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DETERMINANTS OF THE DIVERSITY OF MACROPHYTES IN NATURAL LAKES AFFECTED BY LAND USE IN THE CATCHMENT, WATER CHEMISTRY AND MORPHOMETRY LAKES

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Abstract

This study investigated 14 lakes situated in the Borecka Forest, and the analyzed data covered a period of 10 years. The examined water bodies are at low risk of eutrophication. Three factors explaining 79.1% of total variability in the analyzed natural lakes were identified: 1 – morphometry – use of catchment area, 2 – water chemistry, 3 – lake/catchment area. Those factors determined the patterns of macrophyte distribution in the lakes. The variables applied in the CCA ordination plot explained around 59% of the total variability in plant distribution patterns in the examined lakes. Chlorophyll *a* (chl-*a*) was a statistically significant parameter, which explained 12.4% of the total variability in plant distribution patterns in the analyzed lakes. Morphological, physicochemical and catchment area variables have a significant effect on the development of vegetation in the Natura 2000 sites. The results of this study provide the basis for formulating general management guidelines for the investigated lakes and their catchments, which belong to the Natura 2000 ecological network of protected areas. A comprehensive protection plan should be proposed for interdependent habitats. Forest cover in the lakes' catchment areas should be maintained or expanded, and the share of intensively farmed land should be reduced. Clear cutting in areas adjacent to the lakes should be prevented, and the inflow of biogenic elements, nitrogen and phosphorus (which affects Chl-*a* concentrations) should be reduced. The above goals can be achieved, among others, by preserving the existing water relations and species composition of tree stands in the lakes' catchments areas.

Keywords: catchment, CCA, macrophytes, Natura 2000 sites, spatial structure.

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UWARUNKOWANIA RÓŻNORODNOŚCI MAKROFITÓW W JEZIORACH NATURALNYCH POD WPŁYWEM ZAGOSPODAROWANIA TERENU ZLEWNI, CHEMII WODY I MORFOMETRII JEZIOR

Abstrakt

Obiektem badań było 14 jezior usytuowanych na terenie Puszczy Boreckiej. Dane do analiz obejmowały okres 10-letni. Jeziora te należą do zbiorników słabo zagrożonych eutrofizacją. Ustalono 3 czynniki wyjaśniające 79,1% całkowitej zmienności badanych jezior naturalnych. Są to: czynnik 1 – morfometria jeziora/użytkowanie zlewni, czynnik 2 – chemia wody, czynnik 3 – powierzchnia zlewni/jeziora. Czynniki te wpływają na wzorzec rozmieszczenia roślinności w badanych jeziorach. Zastosowane w ordynacji CCA zmienne tłumaczą ok. 59% ogólnej zmienności wzorca rozmieszczenia roślinności badanych jezior. Ustalono, że parametrem istotnym statystycznie jest koncentracja chlorofilu *a*, co tłumaczy 12,4% ogólnej zmienności wzorca rozmieszczenia roślinności w badanych jeziorach. Zróżnicowanie morfologiczne zbiorników, cech chemicznych oraz parametrów zlewniowych jezior ma decydujący wpływ na wykształcanie się poszczególnych typów roślinności, charakteryzujących siedliska Natura 2000. Na podstawie badań możliwe jest sformułowanie generalnych zaleceń, które mimo różnych charakterystyk badanych jezior są podobne. Zarządzanie siedliskami Natura 2000, jakimi są badane jeziora, wymaga właściwego zarządzania na poziomie obszaru zlewni. Właściwym działaniem jest objęcie ochroną całościową wzajemnie współzależnych siedlisk. Korzystne dla utrzymania i zachowania siedlisk Natura 2000 obejmujących badane jeziora jest zwiększanie lub utrzymanie na istniejącym poziomie powierzchni leśnych w zlewni jezior i ograniczanie intensywnego rolniczego użytkowania zlewni jezior. Wskazane jest zapobieżenie całkowitym wyrębom drzewostanu ze stref przyległych do zbiorników, ograniczenie dopływu pierwiastków biogennych: azotu i fosforu, co wpłynie na wielkość koncentracji chlorofilu *a*. Można to osiągnąć, m.in. utrzymując w zlewni istniejące stosunki wodne oraz zachowując zgodny z siedliskiem skład gatunkowy drzewostanów na obszarze zlewni tych jezior.

Słowa kluczowe: zlewnia, CCA, makrofity, Sieć Natura 2000, struktura przestrzenna.

INTRODUCTION

Similarly to most sessile organisms, macrophytes show a long-term response to changes in environmental conditions (NURMINEN 2003, OBOLEWSKI et al. 2009, NAPIÓRKOWSKA-KRZEBIETKE et al. 2012). The discriminating power of macrophytes along lake size and depth gradients is complex (MURPHY 2002, NURMINEN 2003), and the occurrence of species is more likely determined by biological and stochastic factors than by simple environmental determinism (SØNDERGAARD et al. 2010). The main environmental factors affecting macrophyte abundance in lakes are general water chemistry (SPENCE 1982, JEPPESEN et al. 1994, 2000, GLIŃSKA-LEWCZUK 2009, GLIŃSKA-LEWCZUK, BURANDT 2011, GRZYBOWSKI et al. 2010*a*,*b*), the trophic status of a lake (SPENCE 1982, KOLADA 2010) and light availability (CANFIELD et al. 1985). Macrophytes affect the physical, chemical and biological parameters of lakes, and they reflect the impact of various environmental factors such as lake morphometry, water chemistry and biotic interactions (CHERUVELIL, SORANNO 2008, KOLADA 2010). The structure of aquatic vegetation can be used to determine the diversity of flora and lake habitats (CIECIERSKA 2006) and, above all, the factors that change with the depth gradient (Murphy 2002). The combined, long-term effects of those factors diversify aquatic vegetation along the environmental gradient (Spence 1982, Banaś et al. 2012).

The objectives of this study were to: (a) determine the factors that affect macrophyte distribution in natural lakes, (b) identify the factors that affect the patterns of plant distribution in the analyzed lakes. The research hypothesis was as follows: macrophyte distribution patterns in natural lakes are determined by lake-type-specific variables. Another aim of the study was to propose management recommendations for lakes which are protected sites included in the Natura 2000 network.

