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Plant replacement trend in soft-water lakes with isoetids

by

Rafał P. Ronowski*, Krzysztof Banaś, Marek Merdalski, Józef Szmeja

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University of Gdańsk, Faculty of Biology, Department of Plant Ecology, ul. Wita Stwosza 59, 80-308 Gdańsk, Poland

Abstract

A number of small, shallow inland lakes in the Northern Hemisphere are acidic, soft-water water bodies, mostly fed by precipitation. Some of these lakes are home to *Lobelia dortmanna* and other aquatic macrophytes from the isoetid group. The present study identifies a plant species replacement trend along the main environmental gradient in such lakes, i.e. pH of water.

In 70 lakes covered by the study and ordered along the gradient of increasing alkalinity, bryophytes gradually decline. Their decreasing frequency is 86.8% (pH 4.0), 32.5% (pH 6.5) and < 10% (pH 6.6–9.5). At the same time, the frequency of vascular plants increases from 13.2% in strongly acidic lakes up to 92.8% in alkaline ones. The majority of isoetids usually occur at pH 5.5–6.7, but one of them (*Littorella uniflora*) often (frequency 40.5%) occurs also in eutrophic, alkaline lakes (pH 9.0–9.5), where it forms large populations. In lakes ranked according to the decreasing alkalinity gradient, bryophyte populations have been found to be smaller, while vascular plants become more abundant. The decreasing water acidity leads to partial or total elimination of bryophytes, which are replaced by eutrophilic vascular plants, frequently accompanied by some stonewort species.

Key words: soft-water lakes, alkalinization of lakes, macrophyte replacement

* Corresponding author: rafal.ronowski@phdstud.ug.edu.pl

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Introduction

In the northern and northwestern part of the Northern Hemisphere, a significant fraction of lakes is represented by small and mostly shallow lakes located on the acidic substrate and fed mainly by precipitation. This makes them soft-water lakes, poor in dissolved salts of mainly calcium (< 7.0 mg Ca l^{-1}), usually acidic (pH 4.5–6.7) or only slightly alkaline, oligo- or mesotrophic and highly vulnerable to human activity (Murphy 2002). In some of these lakes, we can observe isoetids (a group of aquatic macrophytes), such as *Isoëtes lacustris* L., *Lobelia dortmanna* L. and *Littorella uniflora* (L.) Asch. (Vestergaard & Sand-Jensen 2000; Chmara et al. 2015). They are included on the IUCN Red List (2015) and in the Red Books in many countries and are protected by law.

In Europe, lakes with isoetids are located on the Scandinavian Peninsula, the British Isles, in France, the Netherlands, Germany and Poland (Hultén & Fries 1986). The EUNIS habitat classification system lists them under code 3110. In Poland, there are about 200 lakes with isoetids (Szmeja 1996) located in Pomerania (NW Poland) in the area of end and ground moraines and outwash. The phytolittoral substrate of such lakes is acidic, mineral and organic, highly hydrated, fairly well oxygenated and lighted, usually free from wind wave pressure or other hydrodynamic forces, located at a depth of 0.3–6.5 m (2.0–5.0). In Poland, most lakes with isoetids are characterized by their location in forest and are protected by law, while others are located in close proximity to cultivated land or buildings and are exposed to intense human activity (Szmeja 2006).

Research on lobelia lakes has a long history and relates mainly to ecophysiology (Sand-Jensen 1978; Sand-Jensen & Borum 1984; Madsen 1985; Boston 1986; Boston et al. 1987) as well as habitat requirements of isoetids (Seddon 1965; 1972; Mäemets 1974; Rørslett 1991; Vöge 1992; Szmeja et al. 1997). There are few studies exploring the structure of submerged vegetation and its transformation caused by environmental factors and anthropogenic pressure.

Specific environmental conditions in lakes with isoetids are subject to alkalinization (Arts 2002), affecting the appropriate carbon content for photosynthesis and disrupting the metabolism (Sand-Jensen 1978; Pulido et al. 2011; Chmara 2014). Our hypothesis is that alkalinization of lakes is responsible for plant species replacement. The exploration of such lakes to date (Chmara et al. 2015) indicates that acidophytic mosses and isoetids may be replaced by some vascular plants and charophytes. Identification of a plant replacement trend that would closely correlate with environmental characteristics of the aquatic environment affected by human impact may contribute to more effective biodiversity conservation within this group of lakes throughout their geographic range.

Materials and methods

Study area and sampling

The study was conducted between 1998 and 2018 in 70 soft-water lakes of northwestern Poland (Fig. 1), where 12 702 plant samples and 38 106 water samples were collected (the latter were collected in places with plants). In each of these lakes, one transect perpendicular to the shoreline was delineated and divided into strips parallel to the shore at 1 m depth intervals. They are referred to as depth zones throughout this study (Fig. 2). In each of the depth zones, a diver randomly delineated 10 to 20 square fields of 0.1 m^2, registered all plants present in these fields, determined their abundance (expressed as % of a sample). Data from such fields are called plant samples in this study.

