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Improved empirical models for predicting nitrogen retention in lakes and reservoirs

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ABSTRACT

Anthropogenic activities have significantly increased the movement of nitrogen (N) from land to freshwaters and to coastal waters and have led to severe environmental consequences. The flow of N is moderated by retention processes in terrestrial, freshwater and marine ecosystems. Freshwater ecosystems have the highest areal N retention rates. The proportion of N retained in aquatic ecosystems depends on the areal hydraulic load and is described by relatively simple semi-empirical or strictly empirical models. Here I compared the predictive power of several models, that predict the annual mean proportion of total N (TN) and dissolved inorganic N (DIN) retained in lakes and reservoirs and developed an improved version of the models currently in use by inclusion of additional relevant parameters. The study shows that models derived from mass balances describing the proportion of annual mean retention of TN and DIN as a sigmoid function of the areal hydraulic load can be approximated by a linear function on the logarithm of the areal hydraulic load. Stepwise multiple linear regression analyses identified the logarithm of the areal hydraulic load as the main explanatory variable for the proportion of retained TN, followed by the ratio between the DIN and the TN load and the ratio between in-lake concentrations of TN and total phosphorus (TP). The logarithm of the areal hydraulic load, the ratio between the DIN and the TN load and the logarithm of the in-lake concentration of TP explained the largest proportion of retained DIN. Addition of the second and third explanatory variable decreased the normalized root mean square deviation between the observed and predicted proportion of retained TN from 37%, to 31% and to 30% and between the observed and predicted proportion of retained DIN from 39%, to 35% and to 32%.

1. Introduction

The global cycling of nitrogen (N) has almost doubled over the last century due to the large increase of anthropogenic N fixation through production of fertilizers, cultivation of legume crops, and combustion of fossil fuels (Galloway et al., 2004). Almost all N originating from land-based sources is retained from the three main ecosystem types: terrestrial (soils: 40%), freshwater (groundwater, lakes and reservoirs, rivers: 35%) and marine (estuaries, continental shelves, oxygen minimum zones: 25%); with rates per unit area in rivers/lakes that are up to 10 times higher than in soils (Seitzinger et al. 2006). Understanding and quantifying N retention processes is extremely important for managing and mitigating the severe environmental consequences associated with N pollution (Boyer et al., 2006). The main N retention processes are microbial-mediated emissions of N_2 gas, permanent storage in soils and sediments and uptake by primary producers. In aquatic ecosystems uptake of N by macrophytes and algae is usually only temporary as most nutrients assimilated during the growing phase are mineralized and released again in autumn (Clarke, 2002). The primary permanent N retention mechanism in aquatic systems is generally denitrification (Nixon et al., 1996; Saunders and Kalff, 2001a; Seitzinger, 1988), although more recently anaerobic ammonium oxidation (anammox) has been reported to contribute significantly to N retention (Lu et al., 2018). Denitrification occurs at oxic-anoxic interfaces. In aquatic systems these are located in the anaerobic layer of the sediments, in the suboxic bottom waters (Seitzinger et al., 2006) and in biofilms of submerged macrophytes or other substrates (Weisner et al., 1994). Nitrate can be supplied either from the overlaying water or produced in the sediment by nitrification of ammonium (coupled nitrification-denitrification). The first pathway may prevail in waters with a high external input of nitrate, the second when water column nitrate becomes limiting (de Klein, 2008). Measurements of denitrification rates in lakes show that nitrate concentration in the water above the sediment is the most important factor for predicting denitrification at variable geographical scales (McCrackin and Elser, 2012; Rissanen et al., 2013), but dependence on temperature (Ahlgren et al., 1994, Saunders and Kalff, 2001b, Veraart et al., 2011) and organic matter (Saunders and Kalff, 2001b) have also been reported. Because of the complexity of the N cycle, before N is finally retained from the aquatic ecosystem, it can undergo numerous reactions (assimilation,

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mineralization, nitrification, dissimilatory nitrate reduction to ammonium), that depend on a variety of environmental parameters such as concentrations of N, P, carbon (C) and oxygen, hydrology, morphology, and temperature. N occurs in different forms and oxidation states (nitrate, ammonium, nitrite, nitrous oxide, dinitrogen, organic nitrogen). Given this complexity, it is surprizing how well relatively simple empirical models are able to predict the proportion of TN retained in aquatic ecosystems ($\%R_{TN}$). Most such models have been derived from N input-output budgets (Kelly et al., 1987; Alexander et al., 2002). Basically two main approaches for modelling $\%R_{TN}$ have been applied: models that predict directly $\%R_{TN}$ (Alexander et al., 2002; Jensen et al., 1990; Molot and Dillon, 1993) and models that are based on the assumption that most N is retained on account of the imported nitrate and estimate $\%R_{TN}$ indirectly from models that predict the proportion of retained dissolved inorganic nitrogen ($\%R_{DIN}$) (Hindar et al., 2001; Seitzinger et al., 2002). Both $\%R_{TN}$ and $\%R_{DIN}$ correlate positively with the water residence time (τ) and negatively with the mean depth of the water column ($\bar{Z}$) (Molot and Dillon, 1993). τ and $\bar{Z}$ affect the duration and the extent of the contact between the water column and the sediment surface influencing the N uptake by the sediment (Coppens et al., 2015).

Some of these relations have been used to make predictions of N retention rates at regional and global scales (Alexander et al. 2002; Beusen et al., 2016; Harrison et al., 2009; Seitzinger et al., 2010; Wollheim et al., 2008). Several studies suggested that parameters other than τ and $\bar{Z}$ may significantly influence the proportion of N retained in lakes: in-lake concentration of P (Berge et al., 1997; Coppens et al., 2015; Kaste and Lyche-Solheim, 2005) and nitrate (Mulholland et al., 2008), the TN:TP ratio (Guildford and Hecky, 2000), temperature (Coppens et al., 2015; Rissanen et al., 2013), the presence of organic matter and the quality of the N loads (i.e. less easily recyclable inorganic N; Rissanen et al., 2013).

The aim of this study was to compare the predictive power of existing simple empirical annual mean TN and DIN retention models for lakes and reservoirs and to develop an improved version of the models currently in use by inclusion of other relevant parameters. The purpose is to predict the amount of annual mean TN and DIN that is retained.

2. Material and Methods

2.1. Derivation and calibration of the models currently in use

Existing empirical N retention models can basically be divided into semi-empirical and strictly empirical models. Semi-empirical models are derived from N mass-balance equations of lakes or river sections, they are calibrated with measured environmental variables, and they describe the proportion of retained N as a function of τ and $\bar{Z}$. Empirical models are a based on statistical relationships between $\%R_{TN}$ and τ, $\bar{Z}$.

2.1.1. Semi-empirical model

According to the mass balance of a lake/reservoir, at steady-state retention of TN (TN_{ret}) can be expressed as (see Fig. 1):

$$TN_{ret} = TN_{in} - TN_{out} \tag{1}$$

with TN_{in} and TN_{out} referring to the TN input and output, respectively, $\%R_{TN}$ corresponds to (Kelly et al., 1987):

$$\%R_{TN} = \frac{TN_{ret}}{TN_{in}} = 1 - \frac{TN_{out}}{TN_{in}} = 1 - \frac{TN_{out}}{TN_{ret} + TN_{out}} \tag{2}$$

Assuming completely mixed conditions and considering N retention a first-order reaction, Eq. 2 can be rewritten as follows (with volumetric units per unit area):

$$\%R_{TN} = \frac{R_{TN}}{L_{TN}} = 1 - \frac{\frac{Q}{A}C_{TN}}{q_{TN}C_{TN} + \frac{Q}{A}C_{TN}} = 1 - \frac{q}{q_{TN} + q} = \frac{q_{TN}}{q_{TN} + q} \tag{3}$$

where R_{TN} is the areal TN retention rate, L_{TN} the areal load, Q is the outflow discharge ($m^3\ yr^{-1}$), A the area of the lake/reservoir (m^2), C_{TN} the in-lake concentration of TN (mg N m^{-3}). q $(=Q/A)$ is the water discharge height or areal hydraulic load, and corresponds also to the ratio between $\bar{Z}$ and τ. q_{TN} represents the biological activity in the form of the uptake velocity (Wollheim et al., 2008) and is also called "mass transfer coefficient" (Kelly et al., 1987) or "apparent settling velocity" (Alexander et al., 2002). In addition to being proposed for modelling retention of TN (Molot and Dillon, 1993), Eq. 4 has also been used for predicting retention of DIN ($\%R_{DIN}$) (Kaste and Dillon, 2003; Kelly et al., 1987; Molot and Dillon, 1993):

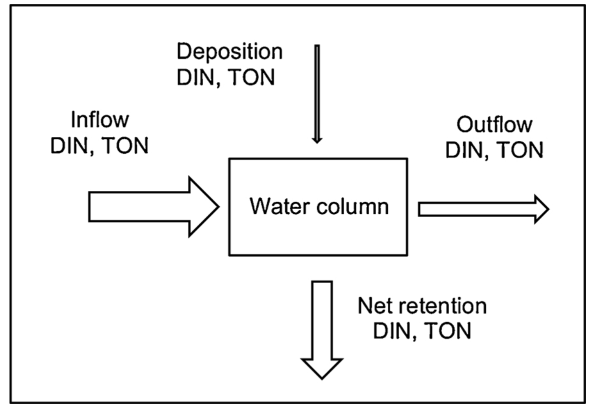

Fig. 1. A conceptual diagram illustrates the N mass balance used in this study.

$$\%R_{DIN} = \frac{R_{DIN}}{L_{DIN}} = \frac{q_{DIN}}{q_{DIN} + q} \tag{4}$$

According to Eq. 3 and Eq. 4, for very low and very high q, $\%R_{TN}$ and $\%R_{DIN}$ approach 1 and 0, respectively.

A sigmoid dependence of $\%R_{TN}$ from q is also described by mathematically different functions, first used to model retention of TN in rivers (Alexander et al., 2002; Wollheim et al., 2008) and then adapted to lakes/reservoirs (Alexander et al., 2002; Harrison et al., 2009). These functions were derived from the solution of the differential equation that describes changes of C_{TN} along a river assuming a first-order reaction for TN retention, steady-state conditions and a completely mixed river section:

$$\%R_{TN} = 1\text{- exp}(\frac{-q_{TN}}{q}) \tag{5}$$

and likewise for DIN:

$$\%R_{DIN} = 1\text{-exp}(\frac{-q_{DIN}}{q}) \tag{6}$$

2.1.2. Strictly empirical models

For not too small and not too high values of q, Eqs. 3–6 can be approximated by a linear equation describing $\%R_{TN}$ and $\%R_{DIN}$ as a function of $\log_{10}q$ (Fig. 2A and Fig. 2B, respectively):

$$\%R_{TN} = a_1 + b_1\log_{10}q \tag{7}$$

$$\%R_{DIN} = a_2 + b_2\log_{10}q \tag{8}$$

Power function regressions between $\%R_{TN}$ and q and between $\%R_{DIN}$ and q were proposed by Windolf et al. 1996 and Seitzinger et al. 2006, respectively:

$$\%R_{TN} = a_3q^{b_3} \tag{9}$$

$$\%R_{DIN} = a_4q^{b_4} \tag{10}$$

With a_1, a_2, a_3, a_4 and b_1, b_2, b_3, b_4 being the constants derived from the regressions.

