# Does resuspension prevent a shift to a clear state in shallow lakes during reoligotrophication?

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#### *Abstract*

Water managers often debate whether resuspension of sediment with high organic matter and water content accumulated during eutrophication delays improvement of water clarity after reduction of external nutrient loading. Using data from 15 shallow (mean depth  $\leq$  5 m) eutrophic lakes surveyed during 8–12 yr, we show that the reduction in phytoplankton biomass after external loading reductions of phosphorus or changes in the abundance of planktibenthivorous fish was accompanied by a proportional or nearly proportional reduction in detritus and inorganic suspended solids. The reduction occurred irrespective of lake size (0.1–40 km<sup>2</sup>), extent of phytoplankton biomass reduction (up to 10-fold), and despite dominance of sediments with high water and organic content. Therefore, we conclude that recovery of shallow lakes after nutrient loading or fish stock reduction is apparently not significantly delayed by resuspension of organic or inorganic matter accumulated in the sediment during eutrophication.

World-wide, many lakes suffer from eutrophication due to high external loading from sewage, industries, and runoff from cultivated soils. Large efforts have been made during the last two decades to combat eutrophication by reducing

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excess loading (Sas 1989; Van der Moelen and Boers 1994), and this has led to improvement of the ecological state and water quality of some lakes (Sas 1989; Jeppesen et al. 2002). However, many lakes show great resistance to improvement due to high internal loading of phosphorus (Sas 1989), homeostasis in the fish community (Gulati et al. 1990; Perrow et al. 1997), and waterfowl grazing (Søndergaard et al. 1997). Furthermore, it has been argued that resuspension of the sediment with high organic matter and water content accumulated during eutrophication also delays or even prevents a shift to the clearwater state in large, shallow, windexposed lakes (Bachmann et al. 1999; Meijer et al. 1999). The arguments suggest that continuous resuspension of detritus reduces the light climate sufficiently to prevent growth of submerged macrophytes (Bachmann et al. 2001*a*) or that the sediment in the reoligotrophication phase is too loose

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54 1.1 53 0.9 32 0.4

Table 1. Physicochemical characteristics of the 15 study lakes. The chemical data represent summer averages (1 May–1 Oct 1989–2000).

and therefore unsuitable for establishment of rooted plant communities (Meijer et al. 1999). Yet plant establishment has occurred in several large shallow reoligotrophic lakes, like Lake Veluwe and Lake Wolderwejd in The Netherlands (Hosper 1997) or following fish manipulation as seen in the U.S.A. (Hanson and Butler 1990). Lowe et al. (2001) also observed a reduction in suspended solids roughly proportional to the reduction in Chl *a* in large Lake Apopka in Florida, where plant establishment remains poor (Lowe et al. 2001). The ongoing debate on the future perspectives of trophic state and management for Lake Apopka (Bachmann et al. 1999; Lowe et al. 2001; Bachman et al. 2001*a,b*; Schelske and Kenney 2001) illustrates well the lack of consensus on the role of resuspension for lake recovery.

Secchi depth (m)

Nonalgal organic suspended solids: SS (%)

We contribute to the debate by presenting data on inorganic and organic fractions of suspended matter from 15 shallow Danish lakes after major reductions in external total phosphorus (TP) loading (Jeppesen et al. 2002; Søndergaard et al. 2002). The lakes vary in size from 0.1 to 40 km2 and in mean depth from 1.0 to 4.6 m and were generally eutrophic (Table 1).

#### Materials and methods

Water samples (depth-integrated samples from the photic zone) for analyses of chemical variables and phytoplankton biovolume were taken at a midlake station biweekly during summer (1 May–1 October) and monthly during the remainder of the year. Phytoplankton was counted on Lugol-fixed samples using an inverted microscope. Biovolume was calculated by fitting the different species and genera to geometric forms. A factor of 0.29 was used to convert phytoplankton biovolume (mm<sup>3</sup>  $L^{-1}$ ) to biomass (mg organic dry weight  $L^{-1}$ ) (Reynolds 1984).

