

Seasonal Translocations of Nitrogen and Phosphorus in Two Lobelian Lakes in the Vicinity of Bytów, (West Pomeranian Lake District)

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Abstract

The aim of this paper was to determine the nutrient translocations between different chemical forms (mineral and organic), as well as between different parts of a lake system (pelagic and benthic; epi- meta- and hypolimnion) in an annual cycle. Nitrogen and phosphorus content in lakes Jeleń and Mały Borek were estimated in monthly intervals (except periods of ice cover).

In both lakes the biggest amounts of pelagic P and N were recorded in autumn. With the beginning of the growth season the quick decrease of P-total in both lakes was observed, attributed to the sedimentation of the particulate organic material. At the end of spring phosphorus resources dropped by about 50%, and the biggest reduction was observed in epilimnion. Translocations of nitrogen during the vegetative period were poorly synchronized with phosphorus translocations. N-total stocks in water column during spring were increasing or stable. The increase was especially intensive in lake Jeleń and was associated with cyanobacterial nitrogen fixation. This process was stopped and nitrogen resources started to decrease when phosphorus resources attained a minimum level. In the second half of summer (before autumn overturn) the amounts of N and P started to increase, due to enhanced migration of nutrients from sediments. During the winter period extensive nitrification was manifested by the downfall of ammonium and simultaneous growth of nitrate stocks. The lakes differ substantially in such features as the levels of ammonium concentration, rate of phosphate and ammonium accumulation in hypolimnion, or intensity of nitrogen fixation. Symptoms of internal loading with phosphorus and extensive nitrogen fixation were found in lake Jeleń, one of the clearest lakes in Poland.

Keywords: nutrients, eutrophication, stratification, lake water quality, biogeochemical cycle

Introduction

Knowledge of nutrient status, mainly nitrogen (N) and phosphorus (P), is essential to assess the present state of a lake ecosystem, to predict its further development, and to propose, if necessary, measures to prevent its degradation [1, 2]. Both phosphorus and nitrogen are highly biologically

and chemically active elements, undergoing numerous transformations and moving between the particulate, dissolved, and gaseous (nitrogen) phases. The nutrient pathways consist of inputs from surface and groundwater drainage, and from the atmosphere (rainfall/deposition), outflow from the basin, biological uptake, transformation and remineralization, sedimentation, benthic accumulation and fluxes across the water-atmosphere (N₂ exchange) and sediment-water interfaces [3-6]. Nutrient fluxes are controlled

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Table 1. Characteristics of Mały Borek and Jeleń lakes.

	Lake Mały Borek	Lake Jeleń
Surface area, [ha]	7.6	89
Total volume, [thous. m ³]	456	8,461.2
Maximum depth, [m]	11	32
Active bottom relative area, %		
in May	15-20	25-40
in August	30-35	35-50
in October	50-70	50-70
Hypolimnion relative area, %	31	39
Hypolimnion relative volume, %	7.5	31
Relict flora	scanty population of <i>Littorella uniflora</i>	rich populations of <i>Lobelia dortmanna</i> , <i>Isoetes lacustris</i> , <i>Littorella uniflora</i>

by meteorological and hydrobiological conditions and geographical and geochemical properties of the catchments, as well as by a variety of anthropogenic factors [7, 8]. The cycle of nitrogen and phosphorus in an aquatic system is thus very complex and its proper understanding requires detailed analyses of the distribution of all components in time and space.

The aim of this paper was to determine the seasonal changes of N and P distribution in two thermally stratified lakes of different morphology: Jeleń and Mały Borek, located in the vicinity of Bytów (West Pomerania). Our intention was to determine the nitrogen and phosphorus translocations between different chemical forms, as well as between different parts of lakes (epi- meta- and hypolimnetic; pelagic and benthic). The chosen lakes are devoid of surface inflows and outflows, which makes studies of their internal nutrient translocations easier.

Material and Methods

Both studied lakes are lobelian. The group of lakes called "lobelian" is characterized by the presence of post-glacial relict flora such as *Lobelia dortmanna*, *Isoetes lacustris*, *Isoetes echinospora*, *Littorella uniflora* and by specific physico-chemical properties of water i.e. low concentration of phosphorus (usually below 120 µg P·dm⁻³; on average about 30 µg P·dm⁻³) and calcium (below 30 mg Ca·dm⁻³; on average about 7.5 mg Ca·dm⁻³) and relatively high transparency (about 4 m from 1 to above 11 m) [9-13]. They are characterized by low conductivity and alkalinity and high concentration of free carbon dioxide. Most of them are oligotrophic or mesotrophic; very rarely they can constitute early development stages of dystrophic lakes.

The typical lobelian lake in Poland is a small reservoir (about 30 ha), with maximum depth of about 12 m and volume about 4 million m³ [14].

Lakes Jeleń and Mały Borek are dimictic closed water bodies with thermal stratification during the vegetative season. The lakes are located in a similar geological environment – in a morainic landscape, with about half the drainage basins forested and another half composed of fields, meadows, pastures and barren land. The main parameters, which indicate differences between the lakes, are presented in Table 1. In the 1980-ties and 1990-ties Jeleń was classified as the clearest among all monitored lakes in Poland.

The vertical distribution of various phosphorus and nitrogen forms was measured in both lakes in monthly intervals from spring until autumn 2005. In Mały Borek measurements continued until December 2006, except for a period of ice cover (in February). In Jeleń some measurements were done only in the second half of 2006. Nitrogen (N-NH₄⁺; N-NO₃⁻, N-total) and phosphorus (P-PO₄⁻; P-total) measurements were conducted in each lake at 5-7 sites arranged in a profile from the coast to the central part of the lake. At each site water samples were collected from the surface (1 m under surface) and near-bottom layer, as well as from above and below the thermocline zone. The chemical analyses of nitrogen and phosphorus determination have been performed according to respective colorimetric methods described in Hermanowicz et al. [15]. Phosphate concentration was measured spectrophotometrically at 690 nm, after reaction with ammonium molybdate. Nitrate concentration was determined at 410 nm, after reaction with sodium salicylate. Ammonium concentrations were measured at 690 nm, using the ammonium test spectroquant (Merck). Total nitrogen and phosphorus were determined after their oxidation to nitrates and phosphates by autoclaving and digestion in perchloric acid. Concentration of organic forms of N and P were calculated as a difference between concentrations of total and mineral forms. Water temperature was measured with WTW TA 197-Oxi probe at 1 m depth intervals. Seasonal evolution of oxygen conditions, chlorophyll_a concentrations and primary production during the period of study has been presented elsewhere [16].

