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Habitat conditions of the *Salvinia natans* phytocoenoses in the Vistula and Odra river valleys in Poland

Standortsbedingungen von *Salvinia natans*-Beständen in den Tälern der Weichsel und Oder in Polen

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Abstract

The Floating Fern, *Salvinia natans*, is a species of fern associated with stagnant water, primarily oxbow lakes, but also ponds clay pits, low-flow drainage canals and ditches. In these ecosystems, it most often forms phytocoenoses of *Salvinio natantis-Spirodeletum polyrhizae*. Due to anthropogenic changes in the river valleys where this species and its communities usually occur, they are under threat of extinction in many parts of Europe. The floristic composition and structure of the phytocoenoses dominated by *S. natans* in Poland and other parts of Europe is well-recognized. However, there is not much information about their ecology, especially the physical and chemical properties of water in which they develop. Therefore, the main purpose of the paper was to determine the range of habitat conditions necessary for phytocoenoses dominated by *S. natans*, in its common areas of occurrence in Poland (which are in the Vistula and Odra River valleys), and to specify the conditions necessary for their protection. In addition, an attempt was made to determine the degree of habitat distinction of *Salvinio natantis-Spirodeletum polyrhizae* phytocoenoses in relation to the most common phytocoenoses of *Lemno-Spirodeletum polyrhizae* in the same areas. 53 stands of *Salvinio natantis-Spirodeletum polyrhizae* were tested for phytosociological and habitat characteristics, and the results compared to data collected from 48 stands of *Lemno-Spirodeletum polyrhizae*. 12 physical and chemical water properties were tested for: water depth, pH, colour, phosphate concentration, ammonium nitrogen, nitrates, calcium, magnesium, sodium; potassium, total iron, and soluble silica. The analyses showed the difference between *Lemno-Spirodeletum polyrhizae* and *Salvinio natantis-Spirodeletum polyrhizae* in range of floristic composition. *Salvinio natantis-Spirodeletum polyrhizae* phytocoenoses had a greater share of aquatic species (*Potamogetonetea* class) and rush plants from the *Phragmito-Magnocaricetea* class. The phytocoenoses of *Salvinio natantis-Spirodeletum polyrhizae* more often inhabited deeper, more alkaline waters that were richer in soluble silica and total iron, and poorer in calcium and potassium. In addition to methods for the protection of *S. natans* and its phytocoenoses a permanent hydrochemical monitoring of the richest *S. natans* sites in both river valleys should be carried out. It is particularly important to maintain proper water depth (> 0.5 to +/-1.5 m), alkaline pH and the concentrations of other properties that differentiate the water habitats of *Salvinio natantis-Spirodeletum polyrhizae* from *Lemno-Spirodeletum poyrhizae*.

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Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

The Floating Fern, *Salvinia natans* (L.) All. is a pleustonic aquatic fern species with an extensive geographical range from Central and Eastern Europe to south-eastern Asia (KRAWCZYK & MAJKUT 2008 for MEUSEL et al. 1965). The plant is associated with areas of sub-oceanic temperate, subtropical and tropical climates (ROTHMALER et al. 1986). It mainly occurs in stagnant and slow-moving waters (oxbow lakes, ponds, slow-flowing rivers, canals, drainage ditches, clay pits and astatic reservoirs), where it often forms extensive and compact phytocoenoses of *Salvinio natantis-Spirodeletum polyrhizae* association Slavnić 1956 = *Lemno minoris-Salvinietum natantis* (Slavnić 1956) Korneck 1959 = *Lemno-Salvinietum natantis* Miyawaki et Tüxen 1960 (MATUSZKIEWICZ 2008, ŠUMBEROVÁ 2011, CVIJANOVIĆ et al. 2018). This association belongs to the class *Lemnetea* O. de Bolós et Masclans 1955, order *Lemnetalia minoris* O. de Bolós et Masclans 1955 and alliance *Lemnion minoris* O. de Bolós et Masclans 1955 (MUCINA et al. 2016). Due to anthropogenic changes in the ecosystems of water and river valleys, this species is now being threatened with extinction in many European countries, and has already extinct in some of them (including France, Belgium and the Netherlands – TUTIN et al. 1964). Therefore, it has been placed under the protection of the Berne Convention.

In Poland, *S. natans* can be found mainly in aquatic ecosystems running through the valleys of the largest Polish rivers, the Vistula and Odra, and some of their tributaries (WOŁEK 1974, TOMASZEWICZ 1979, ZAJĄC & ZAJĄC 2001, MICHALSKA-HEJDUK & KOPEĆ 2002, MARKOWSKI et al. 2004, KRAWCZYK & MAJKUT 2008, 2012). *Salvinia natans* is under strict protection and is considered by various authors as an endangered species on the national scale, or at least in some of the regions in which it is present (PROĆKÓW 2002, MARKOWSKI & BULIŃSKI 2004, ZARZYCKI & SZELĄG 2006, BRÓŻ & PRZEMYSKI 2009, OLACZEK 2012).

The distribution of *S. natans*, the floristic composition and the structure of the phytocoenoses of this species are relatively well known in Poland (see the above-cited papers). A lot of phytosociological data about *S. natans* communities has also been cited in works from other parts of Europe (including PASSARGE 1978, SCHWABE-BRAUN & TÜXEN 1981, SCOPPOLA 1982, SANDA et al. 1987, ŠUMBEROVÁ 2011, CVIJANOVIĆ et al. 2018). Although it seems that there is comprehensive floristic and phytosociological knowledge about phytocoenoses dominated by *S. natans*, detailed data on the ecology of the plant and its communities are still missing. This includes data on the physical and chemical properties of a large number of aquatic habitats in a large area. Foreign works only sometimes quote data concerning water properties from one or several aquatic ecosystems with the occurrence of *S. natans* (KÁRPÁTI 1963, ZUTSHI & VASS 1971, PAPASTERGIADOU & BABALONAS 1993a, b; STOJANOVIĆ et al. 2004, SCHWARZER 2005, SCHWARZER & WOLFF 2005). In Poland, information on *S. natans* ecology has, for many years, originated from floristic and phytosociological works (TOMASZEWICZ 1979). Some of these (WOŁEK 1974, 1997) have presented data on the dependence of pleustonic communities, including *S. natans* phytocoenoses, on water pH-value. In recent years, apart from one paper (MICHALSKA-HEJDUK et al. 2009)

that provided the results of water analyses of 6 oxbow lakes inhabited by *S. natans* on the River Bug, other papers have begun to appear in Poland, taking into greater account the various habitat data from *S. natans* sites and its phytocoenoses (WOŁEK & KOŚCIÓŁEK 2012, GAŁKA & SZMEJA 2012). These works brought new data from the habitats of this species, however, they are limited to rather small regions: WOŁEK & KOŚCIÓŁEK (2012) in Małopolska, and GAŁKA & SZMEJA (2012) in the Vistula delta (Baltic Sea Region). As a result, there is a lack of data on the water chemistry of *Salvinia*'s habitats and its phytocoenoses across the entire range of their occurrence in Poland (i.e. in the Vistula and the Odra River valleys). Obtaining such data would allow for a more complete understanding of the *Salvinia*'s ecology and the communities it creates, as well as clarifying the conditions necessary to protect this rare species.

