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Submerged macrophytes as bioindicators of environmental conditions in shallow lakes in eastern Poland

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Abstract – We investigated the responses of submerged macrophytes to environmental conditions in shallow lakes to evaluate the role of macrophytes as bioindicators of water quality and anthropogenic disturbances (such as eutrophication) of shallow lake ecosystems. The studies were conducted on a group of ten shallow lakes situated on the area of Polesie Lubelskie (eastern Poland). The lakes represented five types of macrophyte communities, *Chara*- *Stratiotes*-, *Myriophyllum*-, *Potamogeton*- and *Ceratophyllum*-dominated. The total biomass of macrophytes and their distribution were significantly negatively correlated with the trophic status of the lake. Principal component analysis confirms the separation of the lakes with regard to trophic status and macrophyte species richness and biomass. The results of the Monte Carlo permutation test (RDA analysis) indicated the significant effect of Secchi disc depth, pH, conductivity, chlorophyll-*a*, P_{tot}, P-PO_4, N-NO_3 and N-NH_4 on the biomass and distribution of submerged macrophytes in the lakes.

Key words: Macrophytes / bioindicators / environmental conditions / shallow lakes

Introduction

Submerged macrophytes constitute a key element in the functioning of shallow lakes and promote clear water conditions (Scheffer *et al.*, 1993; Jeppesen *et al.*, 2007). Macrophytes provide a refuge for small animals against predation, change the nutrient dynamics of the ecosystem, and prevent resuspension of the sediments, thus regulating water turbidity with consequences for physicochemical water quality and biotic communities (Kristensen *et al.*, 1992; Horppila and Nurminen, 2001).

One of the most important ways in which macrophytes influence the lake status is their role in nutrient cycling. Due to the production of high biomass, aquatic plants have a high capacity for accumulation of biogenic compounds (Clarke and Wharton, 2001; Abdo and Da Silva, 2002). In general, the structural complexity and biomass of submerged macrophytes are regulated by nutrient enrichment. Phosphorus and nitrogen control are of great importance in maintaining the biodiversity of lake ecosystems. Phosphorus is considered to be a major determinant of primary production in lakes, particularly for phytoplankton (Kalff, 2001). The relationship between total phosphorus and chlorophyll-*a* concentrations in water is strongly affected by the percentage of water column and bottom area infested by macrophytes (Canfield *et al.*, 1984; Faafeng and Mjelde, 1998). Nitrogen, which may be lost through denitrification processes within lake ecosystems, appears to be a limiting factor for some macrophytes and algal populations in macrophyte-dominated shallow lakes (James *et al.*, 2005; Moss *et al.*, 2005). Under nutrient enrichment, changes of macrophyte structure follow the general sequence of growth forms: from charophytes via elodeids to phytoplankton. In shallow hypertrophic lakes, submerged species are absent or reduce to one or two species appearing in the form of stray shoots or small patches (Rørslett, 1991; Toivonen and Huttunen, 1995; Egertson *et al.*, 2004).

Macrophytes are known to be confined to specific habitats and react to many different changes in their optimal habitat (Barko *et al.*, 1986; Murphy, 2002; van Geest, 2005). It is therefore often suggested that macrophytes are sensitive to anthropogenic disturbances, including sedimentation (Mahaney *et al.*, 2004), hydrological modifications (Squires and van der Valk, 1992) and eutrophication (Penning *et al.*, 2008) and can be used as an indicator assemblage.

Eutrophication, as a human-induced factor, affects the trophic status of shallow lake ecosystems in Europe. Such negative relations are observed in the Polesie Lubelskie region (eastern Poland) (Kornijów and Radwan, 2002;

