Freshwater Biology (2005) **50,** 1747–1771 doi:10.1111/j.1365-2427.2005.01415.x

Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies

ERIK JEPPESEN,[1,2] MARTIN SØNDERGAARD,[1] JENS PEDER JENSEN,[1] KARL E. HAVENS,[3] ORLANE ANNEVILLE,[4] LAURENCE CARVALHO,[5] MICHAEL F. COVENEY,[6] RAINER DENEKE,[7] MARTIN T. DOKULIL,[8] BOB FOY,[9] DANIEL GERDEAUX,[4] STEPHANIE E. HAMPTON,[10] SABINE HILT,[11] KÜLLI KANGUR,[12] JAN KÖHLER,[11] EDDY H.H.R. LAMMENS,[13] TORBEN L. LAURIDSEN,[1] MARINA MANCA,[14] MARÍA R. MIRACLE,[15] BRIAN MOSS,[16] PEETER NÕGES,[17] GUNNAR PERSSON,[17] GEOFF PHILLIPS,[18] ROB PORTIELJE,[13] SUSANA ROMO,[15] CLAIRE L. SCHELSKE,[19] DIETMAR STRAILE,[20] ISTVAN TATRAI,[21] EVA WILLÉN[17] AND MONIKA WINDER[10]

[1]*Department of Freshwater Ecology, National Environmental Research Institute, Silkeborg, Denmark*
[2]*Department of Plant Biology, University of Aarhus, Aarhus, Denmark*
[3]*Department of Fisheries and Aquatic Sciences, University of Florida, FL, U.S.A.*
[4]*INRA, Centre Alpin de Recherche sur les Réseaux Trophiques des Ecosystèmes Limniques, Station d'Hydrobiologie Lacustre, Université de Savoie, Cedex, France*
[5]*Centre for Ecology and Hydrology, Edinburgh, Bush Estate, Penicuik, Scotland*
[6]*Water Resources Department/Environmental Sciences Division, St Johns River Water Management District, Palatka, FL, U.S.A.*
[7]*Brandenburg University of Technology (BTUC), Research Station Bad Saarow, Bad Saarow, Germany*
[8]*Institute for Limnology, Mondsee, Austria*
[9]*Agricultural and Environmental Science Division, Newforge Lane, Belfast, U.K.*
[10]*University of Washington, School of Aquatic and Fishery Sciences, Seattle, WA, U.S.A.*
[11]*Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany*
[12]*Võrtsjärv Limnological Station, Institute of Zoology and Botany, Estonian Agricultural University, Estonia*
[13]*RIZA, Lelystad, The Netherlands*
[14]*CNR, Pallanza, Italy*
[15]*Área de Ecología, Facultad de Biología, Ed. Investigación, Campus Burjasot, Valencia, Spain*
[16]*School of Biological Sciences, Derby Building, University of Liverpool, Liverpool, U.K.*
[17]*Department of Environmental Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden*
[18]*Environment Agency, National Ecology Technical Team, Reading, U.K.*
[19]*Department of Geological Sciences, Land Use and Environmental Change Institute, University of Florida, Gainesville, FL, U.S.A.*
[20]*Limnologisches Institut, Fachbereich Biologie, Universität Konstanz, Konstanz, Germany*
[21]*Limnological Research Institute, Hungarian Academy of Sciences, Tihany, Klebelsberg, Hungary*

SUMMARY

1. This synthesis examines 35 long-term (5–35 years, mean: 16 years) lake re-oligotrophication studies. It covers lakes ranging from shallow (mean depth <5 m and/or polymictic) to deep (mean depth up to 177 m), oligotrophic to hypertrophic (summer mean total phosphorus concentration from 7.5 to 3500 μg L^{-1} before loading reduction), subtropical to temperate (latitude: 28–65°), and lowland to upland (altitude: 0–481 m). Shallow north-temperate lakes were most abundant.

2. Reduction of external total phosphorus (TP) loading resulted in lower in-lake TP concentration, lower chlorophyll *a* (chl *a*) concentration and higher Secchi depth in most lakes. Internal loading delayed the recovery, but in most lakes a new equilibrium for TP

Correspondence: Erik Jeppesen, Department of Freshwater Ecology, National Environmental Research Institute, Vejlsøvej 25, DK-8600 Silkeborg, Denmark. E-mail: ej@dmu.dk

was reached after 10–15 years, which was only marginally influenced by the hydraulic retention time of the lakes. With decreasing TP concentration, the concentration of soluble reactive phosphorus (SRP) also declined substantially.

3. Decreases (if any) in total nitrogen (TN) loading were lower than for TP in most lakes. As a result, the TN : TP ratio in lake water increased in 80% of the lakes. In lakes where the TN loading was reduced, the annual mean in-lake TN concentration responded rapidly. Concentrations largely followed predictions derived from an empirical model developed earlier for Danish lakes, which includes external TN loading, hydraulic retention time and mean depth as explanatory variables.

4. Phytoplankton clearly responded to reduced nutrient loading, mainly reflecting declining TP concentrations. Declines in phytoplankton biomass were accompanied by shifts in community structure. In deep lakes, chrysophytes and dinophytes assumed greater importance at the expense of cyanobacteria. Diatoms, cryptophytes and chrysophytes became more dominant in shallow lakes, while no significant change was seen for cyanobacteria.

5. The observed declines in phytoplankton biomass and chl *a* may have been further augmented by enhanced zooplankton grazing, as indicated by increases in the zooplankton : phytoplankton biomass ratio and declines in the chl *a* : TP ratio at a summer mean TP concentration of <100–150 $\mu g\ L^{-1}$. This effect was strongest in shallow lakes. This implies potentially higher rates of zooplankton grazing and may be ascribed to the observed large changes in fish community structure and biomass with decreasing TP contribution. In 82% of the lakes for which data on fish are available, fish biomass declined with TP. The percentage of piscivores increased in 80% of those lakes and often a shift occurred towards dominance by fish species characteristic of less eutrophic waters.

6. Data on macrophytes were available only for a small subsample of lakes. In several of those lakes, abundance, coverage, plant volume inhabited or depth distribution of submerged macrophytes increased during oligotrophication, but in others no changes were observed despite greater water clarity.

7. Recovery of lakes after nutrient loading reduction may be confounded by concomitant environmental changes such as global warming. However, effects of global change are likely to run counter to reductions in nutrient loading rather than reinforcing re-oligotrophication.

Keywords: fish, macrophytes, nutrient, oligotrophication, plankton, resilience

Introduction

During the past 10–30 years, major efforts have been made in many countries to improve the ecological quality of lakes by combating external nutrient loading (Marsden, 1989; Sas, 1989), sometimes in combination with additional restoration measures such as biomanipulation (Benndorf, 1990; Gulati *et al.*, 1990) or physico-chemical methods (Cooke *et al.*, 1993). The effects of biomanipulation have been described in several recent reviews (Perrow *et al.*, 1997; Hansson *et al.*, 1998; Drenner & Hambright, 1999; Meijer *et al.*, 1999; Benndorf *et al.*, 2002; Mehner *et al.*, 2002). Since the extensive reviews in the 80s and early 90s (Marsden, 1989; Sas, 1989), there have also been several summaries of lake responses to reductions in nutrient loading without the confounding effect of biomanipulation (e.g. Cooke *et al.*, 1993; Van der Moelen & Portielje, 1999; Willén, 2001a; Jeppesen, Jensen & Søndergaard, 2002; Søndergaard *et al.*, 2002). Most have focused on nutrients and phytoplankton, whereas other biological components have been only briefly covered.

The aim of this paper is to evaluate 35 case studies on lake re-oligotrophication based on information given in questionnaires filled in by scientists and in follow-up communications. We focus on changes in water clarity, nutrients, fish, plankton, submerged macrophytes, as well as resource and top-down control of phytoplankton. Based on previous studies we hypothesized that reduction in P loading, N loading or both would result in:

1 A notable delay in the reduction of in-lake total phosphorus (TP) concentrations because at least three retention times are needed to wash out 95% of the excess P pool in the water column of fully mixed lakes, unless P is permanently lost to the sediment, (Sas, 1989), and because internal loading continuously replenishes the P pool in the water column (Søndergaard, Jensen & Jeppesen, 2003; Nürnberg & LaZerte, 2004).

2 A quick response of the total nitrogen (TN) concentration to reduction in N loading, because N loss by denitrification results in negligible internal N loading (Jensen *et al.*, 1992). Any delays might be greater in deep than in shallow lakes because of often longer hydraulic retention times in deep lakes, and a reduced denitrification capacity arising from a lower ratio of sediment area to water volume.

3 An increase in the in-lake TN : TP ratio because of an often higher TN : TP ratio of inflowing water, a decrease in internal P loading and, ultimately, when low TP concentrations have reduced primary production, reduced denitrification as organic carbon becomes limiting for denitrification (Levine & Schindler, 1989).

4 An increase in particle-bound P because P limitation of phytoplankton will gradually replace limitation by light or N (Sas, 1989), resulting in lower soluble reactive phosphorus (SRP) : TP ratios. Moreover, the number of free inorganic binding sites for P may increase (e.g. because of a higher Fe : P ratio in inflowing water), thereby facilitating precipitation of inorganic P and thus lowering the SRP : organic P ratio and consequently the SRP : TP ratio.

5 A unimodal response of the chlorophyll *a* (chl *a*) : TP ratio (McCauley, Downing & Watson, 1989). The increase in the chl *a* : TP ratio from high to moderate TP concentrations occurs because light limitation of phytoplankton growth by self-shading is replaced by increased P limitation because of a lower SRP : TP ratio (Sas, 1989; Reynolds, 2002). In deep lakes, a high P concentration in the hypolimnion favours motile dinophytes, which may assimilate P in the hypolimnion and transport it to the epilimnion. This, in turn, may lead to a greater chl *a* : TP ratio in the epilimnion when TP concentrations decrease in the illuminated water layer (Anneville, Gammeter & Straile, 2005; Dokulil & Teubner, 2005). In contrast, increased grazing (Jeppesen *et al.*, 2003) and higher water transparency may lead to a decline in the chl *a* : TP ratio at low TP concentrations (Portielje & Van der Moelen, 1998).

6 A reduction in phytoplankton biomass because of a lower TP concentration and an increased importance of taxa occurring under oligotrophic conditions (e.g. Edmondson & Lehman, 1981; Wojciechowski *et al.*, 1988; Ruggio *et al.*, 1998; Willén, 2001b; Reynolds, 2002).

7 No consistent response of the fish fauna. There is a general perception, particularly amongst those studying shallow lakes (Scheffer *et al.*, 1993), that the fish community responds only slowly to loading reductions because large organisms such as fish have slow growth rates and high longevity, especially key fish species in nutrient-rich turbid lakes, such as common bream (*Abramis brama* L.) and carp (*Cyprinus carpio* L. and *Carassius auratus* L.). This hypothesis is challenged, however, by the fast responses observed in several reservoirs (Yurk & Ney, 1989; Kalff, 2002) and natural lakes, both deep (Müller & Meng, 1992; Eckmann & Rösch, 1998) and shallow (Jeppesen *et al.*, 2002).

8 A reduction in zooplankton biomass (Gliwicz, 1969; Bays & Crisman, 1983; Hanson & Peters, 1984; Manca & Ruggio, 1998). However, as the predation pressure by planktivorous fish is also likely to decrease, zooplankton biomass is expected to decrease proportionately less than phytoplankton biomass (Jeppesen *et al.*, 2003). The resulting increase in the zooplankton : phytoplankton biomass ratio would augment the relative grazing pressure on phytoplankton.

9 A greater Secchi transparency and therefore a spread of submerged macrophytes. However, macrophyte recolonisation may be slow owing to, for instance, limited seed banks and/or grazing on macrophytes by waterfowl (Mitchell & Perrow, 1997).

Methods

Our analysis is founded on an elaborate questionnaire. In addition, loading data and summer and annual mean values of various lake attributes were examined for the time of maximum external loading, and every 5 years thereafter. Data were averaged from typically 3 years around each 5-year period (−1, 0, +1) to reduce the effect of inter-annual variation. In about 20% of the cases, lack of data reduced the period covered to 1–2 years or larger than 3 years (to cover more variables). Some of the case studies used in this synthesis are described in greater detail in other papers published in this special issue of *Freshwater Biology* (Anneville *et al.*, 2005; Coveney *et al.*, 2005; Dokulil & Teubner, 2005; Jeppesen *et al.*, 2005a; Köhler *et al.*, 2005; Moss *et al.*, 2005; Phillips *et al.*, 2005; Romo *et al.*, 2005; Søndergaard, Jensen & Jeppesen, 2005).

Basic information on the lakes is given in Table 1. Our data set includes both shallow (mean depth <5 m or polymictic) and deep (mean depth up to 177 m) lakes, with trophic status prior to restoration efforts ranging from mesotrophic to hypertrophic. Included are lakes from the subtropics to the temperate zone (latitude : 28–65 °) in North America and Europe. All warm-temperate and subtropical lakes were shallow. All lakes have been subjected to a reduction in P loading, with or without additional measures to reduce N loading. The loading reductions typically began in the 1970–1980s. For most lakes nutrient reduction in the lake inlets was the only restoration measure taken, but in three lakes it was followed by a major (Lake Balaton) or moderate (Veluwemeer, Apopka) removal of fish. The recovery periods studied range from 5 to 35 years (mean = 15.6 years) but typically varied between 10 and 20 years (Table 1).

We have synthesised the questionnaire answers and data in Tables 1–4 and Appendices 1–3. The direction of change (Table 4, Appendices 1 and 3) is based in most cases on statistical tests and in a few cases on qualified evaluations given by the data supplier. In cases where the questionnaire respondent expressed reservations for the direction of change (for instance because of large inter-annual variations), the sign (plus or minus) is bracketed. We used a chi-square test for analysing whether the direction of the changes in selected variables was significantly different from the expectations (SAS Institute, 1989). As Danish lakes comprise a relatively large share of the data set (36% of the shallow and 31% of the deep lakes), and as some of our hypotheses are based on earlier observations from Danish lakes, we ran the tests with and without the data from the Danish lakes. Where percentage values were calculated, they were based on the full data set and on the reduced set excluding Danish lakes. The latter are shown in parentheses. When data were scarce or scattered, we used LOESS regression (SAS Institute, 1989) to give an indication of the direction of changes on the data set divided into shallow and deep lakes. Here the Danish data were included. The LOESS procedure allows smoothing of data but provides no firm statistical tests. In addition, we used multiple regressions (forward procedure) on log-transformed data, with data for deep and shallow lakes pooled. Although these relationships may include transient effects, we believe that they are robust because they cover a very large gradient in mean depth and nutrient status compared to the changes in nutrient loading and concentrations experienced by each lake during the study period.