Suspended solids (SS) were determined as matter retained on GF/C filters after drying at  $105^{\circ}$ C for 24 h and the organic content as loss-on-ignition (LI)  $(550^{\circ}C, 2 h)$  of SS. LI may potentially include some  $CaCO<sub>3</sub>$ , thereby overestimating the organic content. Yet parallel measurements of LI and particulate COD (chemical oxygen demands) on 1,811 samples, however, show good correspondence between the two measures (Jeppesen et al. 1999). Calculations were made to determine nonalgal organic suspended solids (naorgSS) by subtracting phytoplankton biomass from LI, inorganic

suspended solids (inorgSS) by subtracting LI from SS, and nonalgal suspended solids (naSS) by summing up naorgSS and inorgSS. Chlorophyll *a* (Chl *a*) was measured after ethanol extraction of matter retained on a GF/C filter.

88 2.0

Total discharge of tributaries and outlets  $(Q<sub>out</sub>)$  was measured monthly with an OTT-propeller. Water level (H) in the inlet streams was automatically and continuously recorded and daily discharge calculated by use of the relationship obtained between H and  $Q_m$ . Daily TP loading was estimated for each inlet as the product of the daily water discharge and phosphorus concentration obtained by linear interpolation. Loading from the lake catchment not covered by streams was calculated as  $Q_{\text{out}} - Q_{\text{in}}$  assuming TP to equal the *Q*-weighted mean concentrations in the measured inlets. Atmospheric deposition on the lake surface was estimated using an average rate for Denmark of 0.2 kg P ha<sup>-1</sup> yr<sup>-1</sup>.

Sediment cores were taken with a Kajak sampler (5.2 cm in diameter) at 4–7 midlake stations in each of four lakes, then sliced and analyzed for wet weight, dry weight, and loss-on-ignition  $(550^{\circ}C, 1 h)$  and total phosphorus (TP) (as molybdate reactive phosphorus after extraction of ash-free sediment with 1 mol HCl  $L^{-1}$ ). Only data on the upper 5 cm of the sediment was used in the present analyses.

To test trends in the time series at selected physicochemical variables, we used the seasonal Kendall trend test (Hirsch and Slack 1984). This test is a robust nonparametric statistical method commonly used in environmental science for testing seasonal trends in time series. We used data from 7 yr, from the months of April to October, inclusive. The other calendar months were excluded because of too many missing values. For a given year and month, we averaged all observations before analysis.

#### Results and discussion

*Regression analyses*—The 15 lakes are shallow and nutrient rich (summer mean:  $0.064 - 0.850$  mg P  $L^{-1}$ ) with high phytoplankton biomass (Chl *a*), high concentrations of SS (Table 1), and, accordingly, low Secchi depth (summer mean: 0.4–2 m). The contribution of both naorgSS and that of inorgSS to SS were overall high, which is typical of shallow Danish lakes (Jeppesen et al. 1999), and reflects the shallowness of the lakes and the frequent occurrence of resuspension. NaorgSS averaged 54% and inorgSS 26% dur-

Table 2. Pearson correlation coefficients for some selected physicochemical variables in 15 study lakes over 8–12 years. Number of samples ranged between 1,775 and 3,144. All pairwise comparisons were significant ( $P$ <0.0001), though the weakest ones must be interpreted with care because of the large number of samples.

