

An empirical model describing the seasonal dynamics of phosphorus in 16 shallow eutrophic lakes after external loading reduction

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Abstract

Based on monthly mass balances on 7–8 yr of data from 16 shallow (mean depth: 1–10 m), eutrophic, unstratified, or only temporarily stratified Danish lakes, we developed a simple empirical model relating the seasonal variation in lake total phosphorus (TP) concentrations to external loading, accumulated phosphorus in the sediment, hydraulic retention time, and water temperature. The aim was to describe the early recovery phase following an external loading reduction, i.e., when internal phosphorus loading is high, and to include seasonal dynamics. We calibrated a common set of model parameters for all 16 lakes and lake-specific estimates of the exchangeable phosphorus pool in the sediment (P_s). Estimated annual mean TP deviated on average 12% from observed values in the 16 lakes. Moreover, the estimated seasonal dynamics and trend following the external loading reduction closely mimicked the observed pattern. The model was successfully tested on nine of the lakes for which data were available for an additional 7-yr period. The results suggest that TP in the sediment does not provide an adequate description of the exchangeable P pool. In Lake Arreskov, which has shifted from a turbid to a clear-water state following fish kill and biomanipulation, the model significantly overestimated TP, indicating that the model is inadequate for describing seasonal dynamics during the shift from a turbid to a clear-water state. Although simple, the empirical model predicts reasonably well the seasonal dynamics of TP following a P-loading reduction in a variety of shallow turbid lakes.

Cultural eutrophication has considerably impaired lake ecosystems worldwide (Hutchinson 1973; Sas 1989). In northern temperate lakes, total phosphorus is regarded as the key factor of eutrophication (Schindler 1975). To improve water quality, many countries have during the last two decades reduced the external nutrient loading of lakes by improving wastewater treatment, including P removal; by increasing catchment retention capacity; and by reducing the phosphorus content of fertilizers and detergents (Phillips et al. 1999; Van der Molen and Boers 1999). However, following the external loading reduction, many lakes suffer from high internal loading, which delays recovery (Marsden 1989; Sas 1989; Jeppesen et al. 2005b).

To help managers define acceptable external phosphorus loading levels and predict the effects of various measures to reduce the loading, numerous simple empirical and dynamic models have been developed. The most simple of the models relate lake water total phosphorus (TP) to external loading and require that the lakes be in a steady state (Dillon and

Rigler 1974; OECD 1982). These models cannot, however, describe the transient phase following a loading reduction when internal loading is high. They often considerably underestimate lake water TP, since internal loading may in some cases prevail for more than two decades after external loading reduction (Sas 1989; Nürnberg 1998; Søndergaard et al. 2003). To account for internal loading, the sediment pool and sediment release rates have been included in a number of empirical and dynamic models (Nürnberg and LaZerte 2004). These models most frequently belong to the two-compartment type that includes a water and a sediment phase plus an interchange between the two (sedimentation and release). Two-compartment models typically operate with time steps of 1 yr and cannot, therefore, describe the seasonal variation in in-lake TP concentrations. Seasonal dynamics are, however, included in several complex dynamic models, but these models often require comprehensive knowledge of numerous variables, as well as calibration and selection of a large number of unknown parameters (Jørgensen and Mitsch 1983). To our knowledge, no simple models describe changes in seasonal TP in the period following nutrient loading reduction.

From 1989 to 2003, mass balances have been developed on 16 Danish shallow lakes, the majority of which are in a transient state following a TP-loading reduction (Søndergaard et al. 1999). We used the data from 1989 to 1996 to develop a phosphorus model that, based on information on external loading and the exchangeable phosphorus pool in the sediment, allows prediction of the seasonal dynamics of in-lake total phosphorus concentrations of lakes in equilibrium and during the transient state following changes in the external phosphorus loading. The model was subsequently tested on the data from 1997 to 2003. The model was also tested on a biomanipulated lake (Lake Arreskov), which has shifted from turbid to a clear-water state.

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Materials and methods

Sampling and analysis—The 16 lakes included in the study were all encompassed by The Danish Nationwide Lake Monitoring Programme, and the applied sampling procedures and nutrient analyses followed its standardized guidelines (Kronvang et al. 1993). For nutrient analyses, the main inlets of each lake were sampled 18–26 times annually, depending on seasonal variation in discharge, while the minor inlets were sampled less frequently, depending on their relative contribution to total hydraulic and nutrient loading. Lake waters were collected fortnightly during summer and monthly during winter, i.e., 19 times annually. TP was measured as orthophosphate using the method of Murphy and Riley (1972) after persulphate digestion (Koroleff 1970), and chlorophyll *a* was determined after ethanol extraction (Jespersen and Christoffersen 1987).

Total discharge in the main inlets and outlets (Q_m) of the lakes was measured monthly using an OTT propeller. The water levels (H) in the inlet and outlet streams were automatically recorded during the entire study period. Daily discharge (Q_d) was calculated by the use of the relationship obtained for H and Q_m in the inlet and outlet, respectively. In minor inlets, discharge (q) was measured with an OTT propeller and daily discharge values were calculated from q/Q_d relationships.

Monthly water balances were calculated for each lake using the following equation: $Q_{\text{inm}} + Q_{\text{inu}} + \text{Prec} = V_{\text{dif}} + Q_{\text{outm}} + Q_{\text{outu}} + \text{Evap}$, where Q_{inm} and Q_{outm} are the total discharges measured in inlets and outlets, respectively. Prec and Evap are monthly evaporation and precipitation obtained from meteorological stations situated in the vicinity of the lakes. V_{dif} is the monthly variation in lake volume. Q_{inu} and Q_{outu} are the unmeasured input from the catchment without stream inlet and the output from the lake, respectively. The net value of Q_{outu} and Q_{inu} was determined monthly by adjusting the water balance, if $V_{\text{dif}} + Q_{\text{outm}} > Q_{\text{inm}} + \text{Prec}$, then Q_{inu} equals to the difference; otherwise, Q_{outu} is equal to the difference.

