TEMPORAL AND SPATIAL VARIATION OF HABITAT CONDITIONS IN THE ZONATION OF VEGETATION IN THE LATE STAGES OF LAKE OVERGROWTH

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ABSTRACT

The water and substrate properties in the vegetation zones characteristic of the late stages of lake overgrowth were determined. It was demonstrated that the spatial distribution of plant communities conformed with the spatial gradient of habitat conditions. With regard to water properties the largest differences between the zones were found in Mg^{2+} , Ca^{2+} , electrolytic conductivity and NH_4^+ . In the case of substrate the zones differed significantly in Ca^{2+} , total Fe and organic matter content. The water properties varied greatly during the vegetative season in the successive zones. The temporal changes often proceeded at a different level of a given component or factor in most zones. The differences between the zones were, however, maintained. It appears that the plant communities can alter their habitats to a large extent. In the lake studied, the invasion of raised and transitional bog vegetation was observed. The process of dystrophy proceeded from the terrestrialized peripheral parts of the lake to the centre of the lake.

KEY WORDS: late stages of lake overgrowth, mires, zonation of vegetation, water and substrate chemistry, process of dystrophy.

INTRODUCTION

Every lake is, geologically speaking, only a temporary entity. Over the course of time lake basins are steadily filled in with sediment, overgrown with vegetation and eventually turn into mire or terrestrial formation (Moor 1969; Podbielkowski and Tomaszewicz 1982; Marek 1992 and others).

Aquatic and reedswamp communities occupying the littoral zone of the lake play an important role in the process of overgrowing and shallowing of lakes, that is terrestrialization. As the lake becomes more shallow, successional changes in vegetation take place (Tomaszewicz 1977, 1979; Rejewski 1981; Pott 1983; Kłosowski 1990, 1999; Lorens and Sugier 1999). In the classical scheme of successional changes of vegetation outlined by Moor (1969), the lakes are initially colonized by deep-water communities, which yield to those of shallow water. The former communities move gradually inward toward the centre of the lake giving way to floating-leaved vegetation. These are in turn replaced by emergent reedswamp communities, which are displaced by sedge communities and then themselves succeeded by sedge-moss and shrub communities. The area overgrown with vegetation increases and gradually extends inward to the centre of the lake. As a result of this the zone of open water disappears. Under natural con-

ditions the successional changes may be slow or rapid depending on the size of the lake, lake bottom configuration, water depth, catchment area etc. Surveys carried out in north-eastern Poland show that the rate of successional changes occurring in mesotrophic and eutrophic lakes which are not subject to strong anthropopressure (Kłosowski 1999) is accelerated when most of the lake basin fills in with organic-mineral sediments which are highly hydrated in the upper layers. Consequently a zonation of vegetation typical of the late stages of lake overgrowth and formation of a floating mat are observed (Tomaszewicz 1977, 1979; Kłosowski 1999). The phytocoenoses of *Hydrocharitetum morsus-ranae* occupy the open water, where they are one of the last stages in the development of aquatic vegetation. From the land side a floating mat formed by *Thelypteridi-Phragmitetum*, *Cicuto-Caricetum pseudocyperi* or *Caricetum acutiformis* communities, representing the final stages in the development of reedswamps, moves gradually inward toward the open water. These are succeeded by sedge-moss, moss or shrub and forest communities. The data of Kłosowski (1990, 1992, 1999) and other authors (Tomaszewicz 1977, 1979; Rejewski 1981; Kraska 1986) showed that most of the lakes investigated went through a stage of a floating mat and dominance of *Hydrocharitetum morsus-ranae* phytocoenoses in their late stages of overgrowth.

