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The control of the indirect effects of biomanipulation

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Results from long-term investigations on biomanipulation show that indirect effects are at least as important as direct effects are for the stability of biomanipulation. Three types of indirect effects can be distinguished: (1) a change in quantity or quality of the resource base, (2) behavioural change of the prey, and (3) development of anti-predator traits. Although indirect effects of type (2), (e.g. a change in the pattern of vertical migration of zooplankton), and type (3), (e.g. development of helmets and neck teeth in *Daphnia*), are important mechanisms, the most essential indirect effects regarding biomanipulation belong to type (1). An example of the latter will be demonstrated: the complex of indirect effects of enhanced grazing by large herbivores on the phosphorus metabolism of the lake.

It is concluded that control of the indirect effects is absolutely necessary to stabilize biomanipulation measures, but this is much more difficult than the control of direct effects and needs deeper insights into the structuring mechanisms of food webs. Proper management of fish stocks, in combination with the control of phosphorus load and/or the physical conditions, seems to be the most promising way of controlling the indirect effects of biomanipulation.

Introduction

Biomanipulation is regarded as a new tool for water management (Gulati *et al.* 1990). The development of this new tool was possible because water quality depends to a large extent on the structure and function of aquatic food webs. In turn these food webs are mainly controlled by two complex factors: (1) resource limitation ("bottom–up control") and (2) predation ("top–down control" or biomanipulation).

Hitherto, much of the research performed on biomanipulation was focused on the direct effects of predation and consumption (Fig. 1). Some studies also took into consideration the resulting feedback effects which must be regarded as direct and indirect bottom–up effects, caused by the top–down induced change of the resource base (Fig. 1). In recent years it has become increasingly obvious that the complexity of top–down mechanisms, and hence the reliability of biomanipulation as a water-management tool, cannot be understood without taking into consideration the numerous indirect effects (Kerfoot & Sih 1987; Benndorf 1988; Carpenter 1988; Lammens *et al.* 1990). The purpose of this paper consists in demonstrating that indirect effects could be at least as important for the stability of biomanipulation as direct effects, and this insight leads to essential consequences regarding the principal control strategy in water quality management.

Types of indirect effects of biomanipulation

Three types of indirect effects can be distinguished: trophic linkage, behavioural, and morphological (Fig. 2).

The typical character of a trophic linkage indirect effect consists in changing the abundance of a population (A in Fig. 2) which is not directly connected with the "key" population (C in Fig. 2), by influencing the *abundance (or concentration)* of an intermediate population (or

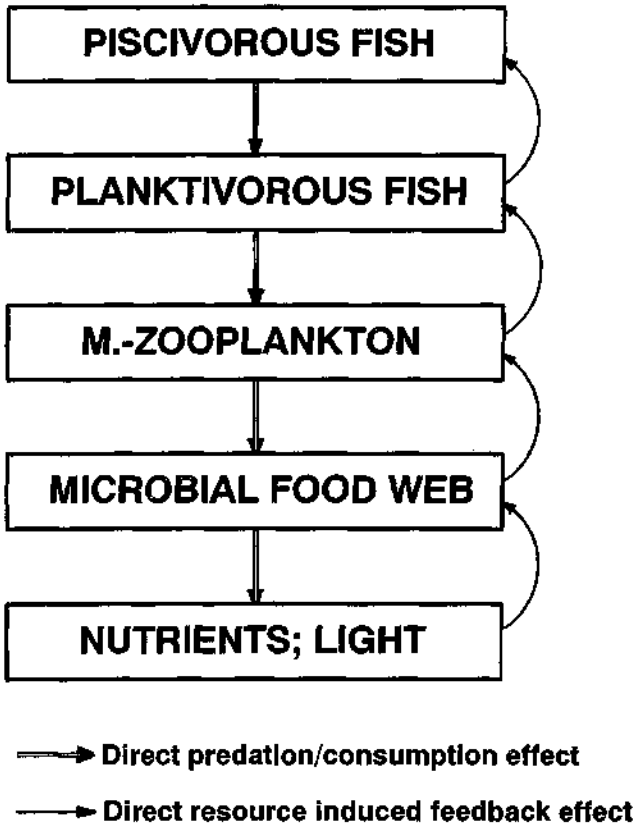

Figure 1. Schematic representation of a simple food chain.

compartment), (B in Fig. 2). Three numerous and typical cases of trophic linkage indirect effects are demonstrated in Figure 3.