TP loading was then estimated for each inlet as the product of the daily water discharge and phosphorus concentration (obtained by linear interpolation). TP concentrations of the unmeasured discharges to and from the lake (Q_{inu} , Q_{outu}) were assumed to equal the Q -weighted concentrations in the measured inlets and outlets. Atmospheric deposition on the lake surface was estimated using an average rate of 20.0 kg P km⁻² yr⁻¹ (Hovmand et al. 1993).

Lake sediment was sampled during winter months and analyzed at least once during the investigation period. Dry weight was determined by drying at 105°C for 24 h and loss on ignition was subsequently determined by drying to constant weight at 550°C. Total phosphorus in the sediment (sed-TP) was analyzed spectrophotometrically as molybdate reactive phosphorus after extraction of ash-free sediment with 1 mol L⁻¹ HCl. Phosphorus in depths from 0–5, 5–10, and 10–20 cm was fractionated according to the sequential extraction technique of Hieltjes and Lijklema (1980) into NH₄Cl-P, NaOH-P, HCl-P, and residual phosphorus (Res-P). Res-P was calculated as the difference between sed-TP and

the sum of NH₄Cl-P, NaOH-P, and HCl-P. For more details of sampling and analysis, see Søndergaard et al. (1996). The exogenous variables (inlet TP, temperature, and hydraulic loading) were interpolated linearly to daily values or with shorter time intervals to match the time scale needed for solving the differential equations with sufficient accuracy. The differential equations were solved by means of either the Euler-scheme or the fourth order Runge-Kutta scheme. The unknown model parameters were estimated by means of a least squares method, where the least square contributions of the lakes are weighted by the number of observations (minus one) per lake and added on a logarithmic scale, i.e., if σ_k^2 and n_k denote the mean squared errors and the number of observations minus one, respectively, for the k th lake, then the total criterion function to be minimized is given by $\sum_{k=1}^{16} n_k \log \sigma_k^2$. Hence, a common set of model parameters was estimated for the 16 lakes. The criterion function was minimized by means of the downhill simplex method (Nelder and Mead 1965; Press et al. 1989).

The model—The model has two state variables: total phosphorus in the lake water (in-lake TP) and exchangeable TP in the sediment. The driving variables in the model are the monthly inlet concentration of TP, the corresponding monthly water discharge, and the lake water temperature.

The dynamics of in-lake TP are given by the difference between input and output, the sedimentation of TP is deducted, and the release of TP from the sediment is added.

$$\frac{dP_l}{dt} = \frac{Q}{V} \times (f_d \times P_i - P_l) - \text{SED} + \text{REL} \quad (1)$$

where P_l is in-lake TP (g m⁻²), P_i inlet TP (g m⁻²), SED sedimentation of phosphorus (g P m⁻² d⁻¹), REL sediment release of phosphorus to lake water (g P m⁻² d⁻¹), f_d the fraction of P_i entering the lake water pool (the rest enters the sediment pool). f_d is defined as $1/(1 + \sqrt{V/Q/365})$, thus declining with increasing hydraulic retention time.

Accordingly, the change in TP in the sediment is given by the following equation:

$$\frac{dP_s}{dt} = \frac{Q}{V} \times (1 - f_d) \times P_i + \text{SED} - \text{REL} \quad (2)$$

The sedimentation of TP is calculated as a constant (bS) multiplied by in-lake TP. The temperature dependence of this process is modeled by a standard Van Hoff's equation.

$$\text{SED} = bS \times (1 + tS)^{T-20} \times \frac{P_l}{Z} \quad (3)$$

where tS is the temperature correction for bS and T is lake water temperature (°C).

The release is a first order reaction:

$$\text{REL} = bF \times (1 + tF)^{T-20} \times P_s \quad (4)$$

where bF is a constant, tF the temperature correction for bF , and P_s exchangeable phosphorus in the sediment.

The model was implemented in Delphi 3 (Borland International Inc. 1997). The SAS package (SAS Institute 1990) was used for additional graphical and statistical processing of input data and model output. We generally used the Euler

Table 1. Selected physicochemical variables for the 16 lakes (annual mean values for the years 1989–1996).

Lake	Lake area (km ²)	Mean depth (m)	Max depth (m)	Water retention time (d)	Inlet P (annual) (mg P L ⁻¹)	Lake P (annual) (mg P L ⁻¹)	Lake P (summer) (mg P L ⁻¹)	Chlorophyll <i>a</i> (summer) (μg L ⁻¹)	Secchi depth (summer) (m)
Borup Sø	0.10	1.1	2.0	24	0.128	0.149	0.217	115	0.6
Byrup Langsø	0.38	4.6	9.0	82	0.116	0.090	0.086	38	2.0
Dons Nørresø	0.36	1.0	1.5	18	0.094	0.169	0.262	350	0.4
Fuglesø*	0.05	2.0	2.8	56	0.151	0.223	0.332	135	0.7
GundSømagle Sø	0.32	1.2	1.9	30	0.963	0.849	0.991	269	0.4
Hejrede Sø	0.51	0.9	3.5	53	0.170	0.139	0.148	66	0.5
Hinge Sø	0.91	1.2	2.6	18	0.114	0.126	0.172	131	0.5
Jels Oversø†	0.09	1.2	1.9	7	0.136	0.274	0.387	160	0.6
Kilen	3.34	2.9	6.5	266	0.150	0.168	0.239	154	0.5
Langesø	0.17	3.1	4.5	200	0.207	0.275	0.309	96	1.0
Lemvig Sø	0.16	2.0	3.7	30	0.212	0.286	0.463	110	0.5
St. Søgård Sø†	0.60	2.7	6.6	82	0.230	0.442	0.561	67	0.8
Søgård Sø	0.27	1.6	2.7	24	0.142	0.229	0.366	193	0.4
Tystrup Sø	6.62	9.9	21.7	180	0.295	0.257	0.215	58	1.6
Vesterborg Sø	0.21	1.4	2.9	26	0.146	0.217	0.310	111	0.5
Øm Sø	0.42	4.0	10.5	18	0.124	0.094	0.100	53	1.4
Min	0.05	0.9	1.5	7	0.094	0.090	0.086	38	0.4
Median	0.34	1.8	3.2	30	0.148	0.220	0.286	113	0.6
Mean	0.91	2.5	5.3	70	0.211	0.249	0.322	132	0.8
Max	6.62	9.9	21.7	266	0.963	0.849	0.991	350	2.0

* 1989–1990, 1992–1996.

