Differences in the exploitation of bream in three shallow lake systems and their relation to water quality

E. H. R. Lammens,* E. H. Van Nes† and W. M. Mooij‡

SUMMARY 1. The development of bream populations, water transparency, chlorophyll-a concentration, extent of submerged vegetation and densities of the zebra mussel, *Dreissena polymorpha*, were analysed in three shallow eutrophic lake systems subject to different fish management.

2. In Lake Veluwemeer, the bream population was reduced from c. 100 to 20 kg ha\(^{-1}\) after 5 years of fishing. The mortality caused by the fishery was estimated at 38% of bream >15 cm in addition to a 13% natural mortality of bream >17 cm. The decline was followed by an expansion of the *Chara* beds present in the shallow parts, an increase in water transparency in the open-water zone, an increase in the density of zebra mussels and a decrease in chlorophyll-a concentrations.

3. The newly created Lake Volkerak showed trends opposite to those in Lake Veluwemeer. Bream colonised the lake in 1988 and reached a biomass of c. 140 kg ha\(^{-1}\) in 1998. The water transparency decreased from a maximum of 3 m to c. 1 m and the chlorophyll-a concentration increased from 5 to 45 µg L\(^{-1}\). Submerged vegetation colonised up to 20% of the total lake area in the first 5 years after creation of the lake in 1987 but decreased to 10% as turbidity increased.

4. Seine fishery in the Frisian lake system did not appear to affect the bream population despite annual catches as high as 40—50 kg ha\(^{-1}\). The estimated natural mortality of fish >15 cm was 15% and mortality by fishery was 26%. The high loss was apparently compensated by good recruitment and high growth rates resulting from a c. 1 °C higher water temperature during the years when bream were removed by fishing. There was only a slight decrease in chlorophyll-a concentrations and a slight increase in water transparency.

5. The results of this study suggest that the effects of bream exploitation in eutrophic lakes can vary depending on the efficiency of the fishery, recruitment success and temperature regime. In the absence of fishery, bream dominated the fish community in the study lakes and apparently prevented *D. polymorpha* and submerged vegetation from establishing because of physical disturbance, enhanced internal P-loading and resettling of resuspended sediments.
Biomanipulation of lake ecosystems: an introduction

P. Kasprzak, *J. Benndorf, † T. Mehner‡, and R. Koschel*

SUMMARY1. This paper is an introduction to a special issue of *Freshwater Biology* containing selected papers from an international symposium on *Food Web Effects of Fish in Lake Ecosystems: Research Progress, Water Quality and Fisheries Management* held from 31 May to 3 June 2000 in Rheinsberg, Germany. The primary goal of the workshop was to enlarge the current view of fish-induced effects on lake ecosystems. An additional goal was to promote biomanipulation as a multiple-use tool for managing freshwater ecosystems.

2. The three main topics addressed at the workshop were: (i) mechanisms involved in biomanipulation, (ii) whole-lake case studies and (iii) management aspects in water quality and fisheries.

3. Mortality of *Daphnia*, nutrient recycling, habitat selection and fish predation are reported as important mechanisms governing food-web effects as a result of biomanipulation.

4. Whole-lake case studies indicate that repeated fish removal can help improve water quality of shallow lakes, but successful biomanipulation of deep, thermally stratifying lakes remains difficult.

5. In many cases, biomanipulation of lakes has proved to provide benefits in addition to improving water quality. As all lake users are potentially affected when biomanipulation is used as a lake management tool, their concerns need to be clearly recognised if biomanipulation is to be successful in practice.