From each of the bottom zones or depth zones with 1 m intervals, the diver collected three water samples (a total of 1.5 dm^3) 5 cm above the plants or sediment. The water samples were analyzed chemically and physically according to the methods proposed by Hermanowicz et al. (1999) and Eaton et al. (2005). The concentration of calcium, total nitrogen, total phosphorus and humic acids, as well as the hardness of water and its color, pH, redox and conductivity were determined. During the fieldwork, photosynthetically active radiation (PAR), water clarity, water temperature and oxygenation were measured.

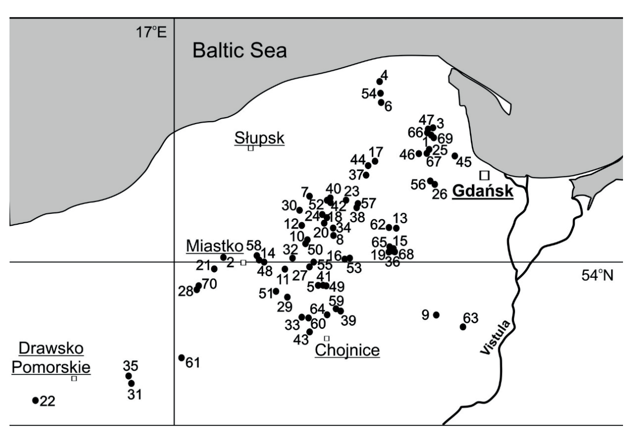

Figure 1

Distribution of the surveyed lakes

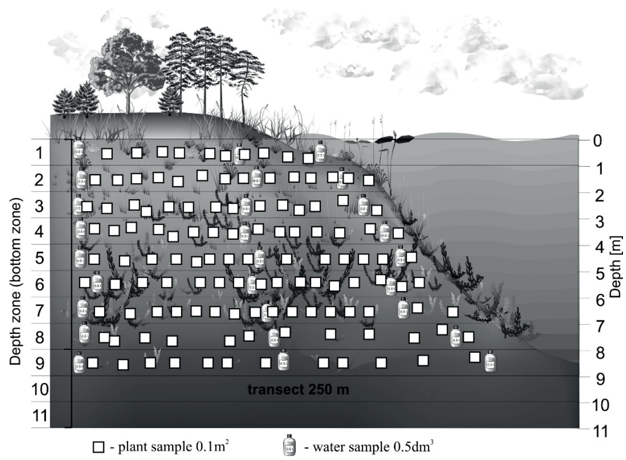

Figure 2

Sampling scheme

The environmental factors were determined in the depth zones as per the following parameters:

1. depth (m) – using NEXUS DEPTH or Eagle TriFinder depth finders;

2. reaction – pH-meter 320/SET1 with a SENTIX 97T measuring electrode;

3. water clarity (m) – Secchi disk with no glass pane on water surface;

4. calcium concentration (mg Ca dm^{-3}) – complexometric titration, titrating 50 dm^3 of water against EDTA disodium, with calconcarboxylic acid as an indicator;

5. water oxygenation (%) and temperature (°C) – WTW OXI 197 oxygen meter with an EOT 196 electrode;

6. general water hardness (mg CaO dm^{-3}) – complexometric titration with Eriochrome Black T as an indicator;

7. humic acid concentration (mg KH dm^{-3}) – spectrophotometrically, using a UV-VIS Aquamate spectrophotometer at 330 nm wavelength;

8. water color (mg Pt dm^{-3}) – a comparative method, using the Platinum-Cobalt Reference Standards;

9. photosynthetically active radiation (PAR, in %) – Licor LI–250 Light Meter, % of the light reaching the water surface;

10. total nitrogen – Merck Spectroquant Cuvette Test;

11. total phosphorus – microwave mineralization in the presence of nitric and sulfuric acids, followed by the determination of total phosphorus using the Merck Spectroquant test for phosphate determination.

Data analysis

The obtained data were entered into a spreadsheet allowing also for species abundance in plant samples and data describing the environmental factors in the depth zones. For plant samples, species diversity was calculated using the *H'* index (Shannon & Weaver 1949; Huston 1996) according to the formula: $H' = -\Sigma[(mj/m) \times \log mj/m]$, where: *mj* – abundance of species *j* in a sample [%], *m* – abundance of all plants in a sample. The frequency of species in plant samples (*F*, in %; 100% = 12 702 samples), as well as the frequency of species groups (mosses, stoneworts, vascular plants, isoetids) and the contribution of specific species to the vegetation as a quotient of the abundance of a given species and the abundance of other species in samples (S, %) were also calculated.

