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Nitrogen dynamics in the steeply stratified, temperate Lake Verevi, Estonia

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Abstract

The dynamics of different nitrogen compounds and nitrification in diverse habitats of a stratified Lake Verevi (Estonia) was investigated in 2000–2001. Also planktonic N_2-fixation (N_2fix) was measured in August of the observed years. The nitrogen that accumulated in the hypolimnion was trapped in the non-mixed layer during most of the vegetation period causing a concentration of an order of magnitude higher than in the epilimnion. The ammonium level remained low in the epilimnion (maximum 577 mgN m^{-3}, average 115 mgN m^{-3}) in spite of high concentrations in the hypolimnion (maximum 12223 mgN m^{-3}, average 4807 mgN m^{-3}). The concentrations of NO_2^- and NO_3^- remained on a low level both in the epilimnion (average 0.94 and 9.09 mgN m^{-3}, respectively) and hypolimnion (average 0.47 and 5.05 mgN m^{-3}, respectively). N_2fix and nitrification ranged from 0.30 to 2.80 mgN m^{-3} day^{-1} and 6.0 to 107 mgN m^{-3} day^{-1}, respectively; the most intensive processes occurred in 07.08.00 at depths of 2 and 5 m, accordingly. The role of N_2fix in the total nitrogen budget of Lake Verevi (in August 2000 and 2001) was negligible while episodically in the nitrogen-depleted epilimnion the N_2fix could substantially contribute to the pool of mineral nitrogen. Nitrification was unable to influence nitrogen dynamics in the epilimnion while some temporary coupling with ammonium dynamics in the hypolimnion was documented.

Introduction

Nitrogen (N) is one of the main building blocks for the production of organic matter on the planet Earth and it is required in greatest quantities (Stolp, 1996; Williams et al., 2002). N, as many other elements in the world, is involved in cyclical transformations. Non-biological transformations have little importance in the nitrogen cycle by contrast with biological transformations, which are primarily controlled by microorganisms (Gorlenko et al., 1977; Sprent, 1987; Stolp, 1996; Voytek et al., 1999). A nitrogen cycle consists of four main components: molecular nitrogen (N_2) fixation (N_2fix), mineralization of organic N (ammonification), nitrification, and denitrification.

Only prokaryotes are capable of N_2fix. In aquatic ecosystems cyanobacteria appear responsible for most of the planktonic N_2fix while heterotrophic bacteria are most important N_2 fixers in lake sediments. The fixation of N_2 by microorganisms is the only process in nature that counteracts the nitrogen losses from the environment by denitrification. The central compound of the nitrogen cycle is ammonium (NH_4^+) which is released into the water by zooplankon and represents the main decomposition product of urea of other animals like fish. In anaerobic hypolimnion where animals are scarce, ammonium is formed at amino-acid degradation of proteins carried out by ammonificating bacteria, occurring in the water column and sediments (Gorlenko et al., 1977;

Howarth et al., 1988a; Stolp, 1996). Nitrification is a two-step oxidation of NH_4^+ through nitrite (NO_2^-) to nitrate (NO_3^-), carried out mainly by chemolithoautotrophic bacteria in aerobic conditions. The most important and intensive site in lakes for nitrification are aerobic sediments while planktonic nitrification could be also significant. Denitrification is an anaerobic heterotrophic process, which shares many of the same substrates and intermediates as nitrification. Denitrification leads to gaseous nitrogen (N_2, N_2O) losses counteracting N_2fix (Gorlenko et al., 1977; Hall, 1982; Henriksen et al., 1993; Stolp, 1996; Voytek et al., 1999). In stratified lakes phytoplankton takes up epilimnetic mineral nitrogen and transports it to the hypolimnion via sedimentation. N may accumulate in the hypolimnion during stratification period while in the epilimnion N deficiency may occur if resupply from the inflows is limited (Scheffer, 1998).

The aim of the present study was to investigate the dynamics of different nitrogen compounds as well as the rates of N_2-fixation and nitrification in diverse habitats of a stratified partly meromictic lake. The main processes of transformations (Fig. 1) were followed on the background of the dynamics of the physico-chemical stratification regime.

