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Aquatic and swamp plant communities as indicators of habitat properties of astatic water bodies in north-eastern Poland

Stanisław Kłosowski, Ewa Jabłońska*

Department of Environmental Botany, Institute of Botany, University of Warsaw, Al. Ujazdowskie 4, 00-478 Warsaw, Poland

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Abstract

Phytosociological and habitat studies were conducted on the water and swamp vegetation of astatic water bodies within north-eastern Poland. The phytocoenoses were selected on the basis of dominance of species forming the particular communities. The analysis of 147 relevés showed the existence of 10 vegetation types: *Lemnetum minoris, Spirodeletum polyrrhizae, Riccietum fluitantis, Elodeetum canadensis, Polygonetum natantis, Typhetum latifoliae, Caricetum elatae, Calletum palustris, Potentilletum palustris, Menyanthetum trifoliatae.* Among the properties of water analysed water depth, SO_4^{2-} , pH, total and carbonate hardness, PO_4^{3-} , Ca^{2+} , Mg^{2+} and Na⁺ were found to be most important in differentiating the habitats of the vegetation types studied. Substrate properties, which best differentiated the habitat conditions occurring in astatic water bodies, particular phytocoenoses distinguished on the basis of dominance of one species were associated with specific habitats. The particular phytocoenoses or groups of phytocoenoses could be good indicators of various habitat conditions that occur within astatic water bodies or changes taking place in these habitats.

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Keywords: Astatic waters; Kettle holes; Aquatic and swamp vegetation; Habitat indicators

Introduction

In Central Europe, astatic water bodies (kettle holes) are a characteristic element of the young glacial Lake District landscape. A wide variability of habitat conditions is observed within these bodies of water, e.g. considerable fluctuations of water level as well as a wide variation of physical and chemical properties of water (Nieckuła and Podyma 1985; Mierwald 1988; Kłosowskiet al. 1995; Gloede 2005; Zander 2005, Joniak et al. 2007) and substrates (Nieckuła and Podyma 1985;

*Corresponding author. Tel.: +48 22 553 05 62;

E-mail address: e.jablonska@uw.edu.pl (E. Jabłońska).

Kłosowski et al. 1995). These features distinguish astatic water bodies from larger and more stable aquatic ecosystems, particularly lakes. Occurring in high numbers astatic water bodies play an important role in the landscape. They have a beneficial effect on the water balance, take part in the retention of some mineral elements, and constitute a refuge for a number of rare species of animals, plants as well as plant communities (Kaźmierczak et al. 1995; Bosiacka and Radziszewicz 2002; Kraska et al. 2002). Therefore, they have significant impact upon the biological diversity of Lake District areas. The important role these small water reservoirs play in the landscape is being more widely appreciated. A number of international conferences were held which dealt with the ecology of astatic water

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bodies (e.g. Kettle Hole Workshops – Zander 2005; Nagengast et al., 2007).

Aquatic and swamp plant communities are an important biotic component of astatic water bodies (kettle holes) and have been described in a number of different papers (Solińska 1963; Mierwald 1988; Bosiacka and Radziszewicz 2002, 2003; Kraska et al. 2002). Compared with lakes and other bigger bodies of water, the vegetation of astatic water bodies has a higher proportion of reedswamp and pleustonic communities (classes Phragmitetea and Lemnetea), and is represented by a smaller group of *Potametea* communities (Podbielkowski and Tomaszewicz 1996). There is, however, maintained a typical feature of aquatic vegetation - the phytocoenoses are formed by one dominant species (Kłosowski et al. 1995; Podbielkowski and Tomaszewicz 1996; Bosiacka and Radziszewicz 2002, 2003; Kraska et al. 2002). Studies conducted on the vegetation of astatic water bodies mainly focused on their floristic composition and phytocoenosis structure. However, little seems to be known about the relationship between these plant communities and their habitats (physical and chemical properties of water and substrates). Although the number of papers (studies) dealing with this subject has increased recently (Rudat and Kalettka 2005; Joniak et al. 2007), they present different approaches to this problem and hence, the results cannot be directly compared.

A distinct relationship between plant communities and the particular habitat parameters was determined for various types of water bodies, especially lakes (e.g. Moyle 1945; Spence 1967; Toivonen and Huttunen 1995; Kłosowski 2006; Papastergiadou and Babalonas 1993a, b; Szańkowski and Kłosowski 2006). Therefore, the main objectives of this study were to determine whether, in spite of the wide variability of habitat conditions occurring within the astatic water bodies, the particular plant communities distinguished on the basis of dominance of one species were distinct with respect to their habitats, and to establish if the above communities could be used as indicators of the various habitat conditions or processes occurring within these bodies of water.

Material and methods

The data used in this study were collected since 1978, at the height of the growing season (July–August), when investigations on the ecological amplitude and bioindicator value of aquatic, reedswamp and mire vegetation were initiated in Poland. The investigations were conducted on 106 permanently flooded astatic water bodies having an area ranging from 50–90 to $800-1000 \text{ m}^2$ and water level fluctuations between ± 10 and 50 cm during the growing season.

Specific phytocoenoses were selected on the basis of dominance of species forming the particular communities. Phytocoenoses which occurred only along the moist edge of a water body and, therefore, were not directly associated with the water environment were not taken into consideration.

