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Conditions for effective biomanipulation; conclusions derived from whole-lake experiments in Europe

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Abstract

Since indirect effects, feedback mechanisms and time lag play an important role in top-down manipulated food webs, conclusions regarding the reliability of biomanipulation as a management tool should be derived only from whole-lake studies, the results of which were followed for at least three to five years. There are only a few experiments and applications of that type from which the following conclusions can be drawn: (1) Food web manipulation should be combined with resource limitation measures (nutrients or light) if a 'biomanipulation-efficiency threshold of the phosphorus loading' is exceeded. (2) The critical biomass of undesirable fish shows a very wide range of variation (20–1000 kg ha^{-1}) and depends on several factors, like species and age of fish, total food assemblage, refugia etc. (3) The maximum possible stability of food web manipulation is probably achieved at a biomass of undesirable fish a little below the critical biomass rather than by extermination of these fish. (4) High piscivore diversity increases stability and reliability of food web manipulations. (5) Various techniques of food web manipulation should be combined, except poisoning the entire fish community.

Introduction

Water quality results from ecosystem-external impacts (energy, matter, information) and their transformation through complex interactions within the aquatic ecosystem. Consequently, control of external impacts as well as control of internal ecological processes (i.e. 'ecotechnology') can be employed in water quality management. The strategy of ecotechnology aims at a desirable physical, chemical and biological structure of the ecosystem. In eutrophication control of lakes and reservoirs, for instance, the following basic ecological control variables can be used in ecotechnology (Straškraba, 1979; Benndorf, 1988): internal phosphorus (P) load from the sediment, P-export by discharge, P-export into the sediment, temperature stratification and mixing depth, water residence time, light extinction, phytoplankton sedimentation, phytoplankton mortality, zooplankton growth, zooplankton mortality, reproduction and growth of fish, and fish mortality. Most of these variables are used as physical, chemical and biological measures (see Benndorf, 1988) for controlling the trophic pyramid from the bottom to the top (bottom-up), i.e. this control is oriented to resource limitation (light, nutrients, food). Only mortality caused by predation on all trophic levels provides the possibility of a top-down control of the community structure. The term 'food web manipulation' (or 'biomanipulation' according to Shapiro *et al.*, 1975) is recently used synonymously with 'top-down control' but it should be mentioned that Shapiro *et al.* (1975) originally included in 'biomanipulation' all methods (top-down as well as bottom-up) by which the biological structure of an ecosystem could be manipulated. This paper is mainly directed to the role of fish in top-down mechanisms. Bottom-up control is taken into consideration only if it plays an essential role in governing ecosystem structure and water quality as an indirect effect following top-down control.

Recently, there has been a controversial discussion of whether or not top-down control can be used in eutrophication control as the sole management tool, i.e. without controlling bottom-up mechanisms. Most of the published results cannot be generalized in a simple way in order to answer this question. Some show very clearly all of the top-down effects that are predicted from the biomanipulation concept (Shapiro *et al.*, 1975). and the 'cascading trophic interactions' hypothesis (Carpenter *et al.*, 1985). The latter hypothesis proposes that variance in structure and function of ecosystems, which cannot be explained by physical or chemical factors, must be attributed to variations in predator-prey interactions transmitted to primary producers. Other results seem to be in contradiction to the biomanipulation and cascading trophic interactions concepts. These results show that top-down effects are strong at the top (fish, zooplankton) but weaken towards the basis of the food web (phytoplankton, phosphorus). From this latter group of findings the 'bottom-up: top-down' model was derived (McQueen *et al.*, 1986) which predicts that maximum attainable biomass on each trophic level is determined by resource availability (nutrients, light), but that actually realized biomass is determined by the combined effects of top-down and bottom-up mechanisms.

Nevertheless, there is no real contradiction between the different concepts and experimental findings if the complexity of real food webs as well as the great differences in experimental design and implementation are taken into account. Thus, the only way to solve the problem and to identify the usefulness and limits of top-down control of food-webs as a management tool is to achieve a deeper insight into the complex interactions in aquatic ecosystems. The objective of this paper consists in contributing to this process by evaluating the available information about European whole-lake studies in biomanipulation.

Types of whole-lake experiments in biomanipulation

There are four general types of whole-lake studies which are relevant to biomanipulation. These types can be characterized as follows: (1) Unintentional or 'natural' changes in fish stocks occur the consequences of which for the entire food web are then followed. (2) Fish stocks are intentionally changed to improve fish production; in most cases only the response of the higher trophic levels (fish, zooplankton, zoobenthos) is observed and recorded; the response of the entire food web remains unknown. (3) Fish stocks are intentionally changed to improve water quality but only a few criteria of water quality (e.g. Secchi depth) are observed and recorded. The response of the entire food web remains unknown, (4) Fish stocks are intentionally changed to study the response of the entire food web and the consequences for water quality.

Each of these four types of studies can reveal three patterns of temporal response: (a) The change or manipulation of the fish stocks does not lead to a new stable state. After a short period of one or two years, the fish community is restored to the original state. (b) The change or manipulation of the fish stocks causes a new stable state of the fish community, but the duration of this new state is shorter than 3 to 5 years. (c) The change or manipulation of the fish stocks causes a new stable state of the fish community and this new steady state lasts 3 to 5 years or longer.

It becomes evident from Table 1 that 10 out of the 12 possible combinations of these different

Table 1. Whole-lake biomanipulation experiments and related studies in Europe. Types: (1) Unintentional changes, (2) manipulations to improve fish production, (3) manipulations to improve water quality, (4) manipulations with various objectives. Types (1) and (4) involve the investigation of the response of the entire food web, whereas only a few criteria are investigated in types (2) and (3). Time patterns: (a) Fish stock changes are not stable, (b) changes are stable for a short period of 1 or 2 years, (c) changes are stable for at least 3 to 5 years.