† 1990–1996.

integration routine. However, final results were always recalculated using the Runge-Kutta integration routine to ensure adequate precision of the calculations.

Table 2. Parameters used for testing the model. The parameter values are obtained from the calibration on the data from 1989 to 1996.

Parameter	Calibrated value measured
Sedimentation rate, <i>bS</i> (m d ⁻¹)	0.0470
Temperature dependence of <i>bS</i> , <i>tS</i>	0
Sediment release rate, <i>bF</i> (d ⁻¹)	0.000595
Temperature dependence of <i>bF</i> , <i>tF</i>	0.0800
Phosphorus in sediment, <i>P_s</i> (<i>t</i> =0) g P m ⁻²	
Borup Sø	20.9
Byrup Langsø	13.8
Dons Nørresø	42.4
Fuglesø	47.9
Gundsømagle Sø	90.3
Hejrede Sø	12.9
Hinge Sø	26.2
Jels Oversø	68.7
Kilen	32.0
Langesø	48.0
Lemvig Sø	63.7
St. Søgård Sø	95.1
Søgård Sø	48.5
Tystrup Sø	40.0
Vesterborg Sø	33.4
Øm Sø	0.00

Results

Test data set—The 16 turbid lakes used for testing the model were shallow with a mean depth ranging between 0.9 and 9.9 m and without permanent summer stratification (Table 1). Lake surface area ranged between 0.05 and 6.62 km². All lakes had a short water retention time (7 to 266 d). The annual mean inlet and in-lake TP concentrations were high (0.094 to 0.963 mg P L⁻¹ and 0.090 to 0.849 mg P L⁻¹, respectively), chlorophyll *a* thus being high (38–350 μg L⁻¹) and Secchi depth low (0.4–2.0 m). During the past 10–20 yr, the external phosphorus loading to most of the lakes has been reduced, and they accordingly suffer from internal loading (Søndergaard et al. 1999). Consequently, the median of annual mean TP was higher in the lake water than in the inlet, and in-lake TP exceeded inlet TP in 11 of the 16 lakes (Table 1).

Since the exchangeable sediment pool is difficult to estimate using measured data (Søndergaard et al. 2003), we first calibrated initial *P_s* on the entire data series for each lake. *P_s* is given in Table 2 and observed and estimated in-lake TP values are shown in Fig. 1. Generally, we observed good correspondence between observed and estimated TP. CV ranged between 26% and 75% (mean = 41%) and root mean square error (RMSE) of predictions between 0.03 and 0.38 (median = 0.07). With the exception of Lake Borup, the inlet concentrations differed significantly from the in-lake concentration, particularly during summer, suggesting that the seasonal dynamic of internal loading is traced well by the model. In the 16 lakes, the estimated annual mean lake water TP during the 7–8 yr of study only deviated 0–44%

