D(P_S - P_I)$$

$$\dot{G}_S = r_G G_S \frac{P_S^f}{h+P_S^f}\frac{1}{1+q_G E_S} - d_G G_S - \delta G_S - D(G_S - G_I)$$

$$\dot{B}_S = r_B B_S \frac{P_S^f}{h+P_S^f}\frac{1}{1+q_B E_S} - d_B B_S - \delta B_S - D(B_S - B_I)$$

$$\dot{G}_I = r_G G_I \frac{P_I^f}{h+P_I^f}\frac{1}{1+q_G E_I} - d_G G_I - D(G_I - G_S)$$

$$\dot{B}_I = r_B B_I \frac{P_I^f}{h+P_I^f}\frac{1}{1+q_B E_I} - d_B B_I - D(B_I - B_S)$$

where

$P_S^f = P_S - G_S - B_S$ = available nutrient in *S* compartment [mgP/L]

$P_I^f = P_I - G_I - B_I$ = available nutrient in *I* compartment [mgP/L]

$E_S = k_G G_S + k_B B_S$ = turbidity in *S* compartment [m^{-1}]

$E_I = k_G(G_S+G_I) + k_B(B_S + B_I)$ = turbidity in *I* compartment [m^{-1}]

(background turbidity due to other suspended material has been neglected)

As for parameter meaning and the corresponding units of measurement (in square brackets), we have:

δ = flush-rate [d^{-1}]

P_0 = nutrient input [mgP/L]

D = mixing rate [d^{-1}]

r_G (r_B) = maximum growth rate of green (blue-green) algae [d^{-1}]

h = half-saturation constant [mgP/L]

q_G (q_B) = shade sensitivity of green (blue-green) algae [m]

d_G (d_B) = loss rate of green (blue-green) algae [d^{-1}]

k_G (k_B) = extinction coefficient for green (blue-green) algae

Moreover,

δP_0 = nutrient inflow in *S* compartment

δP = nutrient outflow from *S* compartment

$D(P_I - P_S)$ = nutrient exchange between compartments due to mixing *D*

$D(G_S - G_I)$ = green algae exchange between compartments due to mixing *D*

$D(B_S - B_I)$ = blue-green algae exchange between compartments due to mixing *D*

As for initial conditions, the following settings must be satisfied:

$G_S(0) + B_S(0) \le P_S(0)$ and $G_I(0) + B_I(0) \le P_S(0)$

For parameterization (see Table I), data from experiments with *Planktothrix agardhii* and *Scendesmus protuberans* were used as examples of the two respective groups [12-17].

TABLE I

Symbol	Quantity
r_G	1.2
r_B	0.6
q_G	2
q_B	1
d_G	0.12
d_B	0.06
k_G	5
k_B	10
h	0.003

TableI. Values of the parameters used to produce the figures.

Parameters P_0, δ and *D* are free to move because they are the parameters on which it is possible to act to control the ecosystem in order to favour situations of green algae dominance or, where it is not possible, of a good water quality, i.e. low turbidity both in *S* and *I* compartment.

As a remark, at equilibrium $\dot{P}_j = 0$ so that $P_j(t)$ tends to P_0 (for *j* = *S*, *I*). Nevertheless, the first two equations are left in the model due to the fact that, in further investigations, parameters P_0 and D might be periodically varied (for example, P_0 as a result of human activity, D as a result of water temperature variation).

Notice that homogenous case [3] corresponds to very high values of mixing rate D, while $D = 0$ describes the case in which there is no mixing between superior and inferior compartments (if so, one could expect that S compartment behaves as the homogenous case, while in the I compartment, B algae are dominant due to an excess of turbidity that comes from the material in the upper area).

II. Model Analysis

Assuming D high (a nearly homogeneous lake), we can expect alternative dominance of G or B algae in both S and I compartment and a hysteretic behavior depending on the values of P_0 and δ (see Fig. 2, analogous to Fig. 9 in [3]).