Comparisons of successive measurements showed that in the case of lake Mały Borek location of sampling sites and number of collected each time water samples (ca. 15) was adequate for proper assessing of total amounts of nutrients in the lake. The temporal changes revealed a regular pattern and the scatter of calculated values was rather small. In the case of lake Jeleń, where a similar number of samples was collected each time as in Mały Borek, the scatter was greater, suggesting worse representativeness of the sample set for the whole-lake assessments. The volume of Jeleń is almost 20 times greater than the volume of Mały Borek and the morphometry of Jeleń is more complex, therefore total amounts of nutrients in this lake were estimated less precisely. Nevertheless, the range of values in both lakes was well established and the general pattern of seasonal changes was clearly reproduced, allowing us to describe major translocations of nitrogen and phosphorus in the lakes in an annual cycle.

Results and Discussion

Deeper lakes in the Pomeranian Lakeland area are traditionally classified as dimictic. However, during our two-year study only in autumns there were several weeks lasting periods of complete vertical water mixing, from the surface to the bottom, while in springs, even a few days after ice melting, water was distinctly thermally stratified due to intensive solar radiation in this season (Fig. 1). The studied lakes differ in depth ranges of epilimnion and hypolimnion. In Mały Borek, for most of the vegetative period, the epilimnion came down to 3-4 meters (average volume 260 thous. m³, about 58% of total lake volume) and the metalimnion spread out from 3-4 to 7-9 meters (160 thous. m³, 35%). Hypolimnion comprised only 7% (35 thous. m³) of total lake volume. In lake Jeleń the epilimnion usually come down to 4-8 meters (average volume 4,100 thous. m³, 48% of lake volume), metalimnion extended from 4-8 to 10-12 meters (2,100 thous. m³, 24%) and hypolimnion comprised almost 4 times bigger part of a lake volume (127.7 thous. m³, 28%) than in Mały Borek.

In winter season 2004/05 the Mały Borek was frozen for 81 days (from December 26 to January 3, and from January 24 to April 5). In winter 2005/06 the ice season lasted 115 days, from December 19 to April 12. In lake

Jeleń the ice cover appeared and disappeared with a few days delay, as compared to Mały Borek, but the number of days with ice was similar in both lakes.

In summer 2005 maximum surface temperatures occurred in July and reached 22°C in Mały Borek and 21°C in Jeleń. The beginning of summer 2006 was exceptionally warm. In Mały Borek the surface water temperature in July exceeded 26°C, and the 25°C – isotherm went down to almost 3 meters depth (Fig. 1).

In both lakes the biggest amounts of pelagic phosphorus and nitrogen were recorded in the second part of the vegetative period. In the autumn of 2006 (October–November) the total phosphorus (P-total) and total nitrogen (N-total) resources in Mały Borek amounted to about 50-60 kg P and 700-800 kg N, respectively (Figs. 2A, 3A) whereas in Jeleń it was 550-670 kg P and 11,000-12,000 kg N (Figs. 4A, 5A). If we take into account the differences in lake size (19 times in volume and 12 times in surface area), we can notice that the average amounts of nutrients, expressed per volume unit, were higher in Mały Borek (about 1.65 gN·m⁻³ and 0.12 gP·m⁻³) than in Jeleń (about 1.35 gN·m⁻³ and 0.07 gP·m⁻³), whereas the amounts of nutrients calculated per surface area were in the case of phosphorus similar (about 0.7 g·m⁻² in both lakes) and in the case of nitrogen – higher in Jeleń (about 13 g·m⁻²) than in Mały Borek (about 10 g·m⁻²).

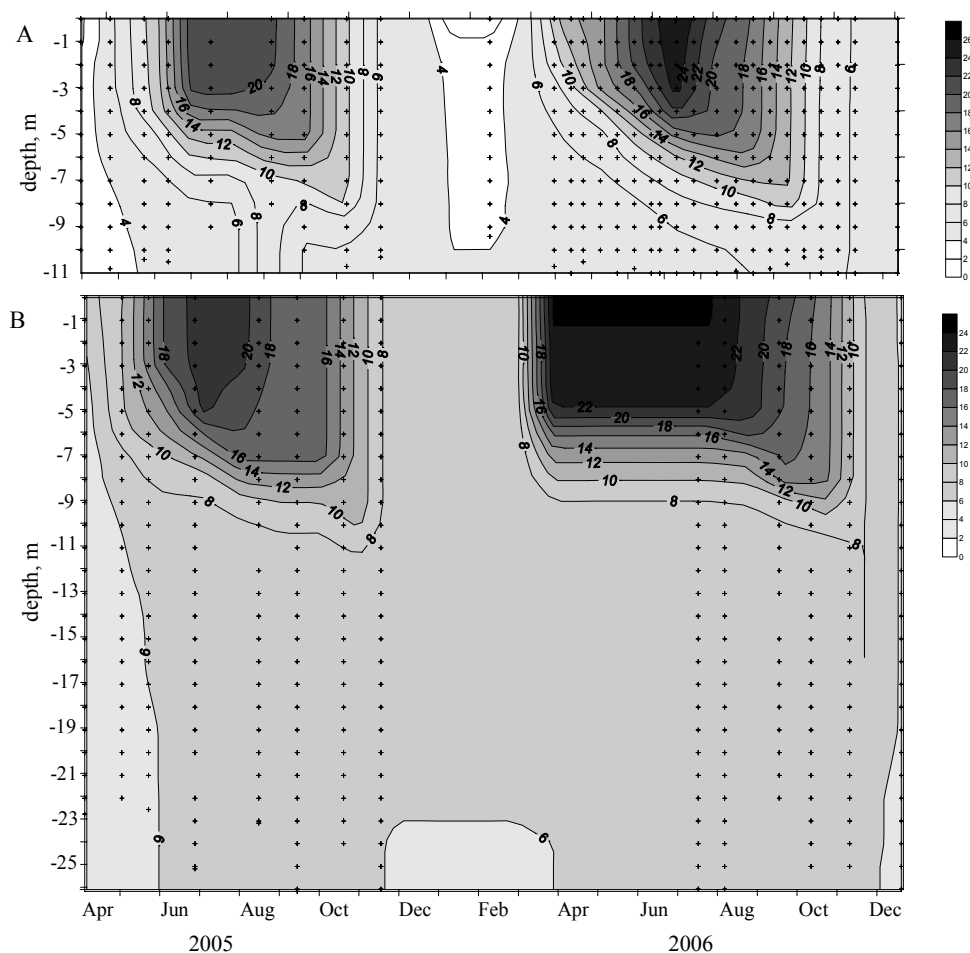


Fig. 1. Seasonal changes of water temperature: A) Lake Mały Borek, B) Lake Jeleń.