Materials and methods

Lake Verevi (0.126 km^2, mean depth 3.6 m, maximum depth 11 m) is a small stratified hypertrophic (see Ott et al., the present issue) lake in South Estonia. The lake is characterized by strong stratification from April to September and an anoxic hypolimnion. The main N_2fix cyanobacterium in Lake Verevi during the years 2000 and 2001 was *Aphanizomenon klebahnii* (Elenkin) Pechar *et* Kalina (Kangro et al., the present issue).

The water samples for nitrogen determination were collected from April to December 2000 and from March to August 2001. In the year 2000 eight and in 2001 three to eight vertical samples were taken at different depths of the epi-, meta- and hypolimnion. The water from the surface layer (0.5 m) was taken directly into the bottle, for other depths a Masterflex pump was used (for details see Zingel, the present issue). Total nitrogen (TN), NH_4^+, NO_2^- and NO_3^- was analysed at the laboratory of Võrtsjärv Limnological Station using the methods described by Grasshoff et al. (1983). For more detailed description of TN determination see Ott et al. (present issue). Ammonium was determined (detection error ± 5.5%) with indophenol blue method (Hansen & Koroleff, 1999). Nitrate was reduced to nitrite, and sulphanil-amide and

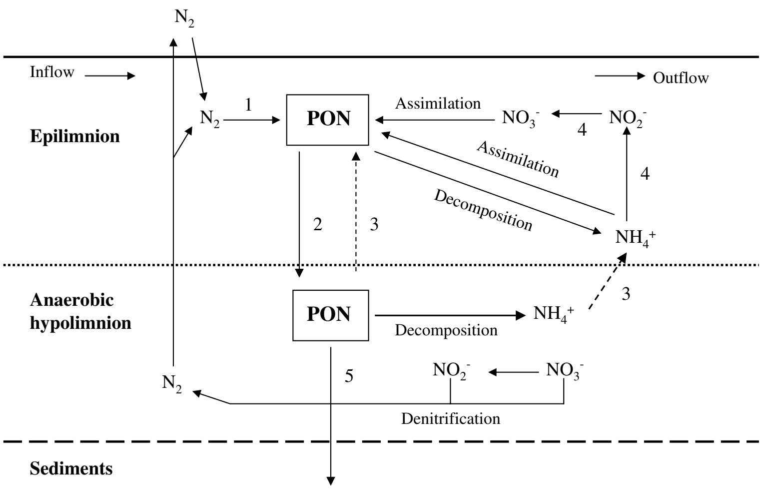

Figure 1. Conceptual scheme of the main processes of the nitrogen cycle in a stratified lake according to Lampert and Sommer (1997): 1 – planktic molecular nitrogen fixation (N_2fix); 2 – a part of the PON (particular organic nitrogen) sinks to the hypolimnion; 3 – due to water mixing some PON is carried from hypolimnion to epilimnion; 4 – in epilimnion ammonium (NH_4^+) is subject to nitrification; 5 – a part of PON is switched off from nitrogen cycle due to sedimentation.

N-(1-naphthyl)-ethylenediamine dihydrochloride was used (detection error ± 2%) for the determination of NO_2^- (Koroleff, 1982). The total amounts of measured nitrogen forms in the epilimnion, hypolimnion and in the whole water column for both years were calculated by integrating the concentrations of the compounds in different water layers. For a detailed description of the calculation method see Nõges et al. (in the present issue).

N_2-fixation in Lake Verevi was measured on August 7, 2000 at one, on August 28, 2000 at two, and on August 2, 2001 at four different depth horizons in the epilimnion (Table 1) applying the acetylene reduction method (Stewart et al., 1967; Présing et al., 1996). Three 60-ml glass bottles were filled with lake water from each depth horizons and exposed for 4 h in the incubator at a constant illumination of 120 W m^{-2} *in situ* temperature. For details see Tõnno & Nõges (2003).

Depths for the nitrification measurement were selected according to the supposed NH_4^+ and oxygen content (Table 1). At each depth four dark glass scintillation vials (two 'samples' and two 'blanks') with a capacity of 24 ml were filled with

Table 1. Dates, sampling depths and measured parameters in Lake Verevi in 2000–2001