The following research objectives were set: (1) define the range of habitat conditions in which phytocoenoses with dominance of *S. natans* develop in the main area of its occurrence in the Vistula and Odra River valleys; (2) check the distinctions between habitats of *Salvinio natantis-Spirodeletum poyrhizae* phytocoenoses and the most common pleustonic phytocoenoses in Poland *Lemno-Spirodeletum poyrhizae* Koch 1954 (from the same phytosociological class, order and alliance) developing in the same area; (3) determine the conditions that need to be met for effective protection of the species and its phytocoenoses.

2. Material and methods

2.1 Data set

The phytosociological and ecological study was carried out in 2009–2017 (from mid-July to September 20th) in the area of the Vistula and Oder River valleys. Material was collected from various types of water reservoirs (oxbow lakes, ponds, clay pits, astatic reservoirs), and from slow-flowing rivers, canals and drainage ditches. Phytosociological relevés were made using the Braun-Blanquet method at the designated study sites, i.e. in patches of *Salvinio natantis-Spirodeletum polyrhizae*, and for comparison, in the *Lemno-Spirodeletum polyrhizae* phytocoenoses. In each of the relevés, a list of plant species was made, with a quantitative evaluation of each species according to the following six-point quantitative cover-abundance scale: + < 5%, 1 = 5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–100% (BRAUN-BLANQUET 1964). Patches with pleustonic dominant species (cover-abundance values 3–5) were taken into account. *Salvinio natantis-Spirodeletum polyrhizae* included patches with dominance of *Salvinia natans*, while *Lemno-Spirodeletum polyrhizae* included phytocoenoses with dominance or co-dominance of *Spirodela polyrhiza*, *Lemna minor*, as well as *L. trisulca*.

Additionally, within each patch, the average water depth was measured and a surface water sample was taken for physico-chemical analyses. A total of 101 phytosociological relevés of an area 2–10 m^2 (mainly 5 m^2) were made, and 101 water samples were collected. 53 relevés were made in *Salvinio natantis-Spirodeletum polyrhizae* stands (34 came from the Vistula River valley and 19 from the Odra River valley), and 48 in stands of the *Lemno-Spirodeletum polyrhizae* (19 from the Vistula River valley and 29 from the Odra River valley). The distribution of the studied pleustonic phytocoenoses was shown (Fig. 1).

2.2 Data analysis

The phytosociological relevés were listed in a synoptic table (Table 1), that considered constancy and abundance as well as the cover coefficient of all species. The author's relevés were also transferred to the Polish Vegetation Database (GIVD ID: EU-PL-001 Database; KĄCKI & ŚLIWIŃSKI 2012). Cover coefficient was calculated as follows: mean percentage cover of species in relevés of table (according to

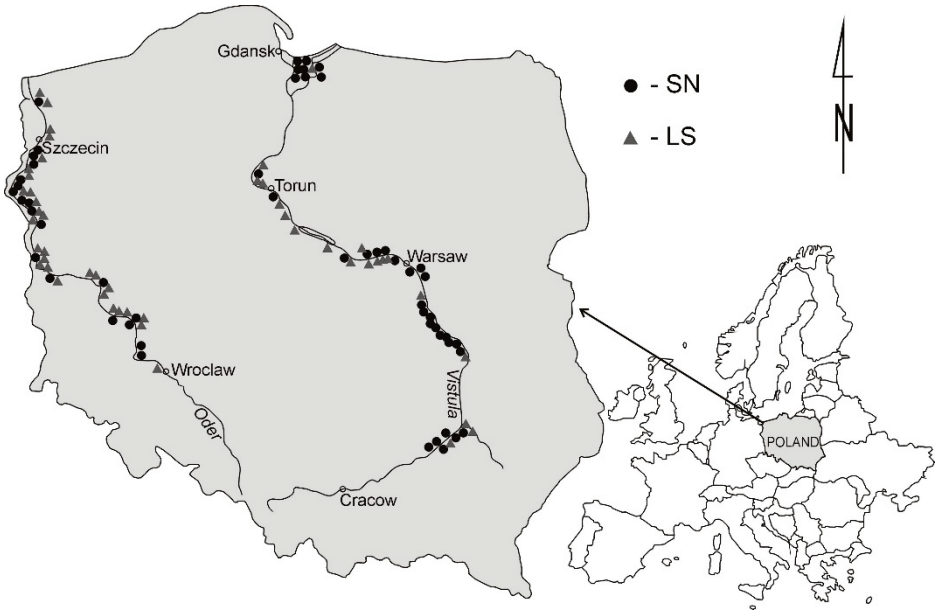

Fig. 1. A distribution map of localities of *Salvinio natantis-Spirodeletum polyrhizae* (SN) and *Lemno-Spirodeletum polyrhizae* (LS) phytocoenoses in the aquatic ecosystems of the Vistula and Odra river valleys in Poland.

Abb. 1. Karte der Verbreitung des *Salvinio natantis-Spirodeletum polyrhizae* (SN) und des *Lemno-Spirodeletum polyrhizae* (LS) in den Flusstälern von Weichsel und Oder in Polen.

a Braun-Blanquet scale, where the respective data corresponded to the following numbers: + = 1%, 1 = 10%, 2 = 20%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%, ETTER 1949) and multiplied by 100. Differences in number of localities of species between the two communities were analysed using a Mann-Whitney U test ($p \geq 0.05$). Taxonomic nomenclature was adopted from THE PLANT LIST (2013), and the names of plant associations studied after ŠUMBEROVÁ (2011). Syntaxonomic nomenclature of higher phytosociological units (class, order, and alliance) was adopted after MUCINA et al. (2016).

Surface water samples were collected into two-litre plastic containers. Water in one container (for PO_4^{3-}, $NH4^+$, NO_3^- and total Fe analyses) was fixed by adding 1 ml of concentrated sulfuric acid. All samples were transported to a laboratory and immediately analyzed. The samples were first filtered and refrigerated at 4 °C until all determinations were complete. 12 physical and chemical water properties were taken into account (including depth): pH using a portable field pH meter; PO_4^{3-} using molybdenum spectrophotometry; NO_3^- using phenyl disulphonic acid spectrophotometry; NH_4^+ using distillation and Nessler spectrophotometry; total iron using rhodanate spectrophotometry; soluble silica using molybdenum spectrophotometry; colour, using spectrophotometry on the platinum-cobalt scale; Ca^{2+}, Na^+ and K^+ on a JENWAY PFP7 flame photometer, and Mg^{2+} on a UNICAM 939 atomic absorption spectrophotometer. K^+ and Na^+ concentrations were determined in 100 mL solutions extracted with 2 mL of HCl 1 + 1 (one part concentrated acid to one part demineralised water, from evaporated and burnt 100 mL water samples). All analyses were carried out according to the procedures described by HERMANOWICZ et al. (1999), and the HACH COMPANY (1992).

The properties of the habitats of the studied pleustonic communities were compared, taking into account their ranges, medians and interquartile ranges. The non-parametric Wilcoxon test was used to demonstrate the significance of the differences. The relationships between all analyzed habitat factors and pleustonic communities were determined based on Canonical Correspondence Analysis (CCA), using CANOCO 5 (ŠMILAUER & LEPŠ 2014). All statistical analyses were performed using Statistica 6.1 (STATSOFT 2003).

