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SECRETS OF SHALLOW LAKES

Recovery of lakes from eutrophication: changes in nitrogen retention capacity and the role of nitrogen legacy in 10 Danish lakes studied over 30 years

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Abstract Using data on 23 Danish lakes, we conducted mass balances to develop total nitrogen (TN) models for predicting annual mean TN in lakes based on external TN loading and found high predictability when including lake hydraulic retention time and mean depth in the model. We further used a unique 30-year mass balance data series from 10 Danish lakes with contrasting mean depths and hydraulic retention times to elucidate the effect of external TN loading reduction and N legacy on lake TN. We found that the TN retention percentage during the 30 years was generally not sensitive to an often major reduction in the external TN loading; it overall followed the pattern of the above model predictions, suggesting a low TN legacy effect. Moreover, the TN retention percentage was not affected by changes in TP. Our results, therefore, show a fast response to TN loading reduction, indicating that we can expect an immediate effect on lake water quality in shallow lakes suffering from internal phosphorus loading during re-oligotrophication provided that inorganic N is low enough to become a growth-limiting nutrient.

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Introduction

Riverine and groundwater-derived nitrogen (N) is retained or denitrified when passing through lakes, and the loss percentage is particularly affected by the hydraulic retention time (OECD, 1982; Bachman, 1984; Lijklema et al., 1989), lake depth (Windolf et al., 1996) and trophic structure (Jeppesen et al., 1998). Several simple empirical models have been developed to describe the concentration and loss (denitrification + accumulation in the sediment) of N in lakes on an annual (OECD, 1982; Bachman, 1984; Saunders and Kalff, 2001) or seasonal scale (Windolf et al., 1996) as a function of the external N loading.

For Danish eutrophic, turbid lakes, these simple models provide a relatively precise prediction of the annual and seasonal dynamics of N (Windolf et al., 1996), except in lakes with major changes in trophic structure due to restoration by fish manipulation, where a substantial increase in N retention occurred following a shift to a clear-water state (Jeppesen et al., 1998).

Much effort has been devoted worldwide to nutrient control with the purpose of restoring eutrophicated lakes (e.g. Sas, 1989; Jeppesen et al., 2005; Steinman & Spears, 2019). Special focus has been on reducing the external phosphorus loading as phosphorus (P) is often considered the most important factor for eutrophication (Schindler, 1978) and as P control in wastewater treatment is considered easier and cheaper than N control (Tammeorg et al, 2023). More recent studies, however, have highlighted that N may play a far more important role in the shift from a clear to a turbid state in shallow lakes than hitherto anticipated (Moss, 2001; González Sagrario et al., 2004; Jeppesen et al, 2007; Olsen et al., 2015; Søndergaard et al., 2017; Shatwell & Köhler, 2019; Jeppesen et al., 2021). In Europe, in the past few decades, focus has been directed at reducing not only P but also N, while P reduction has been of key importance in most other places, e.g., USA. Slow responses to external P loading reduction have been observed in many studies (Steinman & Spears, 2019). This is due to internal P release from the sediment, which may result in prolonged negative retention (Søndergaard et al., 2003, 2013). In contrast, the N response seems faster (Jeppesen et al., 2005; Shatwell and Köhler, 2019), which has been attributed to loss by denitrification, leading to less accumulation of N than of P in the sediment. However, few long-term studies of N retention are available on lakes undergoing re-oligotrophication, and to what extent an N reduction will affect the N retention capacity in the short and longer term in lakes is an open question.

In this study, we developed models for predicting the annual mean total nitrogen (TN) in lakes in relation to external TN loading, lake hydraulic retention time (retention time) and mean depth using data on 23 Danish lakes collected in the period 1989 to 2004. We further exploited a unique 30-year mass balance data series from 10 Danish lakes with contrasting mean depths (1 to 16.5 m) and hydraulic retention times (0.05–12.2 years) to elucidate the effect of an external TN loading reduction and N legacy on TN in the lakes. These 10 lakes had also been subjected to various degrees of external P loading reduction, allowing us to also evaluate the effect of N:P ratios and P concentrations on TN retention. We hypothesised that the response of in-lake TN to TN loading reduction would be fast and that the role of legacy N therefore would be low.

