

# Reconstructing trophic interactions as a tool for understanding and managing ecosystems: application to a shallow eutrophic lake

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**Abstract:** Consequences of disturbance and human intervention on lake ecosystems are difficult to anticipate solely by intuition because of the complex interactions that characterize lake communities. Understanding how the structure of the interactions buffers or amplifies external impacts may have beneficial effects on lake management. In this paper, the food web of a moderately eutrophic lake (Lake Mosvatn, Norway) is reconstructed by using the effects of biomanipulation in combination with loop analysis, a qualitative algorithm. The outcome is a signed digraph that predicts changes in the level of the variables for input entering the system through any component. Model predictions explain the observed patterns of abundance, and this suggests that the graph is a plausible description of the main trophic interactions in Lake Mosvatn. As such, it is used as a predictive tool to discuss problems related to nutrient enrichment. When multiple causes are responsible for the observed effects, explaining their relative contribution to the net outcome is a difficult task. By discussing patterns of abundance observed in Lake Mosvatn as due to different inputs, this paper illustrates how qualitative predictions can help in this respect.

**Résumé :** Les conséquences de la perturbation et de l'intervention humaine sur les écosystèmes lacustres sont difficiles à prévoir si l'on se fie seulement à l'intuition, à cause des interactions complexes qui caractérisent les communautés lacustres. Le fait de comprendre en quoi la structure des interactions amortit ou amplifie les impacts externes peut avoir une incidence positive sur la gestion des lacs. Dans notre étude, nous reconstituons le réseau trophique d'un lac modérément eutrophe (lac Mosvatn, Norvège) en combinant les effets de la biomanipulation à l'analyse de boucle, un algorithme qualitatif. Le résultat est un bigramme signé qui prédit les changements dans le niveau des variables d'entrée introduites dans le système par n'importe quelle composante. Les prédictions du modèle expliquent les patrons d'abondance observés, ce qui permet de penser que le graphique constitue une description plausible des principales interactions trophiques dans le lac Mosvatn. À ce titre, il sert d'outil de prédiction pour analyser les problèmes liés à l'enrichissement en matières nutritives. Quand les effets observés ont des causes multiples, il peut être difficile d'expliquer leur contribution relative au résultat net. En analysant les patrons d'abondance observés dans le lac Mosvatn en regard de différents apports, notre étude montre en quoi les prédictions quantitatives peuvent être utiles.

[Traduit par la Rédaction]

## Introduction

Human impacts and natural perturbations often take the form of food web alterations. These alterations include the addition or removal of species or may also act on populations by changing one or more parameters that govern their growth rate. The ability to predict the effects of such impacts is crucial for the management and conservation of ecosystems. Yet, populations are often the targets of intentional manipulations. Here, managers need to be able to anticipate the effects of their actions if they want to achieve the desired goals and avoid unintended side effects (Crowder et al. 1996).

The multiple reticulate connections that characterize ecosystem food webs create such a complex scenario that causal linkages are inherently difficult to understand, and this reflects on the ability to make predictions (Yodzis 1988; Polis and Strong 1996). Lake ecosystems are not exceptions in

this respect. Although heuristically useful, the cascading trophic interaction theory (Carpenter et al. 1985; Carpenter and Kitchell 1987) and the biomanipulation idea (Shapiro and Wright 1984; Gophen 1990) have a limited potential for prediction. The number of cases in which interventions carried out in lakes contradicted the general expectation of the cascade hypothesis is noteworthy (Shapiro 1990; Carpenter and Kitchell 1993). The linear sequence of events that form the basis of the cascade paradigm cannot always provide a correct grasp of how the diverse array of connections in a lake affect the dynamics of the food web and its response to external impacts. In this perspective, elucidating the pattern of interactions in a lake becomes a major target of investigation.

Detecting complex interactions requires tracking a signal generated by a change in some component as it spreads to other parts of the community. Thus, biomanipulation or enrichment experiments, which are common practice in ecological research, can be used to unravel the structure of the interactions in a lake. To discuss this possibility, I use here the results of a biomanipulation experiment conducted in Lake Mosvatn (Norway), which have been previously published by Sanni and Waervagen (1990). Lake Mosvatn, a shallow, moderately eutrophic lake, appears particularly suit-

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able for this kind of analysis because of the relative simplicity of its ecological network and the completeness of observations by Sanni and Waervagen (1990), who monitored the lake over a period of at least 1 year following biomanipulation. The first objective of this work is reconstructing a model of the food web of this lake using changes observed in lake components as biomanipulation propagated its effects through interaction pathways.

The reconstruction uses the algorithm of a qualitative technique, loop analysis, under the hypothesis of moving equilibrium (Puccia and Levins 1985). In moving equilibrium, one assumes that parameters such as mortality rate, feeding rate, and so forth change slowly enough so that the system may reach a new equilibrium. This approach might seem too restrictive to study natural systems, as it is commonplace that in nature, changes occur rapidly enough to prevent the temporary establishment of any equilibrium (Walters et al. 1987). I have, however, elsewhere offered evidence of its validity based on experimental observations (Bodini 1988), while in other cases, this approach was successfully applied to empirical data (Lane and Collins 1985).

The second objective of this work is to assess the plausibility of the model in order to use it as a predictive tool. As it is a signed digraph that qualitatively predicts changes in the level of the variables in response to parameter changes, predictions are compared with the patterns of abundance in Lake Mosvatn. Because predictions obtained from the graph explain the variations observed in lake components, the model is used to discuss potential effects of selected impacts, also considering cases from the literature.