3. Results

3.1 Phytosociological and habitat characteristics of the studied phytocoenoses

The analysis presented in Table 1 indicates that in phytocoenoses dominated by *Salvinia natans* (which achieve the highest cover coefficient among the pleustonic species), also *Spirodela polyrhiza* and *Lemna minor* had high constancy (respective classes V and III). *Lemna trisulca* had also quite high cover-coefficient. But these three pleustonic species had still smaller percentage cover apart from *S. natans*, on the whole. In some patches, they achieved a considerable degree of cover – just slightly less than the dominant plant. However, their cover coefficients were much lower (Table 1). Other pleustonic species, such as *Ricciocarpos natans*, *Riccia fluitans*, and *Wolffia arrhiza*, occurred sporadically. What is noteworthy there was the important contribution of species of the *Potamogetonetea* Klika in Klika et Novák 1941, primarily *Ceratophyllum demersum* and *Hydrocharis morsus-ranae* (constancy class IV), as well as *Nuphar lutea* (constancy class III) and *Myriophyllum verticillatum*, *Elodea canadensis* and *Stratiotes aloides* (constancy class II). At the same time, these species also achieved high cover coefficients. Species of the *Phragmito-Magnocaricetea* Klika in Klika et Nowák 1941 also had a large share, but only three of them (*Phragmites australis*, *Glyceria maxima* and *Sagittaria sagittifolia*) occurred frequently enough (constancy class II). In individual patches, plant species range from 4 to 12, with 8 being the average.

In the comparable phytocoenoses of *Lemno-Spirodeletum polyrhizae* among pleustonic species, only two dominants achieved the V constancy class (*Lemna minor* and *Spirodela polyrhiza*), and IV class (*Lemna trisulca*). It is worth noting that *S. natans* played an important role in these patches (constancy class III). Among the dominants, *L. minor* achieved the highest cover coefficient (Table 1). Other pleustonic species occurred sporadically. Among species from the *Potamogetonetea* only *Hydrocharis morsus-ranae*, *Ceratophyllum demersum* (constancy class III) and *C. submersum* (constancy class II) were more common. These species also achieved a fairly high cover coefficient (Table 1). Except for individual cases, species characteristic of the *Phragmito-Magnocaricetea* were not important in forming *Lemno-Spirodeletum polyrhizae* phytocoenoses. In individual patches, plant species number ranged from 1 to 12, with 6 on average. In comparison with phytocoenoses of *Salvinio natantis-Spirodeletum polyrhizae*, the patches of *Lemno-Spirodeletum polyrhizae* were floristic poorer.

When comparing the number of localities from the two analysed types of water communities, statistically significant differences were found between 8 species (Table 1). Among the dominants, these differences were demonstrated only in *S. natans.* By contrast, highly important differences occurred between the dominant species in terms of cover coefficient.

Phytocoenoses of *Salvinio natantis-Spirodeletum polyrhizae* developed in the both river valleys, mainly in the oxbow lakes, but depending on the landforms and nature of the valley, also in the slow-flowing rivers and canals (for example, in the Żuławy Wiślane or the lower section of the Odra near Gryfino), and less so in fishponds and clay pits. A characteristic feature of these phytocoenoses was their fairly high density (Fig. 2) and that they occupied considerable areas in calm, shallow and stagnant waters. In the case of small oxbow lakes and other smaller reservoirs, they usually covered the entire water surface. In the canals they often occupied large sections, from a dozen to several dozen or even several hundred meters.

Table 1. Synoptic table of floristic composition of *Salvinio natantis-Spirodeletum polyrhizae* association (SN) and *Lemno-Spirodeletum* association (LS). Constancy: I, II … V; abundance: +, 1, 2 … 5. Significant differences between SN and LS associations based on number of localities of following species were checked by the Mann-Whitney U test; *0.05 ≥ p ≥ 0.01; **0.01 > p ≥ 0.001; ***0.001 > p ≥ 0.0001; ****p < 0.0001.

Tabelle 1. Stetigkeitstabelle des *Salvinio natantis-Spirodeletum polyrhizae* (SN) und des *Lemno-Spirodeletum polyrhizae* (LS). Stetigkeit: I, II … V; Abundanz: +, 1, 2 … 5. Signifikante Unterschiede zwischen den Assoziationen SN und LS in Bezug auf die Zahl der angeführten Arten wurden durch die Anwendung des nicht-parametrischen Mann-Whitney U-Test bestimmt; *0,05 ≥ p ≥ 0,01; **0,01 > p ≥ 0,001; ***0,001 > p ≥ 0,0001; **** p < 0,0001.

Type of community	SN		LS		SN	LS
Number of relevés	53		48			
Average number of species	8 (range 4–12)		6 (range 1–12)			
Average cover of layer [%]	90		95			
Characteristics	Constancy and abundance	Cover coefficient	Constancy and abundance	Cover coefficient	No. of localities	No. of localities
ChCl. *Lemnetea*						
Salvinia natans	V $^{3–5}$	6957	III $^{+-2}$	402	53 ****	25
Spirodela polyrhiza	V $^{+-3}$	695	V $^{+-5}$	1980	44	41
Lemna minor	V $^{+-3}$	642	V $^{+-5}$	5054	43	48
Lemna trisulca	III $^{+-4}$	784	IV $^{+-5}$	2354	31	31
Ricciocarpos natans	I $^{+-1}$	30	I $^{+-1}$	25	7	3
Wolffia arrhiza	I $^{+}$	4	I ^{2}	83	2	2
Riccia fluitans	I $^{+}$	2	I $^{+-2}$	64	1	3
Lemna species	I ^{1}	19	.	.	1	0
Lemna gibba	.	.	I ^{2}	42	0	1
Azolla caroliniana	.	.	I $^{+}$	2	0	1
ChCl. *Potamogetonetea*						
Ceratophyllum demersum	IV $^{+-3}$	911	III $^{+-4}$	828	39 ***	21
Hydrocharis morsus-ranae	IV $^{+-3}$	791	III $^{+-3}$	549	38 **	23
Nuphar lutea	III $^{+-2}$	562	I $^{+-1}$	67	26 ****	5
Myriophyllum verticillatum	II $^{+-4}$	369	I $^{+-2}$	90	13	6
Elodea canadensis	II $^{+-3}$	107	I $^{+-3}$	205	11	7
Stratiotes aloides	II $^{+-2}$	94	I $^{+-2}$	44	13 **	2
Potamogeton natans	I $^{1-2}$	132	I $^{+-1}$	46	5	4
Potamogeton pectinatus	I $^{+-2}$	41	I $^{1–3}$	99	3	2
Nymphaea alba	I $^{+-2}$	81	I $^{+-2}$	44	5	2
Ranunculus circinatus	I $^{+-2}$	58	I $^{+}$	2	3	1
Utricularia vulgaris	I $^{+-1}$	26	I $^{+}$	4	5	2
Ceratophyllum submersum	I $^{+}$	7	II $^{+-3}$	293	4	10
Hottonia palustris	I $^{+}$	4	I $^{+-1}$	23	2	2
Potamogeton lucens	I $^{+-2}$	40	.	.	2	0
Myriophyllum spicatum	I $^{+}$	4	.	.	2	0
Potamogeton compressus	I $^{+}$	4	.	.	2	0
Callitriche species	.	.	I $^{+-1}$	23	0	2
Polygonum amphibium fo. *natans*	.	.	I $^{+}$	2	0	1
Potamogeton friesii	.	.	I $^{+}$	2	0	1
ChCl. *Phragmito-Magnocaricetea*						
Phragmites australis	II $^{+-1}$	72	I $^{+-2}$	194	11	9
Glyceria maxima	II $^{+-1}$	55	I $^{+}$	4	11 **	1
Sagittaria sagittifolia	II $^{+-1}$	38	I $^{+}$	4	11 **	2
Sparganium erectum	I $^{+-2}$	124	I ^{1}	42	8 *	2