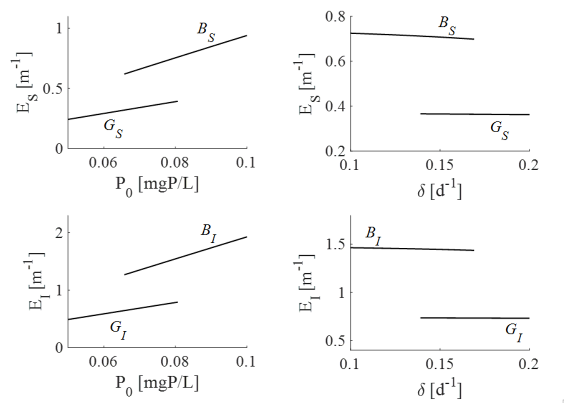

Fig. 2. Hysteresis in the turbidity (E) for S and I compartment (upper and lower row), with respect to the control parameters nutrient input (P_0) and flush-rate (δ) (left and right column). Left (right) column: $\delta = 0.15$ ($P_0 = 0.075$). A high value of D ($D = 0.1$) corresponds to a nearly homogenous lake.

Starting from a point of alternative dominance and introducing a slight mixing in the lake ($D = 0.01$), an algal coexistence in both compartments will occur (Fig. 3). This result confirms the hypothesis that coexistence could be favored in spatially heterogeneous lakes.

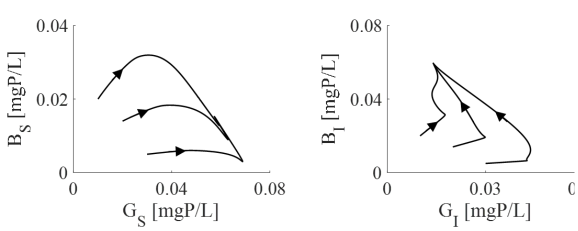

Fig. 3. Trajectories for $P_0 = 0.08$, $\delta = 0.15$ and $D = 0.01$ (heterogenous lake). Both compartments are now characterized by algal coexistence.

The hysteretic behaviour is still present also in the heterogenous case with respect to both control parameters P_0 and δ (Fig. 4). In both cases hysteresis no longer involves the dominant equilibrium of green algae but that of mixed algal coexistence. It could also be noticed that the introduction of a slight mixing in the lake results in hysteresis for higher P_0 values or lower delta values than in the homogeneous case. The turbidity finally worsens, especially in the deep compartment.

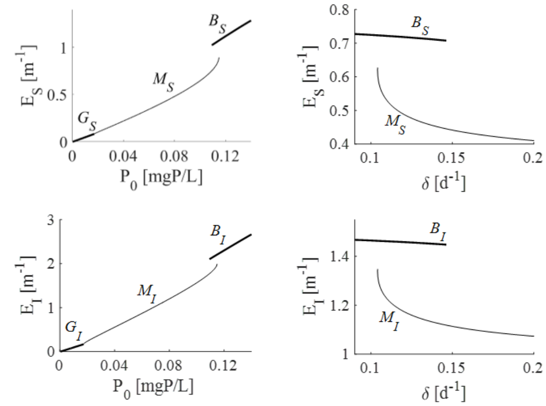

Fig. 4. Hysteresis in the turbidity (E) for S and I compartment (upper and lower row), with respect to the control parameters nutrient input (P_0) and flush-rate (δ) (left and right column) for an heterogenous lake with $D = 0.01$. Left (right) column: $\delta = 0.15$ ($P_0 = 0.075$). Solid (thin) lines correspond to G/B monocultures (mixed coexistence).

In order to better and more rigorously understand these behaviours, we now proceed by making a complete bifurcation analysis of the system [18-20] with respect to the control parameters P_0, D and δ. This will allow us to identify ecosystem behaviours for all possible parametric combinations and, in particular, to understand what control actions need to be taken to ensure the dominance of green algae or, if this is not possible, good water quality (i.e., low turbidity, for example associated with a situation of algal coexistence).

The results of the bifurcation analysis with respect to P_0 and D ($\delta = 0.15$) are shown in Fig. 5. The bifurcation curves (saddle-node SN and transcritical TC) divide the parameter space into eight regions, in each of which the system is characterized by a particular set of attractors, saddles and repellors. It would be boring for the reader to follow a complete discussion of the diagram; therefore, only attractors are shown using simplified sketches.