Date	Depth (m)	Measured parameters					
		Nitrification rate (mgN m^{-3} day^{-1})	TN (mgN m^{-3})	NH_4^+ (mgN m^{-3})	NO_2^- mgN m^{-3})	NO_3^- (mgN m^{-3})	N_2-fixation (mgN m^{-3} day^{-1})
07.08.2000	2.0	–	+	+	+	+	+
07.08.2000	4.0	+	+	+	+	+	–
07.08.2000	5.0	+	+	+	+	+	–
28.08.2000	0.5	–	+	+	+	+	+
28.08.2000	1.0	–	–	–	–	–	+
28.08.2000	5.0	+	+	+	+	+	–
28.08.2000	5.5	+	+	+	+	+	–
23.04.2001	0.5	+	+	+	+	+	–
23.04.2001	5.5	+	+	+	+	+	–
23.04.2001	8.5	+	+	+	+	+	–
30.04.2001	0.5	+	+	+	+	+	–
30.04.2001	5.0	+	+	+	+	+	–
30.04.2001	5.25	+	+	+	+	+	–
30.04.2001	5.5	+	+	+	+	+	–
07.05.2001	0.5	+	+	+	+	+	–
07.05.2001	5.0	+	+	+	+	+	–
07.05.2001	5.25	+	+	+	+	+	–
07.05.2001	5.5	+	+	+	+	+	–
05.06.2001	0.5	+	+	+	+	+	–
05.06.2001	5.0	+	+	+	+	+	–
05.06.2001	5.25	+	+	+	+	+	–
05.06.2001	5.5	+	+	+	+	+	–
02.08.2001	0.5	+	+	+	+	+	+
02.08.2001	1.0	+	+	+	+	+	+
02.08.2001	2.0	+	+	+	+	+	+
02.08.2001	3.0	+	+	+	+	+	+
02.08.2001	4.0	+	+	+	+	+	–
02.08.2001	5.0	+	+	+	+	+	–
02.08.2001	6.0	+	+	+	+	+	–
02.08.2001	7.0	+	+	+	+	+	–

lake water. $NaH^{14}CO_3$ (VKI, Denmark) was added to each vial with a final activity of 0.07 μCi ml^{-1}. To 'blank' vials 100 μl of nitrification inhibitor 2-chloro-6-(trichloromethyl) pyridine (TCMP) was added (final concentration 10 mg l^{-1}). Thereafter the vials were incubated 24 h in thermos flasks containing the water from the same depth where the samples had been taken from. After the incubation 100 μl of water from each vial was taken and mixed with 0.5 ml of β-phenylethylamine (PEA) for the assessment of total radioactivity by using 5 ml of Optiphase solution and LSC RackBeta 1211 (Wallac, Finland). The rest of the water sample from the vials (23.9 ml) was filtered through membranes of 0.20 μm pore size (Millipore, HA). The filters were treated with concentrated HCl fumes for 5 min to remove the excess of inorganic ^{14}C, and air-dried for 24 h. Five milliliters of toluene-PPO-POPOP cocktail was added to filters and their radioactivity was assessed with LSC RackBeta 1211.

Chemosynthetic fixation of CO_2 was calculated by the formula:

$$R = [x * C * 1.05 * 1.06 * V1 * k]/y * V2 * t$$

where R, CO_2 fixation rate (mmole m^{-3} h^{-1}); x, difference of the radioactivities of the filter from the 'sample', and the filter from the 'blank'; C, concentration of HCO_3^- in water (mmole l^{-1}); 1.05, coefficient considering the difference of assimilation efficiencies of $^{12}CO_2$ and $^{14}CO_2$; 1.06, factor considering the respiration losses of the assimilated CO_2 during the exposition; $V1$, volume of the exposition vial (ml); k, 1000 coefficient from litres to cubic meters; y, radioactivity of $NaH^{14}CO_3$ solution added to the vial; $V2$, amount of the filtered water (ml); t, incubation time (h). To estimate nitrification, we used an average conversion factor of 8.3 moles of N oxidized per mole of carbon fixed (Owens, 1986; Joye et al., 1999).

