Long-term biomanipulation of Rimov Reservoir (Czech Republic)

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Received 21 March 1995; in revised form 7 January 1996; accepted 13 February 1997

Key words: biomanipulation, top-down effect, zooplankton structure

Abstract

The history of fish, zooplankton and phytoplankton in Rimov Reservoir during its 14 years existence is documented. After the filling of the reservoir in autumn 1978, the biomass of planktivorous fish increased from near zero to 650 kg ha^{-1} by the fourth year of the reservoir's existence, after which the fish stock continually decreased under various forms of biomanipulative pressure, down to a value of about 100 kg ha⁻¹. This development of fish stock was accompanied by changes in zooplankton size structure, but a cascading effect down to reduction of phytoplankton biomass was not pronounced. The changes of zooplankton body size structure were: increasing or decreasing average size of *Daphnia galeata* (the main cladoceran herbivore species) and changes in relative proportion of cladoceran species, but none of the main zooplankton species was replaced or disappeared. The variation in phytoplankton biomass could be observed lies below 100 kg of planktivorous fish per hectare. An attempt is made to quantify the relationship between fish stock density and the size structure of zooplankton potentially able to influence top-down effects on phytoplankton.

Introduction

The role of fish regulating the structure and function of freshwater ecosystems is now generally accepted in all limnological literature as one of the key forces resulting directly from fish feeding activity or indirectly from size and other forms of prey selectivity and from influences on nutrient cycling and transport. Recognition of this 'top-down' effect, started largely from Czechoslovakian research (Hrbacek Limnological School) in the mid-1950s, was popularized by American and German research (Brooks, Jacobs, and others) in the mid-1960s and has since enjoyed a remarkable upsurge continuing into the 1990s (for review see Northcote (1988)).

Nevertheless, several recent papers have cast some doubts about the validity of this top-down regulation and its application for management of water quality in lakes and reservoirs which is generally known as biomanipulation (DeMelo et al., 1992; Evans, 1990; McQueen, 1990; McQueen et al., 1992). The main thesis of the lake biomanipulation approach for improvement of water quality is based upon suppression of planktivore fish abundance and enhancement of the large-bodied zooplankton leading to reduction in phytoplankton via increased zooplankton grazing pressure and restructuring of nutrient cycling (Benndorf, 1988a; Gulati et al., 1990).

Most of the practical experience of reducing the biomass of planktivorous fish which has led to understanding of top-down effects is limited to small water bodies and to straightforward situations of with and without fish. Very few large and deep water bodies have been subjected to biomanipulative experimentation. Out of twenty-six studies reviewed by DeMelo et al. (1992), the largest water body to be successfully manipulated – that is artificial manipulation of fish stock followed by phytoplankton reduction – was Tuesday Lake, Michigan with a surface area of only 10 hectares (Carpenter et al., 1987). A further set of thirteen studies not reviewed by DeMelo et al. (1992) were presented at the Conference on Biomanipulation in Amsterdam (Gulati et al., 1990). The only successful large-scale biomanipulations reported at this Conference were the whole-lake rotenone poisoning of the shallow Lake Christina (1619 ha) (Hanson & Butler, 1990) and the rudd removal by seining from Lago di Candia (150 ha) (Guissani et al., 1990). None of eleven other lakes manipulated with success were larger than 45 hectares.

In practice, significant changes in fish stock in large and deep water bodies are associated with natural events rather than to deliberate man-managed interventions. Usually, we are passive observers of fluctuating biomass at various trophic levels, trying to reconstruct past events. The best such reconstructed story is that reporting the fourteen-year history of Mendota Lake (Rudstam et al., 1993), which documents the causal link between the natural cycle of the long-lived obligate planktivore *Coregonus ardeti* and the long-term changes of the planktonic community.

In this study, we present data on the fourteen-year history of interactions between fish, zooplankton, phytoplankton and nutrients in the large Rimov Reservoir (210 ha), storaging drinking water for surrounding regions. This reservoir has full legislative protection as single-purpose water body permitting reservoir managers to manipulate fish stock in order to maintain a sustainable water quality (no interference with any angling interests). Nevertheless, the long struggle to suppress planktivorous fish artificially was not strong enough to result in a decisive effect at the phytoplankton level.

Methods

The study was carried out in the canyon-shaped Rimov Reservoir (Czech Republic, ca 170 km south of Prague). Its area is 210 ha, volume 33×10^6 m³ and maximum depth 45 m. The Rimov Reservoir was built by damming the River Malse, which is the main reservoir tributary. The average annual water flow in this tributary varied from 2.1 to 4.9 m³ s⁻¹ during 1979– 1992. The average retention time varied from 80 to 180 days. More hydrological data and comparison with the other Czech reservoirs as well as a bathymetric map of the reservoir were given by Brandl et al. (1989) and Hejzlar & Straskraba (1989).

The zooplankton, phytoplankton and nutrients were monitored at three-week intervals (17 samples per year) throughout the first 14 years of the reservoir's existence since its first filling in autumn 1978. Zooplankton were collected at one station near the dam, by vertical hauls using an Apstein plankton net (net mesh = 200 μ m). The hauls were taken from the bottom to the surface and at least two hauls were combined to get one sample. The sample was divided into three size fractions using two sieves with different mesh sizes 0.71 mm and 0.42 mm (Seda & Dostalkova, 1996). The largest size fraction retained on the 0.71 mm sieve consisted entirely of cladoceran species. The remaining two smaller fractions were separated into Cladocera and Copepoda using the narcoticflotation technique of Straskraba (1964). The biomass of all zooplankton fractions were measured as protein nitrogen by the biuret reaction (Blazka, 1966).

Samples for the determination of species composition of zooplankton were taken at the same time and preserved in 4% formaldehyde. Densities of the main zooplankton species were estimated by the usual method of microscopical counting (McCauley, 1984).

Phytoplankton samples were taken from the uppermost 4 m of the water column using a plastic tube of the appropriate length. Phytoplankton biomass was measured as chlorophyll *a* content (Lorenzen, 1967).

For nutrients, only total phosphorus was analysed in the samples from 0.5 m depth. The total phosphorus was estimated after the oxidation of the evaporated sample by perchloric acid to phosphate (Popovsky, 1970), according to Stephens (1963).