Relationships between the relative abundance of a given species in the vegetation and pH of water near the sediment were determined by the Kruskal–Wallis non-parametric test (Sokal & Rohlf 2012). The frequency of species was calculated from the quotient of their occurrence in the samples. The relationship between the frequency and abundance of plants and the environmental factors was determined by multiple regression and canonical analysis (Gittins 1985; ter Braak 1987). The data included in the analyses were standardized in CANOCO 4.5 (ter Braak & Šmilauer 2002).

Detrended correspondence analysis (DCA) showed that all data on plant abundance and water properties were linear in their structure and represented only a part of the Gaussian distribution (eigenvalues < 2 SD), which required the use of redundancy analysis RDA (ter Braak & Šmilauer 2002). By using the redundancy analysis (RDA; ter Braak 1986; 1987; 1988), we correlate the frequency and abundance of plants with the physicochemical properties of water. Before the analysis, Spearman's rank correlation coefficient (R) was calculated to determine strongly correlated variables. And thus, the following parameters were removed from the RDA analysis: water color, as it was strongly correlated with water clarity (*R* = 0.78), depth and temperature, as they were strongly correlated with PAR (*R* = 0.74), calcium concentration and water hardness, as they were strongly correlated with water conductivity (0.85 and 0.89, respectively). The data were standardized and focused, yet not transformed, on species. The statistical significance of the environmental variables was tested using the Monte Carlo permutation test with 999 permutations.

Results

Frequency, diversity and abundance of plant species groups

A total of 71 species of macrophytes were identified in 12 702 plant samples collected from 70 soft-water lakes with isoetids: 41 vascular plants, including four isoetids, 19 mosses and 11 stoneworts (Table 1). Twenty-two plant species occurred with a frequency (*F*) higher than 1% in the total number of samples (Table 1). The most frequent were vascular plants (present in 6481 samples; *F* = 51.0%), followed by isoetids (4159; *F* = 32.7%), bryophytes (3789; *F* = 29.8%) and stoneworts (2432; *F*=19.1%).

Mosses are the main constituent of submerged vegetation in acidic lakes (pH 4.0–5.5), with usually one species prevailing in a sample (1.0 ± 1.0 species 0.1 m^{-2}). The moss cover is very dense and may reach more than 90%, especially when pH is low. When pH of water is 4, the moss cover is 30.2 ± 41.0%. In waters with neutral to alkaline pH, the number of moss species and their cover gradually decrease. Moreover, species of the genus *Sphagnum* are replaced by other mosses, such as *Fontinalis antipyretica* (Figs 3 & 4). Bryophytes do not occur when pH of water becomes higher than 8.

Vascular plants occur throughout the whole pH range (4.0–9.5). In acidic lakes, the number of species is small, on average 0.6 ± 0.4 species 0.1 m^{-2}. However, as pH increases, the number of species gradually increases and reaches the highest level in alkaline lakes (pH > 8.5). The number of species in such water bodies increases up to 1.9 ± 1.1 species 0.1 m^{-2}. The cover of vascular plants in acidic waters is similar to other plant groups and increases only in alkaline waters, reaching the highest values (40.8 ± 37.8%) at pH = 9.

Like other vascular plants, isoetids occur at pH 4.0–9.5, but the largest number of species (0.7 ± 0.8 species 0.1 m^{-2}) occurs in the pH range of 5.5–6.7. One of the isoetid species (*Isoëtes echinospora*) occurs only in acidic water (pH 4.5–6.0), while the others occur in a much wider pH range. One of the four identified isoetid species, *Littorella uniflora*, forms large populations also in highly alkaline conditions (pH 9.0; Figs 4 & 5).

Few stonewort species occur in soft-water lakes (0.6 ± 0.7 species 0.1 m^{-2}). The largest populations of these plants occur at pH 6.5–8.5 (Fig. 3). Stoneworts do not occur in low pH waters, while their relative abundance in submerged vegetation is negligible when pH is higher than 8.5. The abundance of stoneworts is small and they reach the highest cover (11.4 ± 25.6) in waters with neutral or alkaline pH (7–8.5).