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Correspondence: Peter Kasprzak, Department of Limnology of Stratified Lakes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Alte Fischerhütte 2, D-16775 Neuglobsow, Germany. E-mail:
On the different nature of top-down and bottom-up effects in pelagic food webs

Z. Maciej Gliwicz

SUMMARY

1. Each individual planktonic plant or animal is exposed to the hazards of starvation and risk of predation, and each planktonic population is under the control of resource limitation from the bottom up (growth and reproduction) and by predation from the top down (mortality). While the bottom-up and top-down impacts are traditionally conceived as compatible with each other, field population-density data on two coexisting Daphnia species suggest that the nature of the two impacts is different. Rates of change, such as the rate of individual body growth, rate of reproduction, and each species' population growth rate, are controlled from the bottom up. State variables, such as biomass, individual body size and population density, are controlled from the top down and are fixed at a specific level regardless of the rate at which they are produced.

2. According to the theory of functional responses, carnivorous and herbivorous predators react to prey density rather than to the rate at which prey are produced or reproduced. The predator's feeding rate (and thus the magnitude of its effect on prey density) should hence be regarded as a functional response to increasing resource concentration.

3. The disparity between the bottom-up and top-down effects is also apparent in individual decision making, where a choice must be made between accepting the hazards of hunger and the risks of predation (lost calories versus loss of life).

4. As long as top-down forces are effective, the disparity with bottom-up effects seems evident. In the absence of predation, however, all efforts of an individual become subordinate to the competition for resources. Biomass becomes limited from the bottom up as soon as the density of a superior competitor has increased to the carrying capacity of a given habitat. Such a shift in the importance of bottom-up control can be seen in zooplankton in habitats from which fish have been excluded.
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Top-down control of phytoplankton: the role of time scale, lake depth and trophic state

Jürgen Benndorf, Wiebke Böing*, Jochen Koop and Ivonne Neubauer

SUMMARY

1. One of the most controversial issues in biomanipulation research relates to the conditions required for top-down control to cascade down from piscivorous fish to phytoplankton. Numerous experiments have demonstrated that Phytoplankton biomass Top-Down Control (PTDC) occurs under the following conditions: (i) in short-term experiments, (ii) shallow lakes with macrophytes, and (iii) deep lakes of slightly eutrophic or mesotrophic state. Other experiments indicate that PTDC is unlikely in (iv) eutrophic or hypertrophic deep lakes unless severe light limitation occurs, and (v) all lakes characterised by extreme nutrient limitation (oligo to ultraoligotrophic lakes).

2. Key factors responsible for PTDC under conditions (i) to (iii) are time scales preventing the development of slow-growing inedible phytoplankton (i), shallow depth allowing macrophytes to become dominant primary producers (ii), and biomanipulation-induced reduction of phosphorus (P) availability for phytoplankton (iii).

3. Under conditions (iv) and (v), biomanipulation-induced reduction of P-availability might also occur but is insufficient to alter the epilimnetic P-content enough to initiate effective bottom-up control (P-limitation) of phytoplankton. In these cases, P-loading is much too high (iv) or P-content in the lake much too low (v) to initiate or enhance P-limitation of phytoplankton by a biomanipulation-induced reduction of P-availability. However, PTDC may exceptionally result under condition (iv) if high mixing depth and/or light attenuation cause severe light limitation of phytoplankton.

4. Recognition of the five different conditions reconciles previous seemingly contradictory results from biomanipulation experiments and provides a sound basis for successful application of biomanipulation as a tool for water management.

References  Full Text Article  PDF [376KB]
Hypolimnetic anoxia hampers top–down food-web manipulation in a eutrophic lake

Piotr Dawidowicz, *Andrzej Prejs, *Andrzej Engelmayer, *Andrzej Martyniak, †Jacek Kozłowski, †Lech Kufel‡ and Małgorzata Paradowska§

SUMMARY

1. A biomanipulation experiment was carried out in a small (10 ha), but relatively deep (17 m) and highly eutrophic lake in northern Poland. The lake had been stocked in 1996, 1997 and 1998 with a variety of piscivorous fish (pike, catfish, trout and pikeperch), in order to reduce numbers of cyprinid planktivores.

2. Piscivore stocking was associated with a threefold decrease in the offshore fish density (night echosounding). Despite this reduction, the large planktonic cladoceran, *Daphnia hyalina*, remained scarce, whereas the density of small-sized zooplankton increased greatly.