Results

Total phosphorus

Summer (1 May to 1 October or, in Florida and southern Spain, 1 May to 1 November) mean TP concentration declined in 76% (62% without the Danish lakes) of the shallow lakes and in all deep lakes. Reductions in annual mean TP concentration occurred in 86% (77%) of the shallow lakes and nearly all deep lakes (Appendix 1; Fig. 1). Loading data exist for 17 shallow and 12 deep lakes. To analyse the loading-concentration response pattern, we applied an equation developed by Vollenweider (1976) and OECD (1982):

$$\mathrm{TP} = \mathrm{TP}_{\mathrm{in}}/(1 + t_w^{0.5}) \tag{1}$$

where TP is the annual mean TP concentration in the lake, $\mathrm{TP}_{\mathrm{in}}$ the discharge-weighted annual mean inflow concentration, and t_w the hydraulic retention time (year). During the first 5–10 years, the measured annual mean lake TP concentration was typically higher than predicted from the Vollenweider equation or higher than before the loading reduction (Figs 1 & 2), indicating enhanced internal loading. After 10–15 years, however, measured TP approached the level predicted by the Vollenweider equation or the level attained before loading reduction (Figs 1 & 2).

Total nitrogen

Summer TN concentrations declined in 83% (70%) of the shallow lakes, while no clear pattern was found for deep lakes (Appendix 1). When the Danish lakes

Table 1 Basic information on the study lakes ordered by depth type and decreasing latitude

Lake type	Lake no.	Lake name	Recovery period included (years)	Country	Longitude	Latitude	Altitude (m)	Catchment area (km^2)	Lake area (km^2)	Mean depth (m)	Max depth (m)	Retention time (year)	Summer stratification	Months stratified	TP$_{sum}$ at maximum nutrient loading (μg L^{-1})	TP$_{sum}$ last year included in the study (μg L^{-1})
Shallow	1	Little Mere	10	England	2°24′W	53°20′ N	36	3.5	0.03	0.7	2	0.2	No		3500	135
Shallow	2	Eemmeer	15	Netherlands	5°2′E	52°1′N	0	90	15.7	1.7	6.2	0.05	No		1210	210
Shallow	3	Gundsømagle	10	Denmark	12°11′E	55°43′N	4	66	0.32	1.2	1.9	0.08	No		1176	513
Shallow	4	Gooimeer	15	Netherlands	5°1′E	52°2′N	0	106	25.5	3.5	26.8	0.16	No		620	100
Shallow	5	Veleuwemeer	25	Netherlands	5°4′E	52°25′N	0		30.5	1.5	5	0.14	No		528	44
Shallow	6	Søgård	10	Denmark	9°19′E	55°25′N	9	23	0.27	1.6	2.7	0.05	No		506	267
Shallow	7	Albufera	10	Spain	0°21′W	39°20′N	0	917	23.2	1.2	2	0.1	No		500	300
Shallow	8	Vesterborg	10	Denmark	11°16′E	55°51′N	1	30.3	0.21	1.4	2.9	0.05	No		424	231
Shallow	9	Arresø	10	Denmark	12°7′E	55°58′N	4	216	39.9	3.1	5.9	2.2	No		344	157
Shallow	10	Barton	20	England	1°49′W	52°74′N	1	110	0.57	1.5	2	0.045	No		333	91
Shallow	11	Bagsværd	10	Denmark	12°27′E	55°46′ N	20	7	1.21	1.9	3.2	1.7	No		237	107
Shallow	12	Apopka	5	USA	81°38′W	28°37′N	20	487	124	1.6	4.9	4	No		212	166
Shallow	13	Müggelsee	15	Germany	13°39′E	52°26′N	32	7000	7.3	4.9	8	0.17	Yes	1–2	162	149
Shallow	14	Damhussøen	10	Denmark	12°28′E	55°40′N	7	54	0.46	1.6	2	0.9	No		137	37
Shallow	15	Bryrup	10	Denmark	9°31′E	56°1′N	58	48	0.38	4.6	9	0.15	Temporary		116	62
Shallow	16	Ørnsø	10	Denmark	9°31′E	56°9′ N	19	56	0.42	4	6.6	0.05	Temporary		106	80
Shallow	17	Balaton	15	Hungary	17°5′E	46°8′N	105	5775	596	3.1	11	4.71	No		98	136
Shallow	18	Galten	35	Sweden	16°11′E	65°80′N	0.5	4435	65	3.4	19	0.05	No		89	46
Shallow	19	Okeechobee	20	USA	80°50′W	26°58′N	5	12600	1730	2.7	5.5	2.7	No		69	101
Shallow	20	Leven	15	Scotland	3°22′W	56°12′N	107	145	13.3	3.9	25.5	0.42	No		63	53
Shallow	21	Võrtsjärv	10	Estonia	25°85′E	58°15′N	33.7	3304	270	2.8	6	1	No		58	64
Shallow	22	Peipsi	15	Estonia/ Russia	25–30 E	56–59 N	30	44260	3555	7.1	15.3	2	No		27	39
Deep	23	Rostherne Mere	10	England	2°23′W	53°20′N	30	9.4	0.49	13.6	31	4	Yes	7	350	132
Deep	24	Tystrup	10	Denmark	11°35′E	55°21′N	7	682.5	6.62	9.9	21.7	0.24	Yes	3.5	332	127
Deep	25	Tissø	10	Denmark	11°17′E	55°34′N	2	417	12.3	8.2	13.2	1.5	Yes		129	85
Deep	26	Furesø	10	Denmark	12°25′E	55°48′N	20	696	7.4	16.5	37	14.4	Yes	4	111	75
Deep	27	Ekoln	30	Sweden	16°11′E	59°27′N	0.5	3334	30	15.7	37	0.5	Yes	4	97	37
Deep	28	Constance	25	Germany/ Austria/ Switzerland	9°18′E	47°39′N	395	10500	472	101	252	4.4	Yes	7	87	13
Deep	29	Washington	35	USA	122°15′W	47°38′N	4	1274	87.6	32.9	65.2	2.38	Yes	7	61	14
Deep	30	Scharmützelsee	14	Germany	14°03′E	52°15′N	9	112	12.09	9	29.5	12	Yes	5	55	40
Deep	31	Geneva	25	France/ Switzerland	6°32′E	46°27′N	372	7975	580	153	309	12	Yes	6	43	17
Deep	32	Ravn	10	Denmark	9°50′E	56°6′N	22	57.2	1.8	15	33	1.6	Yes	4	30	23
Deep	33	Mondsee	20	Austria	13°22′E	47°49′N	481	247	14.2	36	68.3	1.7	Yes	5–6	28	9
Deep	34	Maggiore	20	Italy/ Switzerland	8°67′E	45°95′N	190	6599	213	177	374	4	Yes	8	17	9
Deep	35	Vättern	25	Sweden	14°14′E	57°54′N	88.5	6359	1890	39	129	56	Yes	4	8	4

Table 2 Results from multiple linear regression analyses of selected environmental variables (P always <0.0001). The relationships assume potential hysteresis after nutrient loading reduction to be small because of the gradient in nutrients covered is larger than the one the individual lakes have gone through during the study period.

Response variable	Constant	Predictive variable 1	Predictive variable 2	Predictive variable 3	r^2	n
log (TN : TP_{sum})	1.03 ± 0.30	+0.35 ± 0.09 log (TN : TP_{load})	+0.37 ± 0.05 log (Z_{mean})		0.46	77
log (TN : TP_{ann})	1.26 ± 0.31	+0.40 ± 0.08 log (TN : TP_{load})	+0.24 ± 0.10 log (Z_{mean})		0.41	46
log (SRP_{sum})	−3.46 ± 0.43	+1.34 ± 0.08 log (TP_{sum})	+0.25 ± 0.07 log (Z_{mean})		0.80	128
log (DIN_{sum})	−7.05 ± 1.17	+1.55 ± 0.15 log (TN_{sum})	−0.24 ± 0.06 log (t_w)	0.75 ± 0.08 log (Z_{mean})	0.63	102
log (DIN : TN_{sum})	−2.91 ± 0.20	−0.31 ± 0.06 log (t_w)	+0.68 ± 0.09 log (Z_{mean})		0.39	102
log (DIN : SRP_{sum})	6.95 ± 0.77	−1.07 ± 0.44 log (TP_{sum})	+0.30 ± 0.13 log (Z_{mean})	−0.39 ± 0.08 log (t_w)	0.49	121
log ($Phyto_{sum}$)	−3.30 ± 0.28	+1.12 ± 0.07 log (TP_{sum})			0.75	98
log (Chl a_{sum})	−2.30 ± 0.56	+0.93 ± 0.06 log (TP_{sum})	+0.20 ± 0.09 log (TN_{sum})		0.85	107
log (Chl a : TP_{sum})	−2.14 ± 0.58	+0.76 ± 0.22 log (TP_{sum})	−0.10 ± 0.02 (log (TP_{sum}))^2	−0.12 ± 0.05 log (Z_{mean})	0.21	107
log (Zoo_{sum})	4.68 ± 0.60	+0.41 ± 0.11 log (TP_{sum})	−0.28 ± 0.08 log (Z_{mean})		0.62	80
log (ZooPhyt)	0.02 ± 0.037^{NS}	−0.36 ± 0.08 log (TP_{sum})			0.19	79

sum, summer averages; ann, annual averages; load, annual nutrient loading; Z_{mean}, mean depth (m); t_w, annual mean hydraulic retention time (year); Zoo, total zooplankton biomass (μg dry mass L^{-1}); Phyto, phytoplankton biovolume (mm^3 L^{-1}). Chl a, TP, TN, DIN, and SRP = lake water concentrations of chlorophyll a, total phosphorus, total nitrogen, dissolved inorganic nitrogen and soluble reactive phosphorus, respectively, all in μg L^{-1}. ZooPhyt = Zoo_{sum}/Chla_{sum}/66; log = natural logarithm.

Table 3 Results of multiple linear regression analyses of the contribution of selected phytoplankton taxa versus total phosphorus concentration in summer (TP_{sum}; μg L^{-1}) and mean depth (Z_{mean}; m). The relationships assume potential hysteresis after nutrient loading reduction to be small because the gradient in nutrients covered is larger than the one the individual lakes have gone through during the study period.

Response variable	Constant	Predictive variable 1	Predictive variable 2	Predictive variable 3	r^2	n
log (% Chlorophyta + 1)	+3.27 ± 1.01	−1.08 ± 0.50 log (TP_{sum})	+0.17 ± 0.06 [log (TP_{sum})]^2		0.16	103
log (% Cyanobacteria + 1)	−1.27 ± 0.89	+1.72 ± 0.44 log(TP_{sum})	−0.16 ± 0.05 [log (TP_{sum})]^2		0.27	103
log (% Diatoms + 1)	+4.45 ± 0.26	−0.31 ± 0.06 log (TP_{sum})			0.20	103
log (% Cryptophyta + 1)	+2.95 ± 0.19	−0.04 ± 0.01 log (TP_{sum})^2			0.20	99
log (% Chrysophyta + 1)	+4.89 ± 0.64	−1.69 ± 0.32 log (TP_{sum})	+0.15 ± 0.04 [log (TP_{sum})]^2		0.44	103
log (% Dinophyta + 1)	−2.38 ± 1.24	+1.16 ± 0.51 log (TP_{sum})	−0.12 ± 0.05 [log (TP_{sum})]^2	+0.54 ± 0.11 log (Z_{mean})	0.30	103

log, natural logarithm.

Table 4 Answers to questions about responses of submerged macrophytes to reductions in nutrient loading. Lakes 1–22 are shallow, all others are deep.

Question	Answer for lake group 1	Answer for lake group 2	Answer for lake group 3
Does submerged macrophyte abundance increase?	Yes: 1, 5, 13, (17), 26, 27, 31, 32	No change: 7, 23, 29, 33	Decrease: 2, 4, 25
Do the depth limits of submerged macrophytes (excluding mosses) increase?	Yes: 5, 13, 20, 26, 27, 28, 32	No change: 1, 2, 25, 26	Decrease: none
Does percentage coverage or plant volume inhabited by plants increase?	Yes: 5, 12, 14, 26, 28, 32	No change: 13	Decrease: 2, 4, 25
Does the re-establishment of submerged plants occur gradually or abruptly?	Gradually: 13, 14, 26, (27), 32	Abruptly: 1, 12, 17	Exponentially: 5
Are there any changes in species richness, Simpson evenness and Shannon–Wiener diversity of submerged and floating-leaved macrophytes at the species or genus level?	Increase: 4, 5, 13, 30	No change: 20	Decrease: 2, 31
Do changes in macrophyte variables follow patterns different from those observed at increasing nutrient loading?	Yes: 4, 12, 13, 28	No: 5, 20, 21, 31	

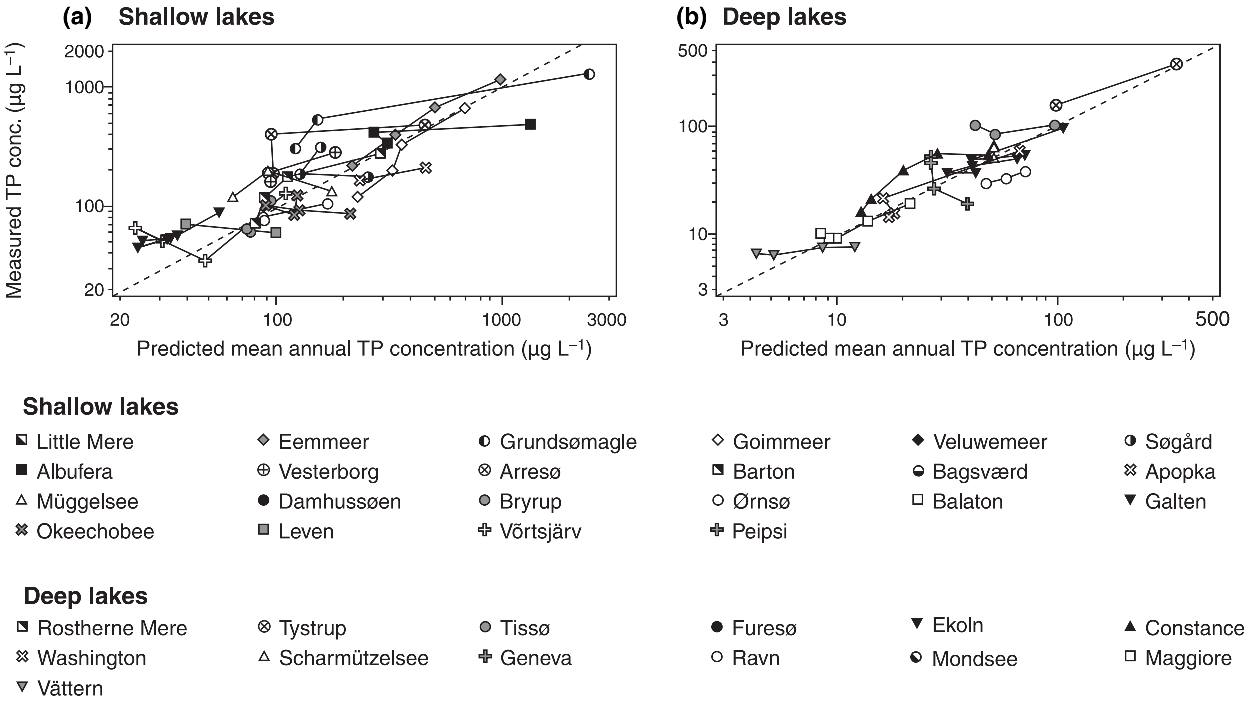

Fig. 1 Annual mean total phosphorus (TP) concentration during the recovery period in the surface water of shallow and deep lakes versus values predicted by the Vollenweider relationship (eqn 1 – see Methods). Lines connect data points at consecutive 5-year intervals for each lake.

were excluded, however, 67% of the deep lakes showed an increase in TN concentration. The marked response observed in shallow lakes may primarily reflect the decline in N loading that occurred in 73% (100%) of the shallow lakes, whereas no consistent pattern was found in N loading reductions in the deep lakes (Appendix 1).