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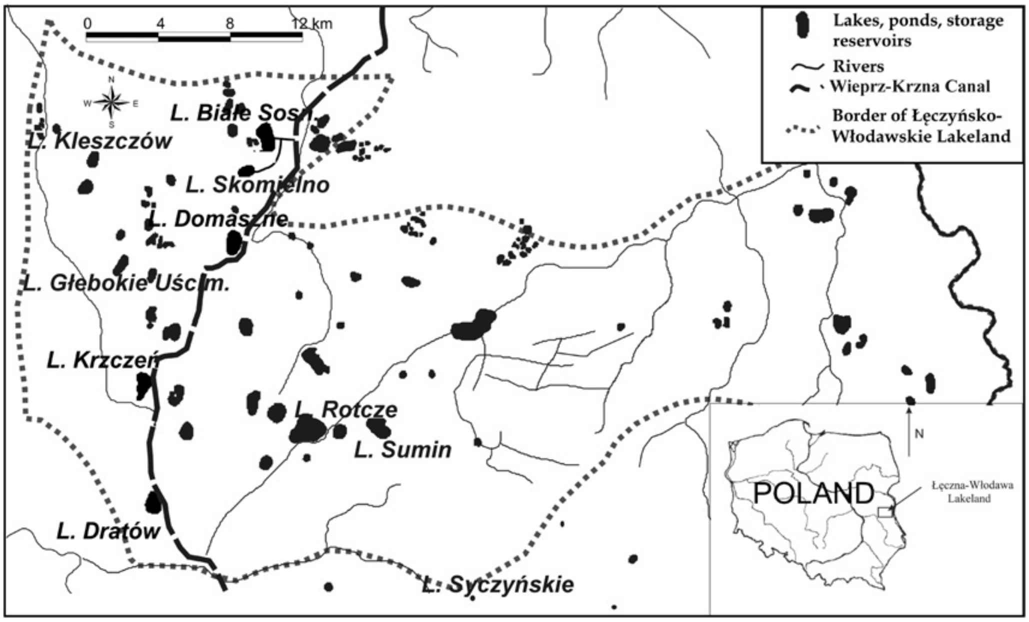

Fig. 1. Location of studied lakes. Kleszczów – *Char*_lake; Rotcze – *Strat*_lake 1; Skomielno – *Strat*_lake 2; Sumin – *Myr*_lake; Głębokie Uścimowskie– *Cer*_lake 1; Domaszne – *Cer*_lake 2; Krzczeń – *Cer*_lake 3; Syczyńskie – *Cer*_lake 4; Białe Sosnowickie – *Pot*_lake 1; Dratów – *Pot*_lake 2.

Small *et al*., 2005). Intensive external loading of nutrients comes from catchments, used mainly for agriculture purposes, animal production and recreational activity, and causes deterioration in the water quality of many lakes. Highly productive lakes are often characterized by permanent and long-lasting cyanobacteria blooms. The group of shallow Polesie lakes is very specific; the origin of these lakes is not clear and still debated (the lakes are situated beyond the range of the last glaciation) (Kolada *et al*., 2005). As a result, the study of the relationships between environmental variables and macrophyte diversity in terms of eutrophication processes will make a significant contribution to the monitoring of shallow lake ecosystems.

As a consequence, the aim of the work described in this paper was to determine the links between the physical and chemical variables of the lakes and the diversity of submerged macrophytes, in an attempt to evaluate the potential of these plants as biological indicators of the environmental conditions of shallow lakes.

The specific objectives of the study were to: (1) describe species structure, biomass and spatial distribution of submerged macrophytes; (2) analyze the relations between macrophyte diversity and trophic state of the lakes; and (3) recognize the significant habitat conditions (environmental variables) affecting macrophyte structure and distribution.

Materials and methods

Study area

The study was conducted in ten shallow, polymictic lakes situated in the area of Polesie Lubelskie (eastern Poland); Kleszczów (51°31′N, 22°53′E), Rotcze (51°22′N, 23°06′E), Skomielno (51°29′N, 23°00′E), Głębokie Uścimowskie (51°28′N, 22°55′E), Domaszne (51°28′N, 23°0′E), Krzczeń (51°23′N, 22°56′E), Syczyńskie (51°17′N, 23°14′E), Sumin (51°22′N, 23°08′E), Białe Sosnowickie (51°32′N, 23°02′E) and Dratów (51°20′N, 22°56′E) (Fig. 1). The morphological parameters and environmental conditions of the lakes are presented in Table 1.

Water sampling and analysis

Water samples used for evaluation of habitat conditions were taken simultaneously with macrophytes, in July of 2011, 2012 and 2013. Samples were collected in the middle lake zone, using a 10 dm^3 tube sampler. *In situ,* a YSI multiparameter meter was used to record water temperature, Secchi disc depth, dissolved oxygen, pH and conductivity. At the laboratory, we determined nutrient compounds ($N\text{-}NH_4$, $N\text{-}NO_3$, P_{tot}, $P\text{-}PO_4$) and chlorophyll-*a* (spectrophotometric method) (Golterman, 1969; Hermanowicz *et al*., 1999).