3. The lack of demographic response in *D. hyalina* was probably due to the anoxia in the hypolimnetic refuge of this vertically migrating species. The anoxic hypolimnion, below 3–4 m depth, was inhabited day and night by numerous *Chaoborus flavicans* larvae.

4. Changes in zooplankton were associated with shifts in the taxonomic composition (from single-cell green algae to filamentous cyanobacteria), size structure (from nano- to net phytoplankton) and seasonal dynamics of phytoplankton, but not in the average biomass of planktonic algae. A clear-water phase, which was absent in the prestocking years, developed in spring, with Secchi depth reaching 2.5 m, a value which had never been recorded in the 20 years preceding the biomanipulation. In general, the lake’s status was switched from hypertrophic to eutrophic.

5. Deteriorating food conditions, resulting from qualitative changes in the phytoplankton community, combined with predation pressure by the remaining fish and *Chaoborus* larvae were associated with the ultimate elimination of *D. hyalina* from the lake.
Contribution of omnivorous tilapia to eutrophication of a shallow tropical reservoir: evidence from a fish kill

Fernando Starling, *† Xavier Lazzaro, ‡ Cristine Cavalcanti † and Ricardo Moreira †

SUMMARY
1. We examined whether a large stock of tilapia (>750 kg ha⁻¹, in littoral areas >1300 kg ha⁻¹), mostly Oreochromis niloticus (L.) and Tilapia rendalli (Boulenger), could contribute to the eutrophication of a tropical reservoir (Lago Paranoá, Brasília, Brazil) by enhancing P-loading.

2. We took advantage of an extensive fish kill (>150 tons removed) during May–August 1997 in a hypereutrophic branch of the reservoir to compare water quality characteristics 1 year before and after this event by means of BACI statistics. We also measured P-excretion rates in laboratory trials to assess the P-loading of the reservoir by the tilapia relative to tributary inputs and loading from a sewage treatment plant.

3. Concentrations of chlorophyll a (decline from 84 to 56 μg L⁻¹, P=0.018) and total P (decline from 100 to 66 μg L⁻¹, P < 0.001) decreased significantly in the branch of the reservoir affected by the fish kill, compared with a similar but unaffected branch that served as a control. Because P-loading by both a sewage treatment plant and tributaries remained high after the incidence, the fish kill was likely to contribute to the observed water quality improvement.

4. Removing 150 tons of dead tilapia corresponded to 20 days of external total phosphorus load (TP-load) to the branch, and resulted in a reduction of 5.1 kg P day⁻¹ in internal recycling via tilapia excretion, which is equivalent to 12% of the external TP-load.

5. Implementing professional tilapia cast-net fisheries could be an efficient biomanipulation approach to improve water quality and limit the occurrence of cyanobacteria blooms and fish kills in hypereutrophic branches of Lago Paranoá and similar tropical lakes.
Activity and food choice of piscivorous perch (*Perca fluviatilis*) in a eutrophic shallow lake: a radio-telemetry study

Lene Jacobsen, Søren Berg, Mads Broberg, Niels Jepsen and Christian Skov

**SUMMARY**

1. Radio transmitters were implanted in large perch (27—37 cm) in a shallow lake in Denmark. Between 6 and 13 perch were tracked every 3 h for 24-h periods twice (summer) or once a month (winter) from August 1997 to July 1998. Activity levels were recorded as minimum distance moved per hour.

2. No significant differences in activity levels of individual fish were observed.

3. Highest activities were observed at daytime with peaks at dawn and dusk or midday. This diel pattern was most pronounced from October to April, whereas diel variations were less in the summer months, with no peaks occurring in midsummer. The general lack of activity at night supports the idea that perch is a visually oriented forager.

