PRIMARY RESEARCH PAPER

Biomanipulation as a useful water quality management tool in deep stratifying reservoirs

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Abstract In six deep, soft-water reservoirs, ranging from oligotrophic to eutrophic, fishery management has been guided by the use of biomanipulation to improve water quality and opportunities for recreational fishing. As evidenced by the establishment of larger-bodied daphnids, a low level of zooplanktivory could be maintained in the newly filled Grosse Dhünn and refilled Brucher and Lingese Reservoirs only by regular stocking of piscivores (*Sander lucioperca*, *Esox lucius*, *Salmo trutta lacustris*, *Onchorhynchus mykiss*) in combination with size and bag limitations for the recreational fisheries. However, in the mesotrophic Pre-Reservoir Grosse Dhünn, Bever Reservoir and the newly filled slightly eutrophic Wupper Reservoir it took between 8 and 10 years before the predator-resistant zooplankton community responded to management with a switch to larger daphnids. Except for oligotrophic Grosse Dhünn Reservoir where angling is prohibited, the expected enhancement of piscivore biomass through stocking not least was prevented by anglers. However, growth of perch (*Perca fluviatilis*) benefited from the changed fishery management relying upon stocking piscivores only allowing them to reach the size of piscivory. The appearance of larger daphnids in Pre-Reservoir Grosse Dhünn and Wupper Reservoir resulted in the biomass of the *Daphnia* spring peak to increase and occur earlier causing prolonged clear water conditions. Although the larger daphnids increased transparency, total summer mean chlorophyll concentrations in the euphotic zone only decreased in the slightly eutrophic reservoirs due to reduced phosphorus availability following unchanged external phosphorus loadings. Reduced phosphorus availability in these reservoirs caused a real oligotrophication. Although the edible seston fraction was controlled ''top down'' the results did not support the *trophic cascade hypotheses* because total phytoplankton remained controlled ''bottom up'', admittedly triggered by ''top down'' forces. In general, the results support the importance of indirect (non-lethal) effects as the driving forces for the successful biomanipulations, particularly in slightly eutrophic reservoirs. Not least, the delayed zooplankton response provides an indication that the underlying change of internal feedbacks was not driven by external forces to stabilize the reservoirs trophic state in these deep stratifying reservoirs.

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Introduction

Reduction of external nutrient loading is a generally accepted concept in water quality management (Vollenweider, 1976) which seeks to limit nutrient input to control biomass; termed ''bottom up''. Conversely, ''biomanipulation'' is a restoration-technique (Shapiro et al., 1975) which relies on ''top down'' forces to control biomass by the application of food-chain theory (Hairston et al., 1960). The underlying simple logic of the *trophic cascade* hypothesis (Carpenter et al., 1985) predicts that a ''rise in piscivore biomass brings decreased planktivore biomass, increased herbivore biomass, and decreased phytoplankton biomass''. Thus, in relation to fish community, the practical target of biomanipulation is to increase the density of piscivores and to reduce the density of planktivores. As most planktivores are size-selective predators reduced predation pressure may result in increased abundance of large-bodied zooplankton which has a more marked effect on their phytoplankton food resources (Gliwicz, 1990; Spaak & Hoekstra, 1997). Consequently, as predicted from the *size-efficiency hypothesis* (Brooks & Dodson, 1965) enhancement of populations of large herbivorous individuals can be taken as indicative of a successful decrease in predation on the zooplankton.

There is overwhelming evidence that biomanipulation is a successful management tool for shallow lakes (Reynolds, 1994; Drenner & Hambright, 1999), but the relevance to deep stratified lakes with a mean depth >5 m is less clear (Benndorf et al., 2002). Long-term success of biomanipulation in shallow lakes, where macrophytes suppress phytoplankton development, is most likely to be achieved with phosphorus levels <100 μg P l^{-1} (Jeppesen et al., 1990). Controlling nutrient levels along with food-web manipulation therefore has the potential to create more permanent effects.

As predicted from the BEThP (Biomanipulation Efficiency Threshold of Phosphorus loading of Benndorf, 1987), a combination of food-web manipulation and nutrient management should be a promising technique for managing deep stratifying lakes. However, biomanipulation in deep reservoirs has often failed or has been less successful than predicted (Seda & Kubecka, 1997; Seda et al., 2000), not least because the P load remained too high (Benndorf et al., 1988). In contrast to most lakes, reservoirs generally contain few macrophytes, sometimes due to a lack of suitable littoral areas and/or large fluctuations in water levels. This reduces refuges and habitat availability, which impacts on fish reproduction and behaviour. In most central European Reservoirs cyprinid (roach, bream) dominance is the last and most stable stage of natural development of the fish stock (Kubecka, 1993) giving rise for high predation pressures on zooplankton. The lack of spatial heterogeneity in the reservoirs tends to intensify predation effects because the linear pelagic food chain of ''nutrients-algae-zooplankton-fish'' dominates. Nonetheless, a deep water refuge for daphnids (Wright & Shapiro, 1990; Dawidowicz et al., 2002) is available in most deep reservoirs.

A growing body of evidence suggests that the appealing but simple logic of a pelagic ''top down''-cascading food chain (Hairston et al., 1960; Carpenter et al., 1985) driven by direct (lethal) effects only works over short time-scales of a few weeks, but it does trigger indirect (non-lethal) effects (Benndorf, 1992) which are of importance for the long-term management success of shallow lakes (Hansson et al., 1998; Scheffer, 2001; Benndorf et al., 2002). Piscivores, for example, may change the behaviour of cyprinids, restricting them to refuges thus reducing the predation pressure upon zooplankton (Braband & Faafeng, 1994; Romare & Hansson, 2003), as well as the transport of nutrients within the lake resulting from a response in the migratory behaviour of fishes and zooplankton (Wright & Shapiro, 1984; Braband et al., 1990; Kairesalo et al., 1999). Since species elemental stoichiometry partially controls biogeochemical cycling (Sterner, 1995), changes induced in zooplankton biomass and community structure by biomanipulation can alter not only the quantity but also the quality of nutrient-cycling (Sterner et al., 1992; Sterner & Hessen, 1994; Attayde & Hansson, 1999), even to the extent of modifying nutrient loss

from the mixed layer (Bloesch & Bürgi, 1989; Mazumder et al., 1992; Houser et al., 2000). If such indirect effects do play an important role in the successful biomanipulation of deep lakes, phosphorus-accumulation in *Daphnia* biomass, in combination with enhanced vertical phosphorus translocation, should result in "oligotrophication", through decreasing phosphorus and chlorophyll-concentrations. As this mechanism only operates in the summer season where a sufficient concentration of epilimnetic phosphorus or a negative epilimnetic phosphorus balance can be achieved (Benndorf et al., 2002), phosphorus concentrations and loadings undoubtedly set boundaries for successful biomanipulation. This emphasizes the need for a combined approach as recommended for shallow lakes (Scheffer, 2001; Benndorf et al., 2002).

This study presents a summary of the long-term results of approximately 15 years from large-scale experiments to examine changes in water quality and sport fishery opportunities by continual piscivores stocking in six deep, stratifying, soft-water reservoirs ranging from oligotrophic to eutrophic. In contrast to the often recommended drastic removal of planktivores (Hansson et al., 1998) continual management is thought to have limited success (Drenner & Hambright, 1999). However, as it is less laborious and may result in a more gradual change in the fish community it is more acceptable for fishers and water quality managers. If biomanipulation by the repeated stocking of piscivores only in combination with size and bag limits for recreational fisheries proved to be an effective water quality management tool I expected to increase the density and size of cladocerans due to reduced predation pressure (Brooks & Dodson, 1965). Nonetheless, the success of biomanipulation and the predictive power of these theories (Hairston et al., 1960; Carpenter et al., 1985) can only be judged by water transparency and chlorophyll concentrations. If indirect effects do play a role the reduction of chlorophyll-concentrations should be coincided by a decrease in phosphorus-availability (Benndorf et al., 2002).

Methods

Site description

The five reservoirs (Grosse Dhünn, Brucher, Bever, Wupper and Lingese) and the Pre-Reservoir Grosse Dhünn are situated in the central area of the Rheinische Schiefergebirge in Western Germany. They are used for controlling the flood regimes of the rivers Dhünn and Wupper. Grosse Dhünn Reservoir is also used for drinking water so, unlike the other reservoirs, public recreation is prohibited. Grasslands with cattle farming and scattered forests dominate land use in the watershed, where there are only small human settlements and farms. Only Wupper and Lingese Reservoirs receive treated sewage and/or storm water effluents. Their morphometric and hydrological features are given in Table 1.

The climate is Atlantic, with mild winters and summers. Stream flow is correlated with rainfall because the non-calcareous bedrock below the clay soils is impermeable. Subsurface runoff, which dominates the water regime, fluctuates widely with peak discharges during winter. Thus, water levels in the reservoirs reach a maximum in spring and a minimum in autumn. The reservoirs, lying at 200–400 m above sea level, are deep (18–52 m max. depth), mostly dimictic, soft water lakes.

Management options for nutrient loading and fish populations

Lingese Reservoir received incompletely treated sewage effluents for 30 years, but these effluents have now been diverted out of the catchment since early winter 1992/1993. Nevertheless, the reservoir still receives effluents from combined sewer overflows. In the year 1990 an artificial mixing system was installed which was improved in 1993. From autumn 1995 to winter 1998/1999 the reservoir was empty and refilling commenced with clearing of the vegetation. In order to reduce internal phosphorus loading from the sediments, the P-rich surface layer of about 30 cm (3.5–4.5 mg P g^{-1} d.w.) was inverted and covered with deeper, nutrient-poor sediment layers (0.8–1.2 mg P g^{-1} d.w.). Further management

Table 1 Morphometric and hydrological features of the reservoirs (R water retention time)

Reservoir	Max. depth (m)	Mean depth (m)	Max. volume (mio m^3)	Max. surface (ha)	R (a)
Lingese	18	6.7	2.6	39	0.3
Brucher	20	7.2	3.3	46	0.7
Pre-Reservoir Grosse Dhünn	28	11.2	7.5	67	0.3
Bever	31	11.9	23.7	200	1.1
Wupper	31	12.2	25.9	211	0.2
Grosse Dhünn	52	20.1	72.0	358	1.5

measures used in the other reservoirs are given in Table 2.