The trophic state of the lakes was determined using the synthetic trophic state index (TSI) (Carlson, 1977). The TSI was calculated as the average value of concentrations of total phosphorus, Secchi disc visibility and Chl-*a* according to the formula:

$$\mathrm{TSI} = \frac{(\mathrm{TSI}_{\mathrm{Ptot}} + \mathrm{TSI}_{\mathrm{SD}} + \mathrm{TSI}_{\mathrm{Chl}-a})}{3},$$

where

$$\mathrm{TSI}_{\mathrm{Ptot}} = 14^{x}\ln(P_{\mathrm{tot}}) + 4.15,$$

$$\mathrm{TSI}_{\mathrm{SD}} = 6014.41^{x}\ln(\mathrm{SD})\ \text{and}$$

$$\mathrm{TSI}_{\mathrm{Chl}-}a = 9.81^{x}\ln(\mathrm{Chl}a) + 30.6.$$

Table 1. Limnological parameters (data according Harasimiuk *et al.*, 1998; Dawidek *et al.*, 2004) and environmental conditions of the studied lakes (mean values July 2011–2013). *Char*_lake-*Chara*-dominated Lake Kleszczów; *Strat*_lake 1 – *Stratiotes*-dominated Lake Rotcze; *Strat*_lake 2 – *Stratiotes*-dominated Lake Skomielno; *Cer*_lake1 – *Ceratophyllum*-dominated Lake Głębokie; *Cer*_lake 2 – *Ceratophyllum*-dominated Lake Domaszne; *Cer*_lake 3 – *Ceratophyllum*-dominated Lake Krzczeń; *Cer*_lake 4 – *Ceratophyllum*-dominated Lake Syczyńskie; *Myr*_lake – *Myriophyllum*-dominated Lake Sumin; *Pot*_lake 1 – *Potamogeton*-dominated Lake Białe Sosnowickie; *Pot*_lake 2 – *Potamogeton*-dominated Lake Dratów.

	*Char*_lake	*Strat*_lake1	*Strat*_lake2	*Myr*_lake	*Cer*_lake 1	*Cer*_lake 2	*Cer*_lake 3	*Cer*_lake 4	*Pot*_lake 1	*Pot*_lake 2
Surface area (ha)	53.9	42.7	75.0	91.5	20.5	95.0	160.7	5.6	167.9	135.8
Maximum depth (m)	2.3	4.3	5.5	6.5	7.1	3.1	5.2	2.9	3.0	2.7
Catchment area (ha)	253.4	157.2	305.0	106.0	173.8	352.2	246.2	458.2	675.5	481.6
Catchment type	Agriculture	Agriculture	Forest	Agriculture	Agriculture	Agriculture	Agriculture	Agriculture	Agriculture	Forest
Temperature (°C)	24.2 ± 1.2	26.1 ± 1.4	21.2 ± 1.1	27.5 ± 1.4	23.4 ± 1.2	20.7 ± 1.1	19.7 ± 0.9	22.3 ± 1.2	21.5 ± 1.1	20.8 ± 1.0
Secchi disc visibility (m)	1.3 ± 0.06	2.3 ± 0.11	2.6 ± 0.13	0.8 ± 0.04	0.7 ± 0.03	0.4 ± 0.02	0.6 ± 0.03	0.5 ± 0.02	0.8 ± 0.04	0.5 ± 0.02
pH	7.3 ± 0.4	7.6 ± 0.38	8.4 ± 0.42	7.4 ± 0.37	6.9 ± 0.34	8.8 ± 0.44	8.8 ± 0.44	7.2 ± 0.36	8.2 ± 0.41	8.2 ± 0.38
Conductivity (μS.cm^{-1})	136 ± 7	226 ± 11	244 ± 12	421 ± 21	247 ± 12	250 ± 13	250 ± 11	574 ± 29	380 ± 19	343 ± 17
Total suspension (mg.L^{-1})	5.3 ± 0.3	3.4 ± 0.2	2.9 ± 0.15	8.3 ± 0.41	13.2 ± 0.66	11.2 ± 0.56	18.4 ± 0.92	14.3 ± 0.72	27.5 ± 1.37	37.8 ± 1.89
Dissolved oxygen (mg.L^{-1})	9.5 ± 0.4	10.1 ± 0.5	9.1 ± 0.45	8.5 ± 0.43	9.1 ± 0.46	12.3 ± 0.62	12.3 ± 0.59	6.7 ± 0.34	11.5 ± 0.57	13.7 ± 0.68
N-NH$_4$ (mg.L^{-1})	0.367 ± 0.02	0.149 ± 0.07	0.098 ± 0.04	0.372 ± 0.02	0.181 ± 0.009	0.164 ± 0.008	0.108 ± 0.005	0.211 ± 0.011	0.148 ± 0.007	0.091 ± 0.005
N-NO$_3$ (mg.L^{-1})	0.381 ± 0.03	0.135 ± 0.06	0.080 ± 0.004	0.221 ± 0.01	0.118 ± 0.006	0.156 ± 0.007	0.120 ± 0.006	0.216 ± 0.010	0.047 ± 0.002	0.085 ± 0.004
P-PO$_4$ (mg.L^{-1})	0.002 ± 0.001	0.006 ± 0.001	0.053 ± 0.002	0.007 ± 0.001	0.044 ± 0.002	0.042 ± 0.002	0.054 ± 0.003	0.330 ± 0.017	0.060 ± 0.003	0.026 ± 0.001
Ptot (mg.L^{-1})	0.022 ± 0.007	0.050 ± 0.009	0.066 ± 0.003	0.032 ± 0.002	0.258 ± 0.013	0.209 ± 0.011	0.231 ± 0.012	0.568 ± 0.028	0.126 ± 0.006	0.080 ± 0.004
Chlorophyll-*a* (μg.L^{-1})	9.66 ± 0.48	8.73 ± 0.43	10.92 ± 0.54	38.89 ± 1.9	41.74 ± 2.1	46.21 ± 2.3	76.9 ± 3.8	50.87 ± 2.5	60.43 ± 3.1	51.18 ± 2.6
TSI	52.6	53.5	54.9	61.3	72.2	78.7	77.9	78.3	69.3	67.5