4. There was no significant relationship between daytime activity during the year and temperature or day length, but nighttime activity was correlated with temperature. In contrast with previous findings, activity levels varied little seasonally, except for high activity levels that occurred concomitantly with high temperatures in August. Instead, we found a significant relationship between the total distances moved per day and temperature, indicating that perch moved at the same average speed in the wintertime, but did so for shorter periods than in summer because of shorter day lengths.

5. Diet of the tagged perch shifted from fish dominance between August and January to invertebrates from February to June. There was no correlation between the diet shift and activity levels, indicating that feeding on invertebrate requires similar activity levels as predation on fish.

6. The results of this telemetry study throughout a year suggest that perch are more active during the winter than previously inferred from gill-net catches. This observation underscores the importance of perch as a predator of 0+ planktivorous fish in lakes and has potential implications for pelagic food web structure and lake management by biomanipulation.

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Comparison of losses of planktivorous fish by predation and seine-fishing in a lake undergoing long-term biomanipulation

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**Keywords**

- fish activity
- fish behaviour
- food choice
- perch
- telemetry

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SUMMARY

1. Piscivore stocking at artificially high densities and fishing are the two common approaches to reduce the amount of planktivorous and benthivorous fish in lake biomanipulation programmes. Both measures have advantages and disadvantages, but their relative efficacy has not previously been directly compared.

2. We calculated the average annual catch of roach and bream in a lake undergoing long-term biomanipulation (Feldberger Haussee, Germany) by seining each year between 1992 and 1998. We compared this value with a bioenergetics estimate of annual consumption rates of the dominant cohorts of piscivores, pikeperch and pike, in 1997 and 1998. We also determined species composition and length distribution of prey fish in stomachs of the piscivores.

3. Roach was the dominant prey species of both pikeperch and pike, whereas bream was rarely taken by either piscivorous species. Seining removed on average larger specimens of roach than were found in the stomachs of the piscivores.


5. Based on these results, a combination of fishing and piscivore enhancement is recommended. Whereas the stocks of adult roach and bream have to be reduced mainly by fishing, the predation of piscivores should be directed predominantly towards the juvenile zooplanktivorous fish. Therefore, small size-classes of piscivorous fish should be promoted by fisheries management, including stocking and harvest regulations.
Biomanipulation of lake ecosystems: successful applications and expanding complexity in the underlying science

Thomas Mehner,* Jürgen Benndorf, † Peter Kasprzak* and Rainer Koschel*

SUMMARY

1. To illustrate advances made in biomanipulation research during the last decade, seven main topics that emerged after the first biomanipulation conference in 1989 are discussed in relation to the papers included in this special issue and the general literature.

2. The substantially higher success rates of biomanipulations in shallow as opposed to stratified lakes can be attributed to several positive feedback mechanisms relating mainly to the recovery of submerged macrophytes.

3. The role of both nutrient loading and in-lake concentrations in predicting the success of biomanipulations is emphasised and supported by empirically defined threshold values. Nutrient recycling by aquatic organisms (such as fish) can contribute to the bottom-up effects on lake food webs, although the degree can vary greatly among lakes.

4. Ontogenetic niche shifts and size-structured interactions particularly of fish populations add to the complexity of lake food webs and make scientifically sound predictions of biomanipulation success more difficult than was previously envisaged.

5. Consideration of appropriate temporal and spatial scales in biomanipulation research is crucial to understanding food web effects induced by changes in fish communities. This topic needs to be further developed.

6. An appropriate balance between piscivorous, planktivorous and benthivorous fishes is required for long-lasting success of biomanipulations. Recommended proportions and absolute densities of piscivorous fish are currently based on data from only a few biomanipulation experiments and need to be corroborated by additional and quantitative assessments of energy flow through lake food webs.

7. Biomanipulation effects in stratified lakes can be sustained in the long term only by continued interventions. Alternate stable states of food web composition probably exist only in shallow lakes, but even
8. Biomanipulation is increasingly used as a lake restoration technique by considering the needs of all lake users (sustainability approach). The combination of water quality management and fisheries management for piscivores with positive effects for both appears to be particularly promising.