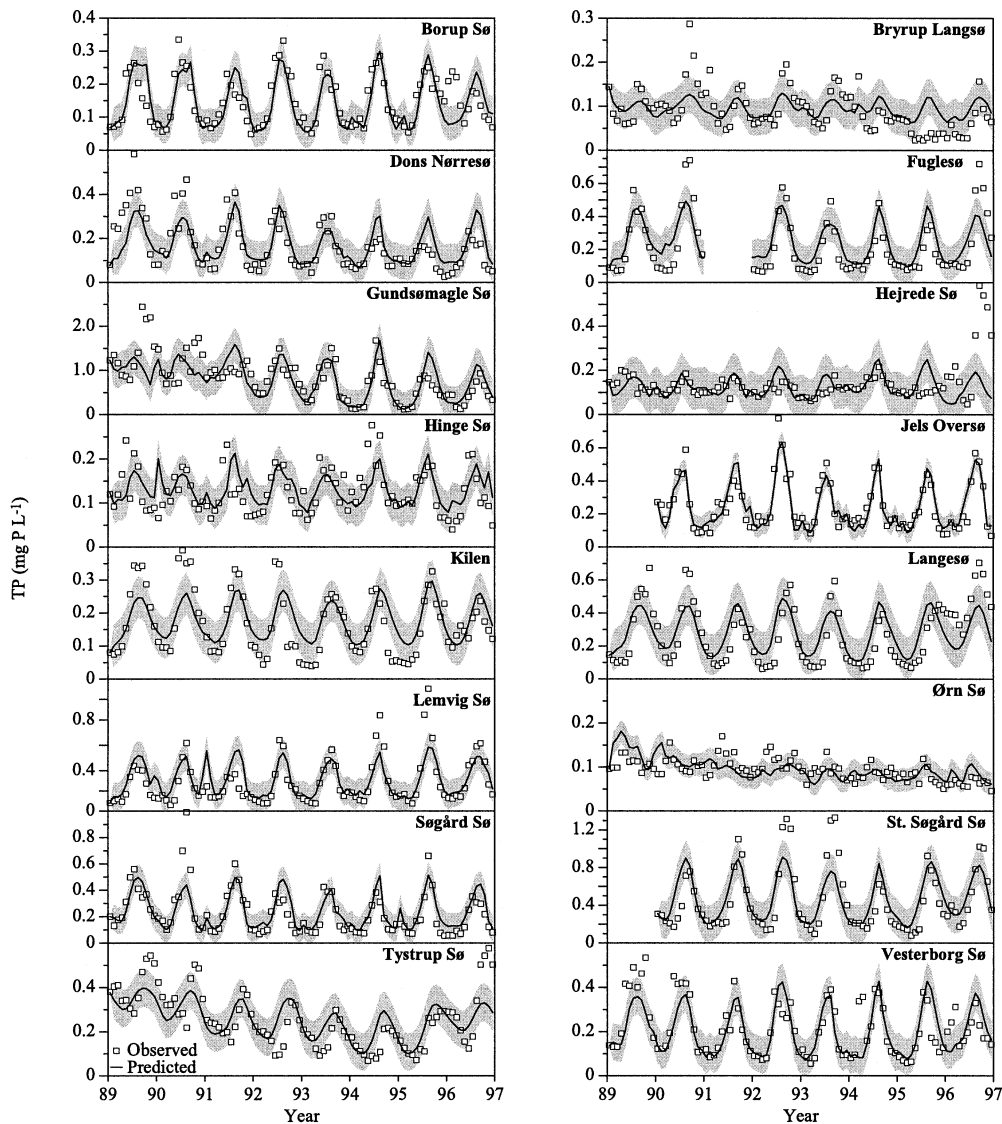


Fig. 1. Observed and predicted total phosphorus (TP) for the 16 shallow lakes during 1989–1996 using the model parameters in Table 2. The gray areas represent predicted values \pm one standard deviation (σ_x in the criterion function).

(mean = 12%) from observed values, while predictions based on the Vollenweider steady state model deviated 2–237% (mean = 56%) (Table 3, Fig. 2).

The estimated P_s in the 16 lakes did not relate significantly to any of the phosphorus fractions in the sediment (Spearman correlation, $p > 0.05$) but was significantly related to the measured TP pool in the uppermost 20 cm of the sediment (Fig. 3; Spearman correlation, $p < 0.05$). The scatter of the relationship was, however, high (Fig. 3). Particularly one lake (Ørn Sø), which has very high iron concentrations in the sediment (140 mg Fe g⁻¹ dry weight, unpubl. data) deviated from the general relationship by having very high TP concentrations in the sediment. By using the measured pools instead of the calibrated ones, estimated annual mean TP deviated 4–176% from observed values (mean = 34%) for the 16 lakes (Table 3).

When calibrating the sediment phosphorus pool, we used

data from all 7–8 yr studied. Since time series of that length are not frequently found, we have also tested how the correspondence between measured and calculated in-lake TP depends on the number of years used for the calibration (Fig. 4). We found only small changes in RMSE when reducing the number of years, median RMSE increased successively from 0.09 to 0.10 and 0.15, when data from the first 7, 4, and 1 yr, respectively, were used for calibration. Likewise, in most lakes only minor reductions in RMSE were found during the first year, when data from this year only were used for calibration (Fig. 4).

Bio-manipulated lake—Lake Arreskov (3.17 km², mean depth 1.9 m) shifted from a turbid to a clear-water state following fish kill in 1991 and a subsequent moderate fish manipulation (Jeppesen et al. 1998; Fig. 5). The shift resulted in a major TP decline, unmimicked by the model.

Table 3. Annual mean total phosphorus concentrations observed and estimated using the calibrated exchangeable pool of phosphorus in the sediment and the measured pool in the upper 20 cm of the sediment.*

Lake	Observed TP (mg P L ⁻¹)	Estimated TP (using calibrated P _s) (mg P L ⁻¹)	Deviation %	Estimated TP (using measured P _s) (mg P L ⁻¹)	Deviation %	Estimated TP (using Vollenweider) (mg P L ⁻¹)	Deviation %
Borup Sø	0.149	0.149	0	0.176	18	0.102	-32
Byrup Langsø	0.090	0.090	0	0.240	166	0.079	-12
Dons Nørresø	0.168	0.168	0	0.131	-22	0.077	-54
Fuglesø†	0.222	0.241	8	0.196	-12	0.108	-51
Gundsømagle Sø	0.839	0.792	-6	0.736	-12	0.728	-13
Hejrede Sø	0.139	0.078	-44	0.251	80	0.125	-10
Hinge Sø	0.127	0.102	-20	0.210	66	0.093	-27
Jels Oversø‡	0.249	0.226	-9	0.285	14	0.118	-53
Kilen	0.167	0.123	-27	0.140	-16	0.081	-51
Langesø	0.272	0.234	-14	0.316	16	0.123	-55
Lemvig Sø	0.285	0.275	-4	0.396	39	0.165	-42
St. Søgård Sø‡	0.447	0.420	-6	0.429	-4	0.158	-65
Søgård Sø	0.228	0.192	-16	0.175	-24	0.113	-50
Tystrup Sø	0.257	0.219	-15	—	—	0.175	-32
Vesterborg Sø	0.216	0.144	-33	0.274	27	0.115	-47
Øm Sø	0.094	0.083	-11	0.254	176	0.102	9
Min	0.090	0.078	-44	0.131	-24	0.077	-65
Median	0.219	0.180	-10	0.251	16	0.114	-44
Mean	0.247	0.221	-12	0.280	34	0.154	-37
Max	0.839	0.792	8	0.736	176	0.728	9

* Also shown is the estimated phosphorus concentration based on the model by Vollenweider (1976), assuming equilibrium with external loading and deviations between the estimated and observed (as percentages of observations) total phosphorus concentrations by the three different calculation methods.

† 1989–1990, 1992–1996.

‡ 1990–1996.

Both when using measured P_s in the sediment and P_s estimated by calibration on the entire study period, highly positive residuals before fish kill and highly negative values afterward were obtained (Fig. 5). The residuals tended to be even more negative after 1991 when P_s was calibrated on data from 1989 to 1990.

Sensitivity analysis—Sensitivity analyses were performed by calculating the relative increase in RMSE in response to halving and doubling the value of each of the parameters *bS*, *bF*, and *tF* in Table 2 and by changing the value of *tS* to 0.08. In each scenario only one parameter value was changed. This was done keeping the initial phosphorus concentrations in the sediment at the estimated values in Table 2 (Fig. 6, upper plot) and by reestimating the phosphorus pool in the sediment (Fig. 6, center plot). For the latter case, box plots of the absolute increases in the estimated initial phosphorus concentration in the sediment are presented in the lower plot in Fig. 6. Our model responds qualitatively as expected to the altered parameters values, and the model appears to be more sensitive to the values of the sedimentation and release rates than to the temperature parameters. However, the most sensitive parameters are clearly the initial P_s values. If these are reestimated, changes in the model parameters imply only moderate changes in RMSE, whereas the reestimated initial P_s values may change quite dramatically. This emphasizes that our model is primarily a model for in-lake TP and that it may model in-lake TP data using sedimentation and release rates at different levels by adjust-

ing the level of the sediment pool accordingly. Hence, lake-specific estimates of the model parameters may, artificially, differ considerably, which is why it may be important to estimate common values of *bS*, *bF*, and *tF* for several lakes.