Lord's range test for comparison of averages (Snedecor & Cochran, 1967) was used to look at the similarities in long-term trends of monitored parameters. This assumes that a seasonal average represents a year characteristic to describe an equilibrium point which is expected to be different as the conditions between the years are changing.

Monitoring of fish in the Rimov Reservoir was started in the autumn of 1984, six years after the first filling of the reservoir. Petersen mark-recapture estimates were carried out during 1985–87. Altogether, 16 113 (July 1985), 6529 (July 1986) and 7005 (July 1987) specimens were marked and released and more than 65 000 fish checked subsequently for marks. Numbers of marked individuals and numbers of fish examined for marks of the three dominant species – Perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and bream (*Abramis brama*) satisfied the criteria recommended for management studies by Robson and Regier (1964).

Catch per unit area by night shore-seining exhibited a good level of agreement with mark-recapture estimates (Kubecka, 1993a) and the fish population censuses in subsequent years (1988–92) were based on the former method. The area sampled by seine net varied between 4 and 7 ha. Confidence intervals were not calculated but the night inshore migration was found to be relatively homogenous along the reservoir (coefficient of variation of the catch in kg per area swept ranged between 10.4% and 35.9% in individual seasons).

Fish abundance in 1979-1984 was reconstructed from 1985 abundances using average age- and speciesspecific survival rates for two intercensus intervals 1985/86 and 1986/87. The coefficients of variation of survival rates for the whole 1985-1992 period were reasonably low: 18.9% for perch, 9.9% for roach and 15.2% for bream; this justified the application of similar survival rates to the whole period 1979-1984. The proportions of other fish species for 1979–1984 were reconstructed using the study of Vostradovsky et al. (1990). Fish biomass was calculated using fish abundance in individual year classes, back-calculated lengths (Frasser-Lee method) and length-weight relationships (Bagenal & Tesch, 1978). More detailed description of the methods applied can be found in Kubecka (in press). Only fish older than one year were included in abundance and biomass estimations.

Biomanipulation measures

Biomanipulative management against undesirable planktivorous fish species in Rimov Reservoir incorporated three strategies: control of spawning success of cyprinids, capture and removal of undesirable fish, and enhancement of predatory-fish populations.

The spawning success of cyprinids was controlled by active water-level manipulation in the years when the hydrological conditions permitted. This involved maintaining high water levels during the period of mass spawning of cyprinids, roach, bream, rudd (*Scardinius erythrophtalmus*), and chub (*Leuciscus cephalus*), in order to encourage spawning in flooded terrestrial vegetation. Water-level was then lowered by 40–60 cm immediately after the end of spawning. This measure destroyed more than 95% of eggs laid in the marginal areas of the reservoir. The same procedure was repeated during bream spawning when the water supply conditions allowed it. This method of reducing cyprinids was especially effective during 1983–1989.

Undesirable fish species, like perch, roach, bream, rudd, chub were captured by the fyke net industry, by shore seining and by electroshocking. The fyke net industry (Kubecka, 1992) was operating during the spawning of perch. Day and night seining and electroshocking was carried out during spawning of 1 0 5 1

cyprinids and night seining only thereafter. Total catches of undesirable species are given in Table 1.

The enhancement of predatory fish was supported by regular stocking and by banning any fishing on predatory fish throughout the existence of the reservoir. The species, numbers and sizes of predatory fish stocked are given in Table 1. In 1985, 1986, 1987, and 1989, the water level was kept as high as possible in early April to facilitate spawning and egg incubation of the autochthonous population of pike, *Esox lucius*.

Results

Fish stock

Thirty-five fish species and five hybrids were found in the Rimov Reservoir (Kubecka, 1990) but only a few of them occurred at ecologically significant levels. The initial development of fish stock in the reservoir was clearly determined by the establishment of several strong year classes of roach, bream and perch in the first years of the reservoir's existence. These year classes were 1979, 1980 and 1981 for roach, 1980 and 1981 for bream and 1981 and 1982 for perch. The appearance of these year classes resulted in an upsurge of fish biomass, which reached 650 kg ha^{-1} in 1982 (Figure 1). All subsequent year classes from 1983-1992 were 100-10000 times weaker due to the successful drying of eggs and to predation by the perch classes of 1981 and 1982. The predatory effect of these two strong classes of perch on the cyprinids and recruitment of perch was important up to 1987, when five- and sixvear-old perch formed nearly 60% of the fish older than one year in the reservoir and when the biomass ratio perch:cyprinids was roughly 1:1. The dominant perch classes decreased sharply in 1988–1989 (Figure 2) due both to the fyke-net industry and to an unidentified perch necrose disease (similar to that reported in Goldspink & Goodwin (1979) and Le Cren (1987)). Their replacement by bream and roach was nearly proportional. Nevertheless, the occasional reproductive success of cyprinids, together with the applied biomanipulative effort has managed to keep the overall biomass of potentially planktivorous fish just between 100 and 150 kg ha^{-1} .

The proportion of other fish was never very high. Non-predatory cyprinids like rudd, chub, dace (*Leuciscus leuciscus*) and bleak (*Alburnus alburnus*) had strong recruitment of fry during 1979–1981, like roach

Table 1. Stocking of predatory fish and removal of non-predatory species during a long-term attempt to generate top-down control in Rimov Reservoir. The numbers of stocked predators are in hundreds per reservoir. Seven piscivore species were evaluated: brook and brown trout, *Salvelinus fontinalis* and *Salmo trutta* (BT); rainbow trout, *Oncorhynchus mykiss* (RT); zander *Stizosteidon lucioperca* (Z); pike *Esox lucius* (P); asp *Aspius aspius* (A); and European catfish *Silurus glanis* (EC). Yearly catch of undiserable fish species (catch removal) is given in tons per reservoir. WAL - weighted average length of stocked piscivorous fish (cm).