Results

In Lake Verevi the concentration of total nitrogen in the hypolimnion (annual average 6646 mgN m^{-3}) was by an order of magnitude higher than in the epilimnion (annual average 948 mgN m^{-3}). TN concentration in the epilimnion and in the hypolimnion from April to September was 781 and 4007 mgN m^{-3}, respectively, increasing by the end of the vegetation period up to 1284 and 11922 mgN m^{-3}, respectively (Fig. 2a). Mean epilimnetic concentration of ammonium from May to August was 6.4 mgN m^{-3}, followed by a sharp increase. In the hypolimnion, the concentration of NH_4^+ was about 35 times higher (average from May to August 2118 mgN m^{-3}) than in the epilimnion but followed the same dynamics (Fig. 2b). The NO_2^- content in the epi- and hypolimnion stayed on a low level from April to October (average 0.21 and 0.16 mgN m^{-3}, respectively), increasing up to 6.8 and 2.9 mgN m^{-3}, respectively by November/December (Fig. 2c). The mean epilimnetic concentration of NO_3^- from April to October was 1.5 mgN m^{-3} increasing abruptly up to 130 mgN m^{-3} by November/December (Fig. 2d). Mean hypolimnetic nitrate concentration in spring was 3.4 mgN m^{-3}, by the end of June it decreased to undetectable values, and two peaks occurred in autumn: in September (4.1 mgN m^{-3}) and in December (58 mgN m^{-3}).

N_2-fixation was measured in 2000 on August 7th at a depth of 2 m (2.80 mgN m^{-3} day^{-1}), and on August 28th at a depth of 0.5 m (0.30 mgN m^{-3} day^{-1}) forming, respectively, 0.31 and 0.043% of TN, and 140 and 15% of the amount of mineral nitrogen in the investigated depth horizons. On August 2, 2001 the N_2fix occurred only at a depth of 3 m (0.38 mgN m^{-3} day^{-1}), taking up 0.05% of TN and 5.37% of mineral nitrogen in the investigated depth horizon.

Nitrification occurred in 2000 on August 7th at a depth of 5 m (107 mgN m^{-3} day^{-1}), and on August 28th at a depth of 5.5 m (54.4 mgN m^{-3} day^{-1}). In 2001 we were unable to detect any nitrification on April 23rd and on May 7th (Table 1) while on April 30th and June 5th nitrification occurred at a depth of 0.5 m (6.0 and 7.5 mgN m^{-3} day^{-1}, respectively) and 5.5 m (13.3 and 17.7 mgN m^{-3} day^{-1}, respectively). On August 2nd we detected nitrification at four depths: 0.5, 3, 6, and 7 m (26.1, 50.7, 79.3 and 308 mgNm^{-3} day^{-1}, respectively).

Discussion

As it is common to stratified lakes (Scheffer, 1998), in Lake Verevi the nitrogen that accumulated in