During the winter period a slight decreasing tendency of nitrogen and phosphorus resources in Mały Borek can be noticed. It was probably a consequence of particulate organic matter sedimentation when the lake was covered with ice. In Jeleń the measurements were not conducted at this time, but the lower amounts of nutrients in spring than in autumn confirm this observation.

With the onset of the growth season a rapid decrease of P-total in both lakes was observed and at the end of spring phosphorus resources achieved the minimum level. In Mały Borek amounts dropped to about 20 kgP and in Jeleń to 200-250 kgP (Figs. 2A and 4A), revealing over 50% reduction as compared to autumn values. The biggest reduction of P-total was observed in the epilimnion as a consequence of particulate material sedimentation. It may be assumed that during the initial stage of the vegetative season the superficial layer of bottom sediments over most of the lakes area was well oxygenated. High redox potential limits the P release from the sediments [17] because of strong adsorption of phosphorus and making the return of its mineralized form to water column difficult.

In 2005 the increase of phosphorus concentration in the water column of both lakes started in autumn, whereas in 2006 in Mały Borek it was observed much earlier – in July. It seems that the increase of phosphorus concentration in water column was a consequence of worsening of oxygen conditions in the upper sediment layer and was associated with this desorption of phosphorus and high water temperature (Fig. 1). High temperature is known to affect phosphorus release [3, 18]. Performed laboratory experiments

[18] showed that the phosphorus release rate from sediments increases fivefold between 2 and 25-35°. In such conditions the microbial decomposition of organic matter was accelerated and the oxygen in sediments was depleted faster, triggering intensive phosphorus desorption [3]. The release of phosphorus from bottom sediments into the water takes place throughout the whole year (as a result of physico-chemical and biochemical processes) but under anoxic conditions the rate of release is significantly higher [17-20]. The phosphorus flux from sediments is largely controlled by the existence of the aerobic surface-sediments layer, in which the iron and other metals (Mg, Al) are oxidized into forms that have strong adsorbing capacities for phosphorus [20]. Under reduced conditions this layer – a barrier suppressing the flux of phosphorus from sediments into the water – disappears, and the phosphorus, especially associated with iron, may be mobilized [3]. Moreover, severe and prolonged anoxia may mobilize even more stable phosphorus fractions.

In effect within 1-2 months, a phosphorus pool in the water column of lakes studied increased by a factor of 2 or more. It should be stressed that restoration of pelagic phosphorus resources in both lakes and in both years took place before autumnal overturn. That means that only the shallower part of a lake's bottom, the contacting with epilimnion so-called 'active bottom' (in August occupying less than 50% of the lake area, Table 1), was the main source of new phosphorus.

In both lakes the mineral phosphorus constituted variable parts of total phosphorus, ranging from several to

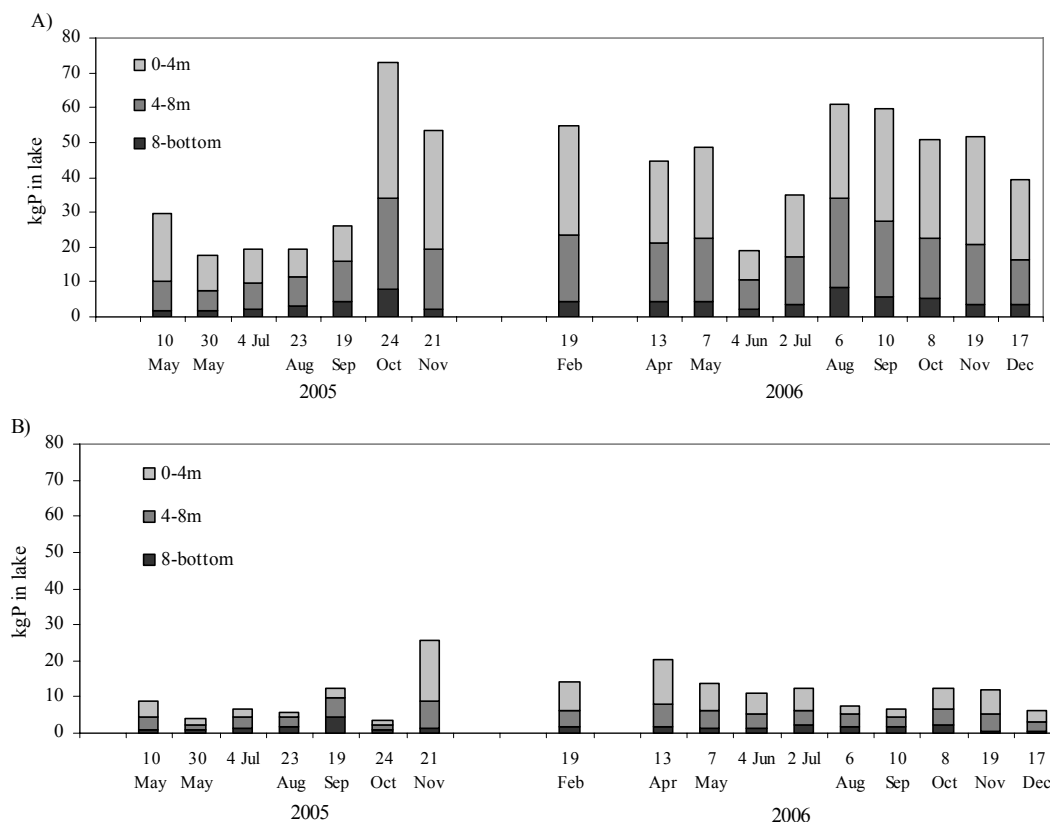


Fig. 2. Seasonal changes of phosphorus content (kg P) in particular water layers in Lake Mały Borek: A) P-total, B) P-PO₄.