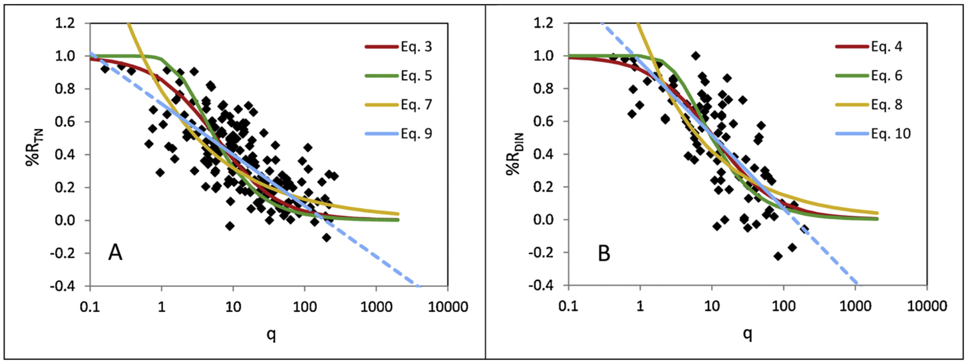

Fig. 2. The proportion of TN (A) and DIN (B) retained as a function of the areal hydraulic load q in lakes and reservoir. The fit of the models described by Eqs. 3–10 is also shown. The dotted extentions of Eq. (9), (10) correnspond to the ranges of q not used in the calibrations. Note the logarithmic scale of the x axes.

2.1.3. Calibration

Eqs. 3,5 and 9, describing $\%R_{TN}$ as a function of q, were calibrated using annual mean $\%R_{TN}$ assessed from TN mass balances of 158 lakes and 20 reservoirs compiled from literature (Appendix: N° 1-178), while Eqs. 4,6 and 10, describing $\%R_{DIN}$ as a function of q, were calibrated using DIN input-output data of 85 lakes and 10 reservoirs (Appendix: N° 141-235,). Lakes that are listed more than once, represent different time periods. Mass balances made for periods shorter than one year were excluded. TN and DIN input included transport from the surrounding watershed and atmospheric deposition directly to the surface of the lake/reservoir. N fixation can also contribute to the N budget. For most published input-output mass balances, however, N fixation was negligible or low (< 10% of the TN input). Budgets with significant N fixation (> 10% of the TN input) were excluded from the analysis, because estimates of N fixation could often not be indicated with sufficient precision. We also excluded lakes/reservoirs with very high q (> 1400 m yr^{-1}), as these are more representative for river ecosystems. For meromictic lakes $\bar{Z}$ and q refer to the mixed lake volume (Appendix: lakes N° 39, 153–156, 199). Models of Eqs. 3–6 were calibrated by minimizing the normalized root mean-square deviation between observed and predicted values (NRMSD), while for the calibration of the models of Eqs. 9–10, the equations were first linearized and the calibration parameters determined by linear regression *of* $\log_{10}\%R_{TN}$ and $\log_{10}\%R_{DIN}$, respectively, on $\log_{10}q$.

Since Eqs. 7 and 8 are valid only for intermediate values of q, only lakes and reservoirs with values of q higher than 1 m yr^{-1} and lower than 100 m yr^{-1} were considered (138 lakes and 16 reservoirs for Eq. 7 and 75 lakes and 9 reservoir for Eq. 8). The range of acceptable q was estimated visually from the data in Fig. 2.

2.2. Improvement of the models currently in use

The linearity of the two strictly empirical models (Eqs. 7–8) gives the opportunity to test the linear dependence of $\%R_{TN}$ and $\%R_{DIN}$ on other possible explanatory variables. In particular, the possibility to improve the models was tested by performing stepwise multiple linear regression analyses between the response variable $\%R_{TN}$ and $\%R_{DIN}$ and the explanatory variables $\log_{10}q$, in-lake concentrations of TP (C_{TP}), its logarithm ($\log_{10}C_{TP}$), the TN:TP ratio (TN/TP), the ratio between the DIN load and the TN load (L_{DIN}/L_{TN}), and absolute latitude (Lat) as possible indicator of temperature. As it has been reported that the efficiency of biotic uptake and denitrification declines with increasing nitrate concentration (Mulholland et al., 2008), inlet concentrations of TN (C_{TNin}) and DIN (C_{DINin}) and their logarithm ($\log_{10}C_{TNin}$ and $\log_{10}C_{DINin}$) were also tested as possible explanatory variables.

The testing of the improvement of Eq. 7 was performed in two steps, because data for the additional explanatory variables were not available for all lakes/reservoirs. For most lakes/reservoirs with TN input-output budgets C_{TP}, TN/TP, C_{TNin} and Lat were available, while C_{DINin} and L_{DIN}/L_{TN} were often lacking. The first step was to carry out stepwise multiple linear regressions not including L_{DIN}/L_{TN} and C_{DINin} as explanatory variables and using data of a larger subgroup of lakes/reservoirs (134 lakes, 13 reservoirs). The second step involved including L_{DIN}/L_{TN} and C_{DINin} as additional explanatory variables using data from a smaller subgroup of lakes/reservoirs (35 lakes, 2 reservoirs). Similarly, the possibility to improve Eq. 8 was tested with the explanatory variables C_{TP}, C_{DINin}, Lat on a larger subgroup of lakes/reservoirs (71 lakes and 2 reservoirs), and the additional variables C_{TNin}, L_{DIN}/L_{TN}, TN/TP on a smaller subgroup (34 lakes and 1 reservoirs).

The multiple linear regression analyses were performed with the statistic software SPSS (SPSS Inc., 2012). A stepping criteria of $p < 0.05$ was considered. The results were tested for normality, homoscedasticity and the absence of multi-collinearity.

2.3. Comparison of model performances

To assess model performance the predicted $\%R_{TN}$ and $\%R_{DIN}$ were compared with the measured values and intercept and slope of the linear regression line were compared. Also the NRMSD between predicted and observed values were calculated and compared (Piñeiro et al., 2008).

3. Results

As expected, $\%R_{TN}$ and $\%R_{DIN}$ increase with decreasing areal hydraulic load q, (Fig. 2). The calculated lake/reservoir specific settling velocities q_{TN} and q_{DIN} varied somewhat depending on the model used for their calculation. In general, q_{TN} and q_{DIN} calculated with the semi-empirical models derived from the mass balance of lake/reservoirs (Eqs. 3 and 4) were slightly higher than if calculated with the semi-empirical models derived from the mass balance of rivers sections (Eqs. 5 and 6). According to Eqs. 3 and 5, q_{TN} ranged from -19 to 95 m yr^{-1} (mean: 10.5 m yr^{-1}) and from -20 to 81 m yr^{-1} (mean: 7.7 m yr^{-1}), respectively. According to Eqs. 4 and 6, q_{DIN} ranged from -19 to 104 m yr^{-1} (mean: 15.2 m yr^{-1}) and from -21 to 42 m yr^{-1} (mean: 7.7 m yr^{-1}), respectively. A two tail t-test for the null hypothesis that the means of q_{TN} of lakes and reservoirs are equal with the assumption of unequal variances could not be rejected, indicating that mean q_{TN} in lakes (9.5 m yr^{-1} for Eq. 3 and 6.8 m yr^{-1} for Eq. 5) and reservoirs (18.2 m yr^{-1} for Eq. 3 and 15.0 m yr^{-1} for Eq. 5) do not differ significantly ($p = 0.11$ for Eq. 3; $p = 0.07$ for Eq. 5). q_{DIN} of lakes and reservoirs was almost identical (15.3 m yr^{-1} (Eq. 4) and 14.4 m yr^{-1} (Eq. 6)). The model values of q_{TN} and q_{DIN}, obtained by minimizing the NRMSD between observed and predicted values, were 5.9 and 3.9 m yr^{-1} for Eqs. 3 and Eq. 5, respectively (q_{TN} in Table 1), and 10.8 m yr^{-1} and 6.9 m yr^{-1} for Eqs. 4 and 6, respectively (q_{DIN} in Table 2). Differences in the predictive power of the semi-empirical models derived from the mass balance of a lake/reservoir (Eqs. 3 and 4) and from the mass balance of a river section were minimal (Eqs. 5 and 6). For both $\%R_{TN}$ and $\%R_{DIN}$, however, slightly better results were obtained with the models derived from the mass

Table 1
$\%R_{TN}$ model equations and coefficients.

model		n	coefficients	R^2 adjusted
Eq. 3	$\%R_{TN}\ \frac{q_{TN}}{q_{TN}+q}$	178	q_{TN} = 5.9 m yr^{-1},	
Eq. 5	$\%R_{TN} = 1-\exp\left(\frac{-q_{TN}}{q}\right)$	178	q_{TN} = 3.9 m yr^{-1}	
Eq. 7	$\%R_{TN} = a_1 + b_1\log_{10}q$	154	a_1 = 0.71, b_1 = -0.31	0.44
Eq. 9	$\log_{10}\%R_{TN} = \log_{10}a_3 + b_3\log_{10}q$	173	a_3 = 0.79, b_3 = -0.39	0.34
Eq. 11a	$\%R_{TN} = a_1 + b_1\log_{10}q$	147	a_1 = 0.71, b_1 = -0.31	0.43
Eq. 11b	$\%R_{TN} = a_{11} + b_{11}\log_{10}q + c_{11}\log_{10}C_{TNin}$		a_{11} = 0.30, b_{11} = -0.30, c_{11} = 0.12	0.48
Eq. 11c	$\%R_{TN} = a_{12} + b_{12}\log_{10}q + c_{12}\log_{10}C_{TNin} + d_{12}\frac{TN}{TP}$		a_{12} = 0.39, b_{12} = -0.29, c_{12} = 0.10, d_{12} = -0.0010	0.50
Eq. 12a	$\%R_{TN} = a_1 + b_1\log_{10}q$	37	a_1 = 0.68, b_1 = -0.28	0.50
Eq. 12b	$\%R_{TN} = a_{13} + b_{13}\log_{10}q + c_{13}\frac{L_{DIN}}{L_{TN}}$		a_{13} = 0.44, b_{13} = -0.27, c_{13} = 0.39	0.64
Eq. 12c	$\%R_{TN} = a_{14} + b_{14}\log_{10}q + c_{14}\frac{L_{DIN}}{L_{TN}} + d_{14}\frac{TN}{TP}$		a_{14} = 0.45, b_{14} = -0.26, c_{14} = 0.43, d_{14} = -0.0016	0.67

Table 2
$\%R_{DIN}$ model equations and coefficients

model		n	coefficients	R^2 adjusted
Eq. 4	$\%R_{DIN} = \frac{q_{DIN}}{q_{DIN}+q}$	95	q_{DIN} = 10.8 m yr^{-1}	
Eq. 6	$\%R_{DIN} = 1-\exp\left(\frac{-q_{DIN}}{q}\right)$	95	q_{DIN} = 6.9 m yr^{-1}	
Eq. 8	$\%R_{DIN} = a_2 + b_2\log_{10}q$	84	a_2 = 0.96, b_2 = -0.45	0.51
Eq. 10	$\log_{10}\%R_{DIN} = \log_{10}a_4 + b_4\log_{10}q$	87	a_4 = 1.16, b_4 = -0.44	0.45
Eq. 13a	$\%R_{DIN} = a_2 + b_2\log_{10}q$	73	a_2 = 0.98, b_2 = -0.45	0.56
Eq. 13b	$\%R_{DIN} = a_{21} + b_{21}\log_{10}q + c_{21}\log_{10}C_{DINin}$		a_{21} = 0.23, b_{21} = -0.41, c_{21} = 0.24	0.71
Eq. 14a	$\%R_{DIN} = a_2 + b_2\log_{10}q$	35	a_2 = 0.95, b_2 = -0.39	0.53
Eq. 14b	$\%R_{DIN} = a_{21} + b_{21}\log_{10}q + c_{21}\log_{10}C_{DINin}$		a_{21} = 0.09, b_{21} = -0.37, c_{21} = 0.29	0.73
Eq. 15a	$\%R_{DIN} = a_2 + b_2\log_{10}q$	35	a_2 = 0.95, b_2 = -0.39	0.53
Eq. 15b	$\%R_{DIN} = a_{22} + b_{22}\log_{10}q + c_{22}\log_{10}C_{TNin}$		a_{22} = -0.20, b_{22} = -0.39, c_{22} = 0.36	0.70
Eq. 16a	$\%R_{DIN} = a_2 + b_2\log_{10}q$	35	a_2 = 0.95, b_2 = -0.39	0.53
Eq. 16b	$\%R_{DIN} = a_{23} + b_{23}\log_{10}q + c_{23}\log_{10}\frac{L_{DIN}}{L_{TN}}$		a_{23} = 0.63, b_{23} = -0.39, c_{23} = 0.50	0.64
Eq. 16c	$\%R_{DIN} = a_{24} + b_{24}\log_{10}q + c_{24}\log_{10}\frac{L_{DIN}}{L_{TN}} + d_{24}\log_{10}C_{TP}$		a_{24} = 0.52, b_{24} = -0.41, c_{24} = 0.46, d_{24} = 0.11	0.69