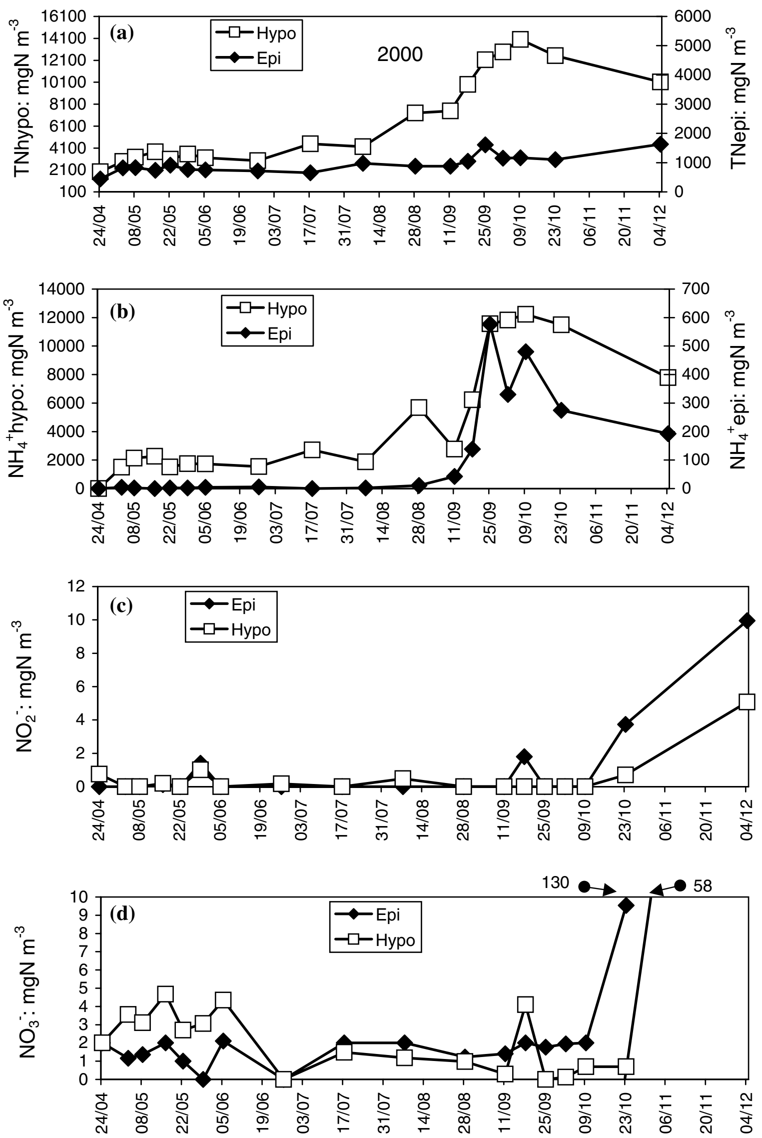

Figure 2. Seasonal course of the epilimnetic (Epi) and hypolimnetic (Hypo) (a) total nitrogen (TN) (b) ammonium (NH_4^+) (c) nitrite (NO_2^-), and (d) nitrate (NO_3^-) in Lake Verevi in 2000.

the hypolimnion was trapped in the non-mixed layer during most of the vegetation period remaining inaccessible to the epilimnetic community.

The concentration of ammonium in the hypolimnion of Lake Verevi was high (maximum 12223 mgN m^{-3}, average 4807 mgN m^{-3}) compared to the other Estonian stratified eutrophic lakes, where according to the database of Võrtsjärv Limnological Station (108 lakes), the average is 742 mgN m^{-3}, and four Canadian lakes, where the NH_4^+ content in the hypolimnion remained below 2000 mgN m^{-3} (Knowles et al., 1981). The high hypolimnetic ammonium concentration implies that most of the epilimnetically derived particulate organic matter was decomposed in this region (Priscu et al., 1986). According to Tammert et al. (present issue) bacteria are one of the most important pools of nutrients (nitrogen, phosphorus) in the hypolimnion of Lake Verevi. In the epilimnion, the ammonium level remained low in spite of high concentrations in the hypolimnion (Fig. 2b). Most probably the metalimnetic barrier but also nitrification detected at the oxic/anoxic interface of the upper section of the hypolimnion were responsible for preventing the penetration of ammonium into the epilimnion in conditions of stable summer stratification. As many microorganisms prefer NH_4^+ as a nitrogen source (Wetzel, 1983; Ahlgren et al., 1994), the ammonium leaking from the hypolimnion could be trapped also by phytoplankton. In Lake Verevi euglenophytes were numerous important in the upper part of hypolimnion, where the concentration of ammonium was high (Kangro et al., in the present issue). Although there was high NH_4^+ content in the hypolimnion, it was trapped and useless for epilimnetic organisms. Such a sharp gradient of nutrients composed a number of niches in the water column for the phyto- and bacterioplankton (see Kangro et al.; Tammert et al., in the present issue). An increase in the epilimnetic ammonium concentration in autumn could be caused by the disturbance of stratification and mixing up of some hypolimnetic water of high ammonium concentration. This assumption is, however, not supported by the results of our measurements showing increasing concentrations both in the epi- and hypolimnion. As the whole year 2000 and the September of 2001 were poor rather than rich in precipitation, a high external loading was not likely either. The only explanation for this pronounced increase could be the mixing up of the nutrient-rich water from the thin near-bottom layer which was not detected by our sampling strategy. It is possible that we could not collect the nearest to the bottom water layer by applied water sampler. As shown by Kõiv & Kangro (the present issue), the concentration of total phosphorus (TP) and SRP in the whole water column also increased in September, which supports the hypothesis that the near-bottom water layer had been mixed up. The hypothesis, however, remains speculative as we have no evidence of such near bottom nutrient rich layer. The concentrations of NO_2^- and NO_3^- remained on a low level both in the epi- and hypolimnion (Fig. 2c, d). The nitrogen mineralized in the epilimnion was probably quickly assimilated by the phytoplankton, causing temporal nitrogen limitation and increase of N_2-fixing cyanobacteria (see Kangro et al., in the present issue). In Lake Verevi denitrification probably could occur not only in the sediments but also in the water column close to the anoxic hypolimnion, and, thus, use nitrite and nitrate, as it was found also in other stratified lakes (Golterman, 1975; Lampert & Sommer, 1997).