| | BT | RT | Z | Р | А | EC | Catch removal (tons per reserv.) |
|--------------------------|--------------|--------------|---------------|--------------|-------------|------------|--|
| 1978 | 300 | 725 | _ | _ | _ | _ | 0.30 |
| 1979 | 20 | 20 | 25 | _ | _ | _ | 0.03 |
| 1980 | _ | _ | 250 | _ | 100 | 5 | 0.00 |
| 1981 | _ | _ | 70 | - | 80 | _ | 0.21 |
| 1982 | _ | _ | 300 | - | 70 | 40 | 0.00 |
| 1983 | _ | _ | 23 | 118 | 100 | _ | 1.17 |
| 1984 | _ | _ | 54 | - | 100 | 21 | 0.09 |
| 1985 | 1 | _ | 20 | 14 | - | 10 | 1.80 |
| 1986 | _ | 3 | 126 | 18 | - | 3 | 6.65 |
| 1987 | _ | _ | 134 | 0.2 | - | 0.2 | 6.25 |
| 1988 | _ | _ | 72 | 98 | 75 | 13 | 5.70 |
| 1989 | _ | _ | 161 | _ | 10 | 8 | 3.00 |
| 1990 | _ | _ | 140 | - | 7 | 7 | 1.58 |
| 1991 | _ | _ | 100 | 8 | _ | _ | 1.40 |
| 1992 | - | - | 100 | 30 | - | _ | 1.90 |
| Yearly average WAL | 21.4 11.0 | 49.4 11.0 | 105.0 10.2 | 19.0 13.0 | 36.1 6.5 | 7.1 8.5 | 2.01 |



Figure 1. Long-term changes of the average annual summed biomasses of the three main planktivorous fish species (perch, roach & bream) in Rimov Reservoir during 1979–1992. The vertical lines for 1985–1987 mark the extent of annual variation which results from the growth dynamics and mortality loses of evaluated fish populations (Kubecka, in press). Only fish older than one year were used.



Figure 2. Long-term changes of the relative proportion of fish species in Rimov Reservoir during 1980–1992. Perch (black), roach (hatched), bream (white) and predatory species – pike, zander, asp and catfish (vertical lines) – were distinguished. The other fish species are summed in crosshatched parts of columns. Only fish older than one year were used.

and bream, and only low reproductive success in subsequent years.

Despite protection and stocking, the abundance of predatory fish has never been high (Figure 2). The pike population was reported to have peaked in 1980 after the filling of the reservoir (Kubecka & Krivanec, 1990), but there are no quantitative data about absolute numbers in the reservoir. This pike peak was insufficient to prevent the development of roach and bream populations and it receded completely by 1982. The average biomass of obligatory fish predators (pike, zander, asp, catfish) was 7.6 ± 2.9 kg ha⁻¹ during 1985–1992. Estimated biomass of predators culminated at 11.7 kg ha⁻¹ in 1987 but then declined to 4.5 kg ha⁻¹ in 1992.

Zooplankton

The species structure of the crustacean zooplankton was relatively stable during the fourteen-years period. The most abundant three cladoceran species were *Daphnia galeata* Sars, *Bosmina longirostris* (O. F. Müller) and *Diaphanosoma brachyurum* (Liévin) and three copepod species were *Cyclops vicinus* Uljanin, *Mesocyclops leuckarti* (Claus) & *Eudiaptomus gracilis* (Sars). More detailed lists of species found, including Rotifera, were published by Seda (1990).

The persistent dominance of *Daphnia galeata* among the five *Daphnia* species recorded in all sam-

ples during the reservoir's existence was surprising. *Daphnia cucullata* Sars was the second most common species of daphnid, restricted usually to the summer months. The proportion of this species was high mainly in years with dense fish stock (1983–1986) when it formed up to 30% of all *Daphnia* individuals. The other three daphnid species, *D. pulicaria* Forbes, *D. pulex* (De Geer) & *D. magna* Straus were sporadic.

The total zooplankton biomass (Figure 3) does not show a clear pattern of increase or decrease during 14 years. The groups of years with high and low fish stock did not significantly differ. The cross-comparison of fourteen average year values by Lord's range test (altogether 91 combinations) showed statistically significant difference (p<0.05) in four cases only. These cases were related to the fact that the lowest average zooplankton biomass within 14 years investigated occurred in 1987 (medium fish stock) and this lowest biomass consecutively displayed differences from four high biomasses years, 1980 and 1981 (low fish stock) and 1983 and 1984 (high fish stock).

As a second step, we analysed the long-term changes of zooplankton for the warm period of each year only, assuming that the strength of biological interactions in planktonic systems increases during the vegetative period of the year. The changes in total zooplankton, cladoceran and copepod biomasses for this period are illustrated in Figure 4. The cross-comparisons of average biomasses of Cladocera,



Figure 3. Long-term dynamics of total zooplankton biomass in Rimov Reservoir during 1979–1992. The zooplankton biomass is expressed in protein nitrogen.

Table 2. The cross-comparison by Lord's range test of fourteen annual values of total zooplankton biomass in Rimov Reservoir from 1979 to 1992. The compared periods cover six months from May to October and the annual values are based on the average of nine analysed samples in each year. The statistically significant differencess are distinguished by asterisks for three levels of significance $(0.1^*, 0.05^{**}, 0.01^{***})$.

| Total zoop | plankton | | | Sigr | nifican | ce of co | mpari | sons | | | | | | | | |
|------------|----------------------|---------|------|---------------|---------|----------|-------|------|-----|----|----|----|----|----|----|----|
| Aver | Max | Min | - | between years | | | | | | | | | | | | |
| biomass | biomass | biomass | | | | | | | | | | | | | | |
| (mg prot.) | N / m ²) | | Year | | | | | | | | | | | | | |
| 199 | 755 | 37 | 1979 | 79 | | | | | | | | | | | | |
| 273 | 574 | 45 | 1980 | _ | 80 | | | | | | | | | | | |
| 292 | 497 | 179 | 1981 | _ | _ | 81 | | | | | | | | | | |
| 233 | 564 | 67 | 1982 | _ | _ | _ | 82 | | | | | | | | | |
| Z35 | 502 | 59 | 1983 | _ | _ | _ | _ | 83 | | | | | | | | |
| 285 | 501 | 151 | 1984 | _ | _ | _ | _ | _ | 84 | | | | | | | |
| 275 | 841 | 94 | 1985 | _ | _ | - | _ | _ | - | 85 | | | | | | |
| 215 | 555 | 128 | 1986 | _ | _ | _ | _ | _ | _ | _ | 86 | | | | | |
| 170 | 238 | 111 | 1987 | _ | * | *** | _ | _ | *** | _ | _ | 87 | | | | |
| 179 | 336 | 103 | 1988 | _ | _ | ** | _ | _ | ** | _ | _ | _ | 88 | | | |
| 158 | 414 | 73 | 1989 | _ | _ | ** | _ | _ | ** | _ | _ | _ | _ | 89 | | |
| 189 | 404 | 103 | 1990 | _ | _ | * | _ | _ | * | _ | _ | _ | _ | _ | 90 | |
| 213 | 513 | 57 | 1991 | - | - | _ | - | _ | _ | - | - | _ | _ | - | - | 91 |
| 158 | 223 | 46 | 1992 | - | * | *** | - | - | *** | - | - | - | - | - | - | - |