We used an empirical model developed for Danish lakes (Windolf *et al.*, 1996) to predict lake water TN concentration:

$$TN = 0.34\,TN_{in} t_w^{-0.16} Z_{mean}^{0.17} \qquad (2)$$

where TN is the annual mean lake TN concentration, TN_{in} the discharge-weighted annual mean inflow concentration, and Z_{mean} the mean depth (m). We found no prolonged delay in the response to N loading reduction; it was typically <5 years and only in a few cases exceeded 10 years (Fig. 3).

TN : TP ratio

Multiple regression analysis showed that the TN : TP ratio in the lakes was positively related to the TN : TP ratio in the lake inflows, both during summer and annually, and was also positively related to depth (Fig. 4; Table 2). With decreasing TP concentration, the TN : TP ratio increased markedly in both deep and shallow lakes (Fig. 4). An increase in the summer TN : TP ratio could be seen in 80% of the lakes receiving water with an increased TN : TP ratio (Appendix 1), but the TN : TP ratio even increased in a few lakes for which the TN : TP ratio of the inflowing water decreased (Appendix 1).

SRP and the SRP : TP ratio

In all lakes except Scharmützelsee, the summer SRP concentration declined with decreasing TP concentration, while no changes or even increases were found in lakes with no changes or increases in summer TP concentration (Figs 5 & 6; Appendix 1). In the deep lakes, summer SRP concentrations approached 10 µg L^{-1} when TP declined below 50–70 µg L^{-1}. In some of the shallow lakes such low concentrations of summer SRP were attained at summer TP levels of more than 400 µg L^{-1}, although typically when TP was below 100–150 µg L^{-1} (Fig. 6). SRP concentrations below 10 µg L^{-1} are often considered to be

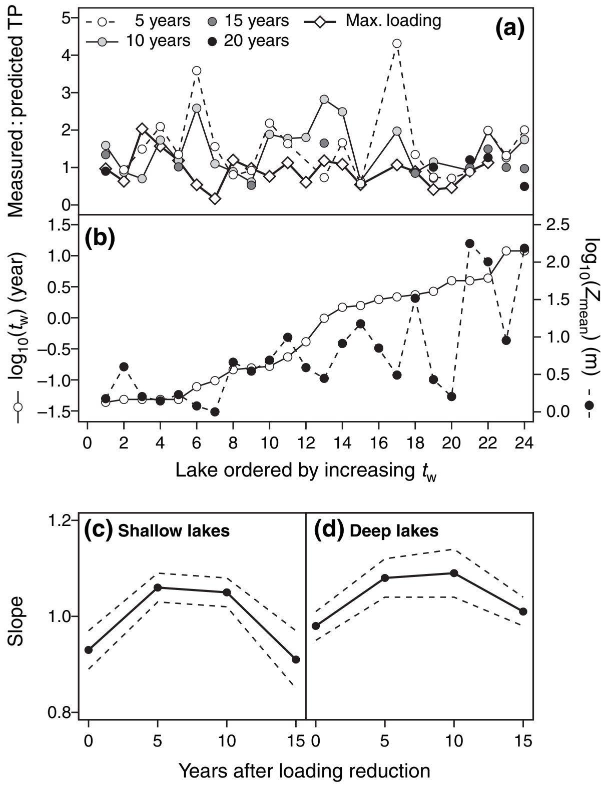

Fig. 2 Ratio of annual mean total phosphorus (TP) concentration measured and predicted (eqn 1, see Methods) in the surface water of lakes at maximum nutrient loading and 5, 10, 15 and 20 years after loading reduction (a); hydraulic retention time (t_w) and mean depth (Z_{mean}) of the lakes (b); and slope (mean ± SE) of linear regressions (forced through the origin) of observed versus predicted annual mean TP concentration in different years following loading reduction in shallow lakes (c) and deep lakes (d). The slopes for 5 and 10 years in shallow lakes and after 5 years in deep lakes were significantly different from the slopes for years 0 and 15 and 10 years in deep lakes ($P < 0.05$, paired *t*-test); however, these differences must be regarded with caution as length of the time series varied across lakes.

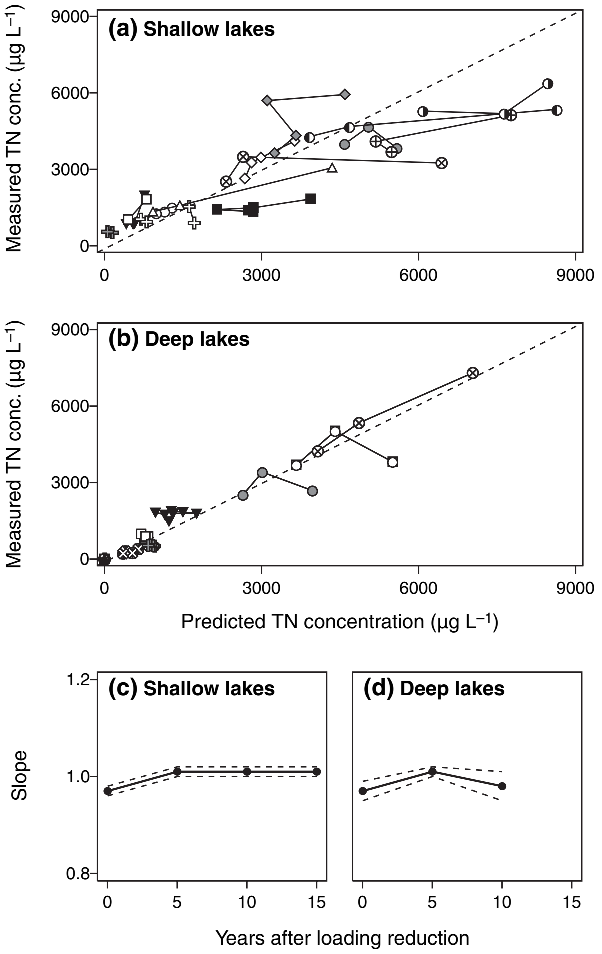

Fig. 3 Annual mean total nitrogen (TN) concentration in the surface water of shallow (a) and deep lakes (b) versus predicted values obtained by an equation developed for Danish lakes (eqn 2 – see Methods); and slope (mean ± SE) of linear regressions (forced through the origin) of observed versus predicted annual mean TN concentrations (eqn 2) in the lake water in different years following loading reduction. The slopes for shallow lakes of 5, 10 and 15 years after loading reduction were significantly different ($P < 0.05$, paired *t*-test) from the slope at 0; however, these differences must be regarded with caution as length of the time series varied across lakes. No significant differences were found for deep lakes. Symbols and time series as in Fig. 1.

indicative of P limitation (Sas, 1989). Multiple regression analysis revealed that the SRP concentration in summer was positively related to the summer TP concentration and mean depth, but was independent of the hydraulic retention time (Table 2).

In all lakes with declining summer TP concentrations, except Scharmützelsee, the summer SRP : TP ratio also decreased markedly (Fig. 6; Appendix 1). An increased ratio, despite no significant change in TP, was found in Müggelsee, which was also subjected to a large TN reduction (Köhler *et al.*, 2005). The different responses of Scharmützelsee and Müggelsee may reflect the fact that the reductions in TN loading exceeded the reductions in TP. Accordingly, dissolved inorganic nitrogen (DIN) decreased markedly after loading reduction in these two lakes (Appendix 1; Fig. 6). The SRP : TP ratio also declined in Lakes Peipsi and Võrtsjärv although the TP concentration remained unchanged or even increased. This may reflect the rising chl *a* values in these lakes (Appendix 1) despite reductions of external TP loading; the increase in chl *a* concentrations has been attributed to a warmer climate in recent years (Kangur *et al.*, 2002).

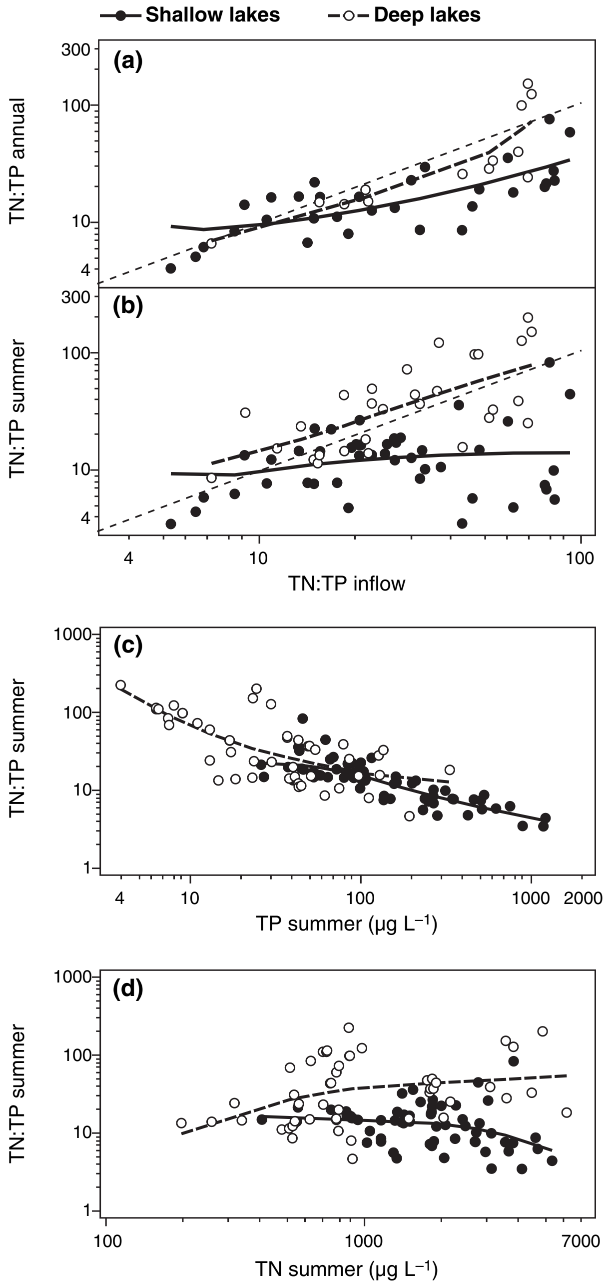

Fig. 4 Ratios of annual and summer mean total nitrogen (TN) concentration to mean total phosphorus (TP) concentration versus the annual mean TN : TP ratio in the lake inlets (a, b) and versus the summer mean TP and TN concentration (c, d). The stippled line in panels (a) and (b) represents the 1 : 1 lines. The curves represent LOESS regression lines.

DIN and the DIN : TN ratio

No clear pattern was observed for DIN in individual lakes (Appendix 1). However, the summer DIN : TN ratio increased in 76% of the shallow lakes (not

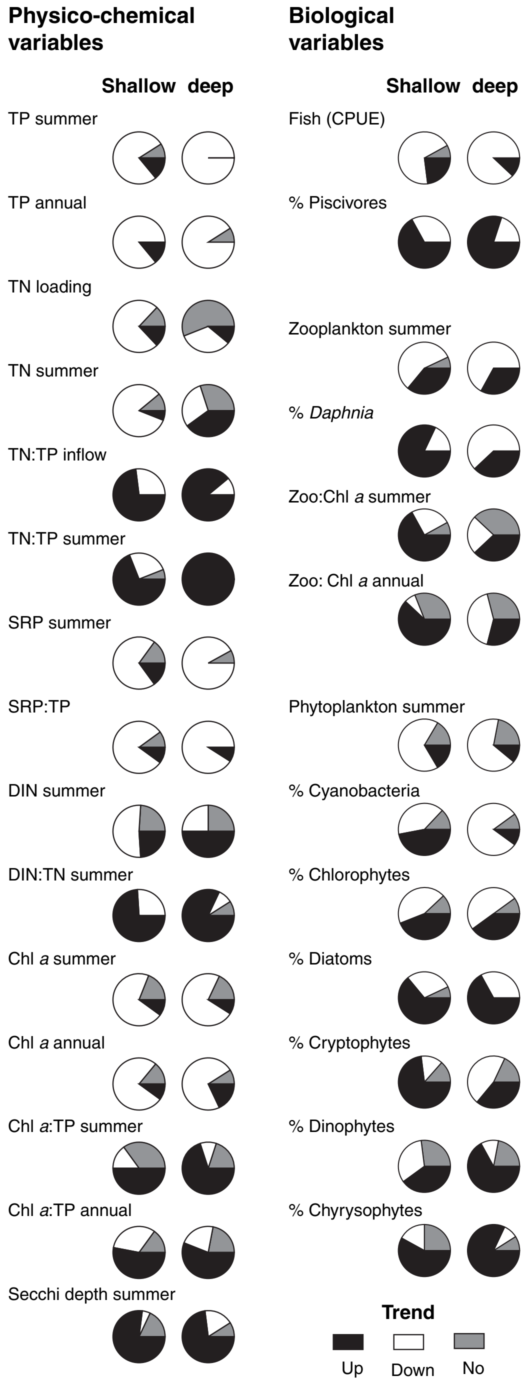

Fig. 5 Summary of key variables of all study lakes divided into three categories according to the direction of responses to reduced nutrient loading: increase = up, decline = down, no change = no. Details are presented in Appendices 1–3. Shallow and deep lake responses are not directly comparable, because the starting levels of total phosphorus (TP) loading and concentrations were generally higher in shallow lakes (Table 1). TN, total nitrogen; SRP, soluble reactive phosphorus; DIN, dissolved inorganic nitrogen; Chl *a*, chlorophyll *a*; CPUE, catch per unit effort by weight; Zoo, total zooplankton biomass in summer.