Model test on data from 1997 to 2003—Equivalent data are available for the period 1997–2003 for 9 of the 16 lakes allowing a further test of the model (Fig. 7). The model was applied to these data using observed values of the exogenous variables in the test period. The relative increase in RMSE for the test period relative to the estimation period 1989–1996 ranged from -51% to 17% with a median of -0.03%, i.e., the RMSE values were generally lower in the test period than in the estimation period.

Discussion

The developed model, though simple using only few parameters, predicted reasonably well the seasonal dynamics of the turbid lakes despite the highly variable hydraulic retention times and external TP loadings. The generally lower RMSE in the test period compared with the estimation period should not be interpreted as evidence of a better model fit in the test period because the explanation is probably that the level of in-lake TP is generally lower in the test period, hence a measure of absolute deviation is likely to be smaller. Generally, the model predicted the observed in-lake TP concentration fairly well, however, with a tendency to overestimation. A conservative model predicting too high TP level

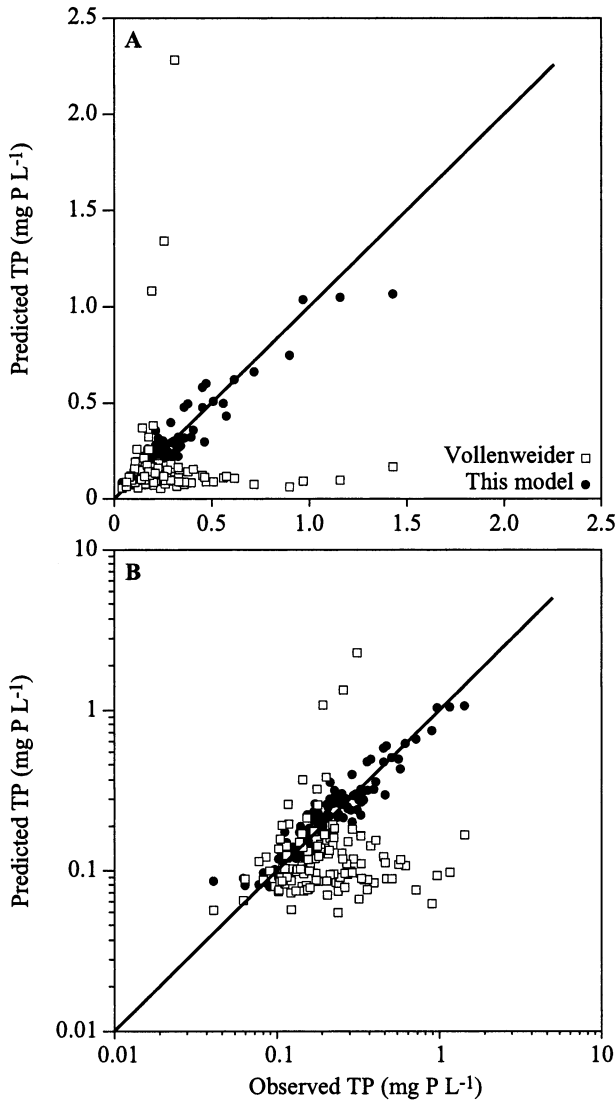


Fig. 2. Inlet, observed, and estimated annual mean (TP) in the lake water showing our model and Vollenweider. The line shows the 1:1 ratio. (A) Linear scale, (B) \log_{10} scale.

and a too long recovery period may to some extent be explained by the fact that the model parameters were estimated on data in a recovery period with, probably, a larger internal loading in the initial phase of recovery (release rate, bF). Furthermore some of the lakes might have shifted in the direction of a more clear-water state (though still relatively turbid) during the study period (Jeppesen et al. 2005a), which will induce a much higher retention of phosphorus

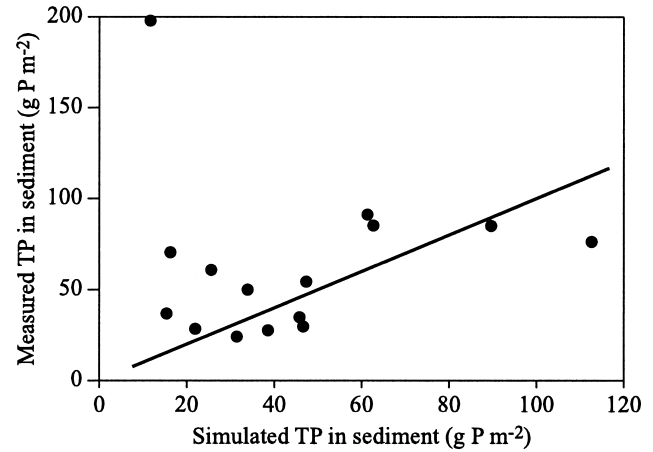


Fig. 3. Observed total phosphorus (TP, g P m^{-2} , 0–20 cm) in the sediment of the 16 lakes and average monthly simulated concentrations of exchangeable P in the sediment. The line shows the 1:1 ratio.