**Materials and methods**

**Method of loop analysis**

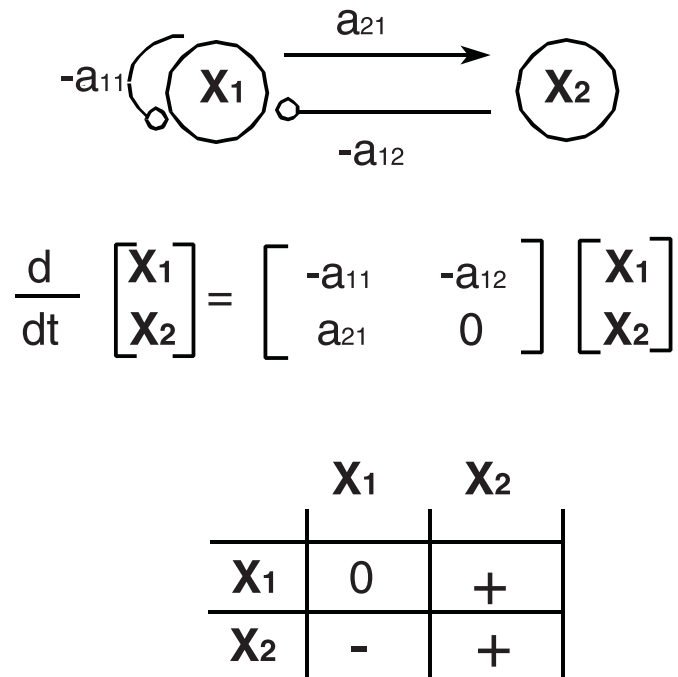
Loop analysis (Levins 1974; Puccia and Levins 1985) uses signed digraphs to represent a network of interacting variables (Fig. 1). System variables are depicted as nodes in the graph, and each connection between two nodes represents a nonzero coefficient of the community matrix. If the connection from variable *i* to variable *j* is as an arrow (circle head), the effect of *i* on *j* is said to be positive (negative), and a positive (negative) coefficient ( $a_{ji}$ ; the first index of this coefficient refers to the affected variable, and the second one identifies the variable producing the effect) enters the community matrix. The diagonal terms of the community matrix are the effect of the system variables on themselves.

Press perturbations (Bender et al. 1984), also called inputs, may act on ecosystems by changing one or more parameters in the growth rate of the variables. Effects of parameter changes may propagate beyond the direct target of the input because of the sequences of biotic interactions that functionally link the components. Loop analysis identifies such pathways and may suggest whether the equilibrium value of system variables is expected to increase, decrease, or remain the same following perturbation. For any variable, the new level can be calculated by the loop formula

$$\frac{\delta x_j}{\delta c} = \frac{\sum_{ik} \left[ \frac{\delta f_i}{\delta c} \right] \times [p_{ji}^k] \times [F_{n-k}^{(comp)}]}{F_n}$$

where *c* is the changing parameter (such as mortality or predation rate),  $\left[ \frac{\delta f}{\delta c} \right]$  designates whether the growth rate of the *i*th variable is increasing (+), decreasing (-), or not changing (0) because of the

**Fig. 1.** Community matrix, related signed digraph, and table of predictions for a simple predator-prey system ( $X_1$ , prey;  $X_2$ , predator). The table of predictions shows variations expected in the level of the column variables when a parameter input affects the row variables.



parameter change, and  $[p_{ij}^k]$  is the pathway connecting the variable that undergoes parameter change,  $x_i$ , with that whose equilibrium value is being calculated,  $x_j$ . The term  $[F_{n-k}^{(comp)}]$  is the complementary feedback, while  $F_n$  indicates the overall feedback of the system. Appendix A explains these notions concisely, and Puccia and Levins (1985) discussed them in detail.

Responses of abundances or biomass to parameter changes are usually arranged in a table of predictions (Fig. 1). The entries in a table denote variations expected in all the column variables when parameter inputs affect row variables. Conventionally, the calculation is done by considering positive inputs,  $\left[ \frac{\delta f}{\delta c} \right] = +$ , those in-

creasing the rate of change of variables. Consequences of negative inputs can be obtained by simply reversing the signs in the table because the only thing that changes in the loop formula is the term  $\left[ \frac{\delta f}{\delta c} \right]$ , which becomes negative.

**Experimental evidence**

In September 1987, the shallow (mean depth 2.1 m, maximum depth 3.2 m), eutrophic Lake Mosvatn was treated with rotenone to eliminate planktivorous fish (mainly whitefish (*Coregonus lavaretus*)) (Sanni and Waervagen 1990). Effects on other variables were observed during the following 2 years. The time-weighted average summer concentration (May–August) of total phosphorus, which was equal to  $42 \mu\text{g}\cdot\text{L}^{-1}$  prior to biomanipulation, decreased and reached a value of  $29 \mu\text{g}\cdot\text{L}^{-1}$  in 1989. The concentration of particulate phosphorus was  $34 \mu\text{g}\cdot\text{L}^{-1}$  in 1987 and  $17 \mu\text{g}\cdot\text{L}^{-1}$  in 1989. Dissolved phosphorus, the form that is readily available to primary producers, showed a different trend: its value, equal to  $8 \mu\text{g}\cdot\text{L}^{-1}$  in 1987, augmented to  $12 \mu\text{g}\cdot\text{L}^{-1}$  in 1989.

The biomanipulation had a very strong restructuring impact on the algal community, as documented by Sanni and Waervagen (1990).

**Table 1.** Quantitative changes observed in the main variables of Lake Mosvatn during the period 1986–1989.

	1986	1987	1988	1989
pH	8.0	8.0	7.9	No data
Secchi depth (m)	1.6	1.7	>2.3	No data
Maximum temperature (°C)	24	18	22	No data
Total phosphorus ( $\mu\text{g}\cdot\text{L}^{-1}$ )	45	42	No data	29
Particulate phosphorus ( $\mu\text{g}\cdot\text{L}^{-1}$ )	32	34	No data	17
Dissolved phosphorus ( $\mu\text{g}\cdot\text{L}^{-1}$ )	13	8	No data	12
Cyanophyceae ( $\text{mm}^3\cdot\text{m}^{-3}$ )	3446	1 005	797	No data
Chlorophyceae plus microalgae ( $\text{mm}^3\cdot\text{m}^{-3}$ )	1345	2 510	3493	No data
<i>Daphnia</i> ( $\mu\text{g dry weight}\cdot\text{L}^{-1}$ )	No data	60	318	No data
Rotifers ( $\text{individuals}\cdot\text{L}^{-1}$ )	No data	10 000	4000	No data

**Note:** Original data are given in Sanni and Waervagen (1990). Values for model variables are time-weighted average summer values. Biomanipulation was carried out in September 1987.

**Table 2.** Qualitative changes observed in the main variables of Lake Mosvatn after biomanipulation (first row) and expected effect of a positive input on planktivorous fish (second row).