9. Biomanipulation research has contributed substantially to progress in understanding complex lake food webs, which should in turn promote a higher success rate of future whole-lake biomanipulations.
Continental-scale patterns of nutrient and fish effects on shallow lakes: introduction to a pan-European mesocosm experiment. *Freshwater Biology* **49:**12, 1517-1524

- T. Mehner & R. Arlinghaus,
- S. Berg,
- H. Dörner,
- L. Jacobsen,
- P. Kasprzak, R. Koschel & T. Schulze,
- C. Skov &


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**Short-term and long-term effects of zooplanktivorous**
fish removal in a shallow lake: a synthesis of 15 years of data from Lake Zwemlust

Wouter J. Van De Bund* and Ellen Van Donk

SUMMARY
1. Removal of zooplanktivorous fish (mainly bream) in 1987 from a shallow eutrophic lake in the Netherlands, Lake Zwemlust, resulted in a quick switch from a turbid state with cyanobacteria blooms to a clear state dominated by macrophytes.

2. The clear state was not stable in the long term, however, because of high nutrient loadings.

3. In 1999, another removal of zooplanktivorous fish (mainly rudd) had similar effects as in 1987, although macrophytes returned more slowly.

4. In the years directly following both interventions there was a 'transition period' of very clear water with high densities of zooplanktonic grazers in the absence of macrophytes; low oxygen concentrations indicate that during those years primary production was low relative to heterotrophic activity.

5. The transition period appears to provide the light climate necessary for the return of macrophytes.

6. Reduction of nutrient loading is necessary to improve water quality in Lake Zwemlust in the long term. In the short term, repeated fish stock reduction is a reasonable management strategy to keep Lake Zwemlust clear.

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Changes in the fish community and water quality
during seven years of stocking piscivorous fish in a shallow lake

C. Skov, * M. R. Perrow, † S. Berg* and H. Skovgaard‡

SUMMARY1. Piscivores (annual stocking of 1000 individuals ha−1 of 0+ pike and a single stocking of 30 kg ha−1 of large 20−30 cm perch) were stocked in seven consecutive years in a shallow eutrophic lake in Denmark. The stocking programme aimed at changing food-web structure by reducing zooplanktivorous and benthivorous fish, with resultant effects on lower trophic levels and ultimately water quality.

2. The fish community and water quality parameters (Secchi depth, concentrations of total phosphorus, chlorophyll a and suspended solids) were monitored between 1996 and 2000 and relationships were evaluated between predatory fish and potential prey and between zooplanktivorous or benthivorous fish and water quality parameters. In addition, potential consumption of piscivorous fishes was calculated.

3. The density of fish feeding on larger zooplankton or benthos (roach >15 cm, crucian carp >15 cm) declined distinctly during the study period. This effect was attributed to predation by large (>50 cm) pike. Based on scale readings, we cautiously suggest that the stocking of 0+ pike boosted the adult pike population to produce an unexpected impact in later years. Conversely, no direct impact of stocked 0+ pike was detected on 0+ roach.

4. A major decline in the recruitment strength of 0+ roach was observed in 2000. A combination of (i) the indirect effect of large pike preying on adult roach, with negative effect on roach reproduction and (ii) the direct predation effect of 0+ pike and/or 1+ and 2+ perch recruited in the lake, provides the most likely explanation of this phenomenon.

5. A marked increase in Secchi depth in 2000 and declining trends in suspended solids, chlorophyll-a and total phosphorus concentrations were observed. These changes may also be attributable to changes in the fish community, although the relationships were not straightforward.

6. This 7-year study indicates that piscivorous fish may be a significant structuring force in shallow eutrophic lakes, suggesting that stocking piscivores can increase predation pressure on cyprinids. However, the general lack of impact of 0+ pike points to the need of refining current stocking practices in several countries across Europe.