Materials and methods

For mass balances, water was sampled in inlets and outlets according to the standardised guidelines of the Danish Nationwide Monitoring Programme (Kristensen et al., 1990; Kronvang et al., 1993). Thus, the main inlet of each lake was sampled 18–26 times annually depending on seasonal variations in discharge, while the minor inlets were sampled less frequently depending on their relative contribution to the total hydraulic and nutrient loading. Outlet samples and depth-integrated lake water samples in the photic zone were collected fortnightly during summer and monthly during winter, i.e. 19 times annually. TN was measured on unfiltered water as nitrite + nitrate after potassium persulphate digestion according to the method of Solórzano & Sharp (1980), and nitrite + nitrate was measured after cadmium reduction. For a period (2007–2014 and 2016—winter 2017) a UV method was used to analyse for TN and TP which underestimated TN and likely also TP. TN was underestimated by 14.6 -16.3% and data corrected accordingly whereas it was not possible to estimate a correction factor for TP (Larsen et al., 2020).

The mass balance calculations differed between the 23 lakes used for developing the nitrogen models and the 10 lakes with long-term data (also included in the 23 lakes for 1989–2004).

Mass balances for the 23 lakes

Total discharge in the main inlets and most outlets (Q_{m}) was measured manually monthly with an OTT-propeller and later also with a Doppler flow meter. The water level (H) was automatically and continuously recorded during the entire study period. Daily discharge (Q_{d}) was calculated by use of the relationship obtained for H and Q_{m}. In minor inlets and a few outlets, discharge (q) was measured, and daily discharge values were calculated from q/Q_{d} relationships.

Yearly water balances were calculated for each lake using the following equation:

$$Q_{\mathrm{inm}} + Q_{\mathrm{inu}} + \mathrm{Prec} = \mathrm{Vol}_{\mathrm{dif}} + Q_{\mathrm{outm}} + O_{\mathrm{outu}} + \mathrm{Evap} \quad (1)$$

where Q_{inm} and Q_{outm} are the total discharge measured in inlets and outlets, respectively. Evap and Prec are mean monthly evaporation and precipitation obtained from meteorological station data from Denmark (interpolated to 10*10 km grids for precipitation and 20*20 km grids for evaporation), and $\mathrm{Vol}_{\mathrm{dif}}$ is the annual change in lake volume. Q_{inu} and Q_{outu} are the unmeasured input from the unmeasured catchment and output (seepage) from the lake, respectively. Q_{inu} and Q_{outu} were determined on an annual basis by adjusting the mass balance; if $\mathrm{vol}_{\mathrm{dif}} + Q_{\mathrm{outm}} + \mathrm{Evap} > Q_{\mathrm{inm}} + \mathrm{Prec}$, then Q_{inu} is equal to the difference, and if the opposite is true $\mathrm{Q}_{\mathrm{outu}}$ is equal to the difference. This approach is rough in the sense that an unmeasured waterflow in and out can be hidden in case that both Q_{inu} and Q_{outu} are high for the same lake. However, this uncertainty is judged to be minor compared to the sampling uncertainty related to the measurement of the nitrogen concentration, where the monthly mean value is calculated based on a limited number of samples without considering the related estimation uncertainty, i.e. often calculated based on a single point measurement assumed to be representative for the concentration level during the entire month.

Daily values for the various N concentrations were calculated by linear interpolation of observed values. N transport was then estimated as the product of the daily water discharge and N concentrations. The input and output of total N were determined using the monthly water balances, the assumption being that the N concentration of the unmeasurable discharges to and from the lake equalled the Q-weighted concentrations in the measured inlets and outlets. In cases where the input of ground water was considerable, information on ground water N concentrations was applied. Atmospheric deposition was added using an average rate for Denmark of 20 kg N and 0.2 kg P ha^{-1} year^{-1} until 1997 (Hovmand et al., 1993) and hereafter 15 kg N and 0.1 kg P ha^{-1} year^{-1} For two of the lakes, no outlet data were available, and inlet Q and $\mathrm{N}_{\mathrm{lake}}$ were therefore used instead. No information on N fixation was available.

N retention values were then calculated using the mass balance model of Messner and Brezonik (1978):

$$\begin{aligned} \mathrm{Retention} &= \text{Total input (apart from } N \text{ fixation)} \\ &\quad - \text{Storage} - \text{Total output} \end{aligned} \quad (2)$$

and retention percentage as Retention/Total input (apart from N fixation)*100.

We conducted a multiple regression relating the annual mean lake TN to the annual mean discharge-weighted inlet TN concentration, mean depth and annual mean water residence time.

Mass balances for the 10 lakes

A different method was used for the 10 lakes with a 30-year record as the method used to predict lake load and release of nitrogen changed from 2015 and onward. The method is described in detail by Sørensen and Nielsen (2023). Briefly, it contains three sub-models: (1) Water balance model; (2) TN and TP concentration model for lake inlet; (3) TN and TP load model. The input for the model is the monthly measured water flow and TN and TP concentration levels in the lake surface water (photic zone), the lake outlet and one or several incoming streams. Atmospheric deposition for phosphorus was estimated as described above.