Regions 1, 2, and 4 are characterized by a unique attractor toward which the system converges for any initial condition: blue/green coexistence, green dominance, and blue dominance, respectively. On the contrary, regions 3, 5 and 6 are characterized by multiple attractors: blue/green coexistence and blue dominance in region 3, blue or green dominance in region 5 (which corresponds to the homogenous lake), blue/green coexistence and green dominance in region 6. In these cases, depending upon initial conditions the system may tend toward an attractor or another.

The regions are bounded by continuous or dashed curves. Continuous curves are catastrophic curves: crossing these curves would result in a sudden change of behavior of the system. For example, starting from a point in region 3 with the system in a mixed behavior, an increase of nutrient inflow

P_0 causing a transition to region 4 would imply a sudden change in system's behavior to a blue dominance and, as a consequence, a sudden worsening of water turbidity. On the contrary, dashed curves are noncatastrophic bifurcation curves: crossing these curves would result in a continuous change of the behavior of the system and of its turbidity. For example, increasing the mixing rate D, causing a transition from region 1 to region 2, would result in a gradual disappearance of blue-green algae from the initial situation of algal coexistence.

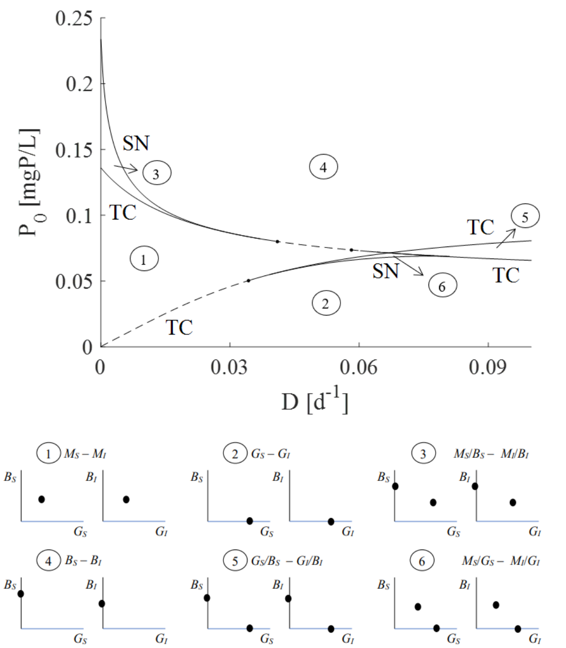

Fig. 5. Bifurcation diagram in (P_0, D) parameter space for $\delta = 0.15$. TC = transcritical bifurcations, SN = saddle-node bifurcations. Dashed (continuous) curves refer to noncatastrophic (catastrophic) bifurcations. For each region, attractors only are shown in the sketches.

This diagram also shows that introducing mixing in the lake may cause coexistence in both compartments (regions 1, 3 and 6). Increasing D, coexistence disappears leading to a blue algal dominance (for high values of P_0) or to a green algal dominance (for low values of P_0). Therefore, while the increase in P_0 still leads to a deterioration in water quality (region 4 with dominance of blue algae), the increase in D has contrasting consequences: water quality improves (worsens) for low (high) values in the nutrient input P_0 (as shown in Fig. 6).

Studying the bifurcation diagram of Fig. 5, it is possible to extract the areas (i.e., parameter combinations) corresponding to green dominance (G), blue-green dominance (B), and mixed algal coexistence (M) (see Fig. 7). G (B) area is present for low (high) input phosphorus values P_0, as expected in [3]. As mixing rate D decreases, lower and lower P_0 values are needed to ensure the dominance of green algae. On the contrary, higher and higher P_0 values are sufficient to eliminate blue-green algae. The algal coexistence is guaranteed for conditions of spatial heterogeneity (not too high values of mixing rate D).