MATERIALS AND METHODS

The analyzed site is situated in the Borecka Forest (geographic coordinates 54°07′31″N; 22°08′54″E) in the north-eastern part of the Masurian Lakeland. This large forest complex occupies a total area of 25 340.1 ha, and it is characterized by low anthropogenic pressure. Agriculture and forestry represent the main types of human activity in the investigated area. Tourism pressure is low, and there are no industrial plants and cities in the vicinity. All of the 14 analyzed lakes (Figure 1, Table 1) are protected sites

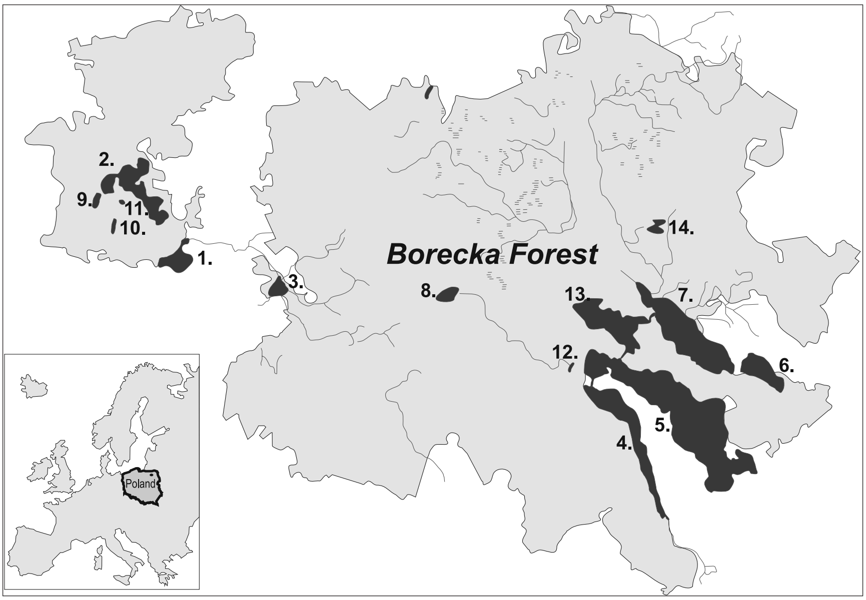

Fig. 1. Geographical location of the studied lakes in the Borecka Forest

Lake types are marked with numbers; stratified lakes: 1 – Zabinki, 2 – Krzywa Kuta, 3 – Lekuk, 4 – Litygajno, 5 – Lazno, 6 – Szwalk Maly, 7 – Szwalk Wielki, 8 – Wolisko; non-stratified lakes: 9 – Biala Kuta, 10 – Smolak, 11 – Kacze, 12 – Dubinek, 13 – Pilwag, 14 – Ciche

Table 1

Characteristic features of the analyzed lakes and their catchments

Lake	Morphometry					Water quality indicators								Catchment				
	no of tran-sect	sur-face area (km^2)	mean depth (m)	max depth (m)	SLD	SD (m)	pH	TP ($mg\ dm^{-3}$)	TN ($mg\ dm^{-3}$)	Chl-*a* ($\mu g\ dm^{-3}$)	Ca ($mg\ dm^{-3}$)	TOC ($mg\ dm^{-3}$)	cond. ($\mu S\ cm^{-1}$)	catch (km^2)	forests (%)	mea-dows (%)	water (%)	agri-cultu-ral (%)
Biała Kuta	4	0.266	1.4	3.2	1.48	1.4	9	0.024	1.32	0.06	27.85	15.83	188	1.53	79.4	3.2	17.40	
Smolak	3	0.063	1.7	5.1	1.34	0.5	7.66	0.026	1.39	7.7	2.87	15.76	27	0.93	93.2		6.80	
Kacze	2	0.018	0.3	0.8	1.07	0.4	6.8	0.032	1.72	3.74	5.71	57.31	40	0.22	91.9		8.10	
Żabinki	5	0.385	9.1	42.5	1.26	3.2	7.93	0.022	0.87	9.41	60.69	13.22	380	24.29	23.2	12.6	1.60	62.6
Dubinek	2	0.182	2.5	6.2	1.10	0.4	7.55	0.022	2.044	4.79	32.13	11.82	204	1.11	83	0.6	16.40	
Pilwąg	14	1.423	1.5	3.6	1.88	0.6	8.05	0.07	2.25	33.5	49.98	18.92	299	9.48	80.79	4.2	15.01	
Litygajno	19	1.668	6	16.4	2.33	1.3	7.78	0.05	1.6	17.2	52.84	12.19	339	16.04	52.3	11.2	10.40	26.1
Łaźno	24	5.712	5.7	18	2.10	4.1	7.75	0.058	1.4	26.7	54.98	12.46	350	142.63	56.2	6.2	4,00	33.6
Szwałk Mały	9	0.711	4.3	6.7	1.64	0.8	7.66	0.043	2.15	23.7	45.7	12.29	302	9.67	56	2.2	7.30	34.5
Szwałk Wielki	15	2.356	4.9	11	1.72	1.1	8.02	0.082	1.9	19.1	53.55	15.51	312	25.35	72.4	12.1	9.30	6.2
Łękuk	3	0.220	4.6	12.5	1.14	1.5	8.05	0.056	1.65	18.6	57.12	18.41	326	14.09	84.9	6.2	1.60	7.3
Ciche	4	0.160	1.0	2.6	1.81	0.5	6.83	0.132	2.488	63.85	59.98	17.33	343	0.98	82.5	1.2	16.30	
Wolisko	2	0.182	4.5	8.6	1.18	1.1	7.74	0.03	2.24	33.4	51.41	11.88	305	2.56	38.6	28.2	7.10	26.1
Krzywa Kuta	15	1.352	6.0	26.5	2.07	2.1	8	0.072	1.82	35.62	41.41	12.67	248	4.13	32.1	7.1	32.70	28.1

No of transect – number of transect, SLD – shoreline development, SD – Secchi depth, TP – total phosphorus, TN – total nitrogen, chl *a* – chlorophyll *a* concentration, TOC – total organic carbon, Cond – conductivity, catch – surface area of catchment of the Natura 2000 network. The studied lakes have a regular shape (ratio of max. length / max. width < 6.0, SLD – shoreline development < 2.3). Their catchment areas are used as farmland and forests (8 lakes) or forests (6 lakes). The lakes were characterized by various water mixing patterns – eight of them were classified as stratified (Zabinki, Krzywa Kuta, Lekuk, Litygajno, Lazno, Szwalk Maly, Szwalk Wielki, Wolisko) and six as shallow, non-stratified water bodies (Biala Kuta, Smolak, Kacze, Dubinek, Pilwag, Ciche).

Water samples were collected twice a year during the summer stagnation period (Table 1), beginning at the depth of 1 m. Three samples were collected each time, and the results are the means of three replicates. Water transparency was measured with the Secchi disc. Physical and chemical analyses of water samples were performed by standard methods (APHA 1999). Total phosphorus, nitrogen and iron content was determined colometrically using the Shimadzu UV 1601 spectrophotometer. Chlorophyll was analyzed by the acetone extraction method (GOLTERMAN 1969) and corrected for pheophytin. Total organic carbon (TOC) concentrations were determined by high-temperature combustion (HTC) using the Schimadzu TOC 5000 analyzer (DUNALSKA 2009). pH and conductivity were determined in situ using the YSI 6600-meter (Yellow Spring Instruments USA).