Although a great number of lakes are densely overgrown with vegetation and a frequent development of the above-mentioned vegetation zones in the final stages of succession is noted a more detailed analysis of their habitat conditions has not been made to date. The lack of hydrochemical data which would describe the habitat conditions in such zonation of vegetation and determine the further direction of changes in the water chemistry and vegetation were the reason for undertaking this study. In the past floristic and phytosociological investigations were carried out in the Elk and Sejny Lake Districts. The preliminary studies were concerned with the zonation of communities overgrowing the bays of larger lakes (Kłosowski 1992; Kłosowski and Migdalska 1998). In the course of these studies it was demonstrated that the bays and their vegetation were distinct with respect to habitat conditions. The present work is, therefore, a continuation of these studies. The main objectives of this study were to:

- determine the temporal and spatial variation of habitat conditions in the zonation of vegetation representing the late stages of lake overgrowth, where the zone of open water had virtually disappeared;
- evaluate whether the zonal distribution of plant communities was accompanied by a similar zonal distribution of water and substrate properties;
- determine the pattern of changes in the evolution of the lake and its vegetation.

MATERIAL AND METHODS

The survey was carried out in a small lake densely overgrown with vegetation, about 7 km north of the village of Sajzy within the Elk Lake District (Fig. 1). The lake, which has no inlet or outlet, is situated in a forest about 700 m from the River Elk flowing from the west southeastward, and raised above the surroundings. An east to west transect about 150 m long was marked out along the vegetation zones of the lake. The following plant communities were examined at the transect: *Eriophoro vaginati-Sphagnetum recurvi* (8 m wide), *Eriophoro-angustifolii-Sphagnetum recurvi* (12 m), *Thelypteridi-Phragmitetum* (4 m), *Hydrocharitetum morsus-ranae* (70 m), *Thelypteridi-Phragmitetum* (4-5 m) and *Carici elongatae-Alnetum* (50 m). When exposed to strong wind action, small pools of open water were observed in the stands formed by *Hydrocharis morsus ranae* occupying the zone of open water. In the present study the above zone was treated as a whole. In each vegetation zone (phytocoenose) one phytosociological relevé was recorded (Table 1). Water and substrate samples were taken and pooled every 2 weeks from mid-June to mid-September of 1993 for physical and chemical analysis. In addition samples were collected in mid-October. Water samples were taken from the intermediate depth at which a given phytocoenose occurred (*Hydrocharitetum morsus-ranae*), from the free water zone beneath the floating mat (*Thelypteridi-Phragmitetum*) and from stagnant water among vegetation (*Eriophoro vaginati-Sphagnetum recurvi*, *Eriophoro angustifolii-Sphagnetum recurvi*, *Carici elongatae-Alnetum*) and immediately transferred to plastic containers. Every water sample was a mixture of a few random subsamples taken within each vegetation zone. Altogether eight samples of water were analysed in each of the six vegetation zones.

Substrate samples were taken from the rhizome-root layer with a tubular bottom sampler and transferred to plastic bags. Each substrate sample contained a mixture of 3 subsamples taken within a phytocoenose. The temporal variability of substrate properties was not investigated as it was difficult to render the changes in sediment chemistry due to the highly mosaic character of the lake bottom deposits. However the spatial gradient of habitat conditions with respect to substrate properties was determined along the transect. In total eight samples of substrate were analysed in each of the vegetation zones and the mean value was calculated.

Both analyses of water and substrate were performed directly after the samples were brought to the laboratory at the University of Warsaw Biological Station in Sajzy. All the determinations were carried out by methods described by Hermanowicz et al. (1976).

In the hydrochemical analyses the following determinations were carried out: pH using pH-meter, electrolytic conductivity with conductivity bridge, Ca^{2+} by flame pho-

Fig. 1. Location of the area studied.

tometry on a Flapho 4 flame photometer, Mg^{2+} with an AAS 1N atomic absorption spectrophotometer, PO_4^{3-} by the colorimetric molybdate blue method, NH_4^+ by Nes-sler's colorimetric method, oxidability (COD $KMnO_4$) as potassium permanganate consumption in acid medium.

In substrate samples, the following properties were as-sessed directly: pH, hydration and organic matter content.

TABLE 1. Basic phytosociological data of the plant communities forming spatial zonation in the investigated lake.