No.	Lake (Author) country	Type	Time pattern	Short description
1	Sobygärd (Jeppesen *et al.*, 1988) DK	1	a	Natural fishkill in the 1970s, subsequent increase in roach and rudd, since 1983 low recruitment
2	Alderfen Broads (Cryer *et al.*, 1986) GB	1	a	Natural two-year periodicy in roach recruitment
3	Lago di Annone (De Bernardi & Giussani, 1978) I	1	b	Natural fishkill in one part, comparison with the undisturbed other part of the lake
4	Queen Elizabeth II reservoir (Duncan, 1975, Steel, 1975) GB	1	c	High natural mortality of perch and roach (disease?), low densities of these fish since the early 1970s
5	Tjeukemeer (Vijverberg & van Densen, 1984, Lammens, 1988) NL	1	c	Increase in body size and biomass of zander due to ending of gill-net fishery in 1977
6	Bolshoy and Maly Okunenok (Gutelmakher & Krylov, pers. commun.) SU	2	b	No fish during 1986/87 in MO, comparison with BO having high stocks of common carp and peled
7	Vörtsjärv (Pihu & Mäemets, 1982) SU	2	c	Stocking with zander and eel, protection of piscivores since 1970
8	Bauernsee and Eiserbuder See (Barthelmes, 1988) DDR	2	c	High stock of zander in BS (no commercial fishery), comparison with ES which is subject to intense fishing
9	Schmachter See (Lampe & Schmidt, 1981) DDR	2	c	Stocking with pike and development of a macrophyte cover since 1980
10	Podhora reservoir (Vostradovsky *et al.*, pers. commun.) CS	3	a	Stocking with pike and zander, selective fishing for cyprinids and perch
11	Lake Trummen (Andersson *et al.*, 1978, Björk, 1985, Andersson & Diehl, 1988) S	4	a	Selective fishing for cyprinids, cyprinid stocks moved back when selective fishing was stopped
12	Hubenov reservoir (Hrbaček *et al.*, 1978, 1986) CS	4	a	Stocking with brown trout since 1972, decline of trout stock and increase in roach and perch stocks after 1977

Table 1. (continued)

No.	Lake (Author) country	Type	Time pattern	Short description
13	Elbe backwaters (Hrbaček *et al.*, 1961) CS	4	b	Poisoning of the whole fish community, stocking with piscivores
14	Feldberger Haussee (Kasprzak *et al.*, 1988) DDR	4	b	Selective fishing for cyprinids (mainly bream) and stocking with zander since 1988
15	Bleiswijkse Zoom (Meijer *et al.*, 1989) NL	4	b	Removal of cyprinids and restocking with 0+ zander in one compartment since 1987, comparison with an untreated second compartment
16	Lake Zwemlust (van Donk *et al.*, 1989) NL	4	b	Removal of cyprinids and restocking with pike fingerlings, improvement of conditions for spawning of pike
17	Lake Vesijärvi (Keto & Sammalkorpi, 1988) SF	4	b	Selective fishing for cyprinids and smelt, stocking with zander since 1987
18	Frederiksborg Slotsso (Riemann, 1988) DK	4	b	Selective fishing for cyprinids in 1985/86
19	Broads at Brundall (Leah *et al.*, 1980) GB	4	b	Stocking of one compartment with pike in 1976, comparison with an untreated second compartment
20	Lake Wyrbel (Gliwicz & Prejs, pers. commun.) PL	4	b	Stocking with pike since 1986
21	Rimov reservoir (Brandl *et al.*, pers. commun.) CS	4	b	Stocking with zander and pike, selective fishing for cyprinids, water level manipulation to eliminate eggs of undesirable species
22	Biesbosch reservoirs (Oskam, 1978 and pers. commun.) NL	4	c	Bad conditions for recruitment of cyprinids, stocking with eel
23	Lake Lilla Stockelidsvatten (Stenson *et al.*, 1978, Henrikson *et al.*, 1980) S	4	c	Poisoning the whole fish stock
24	Experimental water Gräfenhain (Benndorf *et al.*, 1984, Köhler *et al.*, 1989) DDR	4	c	Stocking with piscivores (rainbow trout, perch, pike) since 1980, no fishing
25	Bautzen reservoir (Benndorf *et al.*, 1984, 1988, Benndorf, 1987, Schultz, 1988) DDR	4	c	Stocking with piscivores (zander and pike) since 1977, catch restrictions for zander, pike and eel

types and temporal patterns are represented among a total of 25 European whole-lake studies which were involved in this survey. Although all these studies have contributed essentially to the recent understanding of top-down mechanisms, it should be emphasized that only types 1c and 4c can be used to derive conclusions with respect to appropriate methods and reliability of biomanipulation as a management tool. This results from the fact that indirect effects, feedback mechanisms and time lags play an important role in top-down manipulated food webs. According to Kerfoot & Sih (1987) at least five kinds of indirect effects in top-down impacts can be differentiated. These are: keystone predator effects, cascading effects, effects of behavioral change, chemical induction of antipredator traits and quantitative and qualitative change in the resource base. The latter indirect effect can be taken as an example.

It must be realized that every top-down impact (i.e. every change in predation strength) automatically causes feedback responses in the bottom-up mechanisms. Reduced fish predation on zooplankton, deteriorates the food supply for the increased standing stock of zooplankton. Increased zooplankton biomass, can lead to an improvement of the specific nutrient supply for the remaining phytoplankton through reduced phytoplankton biomass and higher intensity of nutrient remineralisation by zooplankton. Increased zooplankton grazing, can cause higher transparency of the water and hence an increase in photosynthetical activity per unit phytoplankton biomass or enhanced colonization by macrophytes. Increased predation pressure by piscivorous fish on zooplanktivorous fish, can improve the food resources of other zooplanktivorous fish which, consequently grow faster to a critical body size above of which they switch to food resources other than zooplankton (Lammens *et al.*, 1986, Benndorf *et al.*, 1988). There are numerous related feedback loops (Kerfoot & Sih, 1987; Carpenter, 1988). Since many organisms which are involved in that indirect and feedback mechanisms, have generation times of years (fish, other vertebrate predators, *Chaoborus*), a top-down manipulated food web will reach a new steady state only after some years. Thus, many of the mechanisms listed above cannot be investigated in studies of types 1a, 1b, 2a-c, 3a-c, 4a and 4b because either the response of the entire food web or the long-term behaviour or both remain unknown. Because of these factors, only six studies could be used to derive the management implications discussed in this paper (see Table 1). These include: Queen Elizabeth II reservoir (type 1c), Tjeukemeer (type 1c), Biesbosch reservoirs (type 4c), Lilla Stockelidsvatten (type 4c), experimental water Gräfenhain (type 4c), Bautzen reservoir (type 4c).

It seems to be especially important to continue the numerous type 4b-studies, which are still under investigation, so that in the near future a much higher number of 4c-studies will be available for deriving management implications. The principal results of the two type 4c-experiments performed in the GDR will be shown briefly as examples.

Case studies

Table 2 provides a brief description of a few important characteristics of the two experimental waters in the GDR in which type 4c-experiments are under investigation. These two experiments were performed under extremely different conditions regarding lake size (but not mean depth), hydrophysical structure and P-loading (Table 2). Thus, it seemed very probable that a broad spectrum of possible responses to biomanipulation could be observed.

Gräfenhain experimental water

The small lake is a former quarry near Gräfenhain about 40 km north of Dresden. During the prebiomanipulation period the lake was densely populated by zooplanktivorous fish (*Leucaspius delineatus*, mean body weight 3 g, areal biomass 120 kg ha^{-1}). No piscivores were present. *Daphnia* and *Eudiaptomus* were not present and small crustaceans (*Thermocyclops oithonoides*, *Bosmina longirostris*) and rotifers dominated the

Table 2. Characteristics of two experimental waters in GDR.