Type of community	SN		LS		SN	LS
Butomus umbellatus	I $^{+-1}$	24	I $^{+-1}$	23	4	2
Typha latifolia	I $^{+}$	4	I $^{+-2}$	44	2	2
Rorippa amphibia	I $^{+}$	7	I $^{+}$	2	4	1
Phalaris arundinacea	I $^{+}$	4	I $^{+}$	4	2	2
Oenanthe aquatica	I $^{+}$	5	I $^{+}$	2	3	1
Acorus calamus	I $^{+-1}$	24	.	.	4	0
Sparganium emersum	I $^{+-1}$	24	.	.	4	0
Typha angustifolia	I $^{+-1}$	21	.	.	2	0
Mentha aquatica	I ^{1}	19	.	.	1	0
Equisetum fluviatile	I $^{+}$	6	.	.	3	0
Carex rostrata	I $^{+}$	2	.	.	1	0
Carex riparia	I $^{+}$	2	.	.	1	0
Bolboschoenus maritimus	I $^{+}$	2	.	.	1	0
Alisma plantago-aquatica	.	.	I $^{+-1}$	23	0	2
Rumex hydrolapathum	.	.	I ^{1}	21	0	1
Carex acuta	.	.	I ^{1}	21	0	1
Glyceria fluitans	.	.	I ^{1}	21	0	1
Sium latifolium	.	.	I ^{1}	21	0	1
Cicuta virosa	.	.	I $^{+}$	2	0	1
Hippuris vulgaris	.	.	I $^{+}$	2	0	1
Carex pseudocyperus	.	.	I $^{+}$	2	0	1
Accompanying species:						
Agrostis stolonifera	I $^{+-1}$	24	I ^{1}	21	4	1
Agrostis gigantea	I $^{+}$	2	I $^{+}$	8	1	4
Myosotis scorpioides	I $^{+}$	4	.	.	2	0
Bidens frondosa	I $^{+}$	2	.	.	1	0
Chara delicatula	.	.	I ^{2}	42	0	1
Chara vulgaris	.	.	I ^{2}	42	0	1

The phytocoenoses of *Lemno-Spirodeletum polyrhizae* used for comparison occupied the entire surface of the small astatic reservoirs, clay pits and drainage ditches. In the larger reservoirs, they formed smaller concentrations. They also colonized shallower places more often.

3.2 Physico-chemical properties of the water in the phytocoenoses under comparison

The results of the comparative analysis of the 12 physico-chemical properties of the water from the *Salvinio natantis-Spirodeletum polyrhizae* and *Lemno-Spirodeletum polyrhizae* phytocoenoses were presented in Figures 3 and 4. Figure 3 clearly showed that with some of the water properties, there were no significant differences between the habitats of the two types of phytocoenoses. This was true of the basic nutrients, such as phosphates, nitrates, ammonium nitrogen, as well as colour and sodium. The value ranges of those properties in both types of phytocoenoses differed only in their maximum values. For the most part, these overlapped, especially in the 25–75% interquartile range. The relevés differed slightly in the remaining 7 water properties (depth, pH, magnesium concentration, soluble silica, total iron, as well as calcium and potassium). The amplitudes of these water properties compared to the types of phytocoenoses also overlapped to a large extent. However, the 25–75% interquartile value ranges were clearly shifted against each other in both associations, and importantly, the differences between these properties were statistically significant

Fig. 2. Fragments of patches of *Salvinio natantis-Spirodeletum polyrhizae*. Chmielewo, middle Vistula valley (Photo: S. Kłosowski, 2009).

Abb. 2. Fragmente von *Salvinio natantis-Spirodeletum polyrhizae*-Beständen. Chmielewo, Tal der mittleren Weichsel (Foto: S. Kłosowski, 2009).

(Fig. 3). The first five properties reached significantly higher values in the waters of *Salvinio natantis-Spirodeletum polyrhizae*, being lower only for calcium and potassium concentrations. It could be clearly seen that despite the frequent proximity and significant similarity of the types of reservoirs in which phytocoenoses of both sets of plants occurred, there were distinctive differences between them in terms of their physical and chemical water properties. The CCA also clearly indicated the overlapping habitat of parts of *Salvinio natantis-Spirodeletum polyrhizae* and *Lemno-Spirodeletum polyrhizae* phytocoenoses (Fig. 4). However, it also demonstrated that in contrast to the patches of *Lemno-Spirodeletum polyrhizae*, a large part of the phytocoenoses dominated by *S. natans* were grouped within waters with higher values of soluble silica, pH, depth and magnesium (correlating with ordination axis I), and also total iron (correlating with ordination axis II). The opposite was found for calcium and potassium (the higher values of these properties were associated with most of the *Lemno-Spirodeletum polyrhizae* phytocoenoses). Thus, the CCA confirmed the data presented in Figure 4. The two compared pleustonic communities, which often occurred side-by-side and in similar reservoirs, had slightly different optima for the water chemistry of their habitats.

In general, phytocoenoses of both *Salvinio natantis-Spirodeletum polyrhizae* and *Lemno-Spirodeletum polyrhizae* were associated with eutrophic waters in the parts of the Vistula and Odra River valleys studied here (Fig. 1). However, the phytocoenoses dominated by *S. natans* usually colonized deeper, more alkaline waters, with a higher amount of magnesium, soluble silica and total iron, and lower amounts of calcium and potassium, compared to the patches of *Lemno-Spirodeletum polyrhizae*. These conditions could therefore be considered optimal for *Salvinio natantis-Spirodeletum polyrhizae*.