With the exception of Grosse Dhünn, all the reservoirs are co-managed for improve water quality and recreational fisheries including the stocking of common carp (*Cyprinus carpio*) and tench (*Tinca tinca*) at low densities with the beginning of the 1990s (Table 2). Enhancing the piscivorous fish populations has relied mainly upon regular stocking with northern pike (*Esox lucius*), pikeperch (*Sander lucioperca*) and trout (*Salmo trutta lacustris*, *Onchorhynchus mykiss*), in combination with restrictions on the anglers. In contrast to pike and pikeperch, stocked trout do not reproduce in the reservoirs. Minimum sizes (northern pike 55 cm, pikeperch 50 cm, lake-trout 55 cm), bag sizes, e.g. 15 piscivorous fish per angler and season in Wupper Reservoir, and closed seasons for piscivores, e.g. 1 October to 31 May in Wupper Reservoir, restrictions are placed upon the anglers.

Sampling

The reservoirs were sampled between 1988 and 2005 throughout the year bi-weekly at the inflow and from March to October at their deepest point. Secchi depth (m), depth profiles of temperature, oxygen, pH, and chlorophyll, plus integrated samples of the trophogenic layer (taken as 2.3 times the Secchi depth) were taken. Nutrients (DIP Dissolved Inorganic Phosphorus, TP Total Phosphorus, DIN Dissolved Inorganic Nitrogen, DSi Dissolved Silica and DOC Dissolved Organic

Table 2 Management of the reservoirs (AYSR Average yearly stocking rate) from 1988 to 2005

Reservoir	Period	Fish	Size (cm)	AYSR (ind. ha^{-1})	Management measures
Lingese	1988–1990	Pike	30–40	?	1991: Stocking practice—without roach
		Roach	>20	?	
		Common carp	30–40	?	
	1991–1994	Pike	12–18	20	1993: Reduced external P-load; Artificial Mixing
		Pikeperch	12–18	20	
	1999	Minnows		60	1998: Sediment treatment; removal of vegetation
	2000–2005	Rainbow-trout	25–30	20	1999: Refilling; Artificial Mixing in August
		Common carp	20–25	3	
		Tench	15–20	5	
	2000	Pike	3–5	10	
		Pikeperch	12–15	5	
		Eel larvae		25	
	2001/2002	Pike	20–25	10	
		Pikeperch	12–15	10	
		Pikeperch	30–40	3	
	2003–2005	Pikeperch	12–15	10	
		Pikeperch	20–25	5	
Brucher	1994	Minnows		45	1993: Refilling without clearing vegetation; Artificial Mixing
		Sun-bleak		45	
	1994–1997	Brown-trout	15–25	30	
		Rainbow-trout	15–25	25	
		Common carp	20–25	2	

Table 2 continued

Reservoir	Period	Fish	Size (cm)	AYSR (ind. ha⁻¹)	Management measures
Pre-Reservoir Grosse Dhünn	1987/1988	Brown-trout	10–15	40	1988: Introduction of pikeperch
		Rainbow-trout	10–15	45	
		Rainbow-trout	30–35	30	
		Pikeperch	10–15	7	
		Roach	15–30	20	
		Common carp	15–20	15	
		Tench	25–30	4	
		Eel larvae		40	
	1989–1992	Brown-trout	40–50	7	1989/1990: Stocking practice without roach; gradual Reduction of Anglers from 200 to 70 in 2000
		Lake-trout	35–45	8	
		Pikeperch	40–50	2	
		Tench	20–30	15	
	1993–1995	Brown-trout	15–18	15	
		Brown-trout	25–30	20	
		Lake-trout	15–22	90	
		Pikeperch	40–50	2	
	1996/1997	Lake-trout	10–15	120	Angling was closed in 1996/1997
		Lake-trout	30–40	15	
		Pikeperch	18–22	30	
	1998–2000	Lake-trout	10–20	150	1998: Size and bag limitations strengthened
		Pikeperch	18–22	35	
	2001–2003	Lake-trout	30–40	20	
		Pikeperch	18–22	35	
Bever	1989/1990	Pike	30–40	6 (?)	
		Rainbow-trout	25–35	8 (?)	
		Roach	>20	15	
		Common carp	30–40	?	
		Tench	20–25	2.5	
		Eel-larvae		70	
	1991–1993	Rainbow-trout	40–50	2	1991/1992: Stocking practice without roach
		Pike	30–40	5	
		Pikeperch	25–30	3	
		Eel-larvae		30	
	1994–1997	Pike	3–7	50	
		Pikeperch	25–30	2	
	1998	Pike	3–7	40	
		Pikeperch	15–18	10	
		Pikeperch	25–30	1	
	1999–2005	Pikeperch	12–18	10	1999: Stocking practice: Lake-trout
		Lake-trout	25–35	10	
Wupper	1989–1995	Pike	5–7	75	1988: First filling
		Pikeperch	12–15	75	
	1989–1991	Common carp	20–25	10	1992: Reduced external P-load; Piscivores angling opened
	1991	Eel larvae		30	
	1996–1999	Pike	5–7	30	1996: Size and bag limitations strengthened
		Pikeperch	12–15	50	
	1999–2002	Pike	5–7	10	
		Pikeperch	12–15	25	
	2003/2004	No stocking			
Grosse Dhünn	1989–1991	Lake-trout	30–40	6	1984: First filling
		Pikeperch	30–40	4	
	1994	Lake-trout	10–15	30	No recreational fisheries
	2000	Lake-trout	10–15	40	
	2001–2005	Lake-trout	30–40	2	
		Pikeperch	20–25	1	

Carbon) and chlorophyll (CHL) were measured in the integrated samples on the day of sampling according to the methods recommended by Gesellschaft deutscher Chemiker (2004). Seston samples have been taken for elemental stoichiometric analysis (POC Particulate Organic Carbon, PON Particulate Organic Nitrogen, PP Particulate Phosphorus), fractionated into <30 μm and 30–250 μm, filtered with glass-fibre filters and analysed using a Perkin Elmer CHN–2400 elemental analyzer for seston-C and N, and seston-P analysed using the acid molybdate technique after high temperature digestion with persulfate. Phytoplankton samples were fixed with Lugol's iodine. Phytoplankton biomass was estimated by counting cells under an inverted microscope and converting them to biovolume by means of appropriate geometric shapes. Zooplankton was collected by vertical net hauls (100 μm meshes for rotifers and nauplii, 250 μm meshes for crustaceans and copepods and 780 μm for large bodied daphnids and invertebrate predators) from a layer of measurable dissolved oxygen concentrations >0.1 mg l^{-1}. All the nets were conical (100 cm length, 38 cm diameter) with a mouth reducing cone (diameter 17 cm). Preserved samples were enumerated under a microscope, and the biomass of various taxa (daphnids, copepods) determined by measurement of body lengths. Mean individual biomass (μg d.w. dry weight) was calculated for these taxa using a weight–length regression (Bottrell et al., 1976). Less variable taxonomic groups were assigned fixed individual biomass values (Bottrell et al., 1976). All specimens from the *Daphnia galeata—hyaline—longispina* complex are grouped as ''*Daphnia galeata*''. Zooplankton-C was calculated from biomass-d.w. assuming 45% carbon content (Hessen, 1990). Subsequently, *Daphnia*-P concentrations were calculated using a C:P ratio of 80:1 (Hessen, 1990). Internal P Retention/P load was calculated using the formula

$$R = 1 - TP_{Mixing}/TP_{Stratification} \qquad (1)$$

(TP_{Mixing}: January to April and $TP_{Stratification}$: May to September).

Fish stocks mostly were assessed using data on catches from anglers plus qualitative multi-gillnet fishing. Catch records are based on reports of approximately 200 anglers in Wupper and Bever and 85 anglers in Lingese Reservoir. In Pre-Reservoir Grosse Dhünn the number of anglers has decreased gradually from 200 to 70 in the year 2000. Multi-gill net fishing in all reservoirs was irregular, largely qualitative. Nets (5 nets, 30–50 m long, 1.5–2.0 m high and 15, 22, 25, 35, 45, 60 mm mesh size) were set perpendicular to the lake shore, anchored floating 0.5 m below the surface overnight between the end of July and September. All fish were identified, measured and weighed. Subsamples were taken for age determination and stomach content analyses.

In order to estimate fish density, a combination of littoral zone and open water estimates was used in Bever- and Pre-Reservoir Grosse Dhünn in August 2000 and in Wupper Reservoir in August 2003. Whole lake fish biomass for each fish species was determined by comparing species, site and depth distributions of all fishes captured in the multi-gillnets (6.25–55 mm) with corresponding depth strata from the acoustic abundance estimates (SIMRAD EY 500 Splitbeam with 120 kHz operating frequency, 0.1 ms pulse duration). Estimates of fish density and fish-TS (target strength) distributions were based on horizontal and vertical soundings from perpendicular transects, during day and night, taped and digitised with EP 500 postprocessing software (Werner & Schultz, 2004). The TS values were classified into 3 dB classes with minimum TS – 57 dB. Except of Bever Reservoir, where the measured fish lengths (TL) were transformed to acoustic estimates assuming a TS–length dependence TS = 20*log (TL) – 26.0, the relationship TS = 19.1 log (TS) – 63.85 was used. Additionally, electro-fishing from the boat and beach-seining was undertaken in the littoral zone. All fish were identified, measured and weighed. Subsamples were taken for age determination and stomach content analyses.

Data analyses

STATGRAPHICS (Manugistics, 1998) was used for statistical analyses. As not all data were

normally distributed the central tendencies of winter/spring (mixing) and summer growing season (stratification) conditions for each year or time period are presented as medians. Multiple Sample Comparison was performed to test whether the data samples differed. Differences were tested using the Kruskal–Wallis (KW) and Mann–Whitney (W) tests. Box & Whiskers plots were used to visually determine where any differences lay, as recommended by STAT-GRAPHICS. Simple and multiple linear regressions were based on log transformed data to ensure normality and homoscedasticity before quantifying the relationships between variables and chlorophyll-concentrations. Pearson's correlation coefficient was used to measure the strength of association. A P-value of less than 0.01 was taken as highly significant.