above 50% of P-total (on average about 30%, Fig. 6). During the vegetative period the amounts of mineral phosphorus were the smallest (phosphates were rapidly incorporated into the biomass of planktonic algae and bacteria) and increased in autumn – winter period. The average phosphate concentrations in surface water layers during stratification amounted to $0.006 \pm 0.005 \text{ mgP} \cdot \text{dm}^{-3}$ (about 3 kg P in epilimnion) in Mały Borek and $0.009 \pm 0.006 \text{ mgP} \cdot \text{dm}^{-3}$ (about 40 kg P in epilimnion) in Jeleń, whereas during autumn circulation and under ice cover the concentrations were 5-8 times higher. In contrast to the upper layers, concentrations in hypolimnion phosphate during the stratification period were increasing. In lake Jeleń, at the end of summer stratification, most phosphates were assembled in hypolimnion (Fig. 4B), whereas in Mały Borek, although the P-PO_4 concentrations in hypolimnion were usually higher than in epilimnion, the phosphates mass in the bot-

tom layer remained small (Fig. 2B). The rate of phosphate accumulation in hypolimnion may be roughly estimated at $0.61 \text{ mgP} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in Mały Borek and $2.49 \text{ mgP} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in Jeleń. The differences between the intensity of phosphates released in both lakes were significant. Probably the sediments below the hypolimnion layer in Mały Borek were poorer in phosphates. The hypolimnion in Mały Borek, due to its shallowness and relatively small volume, for the most part of the year was anoxic, precluding substantial PO_4 adsorption and accumulation. The situation in lake Jeleń was different. Here the anoxic conditions in the hypolimnion were a relatively new and short-lasting phenomenon, in 2005 appearing only in September and October [16]. In the 1980s and 1990s Jeleń was one of the clearest lakes in Poland (1st class of water quality, acc. to Polish standards) [10, 21], distinguished by low nutrient concentrations, high water transparency (>7 m Secchi depth), and oxygenated

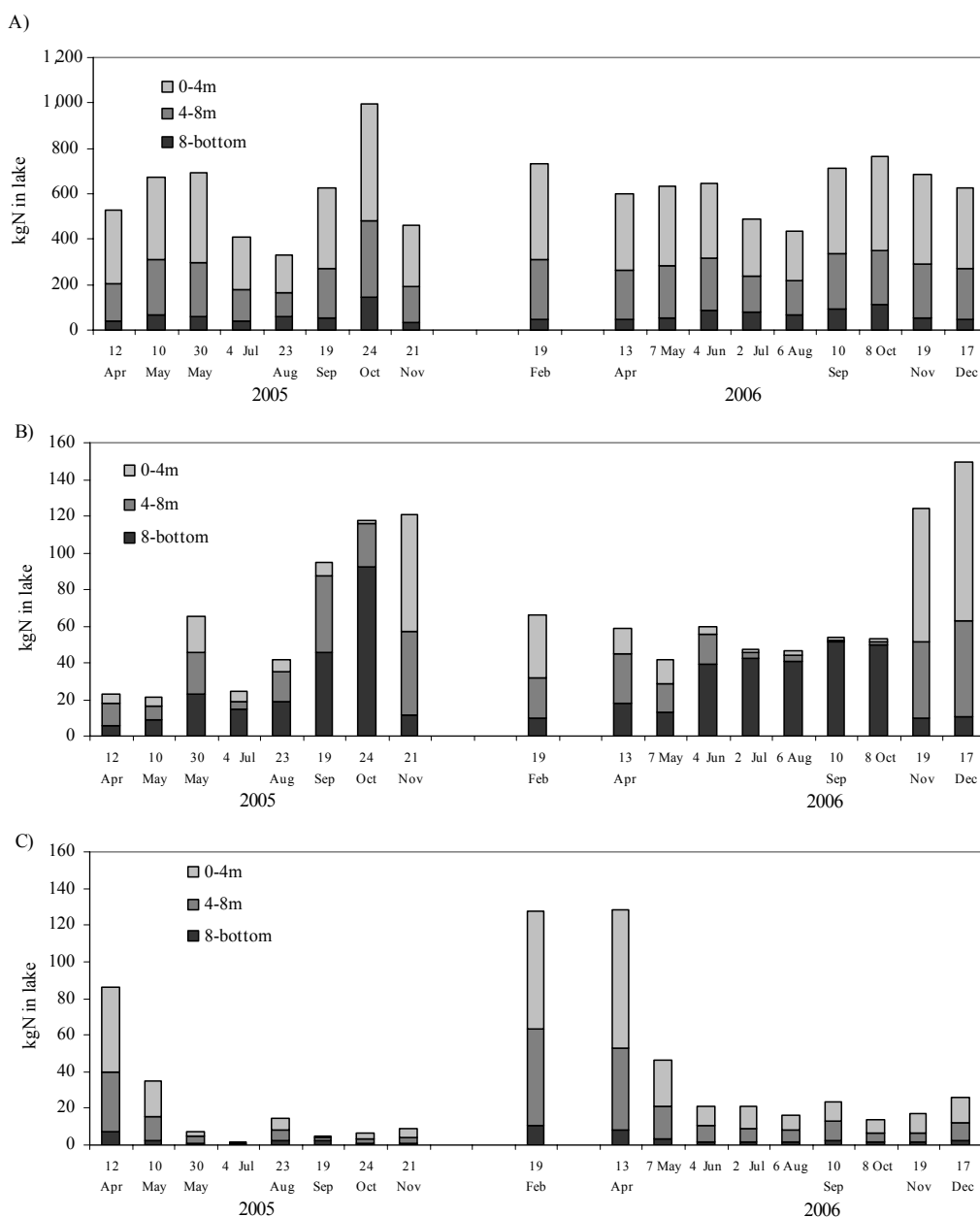


Fig. 3. Seasonal changes of nitrogen content (kg N) in particular water layers in Lake Mały Borek: A) N-total, B) N-NH₄, C) N-NO₃.

hypolimnion (50% and 30% average saturation in August 1986 and 1993, respectively, compared to 10% in August 2005) (Fig. 7; [22, 23]). Apparently, internal loading started in Jeleń in recent years, releasing into the water column phosphorus reserves accumulated during previous years. Sediments can act as new pollutant sources [18, 20, 24] and can account for up to 80% of total nutrient inputs to some lakes [25], and even if external nutrient loadings are reduced, lake recovery can still be significantly retarded by persistently high sediment release rate.