In each phytocoenosis one phytosociological relevé was recorded by Braun-Blanquet (1951) method and water depth was measured in the deepest and the shallowest point of the phytocoenosis. In each relevé, the abundance of each species was estimated according to a modified Braun–Blanquet scale in which + = a few scattered specimens, mean coverage 0.1%; 1 = 1-10%coverage, mean 5%; 2 = 10-25% coverage, mean 17.5%; 3 = 25 - 50%coverage, mean 37.5%; 4 = 50-75% coverage, mean 62.5%; 5 = 75-100%coverage, mean 87.5%. A total of 147 phytocoenoses were investigated.

In each phytocoenosis (within the relevé area) one water (in the pleustonic phytocoenoses) or one water and one substrate samples (in phytocoenoses attached to the bottom) were taken for chemical analyses (147 water and 108 substrate samples together). Both types of samples were collected at the same time as the relevés were performed (July-August). Water samples were taken from an intermediate depth at which a given phytocoenosis occurred and transferred to two 1000 ml plastic containers. Half of the water samples were preserved by the addition of $1 \text{ ml } H_2 \text{SO}_4^{2-}$ for PO_4^{3-} , NO_3^- and total Fe analyses (Hermanowicz et al. 1976). Prior to the analyses all the samples were filtered. Substrate samples were taken from the rhizome-root layer with a tubular bottom sampler and transferred to plastic bags. Each sample was a mixture of three random sub-samples taken within a phytocoenosis.

The collected water and substrate samples were transported to the laboratory within several hours (3-5) and the determinations were carried out immediately. The samples were stored in refrigerators at $4 \,^{\circ}C$ until all the analyses were performed.

The following analyses were carried out in water samples: pH (using pH-meter), total and carbonate hardness using Warthy-Pfeifer sodium mixture, PO_4^{3-} spectrophotometrically by molybdate method, $NO_3^$ spectrophotometrically with phenoldisulphonic acid, total Fe spectrophotometrically by the rhodanate method, dissolved SiO₂ spectrophotometrically by the molybdate method, SO_4^{2-} spectrophotometrically by the nephelometric method, Mg^{2+} with atomic absorption spectrophotometer, Ca^{2+} , K^+ , Na^+ with a flame spectrophotometer (concentrations of K^+ and Na^+ were determined in 100 ml solutions extracted with 2 ml HCl (1+1) from evaporated and ignited 100 ml samples of water).

In the substrate samples, the following properties were assessed directly: pH (in pore water), water content

and organic matter content. Concentrations of $NO_3^$ were determined in solutions extracted by addition of 100 ml demineralised water to a substrate sample containing 1 g of dry matter (water extracts). In the case of solutions used for determinations of total Fe, Ca^{2+} , Mg^{2+} , PO_4^{3-} and SO_4^{2-} each substrate sample containing 1 g of dry matter was first digested in 20 ml HCl (1+1) for 2h and then 100 ml of demineralised water were added (acid extracts). After 24 h all the extracted solutions were filtered, rinsed with small amounts of demineralised water and the final quantities of the solutions were adjusted to 250 ml. Concentrations of K^+ and Na^+ in substrate were determined in 100 ml water solutions extracted with 2 ml HCl (1+1) from ignited samples. The analyses from water and acid extracts, the determinations of K^+ , Na^+ and pH were conducted by the methods described above. Water content 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 h and total N by Kjeldahl's method.

The main types of phytocoenoses were distinguished on the basis of dominance of particular species and then they were compared with respect to each property using quartiles. Because data could not be normalised via transformation, the Kruskal-Wallis test and the nonparametric multiple comparisons (Zar 1984) were applied to determine significant differences of the habitat properties among the vegetation types studied. Moreover, species-habitat relationships were determined by means of canonical correspondence analysis (CCA) using CANOCO for Windows Version 4.0 (Ter Braak and Smilauer 1998). Two sets of data were analysed separately: species - water properties and species - substrate properties. The analysis was performed for all species; however, the diagram presents only the dominant species, which determine the structure and physiognomy of the phytocoenoses.