Plant species diversity expressed by the *H′* index is small (Fig. 6). The *H′* values along the increasing pH gradient of water are contained within a narrow

Table 1

Examined species of macrophytes with frequency of over 1%; F – average value of species frequency in the whole pH range and P – average value of species coverage in the whole pH range

Bryophytes	F	A	Stoneworts	F	A	Vascular plants excluding isoetids	F	A	Isoetids	F	A
Sphagnum denticulatum	14.1	25.8	*Chara delicatula*	8.4	15.5	*Myriophyllum alterniflorum*	19.0	15.2	*Isoëtes lacustris*	27.4	35.0
Fontinalis antipyretica	12.0	12.7	*Chara fargilis*	6.1	32.5	*Elodea canadensis*	12.4	12.8	*Lobelia dortmanna*	13.5	21.8
Warnstorfia exannulata	7.9	7.6	*Nitella flexilis*	3.6	3.2	*Potamogeton obtusifolius*	2.1	2.3	*Littorella uniflora*	8.6	33.3
Drepanocladus sordidus	7.0	9.7	*Nitellopsis obtusa*	1.7	6.1	*Myriophyllum spicatum*	1.8	7.1	*Luronium natans*	2.9	28.8
Fontinalis delecarlica	3.6	12.0	*Nitella gracilis*	1.1	12.3	*Ceratophyllum demersum*	1.6	7.6	-	-	-
Drepanocladus aduncus	1.4	8.8	-	-	-	*Potamogeton natans*	1.1	6.8	-	-	-
Sphagnum fallax	1.1	40.6	-	-	-	-	-	-	-	-	-