Criterion	Bautzen reservoir	Flooded quarry Gräfenhain
Volume (m^3)	39.2 10^6	3,100
Surface area (ha)	533	0.044
Mean depth (m)	7.4	7.0
Mean theoretical retention time of water (d)	193	365
Wind exposure	Extremely exposed	Highly sheltered
Thermal stratification	Unstable, polymictic	Very stable, monomictic
P-loading (g total P m^{-2} y^{-1})	7.1–17.5	0.66
Origin of load	Import by severely polluted river Spree	Import only with precipitation and terrestrial vegetation (falling leaves and pollen)
Eutrophication degree	Hypertrophic	Mesotrophic
Pre-biomanipulation period	1977–1980	1979–1980
Biomanipulation period	1981–now	1981–now

zooplankton. Summer phytoplankton consisted mainly of edible species. Summer Secchi depth averages were *ca.* 2 metres (Fig. 1 and Table 3).

In March 1981 zooplankton-eating fish were completely eliminated by stocking with piscivorous fish. This stocking has continued until the present. In 1981 a total biomass of 117 kg ha^{-1} of piscivorous perch (*Perca fluviatilis*) and rainbow trout (*Salmo gaidneri*) was stocked. The resulting high piscivores/planktivores ratio of 0.98 and the complete lack of refugia for *L. delineatus* led to the extermination of these zooplanktivorous fish within a few weeks. Piscivores could not survive longer than one season in the experimental water due to a regular fishkill in late autumn caused by H_2S-intrusion from the hypolimnion. Only a few species (*L. delineatus, Carassius carassius, Tinca tinca*) are able to tolerate the extremely low oxygen concentration during that autumnal mixing period. Thus, restocking with piscivores (mainly pike, *Esox lucius*, about 20 kg ha^{-1}) was performed every spring after 1981 to avoid recolonisation of *L. delineatus* or other planktivores. Consequently, from 1981 till now there is no predation pressure of vertebrate predators on zooplankton (Fig. 1). This situation and its consequences for the entire food web could hardly be investigated in a larger experimental water.

The short-term responses of the plankton community during the first year of biomanipulation (1981) can be summarized as follows: (1) Biomass of the herbivorous zooplankton increased to nearly 400%. (2) Mean individual body weight of the crustaceans increased to 200 to 300% due to the dominance of *Daphnia hyalina, D. cucullata* and *Eudiaptomus gracilis* which were absent or rare before biomanipulation. (3) The remarkable enhanced grazing pressure of the herbivorous zooplankton on the phytoplankton did not have any effect on the total phytoplankton biomass, but the phytoplankton composition revealed a strong response to the enhanced grazing pressure. The proportion of edible algae decreased (Table 3).

The long-term responses during the fifth, sixth and seventh year of biomanipulation (1985 to 1987) were different from the short-term response in 1981 (Fig. 1 and Table 3): (1) The abundance of *Chaoborus flavicans* strongly increased and showed a pronounced year-to-year fluctuation which appeared to be related to food limitation and the great difference in the generation times of the food organisms and *Chaoborus*. (2) The biomass of the herbivorous zooplankton decreased as a consequence of increased *Chaoborus* abundance and showed reverse year-to-year fluctuations when compared with *Chaoborus*. (3) The