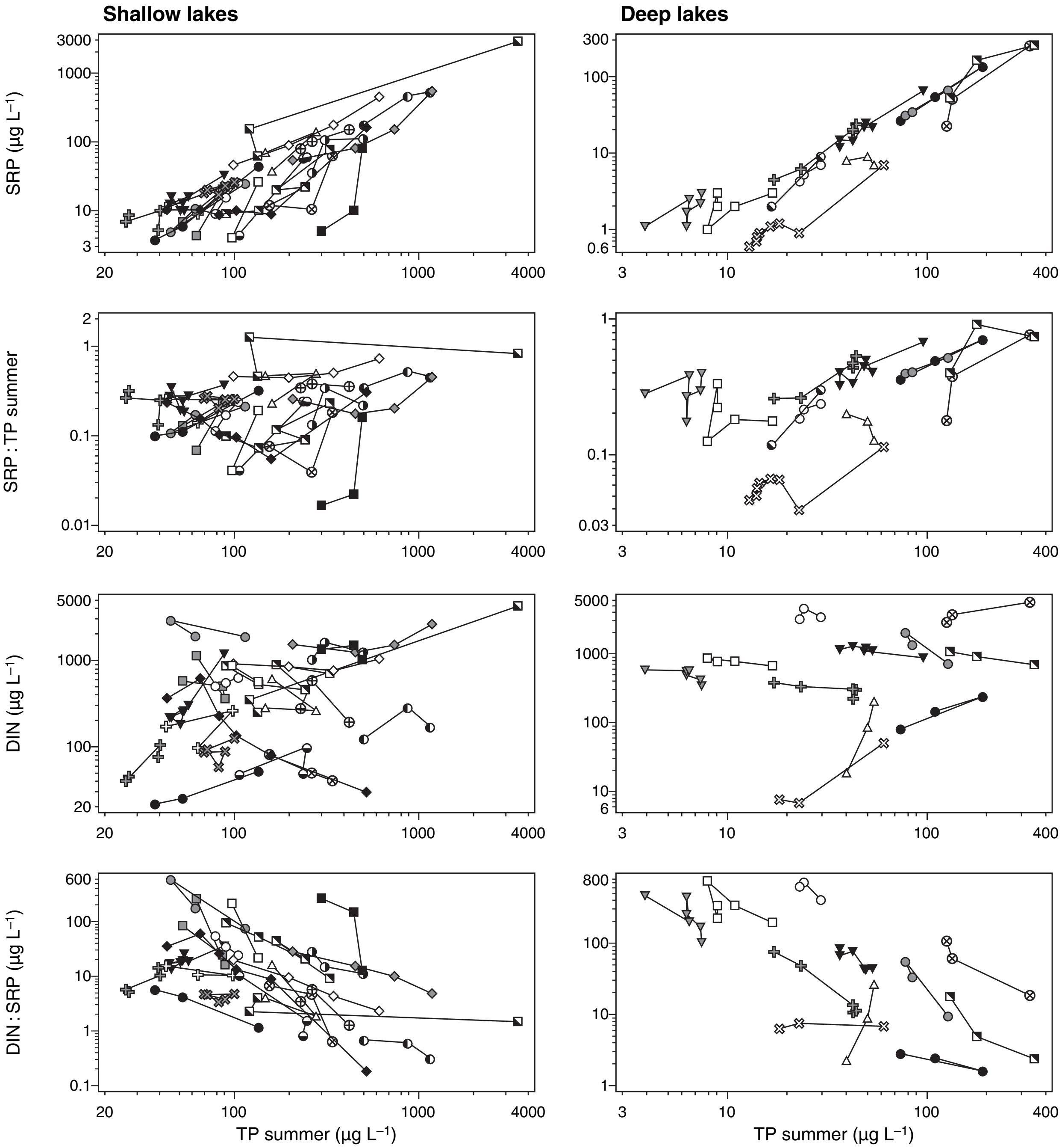

Fig. 6 Changes during the recovery period in summer mean concentrations or ratios of chemical variables versus summer mean total phosphorus (TP) concentration in the surface water of shallow and deep lakes. Symbols and length of time series as in Fig. 1. SRP, soluble reactive phosphorus; DIN, dissolved inorganic nitrogen.

significant without the Danish lakes) and in 82% (86%) of the deep lakes. This indicates a decrease in the organic N fraction of TN, most probably as a consequence of a decreasing phytoplankton biomass. Moreover, increased summer DIN concentrations were found in many of the lakes experiencing decreased N loading (Appendix 1). It is notable that DIN and TN concentrations increased in several of the deep lakes during the recovery period even when N loading remained high or declined (Appendix 1; Fig. 5). However, multiple regressions revealed that summer mean DIN concentration was positively related to the annual discharge-weighted inflow concentration (TN_{in}), or summer TN concentration in the lake and mean depth and negatively related to t_w (Table 2), while being independent of summer TP and chl *a* concentration. The summer DIN : TN ratio was positively related to mean depth and negatively to t_w (Table 2).

DIN : SRP

In 80% (50%) of the shallow and 91% (71%) of the deep lakes, the summer DIN : SRP ratio increased with decreasing TP loading and TP concentration in the lake (Figs 5 and 6). This ratio was below 10 in the majority of the nutrient-rich shallow lakes (summer concentration of $TP > 600\ \mu g\ L^{-1}$), but increased substantially at TP concentrations below $300\ \mu g\ L^{-1}$ in most shallow lakes, and at TP concentrations approximately below $80\ \mu g\ L^{-1}$ in deep lakes (Fig. 4). However, in a few cases, ratios <10 were recorded at summer TP concentrations as low as $20\ \mu g\ L^{-1}$. Multiple regressions revealed that the DIN : SRP ratio positively related to mean depth, and negatively related to the summer mean TP concentration and t_w (Table 2). Interestingly, however, the relation with the TN : TP ratio in the lake inflows was not significant.

Chl a *concentration and the chl* a *: TP ratio*

In 71% (62%) of the shallow lakes and in 69% (78%) of the deep lakes, a decline was found in summer chl *a* concentration with decreasing summer TP concentrations. These were 76% (64%) and 64% (71%), respectively, when chl *a* values were averaged on an annual basis (Fig. 5; Appendix 1). A major decline in chl *a* concentration was found even at summer TP concentrations above $300\ \mu g\ L^{-1}$ in some shallow lakes, and at concentrations of 125–200 $\mu g\ L^{-1}$ in some deep lakes. This indicates that low summer mean TP concentration is not always a prerequisite for a reduction in chl *a* concentration. Both for summer and annual mean values the chl *a* : TP ratio generally increased or remained unchanged during the recovery period (Fig. 7; Appendix 1). The chl *a* : TP ratio was unimodally related to the TP concentration (highest at intermediate TP concentrations), as predicted, although variation among lakes was high (Fig. 7; Table 2). The decline in the chl *a* : TP ratio at low TP concentrations coincides well with an increase in the summer mean zooplankton : phytoplankton biomass ratio, which may suggest enhanced top-down control of phytoplankton biomass and thus chl *a* concentration by grazing at low TP. However, multiple regression analysis showed summer chl *a* concentration to be positively linearly related to the summer TP and TN concentrations (Table 2).

Secchi depth

In 77% (54%, not significant, NS) of the shallow and 82% (86%) of the deep lakes, the Secchi depth increased as nutrient loading decreased (Fig. 5; Appendix 1). In several cases the spring clear-water phase re-appeared after having been absent for many years (e.g. Eemmeer, Loch Leven, Albufera and possibly Mondsee; E.H.H.R. Lammens, L. Carvalho, S. Romo and M. Dokulil, respectively, unpublished data). The time of occurrence varied, from February in the warm temperate Albufera (Romo *et al.* 2005) to May in temperate Loch Leven (L. Carvalho, unpublished data). The spring clear-water phase occurred more frequently in Gooimeer, lasted longer in Müggelsee and, based on greater Secchi depths, was more pronounced in Müggelsee (Köhler *et al.* 2005 and unpublished data) and Lake Geneva (O. Anneville, unpublished data). However, many lakes have not yet reached a state with a spring clear-water phase (e.g. Lakes Apopka, Okeechobee, Balaton, Võrtsjärv and Galten; M.F. Coveney, K.E. Havens, I. Tatraí, P. Nõges and E. Willén, respectively, unpublished data).

Fish abundance and community structure

In most cases fish responded strongly to the reduction in nutrient loading (Fig. 5; Appendix 2). In 82% (90%) of the lakes with available fish data, decreases were noted in the catch of fish by either commercial fishermen, anglers or in fish surveys. These decreases were often substantial. In half of the lakes with quantitative data (in all when the Danish lakes were excluded), the reduction exceeded 25%, and reductions >50% were observed in 18% (83%) of the cases. In addition, the percentage of potential piscivores, such as pike (*Esox lucius* L.), pikeperch (*Sander lucioperca* L.) and perch (*Perca fluviatilis* L.), increased in 80% (75%, although only few data without the

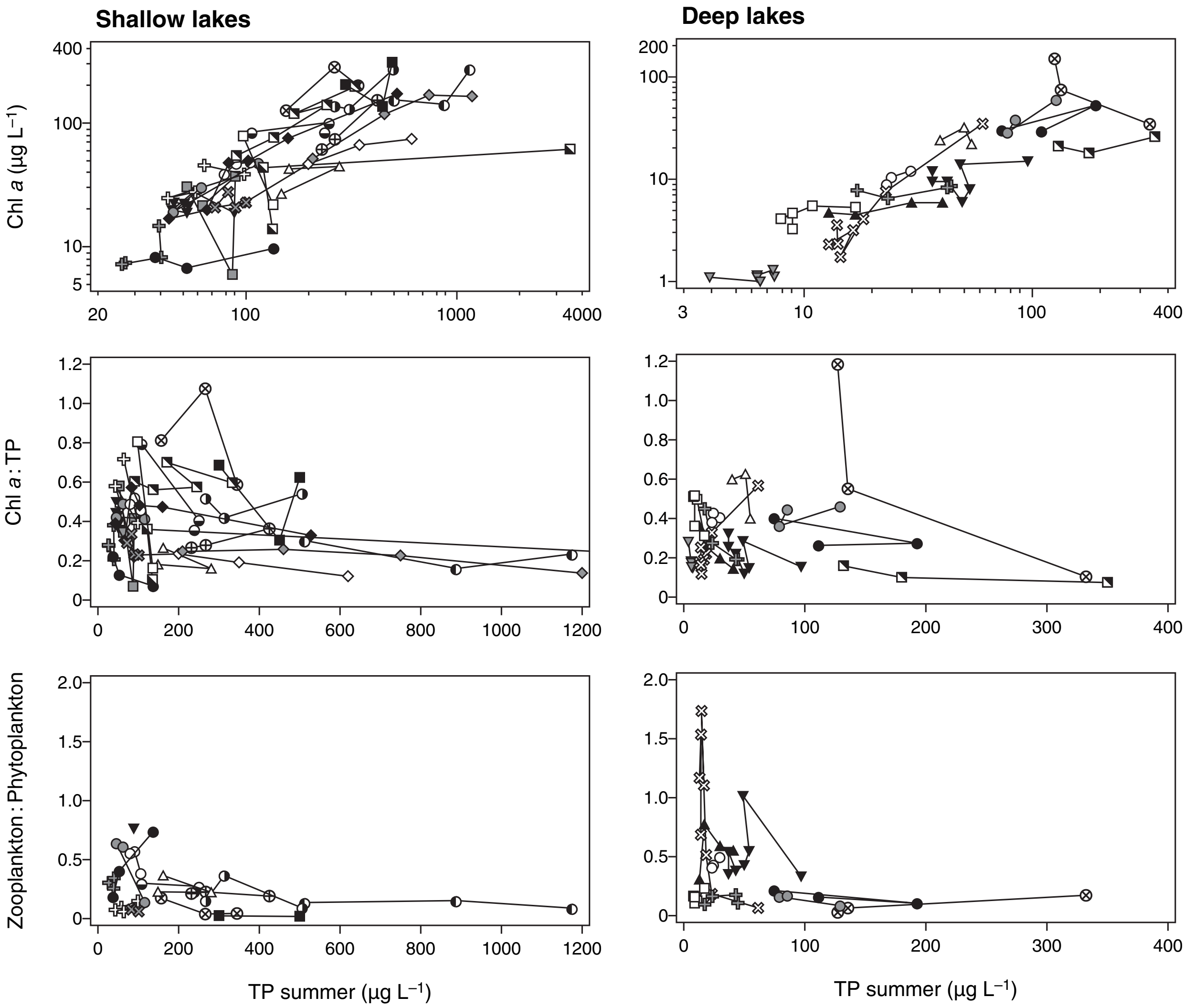

Fig. 7 Changes during the recovery period in summer mean values of chemical and biological variables versus summer mean total phosphorus concentration (TP) in the surface water of shallow and deep lakes. Zooplankton : Phytoplankton refers to the ratio of summer mean zooplankton biomass (mg dry mass L^{-1}) and summer mean phytoplankton biomass (mg dry mass L^{-1}) estimated as Chl *a* × 30 (to convert to carbon) × 2.2 (to convert to dry mass). Symbols as in Fig 1. Chl *a*, chlorophyll *a* concentration.