Plant community	EV	EA	TP1	HM	TP2	CAL
Ch. <i>Oxycocco-Sphagnetea</i>						
<i>Eriophorum vaginatum</i>	3					
<i>Oxycoccus quadripetalus</i>	3	2				
<i>Drosera rotundifolia</i>	+					
<i>Polytrichum strictum</i>	+					
<i>Aulacomnium palustre</i>	+					
Ch. <i>Scheuchzerio-Caricetea nigrae</i>						
<i>Eriophorum angustifolium</i>		2				
<i>Menyanthes trifoliata</i>		1				2
<i>Carex canescens</i>		2			1	
<i>Comarum palustre</i>			+		+	
<i>Sphagnum teres</i>					3	
<i>Epilobium palustre</i>						+
Ch. <i>Phragmitetea</i>						
<i>Carex rostrata</i>		3	2			3
<i>Lysimachia thyrsiflora</i>		+	+			+
<i>Typha latifolia</i>			1		1	+
<i>Carex appropinquata</i>			+		+	+
<i>Carex pseudocyperus</i>					+	
<i>Carex paniculata</i>						+
<i>Ranunculus lingua</i>						+
<i>Peucedanum palustre</i>						+
<i>Scutellaria galericulata</i>						+
Ch. <i>Potametea</i>						
<i>Stratiotes aloides</i>				5		
<i>Hydrocharis morsus-ranae</i>			+	+	+	
Ch. <i>Alnetea glutinosae</i>						
<i>Sphagnum squarrosum</i>			1		3	
<i>Salix cinerea</i>		+			+	1
<i>Lycopus europaeus</i>			+			
Accompanying species						
<i>Sphagnum fallax</i>	5	5	1			4
<i>Thelypteris palustris</i>			5		5	1
<i>Betula pubescens</i> (c)	+	+				
<i>Pinus silvestris</i> (c)	+					
<i>Picea abies</i> (c)	+					
<i>Vaccinium uliginosum</i>	+					
<i>Lemna trisulca</i>			2	4		
<i>Lemna minor</i>			+	+	+	+
<i>Utricularia minor</i>			+		+	
<i>Brachytcheicum rutabulum</i>			1			
<i>Cardamine pratensis</i>			+			
<i>Frangula alnus</i> (b)					+	+
<i>Eurhynchium speciosum</i>					+	
<i>Alnus glutinosa</i> (c)					+	
<i>Alnus glutinosa</i> (a)						3
<i>Alnus glutinosa</i> (b)						2
<i>Betula pubescens</i> (a)						1
<i>Betula pubescens</i> (b)						2
<i>Picea abies</i> (b)						2
<i>Sphagnum palustre</i>						+
<i>Calla palustris</i>						+

EV – *Eriophoro vaginati-Sphagnetum recurvi*; EA – *Eriophoro angustifolii-Sphagnetum recurvi*; TP1 – *Thelypteridi-Phragmitetum* in the east part of the lake; HM – *Hydrocharitetum morsus-ranae*; TP2 – *Thelypteridi-Phragmitetum* in the west part of the lake; CAL – *Carici elongatae-Alnetum*. Tree layer (a); shrub layer (b); herb layer (c)

Other assays were determined after the samples had been mineralized (total nitrogen) or acid extracts were carried out in HCl 1+1 (Ca^{2+} , Mg^{2+} , PO_4^{3-}). The analyses from acid extracts and the determinations of pH were conducted by the methods described above. Hydration was determined by drying substrate samples at 105°C to constant weight, organic matter content by ignition of dry samples at 550°C for 1.5 hrs and total nitrogen by Kjeldahl's method.

Numerical data were evaluated statistically. Mean values were calculated for each component and property, both of water and substrate, from the successive zones. The significance of differences between the mean values of habitat properties of particular vegetation zones was determined by one-way analysis of variance and the Newman-Keuls test (Zar 1984). The pH values were recalculated so as to obtain specific acidity according to Wherry (1922).

RESULTS

Figure 2 shows the temporal and spatial changes of water properties in the six zones of vegetation investigated at the transect. The data relating to the spatial gradient of substrate properties are given in Fig. 3. The results of the statistical analysis applied to determine the significance of differences between the mean values of water and substrate properties in the successive vegetation zones are presented in Table 2 and 3.