Results

Catch records, fish stock data and the impact of anglers

Except for *Brucher Reservoir*, where a trout-minnow system became established (Tables 2, 5) in the second year of refilling (1994), roach (*Rutilus rutilus*) and smaller perch (*Perca fluviatilis*), often in combination with bream (*Abramis brama*), were the main resident planktivores in all the other reservoirs. Additionally, in Bever Reservoir vendace (*Coregonus albula*) was an important planktivore (Table 5).

As became apparent when emptying *Lingese Reservoir* in 1995, there was a huge cyprinid stock (Table 3), mostly roach and bream in poor physical condition (roach 3+, 8–9 cm, 10 g ind.$^{-1}$; bream 4+, 20 cm, 80 g ind.$^{-1}$). As evidenced by analyses of their gut contents, the roach and bream <20 cm preyed heavily upon zooplankton and the bream >20 cm upon chironomids and plants. With changed stocking practice in 1991 (Table 2), anglers piscivorous pike (*Esox lucius*) catch rates dropped from 12.0 ind. ha^{-1} in 1985 to 4.0 ind. ha^{-1} in 1993 and 1.0 ind. ha^{-1} in 2004, whereas pikeperch (*Sander lucioperca*) catch rates reached 1.0 ind. ha^{-1} in 1993 but only 0.1 ind. ha^{-1} in 2004. Adult trout (*Onchorhynchus mysksis*)

stocking was promptly tracked by catch records reaching 7.5 ind. ha^{-1} in 2002/2003. At the same time, benthivorous carp (*Cyprinus carpio*) catch rates declined from 7 ind. ha^{-1} in 1993 to 0.5 ind. ha^{-1}. Anglers' roach catch rates dropped from 120 ind. ha^{-1} in the year 1985 to 45 ind. ha^{-1} in 1993 and 8 ind. ha^{-1} in 2004 as the mean body weight of the roach caught increased from 40 g ind.$^{-1}$ before 1999 to 300 g ind.$^{-1}$ after refilling in 1999. Qualitative multi-gillnetting in August 2002 revealed well-conditioned rainbow-trout that only contained sticklebacks (*Gasterosteus aculeatus*) in their guts. However, the catch was dominated by roach in numbers as well as in biomass.

With the damming of the River Wupper (1988) northern pike, perch, roach and bream entered the slightly eutrophic *Wupper Reservoir* from its pre-reservoir condition. Pike catch rates peaked at 5 ind. ha^{-1} when angling for piscivorous fish was opened in 1992, but declined to 0.8 ind. ha^{-1} after 1995 (Table 2). At the same time, pikeperch catch rates increased from 0.2 ind. ha^{-1}, with a mean body weight of 1.7 kg ind.$^{-1}$, to 0.8 ind. ha^{-1} with 2.6 kg ind.$^{-1}$, although pikeperch stocking was reduced after 1995. Concomitantly, the mean body weight of perch started increasing until 1996 giving rise for perch reaching the size of piscivory. Since 1996, catch rate of cyprinids commenced increasing (Fig. 1a). Echo sounding and gillnetting in August 2003 (Werner & Schultz, 2004) revealed that piscivores contributed approximately 25% of the total fish stock (Table 3). After perch, pikeperch was the dominant piscivore. Roach and age-0 perch (<10 cm) are the dominant planktivores in the pelagic zone, while perch aged 2+ and older (>16 cm) prey heavily upon age-0 perch and ruffe (*Gymnocephalus cernua*). Planktivorous perch preyed heavily upon *Leptodora* in addition to larger daphnids. During the day perch and cyprinids >10 cm occupy the pelagic zone while smaller cyprinids are restricted to the night.

Replacement of the previous put and take fisheries management at the beginning of the 1990s (Table 2) resulted in rapidly declining catch rates in the oligo-/mesotrophic *Pre-Reservoir Grosse Dhünn* and *Bever Reservoir*. In both reservoirs, trout catch rates nearly collapsed after stocking of larger specimens was finished. In

Table 3 Fish stocks and angler catch rates in the reservoirs (without eel, carp and tench)

Reservoir	Year	Standing stock (kg ha^{-1})		Anglers catch rate (kg ha^{-1})	
Pre-Reservoir Grosse Dhünn (65 ha)	2000	Percids > 16 cm	0.9	Percids > 16 cm	1.2
		Lake-trout	0.4	Lake-trout	0.4
		Piscivores	1.3	*Piscivores*	1.6
		Cyprinids	14.5	Cyprinids	0.2
		Total	16.0	Total	1.8
Bever (50/180 ha)[a]	2000	Pike	0.0	Pike	2.4
		Percids > 20 cm	6.2	Percids > 20 cm	2.1
		Piscivores	6.2	*Piscivores*	4.5
		Cyprinids	62.5	Cyprinids	2.7
		Vendace	44.5	Vendace	0.0
		Total	119.0	Total	7.2
Wupper (180 ha)	2003	Pike	0.5	Pike	2.9
		Perch > 16 cm	16.5	Perch > 16 cm	2.7
		Pikeperch > 20 cm	5.0	Pikeperch > 50 cm	3.5
		Piscivores	22.0	*Piscivores*	9.1
		Cyprinids	36.9	Cyprinids	8.3
		Total	92	Total	17.4
Lingese (35 ha)	1993[b]	Pike	4.2	Pike	10.9
	1995	Pikeperch	4.6	Pikeperch	2.5
		Piscivores	8.8	*Piscivores*	13.4
		Cyprinids	207.2	Cyprinids	11.1
		Total	216	Total	24.5

[a] Pelagic fish stock of central basin (50 ha) to which vendace is confined and anglers catch rate from the complete basin (180 ha)

[b] Anglers Catch Record of the year 1993

contrast, intense stocking with smaller lake-trout (*Salmo trutta lacustris*) <20 cm in Pre-Reservoir Grosse Dhünn in the mid 1990s (Table 2) was not tracked by the catch rates which remained on a very low level of 0.3 ind. ha^{-1}. However, after 1998, mean body weight of the trout caught in Pre-Reservoir Grosse Dhünn increased from 300 g ind.$^{-1}$ (mostly rainbow-trout) to 1,200 g ind.$^{-1}$ (lake-trout). Pikeperch were first caught in 1990 with 800 g ind.$^{-1}$. Since 1990, catch rates were in the range of 0.5 ind. ha^{-1} irrespective of increased stocking efforts after 1996/1997. However, pikeperch increased its mean body weight to 2.050 g ind.$^{-1}$ after 1994. In 1996/1997 piscivores angling was closed. Thereafter piscivores catch rates revealed a peak in 1998. Benthivorous carp catches, and tench in Pre-Reservoir Grosse Dhünn declined markedly in both reservoirs (i.e. in Bever Reservoir from 4.0 ind. ha^{-1} to less than 0.1 ind. ha^{-1}). Although, the magnitude of the decline in catch rate of roach and bream is striking in both reservoirs, (i.e. in Bever Reservoir from 30 ind. ha^{-1} roach in the years 1988–

1992 down to 6 ind. ha^{-1} after 1993), neither piscivorous biomass nor numbers were enhanced to any significant extent in the long-term (Table 3). However, perch benefited in growth in Pre-Reservoir Grosse Dhünn after 1993 (Fig. 1b).

As revealed by intense echo-sounding and gillnetting in August 2000 in the central basin of Bever Reservoir (50 ha) (Werner & Schultz, 2001), vendace (*Coregonus albula*) reached stock densities of 45 kg ha^{-1}, accounting for 37% of the total stock biomass (Table 3) and 82% of the abundance of the fish stock living in this area. Vendace are not impacted by anglers. Roach, mostly 23–27 cm, bream and perch aged 1+/2+ (11–16 cm) reached 70 kg ha^{-1}. The perch mainly fed on large daphnids (85%) and *Leptodora* while, vendace mainly consumed *Eudiaptomus*, *Cyclops* (85%) and larger daphnids (15%) during the day in the hypolimnion. Predator biomass (perch >20 cm, pikeperch; northern pike only inhabits the littoral areas) contributed less than 10%.

In Pre-Reservoir Grosse Dhünn intense echo-sounding and gillnetting in August 2000 (Werner
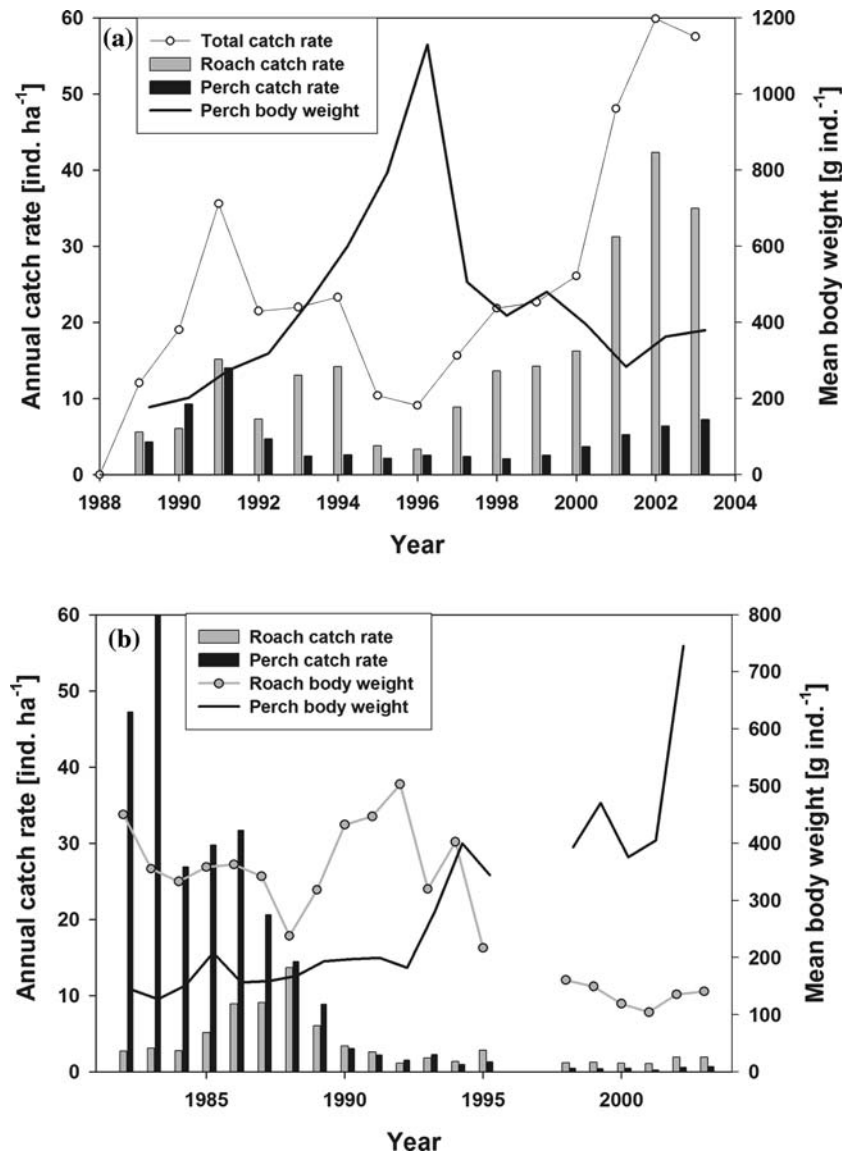
& Schultz, 2002) revealed that about 90% of the total pelagic fish stock (Table 3) was attributable to roach aged 0+ and 1+ (<12 cm) followed by 0+ perch (<10 cm). As the epilimnion was devoid of any fish during the daytime, the roach migrated into the pelagic zone during the night.