	InorgSS	NaorgSS	Chl $a$	TP	Secchi	Area	Mean depth
Suspended solids (SS)	0.84	0.71	0.83	0.74	$-0.90$	0.26	$-0.25$
Inorganic suspended solids (inorgSS)		0.50	0.65	0.63	$-0.76$	0.12	$-0.42$
Nonalgae suspended organic solids (naorgSS)			0.58	0.61	$-0.64$	0.47	$-0.20$
Chlorophyll $a$ (Chl $a$ )				0.71	$-0.84$	0.18	$-0.22$
Total phosphorus (TP)					$-0.77$	0.11	$-0.33$
Secchi depth (Secchi)						$-0.18$	0.32
Lake area (area)							0.28

ing summer (Table 1). Pearson correlation analyses on logtransformed data showed highly significant positive correlations between SS, inorgSS, naorgSS, Chl *a*, and inlake TP (Table 2). In addition, all forms of suspended matter (SS, inorgSS, naorgSS, and Chl *a*) were weakly positively correlated to lake area and negatively so to lake mean depth (Table 2). In a multiple regression, Chl *a,* in-lake TP, lake area, and mean depth contributed significantly to the variation in SS, inorgSS, and naorgSS. We tested for collinearity by calculating a condition index (Rowlings 1988). A condition index around 10 indicates that collinearity affects the regression, a collinearity of 30 and 100 being moderate to strong and values over 100 indicating serious collinearity problems. For the three models with Chl *a,* TP, area, and depth as explanatory variables, we obtained condition indices of around 20, indicating moderate problems. However, by exclusion of TP from the models (Table 3), the index was  $<10.$ 

As Secchi depth is highly significantly related to SS, inorgSS, and naorgSS (Table 2), both detritus and inorganic suspended solids could potentially delay or prevent the clearing up of lakes during the recovery phase following nutrient loading reductions, provided that these variables are not affected themselves by the reduction in phytoplankton biomass. To illustrate how SS, naorgSS, and inorgSS are affected by changes in phytoplankton biomass, we focus on the four lakes with the largest changes in Chl *a* during the survey period, due to either reduced external TP loading prior to (data not shown) or during the course of the investigation (Figs. 1–4). For one lake, Lake Arreskov, in addition to TP reduction, the biomass of planktivorous fish was reduced substantially by fish kills in 1991 and stocking of piscivorous pike in the following years (Fig. 4). For all four lakes, SS followed closely the changes in Chl *a* and also

largely the algal biomass (Figs. 1–4, panels B and C). Accordingly, only comparatively minor changes occurred in the proportion of naorgSS and inorgSS to SS even though contributions to SS were high throughout the year (Figs. 1–4, panel D).

Time series analyses—Lake Dons (0.36 km<sup>2</sup>, mean depth: 1.0 m), showed a significant decline (detrended for seasonal variations) in in-lake TP ( $P = 0.018$ ), Chl *a* ( $P = 0.017$ ), while Secchi depth increased  $(P = 0.010)$ . Summer mean Chl *a* declined from 444 to 232  $\mu$ g L<sup>-1</sup> from 1989–1997 (Fig. 1), SS from 76 to 32 mg  $L^{-1}$ , and LI from 42 to 22 mg  $L^{-1}$ . We found no significant changes ( $P > 0.05$ ) in the fractions of inorgSS, phytoplankton biomass, nonalgae suspended matter to SS or naorgSS, all detrended for seasonal variations.

In Lake Arresø (40 km2 , mean depth: 2.9 m), Chl *a* and SS showed increasing trends until 1993, followed by a major decline coinciding with a reduction of in-lake TP (Fig. 2). The share of nonalgae suspended matter was constantly high except for a reduction at the end of the study period, while the proportion of inorgSS tended to increase. Considering the entire period only, in-lake TP showed a significant decline during the period. However, if only the period with a declining trend (1994–2000) was included, a significant decline was found for in-lake TP ( $P = 0.010$ ), Chl *a* ( $P = 0.010$ ) 0.018), SS ( $P = 0.009$ ), while no significant decline ( $P >$ 0.05) was found for the contribution of inorgSS to SS. Only the contribution of naorgss to SS decreased slightly  $(P =$ 0.029).