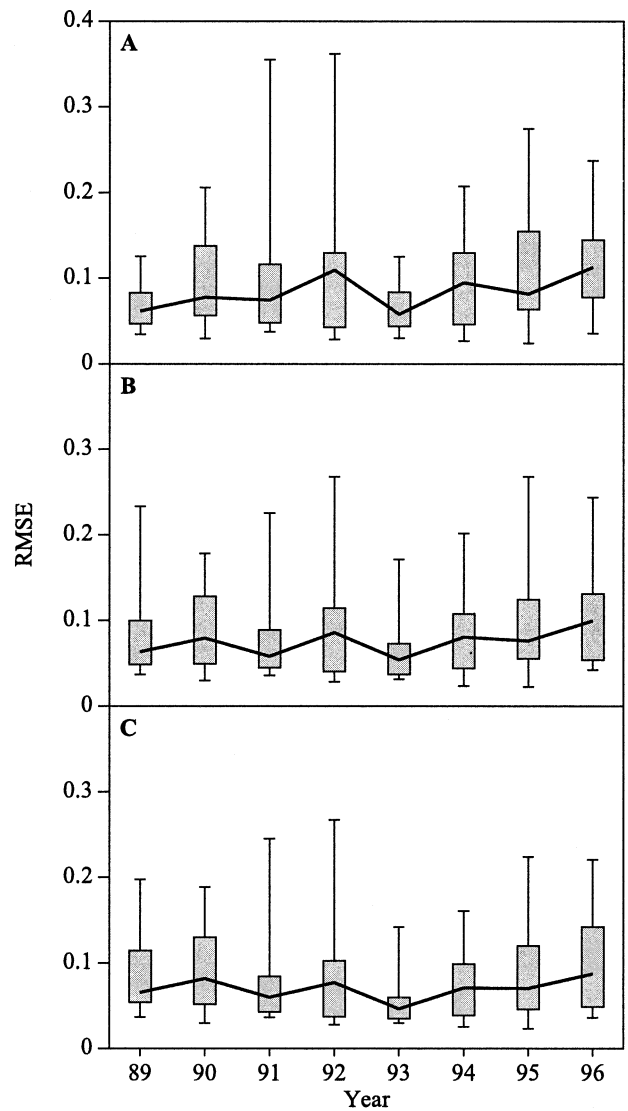


Fig. 4. Box plots showing root mean square error (RMSE) on the prediction of total phosphorus (TP) in the 16 turbid lakes studied during 8 yr, when calibrating the exchangeable P pool in the sediment on (A) the first (upper panel), (B) four (middle panel), and (C) seven (lower panel) years of data, respectively. Full line indicates median values. Also shown are 10%, 25%, 75%, and 90% percentiles.

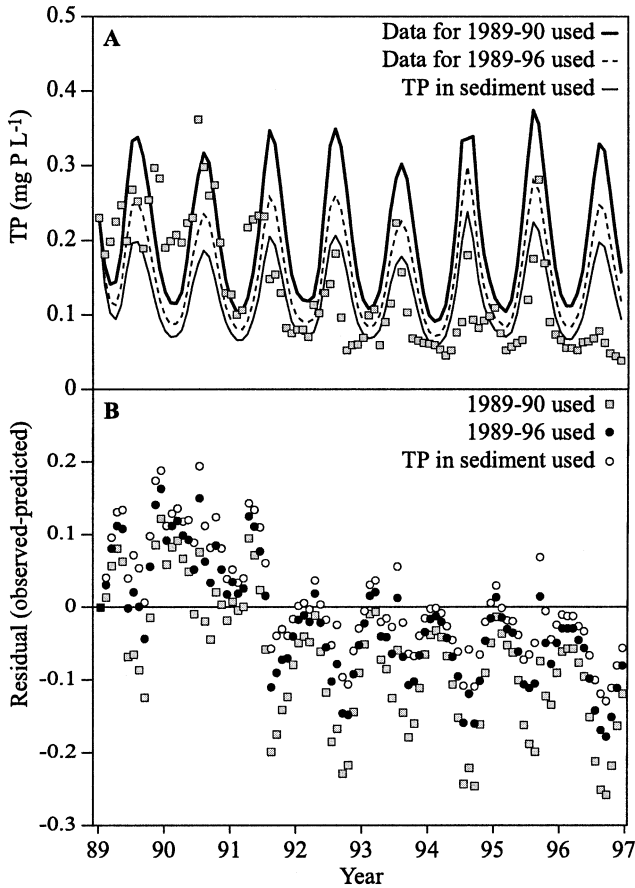


Fig. 5. Lake Arreskov before and after a major fish kill in 1991 and subsequent fish manipulation. (A) Observed and predicted total phosphorus (TP) concentrations based on calibration of P_s on data from 1989 to 1990, data from 1989 to 1996 and measured TP in sediment. (B) Residuals for the same relationships. RMSE was 0.095 when P_s is calibrated on data from 1989 to 1990, RMSE was 0.059 when P_s is calibrated on data from 1989 to 1996, and RMSE was 0.068 when P_s is the measured TP in the sediment.

(Søndergaard et al. 1999), as clearly indicated by the results from biomanipulated Lake Arreskov that has shifted to a clear-water state (Fig. 5). In conclusion, some refinement of the model is needed to make it amenable for long-term predictions.

The calibrated temperature coefficient for phosphorus release from the sediment corresponds to a Q_{10} of 2.2 and is, thus, close to the value of a physiological temperature response. That temperature plays a key role for the seasonal variation in the phosphorus release of shallow lakes has been evidenced by several studies (Boström et al. 1982; Jensen and Andersen 1992). However, the reason is not only increased phosphorus release due to increased mineralization of organic matter, but also the consequence of reduced redox level in the top surface sediment affecting the capacity of iron to retain phosphorus (Mortimer 1941; Stauffer 1981).