Since the river was dammed in 1984, some riverine species, including grayling (*Thymallus thymallus*), brown-trout (*Salmo trutta fario*) (1998) and dace (*Leuciscus leuciscus*) in 2005 have disappeared from the oligotrophic *Grosse Dhünn Reservoir* while perch and roach persisted.

Mean body weight of perch in qualitative multi-gill nettings increased from 165 g ind.[-1] in 1986 up to 300–400 g ind.[-1], with maxima of 1,390 g ind.[-1] after the beginning of the 1990s. At the same time, the proportion of stocked piscivorous lake-trout (*Salmo trutta lacustris*) and pikeperch (*Sander lucioperca*) in the biomass of multi-gill nettings, increased markedly to 40–50%. Gut-analyses of piscivores mainly revealed perch <10 cm.

In general, anglers catch rates of piscivores did not reflect the proportion of piscivores in the

standing stock (Table 3). Not least the harvest rates of piscivores by anglers appear so high that the build-up of piscivore biomass was prevented through stocking. In spite of the restrictions imposed on them, the anglers removed large proportions of the standing stock of piscivores (i.e. 1.3 ind. ha^{-1} of pikeperch >50 cm in Wupper Reservoir) in the face of a standing stock of only 2.2 ind. ha^{-1} >34 cm in August 2003. However, they only took 7 ind. ha^{-1} of piscivorous perch >16 cm, less than 10% of the stock. In Pre-Reservoir Grosse Dhünn 0.3 ind. ha^{-1} and 0.5 ind. ha^{-1}, of lake-trout and pikeperch, respectively, were caught, with quantitative estimations in August 2000 revealing a standing stock of 0.8 ind. ha^{-1}, and 1.5 ind. ha^{-1}, respectively.

Responses of zooplankton, phytoplankton, nutrients and transparency

Due to an intense ''trophic upsurge'' resulting from the sudden decay of the inundated vegetation, phosphorus concentrations in the newly refilled *Brucher Reservoir* peaked in summer 1993 (Table 4). That year, DOC concentrations reached 4–6 mg l^{-1} as lake water became brown-coloured, adversely affecting transparency. Population densities of *Daphnia galeata* in the fishless reservoir remained high throughout the summers with maxima of 37 ind. l^{-1}. In combination with the operation of an artificial mixing system any algal blooms were prevented (Scharf, 2002).

After 1994, as the decay of the inundated vegetation was finished transparency increased coinciding with the reduction in DOC-concentrations to 2 mg l^{-1}. Although *Daphnia galeata* population densities, as well as the proportion of large daphnids >780 μm, declined in 1994 with the implementation of a trout-minnow system (Table 2) it retained its key position in the zooplankton community. In April 1996, even at 7.5°C mean epilimnetic temperature, *Daphnia galeata* reached peak densities of 7.2 ind. l^{-1}, in conjunction with an early spring ''clear water phase'' (c.w.p.) of up to 10 m. Consequently, fishery management was successful in maintaining a low level of zooplanktivory. Nonetheless, as inedible chrysophytes, and occasionally *Sphaerocystis*, developed after 1994 the summer chlorophyll/

particulate phosphorus (CHL/PP) ratios increased from 0.1 in 1993 to 0.6, with maxima of 1.3 in 1995–1997 (KW, $P < 0.0001$) although summer mean chlorophyll concentrations remained unchanged as phosphorus-concentrations were reduced (Table 4).

After sewage diversion reduced the external phosphorus load of *Lingese Reservoir* in 1993, TP-mixing-concentrations responded promptly in winter 1993 (Table 4). As with the development of motile algae (*Cryptomonas ovata*, *C. reflexa*, *C. tetrapyrenoida*) in May, along with small, often single-celled, chlorococcales (*Scenedesmus*, *Tetraedron*, *Coelastrum*), not only summer pelagic chlorophyll-concentrations but also TP concentrations commenced increasing, there was only slight P retention during summer in the pre-restoration period (1988–1992), becoming distinctly negative in the transition period (1993–1995). However, chlorophyll-concentrations decreased markedly and transparency (Fig. 2, Table 4) doubled from 0.7 m to 1.4 m (W, $P < 0.0001$) in the face of a similar summer phytoplankton community composition (Scharf, 1999). *Bosmina*, *Cyclops* and rotifers dominated the zooplankton community, and occasionally densities peaked in the pre-restoration period 1988–1992 (i.e. *Bosmina* with 770 ind. l^{-1} in July 1990). In 1993–1995, summer zooplankton biomass dropped from 330 μg C l^{-1} in the pre-restoration period to 85 μg C l^{-1} (W, $P < 0.0001$). However, although smaller daphnids (*Daphnia parvula*, *Daphnia cucullata*) became increasingly prominent in the transition period, they only reached low population densities of 2–6 ind. l^{-1} as the hypolimnion was still devoid of any oxygen. No c.w.p. occurred until 1995. Consequently, reducing external P-load in combination with changed stocking practices in 1991, was not sufficient to improve ecosystem structure and water quality (Tables 3, 4).

Neither external phosphorus load nor TP mixing concentrations changed significantly (W, $P = 0.36$) during the refilling period. In contrast to previous years, summer TP concentrations were reduced with the onset of the c.w.p. in June enhancing P-retention (Table 4). This coincided with a *Daphnia galeata* peak which may have prevented the formerly summer developments of

**Table 4** Summary of diagnosis variables of biomanipulation

Reservoir	Year period	TP$_{Mix}$ (µg l^{-1})	TP$_{Strat}$ (µg l^{-1})	R$_{Int}$	CHL$_{Strat}$ (µg l^{-1})	SD (m)	D gal (ind. l^{-1})
Lingese	1988–1992	136	130	–0.05	137.0	0.7	0.0
	1993–1995	49	58	+0.16	24.6	1.4	0.2
	1999–2003	44	25	–0.76	6.1	4.0	15.0
Brucher	1993	16	78	+0.8	3.0	2.0	16.6
	1995–1997	12	9	–0.33	3.2	6.3	5.2
Pre-Reservoir Grosse Dhünn	1995–1998	16	9	–0.78	3.7	4.9	0.5
	1999–2002	16	9	–0.78	3.8	6.0	1.1
Wupper	1993–1998	34	24	–0.41	9.5	3.2	0.4
	1999–2005	33	17	–0.94	6.6	5.2	5.1
Bever	1991–1998	13	13	0.00	6.5	4.0	0.0
	2000–2005	11	12	+0.10	6.3	5.2	1.5
Grosse Dhünn	1989	7	6	–0.17	1.5	6.3	3.9
	1997	6	6	0.00	3.3	3.5	0.3
	2003	9	8	–0.12	2.3	6.7	1.4

Median of Total Phosphorus (TP$_{Mix}$, TP$_{Strat}$) and chlorophyll concentrations (CHL$_{Strat}$) during winter/spring mixing and summer stratification (May to September, Bever May to November) in the trophogenic layer along with summer Secchi depth (SD), population density of *Daphnia galeata* and internal P-balance (R$_{Internal}$ = 1 – TP$_{Mix}$/TP$_{Strat}$)

cryptomonads. However, ungrazable summer algae (*Ceratium*, *Peridinium*, *Dinobryon* and *Sphaerocystis*) commenced developing. At the same time, the small, light-scattering and never sedimenting, PP < 30 µm fraction declined (Fig. 3). Phosphorus accumulated in the *Daphnia*-P pool, giving rise to the repartitioning of phosphorus between seston particles of different sizes, and presumably residence time in the pelagic zone. Calculating the P-concentration accumulated in the *Daphnia galeata* population

from density estimations revealed that it accumulated 8.1 µg P l^{-1} (=50%) of the pelagic summer PP pool in 1999, but only 0.2 µg P l^{-1} (<0.1%) in the year 1995 (Fig. 3). Concomitantly, PP < 30 µm concentrations dropped from 23.8 µg l^{-1} (=70%) of the median summer PP pool in 1995 to 4.4 µg l^{-1} (=30%). Since 1999, clear water conditions (SD > 4 m) coincided with low summer TP concentrations of 23.0 µg l^{-1} in contrast to 29.5 µg l^{-1} (W, P < 0.0001) at SD < 4 m. Therefore, as transparency increased