In Lake Vesterborg (0.21 km<sup>2</sup>, mean depth: 1.4 m), a significant decline was observed for in-lake TP ( $P = 0.003$ ), Chl *a* ( $P = 0.007$ ), SS ( $P = 0.001$ ) and phytoplankton biomass ( $P = 0.006$ ), while Secchi depth increased ( $P = 0.001$ ).

Table 3. Multiple linear regression of logarithmically transformed (natural log) total suspended solids (SS), inorganic suspended solids (inorgSS), and nonalgae organic suspended solids (naorgSS) (all in mg DW  $L^{-1}$ ) in the 15 study lakes studied during 8–12 years versus a number of independent variables, chlorophyll *a* (Chl *a*), lake area (area), and mean depth (depth). Other units as in Table 1. In all cases, the relationship was statistically significant ( $P < 0.0001$ ). Total phosphorus was excluded due to collinearity.

	Intercept	Log (Chl a)	Log (area)	$Log$ (depth)	$r^2$	
$log_e$ (SS)	$0.77 \pm 0.05$	$0.57 + 0.01$	$0.13 \pm 0.008$	$-0.32 \pm 0.03$	0.75	1.759
$log_e$ (inorgSS)	$0.03 \pm 0.09$	$0.49 \pm 0.02$	$0.10 \pm 0.02$	$-0.58 \pm 0.08$	0.47	1.759
$log_e$ (naorg $SS$ )	$0.57 \pm 0.7$	$0.47 \pm 0.01$	$0.23 \pm 0.01$	$-0.48 \pm 0.04$	0.61	1.814

**Lake Dons**  $25.$ Lake  $2.0$  $1.0$  $\lambda$ Annual mean in the inlet Phytoplankton (mg L-1)  $0.8$  $20$ Total phosphorus (mg L<sup>-1</sup>) peccui aept  $0.6$  $15$  $04$  $10$ Ξ  $0.2$ 1000 100 R Non-algae suspended solids (%) Suspended solids (mg L<sup>-1</sup>) --- $200$ Chlorophyll a (µg L<sup>-1</sup>) 80 800 150 snspended solids 60 600  $100$  $40$  $400$ 200  $\mathscr{C}_{\mathscr{C}}$  $\theta$  $\overline{93}$ Yea Year

Fig. 1. Lake Dons: (A) discharge-weighted annual mean inlet concentration and lake concentration of total phosphorus, (B) chlorophyll *a* and total suspended solids, (C) biomass of phytoplankton and Secchi depth, and (D) the proportion of nonalgae and inorganic suspended solids of total suspended solids.

Summer mean Chl *a* ranged from 175 to 80  $\mu$ g L<sup>-1</sup> and SS from 43 to 23 mg  $L^{-1}$  (Fig 3). InorgSS was only monitored for the last 3 yr and the analysis is therefore restricted to the naSS, which showed no significant changes during the period ( $P > 0.05$ ).

In Lake Arreskov (3.17 km<sup>2</sup>, mean depth: 1.9 m), a marked reduction in Chl *a* and SS occurred following fish kills in 1991 and a subsequent addition of piscivorous fish, followed by somewhat higher values between 1999–2000 (Fig. 4). If we consider only the period with declining Chl *a* (1989–1997), then the 10-fold reduction in summer mean Chl *a* (from 130 to 12  $\mu$ g L<sup>-1</sup>) was accompanied by nearly similar proportional reductions in SS (from 61 to 6 mg  $L^{-1}$ )

and in LI from 40 to 3 mg  $L^{-1}$ . Accordingly, no significant changes occurred in the contribution of naorgSS or inorgSS to SS during the period. For the entire study period, a significant decline was observed in in-lake TP ( $P = 0.037$ ), Chl  $a$  ( $P < 0.05$ ), SS ( $P < 0.01$ ), and phytoplankton biomass ( $P$  $<$  0.025), while Secchi depth increased ( $P = 0.017$ ).