Results

Plant associations

The following species dominated in the 147 phytocoenoses investigated in the astatic water bodies within north-western Poland (in the case of each species the number of relevés are given in brackets): *Lemna minor* (16 relevés), *Spirodela polyrrhiza* (11), *Riccia fluitans* (12), *Elodea canadensis* (16), *Polygonum amphibium* (11), *Typha latifolia* (9), *Carex elata* (19), *Calla palustris* (21), *Potentilla palustris* (17) *Menyanthes trifoliata* (15). The 10 vegetation types obtained (Table 1) correspond to the following plant associations: *Lemnetum minoris* (Oberd., 1957) Müll. et Görs, 1960, *Spirodeletum polyrrhizae* (Kelhofer, 1915) W. Koch, 1954 em R.Tx. et A. Schwabe, 1974 in R.Tx. 1974, Riccietum fluitantis Slavinić 1956 em. R.Tx. 1974, Elodeetum canadensis (Pign, 1953) Pass., 1964, Polygonetum natantis Soó, 1927, Typhetum latifoliae Soó, 1927, Caricetum elatae Koch, 1926, Calletum palustris (Osvald, 1923) Vanden Berghen 1952, Potentilletum palustris Kłosowski et al. (1995), Menyanthetum trifoliatae (Osvald, 1923) Nowiński, 1927. The analysis of Table 1 showed that some of the associations were distinguished from each other by the presence or absence of certain groups of species. The pleustonic communities (Lemnetum minoris, Spirodeletum polyrrhizae, Riccietum fluitantis) were characterized by a higher proportion of the dominating as well as other Lemnetea species. Species belonging to Lemnetea also occurred with a lower cover in all other communities. The phytocoenoses of Elodeetum canadensis and Potentilletum palustris had the highest frequency of Potametea species. Within the patches of Polygonetum natantis the lowest species diversities were found. In the case of swamp communities, i.e. Typhetum latifoliae and Caricetum elatae, the latter community was richer in species and had a higher proportion of species representing the Molinio-Arrhenatheretea class. Phragmitetea species were also abundant within the phytocoenoses of Potentilletum palustris, Menyanthetum trifoliatae and Calletum palustris. However, the phytocoenoses belonging to the three associations mentioned above were characterised by the highest overall species richness as well as the high cover of mire species (Scheuchzerio-Caricetea nigrae), including bryophytes, and presence of Utricularietea intermedio-minoris species.

Water properties

The water properties which best differentiated the habitats of the associations studied were (Fig. 1): water depth, SO_4^{2-} , PO_4^{3-} pH, total and carbonate hardness, Mg^{2+} and Ca^{2+} . The deepest parts of astatic water bodies were inhabited by the Polygonetum natantis. Typhetum latifoliae and Spirodeletum polyrrhizae developed in only slightly shallower waters than P. natantis. The phytocoenoses of Calletum palustris, Menyanthetum trifoliatae and Potentilletum palustris were associated with the shallowest water. The differences between the habitats of the above two groups of associations were significant (Fig. 1). The SO_4^{2-} concentration differentiated the waters of the associations studied into two groups. The lowest values of SO_4^{2-} were recorded in the waters of Calletum palustris, Elodeetum canadensis and Potentilletum palustris, and the highest in those of Caricetum elatae and Polygonetum natantis (the differences between the above two groups of associations were significant – Fig. 1). With regard to SO_4^{2-} the

Table 1. Synoptic table of plant associations studied

Association	LM	SP	RF	EC	PN	CE	TL	РР	MT	СР
No. of relevés	16	11	12	16	11	19	9	17	15	21
Lemnetea minoris										
Lemna minor	V^5	IV^{1-4}	V^{+-4}	III^+	III^{+-2}	V^{+-3}	V^{+-2}	IV^{+-1}	IV^{+-3}	V^{+-3}
Lemna trisulca	II^+	IV^{+-5}	III^{+-1}	I^+	I^1	III^{+-3}	V^{+-1}	III^{+-2}	II^{+-1}	II^{+-2}
Spirodela polyrrhiza	IV^{+-1}	V ³⁻⁵	H^{+-2}	I ⁺	I^2	Π^+	H^{+-3}	I ⁺	H^{+-1}	I ⁺
Riccia fluitans	I^{+-2}	H^{+-2}	V ⁵	•	П	H^{+-2}	H^{+-4}	I+	H^{+-1}	I^{+-1}
Ricciocarpos natans	I^+		\mathbf{H}^+			I^{+-1}	II^+			
Detemates										
Ceratonhyllum demersum	H^{+-3}	\mathbf{I}^1								
Elodoa canadansis		1		V^5				HH^{+-1}		I +
Potamogaton natans	т+	т+	•	U^{+-1}	•	•	т+	111 1 ⁺	т+	I I +
Murionkullum vorticillatum	1	1	•	11 1 ⁺	·	•	1	и 11 ⁺	1 1+	т т+
	•	•	•	1 1 +	•	т+	•	11 1 ⁺	1 1 +	1 1 +
Hydrocharis morsus-rande	•	•	•	1 11+	·	1	·	1	1	1
Potamogeton friesu	·	• +	• • +	П	•	x + -2	1		• • • • - 1	•
Hottonia palustris		1	1 ' * +		× -4-5	1 * +	П.	II S	II · ·	
Polygonum amphibium	•	•	1	т+	V. s	1	•	•	т+	•
Nymphaea aiba	•	·	•	1	•	•	•	•	1	•
Utricularietea intermedio-minoris		• +	• +	• +	• +	• +	* * 1	•• + - 3	- 1	• +
Utricularia vulgaris	·	1	1	1	1	1	II.		I'	I'
Utricularia minor	•	•	•	•	•	•		$\prod_{i=1}^{i}$	II '	Π^{+-2}
Sparganium minimum	•	•	•	I '	I'	I '	I'	Π^{+-1}	•	•
Warnstorfia fluitans	•	•	•	•	•		•	•	I^+	•
Phragmitetea										
Carex elata			I^+			V^{4-5}	•			I^+
Scutellaria galericulata						II^+			I^+	
Iris pseudacorus					I^+	I^+		I^+		
Phalaris arundinacea						I^+				
Roripa amphibia						I^+				
Oenanthe aquatica						I^+	I^+			
Carex vesicaria	I^+		I^+			II^{+-1}		II^+	I^+	I^+
Peucedanum palustre						I ⁺			\mathbf{H}^+	I ⁺
Carex rostrata						I ⁺		II^{+-1}	H^{+-1}	Π^+
Galium palustre						П+	I +	1 ⁺	П+	H^{+-1}
I vsimachia thvrsiflora						I ⁺	I ⁺	I ⁺	I ⁺	\mathbf{H}^+
Alisma plantago-aquatica	T+	I+	I+	I^{+-1}	I+	и 11 ⁺	1 1 +	и 11 ⁺	и 11 ⁺	111 I ⁺
Fauisetum fluviatile	1	1	1	и+	и 11 ⁺	$I^{+}-1$	1 1 +	11 11 +	V^{+-2}	1 + -1
Typha latifolia	•	•	т+	11	11	1 1 ⁺	V^{4-5}	11 1 ⁺	v II ⁺	111 1 ⁺
	т+	•	1	т+	•	1	$v_{11} + -1$	1 1 +	11 11 ⁺	$r^{+}-1$
Acorus calamus	1 1 +	т+	•	1 1 +	т+	•	11	1 1 +	11 1 +	1 + -1
Eleocharis paiusiris	1	1	•	1 1+	1	•	т+	1 1+	1	11 1 +
Sparganium emersum	• • •	•		1	·	•	1	1 +	•	1
Sparganium erectum	1	•	1	• +	• +	•	•	1 x+	•	• + -1
Glyceria fluitans	•	•	• • +	1	1	•	•	1	•	1 · ·
Carex pseudocyperus	•	•	1	•	•	• • ±	•	•	•	I,
Carex acutiformis	• • ±	•	1'	•	•	1'	•	•	•	• •1
Rumex hydrolapathum	I	•	•	•	•	•	•	•	•	I^{1}
Phragmites australis	I^+	I^+	•	•	•	•	•	•	•	•
Ranunculus lingua			•	•	I^+		•			•
Scheuchzerio-Caricetea nigrae								_		
Comarum palustre	•		I^+	III^+	•	II^{+-1}	•	V^5	III^{+-1}	V^{+-1}
Drepanocladus aduncus	•	•	•	•	•	I^+	II^{+-3}	IV^{+-3}	II^{+-1}	II^{+-1}
Menyanthes trifoliata	•	•		•	•	I^+		•	V^5	I^+
Carex diandra								I^+	II^{+-1}	II^+
Calla palustris								I^+		V^{4-5}
Carex curta								II^+	II^{+-1}	III^{+-1}