Table 3
Intercept, slope and R^2 of the linear regression between observed and predicted $\%R_{TN}$ values and their normalized root mean squared deviation (NRMSD)

model	n	intercept	slope	R^2	NRMSD
Eq. 3	178	0.13	0.67	0.51	49%
Eq. 5	178	0.18	0.56	0.49	56%
Eq. 7	178	0.06	0.86	0.49	43%
Eq. 9	178	0.13	0.71	0.45	50%
Eq. 11a	168	0.06	0.84	0.48	44%
Eq. 11b	168	0.08	0.79	0.51	43%
Eq. 11c	168	0.08	0.81	0.52	42%
Eq. 12a	39	0.00	0.99	0.57	37%
Eq. 12b	39	0.00	0.98	0.69	31%
Eq. 12c	39	−0.01	1.03	0.72	30%

Table 4
Intercept, slope and R^2 of the linear regression between observed and predicted $\%R_{DIN}$ values and their normalized root mean squared deviation (NRMSD)

model	n	intercept	slope	R^2	NRMSD
Eq. 4	95	0.02	0.93	0.61	40%
Eq. 6	95	0.11	0.76	0.59	44%
Eq. 8	95	0.04	0.90	0.62	40%
Eq. 10	95	0.16	0.67	0.48	51%
Eq. 13a	84	0.03	0.91	0.64	38%
Eq. 13b	84	0.03	0.92	0.75	28%
Eq. 14a	38	0.02	0.94	0.55	40%
Eq. 14b	38	0.02	0.92	0.70	33%
Eq. 15a	38	0.02	0.94	0.55	40%
Eq. 15b	38	0.14	0.82	0.69	37%
Eq. 16a	38	0.02	0.94	0.58	39%
Eq. 16b	38	0.02	0.92	0.66	35%
Eq. 16c	38	0.01	0.95	0.72	32%

balance of lakes/reservoirs. This is shown by the fits of the $\%R_{TN}$ and $\%R_{DIN}$ predicting models in Fig. 2, but also by comparing the parameters of the linear regression between the observed and the predicted values: intercepts closer to zero, slopes closer to 1, higher R^2 and lower NRMSD (Table 3 and Table 4, respectively). Among the strictly empirical models approximating the semi-empirical models, the linear relations between $\%R_{TN}$, $\%R_{DIN}$ and $\log_{10}q$ (Eqs. 7 and 8, respectively) gave better results. Both approximations did not worsen the predictive power of the semi-empirical models derived from the mass-balance of lakes/reservoirs: the predictive power of Eq. 8 was similar to that of Eq. 4, while the predictive power of Eq. 7 was even better than that of Eq. 3.

The first improvement of Eq. 7 resulting from the stepwise multiple linear regression analysis between $\%R_{TN}$ and $\log_{10}q$, C_{TP}, $\log_{10}C_{TP}$, TN/TP, Lat, C_{TNin}, $\log_{10}C_{TNin}$ identified $\log_{10}q$ as the most significant explanatory variable (Eq. 11a in Table 1), followed by $\log_{10}C_{TNin}$ (Eq. 11b in Table 1) and TN/TP (Eq. 11c in Table 1). The addition of $\log_{10}C_{TNin}$ and TN/TP to the model increased the adjusted R^2 from 0.43 to 0.48 to 0.50 (Table 1). The improvement of the predictions of $\%R_{TN}$ is also shown by the increase of R^2 of the linear regression between observed and modelled $\%R_{TN}$ from 0.48 to 0.51 to 0.52 and by the decrease of the its NRMSD from 44% to 43% to 42% (Table 3). The second improvement of Eq. 7 resulting from the stepwise multiple linear regression analysis between $\%R_{TN}$ and the same variables as before plus C_{DIN}, $\log_{10}C_{DIN}$ and L_{DIN}/L_{TN}, identified again

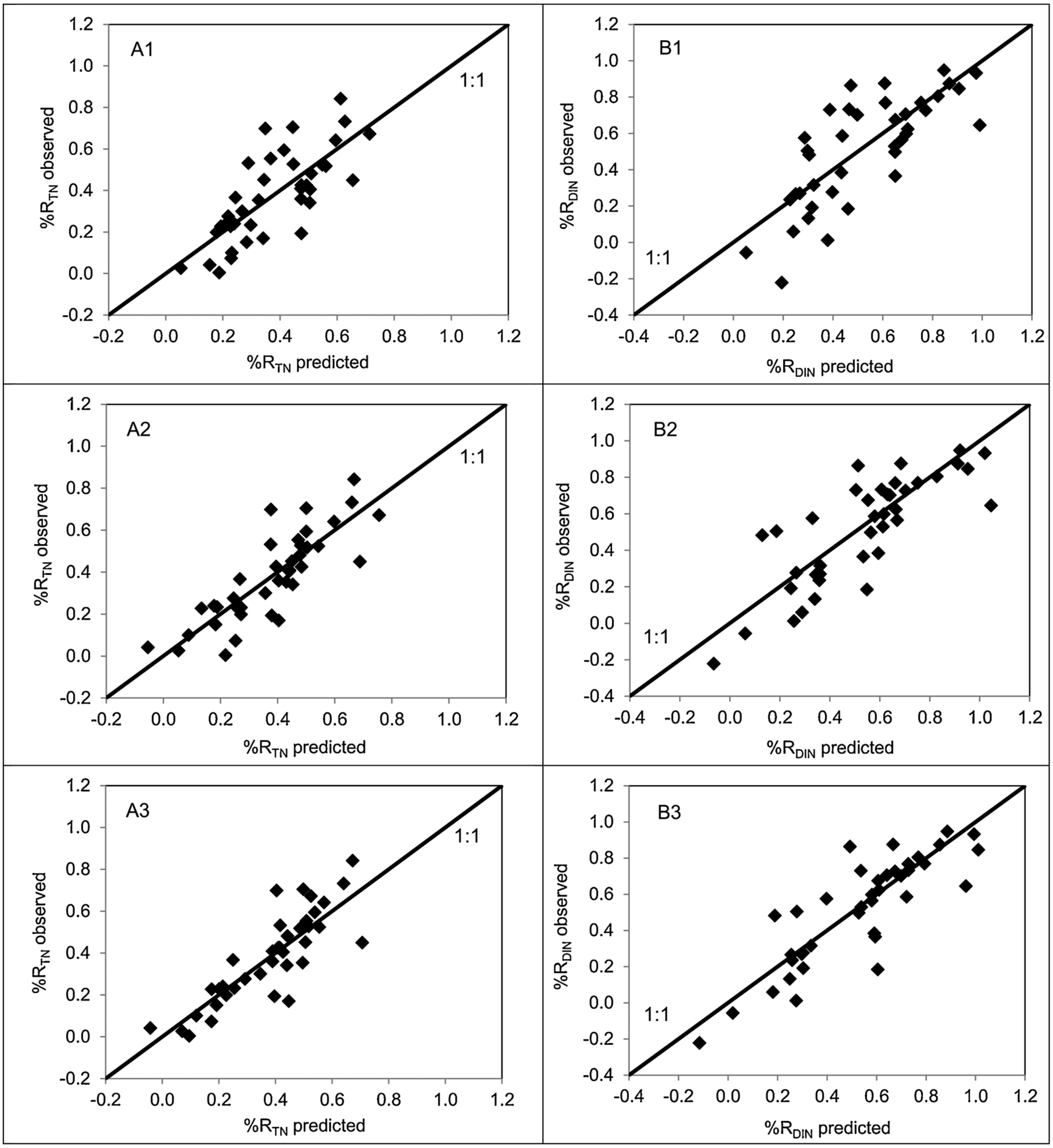

Fig. 3. Observed vs predicted $\%R_{TN}$ calculated by stepwise addition of the explanatory variables $\log_{10}q$ (A1), L_{DIN}/L_{TN} (A2) and TN/TP (A3) and observed vs predicted $\%R_{DIN}$ calculated by stepwise addition of the explanatory variables $\log_{10}q$ (B1), L_{DIN}/L_{TN} (B2) and $\log_{10}C_{TP}$ (B3).

$\log_{10}q$ as the most significant explanatory variable (Eq. 12a in Table 1), followed by L_{DIN}/L_{TN} (Eq. 12b in Table 1) and TN/TP (Eq. 12c in Table 1), whereby the adjusted R^2 increased from 0.50 to 0.64 to 0.67 and the R^2 of the linear regression between observed and predicted $\%R_{TN}$ increased from 0.57 to 0.69 to 0.72 and its NRMSD decreased from 37% to 31% to 30%. Changes in the prediction of $\%R_{TN}$ by successive addition of the parameters $\log_{10}q$, L_{DIN}/L_{TN} and TN/TP to the model are shown in Fig. 3 (A1, A2, A3).

The first improvement of Eq. 8 resulting from the stepwise multiple linear regression analysis between $\%R_{DIN}$ and $\log_{10}q$, C_{TP}, $\log_{10}C_{TP}$, Lat, C_{DINin}, $\log_{10}C_{DINin}$ identified $\log_{10}q$ as the most significant explanatory variable (Eq. 13a in Table 2), followed by $\log_{10}C_{DINin}$ (Eq. 13b in Table 2). The addition of $\log_{10}C_{DINin}$ to the model increased the adjusted R^2 from 0.56 to 0.71 (Table 2). The improvement of the predictions of $\%R_{DIN}$ is also shown by the increase of R^2 of the linear regression between observed and modelled $\%R_{DIN}$ from 0.64 to 0.75 and by the decrease of the its NRMSD from 38% to 28% (Table 4). The same explanatory variables were identified when performing the stepwise multiple linear regression analysis on a smaller subgroup of lakes/reservoirs and by including also C_{TNin}, $\log_{10}C_{TNin}$, L_{DIN}/L_{TN}, TN/TP as possible explanatory variables (Eqs. 14a and 14b in Table 2). If $\log_{10}C_{DINin}$ was excluded, $\log_{10}C_{TNin}$ was identified as an additional explanatory variable after $\log_{10}q$ (Eqs. 15a and 15b in Table 2). If $\log_{10}C_{TNin}$ also was excluded, the identified variables were L_{DIN}/L_{TN} followed by $\log_{10}C_{TP}$ (Eqs. 16a-c in Table 2). Interestingly, the adjusted R^2 of the final models 14b, 15b and 16c (0.73, 0.70, 0.69, respectively, see Table 2) did not differ greatly, nor did the R^2 of the linear regression between the observed and modelled $\%R_{DIN}$ (0.70, 0.69, 0.72, respectively, see Table 4) and its NRMSD (33%, 37%, 32%, respectively, see Table 4). On the contrary, the last added model describing $\%R_{DIN}$ as a linear function of $\log_{10}q$, L_{DIN}/L_{TN} and $\log_{10}C_{TP}$ gave the best predictions. Changes in the prediction of $\%R_{DIN}$ by successive addition of the parameters $\log_{10}q$, L_{DIN}/L_{TN} *and* $\log_{10}C_{TP}$ to the model are shown in Fig. 3 (B1, B2, B3).