Copepoda and total zooplankton were repeated, but the results were similar. The resulting cross-matrices of range tests are shown in Tables 2 and 3a, b. Comparing the fourteen years of data on zooplankton biomass for the vegetative period only, there is a slight tendency of decreasing average biomasses in the second half of years investigated. All differences in Tables 2 and 3a, b were thus related to high biomasses in 1980, 1981, 1883, 1984 and low biomasses in 1987, 1988, 1989, 1990, 1992, independently of fish stock status in pertinent years.

Table 3. The cross-comparison by Lord's range test of fourteen annual values of total cladoceran biomass (upper part) and total copepods biomass (lower part) in Rimov Reservoir from 1979 to 1992. The compared periods cover six months from May to October and the annual values are based on the average of nine analysed samples in each year. The statistically significant differences are distinguished by asterisks for two levels of significance (0.1*, 0.05**).

| Total clad | ocera | | Significance of comparisons | | | | | | | | | | | | | |
|--|--|---|--|--|---|---|--|--|--------------------------|--------------------|--------------------|----------------|--------------|--------------|---------|----|
| Aver | Max | Min | | between years | | | | | | | | | | | | |
| biomass | biomass | biomass | | | | | | | | | | | | | | |
| (mg prot.l | N / m ²) | | Year | | | | | | | | | | | | | |
| 119 | 458 | 8 | 1979 | 79 | | | | | | | | | | | | |
| 128 | 383 | 9 | 1980 | _ | 80 | | | | | | | | | | | |
| 133 | 195 | 47 | 1981 | _ | - | 81 | | | | | | | | | | |
| 128 | 374 | 18 | 1982 | _ | - | - | 82 | | | | | | | | | |
| 134 | 260 | 36 | 1983 | _ | - | - | _ | 83 | | | | | | | | |
| 123 | 187 | 69 | 1984 | - | - | - | - | - | 84 | | | | | | | |
| 104 | 159 | 46 | 1985 | _ | - | - | _ | _ | - | 85 | | | | | | |
| 99 | 145 | 21 | 1986 | - | - | - | - | - | _ | - | 86 | | | | | |
| 91 | 179 | 10 | 1987 | - | - | - | - | - | - | - | - | 87 | | | | |
| 95 | 129 | 61 | 1988 | - | - | ** | - | - | * | - | - | - | 88 | | | |
| 81 | 204 | 42 | 1989 | - | - | * | - | - | * | - | - | - | - | 89 | | |
| 80 | 127 | 35 | 1990 | - | - | ** | - | * | ** | - | - | - | - | - | 90 | |
| 98 | 230 | 18 | 1991 | - | - | - | - | - | - | - | - | - | - | - | - | 91 |
| 83 | 143 | 31 | 1992 | - | - | ** | - | * | ** | - | - | - | - | - | - | - |
| | | | | | | | | | | | | | | | | |
| Total cope | epoda | | | Sigr | nifican | ce of c | ompai | risons | | | | | | | | |
| Total cope Aver | epoda Max | Min | | Sigr betv | nifican veen y | ce of c ears | ompai | risons | | | | | | | | |
| Total cope Aver biomass | epoda Max biomass | Min biomass | | Sigr betv | nifican veen y | ce of c ears | ompai | risons | | | | | | | | |
| Total cope Aver biomass (mg prot.l | epoda Max biomass N / m ²) | Min biomass | Year | Sigr betv | nifican veen y | ce of c ears | compai | risons | | | | | | | | |
| Total cope Aver biomass (mg prot.] | epoda Max biomass N / m ²) 297 | Min biomass 4 | Year 1979 | Sigr betv 79 | nifican veen y | ce of c ears | ompai | risons | | | | | | | | |
| Total cope Aver biomass (mg prot.1 80 145 | epoda Max biomass N / m ²) 297 408 | Min biomass 4 31 | Year 1979 1980 | Sigr betv 79 – | nifican veen y 80 | ce of c ears | ompai | risons | | | | | | | | |
| Total cope Aver biomass (mg prot.) 80 145 155 | epoda Max biomass N / m ²) 297 408 302 | Min biomass 4 31 45 | Year 1979 1980 1981 | Sigr betv 79 – | iifican veen y 80 – | ce of c ears | ompar | risons | | | | | | | | |
| Total cope Aver biomass (mg prot.] 80 145 155 102 | epoda Max biomass N / m ²) 297 408 302 210 | Min biomass 4 31 45 14 | Year 1979 1980 1981 1982 | Sigr betw 79 – – | Nifican veen y 80 – – | ce of c ears 81 – | eompar | isons | | | | | | | | |
| Total cope Aver biomass (mg prot.) 80 145 155 102 101 | epoda Max biomass N / m ²) 297 408 302 210 241 | Min biomass 4 31 45 14 19 | Year 1979 1980 1981 1982 1983 | Sigr betv 79 – – – | Nifican Veen y 80 – – – | ears 81 – – | 82 – | isons 83 | | | | | | | | |
| Total cope Aver biomass (mg prot.1 80 145 155 102 101 158 | epoda Max biomass N / m ²) 297 408 302 210 241 330 | Min biomass 4 31 45 14 19 29 | Year 1979 1980 1981 1982 1983 1984 | Sigr betv 79 – – – – – | 80 - - | 81 - - | 82 – – | 83 – | 84 | | | | | | | |
| Total cope Aver biomass (mg prot.1 80 145 155 102 101 158 137 | pepoda Max biomass N / m ²) 297 408 302 210 241 330 455 | Min biomass 4 31 45 14 19 29 36 | Year 1979 1980 1981 1982 1983 1984 1985 | Sigr betv 79 - - - - - - - - | 80 | 81 - - - | 82 – – – | 83 – – | 84 | 85 | | | | | | |
| Total cope Aver biomass (mg prot.1 80 145 155 102 101 158 137 109 | pepoda Max biomass N / m ²) 297 408 302 210 241 330 455 372 | Min biomass 4 31 45 14 19 29 36 35 | Year 1979 1980 1981 1982 1983 1984 1985 1986 | Sigr betv 79 - - - - - - - - - - | 80 - - - - - - | 81 - - - - - | 82 - - - - | 83 - - - | 84 _ _ | 85 | 86 | | | | | |
| Total cope Aver biomass (mg prot.) 80 145 155 102 101 158 137 109 75 | ppoda Max biomass N / m ²) 297 408 302 210 241 330 455 372 149 | Min biomass 4 31 45 14 19 29 36 35 24 | Year 1979 1980 1981 1982 1983 1984 1985 1986 1987 | Sigr betv 79 – – – – – – – – – – – | 80 * | 81 - - - - ** | 82 - - - - - | 83 - - - - | 84 ** | 85 _ _ | 86 | 87 | | | | |
| Total cope Aver biomass (mg prot.) 80 145 155 102 101 158 137 109 75 70 | ppoda Max biomass N / m ²) 297 408 302 210 241 330 455 372 149 181 | Min biomass 4 31 45 14 19 29 36 35 24 32 | Year 1979 1980 1981 1982 1983 1984 1985 1986 1987 1988 | Sigr betv 79 | 80 * * | 81 ** ** | 82 - - - - - - | 83 - - - - | 84 ** ** | 85 | 86 _ _ | 87 | 88 | | | |
| Total cope Aver biomass (mg prot.] 80 145 155 102 101 158 137 109 75 70 73 | Pepoda Max biomass N / m ²) 297 408 302 210 241 330 455 372 149 181 202 | Min biomass 4 31 45 14 19 29 36 35 24 32 21 | Year 1979 1980 1981 1982 1983 1984 1985 1986 1987 1988 1989 | Sigr betw 79 | 80 - - - - - * * | 81 | 82 - - - - - - - | 83 - - - - - | 84 ** ** ** | 85 | 86 _ _ _ | 87 | 88 – | 89 | | |
| Total cope Aver biomass (mg prot.) 80 145 155 102 101 158 137 109 75 70 73 102 | epoda Max biomass N / m ²) 297 408 302 210 241 330 455 372 149 181 202 318 | Min biomass 4 31 45 14 19 29 36 35 24 32 21 32 | Year 1979 1980 1981 1982 1983 1984 1985 1986 1987 1988 1989 1990 | Sigr betw 79 - - - - - - - - - - - - - - - - - - | 80 * * * | 81 *** *** *** | 82 - - - - - - - - - | 83 - - - - - - | 84 ** ** ** | 85 | 86 | 87 | 88 _ _ | 89 | 90 | |
| Total cope Aver biomass (mg prot.1 80 145 155 102 101 158 137 109 75 70 73 102 109 | epoda Max biomass N / m ²) 297 408 302 210 241 330 455 372 149 181 202 318 468 | Min biomass 4 31 45 14 19 29 36 35 24 32 21 32 14 | Year 1979 1980 1981 1982 1983 1984 1985 1986 1987 1988 1989 1990 1991 | Sigr betw 79 | 80 - - - * * * - | 81 - - - - ** ** ** - | 82 - - - - - - - - - - - - | 83 - - - - - - - - | 84 ** ** ** | 85 | 86 | 87 | 88 _ _ | 89 - - | 90 - | 91 |