Table 1. (continued)

Association	LM	SP	RF	EC	PN	CE	TL	PP	MT	СР
Agrostis canina									II^{+}	I^+
Stellaria palustris				•	•	III^+				I^+
Carex lasiocarpa						I^{+-1}		I^+		
Straminergon stramineum									I^+	I^{+-1}
Carex nigra				•	•	•				I^+
Calamagrostis stricta									I^+	
Sphagnum subsecundum										\mathbf{I}^1
Eriophorum angustifolium										I^+
Carex echinata								•	I^+	•
Molinio-Arhenaterhetea										
Lythrum salicaria		•	•	•	•	III^+	II^+	II^+	II^+	I^+
Cardamine pratensis						II^+			•	
Lysimachia vulgaris		•	•	•	•	I^+	I^+	•	•	•
Myosotis palustris		•	•	•	•	I^+	•	•	I^+	•
Juncus effusus	I^+									
Galium uliginosum		•	•			I^+		•	•	•
Alnetea glutinosae										
Salix cinerea					I^+	I^+	I^+	II^+	I^+	I^+
Lycopus europaeus				•	•	I^+			I^+	II^+
Solanum dulcamara						I^+	I^+			
Sphagnum squarrosum									I^+	
Alnus glutinosa		•	•					I^+	•	•
Others										
Sphagnum fallax				•	•	•			I^1	I^2
Calliergon cordifolium									\mathbf{I}^1	\mathbf{I}^1
Bryum pseudotriquetrum										\mathbf{I}^1
Alopecurus geniculatus		•	•	•	•		•	•	•	I^+
Agrostis stolonifera	I^+								•	I^+
Calliergon giganteum		•	•	•	•		•	III^{+-4}	II^{1-2}	II^{+-1}
Chara fragilis	•	•	•	I^+	•	•	•	I^+	II^{+-4}	II^{+-4}
Bidens cernua	I^+	I^+	•	•	•	•	II^+	I^+	•	I^+
Epilobium palustre	•	•	•	•	•	•	•	I^+	I^+	I^+
Drepanocladus capillifolius		•	•	•	•		•	II^{+-2}	I^+	I^1
Cardamine amara		•	•	•	•		•	I^+	I^+	I^+
Sphagnum palustre		•	•	•	•		•	•	I^+	•
Polytrichum commune										
Callitriche hamulata			•		•			I^+	•	
Mentha aquatica					I^+				•	
Fontinalis antipyretica			•		I^+				•	
Fraxinus excelsior	•	•	•	•	•	I^+	•	•	•	•
Polygonum nodosum		•	•	•	•		I^+		•	