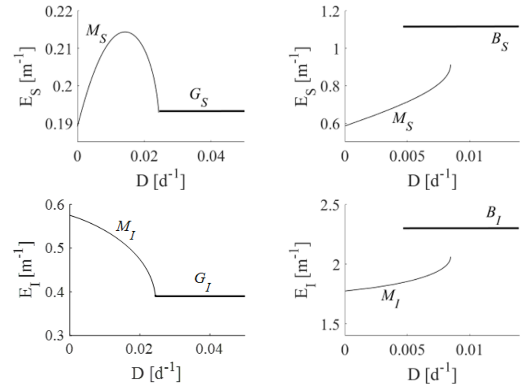

Fig. 6. Turbidity (E) for S and I compartment (upper and lower row), with respect to mixing rate D ($\delta = 0.15$). Left column: $P_0 = 0.04$. Right column: $P_0 = 0.12$. Solid (thin) lines correspond to G/B monocultures (mixed coexistence).

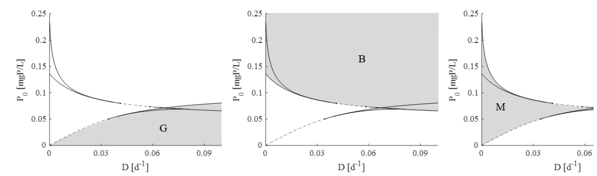

Fig. 7: Regions G, B and M obtained from Fig. 5. For parameter values in region G, the system can evolve toward a green dominance. For parameter values in region B, stable stationary blue-green dominance is possible. Finally, for parameter values in region M, mixed algal coexistence is possible.

Fig. 8 summarized the results of the analysis. It is obtained by superimposing the three diagrams shown in Fig. 7 and indicates only which attractors (G, B, or M) are present in each subregion. Region M where green algae and blue-green algae can coexist is the striped region. The dotted region is the region G∩B where both algal G and B dominance are possible.

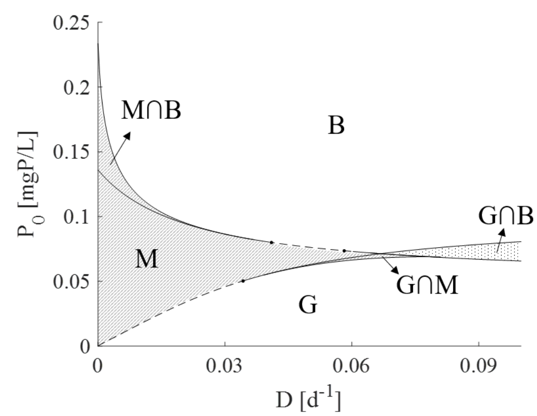

Fig. 8: Superposition of the three graphs shown in Fig. 7. The attractors present in each region are identified by G (green dominance), B (blue-green dominance), and M (mix of green and blue-green algae).

We have repeated this exercise for different values of inflow δ, producing the diagrams analogous to that shown in Fig. 8. The result is shown in Fig. 9, where diagrams from left to right refer to an increasing value of δ (the diagram in the middle corresponds to that reported in Fig. 8; the distinction between catastrophic and noncatastrophic curves has been neglected as the minor regions G∩M).

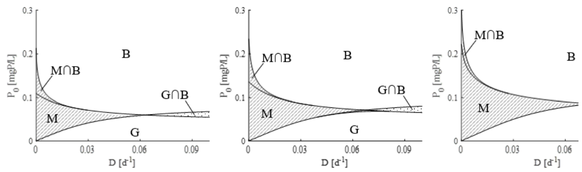

Fig. 9. Bifurcation diagrams in (P_0, D) parameter space for $\delta = 0.125$ (left), $\delta = 0.15$ (middle) and $\delta = 0.175$ (right).

There are no particular differences in the structure of the regions in the three diagrams. However, as in the homogeneous case, not only low flush rate values lead to a shift from green dominance to blue-green dominance but, in the heterogeneous case, they make algal coexistence less likely.

Finally, assuming that only the nutrient inflow and flush rate can be acted upon to control water quality, a bifurcation analysis in the (P_0, δ) parameter space with $D = 0.005$ has been performed. The results are shown in Fig. 10. Now, increasing δ, dominance of green algae is no longer possible for each value of P_0 as it was without mixing (see Fig. 8 in [3]). Moreover, under heterogeneous conditions, in order to eliminate blue-green algae both from a situation of dominance and from the algal coexistence, the nutrient inflow must be reduced much more than in the homogeneous case.