Danish lakes) of the case studies, but the decline was significant in deep lakes only. The density of littoral fish species like tench (*Tinca tinca* L.), Crucian carp (*Carassius carassius* L.) and rudd (*Scardinius erythropthalmus* L.) increased in importance in some cases (Appendix 2), which may indicate enhanced plant coverage.

Zooplankton and the zooplankton : phytoplankton biomass ratio

Zooplankton data were only available from 23 lakes with a strong bias towards Danish lakes (52% of the lakes). Multiple regression analysis revealed total biomass to increase with TP concentration and decrease with depth (Table 2; Fig. 8). However, chi-square tests only showed significant changes for shallow lakes and only when Danish lakes were included (Appendix 3). The contribution of *Daphnia* spp. to total zooplankton biomass increased in 81% of the shallow lakes, whereas no significant pattern was found for deep lakes. The zooplankton : phytoplankton ratio was generally low for TP concentrations >100 μg L^{-1} in both shallow and deep lakes, irrespective of phytoplankton community structure, but increased in many lakes below this threshold

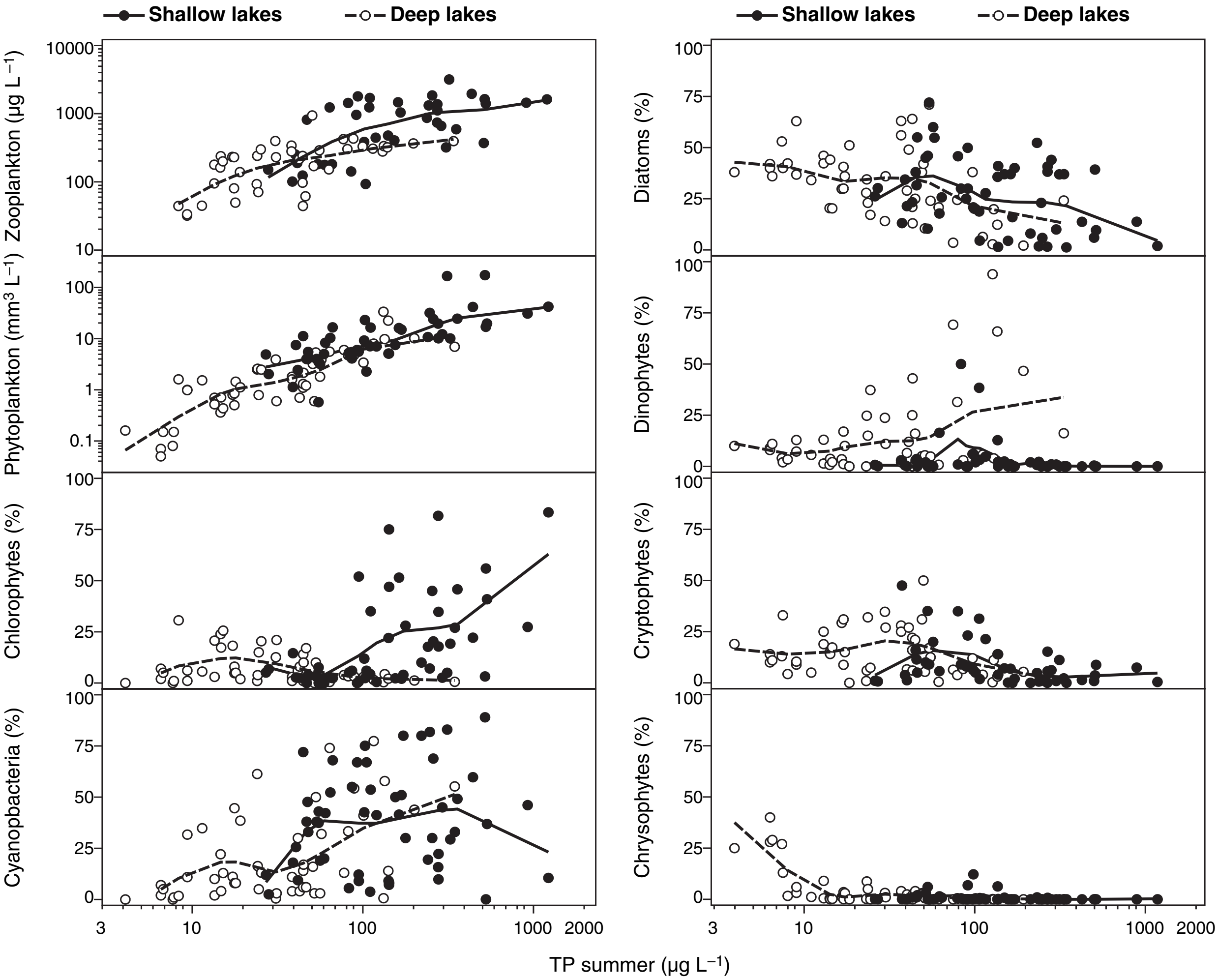

Fig. 8 Summer mean zooplankton biomass and phytoplankton biovolume and proportion of major phytoplankton taxa versus summer mean total phosphorus concentration in the surface water of shallow and deep lakes. Curves represent LOESS regression lines. Data at 5-year intervals are shown from the 23 (zooplankton) or 27 (phytoplankton) lakes for which data were available.

(Fig. 7). The ratio increased in 65% of the shallow lakes, while no clear pattern was found for deep lakes (Appendix 1). Multiple regression analysis showed the ratio to increase with decreasing TP concentration, whereas a significant influence of mean depth was not detected (Table 2).

Phytoplankton biomass and community structure

Phytoplankton biomass followed the pattern for chl *a* concentration (Table 2). It declined in 71% (60%; effect not significant) of the shallow lakes and 70% (67%, NS) of the deep lakes for which data are available (Figs 5 & 8; Appendix 3). The response of the different phytoplankton classes varied among lake types. For shallow lakes, the contribution of diatoms to the total biovolume increased in 69% (63%, NS) of the lakes, and the contribution of cryptophytes and chrysophytes in 63% (50%, NS) and 64% (43%, NS) of the lakes, respectively. No significant pattern was found for the remaining phytoplankton groups. The contribution of chrysophytes also increased in 82% (100%) of the deep lakes. In addition, an increase in dinophytes was found in 75% (89%) and a decline of cyanobacteria in 80% (100%) of the cases (Appendix 3). LOESS smoothing on the entire set of data indicates that the proportion of chlorophytes declined in shallow lakes, from nearly 80% of the total biovolume at high TP concentrations to <10% of the total biovolume at

TP concentrations <100 μg L^{-1}. Deep lakes displayed the opposite tendency, with chlorophytes increasing to near 20% at low concentrations of TP. Cyanobacteria contributed substantially to the total biovolume down to 50 μg TP L^{-1} in shallow lakes and, in some cases, to 10–15 μg TP L^{-1} in deep lakes. The share of diatoms increased steadily with decreasing TP concentrations, such that they constituted the most important group in deep lakes at low TP concentrations. Dinophytes were most important at high to intermediate TP concentrations and were most important in deep lakes. Multiple regression analyses showed unimodal relationships with TP of the biomass proportion of most phytoplankton taxa (Table 3). Mean depth contributed positively for dinophytes only, and the TN concentration was never a significant predictive variable.

Macrophytes

The response of macrophytes to reductions in nutrient loading was not uniform across lakes (Table 4). In most lakes for which data were available, signs of macrophyte spread were apparent, either as an increase in macrophyte abundance, coverage, plant volume inhabited and/or, in the case of submerged macrophytes, depth distribution. These changes occurred gradually in most cases, but in a few instances exponential or abrupt changes were recorded. Species richness also increased in most lakes, although two case studies reported reduced richness. However, in several lakes no changes were observed in submerged macrophyte abundance despite raised water clarity.

Discussion

For both deep and shallow lakes we found clear effects of reductions in nutrient loading (Table 5). For most lakes, lake TP concentrations, chl *a* concentration in the surface water and phytoplankton biomass were lower and Secchi depth was higher. Internal loading apparently delayed the recovery, but in most lakes a new equilibrium between P in the sediment and water column was reached after 10–15 years, thus confirming earlier findings by Ahlgren (1978) and Sas (1989). There was a slight tendency to faster recovery in lakes with a short retention time, despite high TP concentrations when loadings were greatest, and in lakes with a long hydraulic retention time and previously low TP loading (Fig. 2; Table 1). No clear effect of lake depth on recovery was detected (Fig. 2). The latter corresponds well with results from earlier comparisons across lakes by Sas (1989) and Jeppesen *et al.* (1991). A plausible explanation is that lakes with short hydraulic retention times often were more heavily impacted in the past, resulting in higher P accumulation in the sediment and, following nutrient reduction, higher and/or longer internal loading, whose effects overrode the effective P removal through high flushing rates (Jeppesen *et al.*, 1991).

The quick (<5 years) response of lakes to N loading reductions compares well with the results of other studies (Jensen *et al.*, 1992) and may be explained by the fact that surplus inorganic N is lost to the atmosphere via denitrification rather than accumulated in the sediment. For two deep and some shallow lakes with high TN and correspondingly high TP concentrations (see below), the observed TN concentrations were often lower than predicted by the relationship established previously for Danish lakes, but approached the predicted values after 5–10 years (Fig. 3). The general increase in the TN : TP and DIN : SRP ratios in the lake water suggests that P became a more likely limiting nutrient for phytoplankton growth than before reductions in nutrient loading.

The increase in N relative to P may in part reflect that loading reductions have mainly been directed towards P. While this is a wise strategy for deep lakes (Sas, 1989), recent studies show that nitrogen may play a more important role in shallow lakes than hitherto anticipated (Moss, 2001; Gonzáles Sagrario *et al.*, 2005; James *et al.*, 2005). Nitrogen negatively affects both submerged macrophyte species richness (James *et al.*, 2005) and the chances of maintaining a macrophyte-dominated state at moderately high TP levels (Gonzáles Sagrario *et al.*, 2005). At a summer mean TP concentration of 30–150 μg L^{-1}, submerged plants tend to disappear in shallow Danish lakes when the summer TN levels is above 1–2 mg L^{-1} (Gonzáles Sagrario *et al.*, 2005), a threshold exceeded in most of the shallow lakes included in the present study (Fig. 4). Thus, to further improve the ecological quality of shallow lakes, it is important to consider not only P but also N loading (Moss, 2001; Gonzáles Sagrario *et al.*, 2005). However, although a rapid decline in N is to be expected at reduced N loading, it may be difficult to achieve in practice because N in

Table 5 General overview of key findings from the analysed case studies on lake re-oligotrophication. Note that the responses of shallow and deep lake cannot be fully compared as the starting TP level before loading reduction differed, being overall higher in shallow lakes (Table 1).

Response variable	Shallow lakes (mean depth <5 m or polymictic)	Deep lakes (others)
P response time to TP loading reduction	Typically 10–15 years	Typically 10–15 years
N response time to TN loading reduction	Typically <5 years	Typically <5 years
TP summer and annual	Decreased in most lakes	Decreased in all lakes
TN summer	Decreased in most lakes	No clear pattern
TN : TP summer	Increased in most lakes even in some lakes with lower TN : TP in the inlet	Increased in most lakes
SRP summer	Decreased in all lakes when TP decreased	Decreased in all but one lakes when TP decreased
SRP : TP summer	Decreased in all lakes when TP decreased	Decreased in all but one lakes when TP decreased
DIN : SRP summer	Increased in most lakes	Increased in most lakes
Secchi depth summer	Increased in most lakes	Increased in most lakes
Chl *a* summer	Decreased in most lakes	Decreased in most lakes
Chl *a* : TP summer	Increased or no changes	Increased or no changes
Phytoplankton biovolume	Decreased in most lakes	Decreased in most lakes
Phytoplankton community changes	Higher importance of diatoms, cryptophytes and chrysophytes	Decline in cyanobacteria and greater importance of dinophytes and chrysophytes
Fish biomass, judged from surveys, commercial catches or angling reports	Decreased in most lakes	Decreased in most lakes
Percentage piscivorous fish	Increased in most lakes, thus likely resulting in enhanced top-down control of prey fish	Increased in most lakes thus likely resulting in enhanced top-down control of prey fish
Fish community changes in European lakes (examples)	Cyprinids to percids plus cyprinids	Cyprinids to percids plus cyprinids or Percids plus coregonids to coregonids or Coregonids to coregonids plus salmonids, depending on TP levels
Zooplankton biomass	Decreased	No clear pattern
Zooplankton : phytoplankton biomass ratio	Increased in many lakes, probably reflecting release from fish predation	No clear pattern
Submerged macrophytes	No clear pattern	No clear pattern
Indications of enhanced bottom-up control of phytoplankton	Nearly all lakes	Nearly all lakes
Indications of enhanced top-down control of phytoplankton	Many lakes	No clear pattern
Seasonality	Largest reduction in TP and chl *a* concentrations during spring and autumn, later in the recovery phase also in summer. Exceptions are some lakes with major reductions in N loading, showing major effects also in summer in the early recovery phase	Largest effect in summer, later in spring and autumn

lakes typically derives from diffuse sources (Sharpley, Foy & Whiters, 2000).

The large increase in the summer DIN : TN ratio (Fig. 5; Appendix 1) indicates that denitrification could not fully compensate for the reduced uptake of DIN by phytoplankton. The insignificant response of DIN to TN loading reduction (Appendix 1) points in the same direction. No firm conclusions can be drawn on the underlying mechanisms. However, a possible explanation for shallow lakes is that the redox potential in the sediment rose because of lower sedimentation rates of organic matter and the resulting lower sediment oxygen demand. For deep lakes, reduced sedimentation of N to the hypolimnion and higher redox potentials may also play a role, and organic matter may have become limiting for denitrification in some of the deep lakes with low TP concentrations. Finally, an increase in atmospheric nitrogen pollution during the study period may play a role as suggested by results from Lago Maggiore (Mosello *et al.*, 2001).