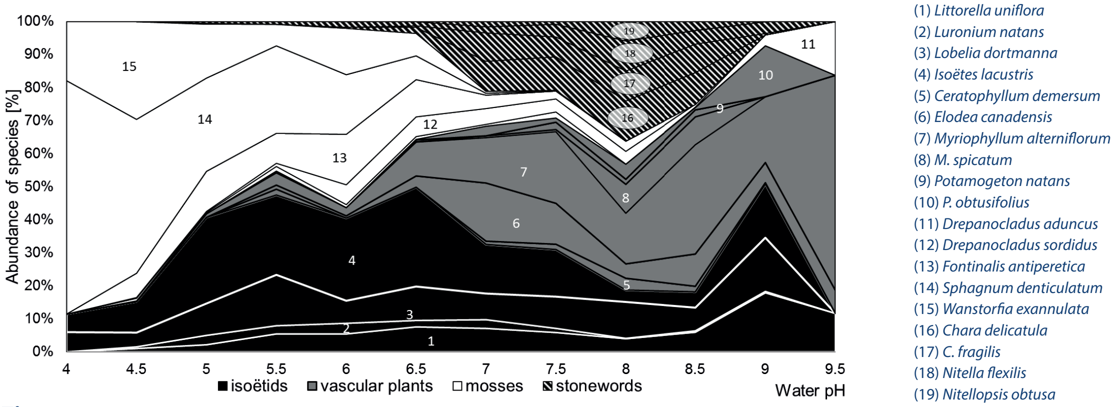

Figure 3

Abundance of plant species in the water pH gradient

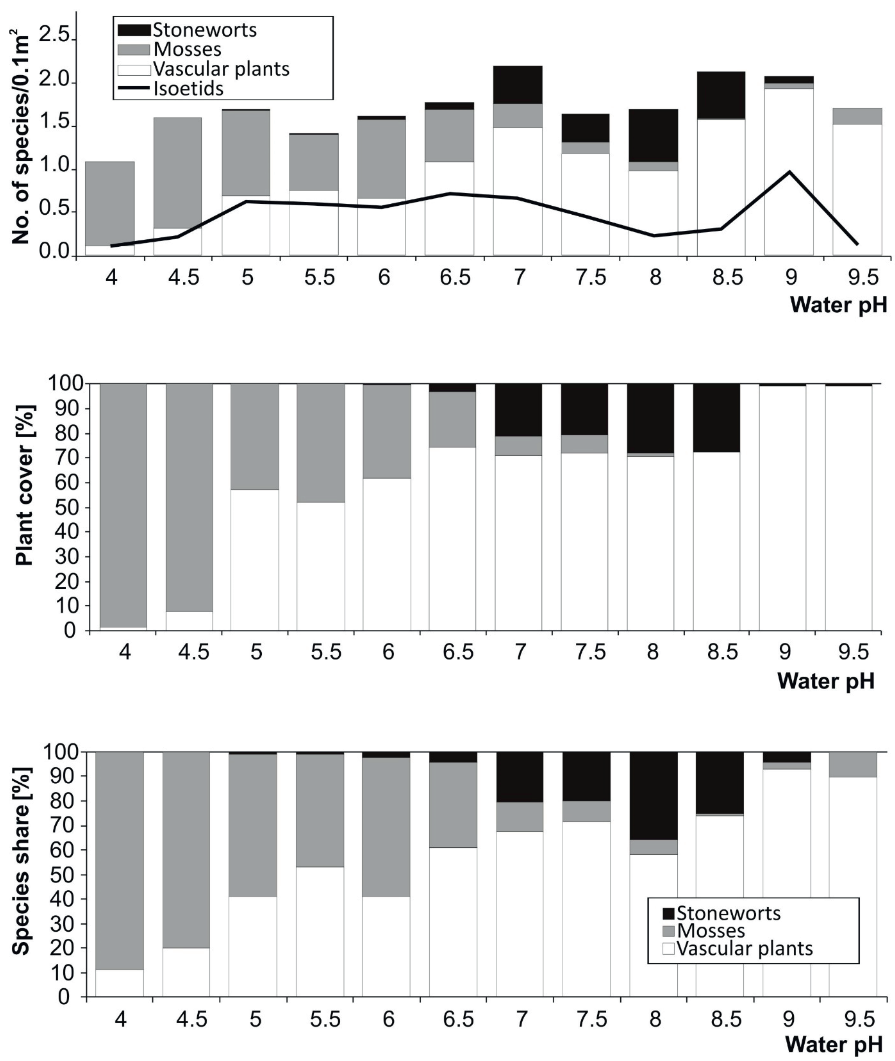

Figure 4

Number of species groups in 12 702 samples (mosses, stoneworts, vascular plants, isoetids; upper graph), their percentage (middle graph) and abundance of plants (bottom graph) in the water pH gradient.

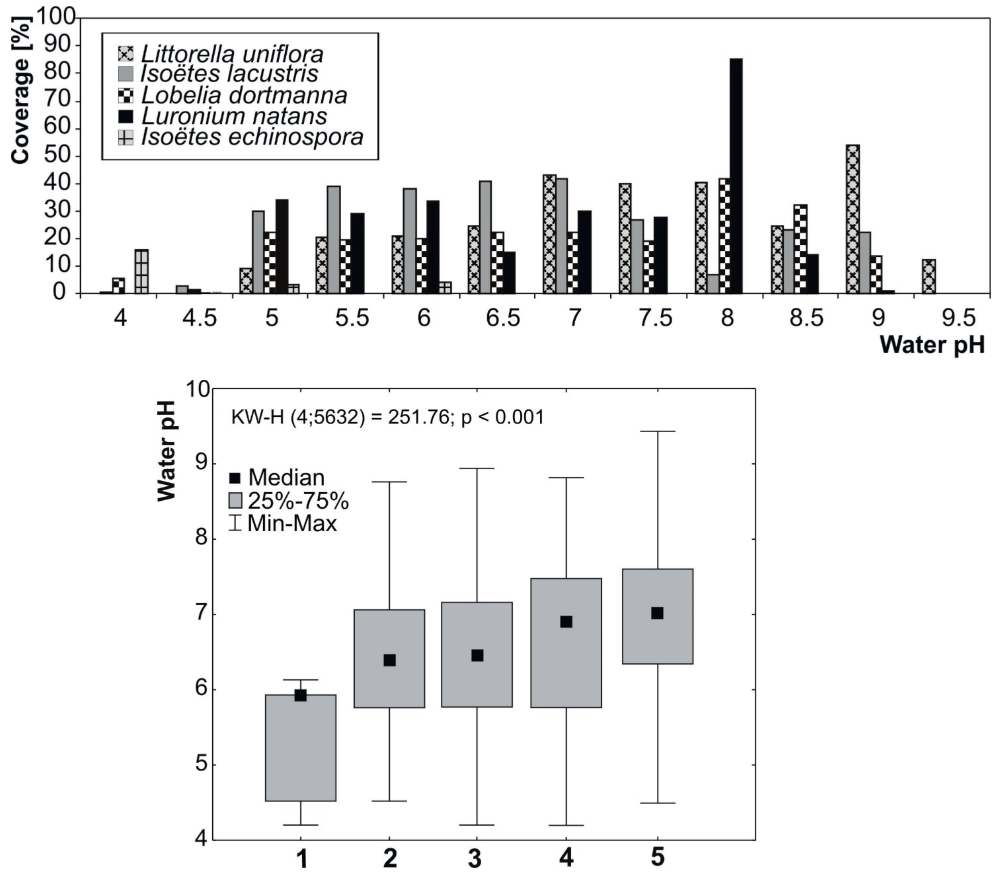

Figure 5

Relationship between water pH and occurrence of isoetid species (1 – 5) in lakes (bottom chart), where: 1 – *Isoëtes echinospora*, 2 – *Luronium natans*, 3 – *Isoëtes lacustris*, 4 – *Lobelia dortmanna*, 5 – *Littorella uniflora* and abundance (coverage) of isoetids in the water pH gradient (upper chart)

range of 0.2–0.4, but the differences are statistically significant ($p < 0.001$). The most statistically significant differences occur in low pH values (pH from 4 to 6),