4. Discussion

The analysis in this paper has shown that the areal hydraulic load q is the key variable for the prediction of both $\%R_{TN}$ and $\%R_{DIN}$. This indicates that $\%R_{TN}$ and $\%R_{DIN}$ increase with increasing τ and with decreasing mean depth $\bar{Z}$. Longer τ increases the chance of nutrients to the be transformed in the water column and lower $\bar{Z}$ increases the chance of nutrients to be transformed at the sediment surface where most denitrification, the main N retention process occurs (Saunders and Kalff, 2001a; Seitzinger, 1988).

The study has also shown that, although the semi-empirical models describe quite well the dependence of $\%R_{TN}$ and $\%R_{DIN}$ from q, lake specific mass-transfer coefficient q_{TN} and q_{DIN} can vary greatly, indicating that other explanatory variables than q must influence $\%R_{TN}$ and $\%R_{DIN}$. Mean q_{TN} was comparable to other studies: 6.2 m yr^{-1} for 75 lakes and reservoirs in the Waitako river basin in New Zealand (Alexander et al., 2002; Eq. 5), 8.3 m yr^{-1} for 16 shallow Danish lakes (Windolf et al., 1996; Eq. 3), 8.9 m yr^{-1} for 115 lakes and reservoirs compiled from literature (Harrison et al., 2009; Eq. 5). Different to this study, Harrison et al. (2009) found a significant difference between mean q_{TN} of lakes and reservoirs (6.8 m yr^{-1} and 13.7 m yr^{-1}, respectively, calculated with Eq. 5) and ascribed it to the increased availability of highly labile organic matter in the reservoirs because of the flooding of previously terrestrial soils and ecosystems. Mean q_{DIN} was slightly higher than reported for 13 oligotrophic P-limited Canadian and Norwegian lakes (Kaste and Dillon, 1993: 2-8 m yr^{-1}; Eq. 4). The latter values are recommended for the estimation of in-lake retention of nitrogen in the calculation of the critical loads of acidity and their exceedances for lake ecosystems (CLRTAP, 2017).

In the strictly empirical models, linear regressions describing variations of $\%R_{TN}$ and $\%R_{DIN}$ as a function of $\log_{10}q$ (Eqs. 7 and 8, respectively) gave significantly better predictions than the power function regressions describing variations of $\%R_{TN}$ and $\%R_{DIN}$ as a function of q (Eqs. 9 and 10, respectively). Eq. 9 has been proposed as a TN retention model by Windolf et al. (1996) with the calibration constants a_3 = 0.15 and b_3 = -0.56. They calibrated the model with hypereutrophic Danish shallow lakes. $\%R_{TN}$ predicted with this model were on average 17% higher than when calculated with the power function in this study. Seitzinger et al. (2002) derived calibration constants a_4 = 0.88 and b_4 = -0.37 for Eq. 10, very close to the values of this study. They used data from about 20 oligotrophic and eutrophic lakes and about 10 rivers.

The study has also shown that the approximation of the semi-empirical models (Eqs. 3–6) by the strictly empirical linear models (Eqs. 7 and 8) did not worsen predictions of $\%R_{TN}$ and $\%R_{DIN}$. On the contrary, predictions with the linear models seemed to be slightly better especially for $\%R_{DIN}$. This result led to search for other possible significant explanatory variables related linearly to $\%R_{TN}$ and $\%R_{DIN}$.

For $\%R_{TN}$, the most important explanatory variable was, as expected, $\log_{10}q$ followed by L_{DIN}/L_{TN} and TN/TP. The variable L_{DIN}/L_{TN} was not as important as $\log_{10}q$ but substantially more relevant than TN/TP. The fact that the $\%R_{TN}$ increases with increasing L_{DIN}/L_{TN} indicates that the "quality" of N entering a lake or reservoir is important for the N retention mechanisms. In most freshwaters, nitrate and DON are the main N species. Between the two, nitrate is generally considered to be the most bioavailable form, because assimilation of DON by plants, algae and microorganisms has been reported, but it seems to become a key resource only in N-limited oligo- to mesotrophic estuaries or freshwaters (Durand et al., 2011). Saunders and Kalff (2001a) have shown that retention of TN occurs mainly by denitrification (80-85%) followed by sedimentation (15-20%). It is therefore not surprising that the supply of DIN to lakes and reservoirs greatly influences retention of TN: directly by providing denitrifying organisms with nitrate and indirectly through uptake by primary producers (transformation into biomass) that can be permanently incorporated in the sediment, or supply denitrifying bacteria with nitrate (coupled nitrification-denitrification) or anammox bacteria with ammonia from mineralization of organic N. The fact, that in the absence of L_{DIN}/L_{TN}, $\log_{10}C_{TNin}$ was identified as explanatory variable is probably due to the positive relation between L_{DIN}/L_{TN} and C_{TNin} in aquatic ecosystems: at low N concentrations (< 1 mg l^{-1}) in ultra-oligotrophic systems DON is the dominant species, while at higher N concentrations nitrate becomes dominant (Durand et al., 2011). C_{TNin} may therefore have acted as a surrogate of L_{DIN}/L_{TN}. The correlation between $\log_{10}C_{TNin}$ and L_{DIN}/L_{TN} is 0.57. TN/TP, the third explanatory variable identified for predicting $\%R_{TN}$, can be seen as an indicator for the proportion of the imported N that can be potentially assimilated into biomass followed by net burial into the sediment, coupled nitrification-denitrification, but also of the supply of organic material to denitrifying bacteria. The slight negative relation found between $\%R_{TN}$ and TN/TP may be the result of all these mechanisms: higher TN/TP infers a lower proportion of N that is transformed into biomass and indirectly contributes to retention of TN. The variable TN/TP is also an indicator for the availability of P relative to N and is often used to discriminate between N and P limitation. Using the criterion of Kelly et al. (2013), 120 of the lakes/reservoirs with TN input-output mass balances and TN/TP data were probably P-limited (TN/TP > 14), 4 were N limited (TN/TP < 3.5) and other 45 co-limited by both N and P, meaning that most lakes/reservoirs of the dataset were at least temporarily P limited. At these conditions we might expect C_{TP} to be a significant indicator for primary productivity and to have a significant influence on TN retention. In contrast to other studies (Berge et al., 1997; Finlay et al., 2013), however, C_{TP} was not identified as a significant explanatory variable for prediction of $\%R_{TN}$. Stepwise multiple linear regression analyses between $\%R_{TN}$ and the variables $\log_{10}q$, C_{TP}, $\log_{10}C_{TP}$, TN/TP, Lat and C_{TNin} and $\log_{10}C_{TNin}$ to lake/reservoirs with TN/TP values > 14 did also not indicate that P concentration was relevant for prediction of $\%R_{TN}$. Concentration of P ($\log_{10}C_{TP}$) was significant only if $\bar{Z}$, C_{TNin} and TN/TP were excluded from the analyses and $\%R_{TN}$ was expressed as a function of $\log_{10}1/\tau$, and $\log_{10}C_{TP}$ (p-value < 0.001, adjusted R^2 = 0.30). The significance of the alternative model, however, was significantly lower. This, together with the high negative correlation between $\log_{10}\bar{Z}$ and $\log_{10}C_{TP}$ (= -0.53), suggests that $\log_{10}C_{TP}$ may in reality just act as a surrogate of $\log_{10}\bar{Z}$. This might explain why Finlay et al. (2013) indicated a positive dependence of $\%R_{TN}$ and R_{TN} on C_{TP} in the plots of $\%R_{TN}$ vs $\log_{10}1/\tau$ and $\log_{10}R_{TN}$ vs $\log_{10}L_{TN}$.

For the improvement of predictions of $\%R_{DIN}$, stepwise multiple linear regression gave the most important explanatory variable as $\log_{10}q$ followed by $\log_{10}C_{DINin}$ (Eq. 13b). Excluding C_{TNin} and C_{DINin} from the analyses, after $\log_{10}q$, L_{DIN}/L_{TN} and $\log_{10}C_{TP}$ were identified as significant explanatory variables (Eq. 16c) and the predicted $\%R_{DIN}$'s were closer to the measured (smaller NRMSD). Again, especially C_{TNin} but also C_{DINin} might here have acted as a surrogate of another parameter: specifically, since $\log_{10}C_{TNin}$ correlates positively with L_{DIN}/L_{TN} (Pearson correlation = 0.57) and $\log_{10}C_{TP}$ (Pearson correlation = 0.69), it might have acted as a surrogate for both variables. This also explains why C_{TNin} was identified as a better significant explanatory variable than either L_{DIN}/L_{TN} or $\log_{10}C_{TP}$ alone. To understand the reason for the significance of L_{DIN}/L_{TN} and $\log_{10}C_{TP}$ for the prediction of $\%R_{DIN}$ a closer look to what $\%R_{DIN}$ represents is necessary. $\%R_{DIN}$ is positively influenced by net retention of DIN by denitrification or sedimentation and by transformation of DIN into TON and negatively by net retention of TON. From the mass-balance equations of TN, DIN and TON it follows:

$$\%R_{DIN} = \frac{R_{TN}}{L_{DIN}} + \frac{O_{TON} - L_{TON}}{L_{DIN}} \tag{17}$$

with L_{TON} and O_{TON} being the areal input and output of TON. The equation indicates that the difference between $\%R_{DIN}$ and R_{TN}/L_{DIN} corresponds to the areal net production of TON relative to L_{DIN} if $O_{TON} - L_{TON}$ > 0 and to the areal net retention of TON relative to L_{DIN} if $O_{TON} - L_{TON}$ < 0. The data in this study show that $(O_{TON}-L_{TON})/L_{DIN}$ increases linearly with increasing L_{DIN}/L_{TN} (Fig. 4A, Pearson correlation = 0.69) and to a lesser extent with increasing $\log_{10}C_{TP}$ (Fig. 4B, Pearson correlation = 0.41), the two additional explanatory variables next to $\log_{10}q$ to be identified for prediction of $\%R_{DIN}$ (Eq. 16c). In other words, from lakes with low values of L_{DIN}/L_{TN} with elevated percentages of TON in the inlets to lakes with high values of

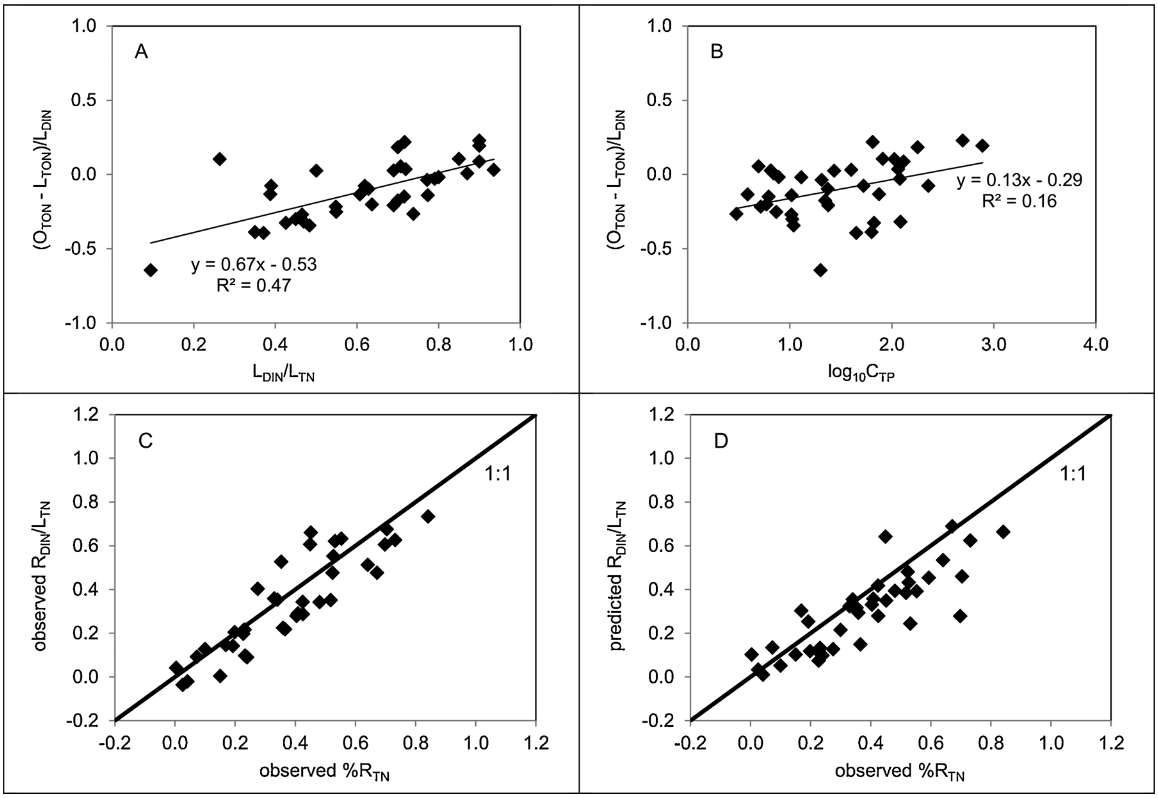

Fig. 4. (A) $(O_{TON} - L_{TON})/L_{DIN}$ vs L_{DIN}/L_{TN}, (B) $(O_{TON} - L_{TON})/L_{DIN}$ vs $\log_{10}C_{TP}$, (C) observed R_{DIN}/L_{TN} vs measured $\%R_{TN}$, (D) predicted R_{DIN}/L_{TN} (Eq. 4) vs measured $\%R_{TN}$.