Behavioural indirect effects are characterised by a change of the *behaviour* of an intermediate population. That change is a direct effect caused by the "key" population (C in Fig. 2) and leads to a change in abundance of another population which is not directly coupled with the "key" population. A typical example was demonstrated by Werner *et al.* (1983). Zooplanktivorous fish (bluegill) exerted a high predation pressure on large-sized *Daphnia* in a shallow lake densely colonized with macrophytes. After the introduction of a piscivorous fish (large-mouth bass), the bluegills took refuge in the stands of macrophytes and, consequently, their predation pressure on *Daphnia* decreased considerably, though there was almost no change in the abundance of the bluegill population.

If a "key" population changes the *morphology or the chemical composition* of an intermediate population in such a way that another (third) population is also affected, this represents a morphological indirect effect. A typical example was observed in the long-term biomanipulation experiment in Gräfenhain (Köhler *et al.* 1989; Benndorf 1990). Some years after the complete elimination of planktivorous fish, the abundance of *Chaoborus flavicans* larvae increased dramatically. Following this increase, small- and medium-sized *Daphnia pulex* produced neck teeth which protect them against predation by *Chaoborus* (Fig. 4). The observed results were a stable and abundant population of *Daphnia pulex*, and a low concentration of all grazable particles in the lakewater.

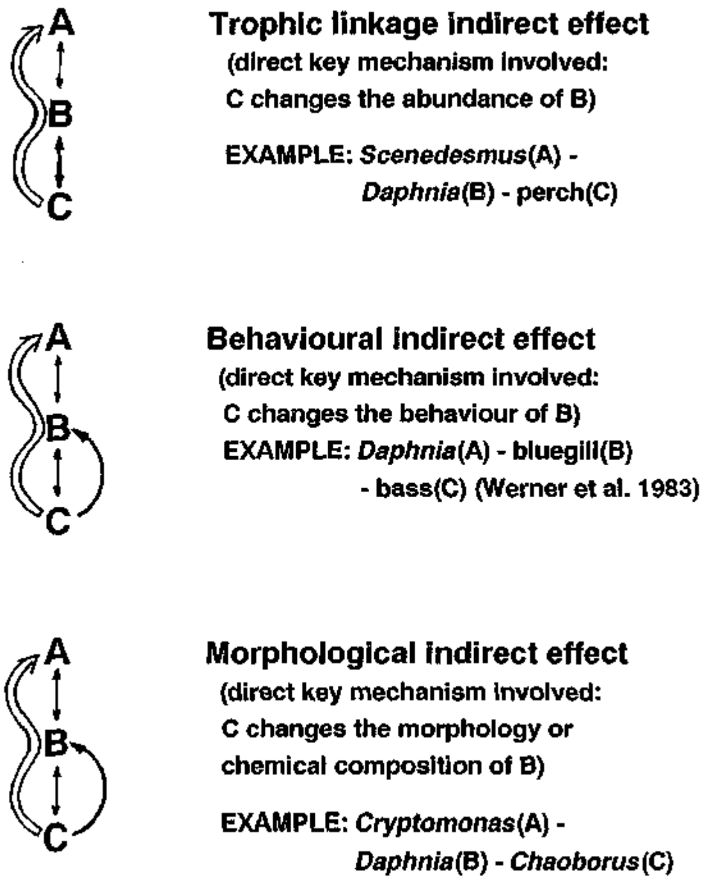

Figure 2. Types of indirect effects. Thick arrows: indirect effects; thin arrows: direct effects (modified after Miller & Kerfoot 1987).

