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ECOLOGICAL CONDITIONS AND TOLERANCE LIMITS OF ISOETIDS ALONG THE SOUTHERN BALTIC COAST

ABSTRACT: The paper describes the limits of ecological conditions tolerated by submerged aquatic plants of the isoetid group (*Isoëtes lacustris* L., *Littorella uniflora* (L.) Aschers. and *Lobelia dortmanna* L.) along the Southern Baltic. Investigations were carried out in 74 lakes, grouped according to the geographical criterion, vegetation in the catchment areas and human pressure. It has been demonstrated that *Littorella* tolerates the widest range of water pH (pH 4.5–9.4), Ca (2.8–32.6 g m⁻³), and total-P (27–620 mg m⁻³). *Isoëtes* withstands total-P concentra-

tions of up to 220 mg m⁻³, *Lobelia* only to 100 mg m⁻³. In lakes with *Littorella* and *Isoëtes* the limits of maximum total-P concentrations are outside the range tolerated by *Lobelia*. Isoetids have become extinct in lakes in which the water pH is permanently below 4.5. *Littorella* is the most resistant to increased water hardness and total-P concentrations, owing to which it best tolerates the effects of lake calcification and eutrophication.

KEY WORDS: lakes, habitat conditions, macrophytes, isoetids, *Isoëtes lacustris*, *Littorella uniflora*, *Lobelia dortmanna*.

1. INTRODUCTION

Isoetid lakes are widespread in northern America, Europe and northern Asia, and in the mountain region of southern America (Hultén and Fries 1986). They also occur in New Zealand (Brown 1975, Ward and Talbot 1984). With a few exceptions, e.g. mountain and volcanic lakes, they are found in the zone of the last glaciation.

In northern Europe, the range of these lakes is determined by the appearance of

Isoëtes lacustris L., *Littorella uniflora* (L.) Aschers. and *Lobelia dortmanna* L. These species occur primarily in postglacial lakes in Sweden, Norway, Finland, Estonia, on Danish islands, the British Isles, in north-western Poland and Ireland. They are less frequent in the natural lakes of North-West Germany (Vöge 1992), Spain (Ballesteros et al. 1989) and France (Szmeja and Clément 1990). There is extensive literature on the distribution

of isoetids in Europe (e.g. Klinsmann 1843, Caspary 1886, Lohammar 1938, Maristo 1941, Seddon 1965, Spence 1967, Farmer and Spence 1986, Mäkirinta 1989, Rørslett and Brettum 1989, Szmeja 1996a). There is also plenty of information on the ecophysiology of isoetids (e.g. Sand-Jensen 1978, Sand-Jensen and Borum 1984, Madsen 1985, Boston 1986, Boston et al. 1987), but much less on the habitat requirements of particular species in various areas of their global or regional distribution (Seddon 1965, 1972, Mäemets 1974, Rørslett 1991, Vöge 1992). It is important to develop geobotanical studies, as in the future, active protection of species will most likely consist of restoration of the optimum habitat conditions and introduction of these species into other lakes.

The aim of the present studies was to determine the ranges of the primary

and secondary (anthropogenic) parameters of chemical and physical properties of the water in lakes with isoetids (*Isoëtes lacustris*, *Littorella uniflora* and *Lobelia dortmanna*) along the Southern Baltic. It was also intended to study the range of the species tolerance by these species of the habitat conditions indicated by the characteristics of the surface and near-bottom water.

It has been assumed in the study that the physical and chemical characteristics of lake water are to some extent determined by the soils and vegetation of the catchment areas, as well as by anthropogenic activity, as exemplified by agriculture, forest management and urbanization of the edge zones. The data presented come from North-Western Poland and are representative of areas located along the Southern Baltic. These data can be useful in conservational work and comparative analyses of similar lakes found in other areas within their global range.

2. MATERIAL AND METHODS

Along the Southern Baltic about 160 isoetid lakes can be found, including 151 in Pomerania (North-Western Poland) (Szmeja 1996a) and several in North-Eastern Germany (Krausch 1985, Vöge 1992). In Pomerania, they represent 4.5% of lakes larger than 1 ha in surface area. Most of them are located in the central part of the region, on terminal-moraine ridges, among acid soils occupied by beech and oak forests. A large group of lakes is also found in the southern part of Pomerania, in outwash-plain soils overgrown with pine forests. There are only 14 such lakes in the western part of Pomerania. They are usually fairly large, deep and situated in beech or oak forests. In North-Eastern Germany, that

is, west of Pomerania, there are only a few such lakes left. In Mecklenburg-Vorpommern *Isoëtes lacustris* and *Lobelia dortmanna* have already become extinct, while *Littorella uniflora* is seriously threatened (Ingelög et al. 1993). In the Schleswig-Holstein region there are still 5 lakes of this type, but their natural diversity is vanishing (Vöge 1992).

The studies were carried out in 74 lakes in Pomerania. The aims of research were to describe the physical and chemical characteristics of the water in lakes selected at random from the whole region (Fig. 1). Also, some data from the papers of Szmal (1959), Szmal Z. and Szmal B. (1965), Kraska et al. (1994, 1995) and Kłosowski (1994)



Fig. 1. Distribution of isoetid lakes along the southern Baltic

have been used. Only those lakes were chosen for study in which *Isoetes lacustris*, *Littorella uniflora* and *Lobelia dortmanna*, or at least one of these species, occurred.

Investigations were carried out on the surface of the water and immediately above the lake bottom, at the deepest point. On the surface, the following parameters were measured: pH, conductivity, hardness and calcium concentration. Above the bottom, free CO_2 , total-P and total-N concentrations were determined.

The pH was measured with a Beckman $\phi 50$ pH-meter, conductivity with an LF 95 conductometer containing a TetraCon 96 electrode, and total-P (in mineralized samples) and total-N were determined spectrophotometrically (Hermanowicz et al. 1976). Hardness, concentrations of free CO_2 and Ca were determined by titration (Golterman 1969). The ecological range of isoetids was established on the basis of the ranges, tolerated by the particular species, of pH, conduc-

tivity, concentrations of calcium, total-P and total-N in the water.