The biomass of large-sized Cladocera (i.e. *Daphnia* retained by 0.71 mm sieve) was the only zooplankton parameter which clearly tracked the development of fish stock in the reservoir (Figure 4). There were conspicuous differences between average biomasses from the period with high fish stock in 1981–1986 and the years with low fish stock in 1979, 1980 at the beginning of the reservoir's existence, or later in 1988–1992, when the fish were significantly decreased. The bio-

mass and density of large-sized *Daphnia* were negligible during period of high fish stock (1982–1984) and gradually increased up to 10% of total zooplankton biomass when the fish stock was reduced.

The differences in small-sized fractions of cladocerans (i.e. cladocerans that passed through 0.71 mm sieve) within analysed period were linked with the biomass allocation between small and large cladocerans and with the total cladoceran biomass levels as well.



Figure 4. Long-term changes of the biomass of large-sized Cladocera (black area), total cladoceran biomass (full line) and total zooplankton biomass (dotted line) in Rimov Reservoir during 1979–1992. Large-sized Cladocera were defined as a fraction retained by 0.71 mm sieve. The numbers in circles show the average value of the biomass of large-sized Cladocera. The vegetative periods from May to October are plotted.

The most significant reduction of the biomass of smallsized Cladocera was in the year with well developed large-sized fraction (1979), or when the presence of some large-sized cladocerans coincided with relatively low levels of total cladoceran biomass (1988–1990, 1992; cf. Figure 4 and Table 4).

Similarly, we examined the long-term changes of biomass of large-sized Copepoda (i.e. Copepoda retained by 0.42 mm sieve, which largely consisted of big adults of *Cyclops vicinus*) but no link with fish population development in the reservoir was found. The registered differences in biomass of large-sized Copepoda were similar to biomass differences of total copepods presented in Table 3b, which are similar to differences in total zooplankton biomass in Table 2.