Fig. 2 Sewage diversion in December 1992 (arrow) resulted in only a slight increase in transparency (SD; median, maximum) in Lingese Reservoir. Commencing with sediment treatment and implementation of a new fish stock, larger daphnids (*Daphnia galeata* > 780 µm) appeared and transparency improved during the refilling period after 1999
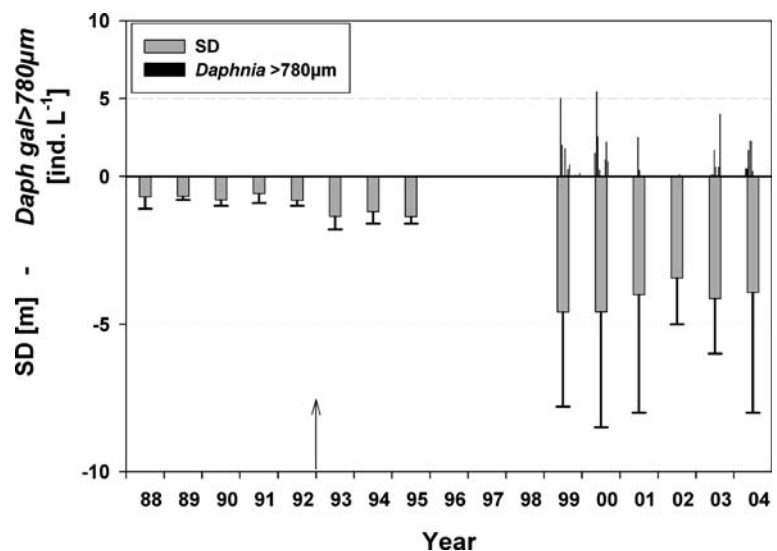
significantly (W, $P < 0.0001$) summer TP concentrations and also chlorophyll-concentrations declined. Although zooplankton biomass in relation to the transition period 1993–1995 remained unchanged at 90 μg C l^{-1}, the larger *Daphnia galeata* since 1999 occupies a key position in the food web which, until 2004, was only altered in 2001 when the daphnid fraction >780 μm disappeared (Fig. 2) as there was a mass development of sticklebacks (*Gasterosteus aculeatus*). *Ceriodaphnia*, *Diaphanosoma* and *Eudiaptomus* densities have also increased since refilling, while *Daphnia parvula* has vanished. In conclusion, zooplanktivory clearly decreased after refilling.

In *Wupper Reservoir* an unchanged external phosphorus load of 3 g P m^{-2} a^{-1} resulted in winter mixing concentrations of 34 μg P l^{-1} after 1992. With settlement of the spring diatom bloom TP concentrations declined. Following a c.w.p. epilimnetic summer phytoplankton (*Sphaerocystis*, *Oocysts*, *Coelastrum*, *Staurastrum*; cryptomonads) developed. In 1999 the larger *Daphnia galeata* suddenly became prominent and c.w.p. became more pronounced while *Daphnia cucullata* declined. Thus, zooplanktivory declined as cyprinid catch rates increased (Fig. 1a). Comparison between the *Daphnia cucullata* years (1993–1998) and the *Daphnia galeata* years (1999–2005) showed that *Daphnia* increased its median share of the summer TP pool as calculated *Daphnia*-P concentrations increased from 0.2 mg P l^{-1} in 1993–1998 to 2.2 mg P l^{-1} in 1999–2005 (Fig. 4).

Concomitantly, the PP < 30 μm fraction of the *Daphnia cucullata*-summer of 1995 did not fall below 5.0 μg l^{-1} (approximately 0.3 mg C l^{-1}), reaching 2.5 μg l^{-1} (approximately 0.15 mg C l^{-1}) in the *Daphnia galeata*-summer of 2002, while transparency increased (W, $P < 0.0001$). In contrast to the previous year's summer, TP concentrations remained low (W, $P < 0.0001$) and chlorophyll-concentrations declined (W, $P = 0.0425$) while CHL/PP ratios of 0.62 and 0.63, respectively, remained unchanged (Tables 4, 5). After 1998, algae increasingly built up populations in the metalimnion (*Planktothrix*; *Tabellaria*; *Dinobryon*).

With the appearance of larger *Daphnia galeata*, the c.w.p. started as early as mid-May (Fig. 5). As an inter-annual comparison revealed, timing of the c.w.p. can hardly be related only to temperature effects.

Bever Reservoir's unchanged external phosphorus load of 0.5 g P m^{-2} a^{-1} resulted in winter mixing concentrations (December to April) of 12 μg P l^{-1}. In contrast to most other reservoirs there was no marked decrease in the pelagic TP concentrations with the onset of thermal stratification (Table 4). As in Wupper Reservoir, small zooplankton species (*Eubosmina*, *Bosmina*, *Cyclops*, rotifers) peaked in 1991. Since 1992, *Ceriodaphnia*, with up to 7 ind. l^{-1}, and *Daphnia cucullata* with up to 12 ind. l^{-1}, have been the main filter feeders, although catch rates of cyprinids did not respond to the changed stocking

Fig. 3 With refilling of the Lingese Reservoir in 1999 there was a repartitioning of phosphorus between seston particles (TP$_{Mix}$ Total Phosphorus during winter/spring mixing; TP$_{Strat}$ Total Phosphorus-, PP Particulate Phosphorus seston fraction < 30 μm and *Daphnia*-phosphorus concentrations) during summer stratification (May–September 1995 and 1999)
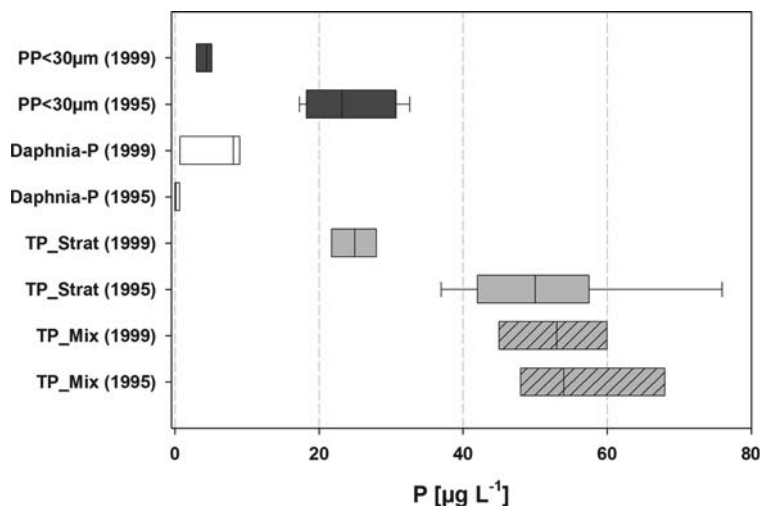
practice that year. In 1998, *Daphnia galeata* appeared unexpectedly in low numbers (up to 1 ind. l^{-1}), while in summer 2000 its population density increased to 13 ind. l^{-1} (Fig. 6) and the large fraction >780 µm appeared. Concomitantly, *Eudiaptomus* increased its density in summer from <1 ind. l^{-1} up to 8–12 ind. l^{-1} while *Ceriodaphnia* disappeared. Hence, there was a shift in zooplankton community size structure, as well as biomass, in 2000 (or 1999 as in Wupper Reservoir and Pre Reservoir Grosse Dhünn) indicating a decrease in zooplanktivory (Tables 4, 5). This was delayed until the distinct decline of roach and bream catch rates after 1993. Although vendace would be an ideal prey for stocked lake-trout (*Salmo trutta lacustris*) and pikeperch the stock density of vendace was still high (Table 3) when the zooplankton community structure shifted. However, vendace were efficient zooplanktivores but did not always strongly select for larger daphnids as evidenced from gut contents. The shift in the zooplankton community structure was accompanied by an increase in median summer *Daphnia*-P from 0.04 µg P l^{-1} (1997) to 1.2 µg P l^{-1} (2001) as the concentration of the PP < 30 µm fraction declined from 4.9 to 3.5 µg PP l^{-1}. The appearance of larger daphnids resulted in stable summer total chlorophyll- (W, $P = 0.205$) and TP concentrations (Tables 4, 5). However, transparency did increase (W, $P < 0.0001$) although the timing of the SD

maximum in June/July was late in contrast to Wupper Reservoir and Pre-Reservoir Grosse Dhünn. While *Planktothrix* only reached low biomass levels of 0.2–0.3 mg l^{-1} fresh weight (f.w.) in winter, it has started increasing its biomass gradually since 1997 and peaked, with up to 3 mg l^{-1} f.w., in the trophogenic layer during summer 2001, accumulating in the upper hypolimnion.

In *Pre-Reservoir Grosse Dhünn*, where the water level did not fluctuate, unchanged external phosphorus loadings of 0.9 g P m^{-2} a^{-1} resulted in mixing concentrations of 16 µg P l^{-1}. With settlement of the diatom spring bloom TP concentrations dropped and low levels of ungrazable summer phytoplankton (chrysophytes; chlorophytes; *Ceratium*, *Cyclotella*, *Aphanothece*) tended to develop predominantly in the metalimnion. As *Daphnia cucullata* was missing from this reservoir the larger *Daphnia galeata* only responded with slightly increased body lengths, as became apparent from the sudden appearance of the size fraction >780 µm in 1999 (Tables 4, 5). With the appearance of larger daphnids not only did the transparency increase (W, $P = 0.0003$) but the summer seston fraction <30 µm declined from 6.5 µg l^{-1} (0.39 mg C l^{-1}) to 3.0 µg l^{-1} (0.24 mg C l^{-1}) in 1999–2002 (W, $P < 0.0001$). If daphnids sequestered 3 µg PP l^{-1} from the small light-scattering fraction <30 µm, this would allow increased densities of about 8–12 ind. l^{-1}. The