The lakes under study have been classified according to: 1. geographical position; 2. kind of vegetation in the catchment area; 3. form of human pressure. In accordance with the geographical criterion, the following lake groups have been distinguished: a) western, b) southern; c) central and eastern parts of Pomerania (Fig. 1). In relationship to the vegetation of the catchment areas, the lakes have been classified as those located in: a) pine forests, b) oak forests, c) beech forests and hornbeam forests. Only lakes without clear signs of human pressure were used for comparison. The forest-kind sequence: pine–oak–beech–hornbeam forests is concordant with the gra-

dient of increasing tropical state of the habitats. The surface area of the different forest types, in a belt 100 m wide around each of the lakes, has been examined by cartographical methods. The forest communities have been identified according to Matuszkiewicz (1984 a).

Lakes with an evident anthropogenic impact have been classified as: mid-field water bodies, lakes located in rural built-up areas, and mid-forest lakes. Dominant in the catchment areas of the latter group are planted pine forests in habitats which were previously deciduous forest. The proportions of farmlands, built-up areas and planted forests in the catchment areas have been determined by cartographic methods.

3. RESULTS

3.1. DIVERSITY OF LAKES

The range of physical and chemical characteristics of the lakes is wide (Table 1). The pH of the 109 lakes studied ranges from very acid (pH 4.5) to highly alkaline (pH 9.4), the number of weakly acidic to acidic lakes (pH < 7) being almost as large as that of alkaline ones (Fig. 2). Very acid lakes (pH 4.5–

5.5) constitute 15 %, moderately acid ones (pH 5.6–6.5) 19.4%. Acid water (4.5–6.5) is found in 34.4% of the water bodies, of which almost all lie in forests. Lakes with a pH range of 6.6–7.5 represent 34.2%, with pH 7.6–8.5 – 25.8%. The latter usually adjoin farmlands. The pH of over a half of the lakes (62%) ran-

Table 1. Physical and chemical characteristics of the surface and near-bottom water*
N – number of lakes studied; SD – standard deviation

	N	Mean ± SD	Median	Range
pH	109	6.9 ± 1.2	6.9	4.5–9.4
Conductivity [$\mu\text{S cm}^{-1}$]	74	75.3 ± 42.8	63.0	23–224
Ca [g m^{-3}]	84	8.3 ± 6.7	5.9	2.0–32.6
Hardness [g CaO m^{-3}]	38	4.7 ± 11.9	9.9	3.2–55.2
*CO ₂ [g m^{-3}]	62	14.9 ± 8.2	14.5	1.5–39.0
*P _{tot.} [mg m^{-3}]	50	81.3 ± 105.0	46.0	27–620
*N _{tot.} [g m^{-3}]	50	1.7 ± 0.8	1.4	0.6–3.9