Macrophyte sampling and analysis

The species structure and spatial distribution of macrophytes were estimated during maximum abundance in July, along horizontal transects according to Jensen (1977). A single transect constituted a minimum width of 30 m and started from the lake shore to a maximum depth of occurrence of vegetation.

The number of transects varied between 6 and 18 and depended on the surface area of the lake. At each point of a transect, water depth, species presence and macrophyte coverage were estimated using a viewer and a rake. Mean macrophyte coverage was calculated according to the Braun-Blanquet scale and was assigned to the following categories: 0,1–1, 1–5, 5–25, 25–50, 50–75 and 75–100% coverage. Based on macrophyte-covered area for each transect, we determined total macrophyte cover in the lake.

Macrophyte biomass was sampled by collecting plants at sediment level at an area of 0.16 m^2. At each sampling date, three random replicates per lake were taken. Each macrophyte sample was put into a separate plastic bag. At the laboratory, the plants were gently washed under running tap water to avoid damaging plant tissues, and blotted to remove surface moisture. Each sample was washed separately. Next, the plants were put into a 105 °C for 10 h to obtain the dry weight (DW).

The species diversity of macrophytes was evaluated using the Shannon-Wiener index, calculated according to the formula (Krebs, 1989):

$$H^{'} = \sum_{i=1}^{s} (p_i)(\log_2 p_i).$$

were: s – number of species, p_i – proportion of individuals belonging to the i species to the total number of individuals.

Data analysis

The influence of the lake (defined as a set of environmental conditions) on the total biomass of macrophytes and the area of macrophyte cover was verified using one-way analysis of variance (ANOVA). The relationships between habitat conditions (lake trophic status) and macrophyte diversity and biomass were determined by calculating Pearson correlation coefficients.

The biomass data (matrices) were used to test the effect of lake type on macrophyte structure and percentage cover using principal component analysis (PCA). The effect of habitat conditions (a group of nine environmental variables: Secchi disc depth, conductivity, pH, dissolved oxygen, N-NH$_4$, N-NO$_3$, P_{tot}, P-PO$_4$, and chlorophyll-*a*) on the structure and spatial distribution of submerged macrophytes was verified using partial redundancy analysis (RDA). The PCA and RDA analyses were applied after detrended correspondence analysis (DCA), which indicated the linear species responses to the environmental

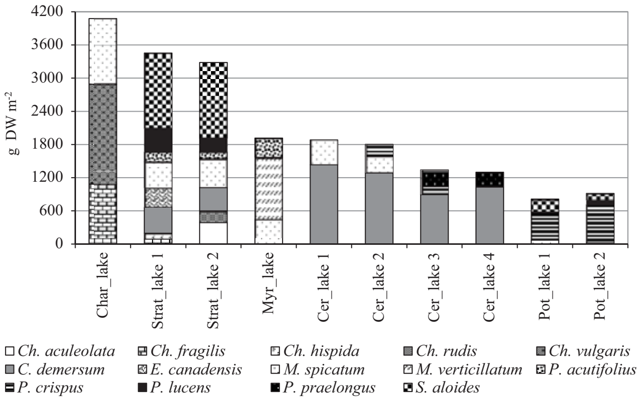

Fig. 2. Total biomass and domination structure of submerged macrophytes in studied lakes (mean values July 2011–2013 per lake; $N = 90$). For lake abbreviations see Table 1.

gradient (length of gradient <2 SD) (ter Braak and Šmilauer, 2002). The Monte Carlo permutation test (499 permutations, full model analysis) was used to determine the variables of significant influence on macrophyte structure and distribution (Lepš and Šmilauer, 2003). The ordination analyses were performed using CANOCO 4.5 for Windows.