Nutrients	Edible green algae	Blue-green algae	Inedible green algae	Macrophytes	Grazers	Rotifers	Invertebrate predators
+	–	–	+	+	+	–	+
–	+	+	–	–	–	+	–

Their findings can be summarized as follows. The time-weighted average summer volume of Cyanophyceae decreased from 1005 to 797  $\text{mm}^3\cdot\text{m}^{-3}$ . Green algae augmented (from 2510 to 3493  $\text{mm}^3\cdot\text{m}^{-3}$ ), but such an increase was due to gelatinous-coated species, while the edible component decreased. After treatment, there was a five-fold increase in the biomass of *Daphnia galeata*, the main grazer in Lake Mosvatn. Its time-weighted summer mean increased from 60 to 318  $\mu\text{g dry weight}\cdot\text{L}^{-1}$ . Rotifers were a significant part of the zooplankton community before biomanipulation; after fish elimination, a notable reduction of both biomass and number of individuals was observed for this group, which passed from a mean value of 10 000  $\text{individuals}\cdot\text{L}^{-1}$  to less than 4000  $\text{individuals}\cdot\text{L}^{-1}$ . This coincided with a higher level of invertebrate predators, mainly individuals of the species *Cyclops abissorum*. As for biomass and number of individuals, however, this species remained well below the values reached by rotifers and grazers. Macrophytes, mainly *Potamogeton pusillus*, responded to biomanipulation by exhibiting a very strong growth, especially in the second year after the intervention, but the authors did not provide quantification of this evidence.

These results form the empirical base upon which the structure of the interactions of Lake Mosvatn is reconstructed. According to the experimental observation, the key variables are assumed to be dissolved phosphorus (N represents nutrients in the model), edible green algae (EG), blue-green algae (BG), inedible green algae (IA), macrophytes (M), grazers (G), rotifers (R), and invertebrate predators (I). Planktivorous fish (PF) are also included in the model. This choice is motivated completely by the variables that were considered of interest by the authors who conducted the experiment.

Table 1 summarizes the quantitative data for some of these variables as they are provided by Sanni and Waervagen (1990) in their paper, which also described the experiment (sampling, chemical analysis, and so forth) in greater detail.

## Results

### Strategy of reconstruction

Rotenone increased fish mortality, and loop analysis classifies this intervention as a negative input on this population. Qualitative changes observed in the other key variables, as

described above, can be used to compile a row in a table of “observations,” or realized predictions, around which a signed digraph for Lake Mosvatn can be assembled. Table 2 summarizes this information. The procedure used for the reconstruction (Bodini 1988) consists of tracing pathways that can be responsible for the observed effects and their complementary feedbacks; according to the loop formula, in fact, a path propagates its effect to the target only if its complementary feedback exists (Appendix A). To compose the pathways and their complementary feedbacks, the links are chosen according to the ecological interactions that likely characterize the variables, as they are documented in the literature.

Ecological realism must guide the reconstruction to avoid absurd situations such as, say, zooplankton that feeds upon dissolved nutrients or planktivorous fish that eat macrophytes. In lake ecosystems, many organisms show a wide spectrum of alimentary preferences, but only their main diets are considered here. For example, planktivorous fish may feed on phytoplankton, but since in Lake Mosvatn they have been described as efficient predators of an abundant population of large herbivores, only their feeding activity on zooplankton is taken into account. On the other hand, organisms cannot efficiently combine different ways of energy intake (Oksanen 1991), and for planktivorous fish it is likely that the energy intake from phytoplankton, if any, should be of minor importance.

The overall feedback,  $F_n$ , is assumed to be negative to reduce the number of unknowns during the reconstruction. This assumption is motivated by the fact that a positive overall feedback would make the equilibrium unstable (although a negative  $F_n$  does not guarantee that the equilibrium is stable; Puccia and Levins 1985). At the end of the graph reconstruction, however, the negative  $F_n$  must become a consequence of the loops formed by the links in the model.

A table of predictions is conventionally constructed assuming positive inputs to system variables. The biomanipulation, on the other hand, produced a negative input

on planktivorous fish. For ease of reconstruction, a positive input on the same variable is assumed; its expected repercussions on the system variables are obtained by simply reversing the signs of the observed changes, and they are summarized in the second row of Table 2. Pathways of interactions have been deduced according to these signs and are illustrated in Fig. 2a.

### Pathway construction

The susceptibility of large-bodied grazers to fish predation is well known (Galbraith 1967), and the expected diminution in the level of grazers can be attributed entirely to predation (Sanni and Waervagen 1990). In pictorial terms, this corresponds to a circle head link connecting planktivores to grazers:  $[PF \rightarrow G]$ .

Green algae and cyanobacteria are expected to increase (expected effects for all the components are given in Table 2); this can be the result of the two pathways that combine the suppression of grazers by fish with the grazing pressure by daphnids over phytoplankton. These paths take the following graphical form:  $[PF \rightarrow G \rightarrow EG(BG)]$ .

The capability of large-bodied zooplankton to dampen blue-green algae has been investigated by many authors with contrasting results (see De Bernardi and Giussani 1990). In many experimental studies, an effective grazing pressure was observed, but concentration, size, and shape of the algae strongly affected their interaction with herbivores (Gliwicz 1990). Neither information about herbivores' feeding activity on BG nor details concerning morphology and toxicity of these algae in Lake Mosvatn were provided by Sanni and Waervagen (1990). Other authors, however, showed that species that dominated the phytoplankton community of this water body, namely *Microcystis aeruginosa* and *Anabaena solitaria/spiroides*, can be grazed by large crustacean herbivores (De Bernardi and Giussani 1990; Lyche et al. 1990; but see Claska and Gilbert 1998); so, hypothesizing a certain grazing pressure on blue-green algae in Lake Mosvatn seems reasonable, in the understanding that additional information should be gathered in this respect.

Table 2 shows that nutrients are expected to decrease. Phosphorus consumption by phytoplankton, two negative links connecting EG and BG to N, yields two pathways that may describe the response of nutrients to biomanipulation:  $[PF \rightarrow G \rightarrow EG(BG) \rightarrow N]$ . Inedible algae grow on dissolved nutrients, and an arrow connecting N to IA completes, with the above pathways, two chains that may explain the expected decrease in IA. These chains are  $[PF \rightarrow G \rightarrow EG(BG) \rightarrow N \rightarrow IA]$ .

Phytoplankton concentration increases lake turbidity (Scheffer et al. 1993). When algae attain high abundance, they may prevent the light from penetrating the water column, thus inhibiting the growth of macrophytes. This action can be depicted as a negative direct link from the three phytoplankton groups to M, and four pathways connecting planktivorous fish and macrophytes emerge. Two of them,  $[PF \rightarrow G \rightarrow EG(BG) \rightarrow M]$ , decrease the level of macrophytes, according to the expectation, whereas the paths  $[PF \rightarrow G \rightarrow EG(BG) \rightarrow N \rightarrow IA \rightarrow M]$  act in the opposite direction. The overall effect of the four pathways is qualitatively ambiguous, but no ecological reason justifies preference for the pathways that confirm the expectation.