The role of indirect effects in food webs

The enormous complexity of interactions in aquatic food webs is not only caused by the high diversity of types of indirect effects. Another important reason is that each trophic level is occupied by numerous species and many indirect effects exist between these species. An attempt to illustrate this fact is made in Figure 5 by assuming the simplest case, where each trophic level is occupied by only two species. We have to realise, for instance, that a piscivorous fish (PiF_I) may be affected indirectly by another piscivore (PiF_{II}) if the latter reduces a planktivorous fish ($PlaF_I$) which happens to be a preferred prey of PiF_I. At the same time, the population of PiF_{II} could also exert a positive indirect influence on population $PlaF_I$ by reducing a planktivorous competitor ($PlaF_{II}$). Similar indirect top–down effects also exist between all species of the other (lower) trophic levels (Fig. 5A).

Similarly, as in the simple food chain shown in Figure 1, each top–down effect automatically causes a feedback response. In almost all cases this feedback response consists of a direct effect and several indirect effects (Fig. 5B). If, for instance, a microbial population, Mi_I (e.g. a

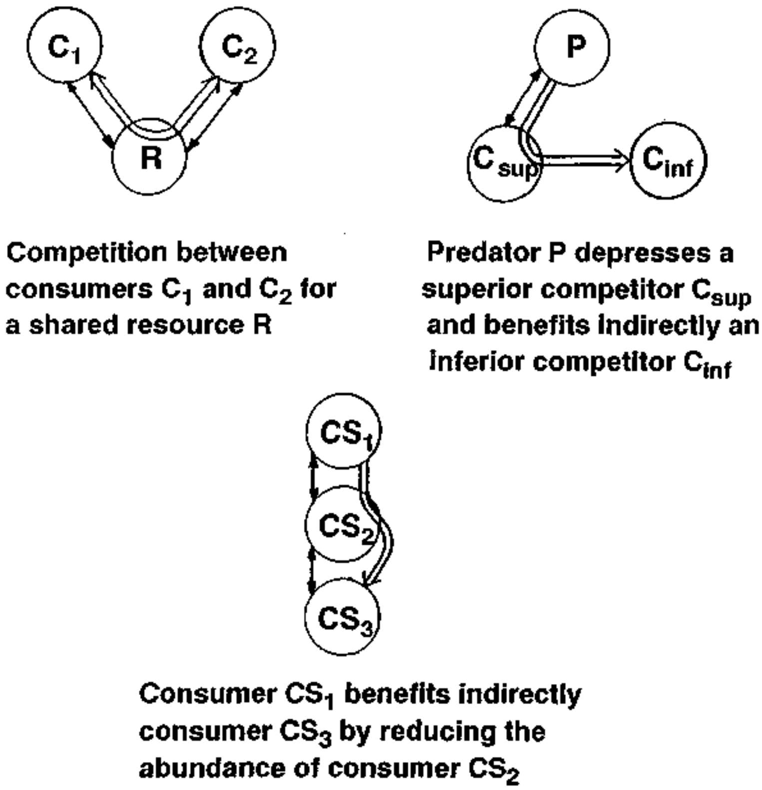

Figure 3. Principal types of trophic linkage indirect effects. Arrows as in Fig. 2 (modified after Crowder *et al.* 1988).

Figure 4. Medium-sized *Daphnia pulex* with neck tooth (arrow) and adult *D. pulex* without neck tooth (left), from the long-term biomanipulation experiment in Gräfenhain. Neck teeth are only formed if the abundance of the predator *Chaoborus flavicans* (right) is high (photograph taken by U. Hornig).