Aquatic vegetation was investigated in 2002-2012. Field studies were carried out at the peak of every growing season (from the second half of June to the end of August) over the ten-year period, in all lakes. Vegetation was examined from boats along shorelines using a scaled rope with a grapnel end. The surveyed objects (plant communities, species) were marked on bathymetric maps with the use of a GPS navigation device (Garmin 60CSx). The experiment involved inventories of plant communities (phytosociological surveys) in the entire phytolittoral zone and mapping of plant colonies in the littoral zone. Plant communities in the investigated lakes (including Characeans, submerged vascular plants, floating-leaved and emergent rush and sedge rush phytocenoses) were fully identified. The following parameters were also determined: maximum colonization depth, total colonized area, percentage share of every identified community in the total phytolittoral area. Plant communities were identified and classified following a phytosociological approach which is widely applied in Polish studies of aquatic ecosystems (BRAUN-BLANQUET 1964). Species abundance was determined based on the BRAUN-BLANQUET (1964) scale which was modified by dividing it into five units, where: 1 = very rare, 2 = rare, 3 = common, 4 = frequent and 5 = abundant. Aquatic vegetation was classified based on the system proposed for Poland by MATUSZKIEWICZ (2002). The phytosociological system of plant community classification was used to identify protected sites of the Natura 2000 network (CID 2011). In line with the International Code of Phytosociological Nomenclature (WEBER et al. 2000), the inventory of plant communities covered: alliance (All.) *Magnocaricion* Koch 1926 – reed beds

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No of transect – number of transect, SLD – shoreline development, SD – Secchi depth, TP – total phosphorus, TN – total nitrogen, chl *a* – chlorophyll *a* concentration, TOC – total organic carbon, Cond – conductivity, catch – surface area of catchment composed of large sedges, natural or anthropogenic communities of tall marshland plants, mostly species of the genus *Carex*; All. *Phragmition* Koch 1926 – reed beds characterized by relatively poor floristic composition, usually found between amphiphytes of the littoral zone and floating-leaved or submerged plants; class (Cl.) *Charetea* (FUKAREK 1961 n.n.) KRAUSCH 1964 – macrophytes rooted in the bottom of oligotrophic and mesotrophic water bodies, mostly large algae belonging to *Charophyta*; All. *Potamion* KOCH 1926 em. OBERD. 1957 – mostly submerged plants rooted in the bottom of natural water bodies, artificial water reservoirs, stagnant and slow-flowing waters; All. *Nymphaeion* OBERD. 1953 – macrophytes rooted in the bottom of water bodies, mostly floating-leaved plants found in shallow stagnant waters; Cl. *Lemnetea* R.Tx. 1955 – pleustophytes floating on the surface of stagnant and slow-flowing waters, often found in communities of aquatic and rush plants; Cl. *Utricularietea intermedio-minoris* DEN HARTOG et SEGAL 1964 em. PIETSCH 1965 – plant communities in shallow dystrophic and oligotrophic water bodies with a naturally accumulated layer of peat, dominated by species of the genera *Utricularia* and *Sparganium* as well as rusty peat mosses and peat mosses.

Macrophyte diversity was described using the phytocenotic diversity index (H) calculated based on the Shannon-Wiener index modified by CIECIERSKA (2006).

The species composition of macrophytes in the analyzed lakes was studied in transects. Transects were mapped in accordance with the method proposed by Jensen (1977) to ensure that survey results were representative. Transects were uniformly distributed along the shoreline. They had the width of 100-200 m, and their length was determined based on the maximum reach of macrophyte communities.

The catchment area of the studied lakes varied from 0.22 to 142.63 km^2. Catchment areas were classified into the following categories based on the predominant type of land use: forests – forests and seminatural areas (including raised bogs, transition mires and quaking bogs, low peat bogs, etc.); meadows – semi-natural hay meadows, dry grasslands, pastures, etc. (land principally occupied by agriculture, with significant areas of natural vegetation); agricultural – arable land, permanent crops, homogenous agricultural areas, etc.; and aquatic. Catchment groups were mapped and their percentage cover was determined (Figure 2). The areas of catchment groups are given in square kilometers. The percentage share of forests, meadows and aquatic catchments is shown in Table 1 (square kilometers were used in analyses).

Statistical analysis

Data were analyzed using factor analysis and nonparametric Spearman's correlation analysis in the Statistica 10 package (StatSoft Inc. 2011). A factor analysis of 15 environmental indices (morphological, physicochemi-

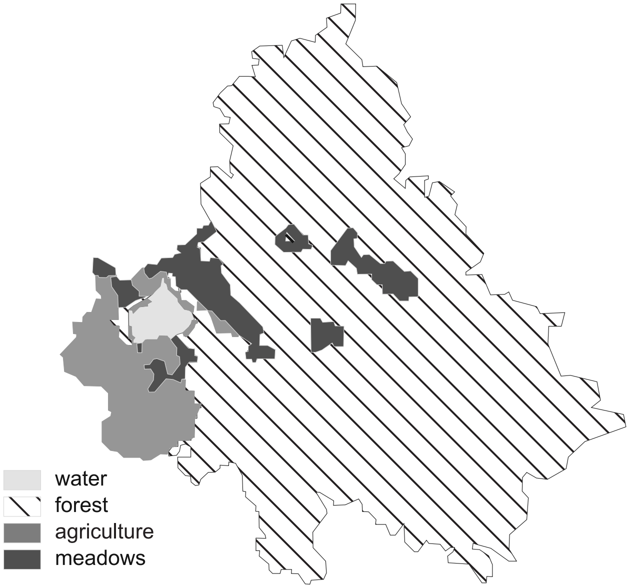

Fig. 2. Land use categories in the catchment area of Lake Leluk

Catchment areas were classified into the following categories: 84.9% – forests (forests and seminatural areas, including raised bogs, transition mires and quaking bogs, low peat bogs, etc.); 6.2% – meadows (semi-natural hay meadows, dry grasslands, pastures, i.e. land principally occupied by agriculture, with significant areas of natural vegetation); 7.3% – agricultural (arable land, permanent crops, homogenous agricultural areas, etc.) and 1.6% – aquatic. Catchment groups were mapped and their percentage cover was determined

cal and catchment area variables) was performed using the 'Varimax-normalized' rotation method. Only statistically significant values were used in further analyses. A preliminary detrended correspondence analysis (DCA) revealed the first gradient length of 2.88 SD, indicating that models based on linear species response models were appropriate for the data structure (Lepš, Šmilauer 2007). A canonical correspondence analysis (CCA) was performed to relate macrophyte species composition to environmental variables in CANOCO (ter Braak, Šmilauer 2002). The composition of aquatic macrophytes in lakes was determined based on the percentage share of species which were reported from more than 5% of transects (i.e. from more than 6 out of the 121 analyzed transects). Statistical significance tests were carried out using Monte Carlo permutation tests. A Monte Carlo test was used to examine the significance of axis eigenvalues generated in the analysis and the species-environmental correlation (using 5000 unrestricted iterations).