Probable explanations for the increase in the chl *a* : TP ratio that we found, notably in deep lakes (Lakes Geneva and Constance), include (i) excess SRP in the early recovery phase, (ii) access to P at high concentrations in the hypolimnion, as suggested by the frequent increase in dinophytes, which may migrate vertically in the water column (Reynolds, 2002), (iii) enhanced mixotrophy and greater P affinity of phytoplankton taxa (Reynolds, 2002; Anneville *et al.*, 2005; Dokulil & Teubner, 2005), (iv) reduced self-shading, and (v), for some lakes, higher water temperatures resulting from global warming. In three lakes, summer chl *a* concentrations even increased, with the increase in one or two of them (Lake Võrtsjärv and possibly also Lake Peipsi) having been attributed to warmer climate (Kangur *et al.*, 2002).

The phytoplankton generally followed patterns observed in earlier studies of oligotrophication (Willén, 2001b; Reynolds, 2002). Diatom growth is dependent on supplies of available silica, which tends to decrease with phosphorus enrichment (Schelske *et al.*, 1986). Therefore, the shift in phytoplankton community structure towards diatoms that we observed at reduced SRP concentrations in shallow lakes may be because of a relaxation of silica limitation in addition to improved competitive capacity for phosphorus (Schelske & Stoermer, 1971). Notable is, however, also the observed shift in the shallow hypertrophic Lakes Gundsømagle and Søgård (Appendix 3), from chlorophytes to cyanobacteria despite a general major increase in the TN : TP ratio in the inflowing water and in the in-lake DIN : TN and DIN : SRP ratios (Appendices 1 and 3). Moreover, when TP concentrations declined and TN : TP ratios increased, N-fixing cyanobacteria were often replaced by heterocystous species (Jeppesen *et al.*, 2002, 2005b; Phillips *et al.*, 2005), indicating that the N : P ratio may be of minor importance for the response of cyanobacteria in these lakes. This is contrary to results obtained in some earlier multi-lake surveys (Smith, 1983; Smith *et al.*, 1995) that encompassed a much narrower range of TP concentrations.

Fish communities showed major responses to reductions in nutrient loading. Catch data suggest that the fish biomass declined in most of the lakes for which quantitative data were available and the proportion of piscivores increased, indicating higher piscivores control of prey fish. In the eutrophic shallow Danish and Dutch lakes, the proportion of percids increased at the expense of cyprinids, and the contribution of pike and pikeperch rose in some cases as well (Jeppesen *et al.*, 2005a; E.H.H.R. Lammens, unpublished data; R. Portielje, unpublished data). Furthermore, in the warm-temperate Albufera, an increase in littoral fish species and a higher contribution of piscivorous species were found during oligotrophication (Romo *et al.*, 2005). In the deep mesotrophic to slightly eutrophic lakes, perch-coregonid communities changed to coregonid dominance (e.g. Lakes Constance and Geneva; Eckmann & Rösch, 1998). However, when TP was reduced further as in Lake Vättern, salmonids increased at the expense of coregonids (Degerman *et al.*, 2001). These results follow the established fish-trophic state relationships (Colby *et al.*, 1972; Persson *et al.*, 1988). Our results suggest, therefore, that fish often respond rapidly to a P loading reduction, and in most cases major changes appeared in both community structure and biomass after <10 years. In subtropical shallow lakes, fish composition differs from that in northern temperate lakes (Schulz, Hoyer & Canfield, 1999), but oligotrophication can result in a similar pattern with a change in composition towards a higher contribution of piscivorous or omnivorous species.

The fast response of the fish community may challenge the idea of using fish manipulation as a lake restoration tool. There are good examples (although also many failures) showing that substantial removal of fish or stocking of piscivores or sometimes continuous fish management have improved the ecological state of lakes and sped up the recovery after reductions in nutrient loading (e.g. Hansson *et al.*, 1998; Lammens, 1999; Meijer *et al.*, 1999; Mehner *et al.*, 2002). Our data indicate that major changes in the fish community often occur <10–15 years after the loading reduction, even without manipulation of the fish stock. Moreover, in lakes with short hydraulic retention times, reduced turbidity of the water column as a result of fish manipulation can result in higher accumulation of P in the surface sediments of the lake than if the water had remained turbid because less particulate P is leaving the lakes and because of higher retention capacity in the sediment (Søndergaard *et al.*, 2003). This would result in lower losses of P via the lake outlet (Hansson *et al.*, 1998; Meijer *et al.*, 1999) and may thus delay the recovery in the long term if the lakes do not remain in the clear-water state (Søndergaard *et al.*, 2003). Although biomanipulation can be a useful tool not least for rapidly shifting turbid shallow lakes to their clear alternative states (Jeppesen *et al.*, 1990; Moss, 1990; Scheffer *et al.*, 1993), we suggest that careful deliberation is needed on the benefits of such measures in the long term.

The greater zooplankton : phytoplankton biomass ratio, smaller chl *a* : TP ratio at summer mean TP concentrations <100–150 μg L^{-1} and the increased contribution of *Daphnia* to zooplankton biomass in shallow lakes are all signs of decreased fish predation on zooplankton and of an enhanced top-down control of phytoplankton (Brooks & Dodson, 1965; Carpenter & Kitchell, 1993; Gliwicz, 2003; Jeppesen *et al.*, 2003). Changes in fish communities have the highest impact on zooplankton in shallow lakes where the overall predation risk appears to be higher (Keller & Conlon, 1994; Jeppesen *et al.*, 2003). Thus, we hypothesise that the often strong response to nutrient loading reduction is a consequence of both enhanced resource and predation control of phytoplankton. Further studies are needed to test this hypothesis. Research is especially needed in the subtropics and tropics, where the dominant fish taxa can often graze both phytoplankton and zooplankton (Lazzaro *et al.*, 2003) and fish predation on zooplankton is likely high even at low TP concentrations (Meerhoff *et al.*, 2003; Jeppesen *et al.*, 2005a), so that the typical trophic cascade type of effects may be less strong (Bays & Crisman, 1983; Crisman & Beaver, 1990).

We found indications of delayed responses of submerged macrophytes to increased water clarity in some case studies (Table 4). It may reflect lack of available seeds and turions and/or hindrance of establishment or spread by waterfowl grazing (Søndergaard *et al.*, 1996) or competition with benthic filamentous algae. Pronounced fluctuations in biomass and species dominance in the early phase of plant re-establishment (Lauridsen *et al.*, 2003) and low species richness at high nutrient levels may reduce the buffering capacity of plants against changes in environmental factors and thus enhance the risk of loss of the plants (Moss, 2001). Shallow eutrophic lakes may also rapidly switch states from clear to turbid and vice versa if water levels vary markedly (Blindow *et al.*, 1993; Havens *et al.*, 2001; Romo *et al.*, 2004). As plants play key roles in shallow lakes (Scheffer *et al.*, 1993; Moss, 2001), it is important to gain better insight into plant responses during recovery from excessive nutrient loading.

Phenological changes were not examined in the present analysis, but are addressed in several papers in this special issue (Anneville *et al.*, 2005; Jeppesen *et al.*, 2005a; Köhler *et al.*, 2005; Phillips *et al.*, 2005; Søndergaard *et al.*, 2005). There is clear evidence that in deep lakes the period in which P limits phytoplankton gradually increases from initially only summer towards inclusion of spring and autumn later in the recovery phase (Anneville *et al.*, 2005). In contrast, in shallow lakes the effect on P and plankton was initially greatest in spring and autumn, progressing later to the summer concurrently with a gradual reduction in internal P loading (Jeppesen *et al.*, 2005a; Phillips *et al.*, 2005; Søndergaard *et al.*, 2005). In shallow lakes experiencing major reductions in external loading of both N and P, the effect on the concentration of TP and chl *a* in the early recovery phase may also be high in summer, despite a continued high internal P loading, because nitrogen can become limiting (Hameed *et al.*, 1999; Köhler *et al.*, 2005). The significant response, particularly in spring and autumn in shallow lakes in the early recovery phase, emphasises the importance of year-round monitoring when evaluating the effect of reductions in nutrient loading rather than only during summer, as is present practice in many countries.

The conclusions derived in the present analysis are based on correlation evidence and interpretation in terms of cause-and-effect relationships may therefore be complicated by confounding factors. One of those is global warming. Although the data presented here are too infrequent (5 year intervals) to elucidate the potential confounding effects of global warming on response to reductions in nutrient loading, climatic effects have been examined for some of the lakes included in the present data set (e.g. Straile & Adrian, 2000; Anneville *et al.*, 2002; Kangur *et al.*, 2002; Nõges *et al.*, 2004). These analyses indicate an earlier onset of the clear-water phase (if any), stratification (if any) and fish spawning, reduced mixing in stratified lakes, and higher surface water temperature promoting higher internal P loading from sediment portions exposed to warm surface water. Moreover, in shallow and some deep lakes cyanobacteria may be more abundant and blooms may persist longer. However, the strong re-oligotrophication signals revealed by our analysis suggest that the observed changes in the lakes included in our data set reflect primarily the impacts of lower nutrient loadings rather than climate change. This conclusion is supported by results from mesocosm experiments which likewise suggest a much stronger effect of changing nutrient loadings than of changing temperatures in shallow lakes (McKee *et al*., 2003; Moss *et al*., 2003).

The general re-oligotrophication response patterns described here can be regarded only as a guideline when discussing the response of a particular lake. Each lake is unique in many respects and may exhibit a specific trajectory, as reflected in the appendices and figures presented (see also Moss *et al*., 2005). Further, although this study covers a wide range of lake types and climate zones, most of the lakes are situated in northern Europe and are relatively shallow Danish lakes in particular contributed importantly to the data set and had also been used previously to generate some of the hypotheses we examined. However, exclusion of the Danish lakes did not radically alter the overall pattern of response reported here. Reduction in the significance of trends was the most obvious difference, but can generally be attributed to reduced sample size (Appendices 1 and 3), although it could also reflect the greater depth gradient and climatic variation among the remaining lakes compared to the Danish lakes. For example we expect that the responses may differ between shallow cold-temperate and tropical or subtropical lakes, for instance owing to faster nutrient cycling and retention, better growth potential for submerged macrophytes, more truncated food webs and probably stronger top-down control of the zooplankton grazers in the warmer lakes (Lazzaro, 1997; Lazzaro *et al*. 2003; Meerhoff *et al*., 2003; Jeppesen *et al*., 2005b; Romo *et al*., 2005). Too few data from warm lakes were available for the present analysis to elucidate such differences in more detail. Thus, different patterns may emerge when examining warm-temperate or tropical lakes and very deep lakes, which also were poorly represented in the present data set.

Acknowledgments

This study was supported by the Danish Natural Science Research Council through the research project 'Consequences of weather and climate changes for marine and freshwater ecosystems. Conceptual and operational forecasting of the aquatic environment' (CONWOY 2052-01-0034), by the National Environmental Research Institute, Denmark, IGBP-PAGES and the EU project EUROLIMPACS (GOCE-CT-2003-505540). We thank the following scientists for contributing data and answering specific questions in the questionnaires: Therese East, Ryan Maki, Bruce Sharfstein, John Beaver, Nadine Angeli, Rita Adrian, Vera Istvanovics, Istvan Kobor, Peter Kozerski, Andreas Nicklisch, Laszlo G. Toth, Norbert Walz, Juta Haberman, Andu Kangur, Peeter Kangur, Reet Laugaste, Anu Milius, Tõnu Möls, Helle Mäemets, Alex Kirika, Iain Gunn, Edgar F. Lowe and Lawrence E. Battoe. We also thank the other participants in the Silkeborg symposium, Carl Sayer, Helen Bennion, Li Shijie, N. John Anderson, Oliver Heiri, Peter Leavitt, Richard W. Battarbee, and Tatyana Moiseenko, for stimulating discussions. Finally, we are grateful to the Danish counties for access to data on Danish lakes. We wish to thank Mark Gessner and two unknown reviewers for most valuable comments that helped tighten up the paper. Thanks are also due to Anne Mette Poulsen for editorial assistance and to NERI's graphical workshop for their patient help with the multiple reworking of figures during the process.

References

Ahlgren I. (1978) Response of Lake Norrviken to reduced nutrient loading. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **20**, 846–850.

Anneville O., Ginot V., Druart J.-C. & Angeli N. (2002) Long-term study (1974–1998) of seasonal changes in the phytoplankton in Lake Geneva: a multi-table approach. *Journal of Plankton Research*, **24**, 993–1007.

Anneville O., Gammeter S. & Straile D. (2005) Phosphorus decrease and climate variability: mediators of synchrony in phytoplankton changes among European peri-alpine lakes. *Freshwater Biology*, **50**, doi: 10.1111/j.1365-2427.2005.01429.x.

Bays J.S. & Crisman T.L. (1983) Zooplankton and trophic state relationships in Florida lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 1813–1819.

Benndorf J. (1990) Conditions for effective biomanipulation; conclusions derived from whole-lake experiments in Europe. *Hydrobiologia*, **200/201**, 187–203.

Benndorf J., Böing W., Koop J. & Neubauer I. (2002) Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. *Freshwater Biology*, **46**, 2282-2295.

Blindow I., Andersson G., Hargey A. & Johansson S. (1993) Long-term pattern of alternative stable states in two shallow eutrophic lakes. *Freshwater Biology*, **30**, 159–167.

Brooks J. L. & Dodson S. I. (1965) Predation, body size, and composition of plankton. *Science*, **150**, 28–35.

Carpenter S.R. & Kitchell J.F. (1993) *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge.

Colby P.J., Spangler G.R., Hurley D.A. & McCombie A.M. (1972) Effects of eutrophication on salmonid communities in oligotrophic lakes. *Journal of the Fisheries Research Board of Canada*, **29**, 975–983.

Cooke G.D., Welch E.B., Peterson S.A. & Newroth P.R. (1993) *Restoration and Management of Lakes and Reservoirs*, 2nd edn. Lewis Publishers, Boca Raton.

Coveney M. F., Lowe E.F., Battoe L.E., Marzolf E.R. & Conrow R. (2005) Response of a eutrophic, shallow subtropical lake to reduced nutrient loading. *Freshwater Biology*, **50**, doi: 10.1111/j.1365-2427.2005.01435.x.

Crisman T.L. & Beaver J.R. (1990) Applicability of planktonic biomanipulation for managing eutrophication in the subtropics. *Hydrobiologia*, **200/201**, 177–195.

Degerman E., Hammar J., Nyberg P. & Svärdson G. (2001) Human impact on the fish diversity in the four largest lakes of Sweden. *Ambio*, **30**, 522–528.

Dokulil M.T. & Teubner K. (2005) Do phytoplankton assemblages correctly track trophic changes? An assessment using directly measured and palaeolimnological data. *Freshwater Biology*, **50**, doi: 10.1111/j.1365-2427.2005.01431.x.