It must be emphasized that there is no information about the seasonality of N_2-fixation in Lake Verevi. As a source of nitrogen, N_2-fixation in Lake Verevi in August 2000 and 2001 was of minor importance. Abundance of N_2-fixing cyanobacteria (mainly *Aphanizomenon klebahnii*) usually increased in August, during the period of temporal nitrogen limitation (Kangro et al., the present issue). Nevertheless, the daily input formed less than 1% of the total amount of TN in the water layer where occurred. The temporary contribution to the algal community could still be important as up to 1.4 times more nitrogen could have been fixed than available in mineral form in the euphotic water layer. According to Kostjaev (1986), in eutrophic lakes N_2fix could form up to 50% of the yearly nitrogen budget.

As an oxygen (O_2) demanding process, nitrification occurred in the epilimnion and the upper part of the hypolimnion (5–5.5 m), where some O_2 was present (Fig. 3). By Tammert et al. (present issue) the total number of bacteria was highest in the hypolimnion. According to Knowles et al. (1981), nitrification has been reported to occur more rapidly at low O_2 concentrations. Accordingly, in Lake Verevi also more intensive nitrification occurred in the upper hypolimnion (except on August 2, 2001). High rates of dark assimilation of $^{14}CO_2$ measured on August 2nd, 2001 in anoxic H_2S-rich water at depths of 6 and 7 m could probably indicate not the nitrification but rather the oxidation of H_2S by sulphur chemoautotrophes, which can also assimilate inorganic carbon in darkness (Gorlenko et al., 1977). Nitrification intensity in Lake Verevi (up to 308 mgN m^{-3} day^{-1}, Fig. 3) was much higher than recorded by Hall (1982) in the hypolimnion of mesotrophic L. Grasmere (in all cases less than 8 mgN m^{-3} day^{-1}). According to Hall (1982), planktonic nitrification in aerobic hypolimnetic water could be important in affecting changes in the water chemistry of this water layer. In Lake Verevi, however, a remarkable influence on nitrogen dynamics

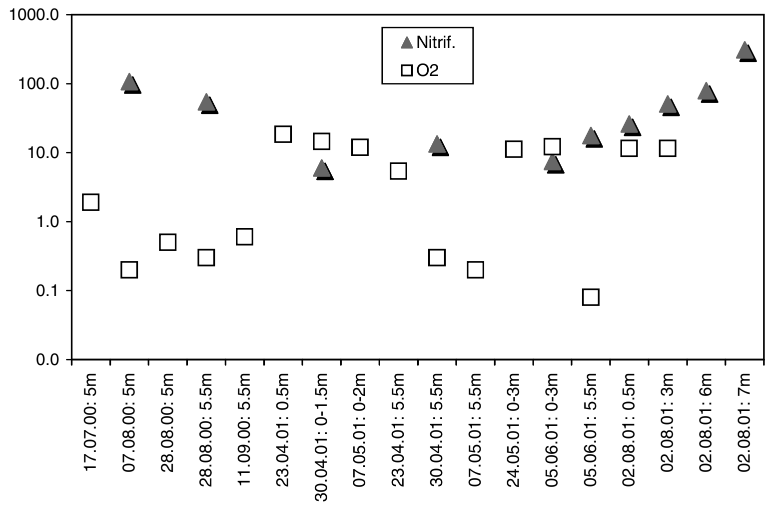

Figure 3. Dynamics of nitrification (Nitrif: mgN m^{-3} day^{-1}) and dissolved oxygen (O_2: mg l^{-1}) in Lake Verevi in 2000–2001 (depth-integrated water samples were collected from water layers 0–1.5, 0–2 and 0–3 m).