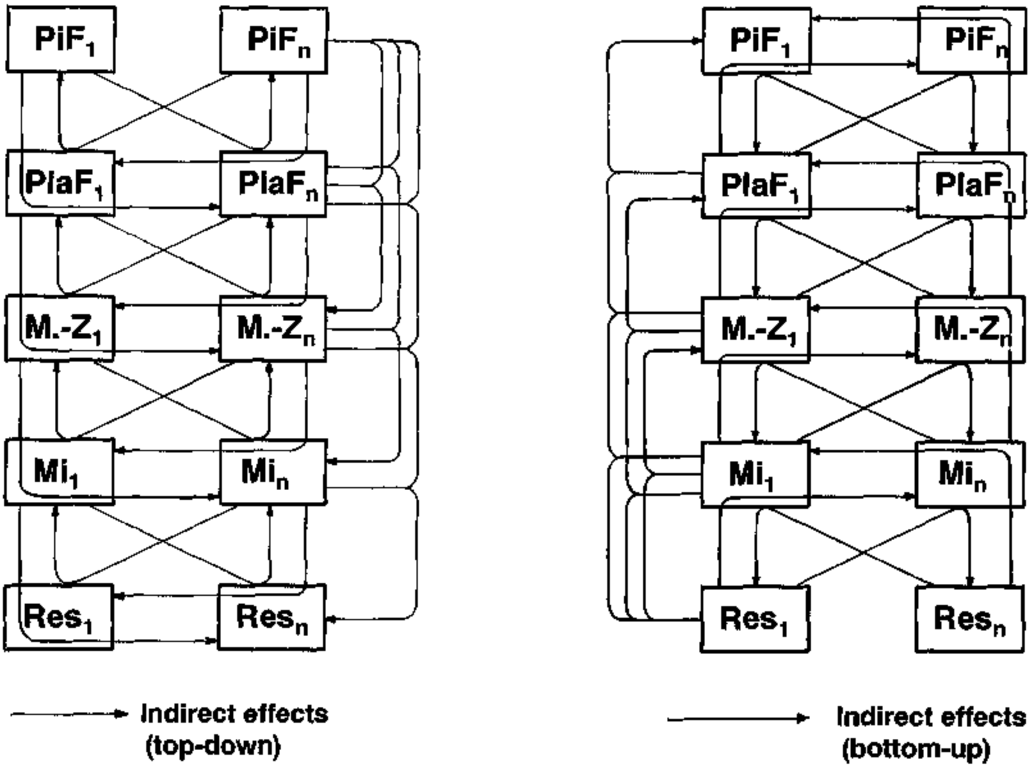

Figure 5. Schematic representation of indirect effects operating top–down (A, left) and bottom–up (B, right) in a simple food web with only two populations on each trophic level. PiF: piscivorous fish, PlaF: planktivorous fish, M.–Z: mesozooplankton/macrozooplankton, Mi:microbial food web (phytoplankton, bacteria, protozoans), Res: resources (nutrients, energy).

grazable microalga), has been reduced as a consequence of top–down mechanisms shown in Figure 1 and Figure 5A, this reduced amount of Mi_I may indirectly affect a mesozooplankton population, $M.–Z_n$ (e.g. a rotifer), through the action of another population, $M.–Z_n$ (e.g. a *Daphnia* species). The inferior competitor ($M.–Z_n$, the rotifer) can not compete successfully with the superior competitor ($M.–Z_i$, the *Daphnia* sp.) under conditions of strong food limitation (Gilbert 1985; Benndorf *et al.* 1988). In similar ways, the other species of all trophic levels are influenced by indirect bottom–up (feedback) effects.

As a comparison of Figures 1 and 5 shows, the number of couplings (i.e. interactions) within and between trophic levels is much greater for indirect effects than it is for direct effects. Thus, it seems already from an *a priori* viewpoint, we should expect that the structuring processes of food webs will be dominated by indirect effects. If this view is correct, then biomanipulation could be much more difficult to control than was assumed (and hoped) originally.

An example: complexity of the indirect effects that enhanced grazing may have on phosphorus concentrations in lakewater

It is well known that in many cases top–down effects are strong at the top of the food web, but in some cases they weaken near the bottom of the trophic pyramid. This "damping phenomenon" is especially pronounced in the more eutrophic water-bodies whereas it seems to be absent under oligotrophic conditions (McQueen *et al.* 1986, Benndorf 1987). There are many indications that this different behaviour of eutrophic and oligotrophic waters is caused by a rather complicated network of indirect effects (Fig. 6).