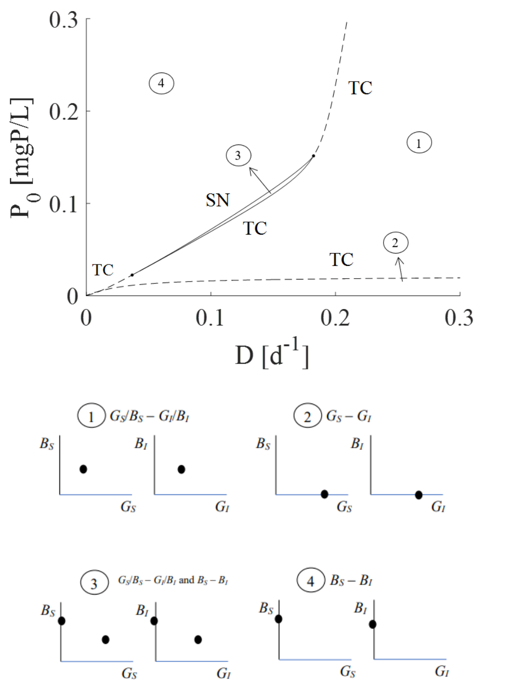

Fig. 10. Bifurcation diagram in (P_0, δ) parameter space for $D = 0.01$. TC = transcritical bifurcations; SN = fold bifurcation. Dashed (continuous) curves refer to noncatastrophic (catastrophic) bifurcations. For each region, attractors only are shown in the sketches.

III. Results and Conclusions

In deep lakes, nutrients and algae can show a considerable vertical variation. Simple experimental thoughts suffice to show that heterogeneity may promote algal coexistence. Imagine a lake stratified in two different compartments: shallow (or superior *S*) and deep (or inferior *I*). Suppose that in case of complete isolation of the regions, blue-green algae can dominate in the deeper part while green algae win the competition in the shallow region. A slight mixing in the lake causes a very small input of the competitive algal group in each part of the lake, but such small change is not sufficient to modify the dominance of each algal group. However, stronger mixing between the parts will cause a more important input of algae between the lake compartments thus preventing competitive exclusion and causing coexistence in all regions. Therefore, it can be assumed that spatial heterogeneity may be in favour of algal coexistence.

In this paper a mathematical model of a lake stratified in two compartments (superior, S, and inferior, I) has been therefore proposed. The analysis of the model has shown that heterogeneity promotes algal coexistence. In fact (see Fig. 8), introducing a small or intermediate mixing rate *D* between the two compartments implies a transition from algal competitive exclusion to algal coexistence.

Moreover, a comparison of all the obtained diagrams shows some interesting patterns and suggests some hints to control water quality in order to obtain green algal dominance or, where it is not possible, a good water quality, i.e. low turbidity both in *S* and *I* compartment, for example, promoting mixed coexistence.

They are as follows:

1. The region of coexistence (striped regions in bifurcation diagrams), which is possible only if the system is heterogeneous, increases with flush-rate δ.
2. For sufficiently high P_0 and *D* (i.e., in the upper right corner of each bifurcation diagram), the system settles irreversibly to a blue-green monoculture B. This condition is therefore always to be avoided.
3. For low nutrient inflow P_0, there is no chance for blue-green algae to be present alone, and the system settles to a green algae monoculture (high *D*) or to a mixed coexistence.
4. Unlike the homogeneous case, the range of nutrients characterizing the hysteresis between the two monocultures increases with δ and decreases with *D*.
5. As in the homogeneous case, fixing *D*, the dominance of green algae (region 2) is obtained by decreasing P_0. Depending on the mixing rate *D*, the value of P_0 that cause the disappearance of blue-green algae (region 2), may be lower (low *D*) or higher (intermediate *D*) than that necessary in the homogeneous case. This value increases with δ.
6. As δ increases, B dominance becomes less likely, as already foreseen in the homogeneous case (high D). However, in this condition, for each P_0 there is a value of δ leading to the disappearance of the B (fig 8 in [3]). With heterogenous lakes this is no longer possible.

All these results suggest that, from a biological point of view, water quality control in non homogenous lakes can be a rather difficult and complex task.

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