L_{DIN}/L_{TN} with elevated percentages of DIN in the inlets, the areal input-output TON mass balance changes from TON net retention to TON net production. More precisely, net production of TON is prevalent in lakes with $L_{DIN}/L_{TN} > 0.8$, and, since L_{DIN}/L_{TN} has been shown to correlate positively with $\log_{10}C_{TNin}$ and $\log_{10}C_{TP}$, at $C_{TNin} > 3\,\mathrm{mg\,l^{-1}}$ and $C_{TP} > 0.3\,\mathrm{mg\,P^{-1}}$, while net retention of TON is prevalent in lakes with $L_{DIN}/L_{TN} < 0.6$, $C_{TNin} < 2\,\mathrm{mg\,l^{-1}}$, $C_{TP} < 0.05\,\mathrm{mg\,P^{-1}}$ and $TN/TP > 50$. For lakes with values in between, both TON net retention or net production can occur.

Several studies estimated $\%R_{TN}$ from models that predict $\%R_{DIN}$, assuming that most N is retained on account of the imported DIN and that there is only minor net transformation of DIN into TON (Hindar et al., 2001; Mayorga et al., 2010). Under these assumptions Eq. 17 becomes:

$$\%R_{DIN} \cong \frac{R_{TN}}{L_{DIN}} \tag{18}$$

and analogously,

$$\%R_{TN} = \frac{R_{TN}}{L_{TN}} \cong \%R_{DIN}\frac{L_{DIN}}{L_{TN}} \tag{19}$$

The comparison between measured R_{DIN}/L_{TN} and measured $\%R_{TN}$ is shown in Fig. 4C. In the presence of a net retention of TON, however, $\%R_{TN}$ and C_{TN} estimated from $\%R_{DIN}$ are under- and overestimated, respectively. The opposite occurs in the presence of a net production of TON. In addition, since it has been shown that the net production of TON is positively correlated with L_{DIN}/L_{TN}, and as it is known that in aquatic ecosystems the ratio between the concentrations of DIN and TN is positively related to concentrations of TN, at low C_{TNin} ($< 2\,\mathrm{mg\,l^{-1}}$), C_{TN} estimated from $\%R_{DIN}$ is somewhat overestimated and at high C_{TNin} ($> 3\,\mathrm{mg\,l^{-1}}$) somewhat underestimated.

Estimation of $\%R_{TN}$ from modelled $\%R_{DIN}$ requires an additional consideration. From the comparison of Eq. 17 with Eq. 16c and the consideration of the linear relation between the second term of Eq. 17 (O_{TON}-L_{TON})/L_{DIN} and L_{DIN}/L_{TN} and $\log_{10}C_{TP}$, it can be derived that R_{TN}/L_{DIN} can be approximated by the first part of Eq. 16c ($a_{24} + b_{24}\log_{10}q$). Therefore measured $\%R_{TN}$ was compared with values estimated from Eqs. 4 and 8 that describe $\%R_{DIN}$ as a function of q alone and have been shown to produce best predictions, and their predictive power compared with that of Eq. 12c that describe $\%R_{TN}$ as a function of $\log_{10}q$, L_{DIN}/L_{TN} and TN/TP (Table 3). The comparison could be made for 37 lakes and 2 reservoirs for which all necessary explanatory variables were known. Almost identical were predictions of $\%R_{TN}$ from Eqs. 4 and 8: intercept, slope and R^2 of the linear regression between observed and predicted values was 0.09, 0.97, 0.72, respectively and the NRMSD was 37% for Eq. 4 and 36% for Eq.8. These values suggest just slightly worse predictions of $\%R_{TN}$ than obtained from Eq. 12c for which the values of the same parameters were -0.01, 1.03, 0.72 and 30%. However, the comparison of measured with predicted $\%R_{TN}$ obtained from $\%R_{DIN}$ models, also showed that $\%R_{TN}$ were underestimated on average by 8% (shown for Eq. 4 in Fig. 4D). The reason is that the lakes/reservoirs used for calibrating the $\%R_{DIN}$ models were probably not equally distributed regarding their TON net retention and net production. The analyses of the subgroup of lakes/reservoirs with available TON input-output mass-balance used for calibration of Eq. 4, showed that the number of lakes with a net retention of TON was higher than that with a net production of TON (25 vs 13) and also the absolute average value of (O_{TON}-L_{TON})/L_{DIN} (0.21 vs 0.15). For the other lakes/reservoirs used in the calibration of Eq. 4 the TON input-output data were not available. However, as it was shown that TON net retention or net production depends also on C_{TP}, the analysis of the representativeness of the lakes regarding this parameter might give further information: in the subgroup of lakes/reservoirs with TON input-output data, 59% of the lakes/reservoirs had C_{TP} values $< 50\,\mathrm{mg\,P\,l^{-1}}$, probable indicator for the occurrence of a TON net retention, 5% had C_{TP} values $> 300\,\mathrm{mg\,P\,l^{-1}}$, probable indicator for the occurrence of a TON net production and the remaining 36% had values in between, where both TON net production of retention can occur. In the larger dataset used for the calibration 37% of the lakes/reservoirs had C_{TP} values $< 50\,\mathrm{mg\,P\,l^{-1}}$, 3% had C_{TP} values $> 300\,\mathrm{mg\,P\,l^{-1}}$ and 61% had values in between, indicating that also in the larger group, lakes/reservoirs with net TON production were probably less represented. As a consequence the calibration curve is more representative for lakes/reservoirs with a TON net retention, leading to an underestimation of $\%R_{TN}$, if the $\%R_{DIN}$ models are used for its estimation. An underestimation of $\%R_{TN}$ (13% on average) was also obtained when it was estimated from $\%R_{DIN}$ modelled with the empirical equation proposed by Seitzinger et al. (2002). Thus $\%R_{DIN}$ models should be used to predict only $\%R_{DIN}$ and not $\%R_{TN}$. The same consideration holds, when calibration of $\%R_{DIN}$ is made only for oligotrophic P-limited lakes, as has been done by Kaste and Dillon (2003). The models are fine if used for prediction of $\%R_{DIN}$ in oligotrophic P-limited lakes, but as at low C_{TP}, the relative to L_{DIN} areal retention of TON might be considerable, predictions of $\%R_{TN}$ from $\%R_{DIN}$ may lead to an underestimation. For example, using an average q_{DIN} of 5 m yr^{-1} proposed by Hindar et al. (2001) for estimating retention of DIN in oligotrophic P-limited lakes, $\%R_{TN}$ of a subgroup of 14 oligotrophic P-limited lakes estimated from $\%R_{DIN}$ using Eq. 4 is underestimated on average by 14%.

Another suggestion for the use of the models presented in this study is to use the best model for which explanatory variables are available. For the prediction of $\%R_{TN}$ the lowest deviations of the measured from the predicted values were given by Eq. 12c, describing $\%R_{TN}$ as a function of $\log_{10}q$, L_{DIN}/L_{TN} and TN/TP. If TN/TP is not known, it can be neglected with not much loss of precision by the use of Eq. 12b. If even L_{DIN}/L_{TN} is not known it can be substituted by $\log_{10}C_{TNin}$ using Eq. 11b and if TN/TP is available by Eq. 11c. If only q is known, then Eq. 9 is recommended, because it has been calibrated with a larger dataset. Predictions of $\%R_{DIN}$ should be approached in a similar way. Eq. 16c that predicts $\%R_{DIN}$ as a function of $\log_{10}q$, L_{DIN}/L_{TN} and $\log_{10}C_{TP}$ gave the best results. In the absence of $\log_{10}C_{TP}$, $\log_{10}C_{TP}$ can be neglected with not much loss of precision and 16b can be used instead. If L_{DIN}/L_{TN} is not known, it may be approximated by C_{DINin} and the use of Eq. 13a, and if q alone is known than Eqs. 4 or 8 should be used for prediction of $\%R_{DIN}$.

Interestingly, the variables C_{TNin} and C_{DINin} were initially introduced as explanatory variables in the expectation of a negative relation with $\%R_{TN}$ and $\%R_{DIN}$, reflecting a decline in the efficiency of N retention at higher N concentrations (Mulholland et al., 2008). Both variables ended up to be positively related to $\%R_{TN}$ and $\%R_{DIN}$, when other more relevant parameters were not available. For the prediction of $\%R_{TN}$, $\log_{10}C_{TNin}$ stood for L_{DIN}/L_{TN} and for the prediction of $\%R_{DIN}$, $\log_{10}C_{DINin}$ stood for both L_{DIN}/L_{TN} and $\log_{10}C_{TP}$.

In addition to the controlling factors identified in this study (q, L_{DIN}/L_{TN}, TN/TP, C_{TP}) other parameters are likely to influence retention of TN and DIN. Temperature for the retention of both TN and DIN and the presence of organic carbon for TN may be relevant as well. Both parameters could not be investigated in this study, because of the lack of data. Latitude was tested as a surrogate for temperature, but was not a significant explanatory variable for $\%R_{TN}$ and $\%R_{DIN}$. Although not object of this study, temperature has been shown to influence seasonality of $\%R_{TN}$ and $\%R_{DIN}$ with generally higher values, especially of $\%R_{DIN}$, during summer (Kaste and Lyche-Solheim, 2005; Windolf et al. 1996). Little has been reported about the influence of temperature on annual mean $\%R_{TN}$ and $\%R_{DIN}$ of aquatic ecosystems. Temperature is generally known to enhance biogeochemical processes in natural aquatic systems (Schwoerbel, 1987). As observed by Veraart et al. (2011), temperature may affect denitrification but also several biogeochemical reactions preceding denitrification such as mineralization and nitrification. As an example, microcosm experiments, field measurements and a simple model approach suggested a doubling of denitrification rates by a temperature increase of three degrees in systems not N limited, when denitrification of nitrate from the water column is the main mechanism, because of the decrease of oxygen concentrations due to lower solubility and due to the steeper increase of respiration compared to photosynthesis (Veraart et al., 2011). However, in N-limited systems, characterized by an increase of the importance of nitrification-denitrification as denitrifying mechanism, the influence of temperature on mineralization and nitrification may be more relevant, and an increase of temperature can theoretically both stimulate nitrification and inhibit nitrification because of lower oxygen concentrations (Veraart et al., 2011). In addition, with increasing temperatures, primary productivity stimulates TN retention by supplying denitrifiers with organic carbon and contributing to net sedimentation, but might also inhibit denitrification by competing for inorganic N (Cabrita and Brotas, 2000). All this indicates that the influence of temperature on N retention might be extremely complex and therefore not easily included in an empirical model as presented here, also because other explanatory variables might be more relevant.