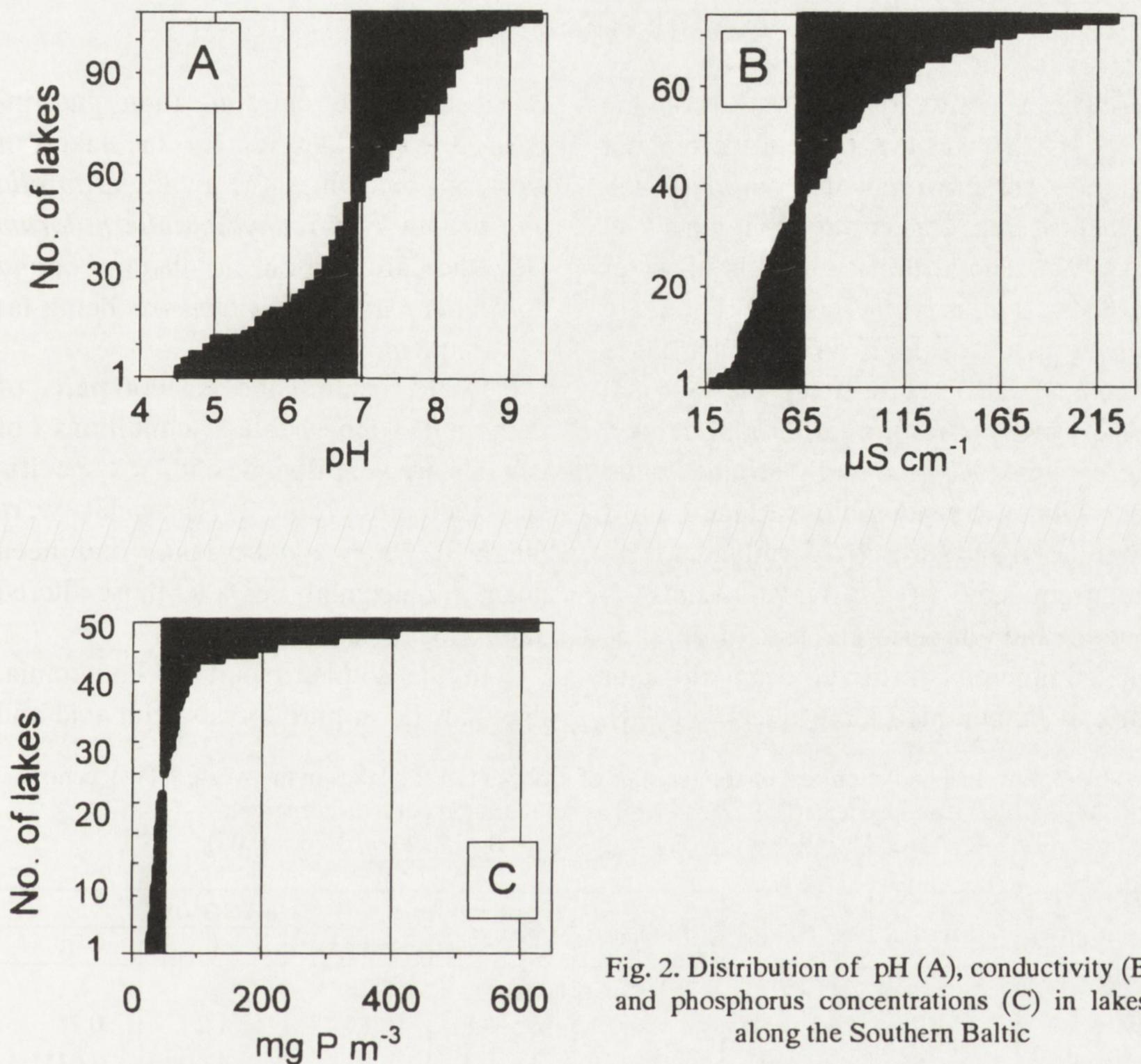


Fig. 2. Distribution of pH (A), conductivity (B) and phosphorus concentrations (C) in lakes along the Southern Baltic

ges from 6.6 to 8.5. About 5.5% of the lakes contain water with a pH > 8.5. Almost all of them adjoin farmsteads.

Conductivity, calcium concentration and hardness are within the ranges typical of softwater lakes. Free CO_2 concentration in the near-bottom water is not high and depends on the pH, hardness and trophic state of the latter. Total-P and total-N concentrations range from values typical of oligotrophic lakes to values found in eutrophic water bodies.

In lakes without any apparent signs of anthropopressure, in the following referred to as "natural", the range of variation of the habitat conditions is narrower than in anthropogenically altered lakes (Fig. 2). Natural lakes have a pH

range of 5.5–8.7, conductivity of 45–160 $\mu\text{S cm}^{-1}$ and concentrations of: Ca 5.0–30 g m^{-3} , free CO_2 3.0–22.9, total-N 0.6–3.4 g m^{-3} and total-P 30–400 mg m^{-3} . We assume that such ranges occurred originally in isoetid lakes along the Southern Baltic.

Human pressure causes a widening of the habitat conditions. Acidification of forest soils results in a pH shift from 5.5 to 4.5 and a free CO_2 concentration decrease from 3.0 to 1.5 g m^{-3} . In anthropogenically eutrophic lakes the concentration of total-P exceeds 400 mg m^{-3} , coming up to as much as 950 mg m^{-3} , while the water reaction is shifted towards a highly alkaline level, ranging from pH 8.8 to 9.4.

3.2. GEOGRAPHICAL DIVERSIFICATION OF THE LAKES

The specific characteristics of the lakes of the western part of Pomerania (Fig. 1) are greater water hardness and higher calcium concentration (B a n a ś et al. 1997). The arithmetic means of water hardness and calcium concentration are almost twice as high as in other lakes (Table 2). This results from the fact that these water bodies are larger and deeper, more intensively fed with ground water and with a considerable surface runoff from limed and fertilized farmlands. Here the frequency of cultivated fields is higher, and the farmers use more lime and commercial fertilizers than in other parts of Pomerania (K o w a l s k i 1994).

Because of the eutrophication and increased water hardness of the lakes of western Pomerania, it is mainly *Littorella uniflora* and *Myriophyllum alterniflorum* DC. that are present in them, *Lobelia dortmanna* and *Isoetes lacustris* being far less frequent.

In the central and eastern parts of Pomerania the habitat conditions of isoetids are very diverse and lack specific characteristics (Table 2). These data were obtained when all the lakes had been taken into account, i.e., also those altered anthropogenically.

In the southern part of Pomerania, the lakes lie in pine forests with acid and

Table 2. Physical and chemical characteristics of the water of the lakes in the western (W), central and eastern (C & E), as well as southern (S) parts of Pomerania
ANOVA: *W ↔ C & E; **C & E ↔ S; ***W ↔ S. ($\alpha = 0.05$)

Lake group	Mean	SD	Median	Range	ANOVA		
					d.f.	F	P
pH							
W	7.4	1.5	8.0	4.5–8.8	86	1.2	0.2*
C & E	7.0	1.0	7.0	4.6–9.4	97	4.4	0.04**
S	6.5	1.6	6.6	4.5–8.4	30	2.5	1.2***
Conductivity [$\mu\text{S cm}^{-1}$]							
W	88.0	52.5	77.0	23–189	56	1.5	0.2
C & E	70.5	38.3	60.0	25–205	76	0.4	0.5
S	65.0	37.6	50.0	26–171	39	2.6	0.1
Ca [g m^{-3}]							
W	13.9	12.4	11.7	2.2–29.0	71	7.2	0.009
C & E	7.4	5.9	6.0	2.0–32.6	89	0.4	0.5
S	7.3	6.0	5.5	2.0–18.8	38	7.8	0.05
Hardness [g CaO m^{-3}]							
W	22.4	19.1	19.2	3.2–55.2	31	6.5	0.016
C & E	11.1	6.4	8.6	4.9–31.9	26	0.2	0.7
S	9.5	7.3	6.0	4.5–17.9	10	4.2	0.03
$\text{P}_{\text{tot.}}$ [mg P m^{-3}]							
W	107.0	116.0	59.5	34–405	39	0.2	0.6
C & E	86.3	118.7	52.0	27–622	40	1.3	0.3
S	44.5	16.1	43.0	28–80	20	3.2	0.09
$\text{N}_{\text{tot.}}$ [g m^{-3}]							
W	1.7	0.7	1.4	1.1–3.0	39	1.2	0.3
C & E	2.0	1.0	1.7	0.6–3.9	40	8.2	0.007
S	1.1	0.4	1.1	0.6–1.9	20	4.5	0.05

barren sand soils. The arithmetic means of the particular traits of the water are lower here than in other regions (Table 2). The differences between these lakes and those found in the central and eastern parts of Pomerania are statistically insignificant.