Results

Environmental parameters

The physical and chemical water parameters of the studied lakes showed high variability (Table 1). Significant differences between the lakes were noted for Secchi disc visibility (ANOVA, $F = 11.87$; $P < 0.001$), total suspension (ANOVA, $F = 5.62$; $P < 0.001$), N-NH$_4$ (ANOVA, $F = 10.13$; $P < 0.001$), N-NO$_3$ (ANOVA, $F = 4.28$; $P < 0.015$), Ptot (ANOVA, $F = 28.94$; $P < 0.011$), P-PO$_4$ (ANOVA, $F = 53.26$; $P < 0.001$) and chlorophyll-*a* (ANOVA, $F = 7.25$; $P < 0.001$).

Macrophyte structure and biomass

The studied lakes represent five macrophyte community types: *Chara*-, *Stratiotes*, *Myriophyllum*-, *Potamogeton*- and *Ceratophyllum*-dominated. These types differed significantly in terms of total area overgrown by macrophytes (ANOVA, $F = 53.18$; $P < 0.001$) and the total biomass of macrophytes (ANOVA, $F = 233.31$; $P < 0.001$). The total biomass ranged from 814.4 g.DW.m^{-2} (*Potamogeton*-dominated lakes) to 4076.6 g.DW.m^{-2} (*Chara*-dominated lake) (Fig. 2). The species richness of macrophytes varied between 2 and 8 species and showed the highest values in *Stratiotes*-dominated lakes (Fig. 3). The highest macrophyte cover was observed in *Chara*-dominated (92%) and *Stratiotes*-dominated lakes (67–84%); the lowest in *Potamogeton*-dominated lakes, at the lakes submerged macrophytes overgrown from 7 to 11% of lake bottom area (Fig. 3).

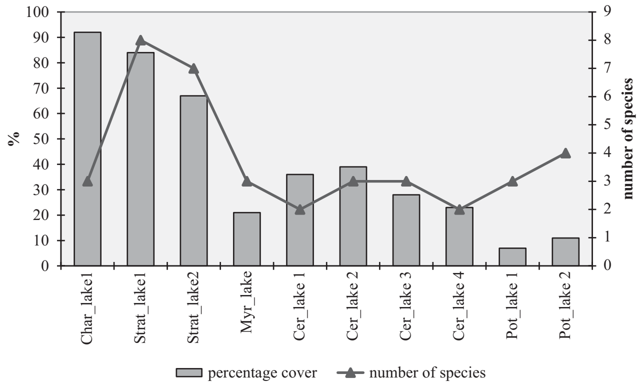

Fig. 3. Percentage cover of submerged macrophytes with regard to the number of species (mean values July 2011–2013). For lake abbreviations see Table 1.

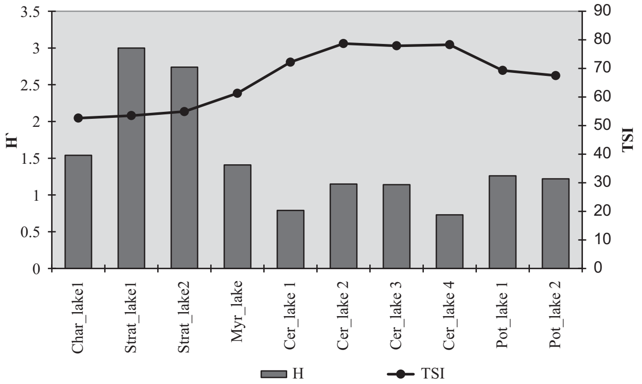

Fig. 4. Species diversity of submerged macrophytes (values of Shannon-Wiener index) with regard to lake trophic status (TSI index) (mean values July 2011–2013). For lake abbreviations see Table 1.