5. Conclusion

In summary, this study showed that empirical models derived from input-output mass balances of TN and DIN describing annual mean $\%R_{TN}$ and $\%R_{DIN}$ in lakes/reservoirs as a sigmoid function of q, can be approximated by a linear function on $\log_{10}q$ with little loss of information and can be significantly improved by focusing on the inorganic N load to the lakes. Nevertheless, the relatively low values of the adjusted R^2 of the models (0.5-0.7) suggests that the here presented models still deliver only estimates of the proportion of retained TN and DIN. The reasons are various. First, not all assumptions the models are based on i.e. lakes at steady state, completely mixed water column, no N_2 fixation, first-order reaction of the N retention mechanism may have been fulfilled by the N mass balances used for the calibration. Second, the mass balances themselves might have been characterized by errors and uncertainties. Third, the water bodies used for the calibrations varied in part enormously in their hydrologic, morphologic, hydrochemical and climatic characteristics, that the here proposed empirical functions were not able to fully reflect. It is clear, that more complex mechanistic models are generally more accurate. However, these models tend to require extensive data that may be difficult to obtain, wherefore they are rather used at local scale. For large scale analyses, the more general empirical models are preferred (Bouwman et al., 2013). Furthermore, empirical N retention models are also used for the calculation of the critical loads of acidity and their exceedances for lake ecosystems (CLRTAP, 2017). That's why the here presented models are still useful tools to estimate TN and DIN retention in lakes and reservoirs. Moreover, since the DIN load has been shown to influence TN retention, the TN and DIN retention models can be combined to model multiple lakes in sequence.

In addition, the accuracy of the presented empirical models might be improved further by repeating the analysis with subsets of lakes/reservoirs that are more homogeneous. It can also be attempted to further improve the models by including N_2-fixation in the mass balance and expressing it as a function of the TN:TP ratio of the external input as proposed by Ruan (2014). Or it can be tried to adapt the models to describe seasonality of N retention by including surface water temperature as proposed by Windolf et al. (1996). Finally, the models might also be calibrated with input-output mass balance data from other types of aquatic ecosystems as well.

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Appendix A. Calibration dataset

Table A1

Table A1
Characteristics of lakes and reservoirs used in the analyses. N° denotes the lake number, $\bar{Z}$ the mean depth (m), τ the residence time (yr), $\%R_{TN}$ the relative retention of TN, $\%R_{DIN}$ the relative retention of DIN, L_{TN} the TN load (g m^{-2} yr^{-1}), L_{DIN} the DIN load (g m^{-2} yr^{-1}), C_{TP} the in-lake concentration of TP, TN/TP the weight ratio between in-lake concentrations of TN and TP. BN: north basin; BS: south basin.

N°	Reference	Name	Type	Period	Location	$\bar{Z}$	τ	%R$_{TN}$	%R$_{DIN}$	L$_{TN}$	L$_{DIN}$	L$_{DIN}$/L$_{TN}$	C$_{TP}$	TN/TP
1	Berge et al. 1997	Bergsvatn	Lake	1992-1994	Norway	4.5	0.1	0.20		75			13	123
2	Berge et al. 1997	Eikenesvatn	Lake	1992-1994	Norway	1.5	0.01	0.28		365			20	60
3	Berge et al. 1997	Grennesvatn N	Lake	1992-1994	Norway	2.3	0.02	0.08		222			18	94
4	Berge et al. 1997	Grennesvatn S	Lake	1992-1994	Norway	1.0	0.005	−0.11					20	
5	Berge et al. 1997	Haugestadvatn	Lake	1992-1994	Norway	1.4	0.01	0.05		215			35	46
6	Berge et al. 1997	Hofreistevatn	Lake	1993-1995	Norway	34.3	0.2	0.00		80			3	121
7	Berge et al. 1997	Ørsdalsvatn	Lake	1993-1995	Norway	138.0	2.6	0.05		18			2	162
8	Dudel and Kohl 1992	Müggelsee	Lake	1978-1984	Germany	4.9	0.1	0.17					168	13
9	Ekholm et al. 1997	Lappajärvi	Lake	unknown	Finland	7.4	2.8	0.59					24	
10	Fleischer et al. 1994	Stjärnap	Lake	1992-1993	Sweden	1.2	0.01	0.10		767				
11	Fleischer et al. 1994	Tjärby 1	Lake	1992-1993	Sweden	2.1	0.04	0.03		1026				
12	Frisk et al. 2006	Hauhonselkä	Lake	unknown	Finland	3.6	1.2	0.52		4			27	26
13	Frisk et al. 2006	Ilmoilanselkä	Lake	unknown	Finland	4.4	1.5	0.91		13			17	26
14	Frisk et al. 2006	Iso-Roine	Lake	unknown	Finland	7.2	6.0	0.91		5			12	33
15	Frisk et al. 2006	Kuohjärvi	Lake	unknown	Finland	9.9	1.8	0.29		3			6	68
16	Frisk et al. 2006	Nerkoojärvi	Lake	unknown	Finland	3.7	1.6	0.53		3			21	28
17	Frisk et al. 2006	Parkanonjärvi	Lake	unknown	Finland	6.8	0.2	0.20		45			31	28
18	Gibbs and White 1994	Horowhenua	Lake	1988-1989	New Zealand	1.3	0.1	0.59		70	60	0.85	173	16
19	Granina 1997	Baikal	Lake	1967,1974,1991,1992	Russia	744.0	330.0	0.51		1			23	8
20	Havens et al. 2001	Donghu	Lake	1997-1998	China	2.2	0.4	0.60		53			400	8
21	Havens et al. 2001	Kasumigaura	Lake	1970-1980	Japan	4.0	0.6	0.69		23			75	15
22	Irfannullah and Moss 2008	Little Budworth Pool	Lake	2001-2003	United Kingdom	1.0	0.02	0.10		577			83	118
23	Jeppesen et al. 1998	Arreskov	Lake	1989-1995	Denmark	1.9	1.8	0.58		16			160	43
24	Jeppesen et al. 1998	Engelsholm	Lake	1989-1995	Denmark	2.6	0.2	0.31		40			95	22
25	Kronvang et al. 2001	Arresø	Lake	unknown,10 years	Denmark	3.1	4.1	0.56		12			430	16
26	Kronvang et al. 2001	Drontermeer	Lake	unknown,11-13 years	The Netherlands	1.1	0.02	0.20		223			240	14
27	Kronvang et al. 2001	Nuldernauw	Lake	unknown,11-13 years	The Netherlands	1.5	0.1	0.43		60			129	21
28	Kronvang et al. 2001	Ravn	Lake	unknown,10 years	Denmark	15.0	2.3	0.53		70			34	
29	Kronvang et al. 2001	Søholm	Lake	unknown,10 years	Denmark	6.5	1.8	0.55		33			78	52
30	Kronvang et al. 2001	Tissø	Lake	unknown,10 years	Denmark	8.2	1.1	0.65		82			110	34
31	Kronvang et al. 2001	Tystrup	Lake	unknown,11-13 years	Denmark	9.9	0.6	0.37		237			250	33
32	Kronvang et al. 2001	Veluwemeer	Lake	unknown,11-13 years	The Netherlands	1.3	0.1	0.52		46			401	6
33	Kronvang et al. 2001	Woldewijd	Lake	unknown,11-13 years	The Netherlands	1.5	0.3	0.37		18			145	17
34	Kvarnäs 2001	Mälaran	Lake	unknown('70-'90),20 years	Sweden	12.8	2.6	0.56					37	17
35	Likens and Loucks 1978	Findley	Lake	1975	USA	7.8	0.1	0.25		7			2	39
36	Likens and Loucks 1978	Mirror	Lake	1970-1975	USA	5.7	1.0	0.30		2			2	65
37	Likens and Loucks 1978	Wingra	Lake	1970-1974	USA	2.4	0.5	0.81		24			24	36
38	Malueg et al. 1975	Shagawa	Lake	1967-1972	USA	5.7	0.6	−0.03		8			57	15
39	Nizzoli et al. 2018	Idro	Lake	2010-2012	Italy	77.1	0.4	0.31		79			110	9
40	Ojanen 1979	Tuusulanjärvi	Lake	1974-1977	Finland	3.1	0.6	0.48		22			105	22
41	Persson 2003	Aspen	Lake	1981-1990	Sweden	16.6	0.1	−0.01		128			10	96
42	Persson 2003	Åsunden	Lake	1989-1991	Sweden	15.0	1.2	0.19		18			20	57
43	Persson 2003	Åsunden + Yttre Ås.	Lake	1989-1991	Sweden	11.9	1.2	0.29		14			18	54
44	Persson 2003	Bolmen	Lake	1980-1984	Sweden	5.0	1.0	0.60		24			14	37
45	Persson 2003	Boren 1	Lake	1973	Sweden	6.0	0.2	0.36		23			26	17
46	Persson 2003	Boren 2	Lake	1976	Sweden	6.0	0.4	0.59		18			15	29
47	Persson 2003	Botjärn	Lake	1972-1973	Sweden	3.3	0.3	0.58		4			14	30
48	Persson 2003	Brunnsjön	Lake	1989-1990,1993-1994	Sweden	2.3	2.4	0.29		24			124	13

(continued on next page)

Table A1 (*continued*)