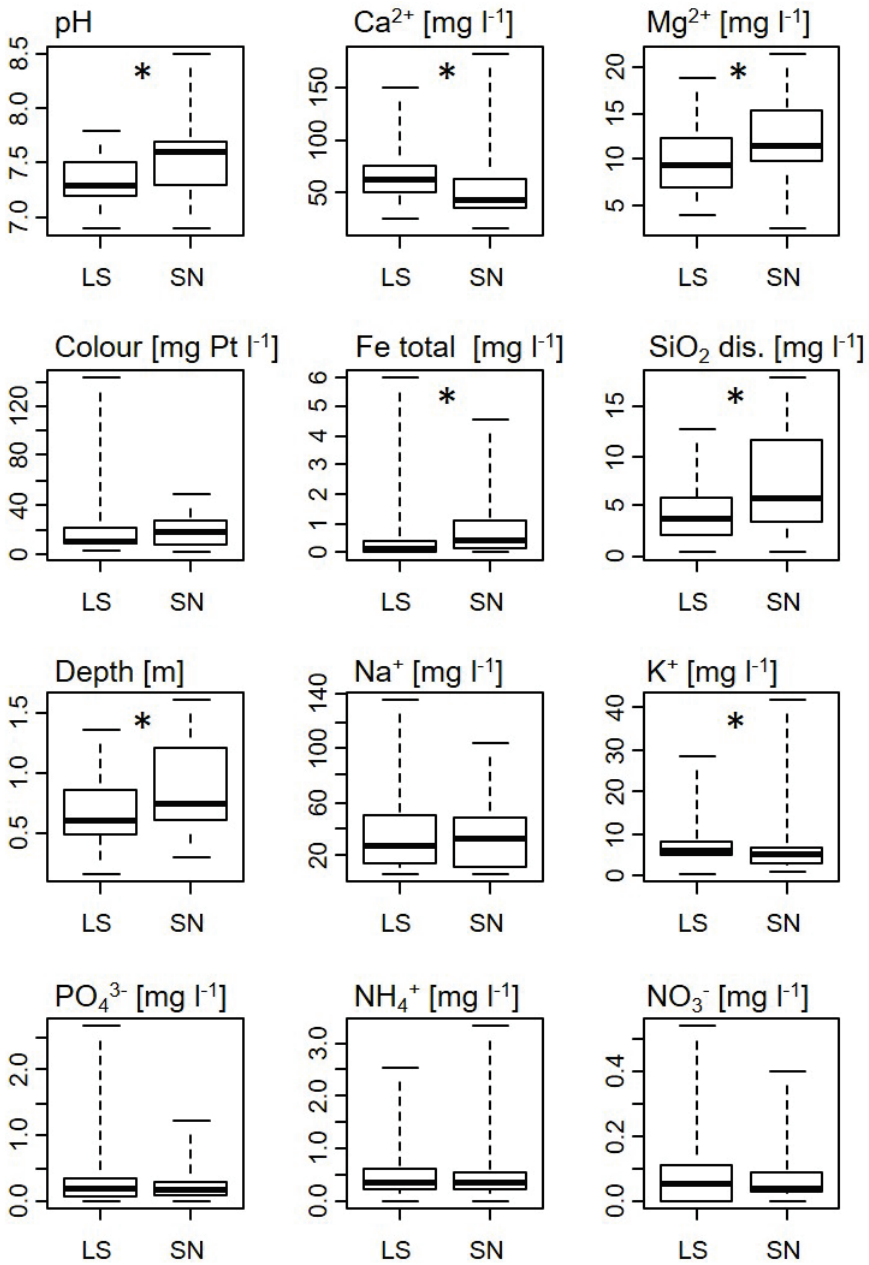

Fig. 3. Differentiation of the two communities studied in relation to 12 properties of water. White boxes show 25–75% interquartile ranges of values, the horizontal black lines in boxes show the medians and asterix mean that the differences between plant communities are significant at $p < 0.05$.
SN – *Salvinio natantis-Spirodeletum polyrhizae*; LS – *Lemno-Spirodeletum polyrhizae*.

Abb. 3. Differenzierung der beiden untersuchten Gesellschaften hinsichtlich der 12 Wassereigenschaften. Die Boxen zeigen die Interquartilsabstände von 25–75 % der Werte und die horizontalen Striche in den Boxen zeigen die Mediane. Mit Sternchen sind signifikante Unterschiede bei $p < 0{,}05$ bezeichnet.
SN – *Salvinio natantis-Spirodeletum polyrhizae*; LS – *Lemno-Spirodeletum polyrhizae*.

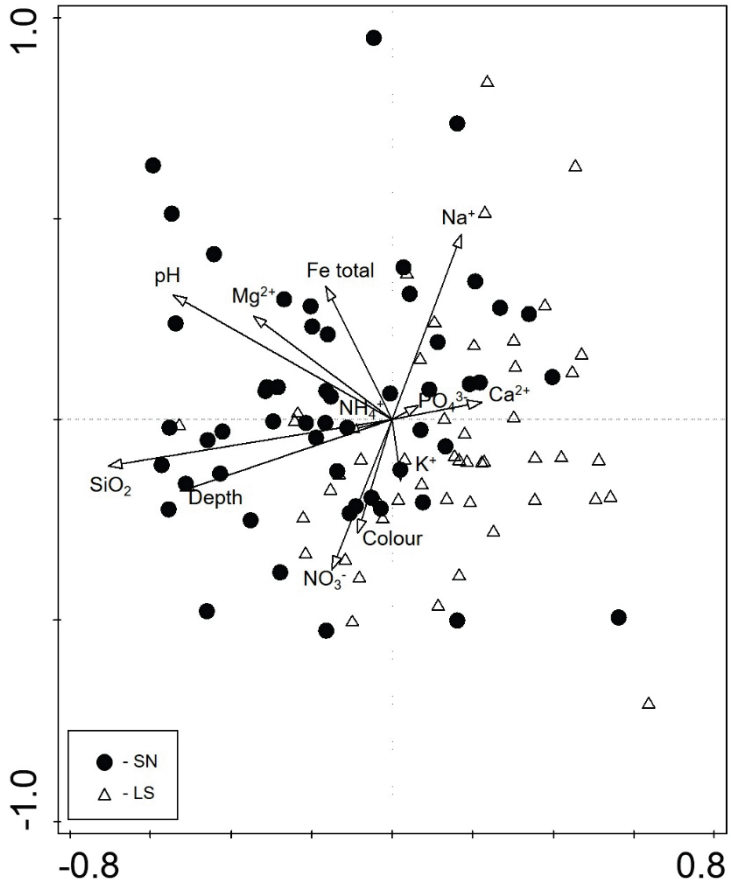

Fig. 4. CCA ordination diagram of 1st and 2nd axes obtained for 12 water properties and 101 relevés of two plant communities studied. Eigenvalues: λ1 = 0.1999, λ2 = 0.1493, λ3 = 0.1243, λ4 = 0.1155. SN – *Salvinio natantis-Spirodeletum poyrhizae*, LS – *Lemno-Spirodeletum polyrhizae*.

Abb. 4. CCA-Ordinationsdiagramm mit der 1. und der 2. Achse, die sich aus 12 Wassereigenschaften und 101 phytosoziologischen Aufnahmen von zwei untersuchten Pflanzengesellschaften ergeben. Eigenwerte der Achsen: λ1 = 0,1999; λ2 = 0,1493; λ3 = 0,1243; λ4 = 0,1155. SN – *Salvinio natantis-Spirodeletum polyrhizae*; LS – *Lemno-Spirodeletum polyrhizae*.

4. Discussion

Salvinio natantis-Spirodeletum polyrhizae and *Lemno-Spirodeletum polyrhizae* are communities from the same phytosociological class and order. In the areas studied, they are often found to coexist in neighbouring and similar reservoirs (oxbow lakes, ponds, canals, etc). It may therefore seem that they differ only in their dominant species, i.e. those that give a specific appearance to their phytocoenoses. The studies carried out indicate that they also differ, to a certain extent, both in terms of floristic composition and habitat requirements.