From Figure 2, it is clear that the fluctuations in water chemistry were considerable in each zone over the vegetative season. The highest temporal changes occurred in the case of properties indicating water richness, namely PO_4^{3-} and NH_4^+ . The lowest fluctuations were found for Ca^{2+} . Independent of the high temporal variability of most water properties considerable differences (spatial variation) were also found between the vegetation zones. In the case of Mg^{2+} and electrolytic conductivity the temporal changes proceeded at a different level in each zone during the vegetative season. The highest values for conductivity and concentrations of Mg^{2+} were found in the water of *Hydrocharitetum morsus-ranae*, the lowest in that of the zone of *Eriophoro angustifolii-Sphagnetum recurvi*, and intermediate levels in both *Thelypteridi-Phragmitetum* zones and *Carici elongatae-Alnetum*, respectively. The *Eriophoro vaginati-Sphagnetum recurvi* zone occupied an intermediate position between the *Carici elongatae-Alnetum* and *Eriophoro angustifolii-Sphagnetum recurvi* zones. The pattern of changes of Ca^{2+} in the successive zones of vegetation was similar but higher levels of Ca^{2+} were observed in the *Thelypteridi-Phragmitetum* zone occupying the west part of the lake. It appeared that the distribution of pH values in the successive zones differed from that of Mg^{2+} concentrations and electrolytic conductivity. Throughout the vegetative season the lowest pH values were noted in the water of the *Eriophoro vaginati-Sphagnetum recurvi* zone, higher in that of *Eriophoro angustifolii-Sphagnetum recurvi* and they increased in the water of the *Carici elongatae-Alnetum* zone. Hence the changes in pH proceeded at a different level in each zone. The water of *Thelypteridi-Phragmitetum* zone in the east sector of the lake showed the highest pH. Slightly lower values of pH occurred only in the waters of *Hydrocharitetum morsus-ranae* and *Thelypteridi-Phragmitetum* from the west part of the lake.

Fig. 2a. Temporal (left and right) and spatial variations (middle) in Mg^{2+} , Ca^{2+} , pH and electrolytic conductivity in waters of the vegetation zones. EV – *Eriophoro vaginati-Sphagnetum recurvi*; EA – *Eriophoro angustifolii-Sphagnetum recurvi*; TP1 – *Thelypteridi-Phragmitetum* in the east part of the lake; HM – *Hydrocharitetum morsus-ranae*; TP2 – *Thelypteridi-Phragmitetum* in the west part of the lake; CAL – *Carici elongatae-Alnetum*.

Fig. 2b. Temporal (left and right) and spatial variations (middle) in NH_4^+ , PO_4^{3-} and COD-KMnO_4 in waters of the vegetation zones. For other explanations see Fig. 2a.

Fig. 3. Spatial variations of substrate properties in the vegetation zones.

The above patterns of changes of water properties in the successive zones were confirmed by the statistical analysis of the differences in the mean values of these properties (Table 2). The highest number of significant differences were found for Ca²⁺, Mg²⁺ concentrations and electrolytic conductivity.

In the case of the remaining properties indicating water richness (NH₄⁺, PO₄³⁻, COD-KMnO₄) a reverse trend was demonstrated. During the vegetative season the highest concentration of NH₄⁺ was noted in the water of *Carici elongatae-Alnetum* and *Eriophoro vaginati-Sphagnetum recurvi* zones, with lower levels in that of *Eriophoro angustifolii-Sphagnetum recurvi*. The lowest NH₄⁺ concentration was observed in the water of both *Thelypteridi-Phragmitetum* zones and in the zone of *Hydrocharitetum morsus-ranae*. The waters of the latter 3 zones had similar levels of NH₄⁺. The highest values for COD-KMnO₄, indicating the content of dissolved organic matter, were recorded in the water of the *Eriophoro vaginati-Sphagnetum recurvi* zone, with lower values in the alder carr and *Eriophoro angustifolii-Sphagnetum recurvi* zones. As in the case of NH₄⁺ the other zones did not vary significantly with respect to dissolved organic matter content. Its level remained constant during the vegetative season and was lower than in the former three communities (*Eriophoro vaginati-Sphagnetum recurvi*, *Carici elongatae-Alnetum* and *Eriophoro angustifolii-Sphagnetum recurvi*). The waters of *Eriophoro vaginati-Sphagnetum recurvi* and *Eriophoro angustifolii-Sphagnetum recurvi* were sharply differentiated from those of the remaining zones in having the highest values for PO₄³⁻ during the vegetative season. Significantly lower levels of PO₄³⁻ occurred in the water of alder carr zone and were the lowest in that of the other three zones (*Hydrocharitetum morsus-ranae* and both *Thelypteridi-Phragmitetum* zones).