Enhanced grazing by large and efficient filtrators (e.g. *Daphnia*) exerts indirect effects, some of which cause an increase and others a decrease of the phosphorus concentration in the production zone of a lake or reservoir. Three indirect effects can cause an increase (Fig. 6, left) and five can cause a decrease of phosphorus in the euphotic zone (Fig. 6, right).

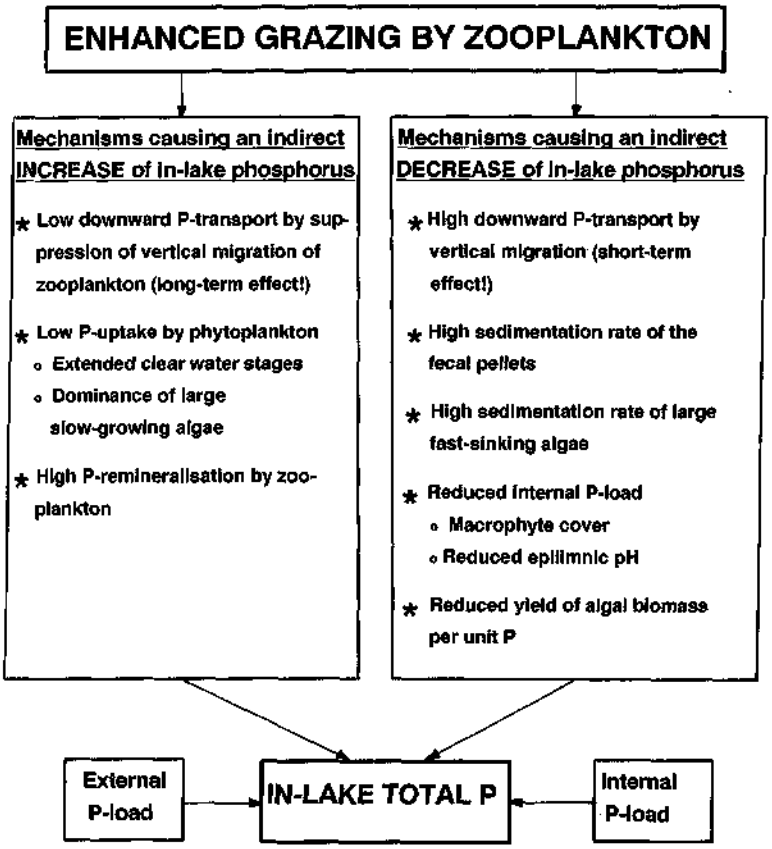

Figure 6. The indirect effects of biomanipulation (enhanced grazing) on the phosphorus concentration in a water-body (modified after Benndorf & Miersch 1991).

Indirect effects that increase the phosphorus concentration in lakewater

(i). The first indirect effect causing an increase in phosphorus concentration is a predator-avoidance mechanism, where the transport of phosphorus from surface waters to deep waters by migrating zooplankters is reduced. Diel vertical migration of the zooplankton, moving to deeper waters in daytime and rising to surface waters at night, must be regarded as a predator-avoidance mechanism which can be shifted by a change in predation pressure. But, as the mechanism is at least partly fixed genetically, a shift in the daily migrating behaviour appears only in a time-scale of months or even years after the change (reduction) in fish predation pressure (Gliwicz 1986; Köhler *et al.* 1989). Therefore, when zooplanktivorous fish are reduced as a management measure, zooplankters will continue their vertical migrations for one or two (or more) following years and thereby continue to transport phosphorus down to the hypolimniom and the sediments. But sooner or later (e.g. after 5 years according to Köhler *et* *al.* 1989) migrating zooplankters will be outcompeted by non-migrating individuals, which are always present due to large genetic variability, because it is much more advantageous to remain in the warmer and food-rich upper layers of the lake throughout the day when there is no longer a risk of predation.

The indirect consequences of zooplankters remaining in the upper layers are a shift to larger, inedible algae (Lampert 1987; Köhler *et al.* 1989) and a reduced downward transport of phosphorus by zooplankton. This predator-avoidance mechanism shows that a positive short-term effect of food-web manipulation can be counterbalanced by the long-term response of the food web.