A mass balance of water for the lake relates the measured inflow and outflow of water in a linear statistical model, where the outflow is explained by the inflow. The accumulation of water in the lake is accounted for by including both the inflow to the lake during the former months and the inflow during the current month in the model to describe the outflow during the current month. Quantification of unmeasured water flow is primarily done using the linear model, where the outflow of the lake is described by the measured inflow (former months and current month), because the estimated slope of the linear relation and the intercept will identify unmeasured water volumes. The linear model is also used to fractionate the unmeasured water into, respectively, ground water and surface-near water, where the lowest measured flow during a year is assumed to be purely groundwater, and changes in unmeasured groundwater flow during the year is described by the interface of the linear model (for details see Sørensen & Nielsen, 2023).

The nutrient concentration (TN and TP) model for the inlet is based on the measured concentration in the inlet water, consisting of a fraction originating from ground water and another from more surface-near water, often showing differing concentrations, and the inlet concentration is considered a mixture of two different concentration levels. However, as the fractions of ground water and surface-near water change from month to month, it is possible to identify the original (latent) nutrient levels in the two water types. For this purpose, a statistical model was developed to identify the two concentration levels as latent concentrations. The unmeasured load to the lake was predicted by multiplying the latent concentration for ground water by the unmeasured volume of ground water and by multiplying the latent concentration for surface-near water by the unmeasured volume of surface-near water.

The two mass balance methods gave comparable results for the nitrogen retention percentage for the lakes and years where both methods were applied (see Appendix).

For each of the 10 lakes, we conducted linear trend analyses (GLM) for the study period.

Results

Model development on 23 lakes (1989–2004)

The key environmental variables for the 23 lakes used for the model development are given in Table 1. The lakes covered a wide range in area, mean depth, mean retention time, TP and TN concentrations.

The calculated TN retention is plotted against the TN loading for the 23 lakes sampled between 1989 and 2004 and shows a generally high loss (denitrification and storage) (Fig. 1, upper panel). We found a strong relationship between the annual mean discharged-weighted inlet TN (TN_{in}, mg l^{-1}) and the annual mean in-lake TN ($TN_{lake,}$ mg l^{-1}) concentrations when including also annual mean retention time (TW, *y*) and mean depth (*Z*, *m*) in the regression (log is natural logarithm):

$$\begin{aligned}\text{Log}\left(TN_{lake}\right) = &-0.80 \pm 0.08 + 0.82 \pm 0.03 \log\left(TN_{in}\right)\\ &+ 0.13 \pm 0.03 \log(Z)\\ &- 0.20 \pm 0.02 \log(TW),\\ &r^2 = 0.75,\ P < 0.001,\ n = 295\end{aligned} \tag{3}$$

and back-transformed to TN_{lake} (Fig. 1, lower panel).

Long-term study of 10 lakes (1990–2020)

Ten of the 23 lakes with a 30-year data series ranged substantially in size (0.2–39.9 km^2), mean depth (1.0–16.5 m) and mean retention time (0.05–3.3 years) (Table 2).

During the 30-year period, hydraulic loading and retention time varied among years but without showing any clear trend (Fig. 2a, b). The external loading of TN (Fig. 2c), in-lake TN (Fig. 2d) and N retention

Table 1 Means (period 1989–2004) of key lake variables for the 23 lakes used in the model development

	Mean	St. Dev	Minimum	Maximum
Lake area (km^2)	3.19	8.47	0.05	39.9
Mean depth (m)	3.62	3.45	0.9	16.5
Retention time (year)	0.62	0.90	0.02	12.2
Total phosphorus (mg l^{-1})	0.18	0.12	0.03	0.57
Total nitrogen (mg l^{-1})	3.64	1.33	1.32	5.74