Drenner R.W. & Hambright K.D. (1999) Biomanipulation of fish assemblages as a lake restoration technique. *Archiv für Hydrobiologie*, **146**, 129–165.

Eckmann R. & Rösch R. (1998) Lake Constance fisheries and fish ecology. *Archiv für Hydrobiologie – Advances in Limnology*, **53**, 285–301.

Edmondson W.T. & Lehman J.T. (1981) The effect of changes in the nutrient income on the condition of Lake Washington. *Limnology and Oceanography*, **26**, 1–29.

Gliwicz Z.M. (1969) Studies on the feeding of pelagic zooplankton in lakes with varying trophy. *Ekologia Polska*, **17**, 663–708.

Gliwicz Z.M. (2003) Between hazards of starvation and risk of predation: the ecology of offshore animals. In *Excellence of Ecology, Book 12*. (Eds O. Kinne), International Ecology Institute, Oldendorf/Luhe.

Gonzáles Sagrario M.A., Jeppesen E., Gomà J., Søndergaard M., Lauridsen T. & Landkildehus F. (2005) Does high nitrogen loading prevent clear-water conditions in shallow lakes at moderately high phosphorus concentrations? *Freshwater Biology*, **50**, 27–41.

Gulati R.D., Lammens E.H.H.R., Meijer M.-L. & Van Donk E. (Eds) (1990) *Biomanipulation – Tool for Water Management*. Kluwer, Dordrecht.

Hameed H.A., Kilinc S., McGowan S. & Moss B. (1999) Physiological tests and bioassays – aids or superfluities to the diagnosis of phytoplankton nutrient limitation? A comparative study in the Broads and Meres of England. *European Phycological Journal*, **34**, 253–270.

Hanson J.M. & Peters R.H. (1984) Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 439–445.

Hansson L-A., Annadotter H., Bergman E., Hamrin S.F., Jeppesen E., Kairesalo T., Luokkanen E., Nilsson P.-Å., Søndergaard M. & Strand J. (1998) Biomanipulation as an application of food chain theory: constraints, synthesis and recommendations for temperate lakes. *Ecosystems*, **1**, 558–574.

Havens K.E., Jin K.R., Rodusky A.J., Sharfstein B., Brady M.A., East T.L., Iricanin N., James R.T., Harwell M.C. & Steinman A.D. (2001) Hurricane effects on a shallow lake ecosystem and its response to controlled manipulation of water level. *The Scientific World*, **1**, 44–70.

James C., Fisher J., Russell V., Collings S. & Moss B. (2005) Nitrate availability and plant species richness: implications for management of freshwater lakes. *Freshwater Biology*, **50**, 1049–1063.

Jensen J.P., Jeppesen E., Kristensen P., Christensen P.B. & Søndergaard M. (1992) Nitrogen loss and denitrification as studied in relation to reductions in nitrogen loading in a shallow, hypertrophic lake (Lake Søbygård, Denmark). *Internationale Revue der gesamten Hydrobiologie*, **77**, 29–42.

Jeppesen E., Jensen J.P., Kristensen P., Søndergaard M., Mortensen E., Sortkjær O. & Olrik K. (1990) Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. *Hydrobiologia*, **200/201**, 219–227.

Jeppesen E., Kristensen P., Jensen J.P., Søndergaard M., Mortensen E. & Lauridsen T. (1991) Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. *Memorie dell'Istituto Italiano di Idrobiologia*, **48**, 127–148.

Jeppesen E., Jensen J.P. & Søndergaard M. (2002) Response of phytoplankton, zooplankton and fish to re-oligotrophication: an 11-year study of 23 Danish lakes. *Aquatic Ecosystem Health and Management*, **5**, 31–43.

Jeppesen E., Jensen J.P., Jensen C., Faafeng B., Brettum P., Hessen D., Søndergaard M., Lauridsen T. & Christoffersen K. (2003) The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: study of 466 lakes from the temperate zone to the Arctic. *Ecosystems*, **6**, 313–325.

Jeppesen E., Jensen J.P., Søndergaard M. & Lauridsen T.L. (2005a) Response of fish and plankton to nutrient loading reduction in eight shallow Danish lakes with special emphasis on seasonal dynamics. *Freshwater Biology*, **50**, doi: 10.1111/j.1365-2427.2005.01413.x.

Jeppesen E., Søndergaard M., Mazzeo N., Meerhoff M., Branco C., Huszar V. & Scasso F. (2005b) Lake restoration and biomanipulation in temperate lakes: relevance for subtropical and tropical lakes. In: *Restoration and Management of Tropical Eutrophic Lakes*. (Ed. M.V. Reddy), pp. 331–349. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Kalff J. (2002) *Limnology – Inland Water Ecosystems*. Prentice-Hall Inc., Upper Saddle River, NJ.

Kangur K., Milius A., Möls T., Laugaste R. & Haberman J. (2002) Lake Peipsi: changes in nutrient elements and plankton communities in the last decade. *Aquatic Ecosystem Health and Management*, **5**, 363–377.

Keller W. & Conlon M. (1994) Crustacean zooplankton community and lake morphometry in Precambrian shields. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2424–2434.

Köhler J., Hilt S., Adrian R., Nicklisch A., Kozerski H.P. & Walz N. (2005) Long-term response of a shallow, moderately flushed lake to reduced external phosphorus and nitrogen loading. *Freshwater Biology*, **50**, doi: 10.1111/j.1365-2427.2005.01430.x.

Lammens E. H.H.R. (1999) The central role of fish in lake restoration and management. *Hydrobiologia*, **395/396**, 191–198.

Lauridsen T.L., Jensen J.P., Jeppesen E. & Søndergaard M. (2003) Response of submerged macrophytes in Danish lakes to nutrient loading reductions and biomanipulation. *Hydrobiologia*, **506/509**, 641–649.

Lazzaro X. (1997) Do the trophic cascade hypothesis and classical biomanipulation approaches apply to tropical lakes and reservoirs? *Verhandlungen der Internationalen Vereinigung für Limnologie*,, **26,** 719–730.

Lazzaro X, Bouvy M., Ribeiro R.A., Oliviera V.S., Sales L.T., Vasconcelos A.R.M. & Mata M.R. (2003) Do fish regulate phytoplankton in shallow eutrophic Northeast Brazilian reservoirs? *Freshwater Biology*, **48**, 649–668.

Levine S.N. & Schindler D.W. (1989) Phosphorus, nitrogen, and carbon dynamics of experimental Lake 303 during recovery from eutrophication. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 2–10.

Manca M. & Ruggio D. (1998) Consequences of pelagic food web changes during a long-term lake oligotrophication process. *Limnology and Oceanography*, **43**, 1368–1373.

Marsden S. (1989) Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. *Freshwater Biology*, **21**, 139–162.

McCauley E., Downing J.A. & Watson S. (1989) Sigmoid relationships between nutrients and chlorophyll among lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1171–1175.

McKee D., Atkinson D., Collings S.E., Eaton J.W., Gill A.B., Harvey I., Hatton K., Heyes T., Wilson D. & Moss B. (2003) Response of freshwater microcosm communities to nutrients, fish and elevated temperature during winter and summer. *Limnology and Oceanography*, **48**, 707–722.

Meerhoff M., Mazzeo N., Moss B., Rodríguez-Gallego L. (2003) The structuring role of free-floating versus submerged plants in a subtropical shallow lake. *Aquatic Ecology*, **37**, 377–391.

Mehner T., Benndorf J., Kasprzak P. & Koschel R. (2002) Biomanipulation of lake ecosystems: successful applications and expanding complexity in the underlying science. *Freshwater Biology*, **47**, 2453–2465.

Meijer M.-L., de Boois I., Scheffer M., Portielje R. & Hosper H. (1999) Biomanipulation in the Netherlands: an evaluation of 18 case studies in shallow lakes. *Hydrobiologia*, **408/409**, 13–30.

Mitchell S.F. & Perrow M.R. (1997) Interactions between grazing birds and macrophytes. In: *The Structuring Role of Submerged Macrophytes in Lakes*. (Eds E. Jeppesen, MA. Søndergaard, MO. Søndergaard, & K. Christoffersen), Ecological Studies, Volume 131. pp. 175–196. Springer Verlag, New York.

Mosello R.A., Barbieri A., Brizzio M.C., Calderoni A., Marchetto A., Passera S., Rogora M. & Tartari G.A. (2001) Nitrogen budget of Lago Maggiore: the relative importance of atmospheric deposition and catchment sources. *Journal of Limnology*, **60**, 27–40.

Moss B. (1990) Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. *Hydrobiologia*, **200/201**, 367–377.

Moss B. (2001) *The Broads. The People's Wetland. The New Naturalist*. Harper Collins Publishers, London.

Moss B., McKee D., Atkinson S., Collings S.E., Eaton J.W., Gill A.B., Harvey I., Hatton K., Heyes T. & Wilson D. (2003) How important is climate? Effects of warming, nutrient addition and fish on phytoplankton in shallow lake microcosms. *Journal of Applied Ecology*, **40**, 782–792.

Moss B., Barker T., Stephen D., Williams A.E., Balayla D., Beklioglu M. & Carvalho L. (2005) Consequences of reduced nutrient loading on a lake system in a lowland catchment: deviations from the norm? *Freshwater Biology*, **50**, doi: 10.1111/j.1365-2427.2005.01416.x.

Müller R. & Meng H.J. (1992) Past and present state of the ichthyofauna of Lake Lugano. *Aquatic Sciences*, **54**, 338–350.

Nõges T., Tonno T. I., Laugaste R., Loigu E. & Skakalski B. (2004) The impact of changes in nutrient loading on cyanobacterial dominance in Lake Peipsi (Estonia/Russia). *Archiv für Hydrobiologie*, **160**, 161–279.

Nürnberg G. & LaZerte B.D. (2004) Modeling the effect of development on internal phosphorus load in nutrient-poor lakes. *Water Resources Research*, **40**, 0W01105. doi:1029/2003WR002410.

OECD (1982) *Eutrophication of Waters. Monitoring, Assessments and Control*. OECD, Paris, 210 pp.

Perrow M.P., Meijer M-L., Dawidowicz P. & Coops H. (1997) Biomanipulation in shallow lakes: state of the art. *Hydrobiologia*, **342/343**, 355–363.

Persson L., Andersson G., Hamrin S.F. & Johansson L. (1988) Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. In: *Complex Interactions in Lake Communities*. (Eds S.R. Carpenter), pp. 45–65. Springer Verlag, New York.

Phillips G., Kelly A., Pitt J.-A., Sanderson R. & Taylor E. (2005) The recovery of a very shallow eutrophic lake, 20 years after the control of effluent derived phosphorus. *Freshwater Biology*, **50**, doi: 10.1111/j.1365-2427.2005.01434.x.

Portielje R. & Van der Moelen D.T. (1998) Relationships between eutrophication variables: from nutrient loading to transparency. *Hydrobiologia*, **408/409**, 375–387.

Reynolds C.F. (2002) Resilience in aquatic ecosystems – hysteresis, homeostasis and health. *Aquatic Ecosystem Health and Management*, **5**, 3–17.

Romo S., Miracle M.R., Villena M-J., Rueda J., Ferrial C. & Vicente E. (2004) Mesocosm experiments on nutrient and fish effects on shallow lake food webs in a Mediterranean climate. *Freshwater Biology*, **49**, 1593–1607.

Romo S., Villena M.-J., Sahuquillo M., Soria J.M., Giménez M., Alfonso T., Vicente E. & Miracle M.R. (2005) Response of a shallow Mediterranean lake to nutrient diversion: does it follow similar patterns as in northern shallow lakes? *Freshwater Biology*, **50**, doi: 10.1111/j.1365-2427.2005.01432.x.

Ruggio D., Morabito G., Panzani P. & Pugnetti A. (1998) Trends and relations among basic phytoplankton characteristics in the course of the long-term oligotrophication of Lake Maggiore (Italy). *Hydrobiologia*, **370**, 243–257.

Sas H. (Ed.) (1989) *Lake Restoration by Reduction of Nutrient Loading. Expectation, Experiences, Extrapolation*. Academia Verlag Richardz GmbH., St Augustin.

SAS Institute (1989) *SAS/Stat User's Guide. Version 6.*, 4th edn. Sas Institute Inc., Volume 1+2, Cary.

Scheffer M., Hosper S.H., Meijer M.-L., Moss B. & Jeppesen E. (1993) Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution*, **8**, 275–279.

Schelske C. L. & Stoermer E. F. (1971) Eutrophication, silica and predicted changes in algal quality in Lake Michigan. *Science*, **173**, 423–424.

Schelske C. L., Stoermer E. F., Fahnenstiel G. L. & Haibach M. (1986) Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 407–415.

Schulz E.J, Hoyer M.V. & Canfield D.E. (1999) An index of biotic integrity: a test with limnological and fish data from sixty Florida Lakes. *Transactions of the American Fisheries Society*, **128**, 564–577.

Sharpley A., Foy B. & Whiters P. (2000) Practical and innovative measures for control of agricultural phosphorus losses to water: an overview. *Journal of Environmental Quality*, **29**, 1–9.

Smith V.H. (1983) Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science*, **221**, 669–671.

Smith V.H., Bierman V.J., Jones B.L. & Havens K.E. (1995) Historical trends in the Lake Okeechobee ecosystem IV. Nitrogen : phosphorus ratios, cyanobacterial dominance, and nitrogen fixation potential. *Archiv für Hydrobiologie*, **107**, 71–88.

Søndergaard M., Olufsen L., Lauridsen T., Jeppesen E. & Vindbæk Madsen T. (1996) The impact of grazing waterfowl on submerged macrophytes: in situ experiments in a shallow eutrophic lake. *Aquatic Botany*, **53**, 73–84.

Søndergaard M., Jensen J.P., Jeppesen E. & Møller P.H. (2002) Seasonal dynamics in the concentrations and retention of phosphorus in shallow Danish lakes after reduced loading. *Aquatic Ecosystem Health and Management*, **5**, 19–23.

Søndergaard M., Jensen J.P. & Jeppesen E. (2003) Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia*, **506/509**, 135–145.

Søndergaard M., Jensen J.P. & Jeppesen E. (2005) Seasonal response of nutrients to reduced phosphorus loading in 12 Danish lakes. *Freshwater Biology*, **50**, doi: 10.1111/j.1365-2427.2005.01412.x.