Macrophyte diversity *versus* lake trophic status

The diversity of submerged macrophytes (values of the Shannon-Wiener index) differed visibly between the lake types (Fig. 4). Values for the H index ranged from 0.73 (*Ceratophyllum*-dominated lake) to 3.0 (*Stratiotes*-dominated lake). Values for the trophic state index were significantly negatively correlated with macrophyte biomass ($r = -0.66$; $P = 0.014$), species diversity ($r = -0.79$; $P = 0.006$) and percentage cover of macrophytes ($r = -0.62$; $P = 0.022$). The lowest values of TSI, 52.6–54.9, were noted in *Chara*- and *Stratiotes*-dominated lakes. In *Myriophyllum*- and *Potamogeton*-dominated lakes, the trophic state index varied between 61.3 and 69.3, and in *Ceratophyllum*-dominated lakes, TSI was the highest (72.2–78.7), typical for hypertrophic lakes (Fig. 4).

Ordination analysis

Axis 1 ($\lambda = 0.426$) and axis 2 ($\lambda = 0.265$) of PCA explained 69.1% of the total variance in macrophyte

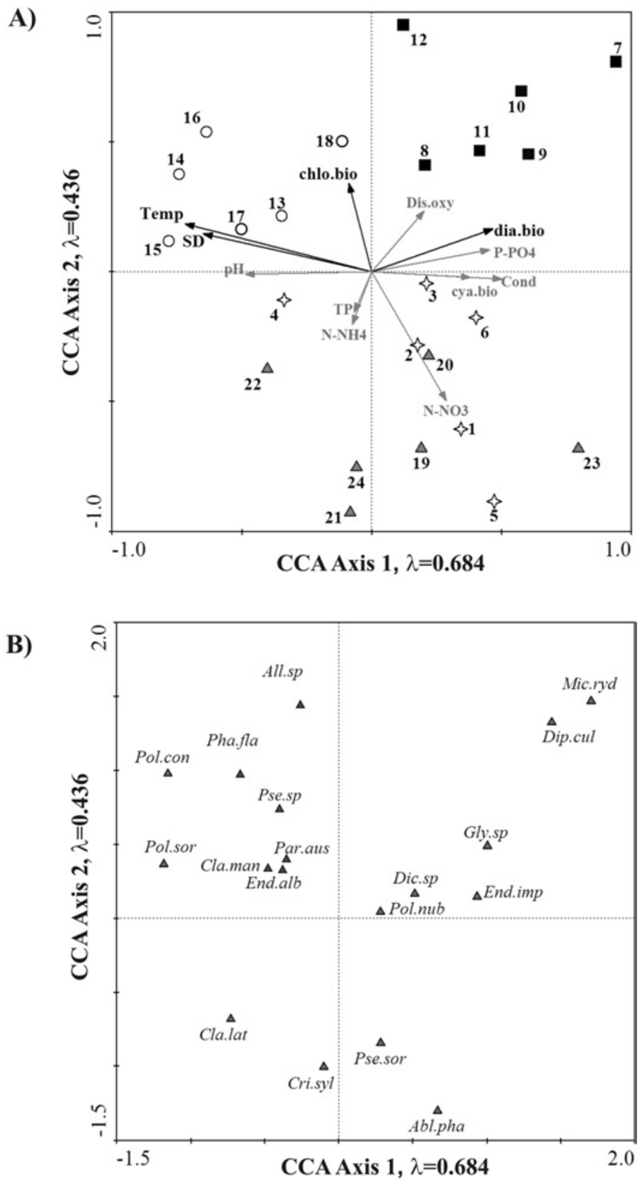

Fig. 5. Principal component analysis (PCA) plot for axis 1 and 2 showing macrophyte samples collected in studied lakes. Axes are derived from the variation in the macrophyte data. Samples collected in studied lakes are marked with an Arabic numeral: 1–9 – *Chara*-dominated Lake Kleszczów; 10–18 – *Stratiotes*-dominated Lake Rotcze; 19–27 – *Stratiotes*-dominated Lake Skomielno; 28–36 – *Myriophyllum*-dominated Lake Sumin; 37–45 – *Ceratophyllum*-dominated Lake Głębokie Uścimowskie; 46–54 – *Ceratophyllum*-dominated Lake Domaszne; 55–63 – *Ceratophyllum*-dominated Lake Krzczeń; 64–72 – *Ceratophyllum*-dominated Lake Syczyńskie; 73–81 – *Potamogeton*-dominated Lake Białe Sosnowickie; 82–90 – *Potamogeton*-dominated Lake Dratów.

distribution. These two axes showed a clear division of the studied lakes into four groups (Fig. 5). *Stratiotes*-dominated lakes (Group II) were visibly separate from *Chara*-dominated lakes (Group I), *Myrophyllum*-lakes (Group III) and Group IV, which included *Ceratophyllum*- and *Potamogeton*-dominated lakes.