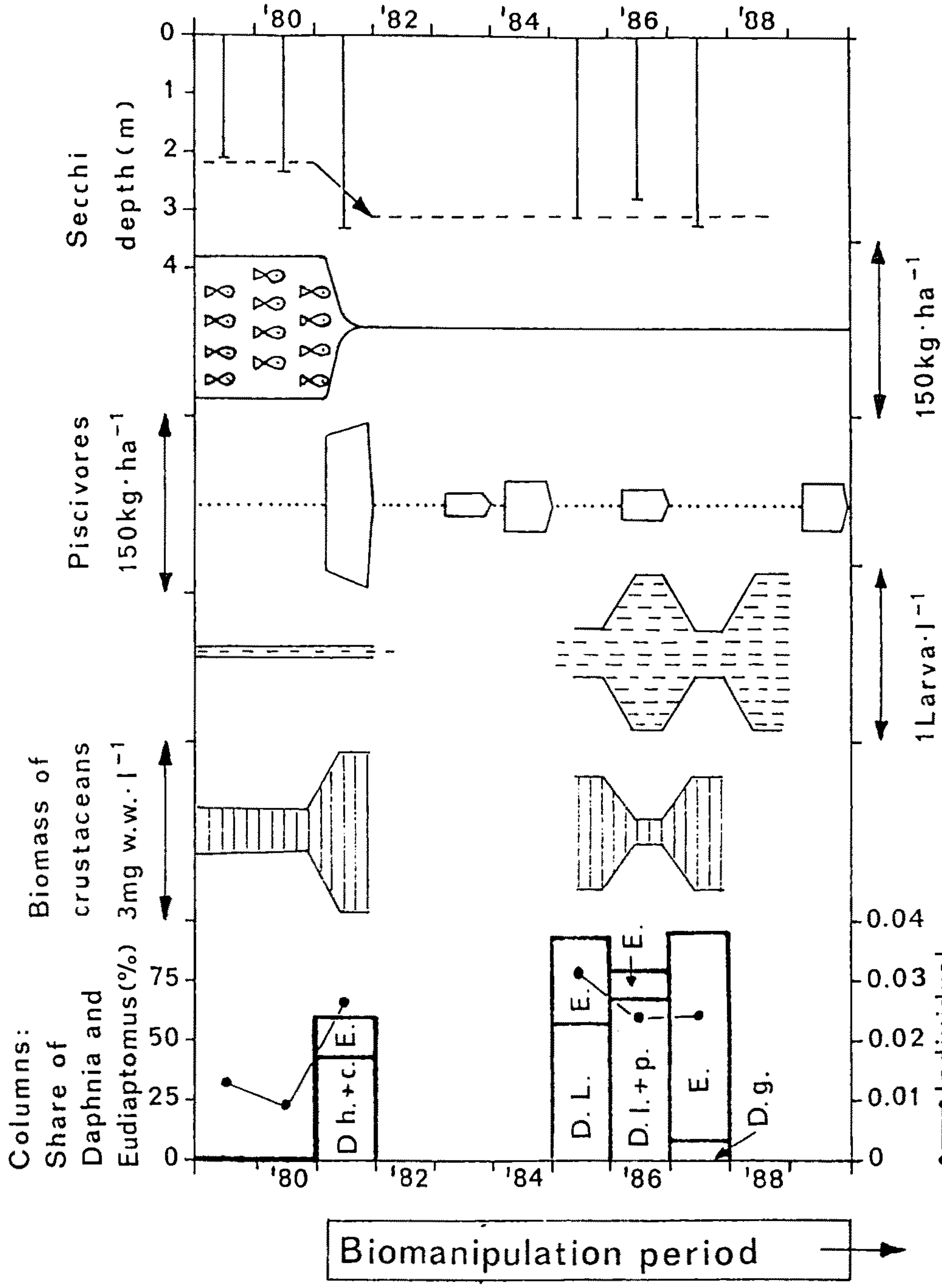


Fig. 1. Long-term changes in fish, zooplankton and Secchi depth in Gräfenhain experimental water. D.h. = *Daphnia hyalina*, D.c. = *D. cucullata*, D.l. = *D. longispina*, D.p. = *D. pulex*, E. = *Eudiaptomus gracilis*, see Table 3 for related results regarding phytoplankton and phosphorus. Partly from Benndorf *et al.* (1984), Köhlet *et al.* (1989).

mean individual body weight of the crustaceans remained high. *Daphnia cucullata* and *D. hyalina* were replaced by larger species (*D. longispina*, *D. pulex*, *D. galeata* and *Eudiaptomus gracilis*). (4) These large herbivores did not longer migrate to deeper layers during day-time, whereas the

Table 3. Comparison of phytoplankton and in-lake phosphorus before and during biomanipulation in Bautzen reservoir and Gräfenhain experimental water (summer averages from Benndorf *et al.*, 1984, 1988 and Köhler *et al.*, 1989). *) The situation in 1976 was characterized by a natural low stock of planktivores; the first strong year class of planktivores appeared in 1977 (see Fig. 2). n.d. = no data available.

Case study	Criterion	*)	Pre-biomanipulation period				Biomanipulation period							
		'76	'77	'78	'79	'80	'81	'82	'83	'84	'85	'86	'87	'88
Bautzen reservoir	Phytoplankton biomass (mg w.w. l^{-1})	13.3	5.3	10.2	n.d.	n.d.	3.0	15.2	21.6	9.4	19.7	22.2	17.2	14.3
	Edible phytoplankton (%)	15	76	78	n.d.	n.d.	9	9	7	44	11	17	26	11
	Total phosphorus (vertical mean, μgP l^{-1})	308	169	171	n.d.	n.d.	n.d.	n.d.	477	729	410	409	443	456
	Dissolved orthophosphate (vertical mean, μgP l^{-1})	219	109	83	n.d.	n.d.	n.d.	n.d.	366	560	278	285	244	294
Gräfenhain	Phytoplankton biomass (mg w.w. l^{-1})				3.5	3.2	3.6	n.d.	n.d.	n.d.	3.5	n.d.	3.6	n.d.
	Edible phytoplankton (%)				80	80	50	n.d.	n.d.	n.d.	30	(27)	12	n.d.
	Total phosphorus (epilimnetic mean, μgP l^{-1})				n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	99	n.d.
	Dissolved orthophosphate (epilimnetic mean, μgP l^{-1})				2.9	9.6	5.2	n.d.	n.d.	n.d.	10.4	n.d.	11.5	n.d.

herbivores did migrate in the first year of biomanipulation (1981). Since there was no fish predation in the epilimnion, but strongly increased *Chaoborus* predation in the hypolimnion in 1985 and following years, this long-term change in the migration behaviour obviously contributed to the pronounced dominance of these large herbivores (biomass: 78% to 95%) in the crustacean zooplankton, (5) Small and medium-sized age classes of *D. longispina* and *D. galeata* developed 'Nackenzähne' as a defense mechanism against *Chaoborus* predation. (6) Phytoplankton biomass has not changed suggesting that they are controlled by nutrients rather than by zooplankton grazing. (7) The percentage of edible algae decreased further, which shows that the grazing pressure on phytoplankton was enhanced. Since the biomass of herbivores decreased, this can only be explained by the altered migration behaviour of the herbivores (Lampert, 1987). (8) Secchi depth remained almost the same as during the first year of biomanipulation.

Unfortunately, no observations are available for the period from 1982 to 1984 so that there is no information about the duration of the transient state between short-term and long-term response of the ecosystem. But the results of the Gräfenhain case study emphasize that, during biomanipulation, the internal ecological time-lag mechanisms must be taken into account even if the transient state should be shorter than five years. The experiment will be continued (see Benndorf *et al.*, 1984 and Köhler *et al.*, 1989 for details).

Bautzen reservoir

Bautzen reservoir is a man-made lake about 70 km north-east of Dresden. It is a typical multipurpose reservoir (cooling water supply for a power plant, water supply for fish ponds situated downstream, flood control, recreation). The intensive recreational use (e.g. camping, boating, surfing, angling, swimming) makes a high demand on the water quality. The main water quality problem is excessive eutrophication caused by high external and internal nutrient loading. Biomanipulation was begun in 1977 by the Dresden University of Technology, the state authorities and the anglers' union of the GDR. This cooperation was a decisive organizational prerequisite for the biomanipulation of such a relatively large water body.

In the first two years after the initial impoundment of the reservoir (1974 and 1975), a large, natural pike population (*Esox lucius*) developed. Thus, pike were abundant in 1976, whereas zooplanktivorous fish were extremely scarce. At this time (May, 1976), angling started at the reservoir and this led to a fast decline in the pike population. The consequence was the development of an abundant stock of small zooplankton-eating perch (*Perca fluviatilis*) belonging to the 1977 year-class (Schultz, 1983).

With the beginning of biomanipulation in 1977, each year (with the exception of 1978, 1979 and 1983) 20000 to 80000 pond-raised zander fingerlings were introduced in autumn and restrictions regarding the catch of piscivores were imposed on anglers after 1979. These restrictions involve the following regulations: (1) Only one specimen of predacious fish may be taken per day and the minimum size must be 60 cm for pike and zander; (2) the use of fish as baits is prohibited and only artificial lures are allowed. Since 1985, additional stocking with pike fry and fingerlings was performed. As a consequence of these measures the pike population was stabilized and an increasing population of zander (*Stizostedion lucioperca*) was established (Fig. 2). It should be stressed that this was only possible by combining both control measures (stocking and catch restrictions). The increased predation pressure of these large piscivores reduced the abundance of zooplanktivorous fish (mainly small perch) without prohibiting the development of a perch population with a sufficiently high proportion of piscivorous age classes. This seems to be a key factor in controlling the young-of-the-year of all fish, including its own species. This control of 0^+ fish has functioned in Bautzen reservoir in most years during the biomanipulation. In 1984, a large proportion of the perch population died after spawning. The probable cause was disease. As a consequence, large numbers of fry were observed in 1984 (perch, roach) and 1988 (zander, ruff, perch). These young fish were reduced to low abundances by zander and pike, but this reduction took place later in the year than was observed in previous years when perch predation on fry was high. The result was no observable reduction of the strong predation of 0^+ fish on zooplankton during summer in 1984 and 1988 (Fig. 2).