It was estimated [21] that in the 1990s, the phosphorus load from the catchment area and from rainfall to lake Jeleń amounted to about 160 kg P·year⁻¹. About 75% of this was coming from the land runoff and 25% of phosphorus was introduced to the lake water with atmospheric deposition. In addition, about 130 kg of P·year⁻¹ was coming from recreation, angling, and permanent and seasonal inhabitants. Total yearly inflow of phosphorus to Jeleń was estimated at about 290 kg (0.33 gP·m⁻² of lake area). This means that in the 1990s permissible lake P-loading was, according to Vollenweider [21] criteria, overdosed almost two times.

The translocations of nitrogen during the vegetative period were only to some extent similar to phosphorus translocations and were not synchronized with them. In contrast to phosphorus, whose biogeochemical cycle doesn't contain a gaseous form and is practically closed, in nitrogen, cycle-free nitrogen (N₂) plays a significant role. Free nitrogen can easily be exchanged between the water phase and atmosphere. In an aquatic environment, N₂ may be a product of

denitrification, but at the same time it can be incorporated into the organic matter by the N-fixing cyanobacteria [4].

During the spring, when the phosphorus pool in lakes was decreasing, the amounts of N-total in the water column were increasing or stable (Figs. 3A and 5A). The increase of nitrogen pool in spring was especially intensive in lake Jeleń and can be attributed to nitrogen fixation. According to our own observations conducted in both lakes during 2005 (unpubl.), the spring phytoplankton in Jeleń (3-12 mg chl a m⁻³ in euphotic layer in April and May) was dominated by filamentous cyanobacteria, with *Oscillatoria sp.* and *Anabaena sp.* being the most numerous taxa. *Anabaena sp.* is known as an efficiently N-fixing cyanobacterium [26]. It was dominated also during the late summer phytoplankton peak (in September) in Jeleń, and was present also in Mały Borek (mainly in April). But its role here was not so spectacular as in Jeleń. As can be inferred from Fig. 5A, between the middle of April and the end of May (46 days), the spring cyanobacterial assemblage in Jeleń might have introduced about 6,000 kg of new nitrogen to the lake system (0.14 gN m⁻²·d⁻¹), doubling initial resources. Nitrogen increment was stopped at the end of May/beginning of June, when phosphorus resources attain a minimum level. Most likely, phosphorus deficiency inhibited further growth of N-fixing cyanobacteria [26, 27]. From this moment nitrogen resources in lakes started to decrease. From June to August filamentous cyanobacteria constituted a minor part of a lake's phytoplankton. In Mały Borek in summer 2006 nitrogen decrease was continuing even in the phase of phosphorus increase (Figs. 2A and 3A). This suggests that

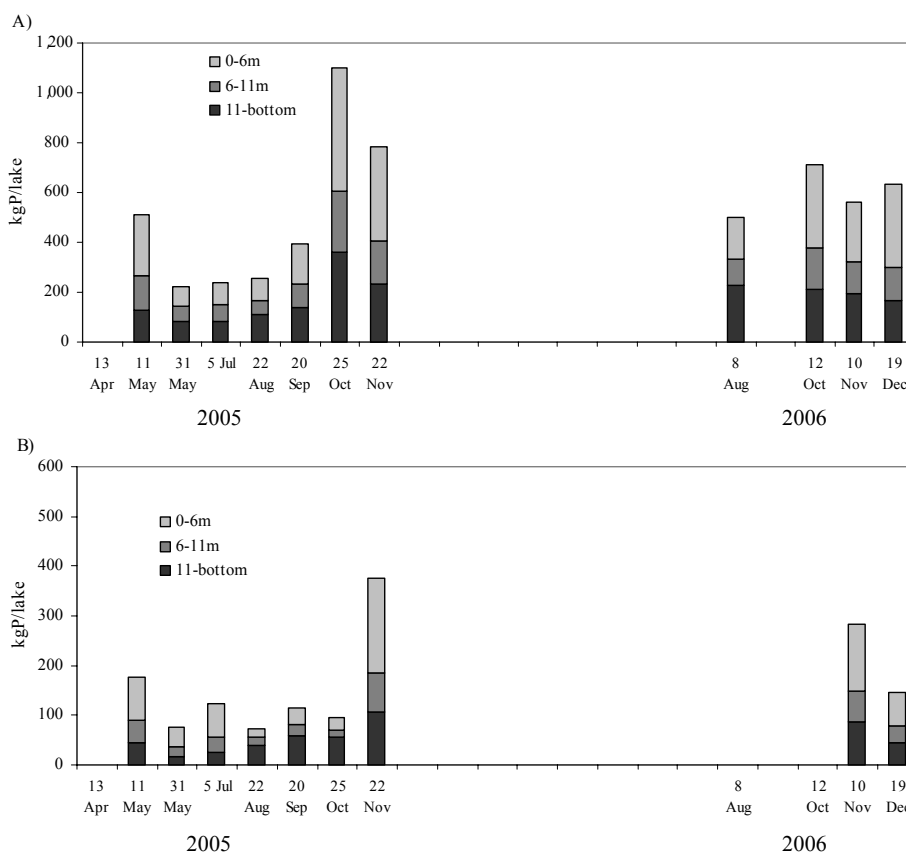


Fig. 4. Seasonal changes of phosphorus content (kg P) in particular water layers in Lake Jeleń: A) P-total, B) P-PO₄.

in the middle of summer losses of nitrogen due to denitrification and sedimentation were higher than gains from N₂ fixation and sediment release. By the middle of summer, total nitrogen resources in Mały Borek were reduced by a half, while in Jeleń – by ca. 1/3, in comparison to autumn levels (Figs. 3A and 5A). In the second part of summer, however, the situation changed and the amounts of nitrogen in water column again started to increase. The greater availability of phosphorus in the second half of summer may have facilitated nitrogen fixation. In autumn the equalization of temperature and weakening of density gradients enhanced the diffusion of nutrients from pore waters into the water column. Additionally, the convection caused by reversing the temperature gradient between water and sediment during periods of quick water cooling might have accelerated migration of nutrients from sediment to water column. By October, pelagic nitrogen resources in lakes attained a maximum level.