(ii). The second indirect effect occurs when phosphorus concentrations remain relatively high because algal uptake is reduced by the low biomass of algae present during zooplankton-induced clearwater stages, and there is a dominance of large, slow-growing algal cells and colonies which cannot be eaten by zooplankters (Sommer *et al.* 1985; Lampert *et al.* 1986).

(iii).The third indirect effect occurs when phosphorus concentrations remain relatively high because the faeces of zooplankters have a high content of mineralized phosphorus. Although the specific excretion of phosphorus (i.e. per unit mass of zooplankton) decreases as the body-size of the zooplankters increases (Esjmont-Karabin 1984; Peters 1987), the overall excretion of phosphorus should increase as a consequence of biomanipulation if there is a considerable increase in total zooplankton biomass.

Indirect effects that decrease the phosphorus concentration in lakewater

(1). An enhanced export of phosphorus from the epilimnion into the hypolimnion and sediments occurs when the zooplankton contains numerous large, vertically-migrating *Daphnia*. These zooplankters feed at night in the upper layers and stay in deeper waters during the day, where a greater proportion of phosphorus is released by excretion (Wright & Shapiro 1984; Dini *et al.* 1987).

(2). The phosphorus-rich faeces of zooplankters have higher sedimentation rates than many small organisms (Benndorf 1979; Carpenter *et al.* 1986; Uehlinger & Bloesch 1987). This settling-out effect is particularly pronounced in oligotrophic–mesotrophic waters where large diaptomids dominate; their faecal pellets sink much faster than the "fluffy", easily disintegrating faeces of *Daphnia*. But even these latter faeces sink faster than the small single cells of algae.

(3). Intensive filtration by zooplankton removes almost all of the small, edible algae, but the large inedible species or strains remain. If the inedible ones are green algae or diatoms, then a higher sedimentation rate of algae-bound phosphorus is to be expected, compared with an algal community dominated by small (slow-sinking) algae.

(4). A reduced internal loading of phosphorus can follow a reduction of algal biomass for two reasons: the development of a macrophyte cover due to an improved underwater light climate (Jagtman *et al.* 1988; Mitchell *et al.* 1988), and phosphorus release from epilimnic sediments is reduced due to lower phytoplankton production and hence a lower pH.

(5). There can be a reduced yield of algal biomass per unit of phosphorus, as a consequence of grazing-induced increases in the population growth rates of phosphorus-limited algae (Olsen 1988).

Indirect effects of grazing in relation to phosphorus loadings

It must be realized that indirect effects which *increase* the phosphorus concentration of lakewater, i.e. (i) to (iii) above, are *independent* of the external and internal phosphorus loadings to the lake. But indirect effects (2) to (5), which *decrease* the phosphorus concentration, are *strongly inhibited* by high external and/or internal phosphorus loadings. The actual concentration of phosphorus in the lakewater is the result of all these indirect effects on the circulation of phosphorus, as well as the external and internal phosphorus loadings to the lake (Fig. 6). Consequently, two constellations or suites of these interactions can be predicted.

Prediction (A). When the external and/or internal phosphorus loading is high, this increases the phosphorus concentration directly and suppresses indirect effects (2) to (5) which decrease the phosphorus concentration. Therefore indirect effects (i) to (iii), which cause an increase in the phosphorus concentration, become dominant. As a result, the in-lake phosphorus concentration remains high (unchanged or increased) and no reduction of the annual average biomass of phytoplankton can be expected.

Prediction (B). When the external and internal phosphorus loading is low, this contributes to a low phosphorus concentration and enhances indirect effects (2) to (5) which also decrease the phosphorus concentration. Therefore indirect effects (1) to (5) become dominant relative to indirect effects (i) to (iii). As a result, the in-lake phosphorus concentration decreases as a consequence of biomanipulation, and the annual average biomass of phytoplankton is also expected to decrease.