Cyprinids increased slightly in abundance during the biomanipulation period. Roach (*Rutilus rutilus*), which feeds on zooplankton, algae, detritus and zoobenthos, were most successful, whereas all the other cyprinids remained at very low abundances. During recent years, the piscivores/(planktivores + benthivores) biomass ratio reached a fairly stable value of 0.3 to 0.5. The strategy of biomanipulation in Bautzen reservoir is to further increase the diversity of piscivores rather than to increase the biomass ratio of piscivores/(planktivores + benthivores) beyond the value of 0.5. A wide and even distribution of age classes in pike and zander and in populations of smaller piscivores (mainly perch and eel, *Anguilla anguilla*) is important to guarantee high predation pressure on a broad spectrum of undesirable fish from large cyprinids down to young-of-the-year.

As a consequence of the described manipulation of the fish community the structure and function of the entire ecosystem during eight years of effective biomanipulation (1981-1988) can be compared with the situation during the period before biomanipulation became effective (1977-1980, Fig. 2 and Table 3). The comparison refers to weighted summer averages (May to October) and shows that: (1) There was only a slight increase (21%) in the biomass of total zooplankton. But the biomass of *Daphnia galeata* rose by about 110 per cent. (2) The mean individual body weight of all crustaceans (including nauplii, but without *Leptodora kindti*) increased by 110 per cent. (3) Biomanipulation led to an enhancement of the abundance of large carnivorous invertebrates (*Chaoborus flavicans*, *Leptodora kindti*), but these predators were controlled to a moderate density by the remaining planktivorous fish. (4) Extended clear water stages with Secchi

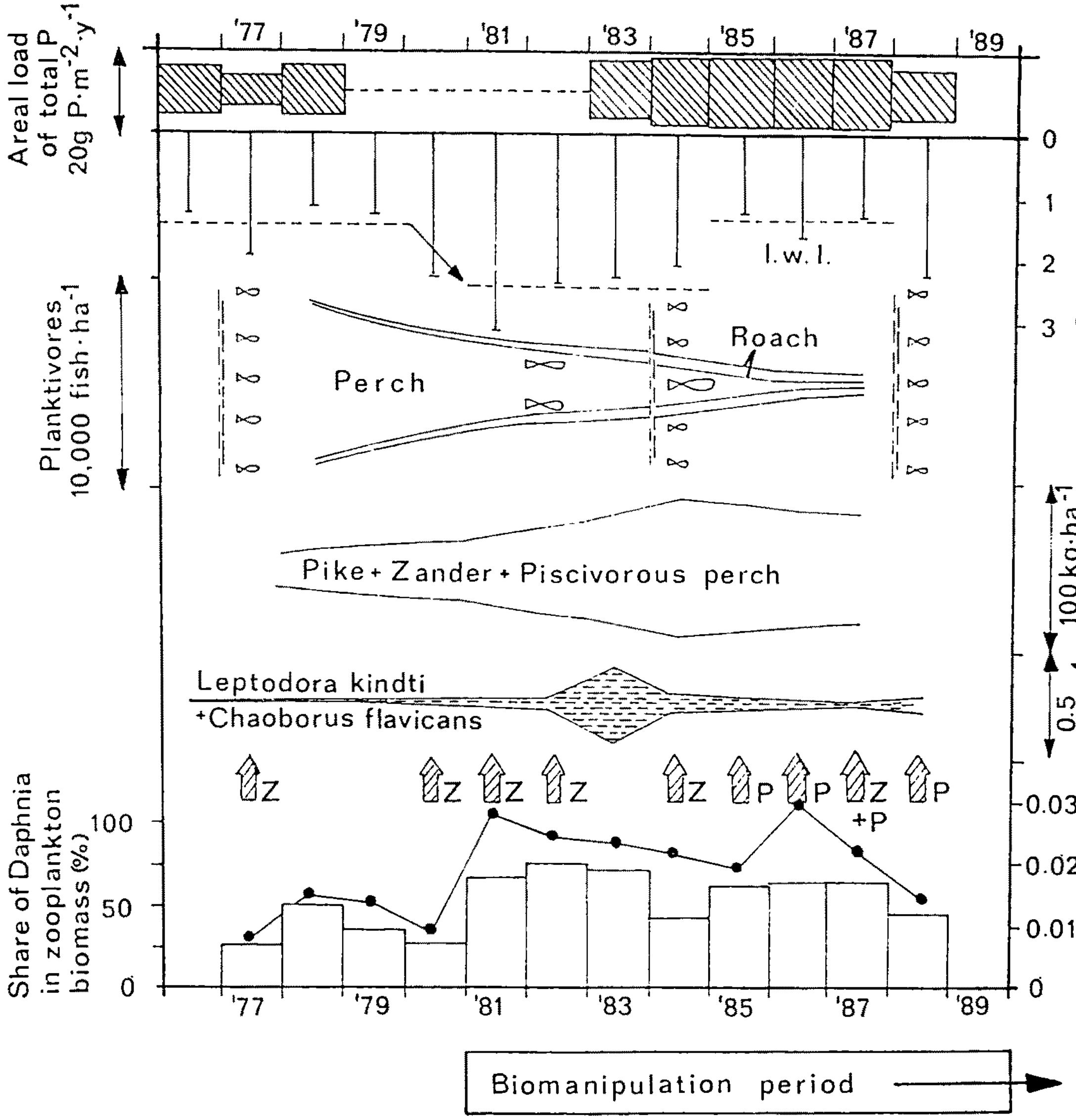


Fig. 2. Long-term changes in fish, zooplankton, Secchi depth and external P-loading in Bautzen reservoir. I.b.w. = Individual body weight, mg = mg wet weight, columns refer to the share of *Daphnia galeata* in the zooplankton biomass, small fish symbols indicate strong recruitment of fish, Z = Stocking with zander fingerlings (*Stizostedion luciopera*), P = Stocking with pike (*Esox lucius*) fry and fingerlings. Partly from Benndorf (1987) and Schultz (1983 and pers. commun.)