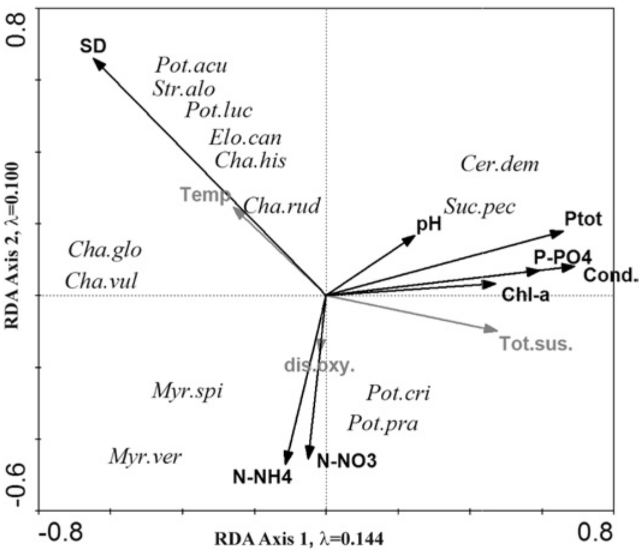

Fig. 6. Redundancy analysis (RDA) biplot for axis 1 and 2 showing macrophyte species biomass and environmental variables. Solid arrows indicate significant variables based on Monte Carlo permutation test ($P < 0.05$). Temp-water temperature; SD – Secchi disc visibility; Cond-conductivity; dis.oxy – dissolved oxygen; N-NH_4 – ammonium nitrogen; N-NO_3 – nitrate nitrogen; P-PO_4 – dissolved orthophosphates; P_{tot} – total phosphorous; Chl-a – chlorophyll-*a*; tot.sus-total suspension. *Cha.glo-Chara globularis, Cha.his-Chara hispida, Cha.rud-chara rudis, Cha.vul-Chara vulgaris, Cer.dem-Ceratophyllum demersum, Elo.can-Elodea canadensis, Myr.spi-Myriophyllum spicatum, Myr.ver-Myriophyllum verticillatum, Pot.acu.-Potamogeton acutifolius, Pot.cri-Potamogeton crispus, Pot.luc-Potamogeton lucens, Stu.pec-Stuckenia pectinata, Pot.pra-Potamogeton praelongus, Str.alo-Stratiotes aloides.*

The results of RDA confirmed the division of macrophyte species with regard to lake tropic status (Fig. 6). We noted the significant effect of eight environmental variables (results of the Monte Carlo permutation test) on the distribution and biomass of macrophyte species within lake types. Secchi disc visibility ($\lambda = 0.11$; $F = 10.39$; $P = 0.002$) showed a significant effect on distribution of large groups of macrophyte species, *Chara globularis, Chara hispida, Chara rudis, Chara vulgaris, Elodea canadensis*, *Stratiotes aloides*, *Potamogeton acutifolius* and *Potamogeton lucens*. These species are associated with *Chara*- and *Stratiotes*-dominated lakes. Chlorophyll-*a* ($\lambda = 0.03$; $F = 3.23$; $P = 0.018$), pH ($\lambda = 0.04$; $F = 4.92$; $P = 0.002$), P-PO_4 ($\lambda = 0.02$; $F = 2.69$; $P = 0.026$), Ptot ($\lambda = 0.03$; $F = 4.09$; $P = 0.008$) and conductivity ($\lambda = 0.10$; $F = 10.46$; $P = 0.004$) were the determinants of biomass and distribution of *Ceratophyllum demersum* and *Stuckenia pectinata* in *Ceratophyllum*-dominated lakes. However, concentrations of N-NH_4 ($\lambda = 0.10$; $F = 1.89$; $P = 0.012$) showed a significant effect on the abundance of *Myriophyllum spicatum* and *Myriophyllum verticillatum*, the dominant species in *Myriophyllum*-dominated lakes. N-NO_3 ($\lambda = 0.44$; $F = 4.09$; $P = 0.006$) was the determinant for the presence of *Potamogeton* *crispus* and *Potamogeton praelongus,* both pondweed species typical for *Potamogeton*-dominated lakes.

Discussion

Macrophyte assemblages showed great potential as indicators of environmental conditions in shallow lakes. We observed visible changes within macrophyte communities through *Chara*, *Stratiotes*, *Myriophyllum*, *Potamogeton* up to *Ceratophyllum* dominance, which reflect the eutrophication process of lake ecosystems.