Straile D. & Adrian R. (2000) The North Atlantic oscillation and plankton dynamics in two European lakes – two variations on a general theme. *Global Change Biology*, **6**, 663–670.

Van der Moelen D.T. & Portielje R. (1999) Multi-lake studies in the Netherlands. *Hydrobiologia*, **408/409**, 359–365.

Vollenweider R.A. (1976) Advances in defining critical loading levels for phosphorus in lake eutrophication. *Memorie dell'Istituto Italiano di Idrobiologia*, **33**, 53–83.

Willén E. (2001a) Four decades of research on the Swedish large lakes Mälaren, Hjälmaren, Vättern and Vänern: the significance of monitoring and remedial measures for a sustainable society. *Ambio*, **30**, 458–466.

Willén E. (2001b) Phytoplankton and water quality characterization: experiences from the Swedish large lakes Mälaren, Hjälmaren, Vättern and Vänern. *Ambio*, **30**, 529–537.

Windolf J., Jeppesen E., Jensen J.P. & Kristensen P. (1996) Modelling of seasonal variation in nitrogen retention: a four-year mass balance study in 16 shallow lakes. *Biogeochemistry*, **33**, 25–44.

Wojciechowski I., Wojciechowska W., Czernas K., Galek J. & Religa K. (1988) Changes in phytoplankton over a ten-year period in a lake undergoing de-eutrophication due to surrounding peat bogs. *Archiv für Hydrobiologie – Advances in Limnology*, **78**, 373–387.

Yurk J.J. & Ney J.J. (1989) Phosphorus-fish community biomass relationships in southern Appalachian Reservoirs: can lakes be too clean for fish? *Lake and Reservoir Management*, **5**, 83–90.

(Manuscript accepted 29 December 2004)

Appendix 1 Changes in physico-chemical variables for surface water and the zooplankton : chl *a* ratio during recovery of 35 lakes from excessive nutrient loading (duration – see Table 1)

Lake no.	Lake name	TP summer	TP annual	SRP summer	SRP : TP summer	TN inflow annual	TN summer	DIN summer	TN : TP inflow annual	TN : TP summer	DIN : TN summer	Chl *a* summer	Chl *a* annual	Chl *a* : TP summer	Chl *a* : TP annual	Zoo : Chl *a* summer	Zoo : Chl *a* annual	Secchi depth summer
1	Little Mere	–	–					–				–	–	+				+
2	Eemmeer	–	–	–	–	–	–	–	+	+	+	–	–	+	+			+
3	Gundsømagle	–	–	–	–	No	–	No	+	+	+	–	–	+	+	+	+	+
4	Gooimeer	–	–	–	–	–	–	–	+	+	+	–	–	+	+			+
5	Veleuwemeer	–	–	–	–		–	+		+	+	–	–	No	–			+
6	Søgård	–	–	–	–	+	–	–	–	+	+	–	–	No	–	+	+	+
7	Albufera	–	–	–	–	–		+	+			–	–	+	+	+	+	No
8	Vesterborg	–	–	–	–	No	–	No	+	+	+	–	–	–	–	+	No	+
9	Arresø	–	–	–	–	–	–	+	+	+	+	–	–	+	+	+	+	+
10	Barton	–	–	–	–			No			+	–	–	No	+			+
11	Bagsværd	–	–	–	–		–	No		+	+	No	–	+	+	+	+	+
12	Apopka		–										–		No			+
13	Müggelsee	No	(–)	+	+	–	–	–	–	–	–	–	–	–	–	–	No	+
14	Damhussøen	–	–	–	–		–	–		+	+	–	No	+	+	–	–	+
15	Bryrup	–	–	–	–	+	–	No	+	+	+	–	–	+	+	+	+	+
16	Ørnsø	–	–	–	–	–	–	–	+	+	+	–	–	+	No	+	+	+
17	Balaton	+	+	+	+	–	–	–	+	–	–	–	–	–	–		+	+
18	Galten	–		–	–	–	–	–	+	–	–	No		+				No
19	Okeechobee	+	+	+	No	–	–	+	–	–	+	No	No	No	No	(–)	No	–
20	Leven	(–)	–	No	No		No	–			(–)	No	No	No	+			(+)
21	Võrtsjärv	No	–	No	(–)	–	No	–	+	No	–	+	+	No	+	No	No	No
22	Peipsi	+	+	No	–	–	+	+	–			+	+					No
23	Rostherne Mere	–	–	–				+				(–)	(–)					
24	Tystrup	–	–	–	–	No	–	–	+	+	+	+	+	+	+	–	–	–
25	Tissø	–	No	–	–	No	No	+	+	+	+	–	–	No	–	+	+	+
26	Furesø	–	–	–	–		–	No		+	No	No	+	+	+	+	–	+
27	Ekoln	–		–	–	–	+	+	+	+	+	–		(+)		No		+
28	Constance	–	–	–	–	+	+	+	+	+	+	–	–	+	+	No	No	+
29	Washington	–	–	–	–	–	–	–	+	+	+	–	–	–	–	+	+	+
30	Scharmützelsee	–	–	No	+			–		+	–	No	No	+	+			
31	Geneva	–	–	–	–	–	+	+	–	+	+	No	No	+	+	No	No	–
32	Ravn	–	–	–	–	No	No	No	+	+	+	–	–	No	No	–	–	+
33	Mondsee	–	–	–	–	No			+			–	–					+
34	Maggiore	–	–	–	–	No	No	No	+	+	+	–	–		No			+
35	Vättern	–	–	–	–		+	+		+	+	–		(+)				+

Lake type	Trend	*P*-value of chi-square test																
Shallow	No, +, –	0.0002	0.001	0.002	<0.0001	0.005	<0.0001	NS	0.07	0.007	0.06	0.0009	0.0002	0.09	0.06	0.04	0.06	0.0001
	+, –	0.003	0.001	0.008	0.001	0.02	0.0005	NS	0.07	0.03	0.06	0.002	0.001	0.03	NS	NS	0.02	0.0003
Deep	No, +, –	<0.0001	0.004	0.002	0.004	NS	NS	NS	0.02	<0.0001	0.003	0.02	0.02	0.05	NS	NS	NS	0.01
	+, –	<0.0001	0.004	<0.0001	0.004	NS	NS	NS	0.02	<0.0001	0.01	0.01	0.09	0.03	NS	NS	NS	0.01
Shallow (–DK)	+, –	NS	0.05	NS	0.06	<0.0001	0.04	NS	NS	NS	NS	0.06	0.05	NS	NS	NS	NS	0.02
Deep (–DK)	+, –	<0.0001	<0.0001	<0.0001	0.04	NS	NS	NS	NS	<0.0001	0.06	<0.0001	<0.0001	NS	NS	NS	NS	0.06

Signs in parentheses are trends that must be interpreted with great caution. Lakes 1–22 are shallow, all others are deep. Also shown at the bottom are results of chi-square tests for differences when all three categories of trends (+, – and no change) were included and when only lakes showing either positive (+) or negative (–) changes were included.

TP, total phosphorus; SRP, soluble reactive phosphorus; TN, total nitrogen; DIN, dissolved inorganic nitrogen; Chl *a*, chlorophyll *a*; Zoo, zooplankton biomass; +, increasing during recovery; –, decreasing; No, no change; empty cells, no data; NS, not significant at the 10% level; –DK, data set excluding Danish lakes.

Appendix 2 Changes in the fish community during recovery of 25 lakes from excessive nutrient loading

Lake no.	Lake name	Fish catch method	Period covered (year)	CPUE	Community change		% Piscivores by weight (including small perch)	
					From	To	From	To
2,4	Eemmeer and Gooimeer	Trawling	20	−35%	Bream-(roach-smelt)	Bream-pikeperch-roach	5	23
3	Gundsømagle	Gill nets	11	−29%	Roach-crucian carp-tench	Roach-perch-pike-crucian carp	5	29
5	Veleuwemeer*	Trawling	25	−75%	Bream-pikeperch	Roach-perch-bream-pikeperch		–
6	Søgård	Gill nets	10	+43%	Roach-bream-perch	Bream-roach perch	16	23
7	Albufera	Commercial/ gill nets	10		Mullets	Mullets	1	
8	Vesterborg	Gill nets	10	−33%	Bream-roach-perch	Roach-bream-perch-pike	9	25
9	Arresø	Gill nets	10	−31%	Bream-roach	Bream-roach-pikeperch	1	32
11	Bagsværd	Gill nets	11	−25%	Bream-roach-pikeperch	Bream-roach-perch	18	11
13	Müggelsee	Commercial	10		Bream-roach			
14	Damhussøen	Gill nets	11	+3%	Perch-tench-roach	Perch-tench-roach	46	39
15	Bryrup	Gill nets	10	0%	Roach-perch	Roach-perch	26	27
16	Ørnsø	Gill nets	5	−8%	Bream-roach-perch	Roach-bream-perch	19	18
17	Balaton	Gill nets	16	−50%*	Bream-roach			+
20	Leven	Sport fishing		(+)				
22	Peipsi	Trawling	15	−67%	Pikeperch-pike-roach-perch	Pikeperch-ruffe-roach	69	70
24	Tystrup	Gill nets	9	−12%	Roach-bream-perch	Perch-roach-bream-bleak	21	50
25	Tissø	Gill nets	11	+22%	Roach-perch-bream	Roach-perch-bream	15	34
26	Furesø	Gill nets	11	−36%	Roach-perch-bream-smelt	Roach-perch-bream	12	53
27	Ekoln			(−)				
28	Constance	Commercial	25	–	Perch-(whitefish)	(Perch)-whitefish, decrease in perch catches and a shift of perch from pelagic to the littoral zone		
31	Geneva	Commercial	25	−40%	Perch-whitefish-(roach)	Whitefish-perch-(pike)		
32	Ravn	Gill nets	6	−20%	Perch-roach-bream	Perch-roach	48	58
34	Maggiore	Commercial		Major reduction	Whitefish-Bleak	Whitefish-shad, bleak Major decline in whitefish and bleak		
35	Vättern	Commercial	5	−60%	Whitefish-salmonids	Increase in salmonids, major decrease in whitefish		

Lake type	Trend	*P*-value of chi-square test	*P*-value of chi-square test
Shallow	No, +, −	0.02	NS
	+, −	0.08	NS
Deep	No, +, −	0.02	<0.0001
	+, −	0.02	<0.0001

*Removal of planktivorous fish in addition to reduction in nutrient loading.

Signs in parentheses are trends that must be interpreted with great caution. Lakes 1–22 are shallow, all others are deep. For chi-square tests at the bottom see legend of Appendix 1.

CPUE, catch per unit effort (or changes in catches when the method is 'commercial'); +, increasing during recovery; −, decreasing; empty cells, no data available.

Appendix 3 Changes in summer mean phytoplankton biovolume, contributions by various taxa to the total phytoplankton biovolume, zooplankton biomass and contribution of *Daphnia* to the total zooplankton biomass during the recovery period

Lake no.	Lake name	Biovolume of phytoplankton in summer	Percentage of phytoplankton biovolume						Biomass of zooplankton in summer	Percentage of *Daphnia* biomass summer
			Cyanobacteria	Chlorophytes	Diatoms	Cryptophytes	Dinophytes	Chrysophytes		
1	Little Mere		−	+		+				
3	Gundsømagle	−	+	−	+	+	−	+	−	+
6	Søgård	−	+	−	No	+	No	No	No	+
7	Albufera	−	No	+	+	+	+		−	No
8	Vesterborg	−	−	−	+	+	+	+	−	+
9	Arresø	−	No	No	+	+	No	No	+	+
10	Barton		−*						−	−
11	Bagsværd	−	−	+	+	+	No	+	+	+
12	Apopka		No	−	+		−			
13	Müggelsee	−	−	No	+	No	No	+	−	
14	Damhussøen	No	+	−	+	+	No	No	−	+
15	Bryrup	No	+	+	−	−	+	+	+	+
16	Ørnsø	−	No	No	+	No	−	+	+	−
17	Balaton	−	−	+	+	+	+	−	−	+
18	Galten	(−)	−		+	−		+		
19	Okeechobee		+	−	−	−	−	−	−	(+)
21	Võrtsjärv	+	+	+	−	No	No	(+)		
22	Peipsi	+	+	−	−	+	+	+	+	
24	Tystrup	+	−	No	−	−	+	+	−	−
25	Tissø	−	No	−	+	−	No	No	+	+
26	Furesø	−	−	+	−	+	+	−	+	−
27	Ekoln	−	−			+	+	+	(−)	
28	Constance	(−)	−	−	+	No	(+)	(+)	−	−
29	Washington	−	−	+	+	+	+	+	(+)	+
30	Scharmützelsee			+		−	+			
31	Geneva		−	−	+		−	+	−	−
32	Ravn	−	+	−	+	−	No	+	−	+
33	Mondsee	−	−	+		+	+	+		
34	Maggiore	No	−	−	+	No	+	+	−	−
35	Vättern	No			−	−	+	+		

Lake type	Trend	All (−DK)	All (−DK)	All (−DK)	All (−DK)	All (−DK)	All (−DK)	All (−DK)	All (−DK)	All (−DK)
Shallow	No, +, −	0.01 (NS)	NS (NS)	NS (NS)	0.007 (NS)	0.03 (NS)	NS (NS)	0.05 (NS)	NS (NS)	0.009 (NS)
	+, −	0.02 (NS)	NS (NS)	NS (NS)	0.07 (NS)	0.02 (NS)	NS (NS)	0.03 (NS)	NS (NS)	0.04 (NS)
Deep	No, +, −	0.05 (NS)	0.008 (<0.0001)	NS (NS)	(NS) (NS)	NS (NS)	0.009 (0.04)	0.003 (<0.0001)	NS (NS)	NS (NS)
	+, −	0.03 (NS)	0.02 (<0.0001)	NS (NS)	(NS) (NS)	NS (NS)	0.01 (0.04)	0.01 (<0.0001)	NS (NS)	NS (NS)

*By number.

Signs in parentheses are tendencies that must be treated with great caution. Lakes 1–22 are shallow, all others are deep. For chi-square tests at the bottom see legend of Appendix 1.

All, *P*-value of chi-square tests for all lakes; −DK, *P*-values of chi-square tests for all lakes except the Danish ones.

+, increasing during recovery; −, decreasing; no, no change; empty cells, no data.