Additional pathways to macrophytes could arise through dissolved nutrients. Luxury nutrient uptake by macrophytes (Meijer et al. 1994), however, seems not to play a significant role in Lake Mosvatn, as this body of water was only moderately eutrophic. In fact, macrophytes absorb nutrients from the sediment through their roots, and only when dissolved nutrients reach very high concentrations in the water column are they exploited by these plants (Carignan and Kalff 1982).

Predation by planktivores can reduce invertebrate predators ( $[PF \rightarrow I]$ ; Porter 1996). Also,  $[PF \rightarrow G \rightarrow I]$ , which combines the suppression of grazers by PF with the positive action of daphnids on invertebrate predators, may contribute to diminish I. In this path, the arrow from G to I refers to predation by invertebrate predators upon grazers that are smaller, such as younger individuals (Porter 1996).

A negative link depicts the suppression of rotifers by invertebrate predators, a key process in lake food webs (Williamson 1983) also mentioned by Sanni and Waervagen (1990) to explain the effect of biomanipulation on rotifers. Input on PF now has two possibilities for percolating to rotifers, producing the expected result  $[PF \rightarrow G \rightarrow I \rightarrow R]$  and  $[PF \rightarrow I \rightarrow R]$ . Algae of small size sustain rotifers, and an arrow from EG to R must be considered in the graph. Yet, it is possible that small zooplankton gathers some food from small blue-green algae (De Bernardi and Giussani 1990). Because of these two links, new connections with a positive effect on R arise:  $[PF \rightarrow G \rightarrow EG \rightarrow R]$  and  $[PF \rightarrow G \rightarrow BG \rightarrow R]$ . All the above pathways are depicted in Fig. 2a.

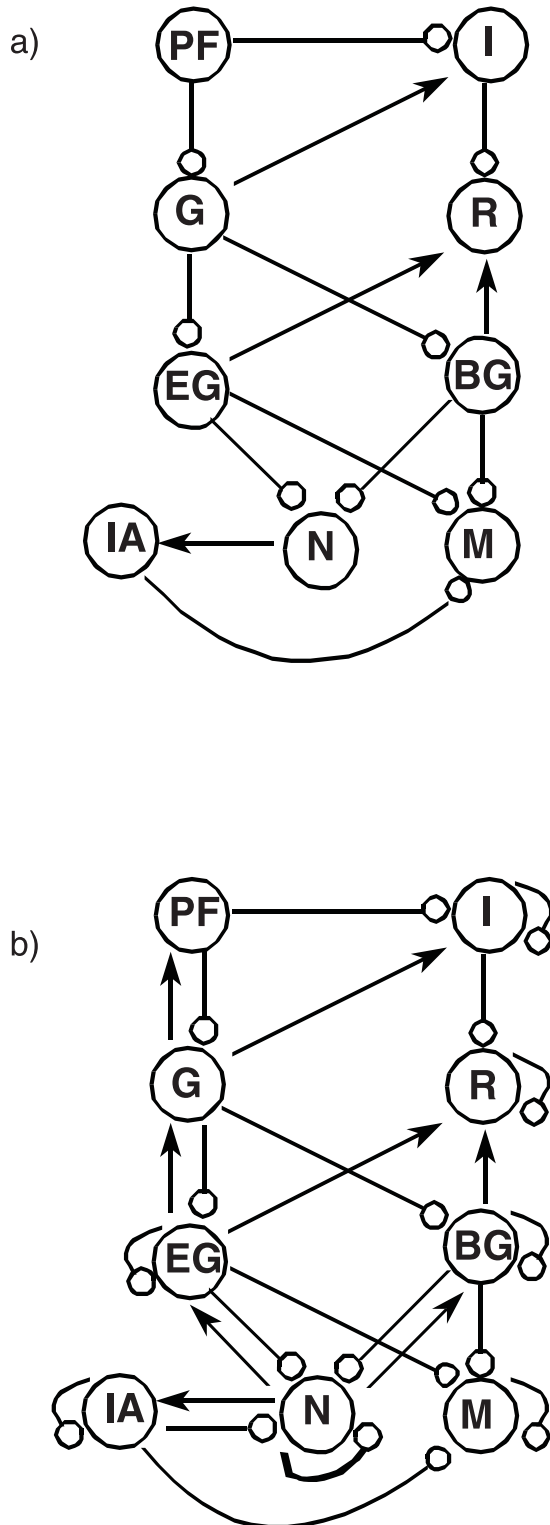
### Complementary feedback for the pathways

All the variables changed following biomanipulation (there are no zeroes in Table 2); this means that each pathway composing Fig. 2a must have its own complementary feedback. Consider first the chain  $[PF \rightarrow G \rightarrow EG \rightarrow N]$ : it leaves out the subsystem  $[IA-M-BG-R-I]$ . According to the loop formula, the sign of the feedback of this subsystem must be negative to confirm the sign of the path. A unique circuit that groups all these variables cannot be identified, so disjunct loops must be combined to yield the complementary feedback (see Appendix A). Since path and complementary feedback must not share variables (Puccia and Levins 1985), inedible algae remain isolated, as they seem not to interact with other variables in the complement. Accordingly, the only possible way that they contribute to the complementary feedback is through a self-damping term. This link may describe a density-dependent growth rate for this variable, as documented in the literature (Scheffer et al. 1993).

A self-damping seems also the only way that macrophytes can contribute to the feedback of this subsystem. This component is neither exploited by the herbivores nor seems to interact with phytoplankton groups to produce feedback loops. Suppression of algae by submerged plants is documented in the literature (Van Vierssen and Prins 1985), but before biomanipulation, macrophytes were restricted to narrow zones along the shores of the lake, and it is unlikely that they could inhibit the growth of algae. The self-damping on M seems ecologically appropriate because these plants acquire phosphorus from the sediment through their roots (Pelton et al. 1998). Nutrients trapped in the sediment, available at a rate independent of their level, would be self-damped,



**Fig. 2.** (a) Structure of the pathways thought to be responsible for the observed effects of biomanipulation and (b) a graph representing the core structure of the food web in Lake Mosvatn as deduced by the reconstruction. N, nutrients; M, macrophytes; BG, blue-green algae; EG, edible green algae; IA, inedible green algae; I, invertebrate predators; R, rotifers; G, grazers; PF, planktivorous fish.



but since they are not explicitly included in the model, their self-damping is passed up to the macrophytes (see Appendix B).