The coefficient of sedimentation was calibrated to 0.047 m d^{-1} or approximately 5% of the in-lake TP pool d^{-1} in a 1-m deep lake. This rate is low compared with those given by Reynolds (1984), but an explanation may be that a con-

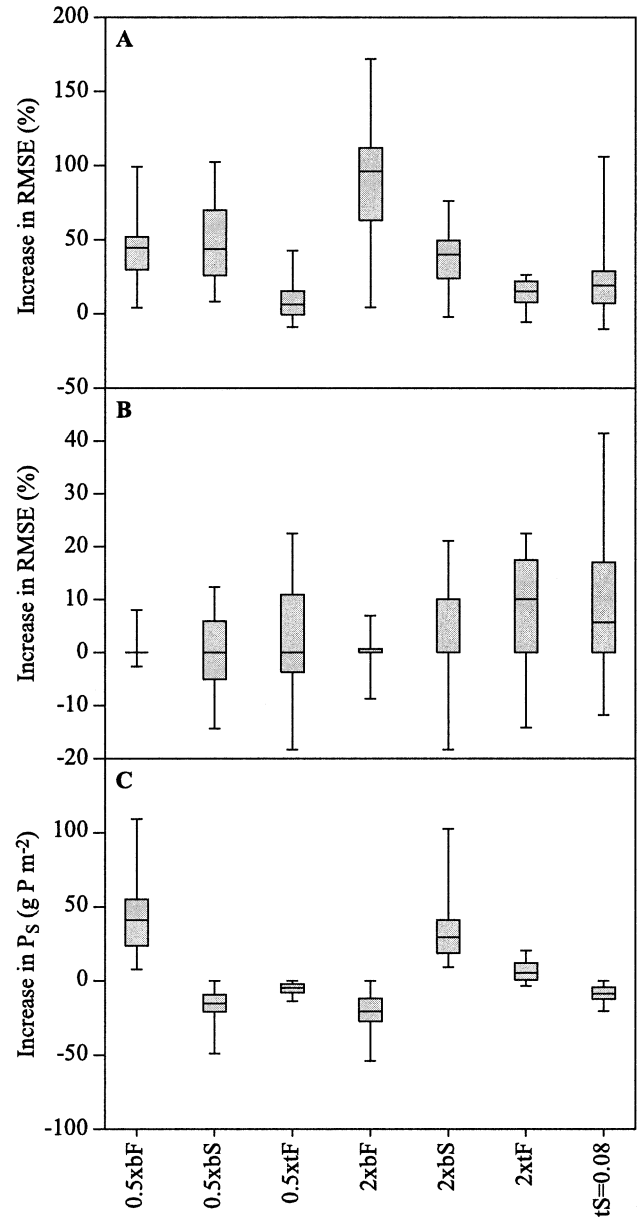


Fig. 6. Box plots of the relative increases in RMSE in response to changing one of the model parameters while keeping the estimated initial P_s values at the estimated values in Table 2 (upper plot) and (B) while reestimating the initial P_s values (center plot). The lower plot shows box plots of the absolute increases in the estimated initial P_s values.

siderable fraction of TP in the lakes consists of orthophosphate during summer (Søndergaard et al. 2005). The sedimentation part of the model could be made more causal if only particulate TP was included. This would, however, require a substantially more complex model including processes for the exchange between dissolved TP and particulate TP and, therefore, as a minimum, additional models (and data) for algal phosphorus uptake and release by grazing. Enhanced complexity would make the model less valuable for managers.

It is remarkable that a simple model is capable of covering

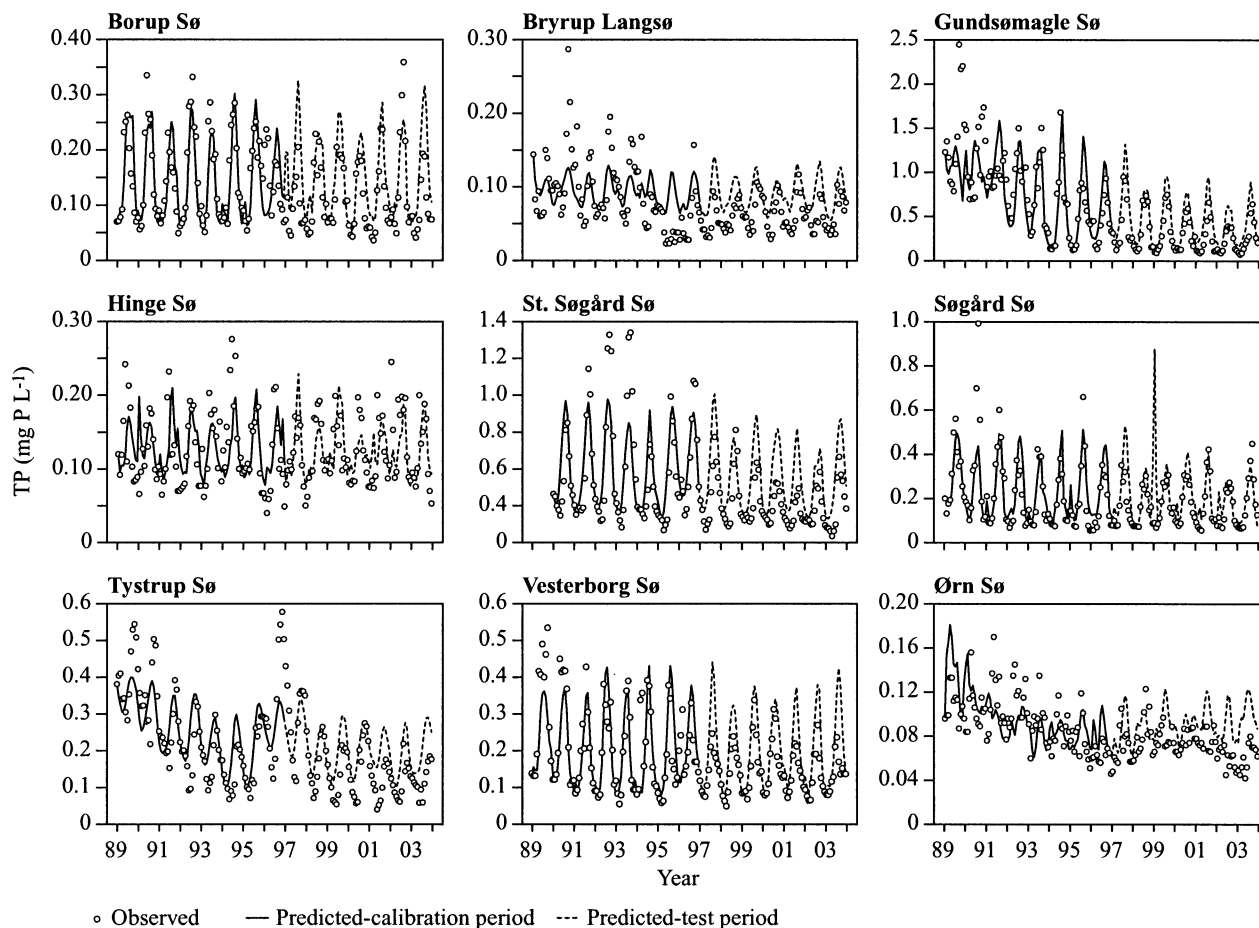


Fig. 7. The model applied to data from 1997 to 2003 for 9 of the 16 lakes using observed values of the exogenous variables for all years. Predicted values in the calibration period 1989–1996 are connected by a solid line and by a dashed line in the test period 1997–2003.