Fig. 4 Increasing calculated *Daphnia*-P-concentrations (median, maximum) coincided with a decline of summer-TP-concentrations (median, 75-percentile) in Wupper Reservoir as water transparency (SD; median, maximum) increased
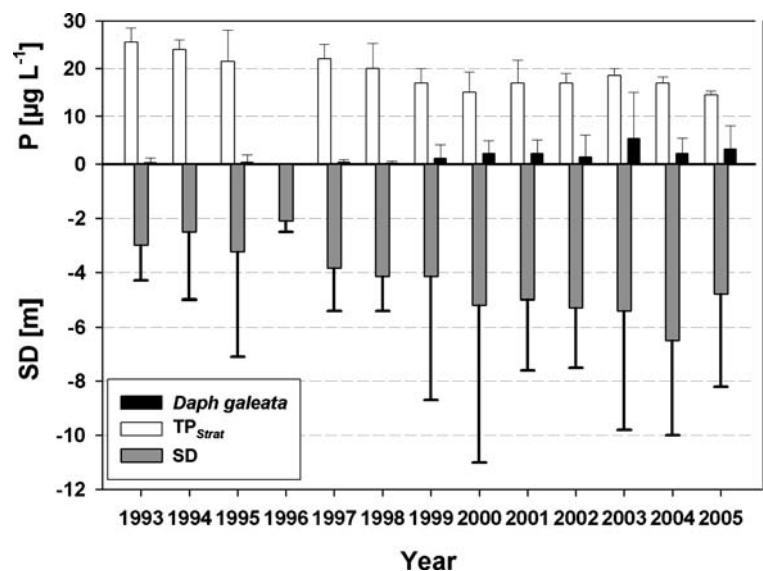
Fig. 5 With the appearance of larger *Daphnia galeata–hyalina* in Wupper Reservoir in 1999, daphnid population density maxima, as well as Sechi-depth maxima (SD), occurred as early as May. There was no "clear water phase" (c.w.p.) in 1996. Mean epilimnetic (0–5 m) water temperature at the end of April
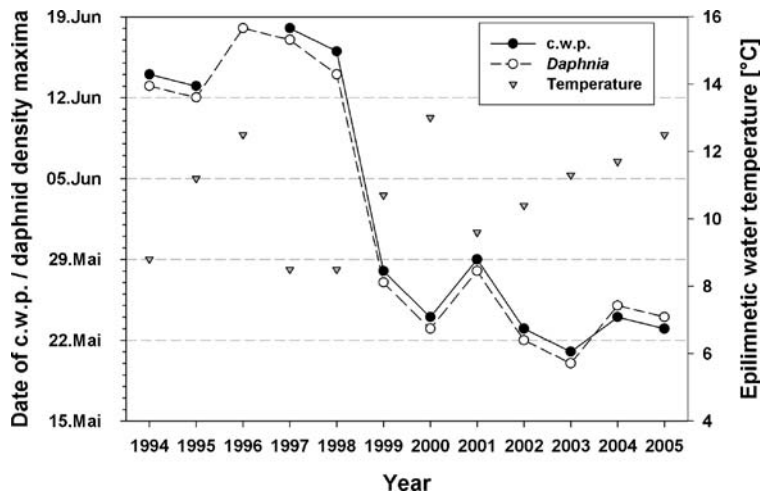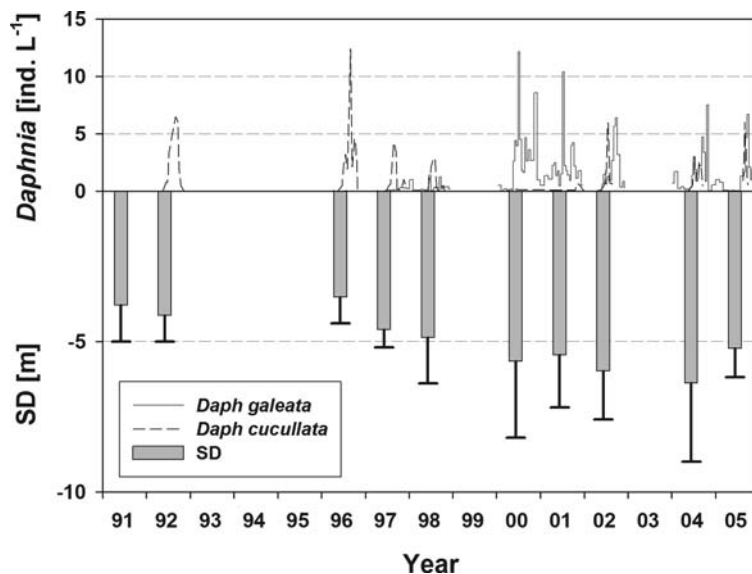

Fig. 6 Commencing in 2000 Sechi-depths (SD; median, maximum) increased as the larger *Daphnia galeata–hyalina* replaced the smaller *Daphnia cucullata* in Bever Reservoir

daphnid population density never peaked to 4–6 ind. l^{-1} before mid-June during 1995–1997, coinciding with the SD maximum; but in later years the daphnids had already peaked by mid-May with 10–18 ind. l^{-1}, as early as in Wupper Reservoir (Fig. 5), resulting in a pronounced c.w.p. lasting until late summer. With the onset of the c.w.p. already in May, lake-P concentrations (W, $P = 0.018$) and chlorophyll-concentrations (W, $P = 0.027$) declined earlier to low levels of 9 μg P l^{-1}. However, summer mean concentrations remained unaffected. As in Wupper Reservoir the earlier timing of the c.w.p. (already in May since 1999), which coincided with an earlier

occurrence and increased biomass of the *Daphnia* spring peak, can be related hardly to increased epilimnetic winter water temperatures or to the standardized North Atlantic Oscillation (NAO) index which was, for example, +1.5 with 12.1°C mean epilimnetic (0–5 m) water temperature on 4th May 1995, when timing was late and –0.2 with 8.5°C on 28th April 2001 with early timing.

An unchanged external P load of 0.15 g m^{-2} a^{-1} resulted in overturn concentrations of 5–8 μg P l^{-1} in *Grosse Dhünn Reservoir*. As became evident from the dominance of *Daphnia galeata*, zooplanktivory never restricted the development of larger daphnids in this reservoir (Tables 4, 5).

Table 5 Summary of results from Biomanipulation in order of total phosphorus concentration during winter/ spring mixing (TP$_{Mix}$): large sized *Daphnia*> 780 μm indicating a low level of zooplanktivory could be maintained in the newly filled/refilled reservoirs or implemented in Bever-, Wupper Reservoir, Pre Reservoir Grosse Dhünn

Reservoir	Manipulation period	TP$_{Mix}$	Predatory stocking	Planktivorous stock	*Daphnia* >780 μm	ZOO	CHL	TP$_{Strat}$	SD
Grosse Dhünn	1989–2005	7	Lake-trout, Pikeperch	Roach, (Perch)	✓	0	0	0	0
Brucher	1994–1998[a]	12	Brown-trout, Rainbow-trout	Minnows, Sun-bleak	✓	0	0	– –[b]	++[b]
Bever	1992–2005	13	Pikeperch, Northern Pike Lake-trout[c]	Vendace, Roach, Bream, (Perch)	✓ (2000)	++	0	0	+
PreResGrosse Dhünn	1990–2005	16	Lake-trout, Pikeperch	Roach, (Perch)	✓ (1999)	+	0	0	+
Wupper	1988–2005	33	Pikeperch, Northern Pike	Roach, Bream, (Perch)	✓ (1999)	++	–	–	++
Lingese	2000–2005[d]	46	Pikeperch, Northern Pike, Rainbow-trout	Roach, Bream, (Perch)	✓	++	– –[e]	– –[e]	++

0 = no change, + increase, – decrease of Zooplankton community size structure (ZOO), Chlorophyll concentration (CHL), total phosphorus concentration during stratification (TPStrat) and summer Sechi depth (SD) in relation to pre-biomanipulation conditions

[a] Added into a fishless reservoir refilled in 1993

[b] Due to the stop of decay of inundated vegetation when refilled in 1993

[c] Since 1999

[d] In relation to 1993–1995

[e] In combination with sediment treatment

Accordingly, the zooplankton did not respond to the successful enhancement of piscivores through stocking as revealed from gill-nettings. However, as the reservoir became more severely phosphorus-limited (Scharf, 1998) at the end of the 1980s *Daphnia galeata* population densities declined, although it still reached a population density maximum of 26 ind. l^{-1} in 1986, whereas it reached only maxima of 5–7 ind. l^{-1} in later years. In those years with low food quality, when *Aphanothece* developed (Table 4: 1997), *Daphnia galeata* nearly vanished, being replaced by *Bosmina* and *Cyclops*. Transparency, which might have been affected by the water filling level in the reservoir and the occurrence of *Daphnia galeata*, revealed no trend in the monitoring period. As *Daphnia cucullata* was missing from this reservoir *Eudiaptomus* attained maxima of only 8–12 ind. l^{-1}.

Comparative analysis

A comparative analysis of the state of the variables spring-TP, as a surrogate for P input, and zooplankton mean body length, as an indicator of zooplanktivory, revealed both nutrient ($r^2 = 0.66$, $P < 0.0001$) and predation effects ($r^2 = 0.40$, $P = 0.0013$) to be related significantly to summer mean chlorophyll concentrations in the reservoirs (Fig. 7a, b). Consequently, a multiple regression predicting summer mean chlorophyll concentrations from both "bottom up" and "top down" forces was highly significant ($r^2 = 0.84$, $P < 0.0001$). However, summer mean chlorophyll in the reservoirs was best predicted from summer mean TP concentrations (Fig. 7c; $r^2 = 0.89$, $P < 0.0001$). Only in two reservoirs—the highly eutrophic Lingese Reservoir in the pre-restoration period governed by small sized zooplankton (*Bosmina*, *Cyclops*, rotifers), and the newly refilled fishless Brucher Reservoir with a predominance of larger daphnids in 1993—did predictions deviate significantly from the regression line (Fig. 7).