The floristic composition and structure of the phytocoenoses dominated by *Salvinia natans* presented in the paper are consistent with earlier observations by other authors. In a synthetic work by TOMASZEWICZ (1979) on aquatic and reedswamp vegetation in Poland, the main species (after the dominant one) creating the *Salvinia* phytocoenoses are listed as

the following *Lemnetea* species: *Spirodela polyrhiza*, *Lemna minor* and *L. trisulca*, and other waterborne plants – *Hydrocharis morsus-ranae*, *Ceratophyllum demersum* and *Nuphar lutea*. Now, the same set of main species (with a high degree of constancy) has been found in the current study. Similar observations have been made by other Polish authors (*inter alia* MICHALSKA-HEJDUK & KOPEĆ 2002, SPAŁEK 2005, AFRANOWICZ 2009, KRAWCZYK & MAJKUT 2012), and some foreign authors (e.g. SANDA et al. 1987). Other European authors (e.g. PASSARGE 1978), as well as researchers presenting data from southern Europe (e.g. SCOPPOLA 1982), also cite *Riccia fluitans* and/or *Ricciocarpos natans*, and often also *Nymphoides peltata*, as being important in the creation of phytocoenoses (CVIJANOVIĆ et al. 2018). The latter species is widespread in the waters of southern Europe, which explains its large contribution in the patches of *Salvinio natantis-Spirodeletum polyrhizae* in those areas.

Floristic differences between phytocoenoses of *Salvinio natantis-Spirodeletum polyrhizae* and patches of *Lemno-Spirodeletum polyrhizae* have not been specifically emphasized in the literature. Analysis of some of the data in earlier papers discussing both types of communities, e.g. AFRANOWICZ (2009), confirms, however, the lower proportion of *Potamion* species in the phytocoenoses of *Lemno-Spirodeletum polyrhizae* in comparison with patches of *S. natans*. This can be associated with a much greater thickness of the *Lemna* sp. cover, especially in smaller water reservoirs. According to TOMASZEWICZ (1979), the thickness of the *Lemna* sp. layer in the *Lemno-Spirodeletum polyrhizae* phytocoenoses can reach up to 5 cm, which prevents the development of submerged plant species. This phenomenon has not been observed in recent studies of *S. natans* patches. A large percentage of aquatic species from the *Potamogetonetea* in the *Salvinio natantis-Spirodeletum polyrhizae* patches could also result from the more frequently observed development of *S. natans* phytocoenoses in deeper waters, which has been confirmed by other authors (TOMASZEWICZ 1979, AFRANOWICZ 2009). On the contrary, the *Lemno-Spirodeletum polyrhizae* patches resist greater water level fluctuations and can also develop well on mud (PIÓRECKI 1975).

Habitat conditions of phytocoenoses dominated by *S. natans* have so far been assessed mainly on the basis of observation of the diversity of their water habitats (oxbow lakes, ponds, clay pits, slow flowing rivers, canals, drainage ditches). Hence, the literature emphasizes their wide ecological amplitude, especially in relation to water trophy, even without conducting detailed physico-chemical analyses (*inter alia* MARKOWSKI et al. 2004, MATUSZKIEWICZ 2008, ŠUMBEROVÁ 2011, KRAWCZYK & MAJKUT 2012, CVIJANOVIĆ et al. 2018). Similar statements have been made about *Lemno-Spirodeletum*, for example, by TOMASZEWICZ (1979), and ŠUMBEROVÁ (2011). Data on water chemistry that can be used with *Salvinia* phytocoenoses can be found in works by some Polish and other European authors (e.g. PAPASTERGIADOU & BABALONAS 1993a, b; STOJANOVIĆ et al. 2004, SCHWARZER 2005, SCHWARZER & WOLFF 2005, KOCIĆ et al. 2008, MICHALSKA-HEJDUK et al. 2009, GAŁKA & SZMEJA 2012), and seem to confirm these observations. The results presented in this paper indicate that the *S. natans* patches have a wide ecological amplitude in relation to the fertility of the water habitats measured, due, amongst others, to phosphates or various forms of nitrogen. However, the statement from a synthetic work on plant communities in Poland (MATUSZKIEWICZ 2008) that *Salvinio natantis-Spirodeletum poyrhizae* is a community with a wide habitat amplitude – from meso-eutrophic to nutrient-poor dystrophic waters – has not been confirmed. In the present study, a connection between *S. natans* phytocoenoses and dystrophic reservoirs was not found. Notwithstanding the broad valence emphasized for both phytocoenoses of *Salvinio natantis-Spirodeletum polyrhizae* and *Lemno-Spirodeletum polyrhizae* in their trophic state, the differences between their

water habitats are also important. In addition to water depth, there are differences in pH and calcium, magnesium and potassium concentration, soluble silica and total iron – properties that are also important in the development and differentiation of various types of aquatic vegetation (KŁOSOWSKI 2006, JABŁOŃSKA & KŁOSOWSKI 2012).

The literature mostly confirms only the alkaline pH in the phytocoenoses of *S. natans* (ZUTSHI & VASS 1971, PIETSCH 1982, PAPASTERGIADOU & BABALONAS 1993b, STOJANOVIĆ et al. 2004, SCHWARZER 2005, SCHWARZER & WOLFF 2005, KOCIĆ et al. 2008, MICHALSKA-HEJDUK et al. 2009, GAŁKA & SZMEJA 2012), as well as the frequent relation between *Lemno-Spirodeletum polyrhizae* patches and lower pH waters (WOŁEK 1974, 1997, OCHYRA 1985, WOŁEK & KOŚCIÓŁEK 2012). Higher concentrations of magnesium, soluble silica and total iron, and lower calcium in the waters of *Salvinio natantis-Spirodeletum polyrhizae* compared to the waters of *Lemno-Spirodeletum polyrhizae* have not had much importance placed upon them until now. In the areas investigated in this paper, this could result, for example, from differences in the processes of dissolving and transferring substances from the substrate to the water. Penetration of silicon into natural waters, for example, often occurs with dissolution of substrate components, and clearly alkaline water pH favours the presence of silica in a soluble form (HERMANOWICZ et al. 1999). There is also the possibility of a larger percentage of groundwater, in usually deeper, *S. natans* reservoirs, which are rich in iron compounds, soluble silica – and depending on the geological conditions of their aquifers – also magnesium (HERMANOWICZ et al. 1999).

The presented data show that phytocoenoses of *Salvinio natantis-Spirodeletum polyrhizae* are characterized by the water habitat properties discussed above, as well as the floristic composition of the small (but still significant) degree of distinction from the most common pleustonic phytocoenoses formed by *Lemna minor*, *L. trisulca* and *Spirodela polyrhiza* from the *Lemno-Spirodeletum polyrhizae* association. The presented value ranges for the water properties studied (25–75% interquartile value ranges) could indicate the optimal conditions for the development of *Salvinio natantis-Spirodeletum polyrhizae* phytocoenoses, as they affect the habitats in their main areas of occurrence. In contrast, species characteristic of *Lemno-Spirodeletum polyrhizae* phytocoenoses are widespread in Poland (ZAJĄC & ZAJĄC 2001), so the range of their habitat properties from the studied river valleys presented in this work could be narrower than the general amplitude of this community. As shown by data from north-eastern Poland (KŁOSOWSKI & JABŁOŃSKA 2009), this is also true in the case of higher concentrations of phosphates or total iron in *Lemno-Spirodeletum polyrhizae* waters in these areas. On the other hand, similarly to the studied river valleys, the *Lemno-Spirodeletum polyrhizae* habitats in north-eastern Poland are characterized by shallower depths (several-dozen cm), neutral or only slightly alkaline pH, high potassium concentration and low soluble silica (KŁOSOWSKI & JABŁOŃSKA 2009). It can therefore be assumed that in the case of the last four water habitat properties, the *Lemno-Spirodeletum polyrhizae* phytocoenoses have more strictly-defined requirements, and the differences observed in relation to *Salvinio natantis-Spirodeletum polyrhizae* are not accidental and have more than a regional meaning.