so well the seasonal dynamics of TP in the 16 turbid lakes used for testing the model, considering that temperature is far from the only factor influencing phosphorus release from the sediment (Boström et al. 1982). The explanation is probably that temperature integrates most of the seasonal mechanisms responsible for the phosphorus release in eutrophic relatively iron-rich lakes. In such lakes, phosphorus release is stimulated in summer when nitrate reaches critically low levels (Andersen 1982) and when pH increases (Boström et al. 1982; Welch and Cooke 1995). Low nitrate and high pH typically occur in summer (in some lakes pH may be high in spring too) when the temperature is high, and this may explain the high predictive power of temperature in our model. We did not deliberately include nitrate and pH in the model because complex mechanisms are included in the seasonal dynamics of these two variables that are difficult to forecast. P release may also be enhanced during spring and summer when the decomposition rate increases, mobilizing both organically bound phosphorus and inorganic phosphorus sorbed to redox-sensitive compounds (mainly iron) because of the diminished oxidized layer of sediment (Søndergaard et al. 2003).

By calibrating P_s , closer correspondence between observed and estimated lake TP was obtained from the 16 test

lakes than by using the observed TP pool in the upper 20 cm of the sediment. This is not surprising, since the exchangeable sediment phosphorus pool is difficult to determine. First, it is difficult to define the maximum depth from which phosphorus is released. Studies of the changes in the sediment phosphorus pool of highly eutrophic Lake Søbygård in Denmark have shown that phosphorus is released from depths down to 20 cm (Søndergaard et al. 1999), and we therefore chose this depth for the present investigation. The “active” depth is, however, likely to vary from lake to lake, depending on factors such as sediment type and shear stress, and sometimes only 10 cm of the upper sediment is considered to be actively involved in the sediment–water interactions (Boström et al. 1982). Second, the exchangeable pool depends on how phosphorus is bound in the sediment (Boström et al. 1988). To identify the exchangeable P pool, several fractionation methods have been developed (Hietjes and Lijklema 1980; Boström et al. 1982; Psenner and Puscko 1988). It is believed that the exchangeable P pool mainly consists of the loosely and iron-bound phosphorus, which can be extracted by ammonium chloride and sodium-dithionite, respectively (Psenner and Puscko 1988). However, the value of using fractionation for determining the exchangeable P pool has been debated extensively

(Stauffer 1981; Boström et al. 1988; Jensen et al. 1992), and so far it has not been possible to establish any distinct relationship. Owing to the difficulties involved in determining the exchangeable P pool, we recommend it to be calibrated. For most lakes, RMSE of the prediction was not sensitive to the number of years used for calibrating the exchangeable P pool. Even when the pool was calibrated on data from a single year only, the model generally had a relatively high predictive power. The very high TP levels measured in the sediment of one lake with high iron concentrations emphasize the importance of iron in binding phosphorus in the sediment (Søndergaard et al. 1996).

While the models using the estimated or measured TP pool in the sediment for some lakes underestimated and for others overestimated annual mean in-lake TP, the predictions by the model developed by Vollenweider (1976) generally and often substantially underestimated lake water TP (Table 3). This was to be expected since the Vollenweider model is based on steady state conditions; most Danish lakes, including the study lakes, are, however, in a transient state following the reduced external loading, resulting increased internal loading (Jeppesen et al. 1991; Søndergaard et al. 1999). As an illustrative example, net retention in eutrophic Lake Søbygård was still negative in 1998, sixteen years after loading reduction (Søndergaard et al. 1999), despite the lake's short hydraulic retention time (approx. 1 month). Thus, our results suggest that the duration of the period with excess internal loading may be long even in lakes with a short hydraulic retention time (<1 month) (Jeppesen et al. 1991; Søndergaard et al. 1999).

The results from the biomanipulated Lake Arreskov indicate that the model was unable to track the changes occurring in the seasonal P dynamics of shallow lakes shifting from a turbid to a clear-water state. The model markedly overestimated in-lake TP in the clear-water state. The response of Lake Arreskov is typical for fish-manipulated lakes, and a number of investigations have shown phosphorus and nitrogen retention to increase considerably after a shift to the clear-water state (Søndergaard et al. 2003; Boers et al. 1991; Jeppesen et al. 1998). This is probably the explanation of the model's inadequacy. Higher P retention may reflect a light-mediated increase in the growth of microbenthic algae enhancing sediment oxidation and thus the phosphorus-binding capacity of iron (Hansson 1989; Van Luijn et al. 1995). However, other factors also may be involved. Hence, lower phytoplankton abundance means lower sedimentation of phytoplankton and accordingly lower oxygen consumption in the sediment, potentially enhancing the redox potential. In addition, an increase in the abundance of benthic invertebrates due to a decline in fish predation pressure (Andersson et al. 1978; Giles et al. 1989) may contribute to higher sediment oxidation, although the role of invertebrates for P release is ambiguous (Andersson et al. 1988). Furthermore, increased abundance of submerged macrophytes due to improved light conditions may also be of importance, though high densities of macrophytes in eutrophic lakes may stimulate sediment P release (Perrow et al. 1994; Moss et al. 1996). For Lake Arreskov, however, uptake by macrophytes cannot be the main reason for the decline in in-lake TP and enhanced TP retention in the sediment (Fig.

7), since the recolonization of submerged plants started 2 yr after the abrupt decline in summer TP (Jeppesen et al. 1998). More complex models need to be established to cover the effects of such changes in trophic structure on the P dynamics of shallow lakes.

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