N°	Reference	Name	Type	Period	Location	$\bar{Z}$	τ	$\%R_{TN}$	$\%R_{DIN}$	L_{TN}	L_{DIN}	L_{DIN}/L_{TN}	C_{TP}	TN/TP
49	Persson 2003	Edsjön	Lake	1972	Sweden	3	0.1	0.12		30			300	9
50	Persson 2003	Erken	Lake	1984	Sweden	9.0	6.3	0.44		2			18	43
51	Persson 2003	Fegen	Lake	1974	Sweden	7.5	1.8	0.44		3			14	30
52	Persson 2003	Finjasjön	Lake	1976-1978	Sweden	3.8	0.4	0.46		33			170	12
53	Persson 2003	Finjasjön 1	Lake	1976-1977	Sweden	3.8	0.4	0.44		31			200	11
54	Persson 2003	Finjasjön 2	Lake	1978	Sweden	3.8	0.4	0.50		37			219	9
55	Persson 2003	Finjasjön 3	Lake	1988-1990	Sweden	3.8	0.4	0.49		45			210	8
56	Persson 2003	Gåran	Lake	1988	Sweden	1.5	0.02	0.12		67			40	20
57	Persson 2003	Glan	Lake	1985-1989	Sweden	9.9	0.3	0.11		47			45	14
58	Persson 2003	Glaningen	Lake	1974	Sweden	1.5	0.1	0.39		40			600	3
59	Persson 2003	Gunillajaure + N + P	Lake	1979	Sweden	6.0	1.5	0.36		7			40	3
60	Persson 2003	Hjälmaren	Lake	1981-1985	Sweden	6.1	3.4	0.77		6			46	17
61	Persson 2003	Hornborgasjön	Lake	1984-1996	Sweden	0.8	0.2	0.43		20			30	53
62	Persson 2003	Hymenjaure N + P	Lake	1979	Sweden	1.3	0.2	0.43		4			70	7
63	Persson 2003	Ivösjön	Lake	1990-1993	Sweden	10.7	1.9	0.57		7			14	57
64	Persson 2003	Kalvsjön	Lake	1974	Sweden	6.2	0.3	0.07		16			12	42
65	Persson 2003	Limmaren	Lake	1991-1992	Sweden	4.6	3.0	0.37		2			80	18
66	Persson 2003	Magnusjaure + N	Lake	1974	Sweden	2.2	0.2	0.35		4			4	100
67	Persson 2003	Mälaren A	Lake	1981-1985	Sweden	3.4	0.1	0.05		60			48	13
68	Persson 2003	Mälaren C	Lake	1981-1985	Sweden	16.9	1.8	0.42		14			29	14
69	Persson 2003	Mälaren D	Lake	1981-1985	Sweden	11.5	1.2	0.31		27			60	14
70	Persson 2003	Mjörn	Lake	1990	Sweden	15.0	1.4	0.38		15			14	68
71	Persson 2003	Norrviken 1	Lake	1961-1962	Sweden	5.4	0.6	0.25		67			260	13
72	Persson 2003	Norrviken 2	Lake	1972	Sweden	5.4	0.9	0.21		7			210	12
73	Persson 2003	Ö. Ringsjön + Sät 1	Lake	1980	Sweden	5.6	0.8	0.44		33			200	11
74	Persson 2003	Ö. Ringsjön + Sät 2	Lake	1990	Sweden	5.6	0.8	0.62		24			60	28
75	Persson 2003	Ö. Storsjön	Lake	1991-1996	Sweden	31.5	0.2	0.23		14			45	16
76	Persson 2003	Oppmannasjön	Lake	1989-1990	Sweden	3.9	2.2	0.90		8			32	31
77	Persson 2003	Oxundasjön	Lake	1972	Sweden	3.3	0.1	0.24		42			140	12
78	Persson 2003	Ralången	Lake	1989-1990	Sweden	2.4	0.1	0.11		32			50	24
79	Persson 2003	Ramsjön	Lake	1974	Sweden	1.8	0.2	0.63		27			300	7
80	Persson 2003	Ringsjön	Lake	1980	Sweden	4.7	1.1	0.68		25			200	12
81	Persson 2003	Ringsjön	Lake	1991	Sweden	4.7	1.1	0.71		20			75	17
82	Persson 2003	Roxen	Lake	1985-1989	Sweden	5.0	0.2	0.16		33			30	23
83	Persson 2003	Rusken	Lake	1985-1989	Sweden	3.5	0.5	0.41		11				
84	Persson 2003	Ryssbysjön	Lake	1974	Sweden	1.8	0.1	0.59		43			200	8
85	Persson 2003	S. Bergundasjön 1	Lake	1973	Sweden	2.4	0.6	0.20		27			1160	4
86	Persson 2003	Södra Barken	Lake	1978-1980	Sweden	5.7	0.1	0.06		30			18	29
87	Persson 2003	Tåkern	Lake	1983-1996	Sweden	0.8	0.7	0.64		5			50	40
88	Persson 2003	V. Ringsjön 1	Lake	1980	Sweden	3.1	0.3	0.49		42			210	12
89	Persson 2003	V. Ringsjön 2	Lake	1990	Sweden	3.1	0.3	0.45		21			70	21
90	Persson 2003	V. Storsjön	Lake	1991-1996	Sweden	4.5	0.7	0.54		5			45	10
91	Persson 2003	Vänern	Lake	1982-1992	Sweden	27.0	9.3	0.30		4			9	97
92	Persson 2003	Väsman	Lake	1978-1980	Sweden	10.6	1.2	0.12		5			15	32
93	Persson 2003	Vättern	Lake	1975-1985	Sweden	40.0	60.0	0.47		2			7	106
94	Persson 2003	Vidöstern	Lake	1990-1998	Sweden	4.4	0.5	0.22		12			17	33
94	Rowe et al. 2014	Michigan	Lake	1994-2008	USA	85.0	99.0	0.86		2			5	90
95	Salas and Martino 1991	Chapala	Lake	1983-1984	Mexico	4.2	11.1	0.91		4			426	2
96	Salas and Martino 1991	Chapala	Lake	1986-1987	Mexico	4.4	15.9	0.94		5			680	2
97	Salas and Martino 1991	La Plata	Lake	1981-1982	Puerto Rico	10.0	0.1	0.44		197			220	5
98	Salas and Martino 1991	Laguna de Sonso	Lake	unknown	Colombia	1.0	0.04	0.22		77			210	12
100	Salas and Martino 1991	Laguna Tortuguero	Lake	1974-1975	Puerto Rico	1.2	0.1	−0.04		15			10	170
101	Salas and Martino 1991	Livingston	Lake	1975	USA	6.3	0.2	0.23		54			20	80
102	Salas and Martino 1991	Loiza	Lake	1973-1974	Puerto Rico	6.1	0.1	0.17		233			330	5
103	Salas and Martino 1991	Requena	Lake	1986-1987	Mexico	5.0	0.3	0.66		98			383	5

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Table A1 (*continued*)

N°	Reference	Name	Type	Period	Location	$\bar{Z}$	τ	$\%R_{TN}$	$\%R_{DIN}$	L_{TN}	L_{DIN}	L_{DIN}/L_{TN}	C_{TP}	TN/TP
104	Salas and Martino 1991	Tequesquitango	Lake	1986	Mexico	16.0	98.5	0.92		1			23	28
105	Schernewski 2003	Belau	Lake	1989-1994	Germany	9.0	0.8	0.50		32			88	18
106	Smith et al. 1989	Kinneret	Lake	1969-1984	Israel	25.0	5.2	0.82		9			20	25
107	Wetzel 2001	Mendota	Lake	unknown	USA	12.7	4.5	0.72		5			110	5
108	Windolf et al. 1996	Borup Sø	Lake	1989-1992	Denmark	0.9	0.05	0.19		147			150	33
109	Windolf et al. 1996	Bryrup Langsø	Lake	1989-1992	Denmark	4.6	0.3	0.49		162			107	39
110	Windolf et al. 1996	Dons Nørresø	Lake	1989-1992	Denmark	1.0	0.05	0.25		148			216	23
111	Windolf et al. 1996	Fårup Sø	Lake	1989-1992	Denmark	5.6	0.5	0.57		44			92	16
112	Windolf et al. 1996	Fuglesø	Lake	1989-1992	Denmark	2.0	0.1	0.54		159			256	16
113	Windolf et al. 1996	Gundsømagle Sø	Lake	1989-1992	Denmark	1.2	0.08	0.37		171			1127	5
114	Windolf et al. 1996	Hejrede Sø	Lake	1989-1992	Denmark	0.9	0.1	0.24		88			123	35
115	Windolf et al. 1996	Hinge Sø	Lake	1989-1992	Denmark	1.2	0.04	0.18		151			122	36
116	Windolf et al. 1996	Jels Oversø	Lake	1989-1992	Denmark	1.2	0.02	0.11		708			273	25
117	Windolf et al. 1996	Kilen	Lake	1989-1992	Denmark	2.9	0.7	0.73		34			187	12
118	Windolf et al. 1996	Lange Sø	Lake	1989-1992	Denmark	3.1	0.6	0.45		76			279	14
119	Windolf et al. 1996	Lemvig Sø	Lake	1989-1992	Denmark	2.0	0.08	0.27		245			239	18
120	Windolf et al. 1996	Ørn Sø	Lake	1989-1992	Denmark	4.0	0.04	0.12		138			108	13
121	Windolf et al. 1996	Søgård Sø	Lake	1989-1992	Denmark	1.6	0.07	0.17		301			272	25
122	Windolf et al. 1996	Store Søgård Sø	Lake	1989-1992	Denmark	2.7	0.2	0.29		187			465	13
123	Windolf et al. 1996	Vesterborg Sø	Lake	1989-1992	Denmark	1.4	0.05	0.21		281			241	22
124	Salas and Martino 1991	Americana	Reservoir	1986	Brazil	7.8	0.08	0.36		357			98	25
125	Salas and Martino 1991	Atibainha	Reservoir	1986	Brazil	12.5	0.4	0.00		29			23	39
126	Salas and Martino 1991	Barra Bonita	Reservoir	1986	Brazil	8.6	0.2	0.46		99			59	23
127	Salas and Martino 1991	Cachoeira	Reservoir	1986	Brazil	10.7	0.1	0.10		72			32	25
128	Salas and Martino 1991	Funil	Reservoir	1987	Brazil	22.8	0.2	0.11		99			41	14
129	Salas and Martino 1991	Funil	Reservoir	1988-1989	Brazil	21.0	0.1	0.27		213			66	9
130	Salas and Martino 1991	Guarapiranga	Reservoir	1986	Brazil	4.9	0.3	0.18		16			44	20
131	Salas and Martino 1991	Itupararanga	Reservoir	1986	Brazil	7.8	0.7	0.68		32			29	31
132	Salas and Martino 1991	Jaguari	Reservoir	1986	Brazil	16.8	1.2	0.53		23			36	22
133	Salas and Martino 1991	Lajes	Reservoir	1988-1989	Brazil	13.6	0.8	0.07		9			18	26
134	Salas and Martino 1991	Paiva Castro	Reservoir	1986	1986	5.4	0.03	0.13		185			23	36
135	Salas and Martino 1991	Paraibuna	Reservoir	1986	Brazil	26.4	1.9	0.23		10			16	36
136	Salas and Martino 1991	Ponte Nova	Reservoir	1986	Brazil	8.3	0.8	0.23		8			25	23
137	Salas and Martino 1991	Taiaçupeba	Reservoir	1986	Brazil	2.2	0.1	0.35		13			31	16
138	Vanni et al. 2011	Acton	Reservoir	2001	USA	3.9	0.1	0.30		380	327	0.86	168	52
139	Tomaszek and Koszelnik 2003	Rzeszów	Reservoir	1999-2001	Poland	0.5	0.006	0.23		1299				
140	Tomaszek and Koszelnik 2003	Solina	Reservoir	1999-2001	Poland	22	0.6	0.12		124				
141	Ahlgren et al. 1994	Norrviken	Lake	1992-1993	Sweden	5.4	0.9	0.19	0.37	8	3	0.39	75	15
142	Ahlgren et al. 1994	Vallentuna	Lake	1992-1993	Sweden	2.5	2.0	0.45	0.85	3	2	0.72	65	18
143	Andersen 1974	Bryrup Langsø	Lake	1972-1973	Denmark	5.0	0.4	0.55	0.70	83	74	0.90	130	20
144	Andersen 1974	Halle sø	Lake	1972-1974	Denmark	2.8	0.1	0.53	0.73	86	73	0.85	82	18
145	Andersen 1974	Kul sø	Lake	1972-1973	Denmark	2.2	0.05	0.23	0.50	109	42	0.39	229	8
146	Andersen 1974	Kvind sø	Lake	1972-1973	Denmark	1.9	0.04	0.28	0.58	162	114	0.70	179	13
147	Andersen 1974	Salten Langsø	Lake	1972-1973	Denmark	4.1	0.2	0.23	0.28	25	9	0.35	63	12
148	Andersen 1974	Stigsholm Sø	Lake	1972-1973	Denmark	1.2	0.03	0.24	0.19	81	38	0.47	122	12
149	Broberg and Persson 1984	Gårdsjörn	Lake	1979-1981	Sweden	4.9	1.0	0.42	0.57	3	2	0.61	4	78
150	Ekholm et al. 1997	Phyäjärvi	Lake	1992	Finland	5.4	3.0	0.84	0.95	3	3	0.77	10	29
151	Gibson et al. 1992	Neagh	Lake	1975-1987	Ireland	8.9	1.2	0.53	0.77	24	17	0.72	115	14
152	Hayward et al. 1993	Lower Lough Erne	Lake	1989	Northern Ireland	11.9	0.4	0.15	0.01	38	14	0.37	45	26
153	ISE-CNR 1981–1990	Maggiore	Lake	1980-1989	Italy/Switzerland	176.5	2.4	0.23	0.27	52	42	0.80	13	56
154	ISE-CNR 1991–2000	Maggiore	Lake	1990-1999	Italy/Switzerland	176.5	2.3	0.23	0.27	50	40	0.80	8	83
155	ISE-CNR 2001–2009	Maggiore	Lake	2000-2009	Italy/Switzerland	176.5	2.1	0.20	0.24	46	40	0.87	7	77
156	UPDA-DT 2001–2007, IST-SUPSI 2008–2012	Lugano BN	Lake	2000-2011	Italy/Switzerland	171.0	6.9	0.70	0.86	28	20	0.70	22	21
157	UPDA-DT 2001–2007, IST-SUPSI 2008–2012	Lugano BS	Lake	2000-2011	Italy/Switzerland	55.0	1.4	0.37	0.32	77	53	0.69	24	52
158	Jensen et al. 1992	Søbygård	Lake	1978-1989	Denmark	1.0	0.06	0.45	0.73	136	122	0.90	495	9