Finally, we examined if body size structure of *Daphnia* and relative changes in proportion of other cladoceran species were related. A comparison of long-term changes in composition of cladoceran species during the spring clear-water period and the late summer cyanobacteria stagnation period is shown in Figure 5a, b. There is a clear pattern of decrease in the relative proportion of *Daphnia* and an increase of *Bosmina* occurrence in spring peaks when fish stocks were high (Figure 5a). In the years with low fish stocks, when the spring peak was dominated by *Daphnia*, this increase usually coincided with biomass maximum of its large

fraction (cf. Figure 4). The long-term changes of cladoceran species composition in late summer seemed to be unaffected by oscillations of fish stock (Figure 5b).

Phytoplankton and nutrients

The observed values of average annual chlorophyll a concentration fell within 10–24 μ g l⁻¹ which was the consequence of phytoplankton development in two consecutive years 1989 and 1990 (cf. Table 5). There was no clear pattern of phytoplankton biomass changes during fourteen years investigated. The length of compared vegetative periods for phytoplankton we put from the middle of April to the end of October (which is longer by half a month than for zooplankton), in order not to omit the maximal value of spring outburst of phytoplankton. These spring peaks formed the year maxima in six years, the rest of reported maximal values in Table 5 ensued from summer bloom of cyanobacteria. The differences in relative proportions of spring and summer algal crops in particular years did not show relationships with long term changes of fish stock in the reservoir.

The cross-comparison of fourteen average year values of chlorophyll *a* (Table 5) showed statistically significant differences in four cases only (p < 0.1). These differences resulted from cross-differences of

Table 4. The cross-comparison by Lord's range test of fourteen annual biomass values of small-sized cladocerans that passed through 0.71 mm sieve in Rimov Reservoir from 1979 to 1992. The compared periods cover six months from May to October and the annual values are based on the average of nine analysed samples in each year. The statistically significant differences are distinguished by asterisks for three levels of significance (0.1*, 0.05**, 0.01***).

| Small-size | | Signi | ficance | e of con | npariso | ons | | | | | | | | | | |
|------------|-------------|---------|---------|---------------|---------|-----|----|-----|-----|----|----|----|----|----|----|----|
| Aver | Max | Min | • | between years | | | | | | | | | | | | |
| biomass | biomass | biomass | | | | | | | | | | | | | | |
| (mg prot.l | N / m^2) | | Year | | | | | | | | | | | | | |
| 66 | 135 | 8 | 1979 | 79 | | | | | | | | | | | | |
| 92 | 209 | 3 | 1980 | _ | 80 | | | | | | | | | | | |
| 130 | 186 | 47 | 1981 | *** | _ | 81 | | | | | | | | | | |
| 128 | 373 | 18 | 1982 | - | _ | - | 82 | | | | | | | | | |
| 134 | 260 | 36 | 1983 | ** | _ | _ | _ | 83 | | | | | | | | |
| 122 | 187 | 60 | 1984 | ** | _ | _ | _ | _ | 84 | | | | | | | |
| 100 | 157 | 42 | 1985 | * | _ | _ | _ | _ | _ | 85 | | | | | | |
| 96 | 137 | 18 | 1986 | _ | _ | _ | _ | _ | _ | _ | 86 | | | | | |
| 79 | 137 | 6 | 1987 | _ | _ | ** | _ | * | * | _ | _ | 87 | | | | |
| 79 | 110 | 40 | 1988 | _ | _ | *** | _ | ** | ** | _ | _ | _ | 88 | | | |
| 69 | 153 | 40 | 1989 | _ | _ | *** | _ | ** | ** | _ | _ | _ | _ | 89 | | |
| 64 | 94 | 33 | 1990 | _ | _ | *** | * | *** | *** | ** | ** | _ | _ | _ | 90 | |
| 81 | 195 | 16 | 1991 | _ | - | * | _ | - | _ | - | _ | _ | _ | - | _ | 91 |
| 73 | 135 | 29 | 1992 | _ | - | *** | _ | ** | ** | - | _ | _ | _ | _ | _ | _ |



Figure 5. Long-term changes of average relative proportion of two main cladocerans at their spring peak during clear-water period (upper part) and during late summer cyanobacteria stagnation (lower part). *Daphnia* spp. (black) and *Bosmina* spp. (hatched) were distinguished. *Ceriodaphnia quadrangula* and *Diaphanosoma brachyurum* are summed in white parts of columns. Three samples from each defined period were averaged.

the two years with relatively high phytoplankton biomass (1981, 1990) and two years where the phytoplankton was relatively low (1985, 1989).

The concentration of total phosphorus in surface water fell within 10–80 μ g l⁻¹. The averages for the

vegetative periods of the years varied between 16 and 41 μ g l⁻¹ of total phosphorus. The data on total phosphorus contrary to chlorophyll *a*, did not significantly differ between the years.

Table 5. The cross-comparison by Lord's range test of fourteen annual values of total phytoplankton biomass (expressed as chlorophyll *a*) in Rimov Reservoir from 1979 to 1992. The compared periods cover six and half months (from mid April to October) and the average values are based on the average of ten analysed samples in each year. The statistically significant differences are distinguished by asterisks for one level of significance $p = 0.1^*$ only. The maximal values which were related with spring phytoplankton peak are marked by $\hat{}$.

| Total phyte | oplankton | | | Sign | ificanc | ce of c | ompar | isons | | | | | | | | |
|-------------|--------------------|---------|------|---------------|---------|---------|-------|-------|----|----|----|----|----|----|----|----|
| Aver | Max | Min | | between years | | | | | | | | | | | | |
| biomass | biomass | biomass | | | | | | | | | | | | | | |
| (mg prot.N | √ m ²) | | Year | | | | | | | | | | | | | |
| 21.7 | 83.7^ | 2.6 | 1979 | 79 | | | | | | | | | | | | |
| 18.4 | 48.1 | 3.5 | 1980 | - | 80 | | | | | | | | | | | |
| 20.5 | 49.8 | 2.5 | 1981 | - | - | 81 | | | | | | | | | | |
| 13.1 | 28.0 | 3.4 | 1982 | _ | _ | - | 82 | | | | | | | | | |
| 14.9 | 35.5 | 1.9 | 1983 | _ | _ | - | - | 83 | | | | | | | | |
| 18.3 | 49.6 | 4.1 | 1984 | - | - | - | - | - | 84 | | | | | | | |
| 11.7 | 25.4 | 3.6 | 1985 | - | - | * | - | - | - | 85 | | | | | | |
| 17.8 | 39.4 | 1.8 | 1986 | - | - | - | _ | _ | - | _ | 86 | | | | | |
| 12.5 | 33.9 | 1.6 | 1987 | - | - | - | - | - | - | - | - | 87 | | | | |
| 19.6 | 81.4 | 2.4 | 1988 | - | - | - | _ | _ | - | _ | _ | - | 88 | | | |
| 10.5 | 24.3 | 1.2 | 1989 | _ | _ | * | - | - | - | - | - | - | - | 89 | | |
| 24.0 | 72.1 | 2.1 | 1990 | _ | _ | - | - | - | - | * | - | - | - | * | 90 | |
| 11.4 | 39.5^ | 0.6 | 1991 | _ | _ | - | - | - | - | - | - | - | - | - | - | 91 |
| 15.2 | 32.7 | 3.3 | 1992 | - | - | - | - | - | - | - | - | - | - | - | - | - |