RESULTS

Based on the average concentrations of total phosphorus and nitrogen, the studied lakes were classified as mesotrophic and eutrophic water bodies [based on different nutrient (N, P) and chlorophyll criteria in trophic status classification methods proposed by WETZEL (1983), OECD (1982) and NÜRNBERG (2001), but their actual trophic class ranged from oligotrophic to hypertrophic. The majority of the investigated lakes (12) are hard-water bodies with a high calcium content and high alkalinity. In summer, the average total phosphorus concentrations were lower in stratified lakes (0.051±0.035 mg dm^{-3}) than in shallow lakes (0.059±0.064 mg dm^{-3}) – Table 1. The average total nitrogen concentrations were also lower in stratified water bodies (1.71±0.77 mg dm^{-3}) than in non-stratified lakes (1.87±0.73 mg dm^{-3}) in the summer season (Table 1). The average TN/TP ratio in the summer epilimnion was higher in shallow lakes (54) than in deep stratified lakes (38). In summer, chlorophyll concentrations were relatively high (>25 μg dm^{-3} in 6 lakes), ranging from 0.006 ±0.003 μg dm^{-3} (Lake Biala Kuta) to 63.9±0.17 μg dm^{-3} (Lake Ciche) on average (Table 1). Secchi disc visibility was determined in the range of 1.4 ± 3.7 m, and it was higher in deep lakes. Total organic carbon concentrations (TOC) did not exceed 20 mg dm^{-3} in most lakes (13).

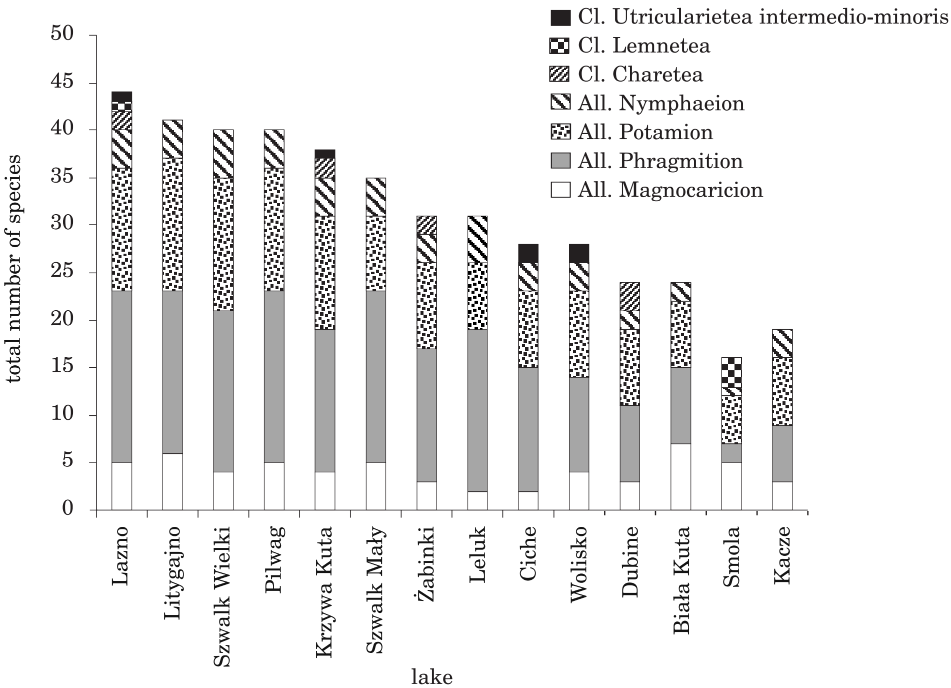

Fig. 3. Total number of macrophyte species from different phytosociological groups in the investigated lakes of the Borecka Forest

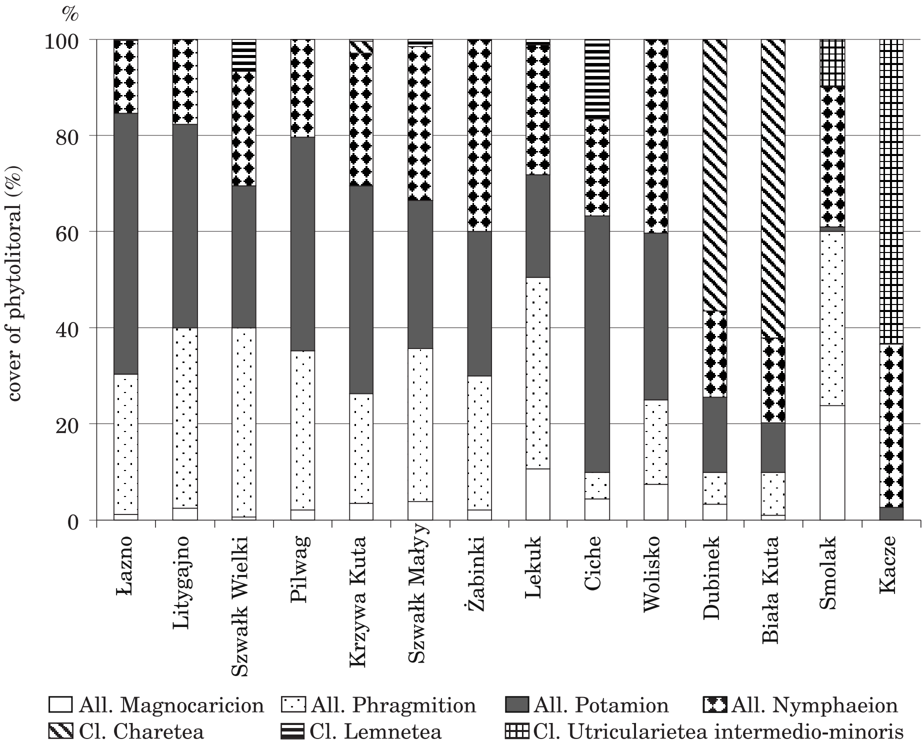

Fig. 4. Variations in aquatic plant communities colonizing the analyzed lakes

In the survey of aquatic vegetation performed in 2002–2012, a total of 123 macrophyte taxa were observed in 14 lakes, including 68 emergent, six floating-leaved, seven free-floating and 42 submerged plant species (including 5 *Characeae* species), although only 19 to 44 macrophyte taxa were determined per lake (Figure 3). The average value of the phytocenotic diversity index (H) was determined at 1.3±0.62 in stratified lakes and at 1.7±0.34 in non-stratified lakes.

Plant communities of the alliances *Phragmition* and *Potamion* had the largest combined share of the phytolittoral zone in most lakes (10). A significant contribution of *Charetea* communities (approximately 60%) was observed in lakes Biala Kuta and Dubinek, and a high share of *Utricularietea intermedio-minoris* communities was noted in lakes Smolak and Kacze (Figure 4).

During factor analysis, abiotic variables (Table 1) were divided into three groups of factors which explained 79.1% of total variability (Table 2, Figure 5). Factor 1 was the morphometry – use of catchment area (mean depth, max. depth, forests and farmland), factor 2 was water chemistry (TP, TN, Chl-a), and factor 3 was the lake/catchment area – (lake area and catchment area).