To sum up, only lakes located in the western part of Pomerania have a clear regional specificity, additionally highlighted by anthropogenic impacts. The differences between the lakes of the remaining two regions are insignificant statistically.

3.3. EFFECT OF THE CATCHMENT AREA VEGETATION

Isoetid lakes are found in pine, oak, beech and hornbeam forests. Such forests are dominant not only in the catchment areas of lakes, but also throughout Pomerania.

The specific nature of the lakes located in pine forests lies above all in the fact that they are poor in total-P, contain less total-N and are usually acid, although lakes with an alkaline reaction of the

water can also be found among them (Table 3). Lakes found in pine forests have sediments poor or rich in CaCO_3 . Those with CaCO_3 -poor sediments are more frequent and always acid. Lakes with sediments rich in CaCO_3 , a component of lacustrine chalk, are alkaline, and the concentration of calcium here is much higher (Table 4). The water pH, conductivity and calcium concentration in both

Table 3. Characteristics of lakes in pine forests (A), oak forests (B), beech- and hornbeam forests (C)

ANOVA: *A ↔ B; **B ↔ C; *** A ↔ C; ($\alpha = 0.05$)

Lake group	Mean	SD	Median	Range	ANOVA		
					d.f.	F	P ($\alpha = 0.05$)
pH							
A	6.4	1.6	6.6	4.5–8.4	32	0.7	0.4*
B	6.0	1.1	6.3	4.5–7.4	26	6.0	0.02**
C	7.0	1.1	6.9	5.7–8.8	35	1.6	0.21***
Conductivity [$\mu\text{S cm}^{-1}$]							
A	65.0	37.6	50	26–171	29	0.001	0.98
B	66.9	26.7	60	32–121	26	0.4	0.55
C	76.5	45.9	64	23–189	32	0.6	0.44
Ca [g m^{-3}]							
A	7.3	6.0	5.5	2.0–18.8	28	1.1	0.32
B	9.5	5.8	7.4	2.2–18.8	26	0.8	0.38
C	12.5	10.2	9.5	2.2–32.6	31	3.3	0.08
$\text{P}_{\text{tot.}}$ [mg P m^{-3}]							
A	44.4	16.1	43.0	28–80	19	7.3	< 0.001
B	146.1	50.8	139.5	91–236	26	1.3	0.27
C	117.3	75.1	122.0	29–263	22	6.8	0.007
$\text{N}_{\text{tot.}}$ [g m^{-3}]							
A	1.1	0.4	0.9	0.6–1.9	19	0.9	0.37
B	1.3	0.7	1.0	0.6–2.9	26	3.1	0.09
C	1.8	0.8	1.5	0.9–3.2	22	6.6	0.02

lake groups differ in a very significant way, whereas the concentrations of total-N and total-P are very low and do not differ at all. Carbonate concentration in the water depends on the size of the surface area of the lacustrine chalk deposits, not covered with acid organic sediments. As a result of the wide range of physical and chemical properties of the water, except for the low total-P concentration, lakes located in pine forests do not differ statistically from those found in oak, beech or hornbeam forests (Table 3).

Lakes found in oak, that is, mixed forests, have a higher total-P concentration than those in pine forests. Other dif-

ferences between these lake groups are insignificant statistically (Table 3). Some of the oak forest-located lakes have the highest acidity and the lowest calcium concentration, especially if the treestand contains a considerable proportion of planted pine or spruce, and also when the lakes adjoin raised or transition bogs.

In broadleaved, i.e., beech or hornbeam forests, the lakes have a slightly higher pH, conductivity and calcium concentration, but they differ in a statistically significant way only from those situated in pine forests. Lakes found in broadleaved forests have higher total-N and total-P concentrations (Table 3).

Table 4. Comparison of mid-forest lakes with sediments poor (A) and rich (B) in CaCO_3

Lake group	Mean	SD	Median	Range	ANOVA	
					F	P
					($\alpha = 0.05$, d.f. = 30)	
pH						
A	4.9	0.3	4.8	4.5–5.5		
B	8.2	0.1	8.2	8.1–8.4	299.3	<0.0001
Conductivity [$\mu\text{S cm}^{-1}$]						
A	44.0	7.6	43	31–55		
B	87.3	14.1	82	66–114	23.0	0.0001
Ca [g m^{-3}]						
A	3.8	1.5	3.0	2.0–6.2		
B	16.7	2.0	16.7	14.7–18.7	140.5	<0.0001
$\text{P}_{\text{tot.}}$ [mg P m^{-3}]						
A	121.4	16.2	103.0	84–216		
B	134.0	28.8	121.0	114–167	0.2	0.68
$\text{N}_{\text{tot.}}$ [g m^{-3}]						
A	1.1	0.2	1.1	0.8–1.3		
B	1.1	0.2	1.0	0.9–1.3	0.05	0.95

3.4. EFFECTS OF HUMAN PRESSURE

In natural lakes, that is, those without apparent signs of human impact, the pH ranges from weakly acid to weakly alkaline, the conductivity is low, and so are the concentrations of total-P and total-N (Table 5). All these lakes lie in forests without any significant changes in the

species composition of the treestands, and without any inflow of water from reclaimed bogs, bog forests or farmlands.