Blue-green algae are not involved in feedback-producing interactions within the subsystem [IA–M–BG–R–I]. Although they are assumed to increase the growth of rotifers (see the positive link in Fig. 2a), the grazing pressure by the rotifers is not strong enough to keep blue-green algae in check (De Bernardi and Giussani 1990; Sanni and Waervagen 1990). Accordingly, the relationship between BG and R remains unidirectional, and a self-damping on blue-green algae becomes necessary to include this variable in the complementary feedback.

What remains to be specified is the way that invertebrate predators and rotifers participate in the complement. Either they form a predator–prey circuit or both are self-damped. A predator–prey relationship requires that an arrow from R to I be added to the graph. This link would create two new pathways with positive effects on invertebrate predators; they are of the form [PF → G → EG(BG) → R → I]. Because of these new paths, the net effect of the input to PF on invertebrate predators would be ambiguous. Conversely, the negative effect would be maintained if R and I were self-damped. The latter solution is accepted at this stage of the reconstruction, in the understanding that it must be justified ecologically and that no disagreement between model predictions and observations will result. Then the predator–prey relationship between I and R should be reconsidered.

The importance of the microbial loop in lake dynamics is widely recognized (Porter 1996). Invertebrate predators and rotifers rely on this microbial food web, as they prey upon bacterial picoplankton, ciliates, and flagellates (Arndt 1993). So their abundance and growth rate are regulated by other variables not in the food web, and this requires that I and R be self-damped.

The pathway [PF → G → BG → N] so far has no complementary feedback because no circuits involving EG can be identified within the subsystem [IA–M–EG–R–I]. Edible green algae do interact with rotifers, but the same argument used to describe the interactions between rotifers and blue-green algae applies here: a typical plant–herbivore interaction would imply a dampening ability of rotifers on phytoplankton, which is a characteristic of large-bodied grazers but would be unrealistic for rotifers (Havens 1993). Thus, a single link, the arrow from EG to R, characterizes this relationship, and edible green algae have to be self-limited to enter the complementary feedback for the path.

According to Fig. 2a, impacts entering the system through planktivorous fish spread to macrophytes along four different routes. The effect produced by [PF → G → BG → M] depends on the feedback of the subsystem [IA–N–EG–R–I]. Invertebrate predators and rotifers can contribute with their self-limiting action, but the way in which dissolved phosphorus and edible and inedible algae participate in the feedback has yet to be specified. N receives continuous supply from outside the system, so a negative self-effect on this variable must be included in the graph (Appendix B). Both edible and inedible algae consume nutrients: to depict these interactions as true resource–consumer relationships, an arrow connecting N to EG and a negative link from IA to N must be added to the graph. The complementary feedback

for the considered path is now complete. It is made of different contributions: one includes all the self-damping on the variables in the subsystem; the others consider the two-node feedback loops between algae (both edible and inedible) and nutrients variously combined with the self-loops on the other variables.

The links discussed so far are sufficient to generate the complementary feedbacks for the other pathways to macrophytes, and the overall effect on *M* remains ambiguous because the paths have different signs. Also, the complementary feedbacks for the pathways to edible phytoplankton and blue-green algae can be identified without introducing other new links. However, for completeness, the interaction between blue-green algae and nutrients requires that an arrow from *N* to *BG* be added, as blue-greens grow on dissolved nutrients. This increases the number of loops involved in the complementary feedback for the path to *EG*.

No further addition of links is required to identify the complementary feedback for the following paths: [*PF* → *G*], [*PF* → *G* → *EG*(*BG*) → *R*], and [*PF* → *G* → *I*]. The path [*PF* → *I*] lacks its complementary feedback; *G*, so far, does not enter any feedback loop with other variables in the complementary subsystem for this path, which is [*G*–*EG*–*IA*–*BG*–*R*–*I*–*M*–*N*]. This inconsistency can be resolved by introducing a positive link from *EG* to *G*. It is also ecologically necessary to complete the interaction between edible green algae and grazers, which is a typical resource–consumer relationship. Because of this addition, a two-node loop takes shape, and it can be variously combined with other one- or two-node loops in the complement to yield the complementary feedback for the considered path. Also, this feedback makes the pathway [*PF* → *I* → *R*] active.

The overall feedback is the feedback of the highest level in a signed digraph (see Appendix A); it must be associated with a circuit or a combination of disjunct loops that comprises all the variables in the graph. No feedback of this type can be calculated from the links so far identified, and this means that links are still missing. In particular, the computation of the overall feedback lacks the contribution of *PF*: this variable does not establish feedback loops with other components, and it is not self-damped. Nevertheless, *PF* and *G* interact as predator and prey, and their feedback plays a key role in the dynamics of lakes (Kerfoot and Sih 1987). To make the structure realistic in this respect, an arrow from *G* to *PF* must be added to the graph. An overall negative feedback for the system can now be identified.

Another possibility is to introduce an arrow from *I* to *PF* so that planktivores and invertebrate predators interact as a predator–prey pair. However, the benefit that planktivores obtain by feeding on Copepoda might be negligible because of the low abundance of these organisms in Lake Mosvatn, so this link is not considered.

The interaction between grazers and blue-green algae is depicted as unidirectional; these algae are of poor nutritional value for zooplankton (De Bernardi and Giussani 1990), and the positive effect on the growth rate of grazers seems negligible. Yet, in representing the interaction between *G* and *I*, no negative impact by the consumer is assumed. Predatory copepods can feed on small individuals, but this may not be enough to control the population of grazers (Carpenter and

Kitchell 1993). The core structure of the food web now seems complete and takes the form of Fig. 2*b*.

The presence of certain paths in the model generates ambiguities about the effect of input to *PF*. In addition, some links that could not be deduced solely from pathway reconstruction have been added to guarantee ecological realism in the structure. Because of this, new pathways may emerge as unexpected combinations of links, and model predictions may not agree with the signs in Table 2. To assess the plausibility of the proposed structure, the graph is qualitatively analyzed by applying the loop formula and its predictions compared with the signs listed in Table 2. Table 3 reports model predictions: one must enter the last row of this table and compare the signs along the columns with those in Table 2. Model predictions confirm the signs of Table 2, and what is depicted in Fig. 2*b* thus seems to be a plausible skeleton of the food web of Lake Mosvatn.