Organic nitrogen was a dominant form of nitrogen in both lakes throughout the whole study period, constituting from 70 to 93% of total nitrogen in lake Mały Borek and over 90% in lake Jeleń (Fig. 8). Organic nitrogen was evenly distributed in the water column and its content in respective lake layers was proportional to the layer volume. The contribution of inorganic nitrogen was smallest during the growth season: from a few to ca. 15% in Mały Borek and only a few % in Jeleń. Its maximum share of inorganic nitrogen was attained in winter.

Through the major part of the year the most important mineral form of nitrogen was ammonium-nitrogen (Fig. 8). During the vegetative period amounts of ammonium nitrogen in epilimnion and metalimnion were low (Figs. 3B and 5B). In summer, N-NH₄ concentrations in the epilimnion of Mały Borek amounted to 0.027±0.019 mg·dm⁻³. In Jeleń, N-NH₄ concentrations were even lower, on average 2 times

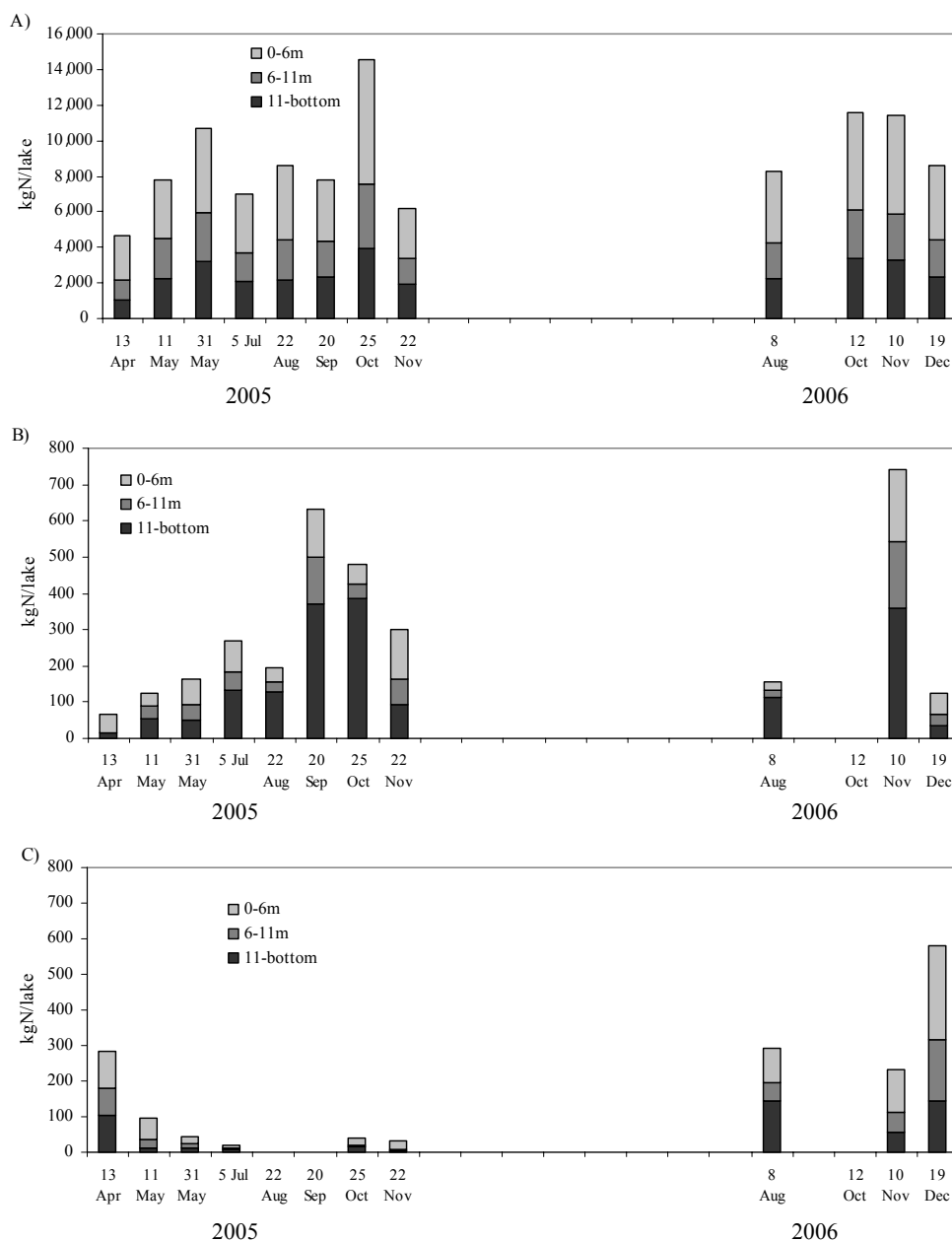


Fig. 5. Seasonal changes of nitrogen content (kg N) in particular water layers in Lake Jeleń: A) N-total, B) N-NH₄, C) N-NO₃.