Discussion

Our long-term study indicate that the only parameter influenced by changes of planktivorous fish stock was the zooplankton body-size structure in Rimov Reservoir. However, no significant differences in total phytoplankton biomass between the years with high and low abundance of large-bodied *Daphnia* were found. This supports the generally observed trend that the top-down trophic cascade is strongly damped and the changes in phytoplankton biomass can be assured only when the fish community is strongly manipulated (McQueen, 1990).

The classic concepts of reduction in average algal crop by biomanipulation presume that this decrease is mediated by increased zooplankton grazing (Shapiro et al., 1975). Nevertheless, some recent insights indicate that, as with zooplankton grazing, there are other factors, mostly connected with nutrient cycling, contributing to final effect (DeMelo et al., 1992; McQueen et al., 1992; McQueen, 1990). This fully supports the proposed criterion of Benndorf (1988b) which stressed that all biomanipulative algal reductions should be considered in the light of known nutrient-phytoplankton relationships (Dillon & Rigler, 1974; Vollenweider, 1976).

We regressed the long-term data of chlorophyll a on total phosphorus in Rimov Reservoir along with the long-term data of two other unmanipulated Czech reservoirs in Figure 6. The set of Rimov data clearly fit the general bottom-up relationship, and shows no tendency for chlorophyll a decrease for the years with high abundance of large bodied Daphnia. The significant phosphorus limitation of phytoplankton was confirmed for summer months in 1989 and 1990 (Nedoma et al., 1993a, b) which again indicate a bottom-up, rather than top-down control of phytoplankton. The importance of zooplankton grazing effect was restricted to the short period of the spring clear-water phase, but there is some evidence that even this phase of low phytoplankton biomass could be mediated by phosphorus deficiency at its beginning (Vyhnalek et al., 1991). All facts about phosphorus in Rimov Reservoir indicate that we did not reduce the planktivorous fish sufficiently and bottom-up forces remained predominant during the whole period investigated.

Most defenders of biomanipulation as an effective tool for reducing algal biomass tacitly presume the manageability of fish stock control in lakes and reservoirs. This presumption becomes more and more fragile with the increasing size of the water body, as planktivorous fish cannot be removed either by poi-



Figure 6. The relationship between the annual average of chlorophyll *a* and total phosphorus in three Czech reservoirs for the warm period of the year (April–October). The black points represented the fourteen years data set of Rimov Reservoir and the numbers indicate corresponding years. Triangles are from Klicava Reservoir 1963–1970 (Hrbacek et al., 1977). Squares are from Slapy Reservoir 1982–1991 (Komarkova, 1993 and Prochazkova et al., in press). The dotted lines mark off the 99% confidence band of the relationship, which is significant at p < 0.001.

soning, or by draining. Any substantial lowering of the impact of planktivory, by enhancing piscivory via artificial addition of predatory fish, requires a massive stocking programme of adult fish predators. The cost-effectiveness of such stocking is often questionable, especially because of the uncertainty of its stability (Laarman, 1978; Barthelmes, 1988). The longterm stabilization of high populations of piscivores is often complicated by cannibalism on recruits (Mills et al., 1987). The proportion of predatory fish in Central European reservoirs seems to be generally low (Kubecka & Bohm, 1991; Kubecka, 1993b) with poor capability for controlling planktivorous fish. Extensive stocking did not enhance the level of predatory fish in Rimov Reservoir to any significant extent probably due to high mortality of stocked individuals.

The most effective biomanipulative measure in the Rimov Reservoir was the lowering of the water level during mass spawning of cyprinids. In the years with high enough discharges to allow the flooding of terrestrial vegetation, the drying of eggs could practically eliminate recruitment. The drying of perch eggs was not so effective because of the species' prolonged spawning season and laying of eggs down to 10 m depth (Kubecka, 1992). Fyke net industry could be rather efficient at reducing perch abundance, but a rather high effort of more than one fyke net per hectare is required for the quick elimination of this species (Svatora, 1989). According to Persson et al. (1988) and Kubecka (1993b) any absolute decrease of total fish stock, especially of cyprinids, could result in stronger perch population. Continuous decrease of the perch proportion shows that some kind of competitive bottleneck may still exist preventing survival of perch recruits.

Elimination of fish biomass was relatively easy in years of high fish biomass. Fish biomass of Rimov Reservoir in 1982–83 was too high for the trophic level of reservoir which resulted in slow growth rates of fish. Much lower biomass in 1989–92 caused lower catch per unit of effort in liquidation catches and the growth rates of fish increased. Further reduction of undesirable fish would require more intensive biomanipulative pressure. This was not possible to achieve in Rimov Reservoir and recent biomanipulative pressure is less intense than it was in 1985–89 (Table 1). The reservoir fish stock seems to have stabilised between 100 and 150 kg ha⁻¹ under this limited effort, which has resulted in partial reappearance of large-sized Cladocera in the zooplankton (cf. Figures 1 and 4).