Chara-dominated lakes are characterized by the highest total biomass of macrophytes (g.DW.m^{-2}). Charophytes, which grow on the bottom of the water column, are known to be negatively affected by nutrient enrichment (van den Bund and van Donk, 2004; Bakker *et al*., 2010). We also observed a significant effect of Secchi disc visibility on the biomass of macrophytes in the lake. This observation can be related to the results of Egertson *et al.* (2004), who indicated the importance of light as a limiting factor for the changes in macrophyte composition and relative abundances as a response to increased turbidity due to agricultural eutrophication. Moreover, *Chara* spp. are known to have an allelopathic effect on algal growth (Mulderij *et al.,* 2003). Studies by Mulderij *et al.* (2007) showed that the allelopathic activity of *Chara* spp. may cause a reduction in phytoplankton growth of 5–10%.

Stratiotes-dominated lakes showed high biomass and species richness of macrophytes. The presence of the macrophyte species *Stratiotes aloides* is evidence of the good ecological status of a lake ecosystem (Smolders *et al*., 2003; Pełechaty *et al*., 2015). As indicated by the study performed by Mulderij *et al*. (2007), *S. aloides* has stronger allelopathic activity than *Chara* spp., which may result in the reduction of phytoplankton biomass even by 80%. Moreover, during the summer, *S. aloides* often floats on the water and has a potential shading effect on phytoplankton. In addition, this macrophyte species had a considerable effect on the reduction of phosphorus levels in the water.

In *Myriophyllum*-dominated lakes, the biomass of macrophytes was quite low, observed in highly eutrophic lakes. Eurasian watermilfoil *(Myriophyllum spicatum*), one of the key species in the lake, is a submerged species exhibiting potent growth and dispersal strategies that enable the plant to rapidly dominate various aquatic systems (Smith and Barko, 1990). Milfoil-dominated lakes usually have low phytoplankton densities (Gross *et al.,* 1996). We observed such a relation in our study. Lower concentrations of planktonic chlorophyll-*a* in *Myriophyllum*-dominated lakes were probably a result of the allelopathic effect of *Myriophyllum* species. *M. spicatum* exhibits a strong inhibitory action against various cyanobacteria, and to a lesser extent to chlorophytes and diatoms (Gross *et al.,* 1996; Körner and Nicklisch, 2002). The production of anticyanobacterial polyphenols has also been reported for another species of the *Myriophyllum* genus, *M. verticillatum* (Aliotta *et al.,* 1992). In the present study, the biomass of *Myriophyllum* species was significantly related to higher concentrations of nitrogen compounds (especially N-NH_4) in water. Large increases in *M. spicatum* biomass, between 30 and 40%, were also observed during experimental studies with ammonium enrichment by Anderson and Kalff (1986). Moreover, studies carried out by Schneider and Melzer (2004) showed that the growth of *M. spicatum* was positively correlated with high water ammonia concentrations.

Ceratophyllum-dominated lakes showed typical hypertrophic conditions; the dominant species, *Ceratophyllum demersum,* may even grow where only 1% of surface water illumination is available (Hutchinson, 1975), which enables its development under high phytoplankton biomass and low water transparency. In the studied *Ceratophyllum*-dominated lakes, we observed a significant effect of total phosphorus and chlorophyll-*a* concentrations on the biomass of *C. demersum* (results of RDA analysis), as well as a positive relationship (Spearman correlation coefficient) between the biomass of macrophytes and concentrations of total phosphorus in water. The presence of *S. pectinata* confirms its tolerance for eutrophic conditions (Grassmuck *et al*., 1995) – the plant forms a canopy to exploit light near the water surface (van den Berg *et al*., 1999). *S. pectinata* can tolerate turbid conditions rather well, but most often does not produce high biomass (Bakker *et al*., 2010; Hidding *et al*., 2010).

In *Potamogeton*-dominated lakes, we observed the lowest biomass of macrophytes and low species diversity. In these ecosystems, curly-leaf pondweed *Potamogeton crispus* dominated. The species is an indicator of eutrophication (Nichols and Shaw, 1986) and is best suited to nutrient-rich water. Curly-leaf pondweed tolerates low light conditions (Tobiessen and Snow, 1984) and turbidity (Nichols, 1992).

In conclusion, the species structure and distribution of submerged macrophytes documented in this study were lake-specific and related to water transparency and the nutrient status of the lake. Moreover, the results of ordination analysis as well as correlation coefficients led us to conclude that abundant growth and high species richness of macrophytes are the combined effect of environmental conditions, such as Secchi disc depth, and concentrations of nutrients and chlorophyll-*a*, specific for a given lake ecosystem.

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