## Discussion

Rotenone treatment in Lake Mosvatn was considered a successful example of biomanipulation (Sanni and Waervagen 1990). Changes observed in the phytoplankton groups, especially the reduced volume of cyanobacteria and edible green algae and the increase in macrophytes, have been associated with the planktivores' elimination. Although the inedible component of the phytoplankton augmented, these modifications were considered as signs of improved trophic conditions for the lake, also because chlorophyll concentration decreased. However, a careful examination of the patterns of abundance reveals that blue-green algae started to decrease before biomanipulation, and this change was accompanied by an increase in inedible green algae. Moreover, the decline in the abundance of blue-green algae that took place between 1986 and 1987 was more pronounced than that assumed to be caused by fish elimination.

Confronted with this evidence, one could argue whether biomanipulation was effectively responsible for the changes observed between 1987 and 1989. An input could have entered the ecosystem before the intervention (1986), imposing trajectories that the variables could have followed during the successive 2 years, showing variations that have been interpreted as consequences of fish elimination. To tackle this problem, one first must show that the variations observed in the level of the components between 1986 and 1987 could be the result of some input. Second, evidence must be found that changes detected after 1987 could be due uniquely to rotenone treatment in order not to confound causes and effects. Model predictions can help in this respect, as patterns of covariation can be diagnostic of the source of change.

The input that supposedly affected Lake Mosvatn in 1986 (or before) must have altered the growth rate of a variable for which the model predicts a negative covariation between *BG* and *IA*, as they changed in opposite directions. In the proposed model, input to nutrients, macrophytes, edible green algae and zooplankton yields positive or no covariation between blue-green algae and inedible algae (see Table 3). Input to Cyanophyceae, planktivorous fish, and inedible algae seems equally acceptable.

**Table 3.** Table of predictions for the core structure of Lake Mosvatn (Fig. 2b).

	N	M	BG	EG	IA	I	R	G	PF
N	+	-	+	+	+	-	+	0	+
M	0	+	0	0	0	0	0	0	0
BG	-	?	+	-	-	+	?	0	-
EG	-	?	-	+	-	-	(+)*	0	+
IA	-	?	-	-	+	+	-	0	-
I	0	0	0	0	0	+	-	0	0
R	0	0	0	0	0	0	+	0	0
G	0	0	0	0	0	-	+	0	+
PF	-	(-)	(+)*	(+)*	-	(-)*	(+)*	-	(+)*

**Note:** (+) means that the pluses outweigh the minuses by two to one; (+)\* means a 3:1 ratio or greater in favor of the pluses. The same is true for (-) and (-)\*, but in favor of the minuses. A question mark means that nothing can be said about the direction of change for the variable. N, nutrients; M, macrophytes; BG, blue-green algae; EG, edible green algae; IA, inedible green algae; I, invertebrate predators; R, rotifers; G, grazers; PF, planktivorous fish.

To decide which component could be the target of the parameter change, predictions must be compared with the patterns of abundance of variables other than phytoplankton. The table suggests that large herbivores change only for input to planktivorous fish. Unfortunately, no information about daphnid abundance before 1987 is available, and attention must focus on other components. Dissolved phosphorus decreased between 1986 and 1987, so the input must have entered the system through the inedible component of phytoplankton. In fact, a negative impact on BG, necessary to reduce the level of the variable itself and to increase inedible algae, would also increase N. The same holds true for input to planktivorous fish.

Model predictions thus suggest that an input prior to biomanipulation could have entered the lake, producing the variations observed in 1986 and 1987. Moreover, this input must have increased the growth rate of inedible algae. This hypothesis is supported by the observation that strong variations in phytoplankton growth and biomass due to meteorological conditions characterized Lake Mosvatn during that period (Sanni and Waervagen 1990). However, it is dubious that such climatic changes affected only inedible algae. A more realistic hypothesis considers that the impact affected BG and EG as well and that the observed patterns of abundance are the net effect of such inputs.

To clarify this point, further indications provided by Sanni and Waervagen (1990) are useful. Water temperature seems to play a crucial role in phytoplankton development in lakes. In particular, the growth of cyanobacteria is enhanced by high temperature (Reynolds 1984; Olsen 1989). In summer 1986, the temperature in Lake Mosvatn reached values well above 20°C (maximum temperature 24°C), favoring the growth of blue-green algae. This may explain the observed dominance of this group over green algae. Similar conditions did not occur in 1987, as the temperature never reached 20°C (maximum temperature 18°C). Lower temperature could have reduced the growth rate of BG while conditions for green algae improved, and the authors considered this event to be responsible for the drop in blue-green algae and the increase in green algae that were observed in 1987.

These temperature variations might have produced a negative impact on blue-green algae and a positive impact on green algae.

In the table of predictions (Table 3), the positive input to IA and the negative input to BG are expected to reduce blue-green algae while increasing inedible green algae. Nutrients, however, are expected to change in the opposite direction following the two inputs. The increased rate of change of EG, on the other hand, reduces blue-green algae, inedible algae, and nutrients.

During the period 1986–1987, a strong decrease in blue-green algae was observed, while the increase in green algae was less pronounced. This may be the consequence of the hypothesized inputs, as all three parameter changes (IA, BG, and EG) are expected to reduce BG, whereas two out of three increase IA and EG. Yet, two inputs (EG and IA) out of three act to reduce the concentration of dissolved nutrients, and this tendency agrees with what was observed in the lake.

The hypothesis that an input entered the ecosystem through phytoplankton before biomanipulation seems plausible. It remains to be shown that the intervention, carried out in September 1987, was really effective. According to model predictions, in fact, changes in the level of BG and IA described as effects of biomanipulation could have been the effect of the input on phytoplankton imposed by temperature fluctuations. Although no data on grazers prior to 1987 are available, the pattern of abundance for this group showed a significant increase after the rotenone treatment; in the model, this can be caused only by a negative input to planktivores. Nutrients increased: if they simply followed the trajectory imposed by the input to phytoplankton, they should have continued to decrease or they could have remained at the same concentration measured in 1987. So biomanipulation really affected the variables in Lake Mosvatn, but the scenario seems more complicated than presented by the authors.