Categorical constancy – I: a species occurs in 1–20% of relevés, II: 21–40%, III: 41–60%, IV: 61–80%, V: 81–100%. Constancy categories of dominant species for particular associations are printed in bold. Ranges of abundance are superscript. Scale for coverage – +:mean coverage 0,1%, 1: 5%, 2: 17,5%, 3: 37,5%, 4: 62,5%, 5: 87,5%. LM – Lemnetum minoris, SP – Spirodeletum polyrrhizae, RF – Riccietum fluitantis, EC – Elodeetum canadensis, PN – Polygonetum natantis, CE – Caricetum elatae, TL – Typhetum latifoliae, PP – Potentilletum palustris, MT – Menyanthetum trifoliatae, CP – Calletum palustris.

habitats of *Riccietum fluitantis* were similar to the first group of communities (*Calletum palustris*, *Elodeetum canadensis* and *Potentilletum palustris*), whereas the waters of *Typhetum latifoliae* contained similar levels of SO_4^{2-} as *Caricetum elatae* and *Polygonetum natantis*. The PO_4^{3-} concentration differentiated the waters of the communities studied into two groups as well. Belonging

to the first group phytocoenoses of *Lemnetum minoris* (the differences were significant in the case of most communities – Fig. 1), *Spirodeletum polyrrhizae* and *Riccietum fluitantis* developed in waters with the highest concentration of PO_4^{3-} . The remaining communities formed the second group, poorer in PO_4^{3-} . The waters of the associations analysed in the study differed



Fig. 1. Differentiation of the 10 plant associations studied in relation to 13 properties of water. Black boxes show 25-75% interquartile ranges of values and white boxes show the medians. LM – *Lemnetum minoris*, SP – *Spirodeletum polyrrhizae*, RF – *Riccietum fluitantis*, EC – *Elodeetum canadensis*, PN – *Polygonetum natantis*, CE – *Caricetum elatae*, TL – *Typhetum latifoliae*, PP – *Potentilletum palustris*, MT – *Menyanthetum trifoliatae*, CP – *Calletum palustris*. Above the boxes abbreviations for significantly different plant associations ($p \le 0.05$) are shown.

considerably with respect to pH as well. The habitats of Calletum palustris were distinguished from those of the other associations by the lowest values of pH (in most cases the waters were slightly acidic). The waters of Menyanthetum trifoliatae and Caricetum elatae were characterized by the similar (only slightly higher) pH values than the habitat of Calletum palustris, whereas the phytocoenoses of Elodeetum canadensis and Polygonetum natantis were more strongly associated with alkaline waters. The remaining communities developed mostly in waters with pH 7-8 (Fig. 1). Statistical differences between the associations studied were only found in the case of Calletum palustris and Elodeetum canadensis (Fig. 1). Total and carbonate hardness differentiated the waters of the communities studied in a similar way (Fig. 1). The Calletum palustris phytocoenoses were associated with the softest waters (the differences were significant for most of the associations analysed in the study - Fig. 1). Potentilletum palustris and Elodeetum canadensis developed in soft waters as well. By contrast, the Lemnetum minoris phytocoenoses showed preference for harder waters (considerable differences were detected for all the above three communities – Fig. 1). With regard to carbonate hardness the waters of Spirodeletum polyrrhizae were most similar to those of Lemnetum minoris (Fig. 1). The lowest concentrations of Ca²⁺ and Mg²⁺ were noted in the waters of *Calletum* palustris, whereas Polygonetum natantis, Typhetum latifoliae, Caricetum elatae and Lemnetum minoris were restricted to waters richer in these elements (the differences were significant - Fig. 1). The waters inhabited by Spirodeletum polyrrhizae were also rich in Mg^{2+} . By contrast, the habitats of *Potentilletum* palustris, Elodeetum canadensis and Menyanthetum trifoliatae had low levels of both Ca^{2+} and Mg^{2+} (Fig. 1).

 Na^+ , K^+ , dissolved SiO₂ and total Fe appeared to be less important in differentiating the habitats of the associations studied (Fig. 1). Only the phytocoenoses of Elodeetum canadensis were restricted to waters rich in Na^+ (significant differences). The lowest levels of K^+ were noted in the waters of *Calletum palustris*, whereas the habitats of Spirodeletum polyrrhizae, Polygonetum natantis, Lemnetum minoris and Caricetum elatae were characterized by higher values of K^+ . The lowest concentrations of dissolved SiO2 were recorded in the waters of Calletum palustris. With regard to this parameter the waters of the above association differed significantly from those of Polygonetum natantis, Caricetum elatae, Lemnetum minoris, Menyanthetum trifoliatae and Typhetum latifoliae. The waters of Elodeetum canadensis, Calletum palustris and Menyanthetum trifoliatae were distinguished from those of Caricetum elatae (poorest in NO₃) by much higher values of NO_3^- (Fig. 1). Similar results were obtained from 13 properties of water and 147 relevés. The character species of the ten plant associations studied were plotted. Eigenvalues: $\lambda_1 = 0.649$, $\lambda_2 = 0.529$, $\lambda_3 = 0.490$, $\lambda_4 = 0.167$. *Cp* – *Calla palustris, Ce* – *Carex elata, Pp* – *Potentilla palustris, Ec* – *Elodea canadensis, Lm* – *Lemna minor, Mt* – *Menyanthes trifoliata, Pa* – *Polygonum amphibium, Rf* – *Riccia fluitans, Sp* – *Spirodela polyrhiza, Tl* – *Typha latifolia,* CCA = Canonical Correspondence Analysis.