Lakes altered as a result of badly executed work in the forests differ from the natural ones by a lower water reaction ($F = 5.6$, $P = 0.02$, d.f. 99). Though a low

Table 5. Physical and chemical properties of the water of natural (N) lakes and those altered by: forest management (F), agriculture (A) and urbanization of the edge zones (U)
ANOVA: * F ↔ A; ** A ↔ U; *** F ↔ U

Lake group	Mean	SD	Median	Range	ANOVA	
					F	P ($\alpha = 0.05$)
pH						
N	6.9	1.1	6.8	5.5–8.7		
F	5.8	1.1	6.0	4.3–7.0	27.9	0.0001*
A	8.1	0.7	8.0	7.0–9.2	0.03	0.85**
U	8.2	1.8	8.8	4.9–9.4	7.8	0.02***
Conductivity [$\mu\text{S cm}^{-1}$]						
N	73.6	44.4	60.0	45–160		
F	68.9	36.6	54.1	32–121	2.1	0.17
A	120.7	82.9	86.5	46–205	0.2	0.65
U	125.5	68.0	109.5	44–207	5.2	0.04
Ca [g m^{-3}]						
N	7.4	6.8	4.8	2.0–30.0		
F	7.2	6.5	5.1	1.8–18.8	2.0	0.2
A	17.4	16.9	11.8	3.5–32.6	0.02	0.8
U	16.3	7.7	16.3	3.3–26.2	4.9	0.05
$\text{P}_{\text{tot.}}$ [mg P m^{-3}]						
N	56.5	27.4	50.0	27–405		
F	55.3	35.4	44.5	29–124	2.9	0.1
A	148.7	218.7	43.0	34–620	0.004	0.9
U	140.3	147.1	62.0	49–310	2.0	0.2
$\text{N}_{\text{tot.}}$ [g m^{-3}]						
N	1.6	0.8	1.3	0.6–3.9		
F	2.6	1.1	2.9	1.2–3.1	0.0	1.0
A	2.6	0.9	2.2	1.3–3.9	2.0	0.2
U	2.0	0.7	2.0	1.0–3.2	1.2	0.3

pH of lakes located in pine, oak or beech forests is a very natural trait, it is surprising that in as high a proportion as 15% the lakes isoetids live at the edge of their tolerance to this ecological factor.

Compared with natural lakes, mid-field lakes have higher values of water-reaction ($F = 11.6$, $P = 0.0008$), conductivity ($F = 11.0$, $P = 0.001$) and concentrations of calcium ($F = 13.7$, $P = 0.0004$), total-P ($F = 12.3$, $P = 0.01$) and total-N ($F = 13.3$, $P = 0.0007$). Differences between natural

lakes and those found in rural built-up areas are equally high. The effects of cultivated lands and villages are manifested by higher concentrations of total-P, calcium, and higher conductivity and pH values. In the group of anthropogenically altered lakes the difference between particular values of the properties of the water are statistically insignificant (Table 5). Thus, one of the effects of human pressure is the unification of the lake characteristics.

3.5. TOLERANCE LIMITS OF HABITAT CONDITIONS

Isoetids are adapted to various habitat conditions (Fig. 3). *Littorella* tolerates water with a pH range of 4.5–9.4, *Isoëtes* pH 4.5–8.8, *Lobelia* pH 4.5–8.7. *Littorella* thus tolerates the widest pH range, while the requirements in this respect of remaining two species are similar. In natural lakes, i.e., those without conspicuous signs of anthropopressure, the range of pH is narrower. In these lakes *Littorella* occurs at pH 5.7–8.7, *Lobelia* at pH 5.7–8.3, *Isoëtes* at pH 5.5–8.2. For all three species the acidity limit that cannot be exceeded is pH 4.5.

The studied species tolerate water with a range of conductivity 23–224 $\mu\text{S cm}^{-1}$ and calcium concentration 2.0–38.9 g m^{-3} . In well preserved natural isoetid lakes the conductivity range of water is 45–160 $\mu\text{S cm}^{-1}$ and calcium concentration 5.0–30 g m^{-3} . In this respect, the re-

quirements of the isoetids are fairly similar except that in natural lakes with *Lobelia* the conductivity is higher by 10–20 $\mu\text{S cm}^{-1}$, and in lakes with *Littorella* the maximum concentration of calcium is about 10 g m^{-3} higher than in those in which the remaining two species occur (Fig. 3).

Lobelia, *Isoëtes* and *Littorella* tolerate low concentrations of total-N (0.6–3.9 g m^{-3}). In natural lakes the range of nitrogen concentration is narrowed down to 0.6–3.4 g total-N m^{-3} . The requirements of isoetids for the concentrations of total-N are rather similar, but they are different in the case of phosphorus. The limits of maximum concentrations of total-P in lakes with *Isoëtes* (662 mg m^{-3}) and *Littorella* (950 mg m^{-3}) are shifted far beyond the values found for lakes with *Lobelia* (100 mg m^{-3}). Of the