Thus, the changes in the proportion of different fractions of SS through time were small or insignificant compared with the major changes recorded in SS and Chl *a* concentrations. The decline in naorgSS and inorgSS concentrations cannot be attributed to a plant-mediated reduction in the shear stress at the lake bottom, as otherwise seen in lakes with abundant plant coverage (James and Barko 1994; Ham-



Fig. 2. Lake Arresø: (A) discharge-weighted annual mean inlet concentration and lake concentration of total phosphorus, (B) lake concentration of chlorophyll *a* and total suspended solids, (C) biomass of phytoplankton and Secchi depth, and (D) the proportion of nonalgae and inorganic suspended solids of total suspended solids.



Fig. 3. Lake Vesterborg: (A) discharge-weighted annual mean inlet concentration and lake concentration of total phosphorus, (B) lake concentration of chlorophyll *a* and total suspended solids, (C) biomass of phytoplankton and Secchi depth, and (D) the proportion of nonalgae and inorganic suspended solids of total suspended solids.

ilton and Mitchell 1996), as no macrophyte colonization occurred in Lake Dons, Lake Arresø, or Lake Vesterborg. Only in Lake Arreskov may plants potentially have contributed to reduce shear stress as macrophyte coverage here increased from zero to a maximum of 61% in these lakes in 1997 and thereafter ranged between 1 and 30% (Hansen 2001). The observed major reductions in naorgSS and inorgSS cannot be attributed to low sensitivity of the sediment to resuspension either, as all four lakes have sediment with high content of water and organic matter in the top 5 cm of the sediment sampled at midlake stations. The water content averaged 89, 90, 94, and 95% in Lake Dons, Lake Arresø, Lake Vesterborg, and Lake Arreskov, respectively, and the contribution

of organic matter to dry weight averaged 22, 23, 36, and 34%, respectively.

Besides the four lakes analyzed above, 7 of the remaining 11 lakes showed a significant  $(P < 0.05)$  decline in Chl *a* or SS during the study period (detrended for seasonal effects). We did not find any significant change in the contribution of inorgSS, naorgSS, or phytoplankton biomass to SS with time  $(P > 0.05)$  for any of these lakes. As could be expected, we did not find any significant  $(P > 0.05)$  changes with time either in the different fractions for the four remaining lakes without significant changes in Chl *a* or SS.

The relatively close correspondence between the SS and Chl *a* reduction in Lake Arresø is particularly noteworthy,



Fig. 4. Lake Arreskov: (A) discharge-weighted annual mean inlet concentration and lake concentration of total phosphorus, (B) lake concentration of chlorophyll *a* and total suspended solids, (C) biomass of phytoplankton and Secchi depth, and (D) the proportion of nonalgae and inorganic suspended solids of total suspended solids. Fish kills occurred in the summer of 1991.

as this lake is large (40 km<sup>2</sup>) and, moreover, situated in a wind-exposed area in a flat landscape close to the sea. A detailed study of resuspension conducted in 1991 (Kristensen et al. 1992) showed that resuspension occurred on average every second day and that the increase in SS due to resuspension alone could reduce Secchi depths to below 1 m. Nevertheless, even in this lake, rapid reduction of naorgSS and inorgSS occurred concurrently with the observed reduction in Chl *a* (Fig. 4).