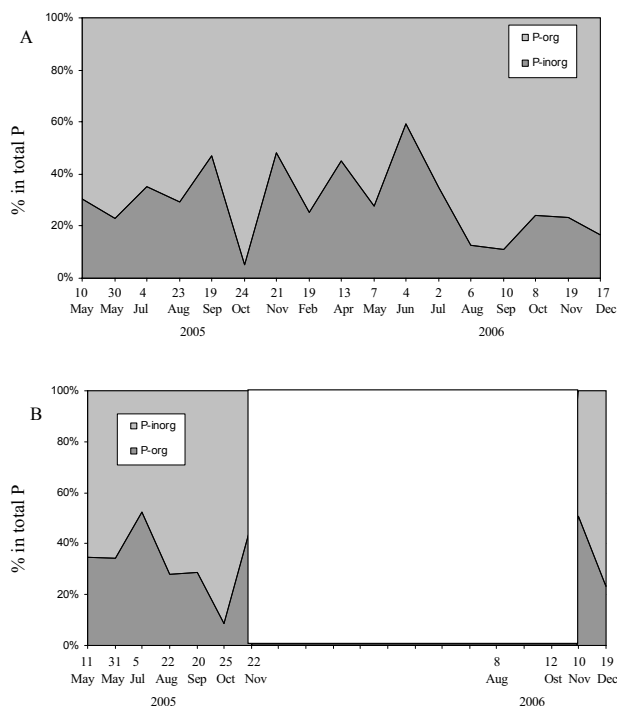


Fig. 6. Seasonal variability of the percentages of inorganic-P and organic-P in total phosphorus, A) Lake Mały Borek, B) Lake Jeleń.

lower than in Mały Borek ($0.014 \pm 0.006 \text{ mg} \cdot \text{dm}^{-3}$). Much higher concentrations occurred in that time in the hypolimnion, but again values in Jeleń (up to $0.4 \text{ mgN} \cdot \text{dm}^{-3}$) were several times lower than in Mały Borek (up to $4 \text{ mg} \cdot \text{dm}^{-3}$). Summer accumulation of N-NH_4 in the bottom layer was associated with water stratification and oxygen deficit. The hypolimnion ammonium (similarly as in phosphates) is generated by the biological decomposition of sedimented organic matter and cannot penetrate to the higher layers of the lake because of water stratification. Moreover, dissolved oxygen concentration impacts rates of nitrification because nitrifying bacteria are obligate aerobes [28]. In the absence of oxygen, as the redox potential is reduced to below about $+0.4 \text{ V}$, bacterial nitrification of NH_4^+ to NO_2^- and NO_3^- ceases [4]. Moreover, in such conditions, i.e. oxygen deficit, the release of NH_4 from sediments is higher [29]. By the end of the stagnation period about 90 and 380 kg of N-NH_4 accumulated in the hypolimnion of Mały Borek and Jeleń, respectively, making over 90% of inorganic nitrogen concentrated in this layer. Contrary to the accumulation of phosphates, the approximate rate of ammonium accumulation in hypolimnion in Mały Borek was greater than in Jeleń ($4.0 \text{ mgN} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ and $2.8 \text{ mgN} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, respectively).

During autumnal circulation, ammonium concentrations were distributed uniformly with depth. In that time, average concentrations of N-NH_4 in lakes Mały Borek and Jeleń were $0.27 \pm 0.05 \text{ mg} \cdot \text{dm}^{-3}$ and $0.056 \pm 0.035 \text{ mg} \cdot \text{dm}^{-3}$, respectively, and the amounts of N-NH_4 in lakes attained maximum levels (Figs. 3B and 5B). It has been observed that the amount of NH_4 in lake Mały Borek was increasing

up to the end of the measurement season (i.e. to November 2005 and to December 2006), whereas in lake Jeleń this increase was stopped in October, and at the end of the season the amount of NH_4 started to decline. Probably in Mały Borek, where oxygen conditions in sediments during stagnation period were worse than in Jeleń, a greater part of sedimented organic matter left unmineralized until autumnal reaeration. Such interpretation is supported by the observation of significantly delayed restoration of oxygen resources during autumnal overturn in Mały Borek, as compared to Jeleń [16]. Evidently in Mały Borek oxygen was intensively consumed and ammonium intensively regenerated even in late autumn.

During the winter period the downfall of ammonium and simultaneous growth of nitrate stocks was observed, indicating extensive nitrification processes occurring in the water column. This process was particularly visible in Mały Borek, as in this lake the measurements were performed also under ice cover (Figs. 3B and C). Low light intensities, slowing down the uptake of nutrients by phytoplankton and high ammonium and oxygen concentrations, created favourable conditions for nitrification, despite low water temperatures. By the end of winter about 120 kg N-NO_3 accumulated in Mały Borek. There were no mid-winter

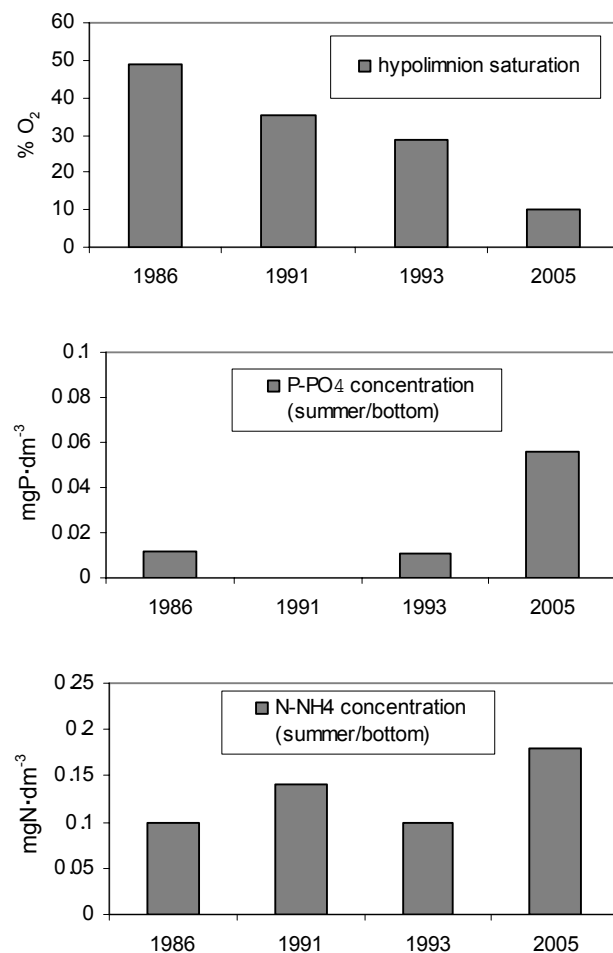


Fig. 7. Changes of some hydrochemical indices in Lake Jeleń in 1986-2005 [22, 23].