In general, these results provide an indication that larger *Daphnia galeata* exploits food resources at low levels reducing PP < 30 μm concentrations to a residual level of about 3 μg

PP < 30 μm l^{-1}. Accordingly, daphnids which can sequester 1 μg P l^{-1}, as in Grosse Dhünn Reservoir, have the possibility to build up densities of 3–4 ind. l^{-1} which corresponds roughly to the observed density maxima. Thus, above a critical TP concentration of >5 μg P l^{-1}, as in Grosse Dhünn Reservoir, food-levels allow the existence of larger daphnids only in small densities. Medium-bodied *Daphnia cucullata* were not collected from the oligotrophic Grosse Dhünn Reservoir but became prominent in meso- to eutrophic reservoirs at high levels of zooplanktivory by exploiting the PP < 30 μm fraction to residual levels of 5 μg PP < 30 μm l^{-1}. With the appearance of larger daphnids the PP < 30 μm seston-fraction was reduced to 2.5–3.0 μg l^{-1} allowing higher daphnid spring biomass peaks

and increased transparency. Although the zooplankton response to changed fishery management was delayed, a shift to larger *Daphnia galeata*, indicating a low level of zooplanktivory, can be induced only in meso- and eutrophic reservoirs (Fig. 8). Seasonally, the lowering of zooplanktivory not only resulted in a shift to larger *Daphnia galeata* but, due to lower residual PP < 30 μm levels, also in greater biomass and earlier timing of the daphnid spring peak causing prolonged clear water conditions. As in mesotrophic reservoirs (e.g. Bever Reservoir and Pre-Reservoir Grosse Dhünn), transparency increased only in the slightly eutrophic reservoirs (e.g. Wupper and Lingese Reservoirs), where summer mean total chlorophyll-concentrations declined in combination with a decrease in TP
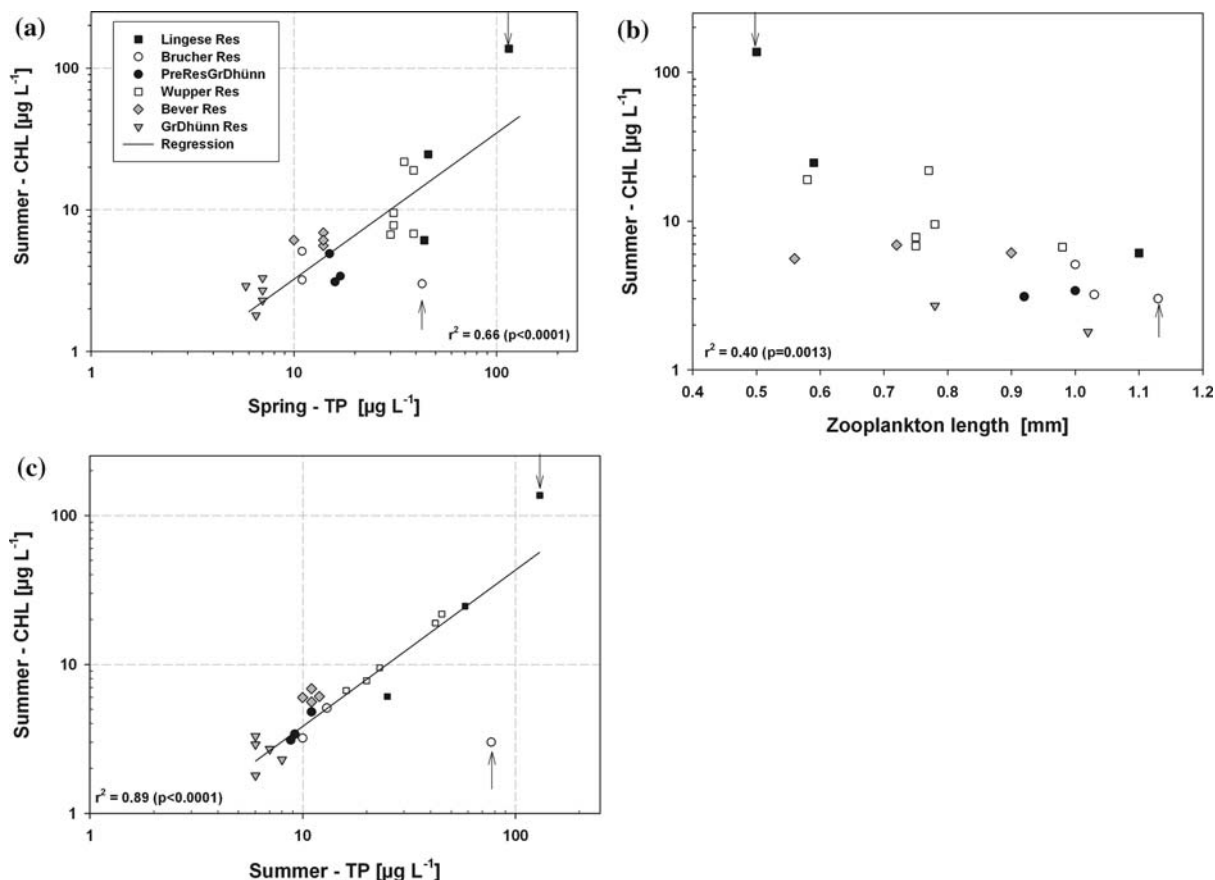

Fig. 7 Scatterplots relating photic zone summer mean total chlorophyll concentrations to (**a**) spring total-phosphorus concentrations and (**b**) mean zooplankton body length, are highly significant. However, chlorophyll concentrations are best predicted from summer mean total-

phosphorus concentrations (**c**). Each point represents the mean of 1–4 summer seasons. Arrows highlight the highly eutrophic Lingese Reservoir without daphnids (1988–1992) and the newly refilled, fishless Brucher Reservoir (1993) with a predominance of larger daphnids

concentrations following unchanged winter mixing concentrations (Tables 4, 5). Consequently, the effectiveness of biomanipulation approached a maximum in these slightly eutrophic reservoirs (Fig. 8).

Discussion

There is no doubt that with the implementation of a fishery management strategy using the principles of biomanipulation in combination with nutrient reduction the recreational value of the reservoirs could be improved not only for anglers, but also for other users who appreciate improved water clarity. Although ''biomanipulation'' through repeated stocking of piscivores in combination with size and bag limits for recreational fisheries may have limited success in deep stratifying reservoirs (Hansson et al., 1998; Drenner & Hambright, 1999), in three (Bever, Wupper, and Pre-Reservoir Grosse Dhünn) out of the six reservoirs considered here, zooplanktivory was reduced by implementing this management practice, as indicated by the appearance of larger

daphnids (Brooks & Dodson, 1965). In the other three newly filled (Grosse Dhünn) and refilled reservoirs (Brucher and Lingese) this management practice ensured the establishment of a low level of zooplanktivory as evidenced by the continued presence of larger daphnids. This long-term success in the reservoirs of the Wupper catchment (Table 5) contrasts with results from Czech Reservoirs (Seda & Kubecka, 1997, Seda et al., 2000). In Rimov Reservoir, for example, although the body sizes of daphnids increased none of the existing daphnid species was replaced (Seda & Kubecka, 1997), as in Bever or Wupper Reservoir.

This study demonstrates that the build-up of piscivorous fish biomass only by stocking, except of Grosse Dhünn Reservoir where angling was prohibited, was prevented not least by the sport fishery in spite of its restrictions (Lathrop et al., 2002). As Seda & Kubecka (1997) pointed out, in Rimov Reservoir extensive stocking did not enhance the level of piscivorous fish due to high mortality of the stocked individuals. In Pre Reservoir Grosse Dhünn, for example, the failure to enhance biomass by stocking smaller trout in

Fig. 8 The effectiveness of biomanipulation approached a maximum in the slightly eutrophic, deep, stratifying reservoirs. While BEThP (=Biomanipulation efficiency threshold of Phosphorus) sets an upper threshold TP$_{Mix}$-concentrations of 8–10 µg l^{-1} set a lower threshold (arrow) for successful biomanipulation
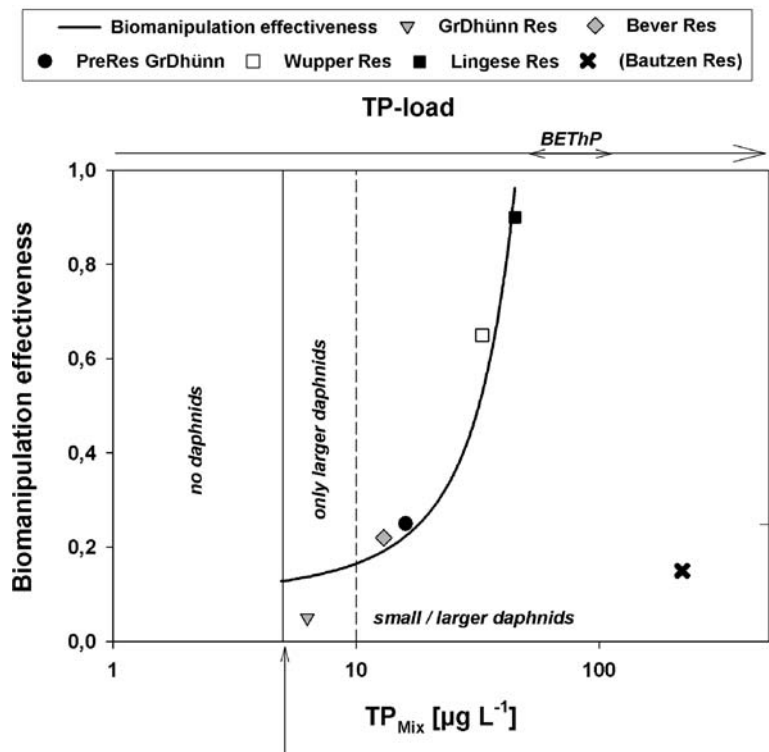
the mid 1990s presumably was due to cormorant predation whereas stocking larger trout in Lingese Reservoir resulted in distinctly increasing catch rates. Nevertheless, as indicated by the shift in zooplankton community structure (Brooks & Dodson, 1965; Spaak & Hoekstra, 1997) zooplanktivory could be decreased by the implementation of a predator management, even without increasing the number and biomass of piscivores directly by stocking. It is expected that direct (lethal) interactions between piscivores and planktivores would cause decreasing numbers of planktivores, with a shift toward larger, invulnerable, often benthivorous specimens. In contrast to these predictions there was often a shift towards smaller cyprinid specimens in anglers' catches as in Pre Reservoir Grosse Dhünn after implementation of a changed stocking practice and in Wupper Reservoir cyprinid catch rates even increased. The decline of larger roach might, in turn, result in reduced fecundity of the population and declining population densities in the long-term. However, as seems likely from the fishing records, in both Pre-Reservoir Grosse Dhünn as well as Wupper Reservoir, the perch concomitantly benefited from growth and size structuring processes promoting "gigantic piscivorous perch which drive the trophic cascade" (Persson et al., 2003) took place in the cannibalistic perch populations. Obviously, this might be the driving force for the whole-lake trophic cascade in Bever and Wupper Reservoirs, and Pre-Reservoir Grosse Dhünn. The failure of successful biomanipulation (e.g. in Lingese Reservoir before 1999), might be attributable to an inability to drive the internal dynamics of the fish population, resulting in a strong piscivorous perch population. I therefore conclude that the presence of a strong well-conditioned perch population, together with roach, under slightly eutrophic conditions as in Wupper Reservoir is generated by successful biomanipulation (Persson et al., 1991; Kubecka, 1993). Indeed, I argue that the build-up of a size structured pikeperch population is a prerequisite for the successful biomanipulation of deep stratifying reservoirs (Braband & Faafeng, 1994; Hölker et al., 2002) which needs the combination of an adequate stocking programme, as in Wupper Reservoir and restrictions to anglers. None-