Our results therefore suggest that, for Danish lakes, resuspension of sediment even with high organic matter and water content does not prevent a shift to the clearwater state during reoligotrophication following reduction in external nutrient loading. This contradicts the view of Bachmann et al. (1999) but supports suggestions forwarded by Lowe et al. (2001). There may be several reasons for the simultaneous decrease in Chl *a* and naSS. First, a reduction in Chl *a* is accompanied by a decline in the abundance of benthivorous fish (Jeppesen et al. 2002). Consequently, disturbance by sediment-foraging fish is also likely reduced. Bream (*Abramis brama*), which is abundant in Danish lakes, and carp (*Cyprinus carpio*) (although absent from the investigated Danish lakes), may have a substantial effect on the concentration of SS in shallow lakes (Hosper 1997). Second, decreased predation by benthivorous fish may enhance the abundance of benthic invertebrates (Andersson et al. 1978) and thereby indirectly also the consolidation of the sediment mediated by tube-building chironomids that also oxidize the sediment by ventilation. Third, enhanced light penetration of the water stimulates benthic algae production, which, in turn, reduces the risk of resuspension (Paterson 2001). Fourth, the consolidation period between resuspension events is prolonged by the less frequent disturbance of the sediment by fish and by the higher biomass of benthic algae and invertebrates, which enhance the shear stress threshold for resuspension, as has been shown after prolonged consolidation periods with stream sediments (Partheniades 1965). Finally, low phytoplankton production reduces the accumulation of ''new'' detritus in the water. It also reduces sedimentation and thus diminishes the amount of detritus that may potentially be resuspended by fish or wave action.

In conclusion, resuspension of loosely organically rich sediment is apparently not a major factor for delaying the recovery of shallow Danish lakes. We emphasize, though, that our analysis does not include lakes with a high content of silt or humic substances nor does it include very large lakes ( $>40 \text{ km}^2$ ). Yet the recent results from large (124 km<sup>2</sup>) and heavily wind-exposed Lake Apopka in Florida (Lowe et al. 2001) suggest that our findings also apply to somewhat larger lakes. Resuspension may, however, indirectly influence the recovery process, as resuspended sediment can release nutrients for phytoplankton growth or sometimes trap nutrients depending on phosphorus adsorption relative to the equilibrium state (Kamp-Nielsen 1974; Søndergaard et al. 1992), just as internal P loading from the undisturbed sediment pool (accumulated during eutrophication) may delay recovery (Sas 1989; Søndergaard et al. 2002).

#### *References*

ANDERSSON, G., H. BERGGREN, G. CRONBERG, AND C. GELIN. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia **59:** 9– 15.