In 1988, the temperature increased again, and, concurrent with biomanipulation, an additional input to phytoplankton must be considered. According to the above discussion, the overall effect of this input would be an increase in dissolved nutrients, a decrease in green algae, and an augmented abundance of blue-green algae. On the contrary, cyanobacteria decreased in 1988, and this may be taken as an evidence that biomanipulation was successful. However, the reduction of blue-green algae could be even stronger: likely, the effect of biomanipulation was partially compensated by the positive input on BG due to the higher temperature.

The biomanipulation and the increased temperature are predicted to act in the same way on edible green algae. It follows that the observed decline of this component could be caused by two inputs instead of biomanipulation only. Inedible green algae are expected to decrease because of the combined effects of the inputs to phytoplankton groups, but their abundance augmented, suggesting that the effect of fish elimination was strong enough to overcome that of temperature. As with edible green algae, it seems that biomanipulation and temperature acted in a synergistic way to set the new level of dissolved nutrients. The combined action of these multiple inputs leads to the conclusion that if



no change were detected in the abundance of blue-green algae after biomanipulation, planktivore elimination could be judged ineffective in reducing blue-green algae and, as such, useless for managing eutrophication. Instead, it simply could not compensate for the input to phytoplankton.

Before biomanipulation, Lake Mosvatn was described by Sanni and his co-worker as moderately eutrophic, and the intervention produced quasi-oligotrophic conditions. Eutrophication, caused by excess input of nutrients, is a widespread problem in lakes. In shallow lakes, this can cause a substantial or complete loss of macrophytes and their replacement by dense phytoplankton populations (Phillips et al. 1978; Moss 1990). According to model predictions, this is also expected in Lake Mosvatn, as a positive input to N lowers the abundance of macrophytes, whereas all phytoplankton groups are predicted to increase.

Other predictions agree with the general phenomena observed in lakes during eutrophication. A typical transformation that takes place is the shift in dominance from large-bodied zooplankton to small grazers (Gliwicz 1969). This shift is also predicted by this model, as for positive input to nutrients, grazers are expected not to change, while rotifers increase. Enrichment experiments conducted in enclosures with and without fish (Levitan et al. 1985) showed that in the absence of planktivores, large zooplankton increased, while phytoplankton remained unaffected; only in the presence of fish did the enrichment lead to an increase in phytoplankton density, while zooplankton remained largely unchanged. The variations predicted by the model seem to be in agreement with those findings: algae increase and no change is expected for grazers following nutrient enrichment.

Other authors found that fish density increased in response to enrichment (McAllister et al. 1972) and was positively related to the nutrient status of lakes (McQueen et al. 1986). The model proposed here for Lake Mosvatn predicts higher fish density for positive impact on nutrients; also, except input to PF, when the level of nutrient augments, so does that of the planktivorous fish.

In a shallow lake, all sorts of different processes not considered here may play a significant role. Consumer-mediated nutrient recycling deserves particular attention. Considerable evidence exists that this process can influence lake community structure and dynamics (DeAngelis 1992; Vanni and Layne 1997), so that it should be included among the key processes. However, recycling links, a series of arrows leaving all the consumer variables and pointing to nutrients, would offset the effects of trophic pathways, and the model would make ambiguous predictions about input to planktivorous fish. Moreover, if recycling links were strong enough to prevail in magnitude over trophic interactions, predictions would be reversed with respect to Table 3. Accordingly, the model, to be in agreement with the data set, requires that trophic interaction prevail over recycling; from a qualitative point of view, recycling can be omitted from the food web with no consequences.

However, this does not mean that recycling in Lake Mosvatn is not relevant: its scarce importance may depend on the trophic status of the lake. In oligotrophic situations (Neill 1988), short feedback loops due to predator-prey and plant-herbivore interactions dominate over longer loops. Since Lake Mosvatn was described as only moderately

eutrophic, it is likely that trophic interaction still prevailed in determining the response of lake variables to biomanipulation. This picture may change during eutrophication, as predicted by the model itself. Because of nutrient enrichment (Table 3), fish density is expected to increase, and this may reflect on how much phosphorus is made available through excretion. Rotifers increase as well, and their contribution to recycling may become more important.

The standing crop of grazers is predicted not to change: as there is more food (algae increase), more individuals are produced, but because of the increased population of predators (planktivores), more grazers are eaten by fish. Thus, the turnover rate of G increases with two interlinked consequences: the age distribution shifts toward younger age-classes and the body size of individuals becomes smaller (Lane and Levins 1977). As the recycling rate is inversely related to mean body size (Peters 1983), it turns out that recycling by large grazers is also expected to increase with eutrophication. Thus, in more eutrophic conditions, the assumption of recycling as a weak force in comparison with trophic interactions would be highly questionable if not completely incorrect.

This study reiterates that most limnetic food webs are more complicated than the simple planktivore-zooplankton-phytoplankton-nutrient chain. In these cases, adopting a one-step linear causality approach may not be appropriate for predicting the effects of environmental disturbance or anticipating the outcomes of manipulative experiments; identifying the structure of the interactions may be useful in this respect. The matrix inversion (Puccia and Levins 1985) is normally used to derive the signs of the interactions in an ecological web, but it requires that press experiments be conducted on all the system variables. By loop analysis instead, as shown here, it is possible to identify relevant interactions even when a limited set of experimental data are available. This case is the rule rather than the exception when ecosystems are subjected to planned press perturbations or presslike natural disturbances. The method presented here, however, may not be generally useful for webs that are very large or have many connections.

The main outcome of a signed digraph is the table of predictions that can be used to forecast the consequences of human interventions or natural perturbations on ecosystems. As many forms of stress act on ecosystems, results of planned interventions may be obscured by such unexpected impacts. In this respect, the table can be used as a diagnostic tool to identify sources of change in the ecosystem and to understand how different causes may contribute to the observed effects.

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**Appendix A**

The loop formula allows one to calculate expected changes in the equilibrium level of variables in response to parameter input. Besides the sign of the input, indicated by the term  $\left[\frac{\delta f}{\delta c}\right]$ , the loop formula makes use of the concepts of path, complementary feedback, and overall feedback. These refer to structural elements that can be identified in any graph. Their meaning can be fully understood by referring to the correspondence between matrix algebra and the formalism of loop analysis and that can be found in Puccia and Levins (1985). Instead, in what follows, criteria to identify such elements in a graph are provided by using the scheme depicted in Fig. A1.