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zooplankton in a mesotrophic reservoir: results from an enclosure experiment

Robert J. Radke and Uwe Kahl

SUMMARY
1. Silver carp, Hypophthalmichthys molitrix (Val.), feeds on both phyto- and zooplankton and has been used in lake biomanipulation studies to suppress algal biomass. Because reports on the effects of silver carp on lake food webs have been contradictory, we conducted an enclosure experiment to test how a moderate biomass of the fish (10 g wet weight m\(^{-3}\)) affects phytoplankton and crustacean zooplankton in a mesotrophic temperate reservoir.

2. Phytoplankton biomass <30 \(\mu\)m and particulate organic carbon (POC) <30 \(\mu\)m were significantly higher in enclosures with silver carp than in enclosures without fish, whereas Secchi depth was lower. Total copepod biomass declined strongly in both treatments during the experiment, but it was significantly higher in fish-free enclosures. Daphnid biomass was also consistently higher in enclosures without fish, although this effect was not significant. However, the presence of fish led to a fast and significant decrease in the size at maturity of Daphnia galeata Sars. Thus, the moderate biomass of silver carp had a stronger negative effect on cladoceran zooplankton than on phytoplankton.

3. Based on these results and those of previous studies, we conclude that silver carp should be used for biomanipulation only if the primary aim is to reduce nuisance blooms of large phytoplankton species (e.g. cyanobacteria) that cannot be effectively controlled by large herbivorous zooplankton. Therefore, stocking of silver carp appears to be most appropriate in tropical lakes that are highly productive and naturally lack large cladoceran zooplankton.

Keywords
biomanipulation
closure experiment
Hypophthalmichthys molitrix (Val.)
plankton
silver carp

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The role of phosphorus release by roach [Rutilus rutilus (L.)] in the water quality changes of a biomanipulated lake

M. Tarvainen,* J. Sarvala* and H. Helminen†

SUMMARY
1. Following fish removal, the water quality in biomanipulated lakes often improves concomitantly with decreased phosphorus (P) levels. Because the decrease in P concentrations
derives most probably either directly or indirectly from fish, which are the main target of biomanipulation, this study examined the P release of 0+, 1+ and 2+ roach \(Rutilus rutilus\) (L.) and changes in the P release during summer in a shallow eutrophic lake in Finland.

2. The P release was separated into P derived from benthic and littoral food items and into recycled P derived from feeding on zooplankton, to estimate the contribution of net P additions to the water column by the fish to the increase in P concentrations of the lake water \((75–110 \text{ mg P m}^{-3})\) in summer 1991–96.

3. Individual P release of roach by both egestion and excretion was estimated with a bioenergetics model. The size of the roach population was estimated with a depletion method and the proportions of different age groups from catch samples, using a programme separating mixtures of normal distributions. The sensitivity of the release estimates to variation in the growth data was estimated with the jackknife technique.

4. The biomass-specific P release by 0+ roach \((0.36–0.54 \text{ mg P g}^{-1} \text{ day}^{-1})\) was higher than that by older roach \((0.07–0.16 \text{ mg P g}^{-1} \text{ day}^{-1})\) throughout the summer. The P release by the whole roach population deriving from benthic and littoral food items \((0.7–2.7 \text{ mg m}^{-3})\) during July to August, representing a net addition to the water column) was 5–19 times lower in 1991–96 than the recycled P release deriving from zooplankton \((8.9–25.7 \text{ mg m}^{-3})\), and too low to explain the increase in the P concentration of the lake water during the summer. Because the biomass-specific P release and roach diet composition vary with fish age, it is important to consider the age structure of fish populations to obtain correct estimates of P release and net additions to the water column.

5. The removal of roach by fishing diminished the roach stock greatly, but the fish-mediated P release to the water column changed little. This effect was because of the high compensation capacity of the roach population, leading to high recruitment of young fish with higher biomass-specific P release rates.