Fig. 2. CCA ordination diagram of 1st and 2nd axes obtained

when the CCA ordination diagram was analysed (Fig. 2), which showed the relationship between the occurrence of the dominant species in the communities and habitat parameters. It appears that the following water properties best differentiated the habitats studied: water depth, SO₄²⁻, Ca²⁺, Mg²⁺ and PO₄³⁻, which correlated with the first ordination axis, as well as total and carbonate hardness, correlated with the second axis. When compared to Fig. 1, the diagram shows a less important role of pH in differentiating the habitats. The relationships described above between the associations studied and the particular water parameters or groups of parameters were confirmed, that is: the waters of Calletum palustris, Potentilletum palustris, Menyanthetum trifoliatae and Elodeetum canadensis were distinguished by low values of the abovementioned main differentiating the habitat water parameters; Polygonetum natantis, Typhetum latifoliae and Caricetum elatae were associated with deeper waters rich in SO_4^{2-} , Ca^{2+} and Mg^{2+} ; whereas Lemnetum minoris and Spirodeletum polyrrhizae were restricted to harder waters rich in PO_4^{3-} .

Substrate properties

The substrate properties which best differentiated the habitats of the associations studied were: NO_3^- , Na^+ , water content, PO_4^{3-} , pH and total N.

 NO_3^- content differentiated the substrates of the associations studied into two groups (Fig. 3). *Polygonetum*





Fig. 3. Differentiation of the seven plant associations studied in relation to 12 properties of substrate. Black boxes show 25-75% interquartile ranges of values and white boxes show the medians. The pleustonic associations were not considered in the analysis. EC – *Elodeetum canadensis*, PN – *Polygonetum natantis*, CE – *Caricetum elatae*, TL – *Typhetum latifoliae*, PP – *Potentilletum palustris*, MT – *Menyanthetum trifoliatae*, CP – *Calletum palustris*. Above the boxes abbreviations for significantly different plant associations ($p \le 0.05$) are shown.

natantis, Caricetum elatae and Typhetum latifoliae were associated with substrates poor in NO_3^- , whereas Calletum palustris, Potentilletum palustris, Menyanthetum trifoliatae and Elodeetum canadensis inhabited substrates significantly richer in this element. The highest values of NO_3^- were found for the Elodeetum canadensis phytocoenoses. A similar trend was determined for Na⁺ concentrations (Fig. 3). The lowest Na⁺ content was noted in the substrates of Typhetum latifoliae, Caricetum elatae and Polygonetum natantis, whereas Calletum palustris, Potentilletum palustris, Menyanthetum trifoliatae and Elodeetum canadensis were distinguished by higher values. The substrates of the latter association had the highest content of this element and the differences were significant (Fig. 3). A slightly different trend was determined for water content (Fig. 3). The phytocoenoses of Calletum palustris, Potentilletum palustris and Menyanthetum trifoliatae were associated mostly with strongly hydrated substrates, whereas Typhetum latifoliae, Polygonetum natantis and Caricetum elatae inhabited slightly hydrated substrates. The differences between the above two groups of associations were significant (Fig. 3). The PO_4^{3-} concentrations differentiated the substrates of the communities studied as well (Fig. 3). The lowest values of PO_4^{3-} were recorded in the substrates of *Caricetum* elatae. The substrates of Calletum palustris were also poor in PO_4^{3-} , whereas those of *Typhetum latifoliae*, Elodeetum canadensis, Menyanthetum trifoliatae and *Potentilletum palustris* were richer in this element. The substrates of the latter four associations differed significantly from that of Caricetum elatae with regard to PO_4^{3-} (Fig. 3). Significant differences were also found between the substrates of Calletum palustris and Elodeetum canadensis, and those of Potentilletum palustris. The substrates of the associations compared differed considerably with respect to pH (Fig. 3). Calletum palustris were associated with the most highly acidic bottoms, whereas Typhetum latifoliae inhabited substrates with the highest values of pH (neutral substrates). The pH values of the substrates of Calletum palustris were more similar to those of Potentilletum palustris, Menyanthetum trifoliatae and Caricetum elatae (the above group of associations, with the exception of Caricetum elatae, differed significantly from Typhetum latifoliae - Fig. 3). The values of pH noted in the substrates of Typhetum latifoliae were similar to those obtained for Elodeetum canadensis and Polygonetum natantis. Total N differentiated the substrates of the associations studied into two groups (Fig. 3). The highest total N content was noted in the substrates of Calletum palustris, Potentilletum palustris and Menvanthetum trifoliatae, with lower levels for Polygonetum natantis, Caricetum elatae and Typhetum latifoliae. The differences between the habitats of Calletum palustris, Potentilletum palustris and Menvanthetum trifoliatae and those of Typhetum latifoliae, and between substrates of Potentilletum palustris and Caricetum elatae were significant (Fig. 3). With regard to Mg^{2+} , the substrates of *Caricetum elatae* were distinguished from those of the other communities by higher values of this parameter (significant differences were detected for Calletum palustris, Potentilletum palustris and Elodeetum canadensis - Fig. 3). Organic matter content, total Fe and K⁺ appeared to be less important in differentiating the habitats of the associations studied. In the case of organic matter significant differences were detected between the substrates of Calletum palustris and Menyanthetum trifoliatae (containing the highest amount of organic matter), and those of Typhetum latifoliae (poor in organic matter). The Calletum palustris phytocoenoses were restricted to substrates poor in total Fe, whereas those of