Table 2

'Varimax-normalized' rotated factor loadings of abiotic variables (abs > 0.7) and the direction of their influence (+ or -) in the investigated lakes

Variable	Factor 1: morphometry – use of catchment area	Factor 2: water chemistry	Factor 3: lake/catchment area
Surface area			0.942
Mean depth	0.880		
Max depth	0.804		
TP		0.764	
TN		0.815	
chl *a*		0.821	
Catch			0.801
Forest	-0.908		
Agricultural	0.827		
Percent of variability	32.3	17.3	29.5

A canonical correspondence analysis (CCA) was performed to relate macrophyte species composition to statistically significant environmental variables. The variables applied in the CCA ordination plot explained around 59% of total variability in plant distribution patterns in the studied lakes. The variables are correlated with the first and second canonical axes, and the longest vectors were Chl-*a* and TP (Figure 6). The first axis expla-

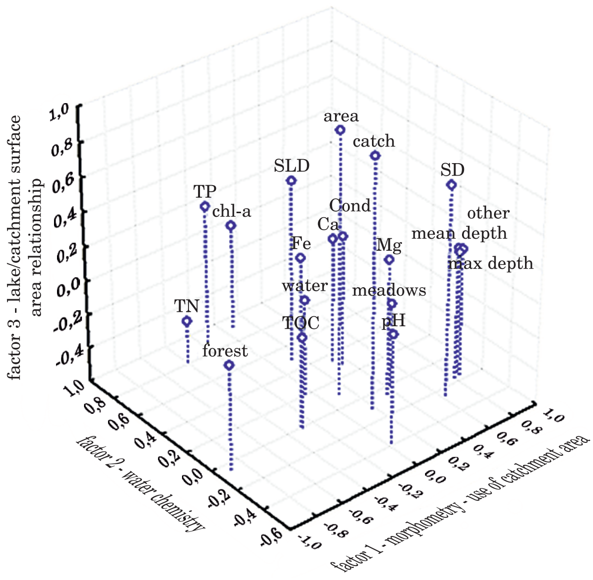

Fig. 5. Abiotic variables described by factors 1-3 in the studied lakes

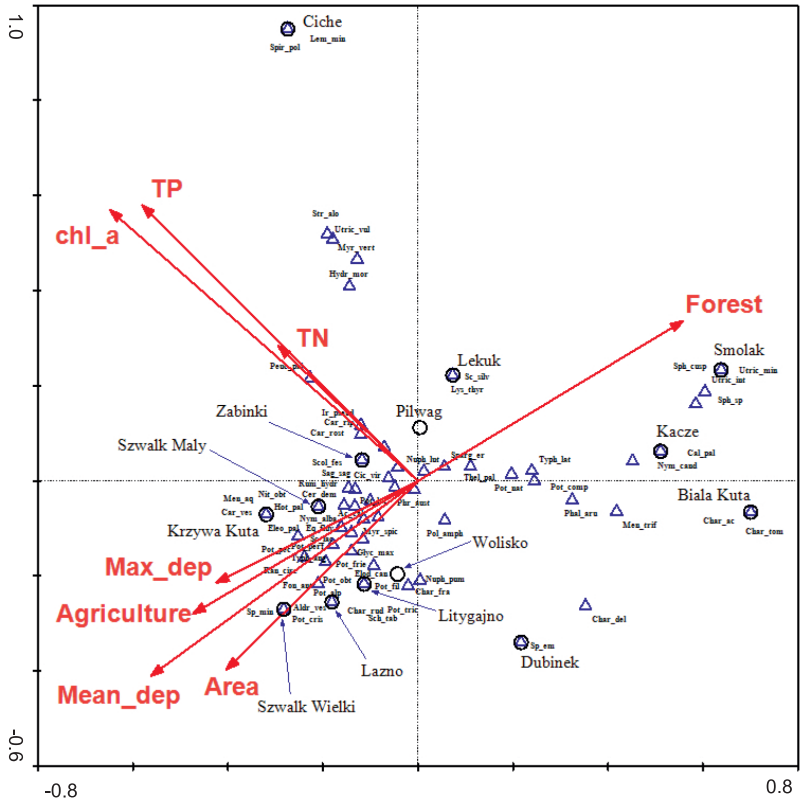

Fig. 6. CCA ordination plots – two first axes

The analysis of the composition of aquatic macrophytes in the lakes was based on the presence and absence of the species and only the common species (present in more than 5% sample sites) were considered in the analysis: *Phr_aust - Phragmites australis, Sc_lac - Scirpus lacustris, Ir_pseud - Iris pseudoacorus, Eleo_pal - Eleocharis palustris, Men_aq - Mentha aquatica, Car_rost - Carex rostrata, Typh_ang - Typha angustifolia, Peuc_pal - Peucedanum palustre, Ac_cal - Acorus calamus, Typh_lat - Typha latifolia, Phal_aru - Phalaris arundinacea, Car_rip - Carex riparia, Eq_fluv - Equisetum fluviatile, Sparg_er - Sparganium erectum, Cic_vir - Cicuta virosa, Glyc_max - Glyceria maxima, Rum_hydr - Rumex hydrolapathum, Sch_tab - Schoenoplectus tabernaemontani, Men_trif - Menyanthes trifoliata, Thel_pal - Thelypteris palustris, Cal_pal - Calla palustris, Scol_fest - Scolochloa festucacea, Lys_thyr -Lysimachia thyrsiflora, Sc_silv - Scirpus silvaticus, Car_ves - Carex vesicaria, Hot_pal - Hottonia palustris, Nuph_lut - Nuphar lutea, Nym_alba - Nymphaea alba, Nuph_pum - Nuphar pumilum, Nym_cand - Nymphaea candida, Pol_amph - Polygonum amphibium f. natans, Pot_nat - Potamogeton natans, Pot_luc - Potamogeton lucens, Pot_pec - Potamogeton pectinatus, Pot_perf - Potamogeton perfoliatus, Pot_frie - Potamogeton friesii, Pot_alp - Potamogeton alpinus, Pot_comp - Potamogeton compressus, Pot_fil - Potamogeton filiformis, Pot_obt - Potamogeton obtusifolius, Pot_trich - Potamogeton trichoides, Pot_crisp - Potamogeton crispus, Cer_dem - Ceratophyllum demersum, Myr_spic - Myriophyllum spicatum, Myr_vert - Myriophyllum verticillatum, Ran_circ - Ranunculus circinatus, Elod_can - Elodea canadensis, Char_tom - Chara tomentosa, Char_ac - Chara aculeolata, Char_del - Chara delicatula, Char_rud - Chara rudis, Char_fra - Chara fragilis, Nit_obt - Nitellopsis obtusa, Hydr_mor - Hydrocharis morsus - ranae, Str_alo - Stratiotes aloides, Sp_em - Sparganium emersum, Sp_min - Sparganium minimum, Sag_sag - Sagittaria sagittifolia, Lem_min - Lemna minor, Spir_pol - Spirodela polyrhiza, Utric_vul - Utricularia vulgaris, Utric_int - Utricularia intermedia, Utric_min - Utricularia minor, Aldr_ves - Aldrovanda vesiculosa, Fon_ant - Fontinalis antipyretica, Sph_sp - Sphagnum sp., Sph_cusp - Sphagnum cuspidatum.*

Circles denote lakes, and triangles denote macrophyte species.