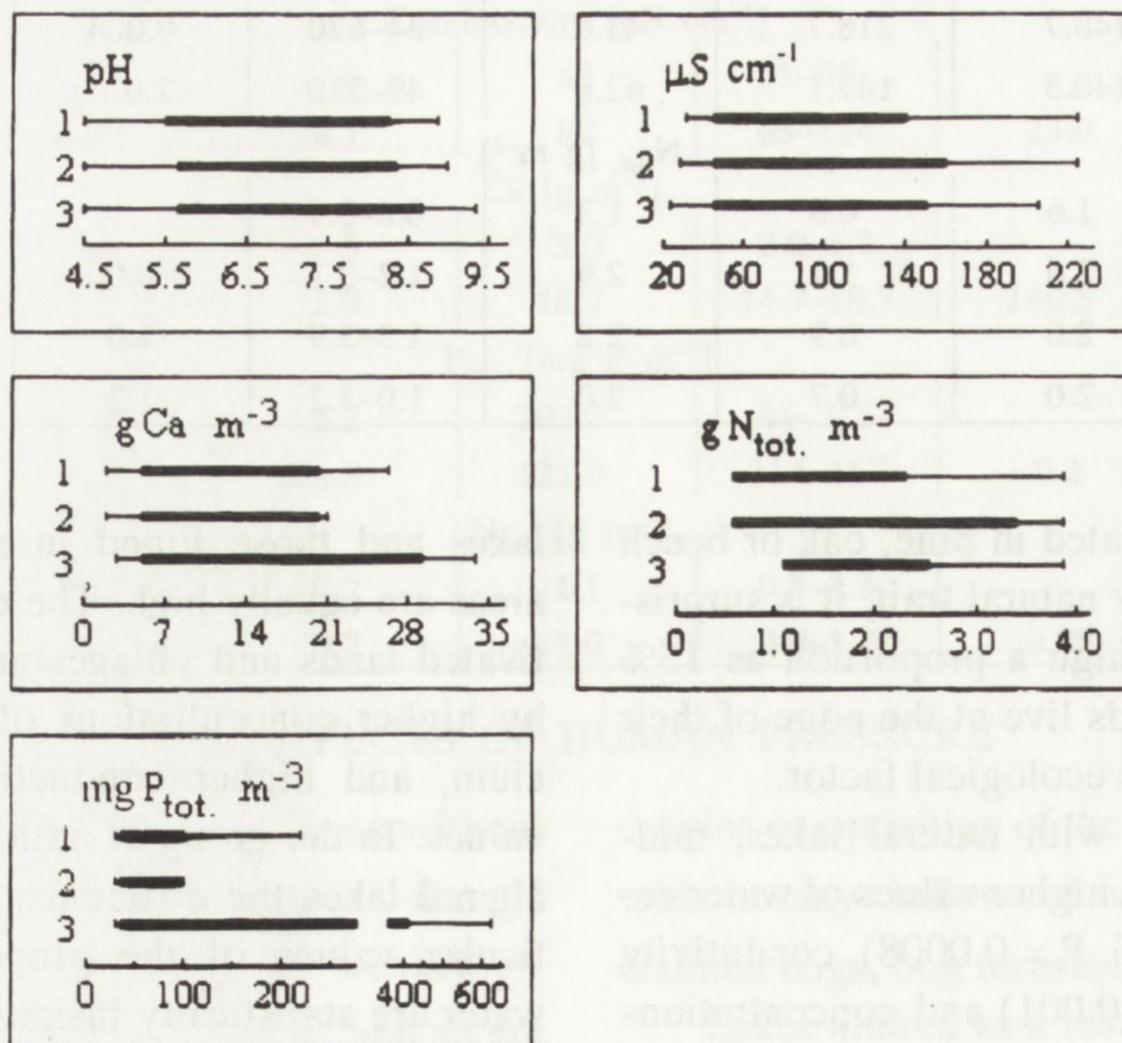


Fig. 3. Ranges of pH, conductivity, Ca, total-N and total-P concentration values tolerated by *Isoëtes lacustris* (1), *Lobelia dortmanna* (2) and *Littorella uniflora* (3). The thick solid line represents the range of characteristics in natural lakes

species studied *Littorella* tolerates the highest total-P concentrations in the water.

To sum up, isoetids can endure in waters anthropogenically or naturally acidified up to pH 4.5. This is indicated by the data from studies of 109 lakes. There is evidence to prove that in lakes

with pH < 4.5 isoetids have become extinct. *Littorella* is the most resistant to increased water hardness and high concentrations of total-P. Therefore its populations can best endure the effects of anthropogenic eutrophication, provided that the concentration of total-N is low, not exceeding 4 g m^{-3} .

4. DISCUSSION

Lakes located along the Southern Baltic are slightly older than those found in Scandinavia, because the basic geomorphological features were formed here at an earlier date. The deglaciation of Northern Poland ended over 10000 years ago and that of Scandinavian countries (Norway, Sweden, Denmark) and Finland, as stated by Rørslett (1991), less than 10000 years ago. However, from the geological point of view, age differences of the relief and lakes are small. As a result, along the Southern Baltic, with the exception of several Northern or Northern-Atlantic species, e.g. *Subularia aquatica* L., *Crassula aquatica* (L.) Schönl. and *Pilularia globulifera* L., the same isoetids are found as in Nordic countries.

On account of the physical and chemical characteristics of the water, isoetid lakes located along the Southern Baltic are similar to the mesotrophic lakes of north European countries, that is, Norway, Sweden, Finland and Denmark. According to Rørslett (1991), in mesotrophic Scandinavian lakes, including those found in Finland, the arithmetic mean of the water pH is 7.07, and that in the lakes under study assumes the value of pH 6.9. Calcium concentration is also similar (7.8 versus 8.3 g m^{-3}). Along the Southern Baltic, the lakes have higher concentrations of total-P and total-N, which is the result of a longer and

stronger anthropopressure, and differences in the structure, age and location of these water bodies. Southern-Baltic lakes are slightly older, usually small, shallow and situated in sandy areas, while the Scandinavian lakes are larger and deeper. Many of them occur among rocky formations and are, above all, subject to the pressure of the severe boreal climate. During the last 10000 years lakes along the Southern Baltic have been enriched, at a faster rate than Scandinavian lakes, with carbonates, nitrogen and phosphorus which are more readily leached from loose and sandy soils than from a rocky substrate.

The development of the southern-Baltic lakes towards softwater acid lakes obviously depends on many environmental conditions, e. g. on the way in which they are fed with water, and also on the kind of soils and vegetation in the catchment areas (Szmeja 1996 b, Szmeja et al. 1996). As oak-, beech- and pine-forest habitats are dominant in Pomerania (Matuszkiewicz 1984 b), and their influence on the physical and chemical characteristics of the water is tolerated by isoetids, we think that here isoetid lakes were once far more common than at present.

There are 151 isoetid lakes in Pomerania (Szmeja 1996 a), and 100 years ago there were at least 220 (Bociąg, un-

published). So far, there is no evidence to suggest that at that time isoetids colonized at least one locality not known before (Szmeja 1992). The floristic and hydrochemical diversity vanished at a rate of 0.65 lakes a year. K. Bociąg analysed floristic papers published from the middle of the 19th century to contemporary times and took into account lakes in which all isoetid species had become extinct. It is known, however, that in many lakes only some of the species had become extinct, e.g. only *Lobelia*, so in reality during the last 100 years the rate of vanishing of their floristic specificity has been higher than specified above. Floristic papers of the 19th century as a rule lack data on the physical and chemical characteristics of the water. Since the botanists of that time mentioned many village isoetid lakes, it may be assumed that the habitat conditions found in them were similar to those which today prevail in areas that are not built-up. At present, no isoetid lakes can be found in villages, except for two eutrophic lakes with vestigial populations of *Littorella uniflora*. In one of them *Isoëtes lacustris* and *I. echinospora* Dur. are also present (Szmeja 1996a).