Menyanthetum trifoliatae and Caricetum elatae occurred

Fig. 4. CCA ordination diagram of 1st and 2nd axes obtained from 12 properties of substrate and 108 relevés. The pleustonic associations were not considered in the analysis. The character species of the 10 plant associations studied were plotted. Eigenvalues: $\lambda_1 = 0.726$, $\lambda_2 = 0.527$, $\lambda_3 = 0.303$, $\lambda_4 = 0.155$. *Cp* – *Calla palustris, Ce* – *Carex elata, Pp* – *Potentilla palustris, Ec* – *Elodea canadensis, Mt* – *Menyanthes trifoliata, Pa* – *Polygonum amphibium, Tl* – *Typha latifolia,* CCA = Canonical Correspondence Analysis.

on substrates significantly richer in this element. With regard to K^+ , considerable differences were marked between the substrates of *Polygonetum natantis* and *Typhetum latifoliae* (poor in this element), and those of *Menyanthetum trifoliatae* (containing higher amount of $K^+ - Fig. 5$). The remaining properties (SO₄²⁻ and Ca²⁺) did not play a significant role in differentiating the habitats compared (Fig. 3).

The CCA ordination (Fig. 4) confirms that the substrates compared were best differentiated by the following parameters: NO_3^- , Na^+ , water content, PO₄³⁻, pH, Mg²⁺. However, total nitrogen was less important than compared to Fig. 3. The relationships presented above between communities and the particular substrate properties were confirmed by the ordination diagram. It appeared that Elodeetum canadensis, Calletum palustris, Menyanthetum trifoliatae and Potentilletum palustris are associated with substrates rich in NO_3^- and Na^+ . The habitats of Caricetum elatae are distinguished from those of the other communities by low PO_4^{3-} level. The phytocoenoses of Calletum palustris develop best on highly hydrated substrates. The diagram shows that pH differentiated the substrates of the communities studied into two groups: Calletum palustris, Menyanthetum trifoliatae, Potentilletum palustris and Caricetum elatae - associated with highly acidic substrates; Polygonetum natantis, Typhetum latifoliae and Elodeetum canadensis – restricted to less-acidic substrates.



PO₄³

 Ec^{\bullet}

0.8

Pa●

Discussion

The knowledge of macrophytes and their communities as biondicators of water quality in kettle holes is scarce, as compared to lakes (Gloede 2005; Gloede and Karlowski 2007). The vegetation-habitat (water and/or substrate) relationships in lakes have been indicated by various authors (e.g. Pearsall 1920; Lohammar 1938; Misra 1938; Spence 1967; Seddon 1972; Catling et al. 1986: Toivonen and Huttunen 1995: Vestergaard and Sand-Jensen 2000; Heegaard et al. 2001; Kłosowski 2006). Regarding astatic water bodies various authors emphasized that the particular phytocoenoses covered only a small area and had a mosaic distribution (Bosiacka and Radziszewicz 2003), that the area occupied by the various phytocoenoses changed considerably even during one growing season (Nagengast et al. 2007) and that the phytocoenoses occurring in astatic water bodies had a relatively short life span (Kaźmierczak et al. 1995). These findings point to the wide variability of habitat conditions within the astatic bodies of water (Solińska 1963; Mierwald 1988; Zander 2005; Kalettka and Rudat 2006) and suggest that it is difficult to determine the relationship between plant communities and particular environmental factors. Plant communities occurring in both astatic bodies of waters and lakes (e.g. Elodeetum canadensis, Polygonetum natantis and Typhetum latifoliae phytocoenoses investigated in the present study) develop under a much wider range of water quality conditions in astatic bodies

of water (e.g. NO_3^- , PO_4^{3-} , K^+ , total Fe, colour – Fig. 5) and are associated mostly with more nutrient-rich habitats, which indicates that the above communities (particularly *Polygonetum natantis* and *Typhetum* latifoliae) have a wide ecological amplitude with respect to properties of water. Wide ecological amplitude is also characteristic for the remaining plant communities compared in the study. It has been confirmed by the hydrochemical data obtained by other authors who investigated the dominant species of the above plant associations (e.g. Elodeetum canadensis - Seddon 1972; Felzines 1977; Wiegleb 1978; Pietsch 1982; Pip 1988; P. amphibium – Wiegleb 1978; Pietsch 1982; Pip 1988; Papastergiadou and Babalonas 1993a, b; L. minor -Felzines 1977; Wiegleb 1978; Pietsch 1982; Gilgen 1989; Papastergiadou and Babalonas 1993a, b; Spirodela polvrrhiza - Felzines 1977; Wiegleb 1978; Pietsch 1982; Gilgen 1989; R. fluitans - Wiegleb 1978; T. latifolia -Felzines 1977; Kłosowski 1992; Toivonen and Huttunen 1995; C. elata - Felzines 1977; Kłosowski and Tomaszewicz 1984). The following question, therefore, needs to be answered: Is it possible to determine specific relationships between habitat conditions and plant communities that have a wide ecological amplitude? The present findings and earlier studies (e.g. Kłosowski et al. 1995) showed that such relationships could be established when investigations were carried out on specific phytocoenoses dominated by a particular aquatic and swamp species. As a result significant differences in habitat conditions were found between the different