depths from 4 to 9 m were observed in the early summer during the biomanipulation period. No such extended clear water stages occurred before 1980. (5) The mean Secchi depth increased by 0.33 m (i.e. 20%) during the entire biomanipulation period. If the three years with extremely low water level (see Fig. 2) are excluded, the increase in transparency was even more pronounced (by 0.70 m or 41%). (6) Inedible algae became dominant during summer of all the years of biomanipulation. The mean as well as the maximum phytoplankton biomasses were either lower (1981), equal (1984), or higher (1982, 1983, 1985, 1986, 1987) than during the pre-biomanipulation period. The probability of the occurrence of extremely dense *Microcystis* blooms has been raised by the increased grazing pressure of *D. galeata* on phytoplankton. There are also indications that the toxicity of *Microcystis* can be enhanced by this strong grazing pressure (see Benndorf & Henning, 1989 for details). (7) Total in-lake phosphorus increased by 140 per cent. But since the external loading also increased, the more interesting finding with respect to P-metabolism, is the decrease in the P-retention of the reservoir from 49 per cent (pre-biomanipulation period) to 36 per cent of the total P entering with inflow during the biomanipulation period. (8) Some responses of the ecosystem to biomanipulation revealed remarkable instability which cannot be attributed directly to year-to-year variations in the fish community (Fig. 2). Such instabilities refer, for instance, to the mean body weight of the crustaceans, strong up- and downward trends in the abundance of *Chaoborus*, strong fluctuations in the abundance of *Leptodora* and to different stable states of the structure of the summer phytoplankton. These instabilities are regarded to be the consequence of the stochastic character of the meteorological conditions as well as the result of time lags and feedback mechanisms within the ecosystem.

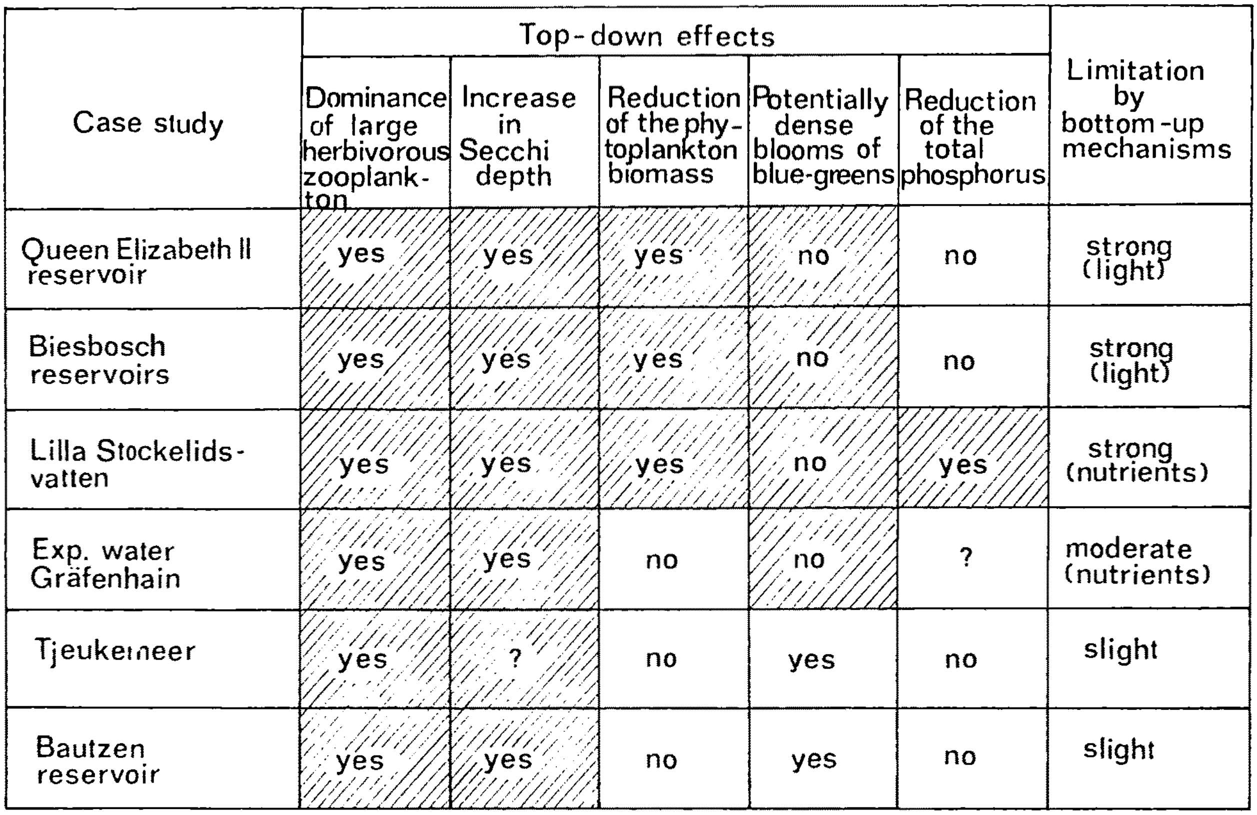
The results of the experiment in Bautzen reservoir demonstrate that it is possible, by proper management of the stocks of piscivores, to stabilize a relatively high stock of different piscivorous fish. This guarantees low abundances of zooplanktivorous fish, even in hypertrophic waters. The fast reduction of 0^+ fish in years with an extraordinarily strong recruitment, is a key problem which has not been solved in Bautzen reservoir. Dominance of large herbivorous zooplankton (mainly *Daphnia galeata*) and increases in Secchi depth due to a change in phytoplankton structure, are the most pronounced biomanipulation effects. Only in one of eight years did biomanipulation cause a reduction of the phytoplankton biomass. The phosphorus concentration as well as the probability of negative side effects (blooms of blue-greens, toxic blue-greens) increased. These findings are an experimental confirmation of the 'bottom-up: top-down' model developed by McQueen *et al.* (1986) and of the hypothesis of a 'biomanipulation-efficiency threshold of the P-loading' (Benndorf, 1987). The experiment will be continued (see Benndorf *et al.*, 1988, Köpke *et al.*, 1988, Schultz, 1988 for details).

Management implications

The six 1c- and 4c-studies (see section of Whole-lake Experiments), which are involved in deriving the following conclusions, represent a rather broad spectrum of waters including: natural as well as man-made lakes, moderate (Gräfenhain) and extremely high external (Queen Elizabeth II, Biesbosch, and Bautzen reservoir) or internal (Tjeukemeer) phosphorus loading. The bioproduction is either nutrient-limited (Lilla Stockelidsvatten, Gräfenhain, Tjeukemeer) or light-limited. Two of the waters exhibit stable thermal stratification (Gräfenhain, Lilla Stockelidsvatten), one is characterized by a short summer stratification (Bautzen reservoir) whereas the others are well mixed during most of the time in a natural (Tjeukemeer) or artificial way (Queen Elizabeth II and Biesbosch reservoirs). Thus, it seems to be sounded to derive some general management implications from these studies.