In Pomerania and North-Eastern Germany, the habitat conditions of isoetids have been changed by the eutrophication of lakes, caused by the chemicalization of farmlands, urbanization of the fringes and development of tourism. The effects of these phenomena in European isoetid lakes have been studied many times (Seddon 1965, 1972, Wallsten 1981, Roelofs et al. 1984, Rørslett and Brettum 1989, Vöge 1992). It must be stressed, however, that in Northern Poland at least 15% of lakes lose the original diversity as a result of their anthropogenic acidification of which the effects are most conspicuous

in small mid-forest lakes. Acidification of lakes entirely or partly surrounded by fields is slower than that of mid-forest water bodies, because the farms have been continually fed with calcium from farmlands treated with lime. In North-Eastern Germany, i.e., to the west of Pomerania, the trends of hydrochemical changes in analogous lakes are similar (Vöge 1992). This means that along the Southern Baltic the isoetids are threatened with extinction because of the impact of the same anthropogenic factors.

The vulnerability of isoetids to eutrophication varies. K. Bociąg (unpublished) says that the most sensitive to eutrophication is *Lobelia*, and the least sensitive *Littorella*. Of eight randomly selected lakes, which have lost their original floristic and hydrochemical diversity, *Lobelia* has become extinct in eight, *Isoëtes lacustris* in seven and *Littorella* in five. According to Vöge (1992), the vulnerability of *Lobelia* to the effects of eutrophication results from its low adaptive plasticity. The germinability of *Lobelia* seeds is high only where there is enough light and oxygen in the sediment (Farmer and Spence 1987, Szmeja 1987), that is, on the light mineral substrate of lakes with transparent water. The probability that seeds will germinate is higher in the area within the reach of the rosette of an adult individual than outside it, and also stronger within an aggregation than outside it (Szmeja 1987, 1994 a). This is connected with the level of oxygenation of the sediments by this plant (Sand-Jensen et al. 1982, Boston et al. 1989). *Lobelia* is the victim of its own highly specialized photosynthesis and little elastic reproductive strategy, whereby an individual can propagate vegetatively only when it flowers (Szmeja 1987), in contrast to *Littorella* which produces runners

throughout the growing season, but when submerged, it reproduces in the most efficient way, that is, vegetatively (S z m e j a 1994a). The higher resistance of *Littorella* to eutrophication results from its growth potential (S a n d - J e n s e n 1978), fast propagation by runners, ability to colonize habitats strongly disturbed by waves, and occurrence in very shallow littoral sites, even on moist sand outside the lake water (S z m e j a 1992, 1994 a, b, c). These are substrates with better oxygenation and light conditions and with smaller amounts of organic matter deposited on them. In acidified lakes they are not overgrown with submerged bryophytes, because they occur in sites which are too shallow.

In eutrophic lakes the areas of submerged aquatic plants are shifted towards shallow waters, this being the result of, among other things, light and oxygen deficiency in the sediments (B o s t o n et al. 1987, V ö g e 1988, 1992, O z i m e k 1990). This type of response of submerged aquatic macrophytes occurred in eutrophic lakes supplied with humic substances from hydrogenic habitats, e.g. bogs or swamp forests. The shrinking of population areas is a significant factor eliminating the macrophytes from lakes.

The process of vanishing of the floristic specificity of isoetid lakes is manifested in various ways. In large, deep, hardwater less often in shallow softwater lakes isoetids are more frequently eliminated by eutrophilous, calciphilous or acidophilous species. There are, however, many deviations from this rule, for in some lakes eutrophication or acidification deprives the littoral of almost all the submerged aquatic vegetation. In eutrophic lakes, higher values are found for pH, conductivity, concentration of calcium, and especially of phosphorus. However, it

is highly unlikely that the water chemistry alone could be the main agent causing quantitative and qualitative changes among macrophytes. Here of decisive importance probably are light (R ø r s l e t t 1991), oxygenation of sediments, chemical processes going on in the latter, and in acidified lakes – competition with bryophytes (R o e l o f s 1983, G r a h n 1986, J a y n e s and C a r p e n t e r 1986, S z m e j a 1994 a, b, c).

Many lakes have lost their former specificity because waters from bogs and swamp forests were discharged into them. In such situations the characteristics of isoetid habitats are determined by large-molecular humic acids which are resistant to biodegradation, sediment becomes absorbed on organic and inorganic suspensions at a fast rate, and can precipitate with calcium carbonate (L a m p e r t and S o m m e r 1996). The effect of this phenomenon on biocoenoses was studied by among others N i l s s e n (1980), A n d e r s s o n (1985), J a n s s o n et al. (1986), B r a n d r u d and J o h a n s e n (1994). Acid sediments limit the occurrence of many submerged aquatic plants, cause changes in the structure of their populations and phytocoenoses (R o e l o f s 1983, G r a h n 1986, S z m e j a 1994 a, c), and lead to the replacement of basiphilous and neutrophilous plants with acidophilous species, mainly bryophytes (S z m e j a 1992). Surface runoff from anthropogenically acidified forest soils, in addition to eutrophication, the main cause of the vanishing of the floristic specificity of these lakes.

It is possible to stop the unfavourable plant succession changes in natural isoetid lakes, but some coordination is needed of all the researches carried on by many scientific institutions in Europe, especially those in the near-Baltic countries.