The validity of these assumptions about the role of indirect effects of biomanipulation on phosphorus metabolism of the water-body, and their consequences for the phytoplankton biomass, can be checked against the results of two independent long-term biomanipulation experiments, using entire lakes of quite different phosphorus loadings (Benndorf *et al.* 1988;

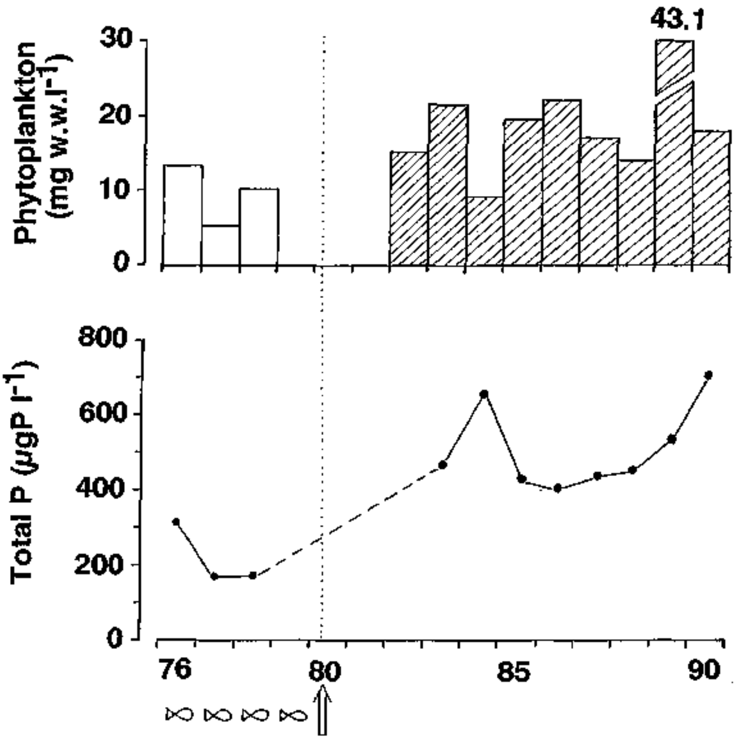

Figure 7. Total phosphorus (µg P l^{-1}) and phytoplankton biomass (mg wet weight per litre of water) before (fish symbols, left, up to 1980) and during (right, after 1980) biomanipulation in the hypereutrophic Bautzen Reservoir (Germany). Volume-weighted vertical averages are shown. (Note: Secchi depth, which is not shown here, was significantly increased due to a change in phytoplankton composition during biomanipulation; see Benndorf *et al.* 1988)

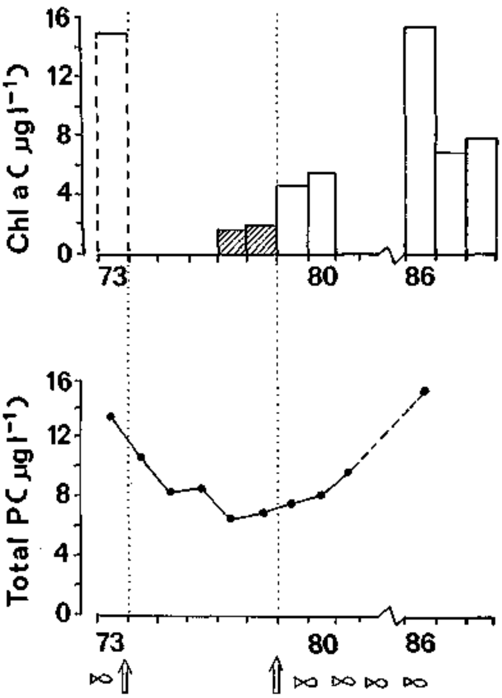

Figure 8. Total phosphorus (µg P l^{-1}) and phytoplankton biomass (as chlorophyll-*a* µg l^{-1}) before and after (fish symbols, up to 1973 and after 1978) as well as during (1974 to 1978) biomanipulation in the oligotrophic Lilla Stockelidsvatten (Sweden). Volume-weighted averages are shown. (From Stenson 1988).