- BACHMANN, R. W., M. V. HOYER, AND D. E. CANFIELD, JR. 1999. The restoration of Lake Apopka in relation to alternative stable states. Hydrobiologia **394:** 219–232.
	- -, AND . 2001*a*. Sediment removal by the Lake Apopka marsh flow-away. Hydrobiologia **448:** 7–10.
- , , AND . 2001*b*. Evaluation of recent limnological changes at Lake Apopka. Hydrobiologia **448:** 19–26.
- GULATI, R. D., E. H. H. R. LAMMENS, M.-L. MEIJER, AND E. VAN DONK [EDS.]. 1990. Biomanipulation—tool for water management. Hydrobiologia **200/201:** 1–628.
- HAMILTON, D. P., AND S. F. MITCHELL. 1996. An empirical model for sediment resuspension in shallow lakes. Hydrobiologia **317:** 209–220.
- HANSEN, K. S. 2001. Arreskov Sø 2000. Vandmiljøovervågning. Fyns Amt, Odense, Danmark. (In Danish)
- HANSON, M. A., AND M. G. BUTLER. 1990. Early responses to food web manipulation in a shallow prairie lake. Hydrobiologia **200/ 201:** 317–328.
- HIRSH, R. M., AND J. R. SLACK 1984. A nonparametric trend test for seasonal data with serial dependence. Wat. Resourc. Res. **20:** 727–732.
- HOSPER, S. H. 1997. Clearing lakes: An ecosystem approach to the restoration and management of shallow lakes in the Netherlands. Ph.D. thesis, Univ. of Liverpool.
- JAMES, W. F., AND J. W. BARKO. 1994. Macrophyte influences on sediment resuspension and export in a shallow impoundment. Lake Res. Mgmt. **10:** 95–102.
- JEPPESEN, E., J. P. JENSEN, AND M. SØNDERGAARD. 2002. Response of phytoplankton, zooplankton and fish to re-oligotrophication: An 11-year study of 23 Danish lakes. Aquat. Ecosys. Health & Mgmt. **5:** 31–43.
- -, AND T. L. LAURIDSEN. 1999. Trophic dynamics in turbid and clearwater lakes with special emphasis on the role of zooplankton for water clarity. Hydrobiologia **408/ 409:** 217–231.
- KAMP-NIELSEN, L. 1974. Mud–water exchange of phosphate and other ions in undisturbed sediment cores and factors affecting exchange rates. Arch. Hydrobiol. **228:** 101–109.
- KRISTENSEN, P., M. SØNDERGAARD, AND E. JEPPESEN. 1992. Resuspension in a shallow eutrophic lake. Hydrobiologia **228:** 101– 109.
- LOWE, E. F., L. E. BATTOE, M. F. COVENY, C. L. SCHELSKE, K. E. HAVENS, E. R. MARZOLF, AND K. R. REDDY. 2001. The restoration of Lake Apopka in relation to alternative stable states: An alternative view to that of Bachmann et al. (1999). Hydrobiologia **448:** 11–18.
- MEIJER, M.-L., I. DE BOOIS, M. SCHEFFER, R. PORTIELJE, AND H. HOSPER. 1999. Biomanipulation in shallow lakes in the Netherlands: An evaluation of 18 case studies. Hydrobiologia **408/ 409:** 13–30.
- PARTHENIADES, E. 1965. Erosion and deposition of cohesive solids. J. Hydraulics Div., HY1. **91:** 105–139.
- PATERSON, D. M. 2001. The fine structure and properties of the sediment surface, p. 127–143. *In* B. Boudreau and B. B. Jorgensen [eds.], The benthic boundary layer: Transport processes and biogeochemistry. Oxford University Press.
- PERROW, M. R., M.-L. MEIJER, P. DAWIDOWICZ, AND H. COOPS. 1997. Biomanipulation in shallow lakes: State of the art. Hydrobiologia **342/343:** 355–365.
- REYNOLDS, C. F. 1984. The ecology of freshwater phytoplankton. Cambridge Univ. Press.
- ROWLINGS, J. O. 1988. Applied regression analysis. A research tool. Wadsworth & Brooks/Cole.
- SAS, H. [ED.]. 1989. Lake restoration by reduction of nutrient load-

ing. Expectation, experiences, extrapolation. Acad. Ver. Richardz Gmbh.

- SCHELSKE, C. L., AND W. F. KENNEY. 2001. Model erroneously predicts failure for restoration of Lake Apopka, a hypereutrophic, subtropical lake. Hydrobiologia **448:** 1–5.
- SØNDERGAARD, M., P. KRISTENSEN, AND E. JEPPESEN. 1992. Phosphorus release from resuspended sediment in the shallow and wind exposed Lake Arresø, Denmark. Hydrobiologia **228:** 91– 99.
- , J. P. JENSEN, E. JEPPESEN, AND P. H. MØLLER. 2002. Seasonal dynamics in the concentrations and retention of phosphorus in shallow Danish lakes after reduced loading. Aquat. Ecosys. Health & Mgmt. **5:** 19–29.
- , T. L. LAURIDSEN, E. JEPPESEN, AND L. BRUUN. 1997. Macrophyte-waterfowl interactions: Tracking a variable resource and the impact of herbivory on plant growth, p. 298–306. *In* E. Jeppesen, M., Søndergaard, M. Søndergaard, and K. Christoffersen [eds.], The structuring role of submerged macrophytes in lakes. Ecological Studies Series 131. Springer.
- VAN DER MOELEN, D. T., AND P. C. M. BOERS. 1994. Influence of internal loading on phosphorus concentration in shallow lakes before and after reduction of external loading. Hydrobiologia **275/276:** 479–492.

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