Combined bottom-up and top-down control

It becomes evident from the selected six whole-lake studies, that some top-down effects are independent or only slightly dependent on limitation by bottom-up mechanisms (Fig. 3). In all cases, reduced predation by zooplanktivorous fish caused the dominance of large herbivorous zooplankton and this, in turn, induced a change in phytoplankton structure to favour algae which are protected against grazing (large cell or colony size, gelatinous sheaths, toxins) or which are characterized by very high growth rates. In almost all cases this structural change in phytoplankton, led to an increase in water transparency, but the increase in Secchi depth is more pronounced if bottom-up control limits bioproduction.



Case study	Top-down effects: Dominance of large herbivorous zooplankton	Top-down effects: Increase in Secchi depth	Top-down effects: Reduction of the phytoplankton biomass	Top-down effects: Potentially dense blooms of blue-greens	Top-down effects: Reduction of the total phosphorus	Limitation by bottom-up mechanisms
Queen Elizabeth II reservoir	▨ yes	▨ yes	▨ yes	▨ no	no	strong (light)
Biesbosch reservoirs	▨ yes	▨ yes	▨ yes	▨ no	no	strong (light)
Lilla Stockelids-vatten	▨ yes	▨ yes	▨ yes	▨ no	▨ yes	strong (nutrients)
Exp. water Gräfenhain	▨ yes	▨ yes	no	▨ no	?	moderate (nutrients)
Tjeukemeer	▨ yes	▨ ?	no	yes	no	slight
Bautzen reservoir	▨ yes	▨ yes	no	yes	no	slight

Fig. 3. Survey of top-down effects, which were observed in six selected long-term whole-lake studies in Europe, in relation to the intensity of bottom-up control. Hatching: desirable top-down effects. See Table 1 for sources. Strong light limitation in Queen Elizabeth II and Biesbosch reservoirs is caused by artificial destratification.

Other top-down effects seem to be strongly dependent on bottom-up mechanisms (Fig. 3). Long-term averages of phytoplankton biomass are reduced by top-down mechanisms, only if a certain degree of resource availability (light, nutrients) is not exceeded. About at the same threshold, the probability of mass developments of inedible algae, especially of blue-greens, increases with decreasing resource limitation.

If bottom-up mechanisms are mainly controlled by phosphorus availability a coincidence between the results related to phytoplankton and the response of in-lake total phosphorus to biomanipulation can be seen: only if total P is reduced by various indirect effects of top-down control (c.f. Wright & Shapiro, 1984, Benndorf & Miersch, 1989) a reduction in phytoplankton biomass occurs. Thus, it seems that the effect of biomanipulation-induced P-decrease is an indispensable prerequisite for long-term phytoplankton reduction. But this P-decrease can only be expected if the external and internal P-load is not too high. The critical P-load cannot be derived exclusively from the six long-term whole-lake studies involved in Fig. 3. From a larger data set including also studies from North America, a 'biomanipulation efficiency threshold of the P-loading', below of which *all* the positive top-down effects shown in Fig.3 can be observed, was estimated to approach a numeric value of about 0.6 g total P $m^{-2}y^{-1}$ (Benndorf, 1987, 1989; Benndorf & Miersch, 1989). This loading threshold is regarded to be a variable in dependence on lake characteristics rather than a fixed value.

The principal conclusion must be drawn that food web manipulation as a management tool should be combined with a resource limitation measure (control of nutrients or light) if the 'biomanipulation-efficiency threshold of the P-loading' is exceeded.

Minimum, critical and optimum fish biomass

Some of the case studies involved in this survey (e.g. the Gräfenhain experiment) as well as studies from North America (e.g. Edmondson & Abella, 1988) show that the complete absence of zooplanktivorous fish does not induce maximum efficiency of food web manipulation. A certain amount of these fish are required to control large invertebrate predators, such as *Chaoborus*, *Leptodora* or *Neomysis*, which would otherwise reduce or even eliminate large herbivorous zooplankton. Moderate fish predation pressure can also increase the stability of *Daphnia* population by avoiding starvation and oxygen depletion as a consequence of extreme overpopulation. Thus, the 'minimum fish biomass' is defined as the biomass of zooplanktivorous fish which is necessary to avoid such negative side effects.

On the other hand, an upper limit of zooplanktivorous fish (the 'critical fish biomass') cannot be exceeded if large herbivores are to dominate the zooplankton. The critical fish biomass, below which large *Daphnia* species can develop great abundances, shows a very wide range of variation which cannot be derived exclusively from the experiments of this survey. The lowest values of about 20 to 50 kg ha^{-1} were found for 0^{+} fish (e.g. Perca flavescens; Mills & Forney, 1983; McQueen & Post, 1986; Perca fluviatilis; Schultz, 1983, Benndorf *et al.*, 1988; cyprinids; Meijer *et al.*, 1989). The availability of refuges for prey, increases critical 0^{+} fish biomass up to 100 kg ha^{-1} (*Perca flavenscens*; McQueen & Post, 1988). Low values ($<$ 120 kg ha^{-1}) were also found for adults of small fish species (e.g. *Leucaspius delineatus*; Benndorf *et al.*, 1984). At a similar small body size as *L. delineatus*, 0^{+} smelt (*Osmerus eperlanus*) need much higher biomasses (up 370 kg ha^{-1}) to drastically reduce *Daphnia hyalina* in Tjeukemeer (Lammens *et al.*, 1985, Lammens, 1988). High turbidity may serve as a refuge in this case. Adult roach (*Rutilus rutilus*) and bream (*Abramis brama*) eliminate large *Daphnia* if their total biomass exceeds the critical level of 200 kg ha^{-1} (Barthelmes, 1988). Extremely high critical fish biomasses with respect to the elimination of large *Daphnia* were reported for common carp (*Cyprinus carpio*) in ponds with additional feeding (650 up to 1000 kg ha^{-1} depending on age class; Barthelmes, 1988).

It can be concluded from the available information of this survey that maximum efficiency of food web manipulation as a management tool is achieved at a 'optimum' biomass of zooplanktivorous fish, the numeric value of which must be sought in the range between critical and minimum fish biomass. It is a key question for successful biomanipulation how wide this range is, but this question can hardly be answered at the present stage of our knowledge.

Optimum structure of the community of piscivorous fish

Besides a sufficiently high proportion of piscivores in the total fish community of about 30–40 per cent, which corresponds to a piscivorous/(planktivores + benthivores) biomass ratio of about 0.28 to 0.66, an optimum structure of the piscivores community is of decisive importance for effective top-down control. The optimum structure should fulfil the following conditions: (1) The desired high proportion of piscivores in the total fish community must be stable in the long-term range. (2) A sufficient proportion of large age classes of piscivores having a large mouth gape must be present in order to exert strong predation pressure on adult zooplanktivorous and benthivorous fish, especially on the large size classes which have an enormous reproductive capacity. (3) There must be high abundances of species and age classes of such piscivores, which prefer 0^{+} fish as prey and which can easily switch to benthic food (but not to zooplankton) if 0^{+} fish are scarce.