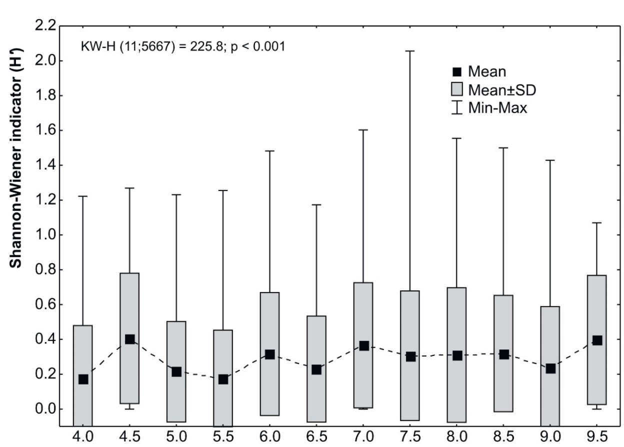

Figure 6

Species diversity along the gradient of water alkalization

and the number of statistically significant differences decreases with increasing pH (Table 2). However, there is no trend in the variation of *H′* in the pH range of 4.0–9.5. The low value of the *H′* index results mainly from the small and fairly similar number of species in the samples and the similar structure of submerged plant communities throughout the gradient, usually dominated by a single bryophyte or vascular species.

Relationship between plant species and environmental factors

The pH of water is a characteristic of the aquatic environment of soft-water lakes with isoetids, which significantly affects the occurrence and abundance of submerged plant species (Fig. 7, Table 3). Other characteristics determining the conditions for the occurrence of plants in lakes, such as PAR, conductivity and water clarity, should also be noted.

The Monte Carlo Test showed that PAR and pH account for most of the variance (lambda 1 in Marginal

Table 2

Differences in the Shannon–Wiener index (*H'*) in different pH ranges (see Fig. 6)

	Shannon–Wiener index (*H'*)											
Mean	0.17	0.41	0.21	0.18	0.32	0.23	0.37	0.31	0.31	0.32	0.24	0.40
SD	0.31	0.37	0.29	0.28	0.35	0.30	0.36	0.37	0.39	0.33	0.35	0.37
pH	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5
4.0		***	-	-	***	*	***	***	***	***	-	*
4.5			***	***	-	***	-	**	*	-	*	-
5.0				-	***	-	***	**	-	**	-	-
5.5					***	-	***	***	***	***	-	-
6.0						*	-	-	-	-	-	-
6.5							***	-	-	-	-	-
7.0								***	**	-	**	-
7.5									-	-	-	-
8.0										-	-	-
8.5											-	-
9.0												-

p > 0.05; * p < 0.05; ** p < 0.01; *** p < 0.001 (post-hoc Dunn's test).

Table 3

Results of RDA analysis of the relationship between plant species and water characteristics in soft-water lakes with isoetids

Axes	1	2	3	4	Total variance
Eigenvalues	0.123	0.020	0.013	0.001	1.000
Species-environment correlations	0.474	0.397	0.377	0.175	
Cumulative percentage variance					
of species data	12.3	14.3	15.6	15.7	
of species-environment relation	77.5	90.3	98.4	99.2	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.158

Effects is 0.06 and 0.02, respectively), but once the environmental variables are successively included in the model (Conditional Effects), PAR accounts for 0.06 of the variation in the vegetation traits, temperature accounts for 0.05, while pH accounts for 0.02 of the variation. The remaining environmental characteristics, although statistically significant, are less important.

The occurrence of isoetids as a species group is largely affected by factors correlated with the first axis (mainly PAR), but it is the factors correlated with the second axis, mainly pH, that have a decisive impact on the occurrence of individual species. *Littorella uniflora* is positively correlated with pH, while *Isoëtes lacustris* correlates negatively.

As far as other species groups are concerned, mosses are associated with high water acidity, while stoneworts are associated with low acidity. The effect of pH on the number of mosses and stoneworts is greater than on the abundance (cover) of their populations. The above analysis indicates that the main course of species turnover along the water pH gradient involves the replacement of mosses by stoneworts, leading to a minor transformation within the group of vascular plants, including isoetids.

Plant species replacement trend in soft-water lakes with isoetids

Mosses occur with the highest frequency in acidic (pH 4.0–6.5) water (Figs 3, 4). *Sphagnum denticulatum* dominates (frequency 69.3%) at pH 4.0–5.0 and is often accompanied by *Warnstorfia exannulata*, less frequently by *Sphagnum fallax* (frequency below 12%). Isoetids are common in such conditions, especially *Isoëtes lacustris* (F = 28.5%), *Lobelia dortmanna* (16.1%) and *Luronium natans* (2.9%).