theless, anglers benefited from this measures not only due to the introduction of new target species (*Sander lucioperca*, *Salmo trutta lacustris*), but also by the increased growth of perch which is a target species not only for biomanipulation but also for recreational fishing. Thus, even if stocking was unable to distinctly increase the predator biomass, as in Grosse Dhünn Reservoir, the biomanipulation induced internal dynamics of the fish stock which promote piscivorous perch trigger positive indirect effects which appear to provide a behaviourally induced "refuge" for daphnids, due to a behavioural response of vulnerable planktivorous fish which eliminates them from the open water habitat (Braband & Faafeng, 1994; Hölker et al., 2002; Romare & Hansson, 2003). Even in Brucher Reservoir, as evidenced from visual observations, it is likely that intense trout predation forced minnows to remain in the littoral macrophytes refuge, which in turn provides a behaviourally induced open water refuge for larger daphnids.

In contrast to Hansson's (1998) recommendations, this biomanipulation was not as intense, and it took about 8–10 years before a decrease in zooplanktivory. In Wupper Reservoir where a predator management was implemented with first filling in 1989, the zooplankton community response was unexpectedly delayed until after 1999 in the face of increasing planktivorous cyprinid catch rates. Although catch rates of roach, dropped rapidly due to the changed stocking practice at the beginning of the 1990s in Pre-Reservoir Grosse Dhünn and Bever Reservoir, the zooplankton community response was delayed until the end of the 1990s. Such a delayed recovery of the predator-resistant zooplankton community is also apparent from the experimental studies of Koenings & Kyle (1997). The unexpected and delayed response of the zooplankton community structure to changes in the fish assemblage, giving rise to a "switch" from smaller daphnids to the larger daphnids of the *Daphnia galeata–hyalina* complex, corroborates the *size-efficiency* hypothesis (Brooks & Dodson, 1965). Because fish not only select larger species but, within each species, select the larger specimens (Mookerji et al., 1998) or hybrids (Spaak & Hoekstra, 1997), even the appearance of larger

daphnids only in the 780 µm net without any switch from medium sized *Daphnia cucullata* to larger sized *Daphnia galeata* as in Pre-Reservoir Grosse Dhünn, might be attributable to decreased zooplanktivory. As further predicted from the *size-efficiency* hypothesis (Brooks & Dodson, 1965) larger daphnids exploiting food resources at low levels did not allow medium-bodied individuals to exist longer (Gliwicz, 1990; Spaak & Hoekstra, 1997). Consequently, as the seston-fraction <30 µm was never above the estimated critical level of 5 µg PP l^{-1}, medium sized *Daphnia cucullata* did not occur in the oligotrophic Grosse Dhünn Reservoir, whereas in those reservoirs where a ''switch'' to larger daphnids did occur the concentrations of the never sedimenting and light-scattering seston fraction <30 µm, often declined to 2.5–3.0 µg PP l^{-1} resulting in increased transparency and the suppression of medium sized *Daphnia cucullata*. Thus, it is likely that edible algal and seston concentrations are controlled directly by ''top down'' forces. However, a decrease in summer mean total chlorophyll concentrations in the trophogenic layer, as predicted from the *trophic cascade* hypotheses (Carpenter et al., 1985), could only be achieved in the slightly eutrophic reservoirs. This decrease in trophogenic summer mean total chlorophyll concentrations always coincided with declining total phosphorus concentrations in summer, following unchanged total phosphorus concentrations in winter and spring. Thus, total chlorophyll-concentrations are controlled ''bottom up'', admittedly triggered by ''top down'' forces due to a biomanipulation-induced decline in phosphorus-concentrations. Due to low lake-phosphorus and chlorophyll concentrations in Pre-Reservoir Grosse Dhünn summer mean concentrations remained unaffected although lake phosphorus concentrations had already dropped to low summer levels in May since the earlier spring biomass peaking of larger daphnids. Furthermore, neither the failure to prevent an increase of summer mean P–CHL relationships (Drenner & Hambright, 2002) in Brucher Reservoir in the face of larger daphnids, nor the development of ungrazable often intense metalimnetic algal developments, support predictions from the *trophic cascade* hypotheses (Car-

penter et al., 1985). In conclusion, reduced P availability due to a shift in food-web structure, giving rise for the repartitioning of phosphorus between seston particles of different sizes and residence times in the pelagic zone, increased vertical phosphorus flux (Mazumder et al., 1992; Houser et al., 2000) in the slightly eutrophic reservoirs, as predicted from the BEThP (Benndorf, 1987, Benndorf et al., 2002) causing oligotrophication in the reservoir. However, increased transparency and vertical phosphorus flux favoured metalimnetic algal developments (Pilati & Wutsbaugh, 2003), in Bever and Wupper Reservoirs, which highlights problems with theories of nutrient resource limitation alone (Reynolds, 1994). Although the improvement in food-web structure of Lingese Reservoir after refilling concurred with reduced internal phosphorus loading, due to the sediment treatment, it undoubtedly generated an internal oligotrophication process mostly due to an increased P-sedimentation rate with declining densities of motile cryptomonads and concentrations of the never-settling seston particles<30 µm (Mazumder et al., 1992). Thus, water transparency increased and reduced P-availability, owing to a negative phosphorus mass balance (Benndorf et al., 2002), resulted in declining algal developments. Reduced P-translocation resulting from cyprinid reduction (Braband et al., 1990) might have been of minor importance for the P-balance in Lingese Reservoir as cyprinids mostly fed on zooplankton.

Summer mean total chlorophyll concentration in the reservoirs could be predicted very well from both ''bottom up'' and ''top down'' forces (Carpenter et al., 1985), however it was best predicted from mean summer TP concentrations which are closely related to winter mixing concentrations and subsequent phosphorus downward flux. Two situations, in Brucher (1993) and Lingese Reservoir (1988–1992), presumably supported by the microbial food web, deviate significantly from the regression line (Fig. 8). In the case of the fishless Brucher Reservoir, it is reasonable to assume that direct ''top down'' effects due to the inundated decaying vegetation (Scharf, 2002), which fuelled the microbial food web, offered an alternative and persistent resource base for larger daphnids

during summer, suppressing any algal growth (Reynolds, 1994).

If the biomanipulation-induced reduction of P availability is a prerequisite for a successful lowering of the chlorophyll-concentrations, then the phosphorus load undoubtedly sets boundaries with respect to achieving a negative phosphorus balance (Benndorf et al., 2002). Benndorf et al. (1988) found that neither lake phosphorus concentrations nor chlorophyll concentrations decreased in the highly eutrophic Bautzen Reservoir when zooplanktivory was lowered, giving rise to the appearance of larger daphnids. This suggests that at higher phosphorus concentrations the effectiveness of biomanipulation is very low. Bever Reservoir and Pre-Reservoir Grosse Dhünn, which are oligotrophic/mesotrophic, only experienced a reduced biogenic turbidity that improved their aesthetic value for recreational users, because productivity cannot be decreased further to a measurable extent by a biomanipulation-induced reduction of P availability (Benndorf et al., 2002). Consequently, this study not only supports the view that there must be an upper boundary to the P load for successful biomanipulation but also that there is a lower boundary within the range of 8–10 µg P l^{-1}. The lower boundary occurs where the system becomes sufficiently productive to support either larger-bodied *Daphnia galeata* or medium-bodied *Daphnia cucullata*, giving rise to the opportunity to induce a shift in the zooplankton community size structure by lowering zooplanktivory.

In conclusion, there appears to be a lower phosphorus threshold for biomanipulation and biomanipulation efficiency approaches a maximum in slightly eutrophic reservoirs as long as the internal phosphorus balance can be improved (Benndorf, 1987). Furthermore, the delayed and non-linear response of the reservoirs in this study, to the changed fishery management practice supports the idea that a change of internal feedbacks not driven by external forces, acts to stabilize the lake's trophic state by a regime shift, not only in shallow lakes (Scheffer, 2001) but also in deep lakes (Carpenter & Cottingham, 1997), such as Wupper and Lingese Reservoirs. If this holds true, for example in slightly eutrophic Wupper Reservoir, there might be no need for

continued intense predator stocking or only the need for a fishery management strategy without cyprinid (roach, bream) stocking and adequate restrictions to anglers' to protect the self reproducing predator population (pike, percids) to sustain improved conditions.

There was a strikingly coherent response among the reservoirs in the delayed shift of zooplankton community size structure occurring in the late 1990s. As already noticed by Lathrop et al., 2002, in Pre-Reservoir Grosse Dhünn and Wupper Reservoir also with the appearance of larger daphnids, *Daphnia* biomass increased earlier in spring, reached greater densities, and lasted longer resulting in an earlier timing and more prolonged c.w.p.. An increasing body of evidence suggests that effects of climate change, measured by the North Atlantic Oscillation (NAO), on winter and spring water temperatures tend to result in higher *Daphnia* growth rates and spring biomass, leading to the earlier occurrence of the c.w.p. (Straile et al., 2003). However, this results do not provide any evidence that the earlier timing of c.w.p. can be related to an increase in epilimnetic winter and spring temperature, nor is it possible to relate the shift in timing in both reservoirs to the standardized seasonal mean winter NAO index. Furthermore, in Bever- and Lingese Reservoir *Daphnia* biomass spring peak and c.w.p. remained late whereas in Brucher Reservoir it already occurred in April at low temperatures. Therefore, this suggests that the observed patterns can be explained by a change in management practice and are not directly attributable to climate change (Van Donk et al., 2003).

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