6. External loading is very low during summer months and therefore it cannot explain the increase in the P concentration of water during that time. Internal loading from the sediment might be as high as \(10.2 \text{ mg P m}^{-2} \text{ day}^{-1}\), i.e. 50 times higher than the maximum net P addition by the total roach population.

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**To cite this article**
SUMMARY

1. We studied the population dynamics of 0+ fish in a eutrophic gravel pit lake in which predation of 0+ Eurasian perch on other 0+ fish was suspected to influence perch growth and the structure of the fish community, with effects on the lake food web.

2. The adult fish community was dominated by piscivorous species, especially perch, and the 0+ fish community was dominated by perch and bream. Bream grew to a total length of 80 mm between May and the end of August, gradually decreased in numbers during the summer, and completely disappeared in autumn. Stomach analysis revealed that 0+ perch ≥28 mm fed on 0+ bream.

3. The initially unimodal cohort of 0+ perch gradually broadened and became bimodal by the end of July. Fish of the larger, piscivorous cohort grew faster (1.4 mm day\(^{-1}\)) than the smaller, zooplankton-consuming fish (0.6 mm day\(^{-1}\)). Although individuals of both cohorts later consumed zooplankton and grew at similar rates (0.5 mm day\(^{-1}\)), only perch of the large cohort (mean TL 125 mm) were found by mid-October. Intraspecific competition for food or cannibalism of older perch may have contributed to the disappearance of the smaller perch.

4. Early piscivory of the fast-growing 0+ perch apparently resulted in the disappearance of 0+ bream by the end of the growing season and precocious maturation of male perch. In contrast to findings in other studies, these large 0+ perch thus avoided the juvenile bottleneck by switching to piscivory early during their ontogenetic development.

5. The observations of this study suggest that early piscivory of 0+ perch can have a long-lasting impact on fish communities in eutrophic lakes, particularly if prey fish are abundant and the structural complexity of the lake is low. Furthermore, early piscivory of 0+ perch may help prevent the expected increase in 0+ cyprinids following reduction of adult cyprinids, which is considered important to ensure the long-term success of biomanipulation experiments.
SUMMARY

1. We used an individual based modelling approach for roach to (i) simulate observed diel habitat shifts between the pelagic and littoral zone of a mesotrophic lake; (ii) analyse the relevance of these habitat shifts for the diet, activity costs and growth of roach; and (iii) quantify the effects of a hypothetical piscivore-mediated (presence of pikeperch) confinement of roach to the littoral zone on roach diet, activity costs and growth.

2. The model suggests that in the presence of pikeperch, roach shifts from zooplankton as the primary diet to increased consumption of less nutritious food items such as macrophytes, filamentous algae and detritus.

3. The growth of roach between May and October was predicted to be significantly higher in the absence of pikeperch, although the net activity costs were about 60% higher compared with the scenario where pikeperch were present.

4. These modelling results provide quantitative information for interpreting diel horizontal migrations of roach as a result from a trade-off between food availability and predation risk in different habitats of a lake.

5. Altering the habitat selection mode of planktivorous roach by piscivore stocking has the potential to reduce zooplankton consumption by fish substantially, and could therefore be used as a biomanipulation technique complementing the reduction of zooplanktivorous fish.
Life history of *Daphnia galeata* in a hypertrophic reservoir and consequences of non-consumptive mortality for the initiation of a midsummer decline

*S. Hülsmann and H. Voigt*

**SUMMARY**

1. Field and laboratory investigations were combined in a 2-year study on the initiation of a midsummer decline of *Daphnia galeata* Sars in a hypertrophic reservoir. Quantitative field samples were taken twice a week, and, adult and juvenile mortality rates were calculated. Patterns of reproduction and survival of daphnids born during spring and early summer under fluctuating food conditions were determined in life-table experiments.

2. The abundance of *Daphnia* increased strongly in early May and declined in June 1998 (midsummer decline). In 1999, *Daphnia* density increased only slowly in spring and remained constantly high throughout the summer.