The first signs of species turnover were observed at low water acidity – pH 6.6–7.5. In plant samples from such lakes, an increase in the frequency of mosses other than those mentioned above, mainly of *Drepanocladus sordidus*, *Fontinalis antipyretica* and *F. delecarlica*, was observed. Their frequency is high in the pH range of 6.0–7.5, while the contribution of mosses to the structure of submerged vegetation is

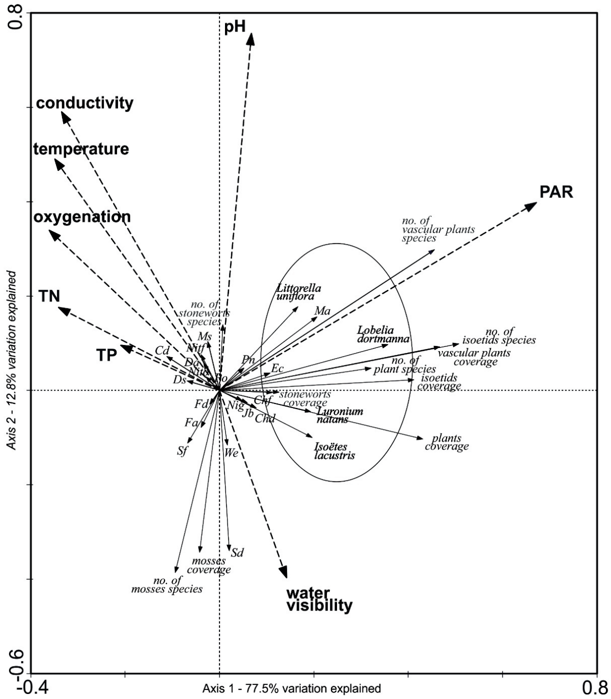

Figure 7

Model of the relationship between plant species and water parameters in soft-water lakes with isoetids, ordered by the RDA method

Abbreviations: TP – total phosphorus, TN – total nitrogen, PAR – photosynthetically active radiation; vascular plants: Cd – *Ceratophyllum demersum*, Ec – *Elodea canadensis*, Ma – *Myriophyllum alterniflorum*, Ms – *Myriophyllum spicatum*, Pn – *Potamogeton natans*, Po – *Potamogeton obtusifolius*; mosses: Da – *Drepanocladus aduncus*, Ds – *Drepanocladus sordidus*, Fa – *Fontinalis antipyretica*, Fd – *Fontinalis delecarlica*, Sd – *Sphagnum denticulatum*, Sf – *Sphagnum fallax*, We – *Warnstorfia exannulata*; stoneworts: Chd – *Chara delicatula*, Chg – *Chara globularis*, Nif – *Nitella flexilis*, Nig – *Nitella gracilis*, Nito – *Nitellopsis obtusa*

relatively small, in terms of phytolittoral coverage, and does not exceed several percent.

The second stage of species replacement was identified in waters with relatively high alkalinity (pH 7.5–9.5). Almost all mosses, as well as isoetids and stoneworts were replaced (Figs 3, 4). Their habitats were occupied by vascular plants. At pH close to neutral, *Elodea canadensis* (F = 17.2%) and *Myriophyllum alterniflorum* accounted for the largest relative abundance; their coverage can be as high as 54.9%, especially when pH of water is very high. At water pH ≥ 8, other species of vascular plants may occur, such as *M. spicatum* or two pondweed species (Table 1). Interestingly enough, *Myriophyllum alterniflorum*, as a species typical of lobelia lakes continues to dominates. Stoneworts occur when pH is 6.5–8.5, but their highest relative abundance is observed in waters with pH above 7. The frequency of *Chara delicatula*, *Chara globularis* and *Nitella flexilis* was very similar (below 12%), while the contribution of *Nitellopsis obtusa* was much smaller and did not exceed 5.9%. *Nitella gracilis* associated with neutral waters (pH 6–7.5) occurred with a low frequency (F ≤ 1.1%). Stoneworts are a group of plants occurring at pH ranging from 6.5 to 8.5, which implies their narrow ecological range. Only one of all isoetids is capable of growing in water with high reaction, i.e. *Littorella uniflora*, which occurs more often in waters with neutral or alkaline reaction and its frequency may be high (17.7%) even at water pH equal to 9. The occurrence of other isoetid species is limited to waters with low reaction. It is also noteworthy that the analyzed H' index does not show the total species replacement along the pH gradient. Individual species of bryophytes and isoetids, such as *Isoëtes lacustris* and *Littorella uniflora*, are eliminated and replaced by eutrophilous species of vascular plants.