From Table 2, it is clear that a high number of significant differences between the zones were found for NH₄⁺ concentration, and a low number in the case of PO₄³⁻.

It was demonstrated that the vegetation zones occurring farther from the centre of the lake were most distinct with respect to habitat conditions. This applied to 7 properties of water analysed. The communities associated with or occupying the open water zone (*Thelypteridi-Phragmitetum*

TABLE 2. The significance of differences in the mean values of water properties between the vegetation zones. + = significant at P=0,05 (pH values were recalculated so as to obtain specific acidity).

Properties	EV-EA	EV-TP1	EV-HM	EV-TP2	EV-CAL	EA-TP1	EA-HM	EA-TP2	EA-CAL	TP1-HM	TP1-TP2	TP1-CAL	HM-TP2	HM-CAL	TP2-CAL
Mg ²⁺	—	+	+	+	+	+	+	+	+	—	—	+	+	+	+
Ca ²⁺	—	+	+	+	+	+	+	+	+	—	+	+	—	+	+
pH	+	+	+	+	+	—	—	—	—	—	—	—	—	—	—
Conductivity	+	+	+	+	+	+	+	+	+	—	—	+	—	+	+
COD-KMnO ₄	+	+	+	+	+	—	—	—	—	—	—	+	—	+	+
PO ₄ ³⁻	—	+	+	+	—	—	—	—	—	—	—	—	—	—	—
NH ₄ ⁺	+	+	+	+	—	+	+	+	+	—	—	+	—	+	+

EV – *Eriophoro vaginati-Sphagnetum recurvi*; EA – *Eriophoro angustifolii-Sphagnetum recurvi*; TP1 – *Thelypteridi-Phragmitetum* in the east part of the lake; HM – *Hydrocharitetum morsus-ranae*; TP2 – *Thelypteridi-Phragmitetum* in the west part of the lake; CAL – *Carici elongatae-Alnetum*

TABLE 3. The significance of differences in the mean values of substrate properties between the vegetation zones. + = significant at P=0,05. For other explanations see Table 2.

Properties	EV-EA	EV-TP1	EV-HM	EV-TP2	EV-CAL	EA-TP1	EA-HM	EA-TP2	EA-CAL	TP1-HM	TP1-TP2	TP1-CAL	HM-TP2	HM-CAL	TP2-CAL
Mg ²⁺	—	+	+	+	—	+	+	+	—	—	—	+	—	+	+
Ca ²⁺	—	+	+	+	—	+	+	+	—	+	+	+	—	+	+
pH	+	+	+	+	+	+	+	+	+	—	—	—	—	—	—
PO ₄ ³⁻	—	+	+	+	—	+	+	+	—	—	—	+	—	+	+
Total Fe	—	+	+	+	—	+	+	+	—	+	—	+	+	+	+
Org. matter	—	+	+	+	—	+	+	+	—	—	+	+	+	+	+
Total N	—	+	+	+	+	+	+	+	+	—	+	—	—	—	+

tum, *Hydrocharitetum morsus-ranae*) were far less distinct with respect to water chemistry except for Mg^{2+} , electrolytic conductivity and Ca^{2+} .