Table 3

Spearman's rank correlation between abiotic variables and aquatic vegetation metrics in two types of lakes in the Borecka Forest ($p < 0.05$)

Macrophyte metrics	Factor 1				Factor 2			Factor 3	
	morphometry – use of catchment area				water chemistry			lake-catchment area	
	mean depth	max depth	forests	agricultural	TP	TN	Chl *a*	lake area	catchment area
Stratified lakes (n = 8)									
No of species					-0.51	-0.61			
H	-0.52			-0.38	-0.59				
Proportion of phytocenoses in different syntaxonomic groups									
%Chara			0.39	-0.39	-0.52				
%Pota					-0.61				
%Nymph	-0.59	-0.67		0.40				-0.38	
%Phra	0.52		-0.38		0.38		0.66	0.38	
%Mcar									
%Lemn									
%Utric									
Non-stratified lakes (n = 6)									
No of species				-0.91					
H			0.67						
Proportion of phytocenoses in different syntaxonomic groups									
%Chara			0.39	-0.62	-0.63	-0.39	-0.71		
%Pota				0.80	0.39				
%Nymph	-0.61	-0.49			0.39	0.45	0.55		
%Phra	0.39		-0.61		0.38	0.58	0.66		
%Mcar									0.44
%Lemn				0.88			0.78		
%Utric	-0.61	-0.51	0.80		0.68	0.67	0.55		

The table includes only abiotic variables which appeared in the factor analysis.
No of species – number of species; H – Shanon index; Cl. – class, All. – alliance; proportion of phytocenoses: %Chara – class *Charetea* %, Pota – alliance *Potamion*, %Nymph – alliance *Nymphaeion*, %Phra – alliance *Phragmition*, %Mcar – alliance *Magnocaricion*, %Lemn – class *Lemnetea*, %Utric – class *Utricularietea intermedio-minoris*; TP – total phosphorus, TN – total nitrogen, Chl*a* – chlorophyll *a*; Cl. – class, All. – alliance; empty cell – no relationship, correlation values

ins 30.5% of total variability, and the second axis – 19.4%, which accounts for 84.6% of explained variability (with 59% total variability). The test of significance of the first canonical axis revealed a significant gradient that determines differences in plant distribution patterns in the analyzed lakes (p = 0.05). The first axis is strongly correlated with Chl-*a* (-0.6), TP (-0.55), Forest (0.53), and Mean depth (-0.53), followed by Agricultural (-0.45) and

Max depth (0.40). The second axis is strongly correlated with TP (0.56) and Chl-*a* (0.55). Chl-*a* (lambda = 0.28, p = 0.002, F = 3.67) was a statistically significant parameter (Monte Carlo permutation test, $p < 0.05$) which explained 12.4% of total variability in plant distribution patterns in the examined lakes.

The correlations between environmental factors and the share of phytosociological groups in stratified and non-stratified lakes were also examined (Table 3). Spearman's correlation analysis examining macrophyte metrics and environmental indices showed that the number of species present in all ecological zones was negatively correlated with nutrient concentrations (TP, TN) in stratified lakes and with agricultural catchments in non-stratified lakes (Table 3). Biological diversity described by SHANNON'S index in stratified lakes increased with a decrease in depth, a decrease in the share of agricultural areas in the catchment and a drop in TP levels (Table 3). The percentage cover of forests in the catchment was positively correlated with biological diversity in non-stratified lakes (Table 3).

The share of phytocenoses of the class *Charetea* increased with the percentage cover of forests in the catchment area, it decreased with a drop in TP concentrations in stratified lakes and with a decrease in TP, TN and Chl-*a* levels in non-stratified lakes (Table 3).

The distribution of nympheids in stratified and non-stratified lakes was negatively correlated with depth (Mean depth, Max. depth), and it was positively correlated with lake area (Area) and the percentage cover of forests in the catchment only in stratified lakes (Table 3). A positive correlation with TP, TN and Chl-*a* was observed in non-stratified lakes (Table 3).

In stratified lakes, the share of *Phragmitetea* class communities was positively correlated with mean depth, TP, Chl-*a* and lake area, and it decreased with an increase in forest cover in the catchment (Table 3). In non-stratified lakes, the share of *Phragmitetea* class communities was positively correlated with mean depth, TP, TN and Chl-*a*. Unlike in stratified lakes, lake area was not a correlated parameter, but correlations were determined with catchment area (Table 3). Similarly to stratified lakes, the share of helophytes of the class *Phragmitetea* decreased with an increase in forest cover in the catchment (Table 3).

In stratified lakes, no significant correlations were noted between the analyzed environmental factors and plant communities of the alliance *Magnocaricion*, class *Lemnetea* or class *Utricularietea intermedio-minoris* (Table 3). In non-stratified lakes, an increase in the share of agricultural catchment area was accompanied by a higher share of pleustophytes in aquatic vegetation, and it was correlated with an increase in chlorophyll a concentrations (Table 3).

No correlations between plant communities of the alliance *Magnocaricion* and environmental factors were determined in stratified lakes. In non-stratified lakes, a positive correlation was observed between the share of plant communities of the alliance *Magnocaricion* and catchment area (Table 3). In stratified lakes, the analyzed environmental factors were not correlated with plant communities of the alliance *Magnocaricion*, class *Lemnetea* or class *Utricularietea intermedio-minoris* (Table 3).

The highest number of significant correlations was observed between plants of the class *Utricularietea intermedio–minoris* in shallow, non-stratified lakes (Table 3). The share of those plant communities increased with the percentage of forest cover in the catchment as well as nutrient and chlorophyll concentrations, and it decreased with depth (Table 3).

DISCUSSION

All of the studied lakes (14) were classified as sites of the Natura 2000 network based on Habitat Directive criteria (EC 1992, CID 2011). The main criterion for classifying water bodies as Natura 2000 sites is the type of aquatic vegetation (plant communities) in lakes. The results of CCA (Figure 7)

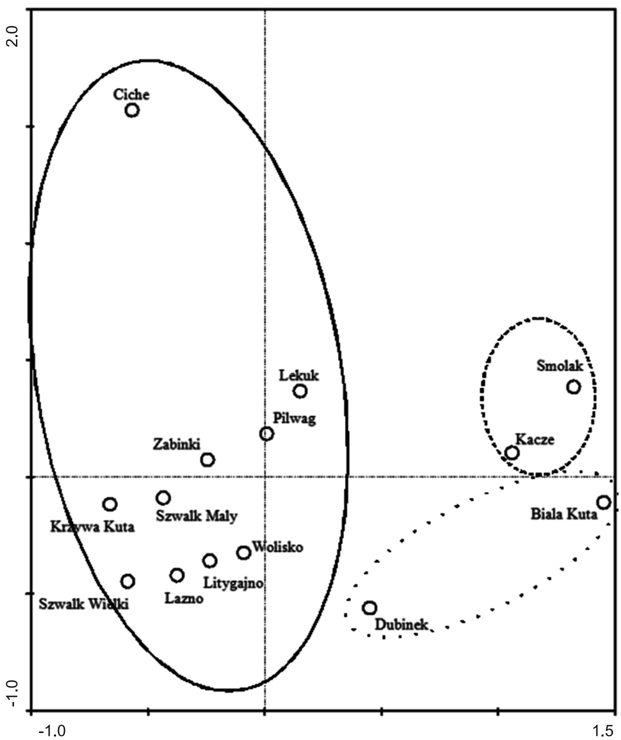

Fig. 7. Generalized CCA ordination plot– two first axes
solid line – eutrophic lakes (3150), dashed line – dystrophic lakes (3160), dotted line – hard oligo-mesotrophic waters with benthic vegetation of Chara spp. (3140); circles denote lakes