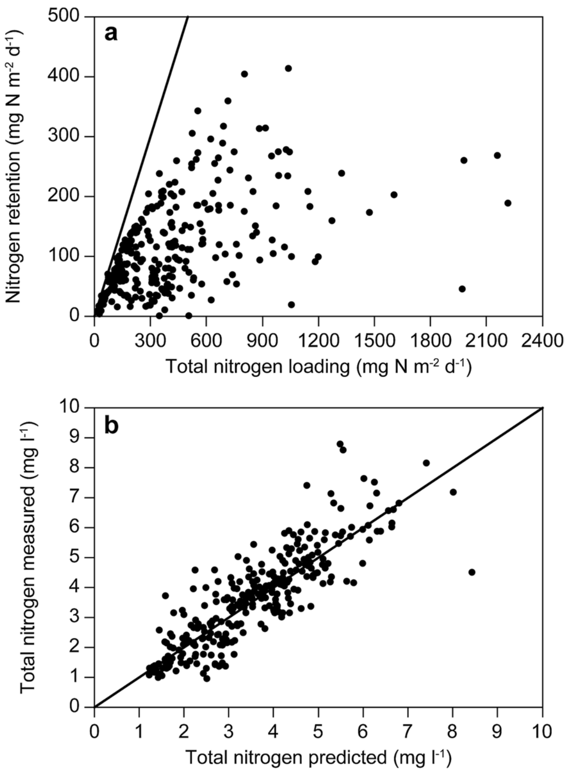


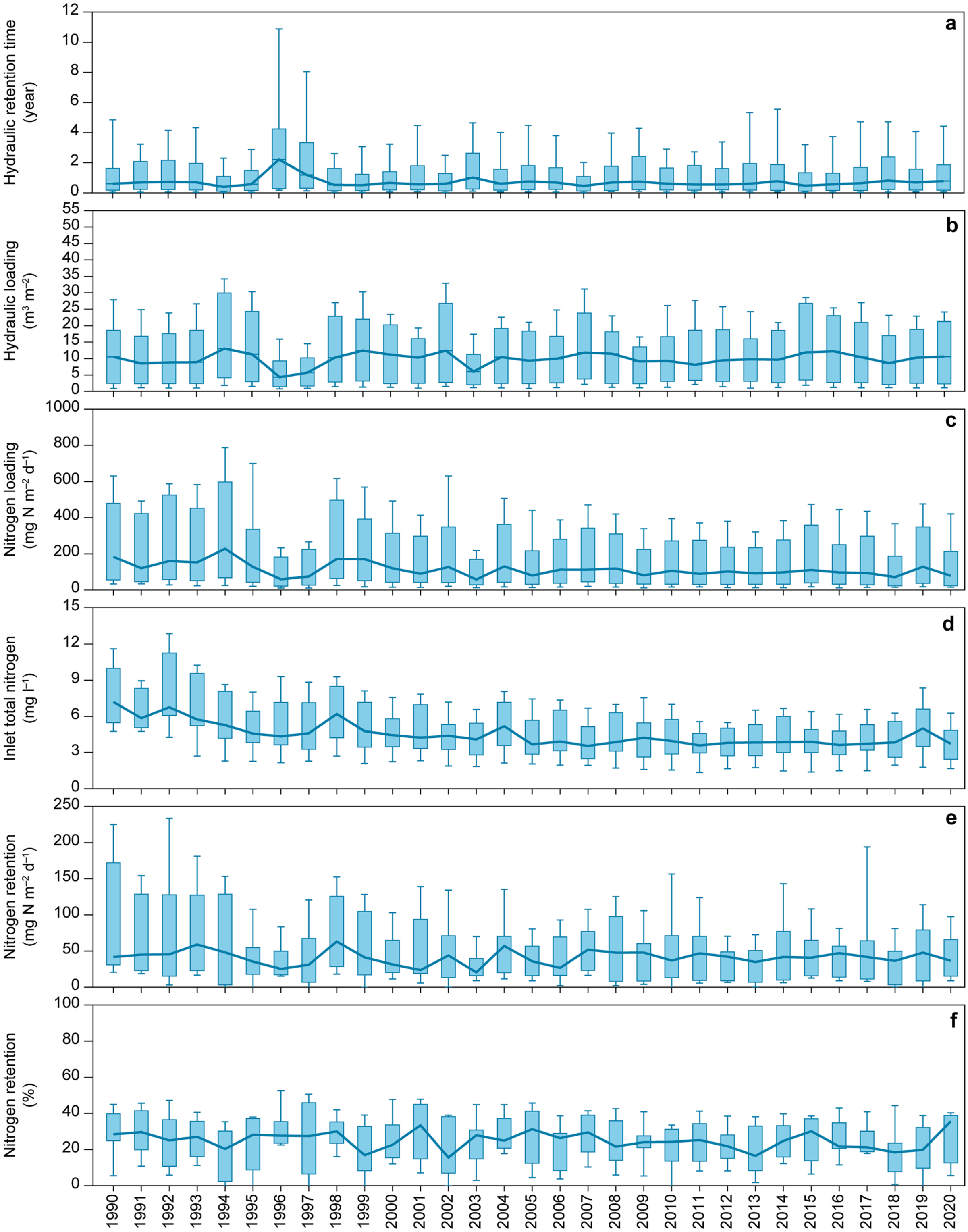
Fig. 1 (Upper) Nitrogen retention related to total nitrogen loading in 23 Danish lakes (295 lake years). Also shown is the 1:1 line. (Lower) Predicted and measured annual mean in-lake concentrations of total nitrogen for the same set of lakes using Formula 3