As the empirical relationship between prey size and body size of the most important piscivores in European lakes illustrates (Fig. 4), condition (2) can be fulfilled only if northern pike (*Esox lucius*) and/or the largest size classes of zander (*Stizostedion lucioperca*) are present. Condition (3) is optimally achieved by a high abundance of eel (*Anguilla anguilla*), but perch (*Perca fluviatilis*) and small zander may essentially contribute to 0^+ fish elimination. High species diversity, as well as a wide distribution of age classes in all populations of piscivores, are both necessary to fulfil conditions (2) and (3), and should also ensure that condition (1) is guaranteed.

The desirable high predation pressure on a wide range of different species and age classes of zooplanktivorous and benthivorous fish is not only achieved by the various abilities of the piscivores to use prey of a particular size (Fig. 4). Great differences in habitat selection, temporal feeding behaviour and tolerance to extreme environmental conditions (pH, O_2, temperature etc.) in different piscivorous fish contribute to high predation pressure and to the stability of the stock of piscivores. With respect to the temporal feeding behaviour, for instance, this can be seen in a piscivores community consisting of northern pike, zander and perch. Pike feed mainly during daytime, perch during the early morning and evening and zander during night (or when the light intensity is low) (Craig, 1987).

It can be easily understood, that such multi-species communities of piscivores fill a much higher number of ecological niches when com-

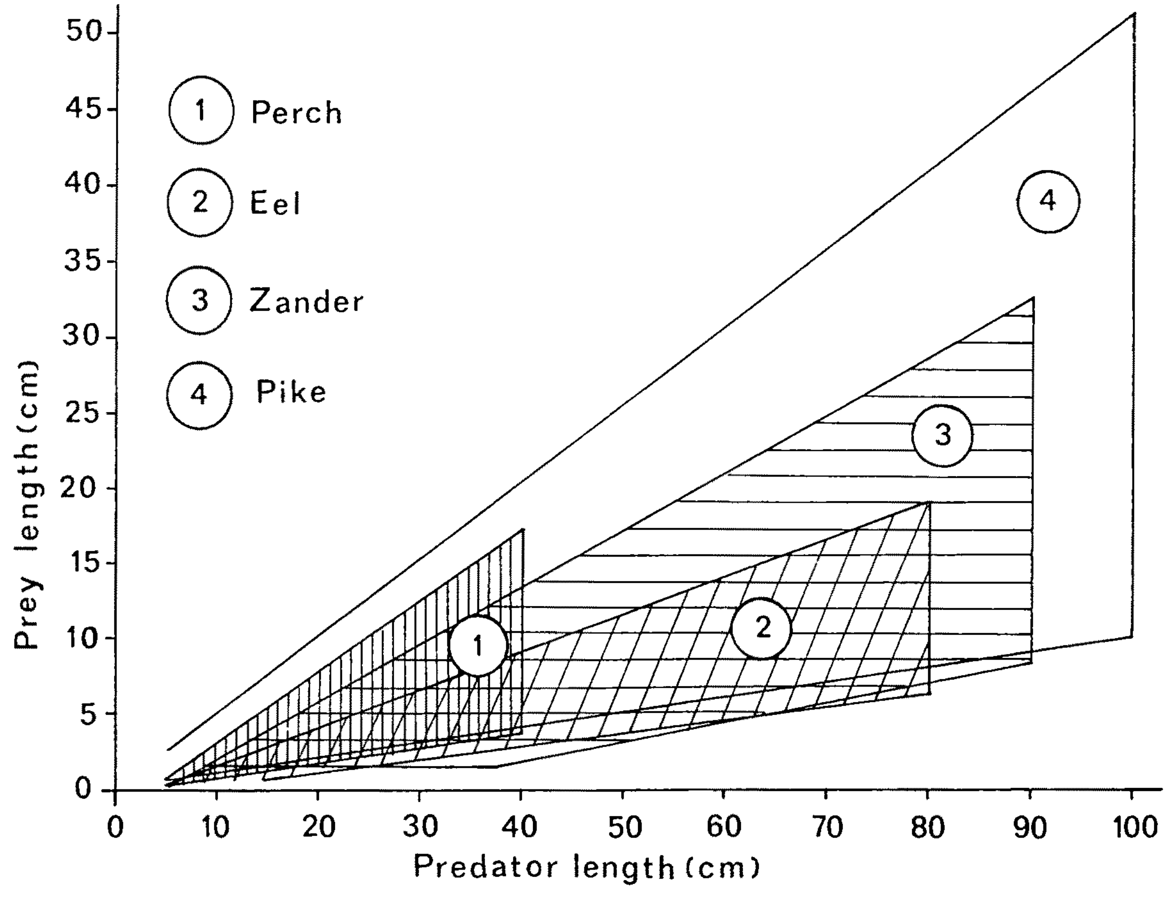


Fig. 4. Range of prey fish lengths which can be eaten by four important types of European piscivores (1 = *Perca fluviatilis*, 2 = *Anguilla anguilla*, 3 = *Stizostedion lucioperca*, 4 = *Esox lucius*). Combined from stomach analyses performed by Popova (1978), DeNie (1987) and Schultz (pers. commun.).

pared to single populations. Thus, food web manipulation should be directed to the creation and maintenance of appropriate multispecies communities of piscivores rather than to simple increases of the abundance of a single population.

Techniques of food web manipulation

The following techniques were used in European whole-lake experiments in biomanipulation (c.f. Table 1): (a) experimental poisoning of the entire fish stock, (b) stocking with piscivorous fish, (c) catch restrictions for piscivorous fish, (d) Selective fishing for undesirable fish, (e) improvement of the conditions of reproduction and survival of desirable fish (e.g. developing a macrophyte cover); (f) deterioration of the conditions of reproduction and survival of undesirable fish (e.g. water level manipulation in reservoirs after spawning to eliminate eggs and fry of undesirable species).

Almost all studies listed in Table 1 reveal that the application of only one of these techniques does not lead to the desired long-term stability of fish community structure. The enormous influence of the stochastic character of meteorological and hydrological events on recruitment of all fish populations, can be damped only by an appropriate combination of different techniques. Furthermore, in some cases, the fish community structure may be in a stable but undesired state (e.g. high abundance of adult bream, *Abramis brama*, van Densen & Grimm, 1988). In these cases, different techniques must be employed to first destroy the undesired stable state, and then to prevent return to that state.

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