Fig. 5. Chosen water properties in plant associations occurring in astatic water bodies and in lakes from the same area. Black boxes show 25–75% interquartile ranges of values and white boxes show the medians. EC – *Elodeetum canadensis*, PN – *Polygonetum natantis*, TL – *Typhetum latifoliae*. Significant differences (Mann-Whitney test, $p \le 0.05$) of a water property between astatic water bodies and lakes are marked with asterix (*).

types of phytocoenoses. A similar approach to the problem was adopted by Joniak et al. (2007), who indicated significant differentiation in the water chemistry between the vegetated and unvegetated zones as well as between the plant communities dominated by particular macrophytes in astatic water bodies. The latter authors confirmed our observations regarding the important role of pH, NO₃, phosphorus and hardness in differentiating the habitats of the vegetation of astatic water bodies. Rudat and Kalettka (2005) also pointed to the necessity of conducting studies on different types of phytocoenoses in order to indicate the relationship between plant communities and their habitats in kettle holes. The correlations between vegetation and site factors were determined by means of transects traversing the various vegetation zones. In each zone vegetation (species coverage) and site factors (hydrology, morphology, chemistry of sediment and water) were analysed. The above authors indicated that in the aquatic zone the shore width, water depth and trophic level of the water were factors with high gradients for differentiation of vegetation unit.

Floristic dominance is a phenomenon often observed in bodies of water where habitat conditions are highly variable, and has special ecological significance (Rejewski 1977). This also applies to astatic water bodies. The floristic dominants play an important role in modifying and utilisation of their habitats. This confirms the findings of Willby et al. (2000) who indicated significant relationships between attribute groups (sets of species characteristics) and habitat utilisation. The dominant species play a significant role in determining the type of substrate that is being deposited within the plant community. They exert influence on such processes as decalcification and oxygenation of water, and can regulate the uptake of biophilous elements. The above processes proceed differently in phytocoenoses dominated by pleustonic species, as well as in submerged, floating-leaved and swamp communities (Podbielkowski and Tomaszewicz 1996).

In the present work investigations were carried out exclusively on specific phytocoenoses distinguished on the basis of dominance of one species. Among the ten main types of vegetation units identified most of the phytocoenoses were distinct with respect to water and sediment chemistry preferences. The following relationships were, therefore, determined between the plant associations studied and their habitat:

Riccietum fluitantis – waters mainly alkaline, poor in SO_4^{2-} , Na⁺, with a relatively high concentration of PO_4^{3-} .

Lemnetum minoris and Spirodeletum polyrrhizae – waters medium hard, alkaline, rich in PO_4^{3-} .

Elodeetum canadensis – waters relatively soft, alkaline, poor in SO_4^{2-} , Ca^{2+} , Mg^{2+} , dissolved SiO₂, with low

 PO_4^{3-} concentration (and having a narrow range), rich in Na⁺ and NO₃⁻; substrates with high NO₃⁻, PO₄^{3-} and Na⁺ contents.

Polygonetum natantis – the deepest waters (mainly within the 0.5–1.1 m depth range), alkaline, relatively rich in Ca^{2+} , Mg^{2+} and SO_4^{2-} ; substrates neutral, poorly hydrated, with low K⁺, Na⁺, NO₃⁻ and total N contents, relatively rich in Ca^{2+} and Mg^{2+} .

Typhetum latifoliae – waters mainly within the 0.35–0.65 m depth range, moderately hard, neutral, with high Ca^{2+} and Mg^{2+} concentrations; substrates mainly neutral, poorly hydrated, with low total N, NO_3^- , Na^+ , K^+ and organic matter contents, rich in PO_4^{3-} .

Caricetum elatae – waters neutral, rich in SO_4^{2-} , Ca^{2+} and dissolved SiO₂; substrates poor in total N, NO_3^- , PO_4^{3-} and Na^+ , with high contents of Mg^{2+} and total Fe.

Calletum palustris – waters shallow (mainly 0.1–0.25 m), mostly acidic, soft, poor in Ca^{2+} , Mg^{2+} , K^+ , PO_4^{3-} , SO_4^{2-} and dissolved SiO₂, relatively rich in NO_3^- ; substrates acidic, organic, highly hydrated, with low Ca^{2+} , Mg^{2+} and total Fe levels, relatively rich in total N, NO_3^- and Na^+ .

Menyanthetum trifoliatae – waters very shallow (mainly 0.05–0.15 m), soft or moderately hard, mostly poor in PO_4^{3-} , relatively rich in NO_3^- ; substrates acidic, highly hydrated, rich in total N, NO_3^- , K⁺ and organic matter contents, poor in Mg^{2+} .

Potentilletum palustris – waters shallow (mainly 0.05–0.25 m), mostly neutral and soft, with relatively high Na⁺ concentrations, poor in PO_4^{3-} ; substrates acidic, highly hydrated, poor in Mg²⁺, relatively rich in PO_4^{3-} and total N.

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