The long-term data on fish and zooplankton development in Rimov Reservoir were used to establish a relationship between size-structure of zooplankton and the biomass of planktivorous fish (Figure 7, Table 6). The size-structure of zooplankton was characterised as the percentage of the biomass of the large Daphnia specimens (retained on a 0.71 mm sieve) in the total zooplankton biomass. The advantage of this relative size index is, that it is much less affected by bottom-up forces, especially when we compare the years, or reservoirs, with different trophic conditions. The planktivorous fish stock was expressed as biomass of 1+ fish and older. The impact of the young-of-the-year fish on zooplankton structure was not apparent in fourteen years' history of Rimov Reservoir. This was mainly because the strongest year classes were born in the years with relatively large zooplankton. In addition, low recruitment and high mortality of fry (Kubecka, 1991) caused little 0+ fish interference with the pronounced effect of 1+ and older fish on zooplankton structure during 1984-1990. Moreover, the adult fish of all three dominant species were recorded to be feeding on pelagic zooplankton on most sampling dates during 1986–1987 (Kubecka & Matena, unpubl.).

The weakness of zooplankton structure versus fish biomass plot in Figure 7 is that there is only one point

Fb RMS d.f. arpRimov 79-92 38.2 (±1.5) 0.989 (±0.004) 2.12 12 34.0 < 0.001 0.86 (8.15)(0.84)Rimov 80-92 $47.4(\pm 1.7)$ 2.24 0.85 11 < 0.001 $0.989 (\pm 0.005)$ 29.7 (5.21)(0.84)Rimov 80-92 & London 93 49.2 (±1.2) $0.989 (\pm 0.003)$ 1.78 0.88 14 50.1 < 0.001

Table 6. The statistics of exponential regression $(y = a \cdot b^x)$ relating the relative proportion of large Cladocera in total zooplankton biomass (%) to the fish biomass (kg ha⁻¹). The numbers in brackets for residual mean square and correlation coefficient refer to Rimov data when a linear model was applied. The data from Figure 7 were analysed.

a, b - parameters of exponential equation (\pm 95% confidence limit); RMS - residual mean square; r - correlation coefficient; d.f. - degrees of freedom; F - variance ratio; p - probability.



Figure 7. The relationship between annual averages of relative proportion of large Cladocera in total zooplankton biomass and the biomass of planktivorous fish stock in Rimov and three of London reservoirs. Data for Rimov Reservoir are marked by circles and triangles and the symbols for different years are identical with Figure 1. The hatched squares represent the characteristics of fish and zooplankton structure in three of London reservoirs in 1993 (Seda, Kubecka & Duncan, unpubl. data).

The white circle with the arrow represents the first year of Rimov Reservoir existence (1979), when unstable conditions connected with decomposition processes interfered. The plotted regression lines are based on the whole 1979–1992 data set for Rimov Reservoir (1), or after ommiting the debatale first year 1979 (2). The statistics for the combined regressions of the presented data are in Table 6.

for the fish biomass below 100 kg ha⁻¹ in Rimov data set. This point represents the first year of reservoir existence when unstable conditions connected with decomposition processes interfered. Omitting or including this debatable point has only little effect on residual mean square of estimated regression, but influenced the intercept of the assumed exponential relationship (Table 6). The lack of data on size-structure of zooplankton when the fish biomass is reduced below 100 kg ha⁻¹ could similarly cast doubt on the exponential relationship in Figure 7 although it fitted better than linear one (Table 6). Moreover, the extent of real values of index on y axes in Figure 7 is clearly connected with the size of dominant species of *Daphnia*, for which the occurrence of larger-bodied species is possible only under low fish predation.

The large *Daphnia* specimens (retained on a 0.71 mm sieve) were formed purely by *Daphnia galea-ta* in the Rimov data set. A theoretical model proposed on the base of Rimov data by Seda (1989) predicted, and field experiments confirmed, that the maximal attainable proportion of large cladocerans in zooplankton was between 22% and 25% when *Daphnia galeata* was the only species present. This is in agreement with study in another Czech reservoir, Hubenov Reservoir, where Hrbacek et al. (1978, 1986) found that the proportion of large *Daphnia* could be more than 30% of the zooplankton biomass when larger species like *Daphnia pulicaria* were also present. In Hubenov Reservoir this was attained by experimentally reducing the planktivorous fish by adding piscivorous salmonids.

Recent analyses of zooplankton structure in nearly fishless London reservoirs (Seda & Duncan, 1994) revealed that the proportion of large *Daphnia* can reach on average 50% when the fish stock is significantly reduced and *Daphnia magna* and *Daphni pulicaria* are the dominant species. To illustrate this we plotted in Figure 7 the preliminary characteristics of fish and zooplankton structure in three London reservoirs investigated in 1993 (Seda, Kubecka & Duncan, unpubl.), which nicely fitted the exponential relationship of fourteen years' Rimov data.

The question remains, if there exists a threshold level of fish predation, or zooplankton status, above which the top-down effects on lowering phytoplankton biomass is apparently pronounced. Judging from long-term data of Rimov Reservoir, the biomanipulative experiment in Hubenov Reservoir (Hrbacek et al. 1978, 1986) and last year's survey in the London reservoirs (Seda & Duncan, 1994) this critical limit lies between 20% and 30% of large daphnids in total biomass, expressed in terms of zooplankton structure.

Combining the relationship presented in Figure 7, the mentioned critical zooplankton structure correspond to relative low value of fish biomass (70–40 kg ha⁻¹). It seems, that the decrease of fish biomass was not intense enough in Rimov Reservoir to break through the monopoly of *Daphnia galeata* for enabling the appearance of another larger-bodied species of daphnids which could significantly change the structure of the whole zooplankton. This is probably the crucial demand with respect of possible reduction of phytoplankton biomass by the biomanipulative approach in Rimov Reservoir.

Acknowledgments

Many people contributed to the field data analysed in this paper. The authors are obliged mainly to P. Blazka, Z. Brandl and M. Straskraba for initiating the program of long-term monitoring of Rimov Reservoir and for contribution to zooplankton analyses. B. Desortova, J. Komarkova and V. Vyhnalek contributed to phytoplankton analyses and J. Kopacek, J. Popovsky and L. Prochazkova conducted the analyses of nutrients. We are grateful to J. Matena for help with fish work essential for this study.

The final version of this paper was completed during J.S.'s stay at Royal Holloway College (University of London) which was realised within the framework of Community mobility action financed by the Commission of European Communities.

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