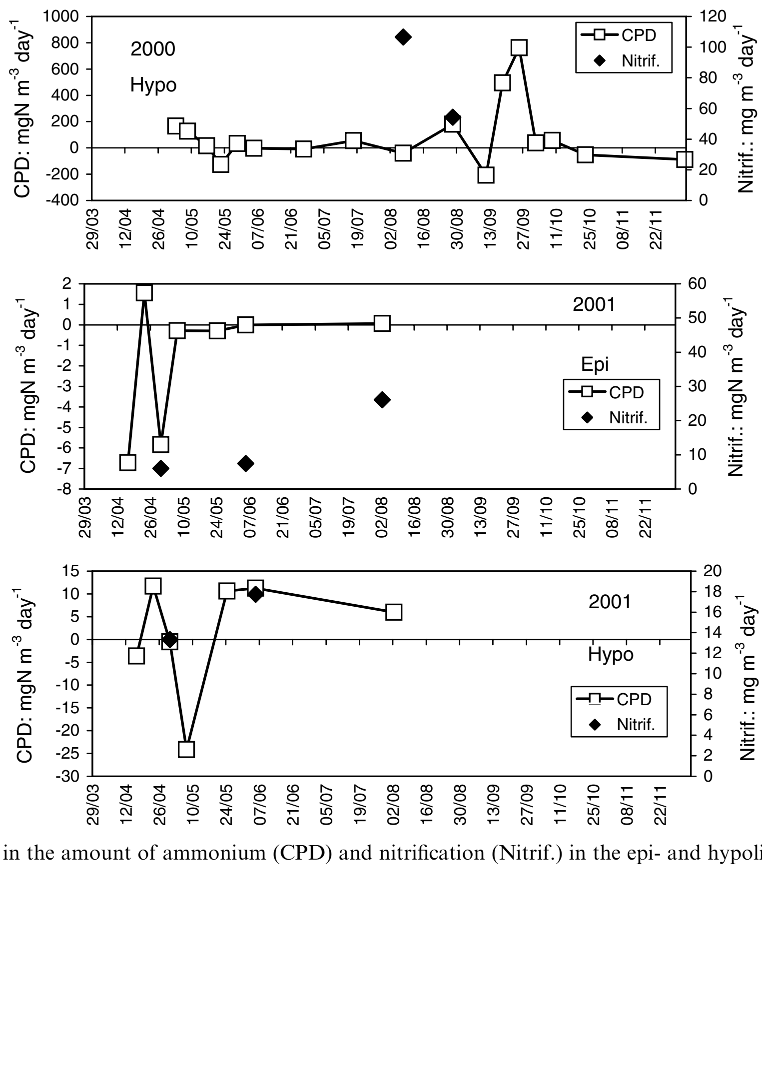

Figure 4. Daily changes in the amount of ammonium (CPD) and nitrification (Nitrif.) in the epi- and hypolimnion of Lake Verevi in 2000–2001.

could be quantified in some cases. For example, a decrease in ammonium during the period after a rather high nitrification rate had been detected in late August/early September 2000, and at the beginning of May 2001 in the hypolimnion (Fig. 4). In the epilimnion the coupling was absent probably because a more open nitrogen cycle involving phytoplankton, which in the euphotic zone quickly consumes all forms of mineral nitrogen.

Conclusions

- In Lake Verevi steep stratification trap ammonium in the hypolimnion during most of the vegetation period causing a concentration that is by an order of magnitude higher than in the epilimnion.
- The role of N_2-fixation in the total nitrogen budget of Lake Verevi in our investigation period was negligible while episodically in the nitrogen-depleted epilimnion N_2fix could substantially contribute to the pool of mineral nitrogen.
- Nitrification was unable to influence nitrogen dynamics in the epilimnion while some temporary coupling with ammonium dynamics in the hypolimnion was documented.

Acknowledgements

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References

Ahlgren, I., F. Sörensson, T. Waara & K. Vrede, 1994. Nitrogen budgets in relation to microbial transformations in lakes Ambio 23: 367–377.

Golterman H. L., 1975. Physiological limnology. An approach to the physiology of lake ecosystems. Elsevier, Amsterdam, Oxford, New York.

Gorlenko, V. M., G. A. Dubinina & C. I. Kuznetsov, 1977. Ekologija vodnyh mikroorganizmov [Ecology of water micro-organisms]. Moscoy.

Grasshoff, K., M. Ehrhardt & K. Kremling, 1983. Methods of Seawater Analysis. Verlag Chemie, Weinheim.

Hall, G. H., 1982. Apparent and measured rates of nitrification in the hypolimnion of a mesotrophic lake Applied and Environmental Microbiology 43: 542–547.

Hansen, H. P. & F. Koroleff, 1999. Determination of nutrients. In Grasshoff, K., M. Kremling & K. EhrhardtMethods of Seawater AnalysisWILEY-VCHWeinheim New York Chichester. Brisbane. Singapore. Toronto,600 pp.

Henriksen, K., T. H. Blackburn, B. A. Lomstein & C. P. McRoy, 1993. Rates of nitrification, distribution of nitrifying bacteria and inorganic N fluxes in northern Bering-Chukchi shelf sediments Continental Shelf Research 13: 629–651.