Discussion

Soft-water lakes with isoetids (or so-called lobelia lakes) are included in the EU Habitats Directive, entry 3110, in the Natura 2000 network (Kolada et al. 2017). They are of great natural value due to specific characteristics of the aquatic environment and the occurrence of rare plant species from the isoetid group, such as *Lobelia dortmanna*, *Isoëtes lacustris*, *I. echinospora*, *Luronium natans* and *Littorella uniflora*. These are species of special concern in the European Union and are included on both national and regional Red Lists and on the list of threatened species published by the International Union for Conservation of Nature (IUCN). In Europe, lakes with isoetids are mainly located in its northern and northwestern parts and in north and northwest of Central European Russia (Jalas & Suominen 1972; Hultén & Fries 1986). Some of these lakes in Europe are located in the mountains (the Alps, the Scandes, the Massif Central, the Pyrenees, the Vosges), 600–2300 m above sea level (Tison & de Foucaul 2014). In Poland, lakes of this type have been sensitive to intense human activity since the mid-20th century (Szmeja et al. 1997). Some of them have undergone eutrophication, other acidification, often as a result of excessive supply of humic substances from drained peatlands in the past (Banaś 2016). Research on the number of plant species, the size of their populations and the diversity of their communities has shown that pH of water and sediment is an important factor affecting the submerged vegetation in such lakes (Szmeja 1992; 2006). It is also important that a group of such lakes (unfortunately increasingly large in Poland) is subject to anthropogenic eutrophication, usually accompanied by alkalinization. Each of these processes interferes with the concentration of inorganic carbon and its availability for photosynthesis (Bowes 1987; Wetzel 1990), which has a negative impact on the populations of isoetids and bryophytes (Szmeja 2010). One of the effects presented in this study involves plant species replacement along the increasing gradient of water alkalinity (Figs 3, 4). Plant turnover leads to shrinking populations of acidophilic bryophytes and some isoetids (*Isoëtes lacustris* and *Luronium natans*), to a lesser extent of *Lobelia dortmanna* and *Littorella uniflora*, and to an increase in the number and abundance of non-isoetid vascular plants (Fig. 3). High alkalinity of water (pH 8.0–9.0) creates optimum conditions for photosynthesis and growth of eutrophilic vascular plants (Madsen & Sand-Jensen 1991; Madsen & Maberly 1991; Frost-Christensen & Sand-Jensen 1995). It is worth noticing that in the lakes under study, with varying pH values, various populations dominated by specific groups of species are formed. Isoetids and bryophytes dominate in acidic waters, isoetids and stoneworts dominate in waters with neutral reaction, while vascular plants, including *Myriophyllum alterniflorum*, *M. spicatum*, *Elodea canadensis*, *Potamogeton obtusifolius* and *Nitellopsis obtusa*, dominate in waters with high pH (< 8). This may suggest that species turnover, as described above, occurs in isoetid lakes that are subject to pH changes (alkalinization or acidification; Gos & Banaś 1999).

As a result of environmental changes caused by pH fluctuations, light intensity in water decreases, massive growth of plankton and epiphytic algae becomes more frequent, while the boundaries of areas occupied by sediment-rooted plants are shifted toward the littoral zone (Szmeja 1992; Banaś et al. 2012). In these conditions, populations of submerged macrophytes disperse and disintegrate (Szmeja & Bociąg 2004; Bociąg et al. 2013).

Apart from the reduced light availability, which could have a negative impact on the occurrence and abundance of individual macrophyte species, other environmental parameters are also very important. The research confirms that oxygenation also plays a significant role. A decrease in the oxygen level leads to the withdrawal of all species from their habitat, irrespective of the group to which they belong. It can therefore be said that it is likely that none of the species under study is able to cope with a significant decrease in water oxygenation.

Another important factor is conductivity, which reflects the content of calcium salts in water, varying along with pH. As conductivity increases, vascular plants are favored, particularly those that acquire carbon for photosynthesis from the breakdown of hydrocarbons, thus they cope better in waters with a higher content of calcium, carbonates and pH fluctuations compared to bryophytes, stoneworts, and isoetids, which quickly withdraw under such conditions.

The specificity of the surveyed water bodies is also important. Isoetid lakes have low pH, which results in their low buffering capacity, thus making them less susceptible to adverse external impact compared to lakes with harder water and higher reaction. It could therefore be assumed that pH, which is the product of many chemical parameters, is largely responsible for the resistance of individual water bodies to environmental changes (Szmeja 2006). Furthermore, the trophic status of these lakes is equally important. These are oligotrophic water bodies where – as shown by the research (cf. Fig. 6) – the content of total nitrogen and phosphorus is insignificant in terms of the occurrence and abundance of individual plant species compared to other types of lakes (Banaś 2016).

Nevertheless, it is important to bear in mind that natural succession of lakes largely affects underwater conditions and may be a determinant of the occurrence of individual species. It determines environmental conditions (Siraj et al. 2011; Feldmann 2012), causes disruption of interspecific relations (Mitchell & Perrow 1998; Szmeja 2010; Szmeja et al. 2010) and transformation of plant communities (Chmara et al. 2013).

Nearly half of the soft-water lakes with isoetids in Poland are located in forest and are under protection. The remaining lakes are, to a varying extent, affected by human activity, especially in the vicinity of towns and cities. Anthropogenic plant species replacement in soft-water lakes with isoetids is common and should be monitored.

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