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Table A1 (*continued*)

N°	Reference	Name	Type	Period	Location	$\bar{Z}$	τ	$\%R_{TN}$	$\%R_{DIN}$	L_{TN}	L_{DIN}	L_{DIN}/L_{TN}	C_{TP}	TN/TP
159	Jeppesen et al. 1998	Søbygård	Lake	1988-1995	Denmark	1.0	0.05	0.35	0.59	86	77	0.90	775	4
160	Jonsson and Jansson 1997	Örträsket	Lake	1991-1992	Sweden	23.0	0.3	0.04	−0.22	27	3	0.09	20	20
161	Kaste and Lyche-Solheim 2005	Nedre Laundetjenn	Lake	1999-2001	Norway	8.5	0.2	0.07	0.13	29	20	0.69	7	91
162	Kaste and Lyche-Solheim 2005	Øvre Laundetjenn	Lake	1999-2001	Norway	7.0	0.1	0.00	0.06	38	27	0.71	5	120
163	Knuuttila et al. 1994	Kotojärvi	Lake	1987-1988	Finland	2.5	0.4	0.43	0.67	10	4	0.43	67	15
164	Knuuttila et al. 1994	Villikkalanjärvi	Lake	1989-1990	Finland	3.2	0.2	0.17	0.18	55	43	0.79	120	14
165	Molot and Dillon 1993	Blue Chalk	Lake	1977-1989	Canada	8.5	5.3	0.73	0.87	2	1	0.72	6	42
166	Molot and Dillon 1993	Chub	Lake	1977-1989	Canada	8.9	2.0	0.40	0.60	3	1	0.47	10	36
167	Molot and Dillon 1993	Crosson	Lake	1977-1989	Canada	9.2	1.6	0.36	0.50	3	2	0.45	11	36
168	Molot and Dillon 1993	Dickie	Lake	1977-1989	Canada	5.0	1.8	0.52	0.73	2	1	0.48	11	36
169	Molot and Dillon 1993	Harp	Lake	1977-1989	Canada	13.3	3.1	0.48	0.62	3	2	0.55	7	51
170	Molot and Dillon 1993	Plastic	Lake	1977-1989	Canada	7.9	3.8	0.64	0.80	2	1	0.64	6	45
171	Molot and Dillon 1993	Red Chalk	Lake	1977-1989	Canada	14.2	2.5	0.41	0.53	3	2	0.55	5	63
172	Nõges et al. 1998	Võrtsjärv	Lake	1995	Estonia	2.8	0.9	0.52	0.77	8	5	0.62	53	22
173	Nõges et al. 2003	Peipsi	Lake	1998	Estonia	7.1	1.6	0.34	0.71	7	3	0.50	27	36
174	Serruya 1975	Kinneret	Lake	1968-70	Israel	25.0	3.4	0.70	0.88	20	15	0.77	21	38
175	Sterner et al. 1989	Superior	Lake	synthesis(1948-1999)	USA	147.0	191	0.67	0.65	1	1	0.74	3	172
176	David et al. 2006	Shelbyville	Reservoir	2002-2003	USA	5.5	0.3	0.33	0.38	207	194	0.94	40	
177	Prochazkova et al. 1973	Slapy	Reservoir	1963-1964	Czech Republik	20.6	0.11	0.03	−0.06	163	102	0.63	24	35
178	Turner et al. 1983	Talquin	Reservoir	1971-1974	USA	4.1	0.09	0.10	0.48	54	14	0.26	106	10
179	Calderoni et al. 1978	Lago Mergozzo	Lake	1975	Italy	45.4	4.7		0.40		9		6	
180	Dillon and Molot 1990	Batchawana South	Lake	1981-1983	Canada	3.3	0.3		0.24				0.2	
181	Dillon and Molot 1990	Clearwater	Lake	1977-1979	Canada	8.3	3.7		0.61				6	
182	Dillon and Molot 1990	Lohi	Lake	1977-1979	Canada	6.2	1.0		0.46				6	
183	Dillon and Molot 1990	Turkey	Lake	1981-1983	Canada	12.2	0.9		0.29				0.2	
184	Höhner and Gächter 1993	Aegerisee	Lake	1947-1951	Switzerland	49.3	7.1		0.42		3		7	
185	Höhner and Gächter 1993	Alpnachersee	Lake	1971-1973	Switzerland	21.1	0.3		0.02		36		25	
186	Höhner and Gächter 1993	Attersee	Lake	1975-1976	Austria	84.2	7.1		−0.04		5		3	
187	Höhner and Gächter 1993	Baldeggersee	Lake	1957-1959	Switzerland	33.1	4.2		0.74		22		175	
188	Höhner and Gächter 1993	Baldeggersee	Lake	1985-1987	Switzerland	33.1	4.2		0.66		53		200	
189	Höhner and Gächter 1993	Baldeggersee	Lake	1975-1976	Switzerland	33.1	0.2		0.62		31		425	
190	Höhner and Gächter 1993	Feldsee	Lake	1974-1975	Austria	15.7	0.5		0.13		7		50	
191	Höhner and Gächter 1993	Greifensee	Lake	1951	Switzerland	19.0	1.4		0.64		46		75	
192	Höhner and Gächter 1993	Greifensee	Lake	1978	Switzerland	19.0	1.4		0.57		54		270	
193	Höhner and Gächter 1993	Greifensee	Lake	1967-1968	Switzerland	19.0	1.4		0.63		48		388	
194	Höhner and Gächter 1993	Hallwilersee	Lake	1988-1990	Switzerland	28.0	3.8		0.56		18		130	
195	Höhner and Gächter 1993	Lac de Neuchâtel	Lake	1985	Switzerland	64.0	8.3		0.61		22		40	
196	Höhner and Gächter 1993	Lac Léman	Lake	1985	France/Switzerland	154.0	12.5		0.41		12		75	
197	Höhner and Gächter 1993	Lac Léman	Lake	1976	France/Switzerland	154.0	12.5		0.46		11		100	
198	Höhner and Gächter 1993	Lunzer Untersee	Lake	1975-1976	Austria	20.0	1.2		0.03		43		7	
199	Höhner and Gächter 1993	Maggiore	Lake	1972-1973	Italy/Switzerland	20.0	2.4		0.30		58		35	
200	Höhner and Gächter 1993	Ossiachersee	Lake	1974-1976	Austria	17.4	1.8		0.64		17		40	
201	Höhner and Gächter 1993	Pfäffikersee	Lake	1951	Switzerland	17.4	2.0		0.69		19		80	
202	Höhner and Gächter 1993	Pfäffikersee	Lake	1967-1968	Switzerland	13.0	2.0		0.74		30		250	
203	Höhner and Gächter 1993	Piburgersee	Lake-	1974-1976	Austria	44.4	2.8		0.39		2		20	
204	Höhner and Gächter 1993	Sempachersee	Lake	1966	Switzerland	44.4	16.7		0.82		7		30	
205	Höhner and Gächter 1993	Sempachersee	Lake	1977-1978	Switzerland	44.4	16.7		0.85		13		100	
206	Höhner and Gächter 1993	Sempachersee	Lake	1984-1986	Switzerland	44.4	16.7		0.86		17		150	
207	Höhner and Gächter 1993	Sempachersee	Lake	1954	Switzerland	44.4	16.7		0.77		4		20	
208	Höhner and Gächter 1993	Türlersee	Lake	1952-1953	Switzerland	14.0	2.1		0.69		8		16	
209	Höhner and Gächter 1993	Zürich-Obersee	Lake	1969-1970	Switzerland	27.5	0.2		−0.17		72		40	
210	Höhner and Gächter 1993	Zürichsee	Lake	1953	Switzerland	44.0	1.4		0.21		27		50	
211	Höhner and Gächter 1993	Zürichsee	Lake	1969-1970	Switzerland	44.0	1.4		−0.05		22		100	
212	Höhner and Gächter 1993	Zürich-Untersee	Lake	1969-1970	Switzerland	49.2	1.2		−0.03		30		100	
213	Kaste and Dillon 2003	Fjellgardsvatn	Lake	1999	Norway	42.7	0.4		0.10		16		4	

(*continued on next page*)

Table A1 (*continued*)

N°	Reference	Name	Type	Period	Location	$\bar{z}$	τ	$\%R_{TN}$	$\%R_{DIN}$	L_{TN}	L_{DIN}	L_{DIN}/L_{TN}	C_{TP}	TN/TP
214	Kaste and Dillon 2003	Heney	Lake	1980-1998	Canada	3.3	1.5		0.62		1		8	
215	Kaste and Dillon 2003	Langtjern	Lake	1987-1988	Norway	2.4	0.2		0.18		1		4	
216	Kaste and Dillon 2003	Røyravatn	Lake	1999	Norway	16.4	0.1		0.09		22		4	
217	Kaste and Dillon 2003	Sandvatn	Lake	1999	Norway	4.5	0.3		0.24		7		4	
218	Kelly et al. 1987	223	Lake	1976-1984	Canada	7.1	8.7		0.98		1		7	
219	Kelly et al. 1987	239	Lake	1981-1983	Canada	10.9	6.2		0.88		1		8	
220	Kelly et al. 1987	302N	Lake	1981-1984	Canada	5.7	5.8		0.70		1		1	
221	Kelly et al. 1987	302S	Lake	1981-1984	Canada	5.1	8.3		0.98		1		1	
222	Kelly et al. 1987	Crystal	Lake	1984	USA	10.6	25.0		0.99		0.3		8	
223	Kelly et al. 1987	Dart's	Lake	1982-1984	USA	7.1	0.06		0.07		36		8	
224	Kelly et al. 1987	Langtjern	Lake	1972-1978	Norway	2.4	0.2		0.36		1		4	
225	Mengis et al. 1997	Baldeggersee	Lake	1989-1990	Switzerland	33.0	4.1		0.84		42		99	
226	Mengis et al. 1997	Zugersee	Lake	1995	Switzerland	84.0	14.4		1.00		9		158	
227	Olsen and Andersen 1994	Kvie	Lake	1989	Denmark	1.2	1.5		0.80		3		80	
228	Schelske 1975	Michigan	Lake	1962-1964	USA	84.0	100.0		0.93	1	1	0.72	10	
229	Garnier et al. 1999	Aube	Reservoir	1994-1995	France	7.6	0.6		0.53		37			
230	Garnier et al. 1999	Marne	Reservoir	1993-1995	France	7.2	0.5		0.50		45			
231	Garnier et al. 1999	Seine	Reservoir	1993-1995	France	8.9	0.4		0.26		104			
232	Kelly 2001	Falcon	Reservoir	1996-1998	USA	11.2	0.8		0.76		4			
233	Kelly 2001	Amistad	Reservoir	1996-1998	USA	47.7	1.6		0.37		5			
234	Kelly 2001	Mead	Reservoir	1996-1998	USA	55.9	3.7		0.00		7			
235	Kelly 2001	Powell	Reservoir	1996-1998	USA	93.0	3.3		0.00		11			

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