(Fig. 2e) generally decreased, while the N retention percentage remained rather constant (Fig. 2f). Specifically, the external TN loading decreased from an average of 308 mg N m^{-2} day^{-1} from the period 1990–1994 to 198 mg N m^{-2} day^{-1} in the period 2015–2019, and the TN retention decreased from 84 to 55 N m^{-2} d^{-1} (Table 3). The mean retention percentage ranged between 21 and 26%, showing a tendency to a slight decrease by the end of the study period.

No significant changes were found in the hydraulic loading for any of the lakes (Table 4). For all lakes, we found a significant decline in the discharge-weighted inlet TN, while the inlet TP declined in eight of the 10 lakes (Table 4). Due to the dual reduction of N and P concentrations, the TN:TP ratio in the inlet did not show a clear response but revealed both an increase, a decrease or no significant change (Table 4). Apart from two lakes (Vesterborg and Søholm), the in-lake TN concentration decreased during the study period, both on an annual basis and in summer. The (annual) in-lake TN:TP ratio showed an increase in six lakes and a decrease in one lake, but apart from two lakes (Arreskov and Ravnsø) these changes did not match the changes in inlet TN:TP (Table 4). The TN retention percentage showed only a minor response, being slightly significantly increasing in Lake Hinge and decreasing in Lake Arreskov, while no significant changes were found for the other eight lakes (Table 4). We also related the TN retention percentage to in-lake TP and found a slightly positive relationship for Lake Engelsholm ($r^2 = 0.17$, $P < 0.02$) and a slightly negative relationship for Lake Bryrup ($r^2 = 0.14$, $P < 0.04$), but no significant relationships appeared for the other eight lakes, and no overall relationship of the total dataset with lakes treated as a class variable was found ($P > 0.05$).

Table 2 Means (period 1990–2020) of key lake variables for the 10 lakes based on long-term data. Measured (%) is the percentage of the water input with direct measurements of TN concentrations. For the remaining part, water input TN is estimated (see methods)

Lake	Area (km^2)	Mean depth (m)	Retention time (year)	Measured (%)
Vesterborg	0.21	1.0	0.06	85.7
Hinge	0.93	1.2	0.05	75.4
Arreskov	3.12	1.9	1.20	41.3
Engelsholm	0.43	2.6	0.21	64.1
St. Søgaard	0.61	2.7	0.20	89.6
Arresø	39.9	3.1	3.23	42.3
Bryrup	0.37	4.6	0.23	81.3
Søholm	0.26	6.5	1.35	62.8
Ravnsø	1.81	15.0	2.04	79.1
Furesø	9.41	16.5	12.2	38.6


a
Hydraulic retention time (year)
0
2
4
6
8
10
12
b
Hydraulic loading ($m^3 m^{-2}$)
0
5
10
15
20
25
30
35
40
45
50
55
c
Nitrogen loading (mg N m^{-2} d^{-1})
0
200
400
600
800
1000
d
Inlet total nitrogen (mg l^{-1})
0
3
6
9
12
15
e
Nitrogen retention (mg N m^{-2} d^{-1})
0
50
100
150
200
250
f
Nitrogen retention (%)
0
20
40
60
80
100
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020

◂**Fig. 2** Changes in annual mean lake retention time (**a**) and loading of water (**b**) and total nitrogen (**c**), inlet discharge-weighted annual mean total nitrogen concentration (**d**) and nitrogen retention as absolute values (**e**) and as percentage of external loading (**f**) in 10 lakes followed for 30 years. Bars are 25% and 75% percentiles, respectively, full line is median. Also shown are the 5 and 95% percentiles