The data providing a picture of the spatial variation of substrate properties at the transect (Fig. 3) also showed considerable differences between the vegetation zones. The substrates of *Eriophoro vaginati-Sphagnetum recurvi*, *Eriophoro angustifolii-Sphagnetum recurvi* and *Carici elongatae-Alnetum* had similar lower levels of Mg^{2+} , Ca^{2+} , total Fe and PO_4^{3-} . In addition they were highly acidic. The zone of *Carici elongatae-Alnetum* was distinguished from the other two zones in having the least acidic substrates. In the remaining zones the content or values of the above properties were much higher and differed more considerably between the zones (e.g. Ca^{2+} , total Fe). The highest sediment Ca^{2+} and Mg^{2+} contents were noted in the zone of *Thelypteridi-Phragmitetum* in the east part of the lake. The substrates of *Hydrocharitetum morsus-ranae* contained the greatest amounts of PO_4^{3-} and total Fe. The highest values of pH were recorded in the substrates of both *Thelypteridi-Phragmitetum* zones. The distribution of total N values was similar to that of the above properties. The lowest content of N-total was found in the substrates of *Eriophoro vaginati-Sphagnetum recurvi* and *Eriophoro angustifolii-Sphagnetum recurvi*, with higher levels in those of *Hydrocharitetum morsus-ranae* and both *Thelypteridi-Phragmitetum* zones. The highest total N contents were, however, noted in the substrates of the *Thelypteridi-Phragmitetum* zone occupying the west sector of the lake. The content of N-total in the substrates of *Carici elongatae-Alnetum* was similar to that of the zones occupying the centre of the lake.

As in the case of Ca^{2+} , Mg^{2+} , PO_4^{3-} and total Fe, the substrates of *Eriophoro vaginati-Sphagnetum recurvi*, *Eriophoro angustifolii-Sphagnetum recurvi* and *Carici elongatae-Alnetum* contained similar levels of dissolved organic matter. However a reverse trend in the distribution of the mean values for the above property was observed. The latter zones were much richer in organic matter than the other zones. The lowest content of organic matter was noted in the *Thelypteridi-Phragmitetum* zone from the east part of the lake.

The above spatial variability of substrates properties and distinct character of the successive vegetation zones were confirmed by the results of the significance test (Table 3). The highest number of significant differences were found with regard to contents of Ca^{2+} , total Fe, total N and organic matter.

DISCUSSION

The results of the present study have shown a distinct spatial variability of habitat conditions with respect to water and substrate chemistry in the lake which was in its last stages of overgrowth. The variation in habitats was associated with the community type. Hence, the spatial (zonal) distribution of plant communities is accompanied by a similar zonal distribution of water and substrate properties. When habitat conditions do not exhibit zonal distribution, the ecological distinction of some communities forming zonation is still observed.

Throughout the vegetative season wide temporal variations in most properties of water were displayed by each

vegetation zone at the transect. In spite of the large temporal changes in water chemistry, the differences between some zones were maintained, irrespective of whether the pattern of changes was similar or not. The changes often proceeded at a different level of a given component or factor throughout the greater part or entire vegetative season (e.g. Mg^{2+} , electrolytic conductivity, pH). The above data demonstrate a clear relationship between the communities and their habitats and reflect the ability of communities to modify the habitat.