A separate issue is that of the degree of threat to the *S. natans* and its communities, and the need to protect. Many works (*inter alia* PROĆKÓW 2002, BRÓŻ & PRZEMYSKI 2009, OLACZEK 2012) emphasized that *S. natans* is an endangered species and under threat of extinction in some parts of Poland. The most common reasons for this are the shallowing and overgrowing of reservoirs, drainage of adjacent areas, disappearance of oxbow lakes and the decline of groundwater levels as a result of river regulation, the draining and cleaning of

ponds, increased eutrophication, pollution with sewage water and liquidation of reservoirs as part of the urbanization process (MICHALSKA-HEJDUK & KOPEĆ 2002, KRAWCZYK & MAJKUT 2008). In recent years, however, a massive increase in *S. natans* and its phytocoenoses has been observed, both in areas where it had been previously found, e.g. the Vistula delta (MARKOWSKI et. al. 2004, GAŁKA & SZMEJA 2012), as well as in new places, such as the Pilica River valley (STOLARZ & STOLARZ 2015). A similar phenomenon was also observed in Germany (WOLFF & SCHWARZER 2005). *Salvinia natans* is considered a thermophilic species (e.g. PASSARGE 1978, SANDA et al. 1987, MARKOWSKI et al. 2004, ŠUMBEROVÁ 2011, KRAWCZYK & MAJKUT 2012), gaining an advantage over underwater species with increased reservoir temperatures (NETTEN et al. 2010). Thus, it seems very likely that the phenomenon of its expansion, and thus the increase in the number of sites and massive development of large-scale phytocoenoses can be associated with directional climate changes, such as global warming (MARKOWSKI et al. 2004, KRAWCZYK & MAJKUT 2012). This has been confirmed by studies carried out in recent years in the Vistula delta (GAŁKA & SZMEJA 2013, SZMEJA et al. 2016).

The observed increase in the number of *S. natans* sites and the surfaces of its phytocoenoses does not mean, however, that threats to this species are disappearing, especially those of an anthropogenic nature related to the transformation of river valleys and the disappearance of oxbow lakes. The data presented in this paper indicate that in addition to previously postulated conservation strategies (counteracting subsequent succession and excessive eutrophication; extensive fishing management; cessation of river regulation and liquidation of small reservoirs, marking larger sites as protected lands – see the works of MICHALSKA-HEJDUK & KOPEĆ (2002) and KRAWCZYK & MAJKUT (2008), permanent hydrochemical monitoring of the richest *S. natans* sites should be carried out in both river valleys. The aim of this monitoring should be the observation of the variability of the level and water chemistry in the habitats of *Salvinio natantis-Spirodeletum polyrhizae* phytocoenoses. It is particularly important to maintain proper water depth (> 0.5 to +/-1.5 m), an alkaline pH and the concentrations of other properties that differentiate the water habitats of *Salvinio natantis-Spirodeletum polyrhizae* from *Lemno-Spirodeletum polyrhizae*.

Erweiterte deutsche Zusammenfassung

Einführung – Der Gemeine Schwimmfarn (*Salvinia natans*) ist an stehende Gewässer gebunden, hauptsächlich an Altgewässer, Teiche und Weiher. Die Art kommt auch in Kanälen und Entwässerungsgräben vor, die nur schwach durchströmt werden. In diesen Ökosystemen bildet sie meistens Phytozönosen der Assoziation *Salvinio natantis-Spirodeletum polyrhizae* Slavnić 1956. Aufgrund der anthropogenen Veränderungen in den Flusstälern, wo *S. natans* meistens auftritt, sind diese Art und ihre Gesellschaften an vielen Stellen in Europa in ihrem Bestand gefährdet. Die floristische Zusammensetzung und Struktur der Phytozönosen mit dem dominierenden Schwimmfarn sind in Polen sowie in ganzen Europa ziemlich gut beschrieben. Ihre Ökologie und besonders die physikalisch-chemischen Eigenschaften der Gewässer, in denen sie sich gut entwickeln, sind aber bisher noch nicht eingehend untersucht worden. Solche Untersuchungen können dazu beitragen, besser die Bedingungen zu verstehen, unter denen der Gemeine Schwimmfarn und die Gesellschaft *Salvinio natantis-Spirodeletum polyrhizae* erfolgreich geschützt werden können. Zielsetzung dieser Arbeit war es, die Standortverhältnisse der Phytozönosen mit der Dominanz von *S. natans* zu untersuchen, um die geeigneten Maßnahmen für ihren Schutz im Hauptgebiet ihres Vorkommens, also in den Flusstälern von Weichsel und Oder, zu bestimmen. Es wurde auch der Versuch unternommen, die standörtliche Eigenständigkeit des *Salvinio natantis-Spirodeletum polyrhizae* gegenüber der in Polen am meisten verbreiteten Pleustophyten- Assoziation *Lemno-Spirodeletum polyrhizae* Koch 1954 zu belegen.

Material und Methoden – In den Tälern der Weichsel und der Oder wurden in den Jahren 2009–2017 (von Mitte Juni bis zum 20. September) pflanzensoziologische und ökologische Untersuchungen durchgeführt. Untersucht wurden verschiedene Gewässertypen wie Altgewässer, Teiche, Weiher und Tümpel, sowie auch langsam fließende Flussabschnitte, Entwässerungsgräben und Kanäle. An den festgelegten Untersuchungsstellen, d. h. in den Beständen des *Salvinio natantis-Spirodeletum polyrhizae* und zum Vergleich in den Beständen des *Lemno-Spirodeletum polyrhizae* wurden pflanzensoziologische Aufnahmen nach der Braun-Blanquet-Methode (BRAUN-BLANQUET 1964) erstellt. Zusätzlich wurde in jedem Bestand die mittlere Wassertiefe gemessen und eine Wasserprobe von der Wasseroberfläche für physisch-chemische Analysen entnommen. Insgesamt wurden 101 Vegetationsaufnahmen auf Flächen von 2 bis 10 m^2 angefertigt und 101 Wasserproben entnommen. 53 Aufnahmen wurden für das *Salvinio natantis-Spirodeletum polyrhizae* erstellt (34 aus dem Tal der Weichsel und 19 aus dem Tal der Oder) und 48 Aufnahmen für das *Lemno-Spirodeletum polyrhizae* (19 aus dem Weichseltal und 29 aus dem Odertal). Die Verteilung der Fundorte der untersuchten Pleustophyten-Gesellschaften zeigt die beigefügte Karte (Abb. 1). Die erstellten pflanzensoziologischen Aufnahmen wurden in einer Stetigkeitstabelle zusammengestellt (Tab. 1), wo außer der Stetigkeit und der Artmächtigkeit auch der Deckungswert für alle Arten nach der Braun-Blanquet-Skala angegeben wird. Der Deckungswert wurde auf folgende Weise berechnet: die mittleren Deckungsprozente einer Art in den Aufnahmen der Tabelle (nach der Braun-Blanquet-Skala, wo den einzelnen Stufen der Skala folgende Zahlen entsprachen: + = 1 %, 1 = 10 %, 2 = 20 %, 3 = 37,5 %, 4 = 62,5 %, 5 = 87,5 %) wurde mit 100 multipliziert. Die Unterschiede in der Zahl der Fundorte einzelner Arten zwischen zwei Pflanzengesellschaften wurden mittels des Mann-Whitney-U-Tests gestestet ($p \leq 0{,}05$).