Figure 3 illustrates the changes in annual mean discharge-weighted inlet concentrations as well as measured and predicted in-lake concentrations of TN for the 10 lakes and shows the decline occurring in both inlet and in-lake concentrations, as also demonstrated in Table 4. Additionally, we found good correspondence between predicted and measured in-lake TN concentrations for most of the lakes (Fig. 3), and when this was not the case (Lake Arresø), there was apparently no systematic change in deviation with time. To elucidate this further, we calculated the difference between the annual mean in-lake TN and the predicted TN (expressed as a percentage of the latter) and analysed the emerging trend (Table 5). Only in one lake, Hinge, did we see a decline in the difference between the predicted and observed TN. By contrast, six of the lakes exhibited a significant decrease in the percentage deviation for TP (and one an increase) when using the OECD (1982) equation:

$$TP_{lake} = TP_{in}\left(1/\left(1 + TW^{0.5}\right)\right) \tag{4}$$

for prediction, where TP_{Lake} and TP_{in} are annual mean lake and discharge-weighted inlet concentrations, respectively, and TW is the annual mean water retention time. Four examples that clearly illustrate the different responses of TP and TN are displayed in Fig. 4.

Discussion

Our study revealed that: (1) the in-lake TN concentration was strongly dependent on and well predicted by the discharge-weighted annual mean TN concentration, the annual mean retention time and mean depth; (2) the TN retention percentage was generally not sensitive to the reduction in external TN loading, suggesting a low N legacy effect; 3) the retention percentage was generally not affected by changes in TP. Our results, therefore, show a fast response in in-lake TN concentrations to TN loading reductions independent of changes in TP.

As in several other studies conducted in rivers, lakes, wetlands and coastal environments (e.g. OECD, 1982; Saunders & Kalff, 2001), we found that in-lake TN concentrations were strongly linked to the discharge-weighted inlet concentration and water retention time. The dependency on retention time can be explained by higher loss by denitrification and higher net sedimentation when the water stands longer in the lakes. Our extensive dataset also revealed that mean depth was a contributory factor (higher loss in shallow lakes), as in the study by Windolf et al. (1996) on a smaller dataset from Danish lakes, which most likely reflects a higher contact between water and sediment in shallow lakes, augmenting denitrification. The slope of 0.82 (Std error = 0.03) on the inlet concentration of TN in Eq. 3 indicates a gradually higher loss in the lakes at increasing inlet TN, which might be explained by higher loss by denitrification at excess N not used by primary producers. This also means that we should expect a slight decrease in the retention percentage when the TN loading (concentration in the inlet) is reduced, as also indicated by the overall picture for the 10 lakes studied for 30 years (Table 3).

Using the developed TN model, we found a generally good correspondence between the predicted and the measured in-lake TN, without any delay (overshoot), indicating a fast response to a TN loading reduction. However, for three lakes (Engelsholm, Arresø and Arreskov), the predicted and measured concentrations differed. For these three lakes, the proportion of the water input with measured TN was relatively low (41.3–64.1%, Table 2) and the mass balance thus somewhat uncertain. Except for one lake (see below), we found no significant change in the TN retention percentage with time despite major reductions in the external TN loading, and also the three lakes for which the predicted in-lake TN differed from measured TN followed this pattern. Moreover, we found no clear effect of TP loading reduction or in-lake TP on the TN retention percentage, as evidenced by the close relationship between predicted and measured in-lake TN for the 23 lakes, irrespective of high variation in TP loading and in-lake TP. The TN retention percentage in the lakes was therefore primarily driven by water residence time and

Table 3 Changes in external loading, retention and retention percentage of total nitrogen in the 10 study lakes for 5-year periods

Period	Mean N loading mg m^{-2} day^{-1}	Mean N retention mg m^{-2} day^{-1}	Mean N retention (%)
1990–1994	308	84	25
1995–1999	213	62	26
2000–2004	199	60	25
2005–2009	182	58	25
2010–2014	172	51	21
2015–2019	193	55	23

mean depth, as indicated by the regression model for in-lake TN (Formula 3).

As we saw both a reduction in external TN and TP loading, we calculated the trend in the relative difference between the measured and the predicted TN concentration (as a percentage of the latter) and did the same for TP. Except for one lake (see next), we found no change in the relative difference in TN during the study period. By contrast, the relative difference declined in six of the 10 lakes for TP, clearly indicating a difference in the legacy role of the two nutrients, with TP and TN showing an overall slow and fast response to loading reduction, respectively. The slow response of TP is well known and can last for decades (Søndergaard et al., 2013; Steinman & Spears, 2019, Rippey et al, 2022), while the fast response for N can be explained by the fact that loss by denitrification of nitrate and through the coupled nitrification–denitrification in the sediment result in a low net release of N from the sediment and thus fast adjustment to the lower external loading.