The most considerable differences in water and substrate properties were found between the communities of *Eriophoro vaginati-Sphagnetum recurvi*, *Eriophoro angustifolii-Sphagnetum recurvi*, *Carici elongatae-Alnetum* and those associated with the open water zone (*Thelypteridi-Phragmitetum*, *Hydrocharitetum morsus-ranae*). This is ascribed to the changing environmental gradients in the lake: eutrophy-ombrotrophy. It is interesting to note that the changes occurring within a small area (a few metres) among the neighbouring communities of *Eriophoro angustifolii-Sphagnetum recurvi* and *Thelypteridi-Phragmitetum* from the east part of the lake and those of *Carici elongatae-Alnetum* and *Thelypteridi-Phragmitetum* from the west sector of the lake were very sharp. The floating mat of *Thelypteridi-Phragmitetum* plays a role of a barrier separating the mire vegetation from the *Stratiotes aloides* phytocoenoses occupying the open water. Hence the stagnant water among the mire vegetation has a distinct and specific chemical composition characteristic of raised and transition bogs. These highly acidic waters are characterized by low Ca^{2+} and Mg^{2+} concentrations and low electrolytic conductivity (Gorham 1956; Schwintzer and Tomberlin 1982; Vitt and Bailey 1984; Lütt 1992). It is worth noting that the concentrations of PO_4^{3-} , NH_4^+ , Mg^{2+} , Ca^{2+} and values of electrolytic conductivity in the water of the raised bog (*Eriophoro vaginati-Sphagnetum recurvi*) were higher than in that of the transition bog (*Eriophoro angustifolii-Sphagnetum recurvi*). This may have been attributed to the slight flooding of the zone representing the raised bog formation which was farthest from the centre of the lake. Even small vertical fluctuations of the water level in this zone can initiate periodically the process of mineralization of accumulated matter. Other authors also pointed out higher concentrations of nitrogen and phosphorous in the water of raised bogs than in that of transition bogs and fens (e.g. Schwintzer and Tomberlin 1982; Łachacz and Olesiński 2000). Higher levels of dissolved PO_4^{3-} and NH_4^+ were also observed in the surface layers of peat bogs (Waughman 1980).

The differences in water chemistry parameters, especially PO_4^{3-} , NH_4^+ and COD-KMnO₄, between the neighbouring zones of *Thelypteridi-Phragmitetum* and *Hydrocharitetum morsus-ranae* were much less marked, which may have been attributed to the mixing of their waters. More pronounced differences were in Ca^{2+} , Mg^{2+} , electrolytic conductivity and pH. This may be associated with the biological activity of *Stratiotes aloides* (Brammer and Wetzel 1984), which is the main constituent of *Hydrocharitetum morsus-ranae* phytocoenoses.

With regard to substrate properties the habitat conditions were much more uniform in the typical mire vegetation (*Eriophoro vaginati-Sphagnetum recurvi*, *Eriophoro angustifolii-Sphagnetum recurvi* and *Carici elongatae-Alnetum*). This is explained by the fact that in the investigated lake,

Sphagna are the primary constituent of mire vegetation. They grow on substrates with a thick layer of much less humified *Sphagnum* peat. These highly acidic peaty soils are characterized by low Ca^{2+} and Mg^{2+} content (Mysłińska 2001) and are rich in organic matter. Moreover they are poor in PO_4^{3-} , which is ascribed to the low degree of decomposition of peat. More pronounced concentration differences between the peat-inhabiting communities were in total N. The alder carr zone (*Carici elongatae-Alnetum*) was sharply differentiated from the *Eriophoro vaginati-Sphagnetum recurvi* and *Eriophoro angustifolii-Sphagnetum recurvi* zones in having much higher concentrations of N. This is attributed to the lower contribution of *Sphagnum* peat to the substrates of *Carici elongatae-Alnetum*, which is poor in N (Gorham 1953; Ingram 1967; Waughman 1980).

The highest mean values of substrate properties (with the exception of organic matter) were found for communities associated with the centre of the lake. The latter communities represent earlier stages of lake overgrowth characteristic of eutrophic bodies of water than those of the mire vegetation. They inhabit lake sediments of the detrital-calcareous gyttja type, which are slightly acidic and have higher calcium content. The substrates of *Thelypteridi-Phragmitetum* differed considerably from those of *Hydrocharitetum morsus ranae* occupying the open water as opposed to the water habitats. It should be noted that the substrates of the *Hydrocharitetum morsus-ranae* zone contained the largest amounts of PO_4^{3-} and total Fe. In these places, where the water is deepest, typical lake sediments are deposited resulting from the death of individual plants such as *Stratiotes aloides* and other organisms floating freely in the water. Unlike the peaty soils of the lake basin overgrown with vegetation, they are highly humified and are therefore rich in total Fe and P.