3. Food conditions (concentrations of POC$_{<30 \mu m}$) for daphnids deteriorated in both years in response to increasing *Daphnia* densities, resulting in a clear-water phase of about 4 weeks. When *Daphnia* abundance declined in 1998, POC$_{<30 \mu m}$ concentrations increased greatly, whereas in 1999 food conditions improved only slightly and Secchi depth remained high.

4. Survival of daphnids in life-table experiments decreased greatly after food became rare and was strongly reduced in those animals born during the clear-water phase compared with those born later. In addition, age at first reproduction was retarded during the clear-water phase, resulting in very low population growth rates. Survivorship patterns in life-table experiments suggest a strong impact of non-consumptive mortality on *Daphnia* population dynamics.

5. Field data of mortality point to differences in mortality patterns between years, probably resulting from different predation impacts of juvenile fish. In both years, however, adult mortality contributed substantially to overall mortality at the end of the clear-water phase. As bottom-up effects on *D. galeata* were very similar in both years, the significance of non-consumptive mortality on the initiation of midsummer declines appears to depend largely on recruitment patterns before the clear-water phase. A high impact can be expected when *Daphnia* populations are dominated by a peak cohort of nearly identical age during the clear-water phase.

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Stocking piscivores to improve fishing and water clarity: a synthesis of the Lake Mendota biomanipulation project


SUMMARY
1. A total of 2.7 × 10^6 walleye fingerlings and 1.7 × 10^5 northern pike fingerlings were stocked during 1987–99 in eutrophic Lake Mendota. The objectives of the biomanipulation were to improve sport fishing and to increase piscivory to levels that would reduce planktivore biomass, increase Daphnia grazing and ultimately reduce algal densities in the lake. The combined biomass of the two piscivore species in the lake increased rapidly from < 1 kg ha^-1 and stabilised at 4–6 kg ha^-1 throughout the evaluation period.

2. Restrictive harvest regulations (i.e. increase in minimum size limit and reduction in bag limit) were implemented in 1988 to protect the stocked piscivores. Further restrictions were added in 1991 and 1996 for walleye and northern pike, respectively. These restrictions were essential because fishing pressure on both species (especially walleye) increased dramatically during biomanipulation.

3. Commencing in 1987 with a massive natural die-off of cisco and declining yellow perch populations, total planktivore biomass dropped from about 300–600 kg ha^-1 prior to the die-off and the fish stocking, to about 20–40 kg ha^-1 in subsequent years. These low planktivore biomasses lasted until a resurgence in the perch population in 1999.

4. During the period prior to biomanipulation when cisco were very abundant, the dominant Daphnia species was the smaller-bodied D. galeata mendotae, which usually reached a biomass maximum in June and then crashed shortly thereafter. Beginning in 1988, the larger-bodied D. pulicaria dominated, with relatively high biomasses occurring earlier in the spring and lasting well past mid-summer of many years.

5. In many years dominated by D. pulicaria, Secchi disc readings were greater during the spring and summer months when compared with years dominated by D. galeata mendotae. During the biomanipulation evaluation period, phosphorus (P) levels also changed dramatically thus complicating our analysis. Earlier research on Lake Mendota had shown that Daphnia grazing increased summer Secchi disc readings, but P concentrations linked to agricultural and urban runoff and to climate-controlled internal mixing processes were also important factors affecting summer readings.

6. The Lake Mendota biomanipulation project has been a success given that high densities of the large-bodied D. pulicaria have continued to dominate for over a decade, and the diversity of fishing opportunities have improved for walleye, northern pike and, more recently, yellow perch.
7. Massive stocking coupled with very restrictive fishing regulations produced moderate increases in piscivore densities. Larger increases could be realised by more drastic restrictions on sport fishing, but these regulations would be very controversial to anglers.

8. If the lake’s food web remains in a favourable biomanipulation state (i.e. high herbivory), further improvements in water clarity are possible with future reductions in P loadings from a recently initiated non-point pollution abatement programme in the lake’s drainage basin.