supported the identification of eutrophic lakes (Natura 2000 code 3150-1: Litygajno, Żabinki, Szwalk Maly, Lekuk, Szwalk Wielki, Wolisko, Krzywa Kuta, Lazno; Natura 2000 code 3150-2: Pilwag, Ciche). Based on trophic state evaluation criteria (OECD 1982, NÜRNBERG 2001), Lake Ciche was classified as a hypertrophic water body. The above assessment was further confirmed by the results of CCA (Figures 6, 7) which revealed that Lake Ciche had a predominance of pleustophytes (*Lemna minor, Spirodela polyrhiza*) and submerged vegetation (*Myriophyllum verticilatum, Stratiotes aloides, Hydrocharis morsus-ranae, Utricularia vulgaris*) which are characteristic of highly fertile waters (KŁOSOWSKI 2006).

Lakes Biala Kuta and Dubinek are hard oligo-mesotrophic waters with benthic vegetation of *Chara spp*. (Natura 2000 code 3140), whereas lakes Smolak and Kacze were classified as dystrophic water bodies (Natura 2000 code 3160). The variations in plant distribution patters in the above lakes were positively correlated with the first cardinal axis. Lakes Biala Kuta and Dubinek were characterized by low phosphorus concentrations (Table 1). Dense stonewort meadows act as nutrient traps by blocking internal sources of biogenic substances, limiting sediment resuspension and impairing phytoplankton growth (VAN DEN BERG 1999, KUFEL, KUFEL 2002). They secrete growth inhibitors and exert allopathic effects on vascular plants and phytoplankton (VAN DONK, VAN DE BUND 2002). Stoneworts are important regulators of water quality (VAN DER BERG 1999, KUFEL, KUFEL 2002). In those lakes, CCA revealed the presence of species characteristic of the class *Charetea,* and correlations with *Sparganium emersum* were also noted in the phytolittoral zone. In non-stratified lakes, plants of the class *Charetea* were significantly correlated with factor 1 (morphometry – use of catchment area), but only in reference to catchment use, and factor 2 (water chemistry) indicators, which confirms the presence of the above relationships. Similar correlations were noted by other authors (KRAUSE 1981, VAN DEN BERG 1999). They are characteristic of oligotrophic or mesotrophic waters with low phosphorus concentrations and high calcium levels (KRAUSE 1981), and lakes Biala Kuta and Dubinek fit the above description. It is believed that stoneworts have a stabilizing effect when stonewort meadows cover more than 30% of the lake's littoral zone (JEPPESEN et al. 1994, PORTIELJE, RIJSDIJK 2003). This condition was met by lakes Biala Kuta and Dubinek.

The catchments of the analyzed dystrophic lakes (Smolak and Kacze) are largely occupied by raised bogs (<70%) which are a source of humic substances. Most humic substances dissolved in surface waters originate from catchment areas (WILKINSON et al. 1997), and only a small fraction has autochthonic origin (WETZEL 1983, DE HAAN 1992). In general, humic substances stain water, they affect the quality and quantity of light in aquatic ecosystems, increase sedimentation, bind calcium, nitrogen and phosphorus, and neutralize oligotrophic and acidic water bodies (RORSLETT 1987). Dissolved humic substances support the formation of complex phosphorus compounds (De Haan 1992), they accelerate and stabilize calcite precipitation. In acidic environments, humic substances limit the solubility of silica (Conzonno, Cirelli 1995), and similar activity is observed in lakes colonized by stonewort meadows (Kufel, Kufel 2002). Humic substances react with water and sediment components to regulate the quantity and availability of nutrients for plants (Banaś et al. 2012). The above mechanisms explain the CCA results reported in this study (Figures 6, 7). The species identified in lakes Smolak and Kacze are typical of dystrophic waters (mainly species of the class *Utricularietea intermedio–minoris)*, and the positive correlation with the percentage cover of forests in the catchment confirms that the type of land use in catchments affects plant distribution patterns in those lakes. In non-stratified lakes, significant correlations between plants of the class *Utricularietea intermedio-minoris* and factor 1 (morphometry – use of catchment area) and factor 2 (water chemistry) indicators further attests to the presence of the above relationships. The results of the study demonstrate that plant communities of the class *Utricularietea intermedio-minoris* are effective biomarkers of catchment parameters and water quality attributes in both lake types. The ecology of plant communities representing the class *Utricularietea intermedio-minoris* remains poorly investigated. The existing studies suggest that this group of plants is a good indicator of habitat quality, in particular humic substance concentrations in lakes (Adamec, Lev 2002, Ditě et al. 2006). Plant communities of the class *Utricularietea intermedio -minoris* were also found to be correlated with water pH and conductivity (Ditě et al. 2006). The results of this study expand our knowledge about the discussed group of aquatic vegetation.

The proportion of agricultural land in the catchment area was correlated with biological diversity indicators in the examined lakes (Table 3; stratified lakes – agricultural use vs. H, non-stratified lakes – agricultural use vs. number of species). The surface area of stonewort meadows was also found to decrease with an increase in the share of agriculturally used land in the catchment (Table 3). In stratified lakes, the proportion of floating -leaved vegetation increased with the share of agriculturally used land in the catchment. In shallow, non-stratified lakes, an increase in the share of agriculturally used land in the catchment was accompanied by a higher contribution of submerged plants and pleustophytes. These results corroborate the findings of Cheruvelil, Soranno (2008) as well as Kolada (2010) who demonstrated that the type of land use in the catchment is an important indicator of macrophyte distribution patterns in lakes.

The percentage cover of forests in the catchment area was also an indicator of plant structure and diversity in the analyzed lakes. These results are consistent with the findings of Kolada (2010). The values of coefficients of correlation between plant parameters and forest cover in the catchment area were higher in shallow lakes (Table 3). A similar trend was reported by Kolada (2010) in 83 lakes situated in Polish lowlands. The described role of plants of the class *Utricularietea intermedio-minoris* makes a new and original contribution to the existing knowledge.

Most lakes had a considerable share of rush plants of the alliance *Phragmition* (>20% of the phytolittoral zone in 9 lakes). The three identified factors (Tables 2, 3) were correlated with plants of the alliance *Phragmition*. A similar correlation was observed by KOLADA (2010).