The zonation of plant communities observed in the studied lake, where *Hydrocharitetum morsus-ranae* formed a well marked community in the centre of the lake and was surrounded by the belt of *Thelypteridi-Phragmitetum* and from the land by the vegetation of transition and raised bogs indicates that the lake has gradually changed its trophic character from eutrophy to dystrophy. The analysis of the topographic maps confirms that the lake used to be of eutrophic character and points to the existence of an inlet. The water course has, however, overgrown with vegetation and disappeared altogether. Consequently the lake has lost its inflow. According to Marek (1992), who presented the theory of lake transformation to mires, a lake must lose its inflow and outflow, which leads to the acceleration of the process of overgrowth, in order to be converted to areas of mire. The author concludes that deep eutrophic lakes with symmetrical bottom line (as in the case of the lake studied) which lost their inflow are transformed to fens in their peripheral parts while the central part attains a stage of dystrophy. The encroachment of a floating mat of vegetation from the fringe of the lake toward its centre gives rise to an invasion of transitional and raised bog vegetation. A reverse trend was, however, determined in the case of the lake studied. The process of dystrophy proceeds from the raised bog in the terrestrialized peripheral parts of the lake (*Eriophoro vaginati-Sphagnetum recurvi*) through transition bogs (*Eriophoro angustifolii-Sphagnetum recurvi* in the east part and *Carici elongatae-Alnetum* developing on me-

sotrophic transitional peats in the west part of the lake), reedswamps and aquatic vegetation, respectively, where the eutrophic conditions in the centre of the lake persist for a longer time than around its periphery. The data of other authors have shown that a number of small postglacial lakes, exhibiting similar spatial sequence of vegetation zones, disappear in this way as well (Łachacz and Olesiński 2000).

The results obtained in the study, however, do not rule out the scheme of lake transformation to mires elaborated by Marek (1992). The process of lake overgrowth depends on a variety of conditions such as local hydrological conditions, location of the body of water, nature of the original substrates in the catchment area and etc.

The present study showed that plant communities exert a much more profound influence on their habitat when the lake is in its last stages of overgrowth and only few communities dominate. The spatial distribution of communities is accompanied by a similar zonal distribution of water and substrate properties, which reflect the nature of the associated direction of changes in the trophy of the lake (eutrophy-ombrotrophy). These findings confirm the data from earlier publications (Tomaszewicz 1979; Kłosowski 1990, 1999), which indicate that the zonation of communities corresponds to the successive stages of succession only when the lakes are in their late stages of overgrowth.

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CZASOWA I PRZESTRZENNA ZMIENNOŚĆ WARUNKÓW SIEDLISKOWYCH W UKŁADZIE PASOWYM ROŚLINNOŚCI Z KOŃCOWEJ FAZY ZARASTANIA JEZIORA

STRESZCZENIE

Zbadano właściwości wody i podłoża w zbiorowiskach roślinnych tworzących układ zonacyjny w jeziorze znajdującym się w końcowej fazie zarastania. Wykazano, iż pasowemu układowi zbiorowisk w dużym stopniu odpowiada pasowy układ warunków siedliskowych. Spośród analizowanych właściwości wody najsilniej różnicują strefy roślinne Mg^{2+} , Ca^{2+} , przewodnictwo elektrolityczne i NH_4^+ , a z właściwości podłoża Ca^{2+} , żelazo ogólne i zawartość substancji organicznej. W przypadku cech wody obserwuje się w poszczególnych strefach roślinnych dużą ich zmienność w ciągu sezonu wegetacyjnego. W większości stref przebiega ona na innym poziomie wartości, tak, że różnice między strefami pozostają zachowane. Zbiorowiska roślinne wykazują więc silny, modyfikujący wpływ na siedlisko. W badanym jeziorze rozpoczęła się faza rozwojowa torfowiska przejściowego i wysokiego. Dystrofia postępuje od brzeżnych, całkowicie zarośniętych i zładowanych partii jeziora do jego partii centralnych.

SŁOWA KLUCZOWE: końcowe fazy zarastania jeziora, torfowiska, zonacja roślinności, chemizm wody i podłoża, proces dystrofizacji.