One of the lakes (Lake Hinge), however, showed a different response as the relative difference between the measured and the predicted TN concentrations decreased with time. The measured values were mostly above the predicted values for TN, and also for TP, until 2006 (Fig. 3), where zebra mussels (*Dreissena polymorpha* (Pallas 1771)) invaded the River Gudenå system to which Lake Hinge belongs (Søndergaard et al., this volume). After the invasion, which led to a reduction of phytoplankton biomass, higher water clarity and colonisation of submerged macrophytes (Søndergaard et al., this volume), the differences became smaller and even negative in several of the years (i.e., the concentrations were lower than predicted) for both TN and TP concentrations. Enhanced N retention percentage was also found in four fish-manipulated lakes following a shift to a clear-water state by Jeppesen et al. (1998), which they attributed to (i) a decrease in organic N in the lake due to the decrease in phytoplankton biomass and thus

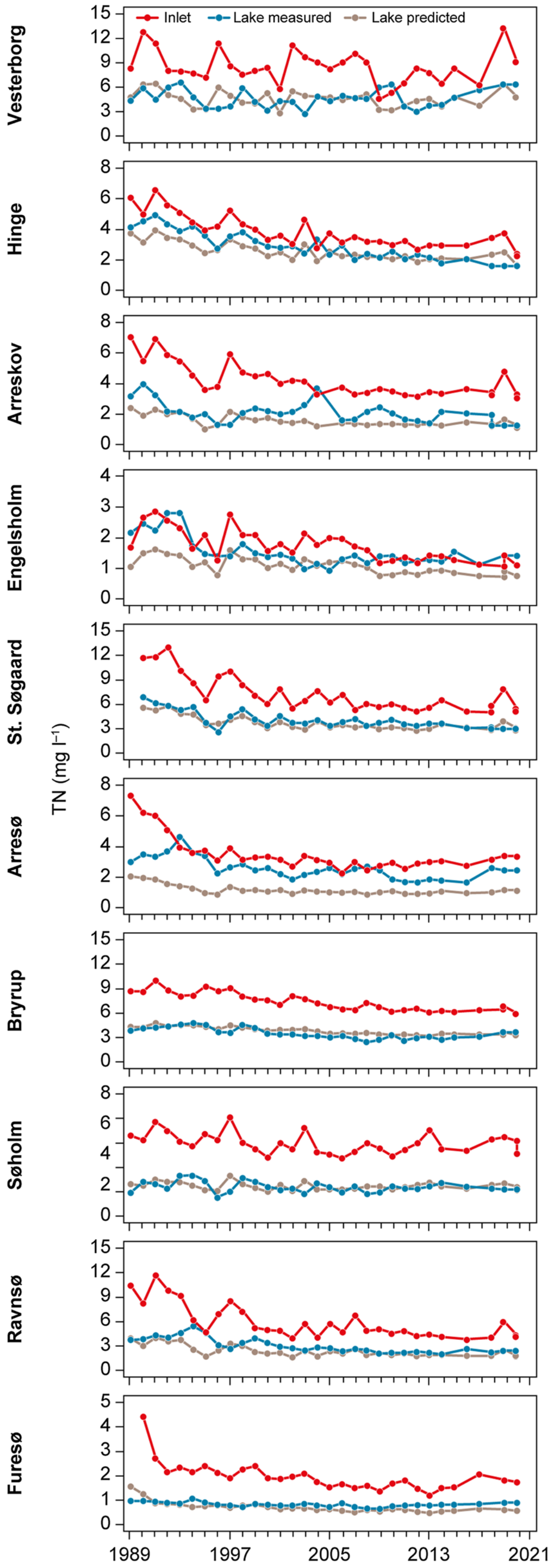
Table 4 Trend analysis (annual or summer means) for the time period 1990–2020 in 10 lakes ordered by increasing depth

Lake	Depth	Area	TW	Qn	TNin	TNlake	STNlake	TNretpro	TPin	TN/TPin	TN/TPlake
	Metre	Km^2	Year								
Vesterborg	1.0	0.21	0.06		***–				**–		***+
Hinge	1.2	0.93	0.05		***–	***–	***–	*+	***–	*–	
Arreskov	1.9	3.12	1.20		*–	***–	**–	*–	***–	*+	*+
Engelsholm	2.6	0.43	0.21		***–	***–	**–			***–	
St. Søgaard	2.7	0.61	0.20		***–	***–	***–		***–		*+
Arresø	3.1	39.9	3.23		***–	***–	**–		*–		***+
Bryrup	4.6	0.37	0.23		***–	***–	**–		***–	*+	
Søholm	6.5	0.26	1.35		***–						**+
Ravnsø	15.0	1.81	2.04		***–	***–	***–		***–	*–	***–
Furesø	16.5	9.41	12.23		***–	**–	*–		***–		***+