Stenson 1988). A comparison of Figures 7 and 8 reveals complete agreement between predictions (A) and (B) and the respective observations on the hypereutrophic Bautzen Reservoir and the oligotrophic Lilla Stockelidsvatten. Likewise, model simulations for Bautzen Reservoir and the oligotrophic Lake Stechlin also show agreement with predictions (A) and (B), (Benndorf & Miersch 1991).

Phosphorus-loading threshold between predictive constellations (A) and (B)

There is obviously a threshold for phosphorus loadings which separates predictions (A) and (B). The existence of this threshold was first hypothesized by Benndorf (1987) and it has been confirmed recently by Søndergaard *et al.* (1990), Jeppesen *et al.* (1990), Sanni & Waervagen (1990) and Benndorf & Miersch (1991). This threshold is assumed to be relatively variable from lake to lake, rather than having a fixed value. But from the available information cited above, it can be estimated that the threshold should range between 0.5 and 2.0 g total P m^{-2} $year^{-1}$. If the phosphorus loading is below this threshold, the combination of direct and indirect effects listed under prediction (B) should ensure the long-term success of biomanipulation. On the other hand, if the threshold is exceeded, only a short-term or temporary success can be expected from biomanipulation.

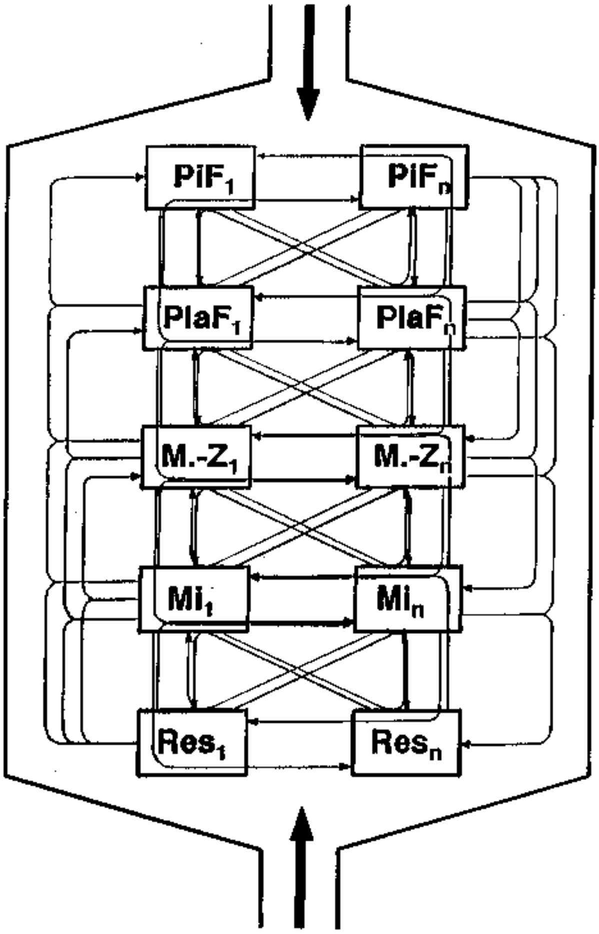

Figure 9. Schematic representation of the food web depicted in Fig. 5, showing all couplings by indirect effects. The high complexity of the system should be controlled simultaneously from the bottom and from the top.

Conclusions

(1). Indirect effects play an essential role in structuring the processes (interactions) of food webs. They can enhance or decrease the stability of biomanipulation measures.

(2). The control of indirect effects is absolutely necessary to stabilize biomanipulation measures, but this is much more difficult than the control of direct effects and needs a deeper understanding of the structuring mechanisms of food webs. For biomanipulation, the problem is how to selectively support the positive indirect effects.

(3). The probability seems not to be high that the lower trophic levels (especially the phytoplankton biomass) can be reduced by controlling the food web exclusively from the top.

(4). The numerous indirect effects can be used optimally (and the positive indirect effects can be selectively enhanced) if strong top–down control (biomanipulation) is combined with maximal limitations at the bottom of the food web, e.g. limitation by phosphorus or light (Fig. 9). This combination is much more efficient than each of the two control strategies alone.

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