Die Auswertung der Daten erfolgte mittels des Moduls von „Statistica 6.1" (STATSOFT 2003). Die taxonomische Nomenklatur richtet sich nach THE PLANT LIST (2013), und die Namen der untersuchten Assoziationen entsprechen ŠUMBEROVÁ (2011). Bei den physikalisch-chemischen Untersuchungen der Gewässer wurden 12 Eigenschaften berücksichtigt: Wassertiefe, pH-Wert, Wasserfarbe, Gehalte an Phosphat, Ammonium, Nitrat, Calcium, Magnesium, Natrium, Kalium, Gesamteisen und gelöstem Silikat. Alle Analysen wurden nach Methoden durchgeführt, die in den Arbeiten von HERMANOWICZ et al. (1976) und HACH COMPANY (1992) beschrieben wurden. Die Standortbedingungen der untersuchten Pleustophyten-Gesellschaften wurden unter Berücksichtigung ihrer Schwankungsbreite, ihrer Mediane und Interquartilsabstände verglichen. Zur Feststellung statistischer Signifikanz der Unterschiede wurde der nicht-parametrische Wilcoxon-Test (STATSOFT 2003) angewendet. Die wechselseitige Abhängigkeit zwischen allen analysierten standörtlichen Faktoren und den Pleustophytengesellschaften wurde anhand der kanonischen Korrelationsanalyse (CCA) mit dem Programm CANOCO 5 (ŠMILAUER & LEPŠ 2014) ermittelt.

Ergebnisse – Die durchgeführten Untersuchungen haben gezeigt, dass die Bestände des *Salvinio natantis-Spirodeletum polyrhizae* sich von den *Lemno-Spirodeletum polyrhizae*-Beständen durch den größeren Anteil der Wasserpflanzen aus der Klasse *Potamogetonetea* Klika in Klika et Novák 1941 und der Röhrichtarten aus der Klasse *Phragmito-Magnocaricetea* Klika in Klika et Novák 1941 unterscheiden (Tab. 1). Die Bestände des *Salvinio natantis-Spirodeletum polyrhizae* entwickeln sich in den beiden Flusstälern hauptsächlich in Altgewässern, aber je nach der geomorphologischen Struktur und dem Charakter des Tals auch in den in Flüssen und Kanälen mit schwacher Durchströmung, z. B. im Weichsel-Nogat-Delta oder am unteren Lauf der Oder bei Gryfino. Seltener sind es Fischteiche oder ehemalige Lehmgruben. Die untersuchten Phytozönosen bildeten meistens zusammenhängende Schwimmdecken und nahmen in stillen, nicht sehr tiefen Gewässern erhebliche Flächen ein. In kleineren Altgewässern oder anderen Kleingewässern bedecken sie meistens die ganze Wasseroberfläche. In den Kanälen besiedeln sie oft lange Strecken von 10 bis 100 Meter Länge, oder sogar noch längere Abschnitte. Die Bestände des *Lemno-Spirodeletum polyrhizae* bedeckten die ganze Wasseroberfläche nur in temporären Kleingewässern, in ehemaligen Tongruben und in Entwässerungsgräben. In größeren Gewässern bildeten sie kleinere Decken. Öfter besiedeln sie auch seichtere Stellen. Beide Pleustophytengesellschaften sind im Untersuchungsgebiet an eutrophe Gewässer gebunden, aber das *Salvinio natantis-Spirodeletum polyrhizae* entwickelt sich häufiger in tieferen Gewässern mit höherem pH-Wert

und höherem Gehalt an gelöstem Silikat und Gesamteisen, die dafür ärmer an Calcium und Kalium sind (Abb. 2 und 3). Solche Standortbedingungen kann man als optimal für die Entwicklung des *Salvinio natantis-Spirodeletum polyrhizae* betrachten.

Diskussion – Die durchgeführten Untersuchungen haben frühere Beobachtungen über die floristische Zusammensetzung und den Aufbau des *Salvinio natantis-Spirodeletum polyrhizae* bestätigt (TOMASZEWICZ 1979, SANDA et al. 1987, MICHALSKA-HEJDUK & KOPEĆ 2002, SPAŁEK 2005, AFRANOWICZ 2009, KRAWCZYK & MAJKUT 2012). Aus den ermittelten Daten wird aber ersichtlich, dass wesentliche floristische und standörtliche Unterschiede zwischen dem *Salvinio natantis-Spirodeletum polyrhizae* und dem *Lemno-Sopirodeletum polyrhizae* bestehen, obwohl diese Gesellschaften zu derselben Klasse und Ordnung gestellt werden und in den beiden untersuchten Flusstälern in benachbarten, ähnlichen Gewässertypen vorkommen. Sowohl das *Salvinio natantis-Spirodeletum polyrhizae*, als auch das *Lemno-Spirodeletum polyrhizae* werden als Gesellschaften angesehen, die sich durch eine breite ökologische Amplitude bezüglich der Trophie auszeichnen (MATUSZKIEWICZ 2008, ŠUMBEROVÁ 2011, KRAWCZYK & MAJKUT 2012, CVIJANOVIĆ et al. 2018 u. a.). Deshalb sind die Unterschiede so wichtig, die zwischen ihren Wasserstandorten festgestellt wurden. Sie betreffen die Wassertiefe, den pH-Wert und die Konzentrationen an Calcium, Magnesium, Kalium, gelöstem Silikat und Gesamteisen, also solche Eigenschaften, die generell von großer Bedeutung für die Entwicklung und Differenzierung verschiedener Typen der aquatischen Vegetation sind (KŁOSOWSKI 2006, JABŁOŃSKA & KŁOSOWSKI 2012). Diese Eigenschaften sollten beim Monitoring von Wasserstandschwankungen und des Wasserchemismus an den reichsten Wuchsorten des *Salvinio natantis-Spirodeletum polyrhizae* berücksichtigt werden, damit getroffene Maßnahmen zum Schutz des Gemeinen Schwimmfarns und seiner Bestände effektiv sein können.

Author contributions

Stanisław Kłosowski: 45% (field research, work on the text)
Paweł Pawlikowski: 35% (field research)
Ewa Jabłońska: 10% (work on the text)
Monika Podgórska: 10% (work on the text)

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