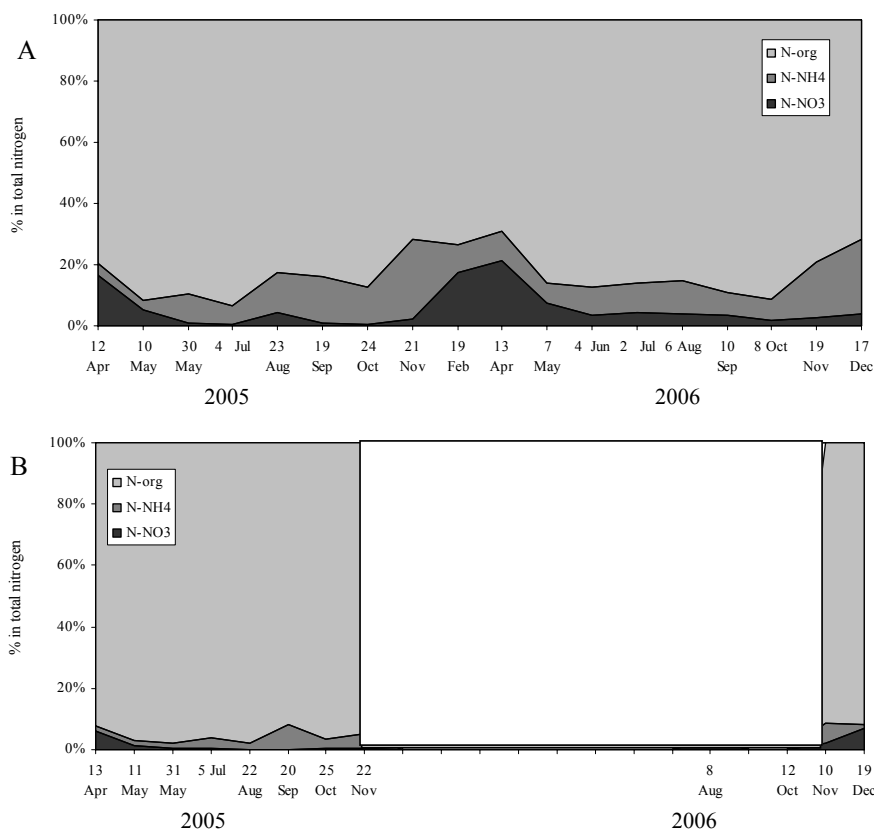


Fig. 8. Seasonal variability of the percentages of NH₄-N, NO₃-N, and organic-N in total nitrogen: A) Lake Mały Borek, B) Lake Jeleń.

data from Jeleń, but at least 580 kg N-NO₃ were present in December 2006 (Fig. 5C).

In April, after ice melt, 70-85% of phytoplankton accessible to inorganic nitrogen was in the form of nitrates. For several weeks high winter stocks of inorganic nitrogen were consumed, but it is not clear which process, assimilation by algae or denitrification, was more important for nitrate utilization.

Although the general pattern of nitrogen and phosphorus translocations in Mały Borek and in Jeleń was similar, there were striking quantitative differences in some of the observed characteristics, especially relating to inorganic components. The rate of phosphate accumulation in the hypolimnion was 4 times higher in Jeleń than in Mały Borek, and this was attributed to the internal loading with phosphorus, starting in recent years in lake Jeleń. In contrast, the rate of ammonium accumulation in hypolimnion was 3.5 times higher in Mały Borek than in Jeleń; ammonium concentrations in epilimnion during stratification as well as concentrations in the whole lake during autumnal overturn in Mały Borek were at least 5 times higher than in Jeleń; while massive spring-time nitrogen fixation occurred only in Jeleń, being rather a small-scale phenomenon in Mały Borek. All this may suggest stronger nitrogen limitation in Jeleń as compared to Mały Borek. However, total N : total P ratio in autumn, i.e. in the period of maximum nutrient pelagic stocks, was higher in Jeleń (about 19 : 1, g/g) than in Mały Borek (13.5 : 1). To explain this apparent paradox, an *ad-hoc* hypothesis may be proposed that organic nitrogen

composition in lakes was different, with refractory fraction more important in Jeleń than in Mały Borek. When inorganic N : inorganic P ratio in epilimnion of both lakes is compared, inorganic nitrogen deficiency in Jeleń during the first half of the vegetative period becomes evident (from April to July N : P between 1 : 1 and 3 : 1; Fig. 9). On the other hand, if due to N-fixation several tonnes of new nitrogen can be imported annually to the system, an opposite flux should be expected, to maintain nitrogen budget in lake Jeleń balanced. This may be achieved by denitrification of the same order of magnitude as N-fixation.

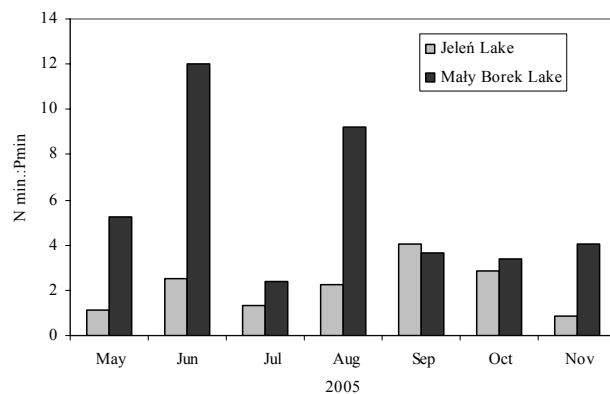


Fig. 9. Inorganic N : inorganic P ratio in epilimnion of lakes Mały Borek and Jeleń in 2005.

Changes in concentrations of various substances, which can be observed in field studies, are only the net effects of a combination of various, partly counteracting processes like biological uptake and mineralization, sedimentation and release, N-fixation and denitrification, etc. Actual rates of these processes can be many times higher than rates of changes of concentrations. Therefore, it is difficult to describe adequately the functioning of a lake ecosystem based only on stock measurements. For this purpose, rate measurements of individual processes are necessary in addition to modelling. Nevertheless, studies on nutrient translocations may help recognize some of the crucial driving factors acting in the ecosystem, indicate peculiarities of a given lake, and help set frames for more detailed investigations.

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