Submerged and floating-leaved plants are an indicator of local environmental conditions (SØNDERGAARD et al. 2010). By supplying nutrients and directly influencing habitats, aquatic vegetation also determines abiotic conditions (BARKO et al. 1991, MURPHY 2002) and the flora and fauna of wetlands at various trophic levels (e.g. NORLIN et al. 2005). Yet an analysis of the correlations between submerged vascular plants (all. *Potametea*) and the parameters described by factor 1 (morphometry – use of catchment area) and factor 2 (water chemistry) revealed that submerged and floating-leaved plants play a minor indicative role. They influenced plant distribution patterns in eutrophic lakes classified under code 3150 in the Natura 2000 network (Figure 7). The alliance *Potametea* is composed mainly of ceratophyllids, myriophyllids and potamida. Other authors have demonstrated that this highly varied alliance is represented by plant communities with a broad ecological amplitude (e.g. MURPHY 2002, KŁOSOWSKI 2006). Vascular plants have very different trophic requirements (JEPPESEN et al. 2000). Therefore, the indicative role of communities representing the alliance *Potamion* seems to be very limited, as demonstrated by the results of this study. A positive correlation with TP was noted in stratified lakes, whereas an inverse relationship and a positive correlation with agricultural use of catchment area was observed in non-stratified lakes (Table 3). Floating-leaved plants of the alliance *Nymphaeion* have less diverse environmental requirements than submerged vegetation representing the alliance *Potametea* (KŁOSOWSKI, SZAŃKOWSKI 1999). In both lake types, floating-leaved plants were more robust environmental indicators than submerged vegetation of the alliance *Potamion*. Significant positive correlations were determined between floating-leaved plants and morphometric parameters of the studied lakes (Mean depth, Max. depth). In stratified lakes, floating-leaved plants were additionally correlated with agricultural use of the catchment and were negatively correlated with lake area. Positive correlations with all parameters described by factor 2 (water chemistry) were reported in non-stratified lakes.

Other authors (PORTIELJE, ROIJACKERS 2003, JEPPESEN et al. 2000) have observed that nympheids are highly tolerant of increased turbidity. In this study, this group of plants was a good indicator of water quality in shallow lakes. Similar results were reported by SCHEFFER, VAN NES (2007) who emphasized the growing role of the analyzed plants in shallow lakes and ponds.

Numerous authors have argued that aquatic vegetation in lakes may exhibit a delayed response to nutrient supply because the phosphorus delivered to and present in lakes may be partially unavailable for producers

(Ciecierska 2006). This explains a strong correlation between plant distribution patterns and chlorophyll concentrations and a weaker relationship with the remaining lake parameters in CCA. Despite the above, a significant correlation between nutrient concentrations (TP and TN) and plant communities suggests that those parameters are important drivers of plant distribution patterns in the analyzed lakes. In stratified lakes, weaker correlations were determined between TP levels and plant groups characteristic of eutrophic lakes (*Potamion, Phragmition*), and an inverse relationship was noted between TP concentrations and stonewort meadows. In non-stratified lakes, nutrient concentrations were significantly correlated with vegetation. Significant correlations were noted for two plant groups which determine habitat types in the studied lakes (class *Charetea* and class *Utricularietea intermedio–minoris)*. Nutrient concentrations were also correlated with plant groups encountered in all lake types (%Pota vs. TP; %Phra vs. TP and TN; %Nymph vs. TP and TN). Plant distribution patterns in non-stratified lakes were significantly correlated with chlorophyll concentrations (Table 3). Those relationships are manifested by different plant zones in lakes with varied trophic status. Similar observations were made by Spence (1982) and Rørslett (1987).

The morphological, physicochemical and catchment area parameters of lakes have a significant effect on vegetation development in protected sites of the Natura 2000 network (Figures 6, 7). Lakes of different trophic status differ with respect to the mechanism of eutrophication (Jeppesen et al. 1994, 2000, Murphy 2002, Nurminen 2003, Portielje, Rijsdijk 2003, Norlin et al. 2005, Cheruvelil, Soranno 2008, Kolada 2010). However, the results of the present study provide a basis for formulating general management guidelines for lakes of different types and their catchments, which belong to the Natura 2000 ecological network of protected areas. A comprehensive protection plan should be proposed for interdependent habitats (e.g. lake-forest-peatland). Forest cover in the lakes' catchment areas should be maintained or expanded, and the proportion of intensively farmed land should be reduced. Clearcutting in the areas adjacent to the lakes should be prevented, and the inflow of biogenic elements, nitrogen and phosphorus (which affects Chl-*a* concentrations), should be reduced. The above goals can be achieved, among others, by preserving the existing water relations and species composition of tree stands in the lakes' catchments areas.

Increased human pressure (including agricultural intensification and a decrease in the proportion of forest communities *compatible* with natural *habitat conditions*) in lake catchments leads to increased inflow of biogenic elements and allochthonous matter, which may be followed by eutrophication or even hypertrophication and, ultimately, by the disappearance of submerged vegetation (Ciecierska 2006). In the group of analyzed water bodies, such a situation was observed in Lake Ciche (Table 1, Figure 6).

Effective catchment management is particularly important in shallow, non-stratified lakes (Table 3, Figure 6) whose buffering capacity is low. Dystrophic lakes Smolak and Kacze (code 3160 in the Natura 2000 network) are non-stratified water bodies with a small surface area, surrounded by coniferous forests and peatlands. They are at risk of degradation due to habitat reduction or destruction in their catchments (BANAŚ et al. 2012). Protecting interdependent habitats (lake-forest-peatland) is essential to ecosystem functioning. The priorities for silvicultural management in the catchments of lakes Smolak and Kacze should include the adoption of forest conservation practices and imposing a ban on timber harvesting. Drainage and land reclamation works should also be prohibited, as they could alter the local hydrographic conditions and increase the input of biogenic substances. In dystrophic lakes, eutrophication is usually caused by permanent lowering of the groundwater table in the catchment (due to e.g. long-term drought), lowering of the lake water level, and sphagnum peatland overdrying (CIECIERSKA 2006, BANAŚ et al. 2012), which affect the amount and composition of humic and mineral substances entering the open water zone (DE HAAN 1992).

Lakes Dubinek and Biała Kuta, classified as hard oligo-mesotrophic waters with benthic vegetation of *Chara spp*., seem to be less prone to eutrophication (Figure 6). The key to preserving Natura 2000 3140 sites is maintaining the existing stonewort meadows which serve as buffer zones in lake ecosystems. The implications of charophyte colonization for lake management have been investigated and described (e.g. KRAUSE 1981, VAN DEN BERG 1999). Increased inflow of biogenic elements and a high proportion of farmland and forests in lake catchments contribute to the disappearance of charophyte algae (Table 3). In order to preserve these unique habitats, land use structure in the catchments of Lakes Dubinek and Biała Kuta should remain unchanged. Preferably, the percentage of catchment area under intensive agriculture should be decreased, and the input of biogenic substances from other sources should be limited.

CONCLUSIONS

Morphological, physicochemical and catchment area variables have a significant effect on vegetation development in Natura 2000 sites. The results of this study provide a basis for formulating general management guidelines for the investigated lakes and their catchments, which belong to the Natura 2000 ecological network of protected areas. A comprehensive protection plan should be proposed for interdependent habitats. Forest cover in the lakes' catchment areas should be maintained or expanded, and the proportion of intensively farmed land should be reduced. Clear cutting in the areas adjacent to the lakes should be prevented, and the inflow of biogenic elements, nitrogen and phosphorus (which affects Chl-*a* concentrations), should be reduced. The above goals can be achieved, among others, by preserving the existing water relations and species composition of tree stands in the lakes' catchments areas.

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