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5. SUMMARY

The authors studied the habitat conditions of *Isoëtes lacustris*, *Littorella uniflora* and *Lobelia dortmanna* in lakes along the southern Baltic (Fig. 1). It has been assumed in the study that the physical and chemical characteristics of lake water are to some extent determined by the soils and vegetation of the catchment areas (Tables 3 and 4), as well as by anthropogenic activity, as exemplified by agriculture, forest management and urbanization of the edge zones (Table 5). The data presented come from North-Western Poland and are representative of areas located along the southern Baltic (Tables 1 and 2). These data can be useful in conservational work and comparative analyses of similar lakes found in other areas within their global range.

The range of physical and chemical characteristics of the lakes is wide (Table 1). The pH of the 109 lakes studied ranges from very acid (pH 4.5) to highly alkaline (pH 9.4), the number of weakly acidic to acidic lakes (pH < 7) being almost as large as that of alkaline ones (Fig. 2). Very acid lakes (pH 4.5–5.5) constitute 15%, moderately acid ones (pH 5.6–6.5) 19.4%. Acid water (4.5–6.5) is found in 34.4% of the water

bodies, of which almost all lie in forests. Lakes with a pH range of 6.6–7.5 represent 34.2%, with pH 7.6–8.5–25.8%. The latter usually adjoin farmlands. The pH of over a half of the lakes (62%) ranges from 6.6 to 8.5. About 5.5% of the lakes contain water with a pH > 8.5. Almost all of them adjoin farmsteads.

In well preserved natural isoetid lakes the pH range of the water is 5.5–8.7, conductivity 45–160 $\mu\text{S cm}^{-1}$, Ca concentration 2.0–30.0 g m^{-3} , total-N 0.6–3.9 g m^{-3} and total-P 27–405 mg m^{-3} . In anthropogenically changed lakes these ranges are wider: pH 4.5–9.4, conductivity 23–224 $\mu\text{S cm}^{-1}$, Ca 2.0–32.6 mg dm^{-3} , total-P 27–620 mg m^{-3} (Table 5).

Littorella tolerates the widest range of water pH (4.5–9.4), concentration of Ca (2.8–32.6 g m^{-3}) and total-P (27–620 mg m^{-3}). *Isoëtes* can withstand total-P up to 220 mg m^{-3} , *Lobelia* only to 100 mg m^{-3} (Fig. 3). In lakes with *Littorella* and *Isoëtes* the range of maximum phosphorus concentration is wider than that tolerated by *Lobelia* which is the least resistant to eutrophication. The acidity limit value, the same for each of the species, is pH 4.5.

6. POLISH SUMMARY

W pracy przedstawiono charakterystykę warunków siedliskowych *Isoëtes lacustris*, *Littorella uniflora* i *Lobelia dortmanna* w jeziorach wzdłuż południowego Bałtyku (rys. 1). W pracy przyjęto założenie, że fizyczne i chemiczne cechy wody w jeziorach są zdeterminowane, do pewnego stopnia, przez gleby i roślinność w zlewniach (tab. 3 i 4), a także przez oddziaływania antropogeniczne, z których uwzględniono gospodarke rolniczą, leśną i urbanizację obrzeży (tab. 5). Prezentowane dane pochodzą z północno-zachodniej Polski (tab. 1 i 2), są reprezentatywne dla terenów położonych wzdłuż południowego Bałtyku, mogą służyć do wykonywania zabiegów konserwatorskich i porównań z analogicznymi jeziorami w innych częściach ich globalnego zasięgu.

Zakres zmienności fizycznych i chemicznych cech wody jezior lobeliowych jest duży

(tab. 1). Odczyn 109 badanych jezior rozciąga się od bardzo kwaśnego (pH 4,5) do wysoce zasadowego (pH 9,4), przy czym kwaśnych (pH < 7) jest niemal tyle samo co zasadowych (rys. 2). Jezior bardzo kwaśnych (pH 4,5–5,5) jest 15%, natomiast umiarkowanie kwaśnych (pH 5,6–6,5) 19,4%. Woda kwaśna (pH 4,5–6,5) występuje w 34,4% zbiorników, z których niemal wszystkie leżą w lasach. Jezior o pH 6,6–7,5 jest 34,2%, o pH 7,6–8,5 jest 25,8%; w pobliżu tych ostatnich zwykle są tereny rolnicze. Ponad połowa jezior (62 %) ma pH 6,6–8,5. Wodę o pH > 8,5 ma 5,5% jezior, z których niemal wszystkie leżą w sąsiedztwie zabudowań wiejskich.

W dobrze zachowanych jeziorach z isoetydami woda ma następujące cechy: pH 5,5–8,7, przewodnictwo 45–60 $\mu\text{S cm}^{-1}$, stężenie wapnia 2,0–30,0 g m^{-3} , $N_{\text{całk.}}$ 0,6–3,9 g m^{-3} i $P_{\text{całk.}}$ 27–

405 mg m⁻³. W jeziorach antropogenicznie przekształconych, zakres fizycznych i chemicznych cech wody w jeziorach jest szerszy: pH 4,5–9,4, przewodnictwo 23–224 μS cm⁻¹, Ca 2,0–32,6 g m⁻³, P_{całk.} 27–620 mg m⁻³ (tab. 5).

Littorella toleruje najszerszy zakres odczynu wody (pH 4,5–9,4), stężenie Ca (2,8–32,6 g m⁻³) i P_{całk.} (27–620 mg m⁻³). *Isoëtes* znosi

stężenie P_{całk.} do 220 mg m⁻³, *Lobelia* tylko do 100 mg m⁻³ (rys. 3). Granice maksymalnych stężeń fosforu w jeziorach z *Littorella* i *Isoëtes* są przesunięte poza zakres tolerowany przez *Lobelia*, która jest najmniej odporna na eutrofizację. Graniczna wartość zakwaszenia jest dla każdego z tych gatunków taka sama i wynosi pH 4,5.

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