Howarth, R. W., J. J. Cole, R. Marino & J. Lane, 1988. Nitrogen fixation in freshwater, estuarine and marine ecosystems. 1. Rates and importance Limnology and Oceanography 33: 669–687.

Joye, S. B., T. L. Connell, L. G. Miller & R. S. Oremland, 1999. Oxidation of ammonia and methane in an alkaline, saline lake Limnology and Oceanography 44: 178–188.

Kangro, K., R. Laugaste, P. Nõges & I. Ott, 2005. Long-term changes and seasonal development of phytoplankton in a strongly stratified, hypertrophic lake. Hydrobiologia 547: 91–103.

Knowles, R., D. R. S. Lean & Y. K. Chan, 1981. Nitrous oxide concentrations in lakes: Variations with depth and time Limnology and Oceanography 26: 855–866.

Kõiv, T. & K. Kangro, 2005. Resource ratios and phytoplankton species composition in a strongly stratified lake. Hydrobiologia 547: 123–135.

Koroleff, F., 1982. Total and organic nitrogen. In K. Grasshoff (ed), Methods of Seawater Analysis. Verlag chemie, 162–168.

Kostyaev, V. J., 1986. Biologiya i èkologiya azotfiksiruyushchih sinezelenyh vodoroslej presnyh vod. Leningrad. [Biology and ecology of nitrogen fixing cyanobacteria from inland water].

Lampert, W. & U. Sommer, 1997. Limnoecology: The Ecology of Lakes and Streams. Oxford University Press.

Nõges, P., 2005. Water and nutrient mass balance of the partly meromictic temperate Lake Verevi. Hydrobiologia 547: 21–31.

Ott, I., T. Kõiv, P. Nõges, A. Kisand, A. Järvalt & E. Kirt, 2005. General description of partly meromictic hypertrophic Lake Verevi, its ecological status, changes during the past eight decades and restoration problems. Hydrobiologia 547: 1–20.

Owens, N. J. P., 1986. Estuarine nitrification: A naturally occurring fluidized bed reaction? Estuarine, Coastal and Shelf Science 22: 31–44.

Présing, M., S. Herodek L. Vörös & I. Kobor, 1996. Nitrogen fixation, ammonium and nitrate uptake during a bloom of *Cylindrospermopsis raciborskii* in Lake Balaton Archiv für Hydrobiologie 136: 553–562.

Priscu, J. C., R. H. Spigel M. Gibbs & M. T. Downes, 1986. A numerical analysis of hypolimnetic nitrogen and phosphorus transformations in Lake Rotoiti, New Zealand: A geothermally influenced lake Limnology and Oceanography 31: 812–831.

Scheffer, M., 1998. Ecology of Shallow Lakes. Chapman & Hall, London.

Sprent, J. I., 1987. The Ecology of the Nitrogen Cycle. Cambridge University Press, USA.

Stewart, W. D. P., G. P. Fitzgerald & R. M. Burris, 1967. In situ studies on N_2 fixation using the acetylene reduction technique Proceedings of the Nnational Academy of Sciences of the U.S.A. 58: 2071–2078.

Stolp, H., 1996. Microbial Ecology: Organisms, Habitats, Activities. Cambridge University Press, USA.

Tammert, H., V. Kisand & T. Nõges, 2005. Bacterioplankton abundance and activity in a small hypertrophic stratified lake. Hydrobiologia 547: 83–90.

Tõnno, I. & T. Nõges, 2003. Nitrogen fixation in a large shallow lake: rates and initiation conditions Hydrobiologia 490: 23–30.

Voytek, M. A., J. C. Priscu & B. B. Ward, 1999. The distribution and relative abundance of ammonia-oxidizing bacteria in lakes of the McMurdo Dry Valley, Antarctica Hydrobiologia 401: 113–130.

Wetzel, R., 1983. Limnology. Saunders College Publishing.

Williams, P. J. le B., D. N. Thomas & C. S. Reynolds (eds), (2002) Phytoplankton Productivity. Carbon Assimilation in Marine and Freshwater Ecosystems. Blackwell Science, UK 109–141.

Zingel, P., 2005. Vertical and seasonal dynamics of planktonic ciliates in a strongly stratified hypertrophic lake. Hydrobiologia 547: 163–174.