**Circuits and feedback**

In loop analysis, a pathway that starts at one node and, by following the direction of links, returns to it without crossing intermediate nodes more than once is called loop, or circuit. Any circuit produces a feedback that can be positive or negative depending on the product of the signs of the links that form the loop. As there may be circuits of different length (1, 2, 3,... variables involved) in a system, there are as many levels of feedback as variables. Each level of feedback considers all the circuits (feedbacks) involving that particular number of variables. In the system in Fig. A1, there are three levels of feedback.

**Overall feedback ( $F_n$ )**

It is computed only once and corresponds to the highest possible level of feedback in a system. In the model in Fig. A1, it is the third level of feedback and includes all the

feedbacks of the circuits involving the three components. No disjunct loop of length 3 exists in the graph, and in this case, the overall feedback comprises all of the product of disjunct loops that have a combined number of variables equal to 3. As disjunct loops are those that share no variables,  $F_n$  is composed by the self-damping on A (a self-effect link is a loop of length 1) plus the two-node loop [B-C]. Its sign is obtained by multiplying the signs of the links involved, further multiplied by  $(-1)^{m+1}$ , where  $m$  is the number of disjunct loops entering the feedback. As the links involved are two negative and one positive, and there are two disjunct loops, the overall feedback is negative.

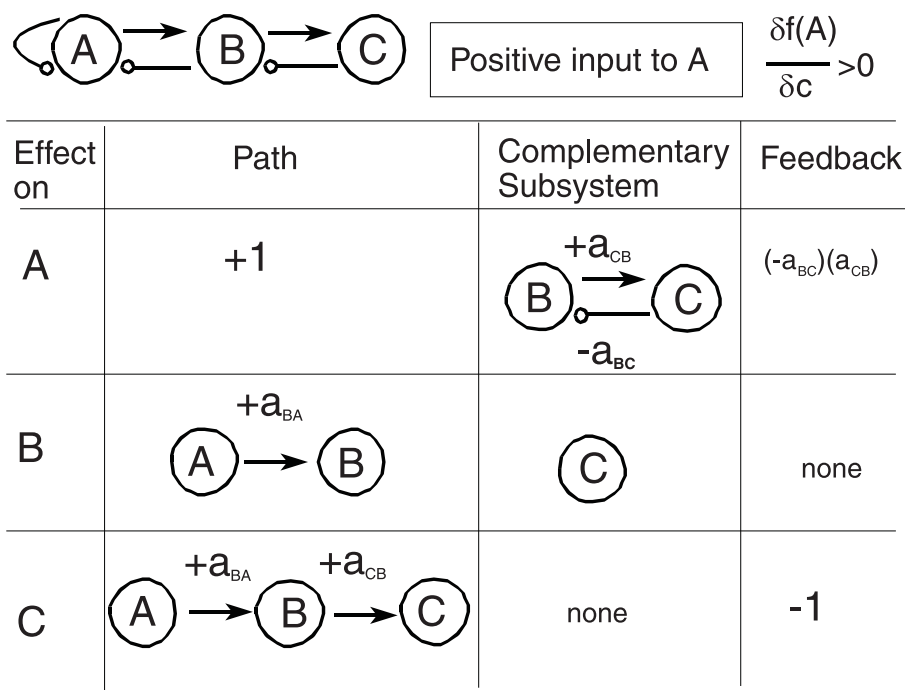
**Path [ $p_{ij}^k$ ]**

A path is a series of links starting at one node and ending on another without crossing any variable twice. Suppose a positive input occurs on A (its rate of change increases,  $\left[\frac{\delta f}{\delta c}\right] > 0$ ). To predict the new equilibrium of, say, C, the path along which the effect travels is the positive link from A to B plus the arrow from B to C. It involves three variables ( $k$ ) and its sign, given by the product of the signs of the links that form the path, is positive.

**Complementary feedback ( $F_{n-k}$ )**

If the  $k$  variables in the path are ideally excluded from the graph, what remains is called complementary subsystem. The complementary feedback is the highest possible level of feedback that can be found in the complementary subsystem. For positive input on A and effect on B, what remains is C, and the highest possible level of feedback is level 1. As C has no self-effect link, there will be a null (0) complemen-

**Fig. A1.** Signed digraph of a three-level trophic chain showing paths, complementary subsystems, and feedback used to calculate expected changes in the equilibrium level of the variables in response to positive input on A.



tary feedback. For completeness, it has to be noted that a path from a variable to itself is equal to 1; if all the variables are in the path (i.e., input to A and effect on C), no complementary subsystem can be identified, but the complementary feedback is equal to  $-1$ . These are two algebraic conveniences. The summation sign in the loop formula considers the fact that two variables can be connected by more than one path.

### Appendix reference

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### Appendix B. Self-damping

If a variable is not self-reproducing, it is usually self-damped. For instance, if nutrient enters a lake at a rate  $\Phi_N$ , because there are tributaries of the lake, and is removed by some consumer plant P, the concentration of usable nutrient in the lake may follow the equation

$$\frac{dN}{dt} = \Phi_N - PN.$$

By taking the derivative with respect to nutrient itself, one obtains

$$\frac{\delta}{\delta N} \left[ \frac{dN}{dt} \right]_* = \frac{\Phi_N}{N^*}$$

and the diagonal term of the community matrix is negative, which translates into a self-loop.

If a model excludes variables that are self-damped, mostly those at the lowest trophic levels such as inorganic nutrients,

then their self-damping property is transferred to variables that interact with the self-damped ones. Consider a nutrient N that enters a system from outside and is consumed by a species S. This interaction can be represented by the following equations:

$$\frac{dN}{dt} = \Phi_N - aNS$$

$$\frac{dS}{dt} = S(bN - \beta)$$

where  $a$  is the rate of nutrient uptake by S,  $b$  is the rate of conversion of N into S, and  $\beta$  is the death rate of S. In this system, N is self-damped, as shown before, but S is not, as taking the partial derivative with respect to S yields a null value. If N is not recognized as a distinct variable, then it can be replaced in the second equation by its expression obtained at equilibrium from the first equation

$$N^* = \frac{\Phi_N}{aS}$$

and the equation for the consumer becomes

$$\frac{dS}{dt} = \left[ b - \frac{\Phi_N}{aS} - \beta \right] S$$

whose partial derivative with respect to S is negative and the variable is self-damped.

Also, a self-damping may originate from a density-dependent growth rate. Its demonstration is not given here, as it follows the same procedure shown for the two previous cases.