Qn hydraulic loading, *TNin* inlet TN, *TNlake* in-lake TN, *STNlake* summer mean in-lake TN, *TPin* inlet TP, *TN/TPin* inlet TN/TP ratio, *TN/TPlake* in-lake TN/TP ratio

*$P < 0.05$ **$P < 0.01$, ***$P < 0.001$. + is increasing and – decreasing. Empty cells means not significant

Fig. 3 Predicted annual mean inlet concentrations of total ▶ nitrogen (TN) (Formula 3) and measured annual mean in-lake TN concentrations during the 30-year study period in the 10 lakes. Also shown is the measured inlet concentration



TN, (ii) reduced resuspension, probably reflecting both a decrease in the number of fish foraging in the sediment and a suggested increase in benthic algal growth, and (iii) higher denitrification in the sediment, reflecting less competition between denitrifiers and phytoplankton for nitrate, (iv) enhanced N retention by phyto- and zoobenthos and (v) an increased coupled nitrification–denitrification rate due to higher oxygen concentrations, the latter reflecting low sedimentation, higher density of zoobenthos and higher oxygen production by benthic algae. Collectively, the results from Lake Hinge and the four fish-manipulated lakes mentioned suggest that the retention capacity for both TN and TP may be higher than predicted by the general formula when shallow lakes shift from a phytoplankton-dominated state to a macrophyte-dominated state with low chlorophyll *a* in the water, at least temporarily.

In conclusion, our study (1) confirmed that the in-lake TN concentration was strongly dependent on and well predicted by the discharge-weighted annual mean TN concentration and retention time, and we additionally revealed a dependence of lake mean depth; (2) showed that the N retention percentage was generally not sensitive to changes (i.e. reductions) in external N loading (unlike what is known for TP), suggesting a low effect of N legacy; (3) revealed that the N retention percentage was generally not affected by changes in in-lake TP in the TP range of the 10 lakes studied. Our results, therefore, identified a fast response in in-lake TN to TN loading reduction independent of changes in in-lake TP. This means that as long as the lakes suffer from high internal P loading and in-lake TP thus remains high, a reduction of external TN loading would have an immediate effect on lake water quality, providing that N acts as the key limiting nutrient for phytoplankton growth. Such an effect of N reduction is nicely demonstrated in

Table 5 Trend analysis of the deviation between measured and predicted annual means in-lake total nitrogen (TN) and total phosphorus (TP) concentrations in the 10 lakes during the study period. For statistical information, see Table 4

Lake	TN	TP
Vesterborg		***-
Hinge	***-	***-
Arreskov		*-
Engelsholm		
St. Søgaard		**-
Arresø		***-
Bryrup		
Søholm		***-
Ravnsø		*+
Furesø		

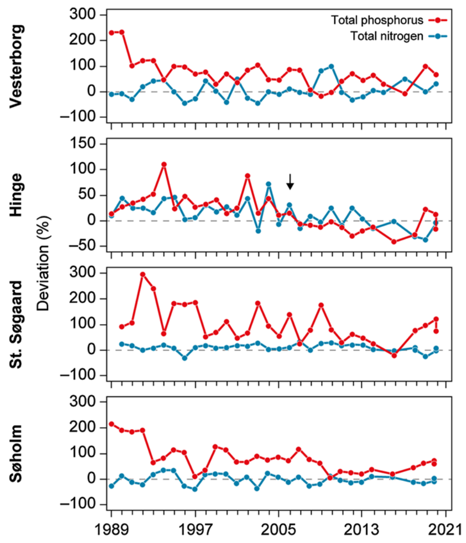


Fig. 4 Changes in deviation (%) from predicted total phosphorus (TP) (Formula 4) and total nitrogen (TN) (Formula 3) in lakes with large changes over time in in-lake TP and TN during the 30-year study period. The arrow for Lake Hinge indicates arrival of zebra mussels (*Dreissena polymorpha*)

the long-term study of Lake Müggelsee, Germany, by Shatwell and Köhler (2019). However, even in lakes with N limitation in summer, P may still be the limiting nutrient in spring and autumn (Shatwell & Köhler, 2019; Jeppesen et al., 2005 and 2021), indicating that external P loading reduction should be continued in such lakes in parallel with the N loading reduction.

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Data availability The datasets generated and/or analysed in the current study are available from the corresponding author upon reasonable request.

Declarations

Competing interest The authors have no competing interests relevant for the content of this article to declare.

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