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Environmental factors affecting pondweeds in water bodies of northwest Poland

Marek Merdalski*, Krzysztof Banaś & Rafał Ronowski

Department of Plant Ecology, Faculty of Biology, University of Gdańsk, Wita Stwosza 59, 80-308 Gdańsk, Poland; ORCID: MM http://orcid.org/0000-0003-2117-4889, KB http://orcid.org/0000-0002-2131-8400, RR http://orcid.org/0000-0002-5638-7131
*corresponding author (e-mail: marek.merdalski@ug.edu.pl)

Abstract. In 32 lakes, 19 watercourses and 11 estuaries located along the southern Baltic coast (NW Poland) taxa of *Potomogeton* and *Stuckenia* genera were determined on the basis of 981/0.1 m^2 plant samples. Environmental factors affecting them were identified on the basis of 212 water samples and 272 sediment samples. Twenty-one *Potamogeton* taxa were found, including four hybrids and two *Stuckenia* species. Twenty-one pondweed species occurred in lakes, thirteen in watercourses and ten in estuaries. There were significant differences in environmental factors in particular types of water bodies ($p<0.001$) except for the content of organic and mineral matter and of humic acids in the sediment.

There was a statistically significant difference ($p<0.001$) between the environmental factors affecting *Potamogeton* and *Stuckenia*, respectively, within each of the waterbody types studied. In lakes, *Potamogeton* occupied poorer habitats than *Stuckenia*, with lower conductivity, redox, PAR intensity, concentration of bicarbonates, calcium and chlorides and lower calcium content in the sediment. In watercourses, *Potamogeton* occurred in less coloured and less oxygenated waters than *Stuckenia*, but richer in CO_2 and chlorides, better insolated and flowing faster. It also occupied less alkaline sediment, but of higher conductivity. In estuaries, *Potamogeton* occurred in waters with a relatively low concentration of chlorides and calcium than *Stuckenia*, lower pH and conductivity, but more coloured and, consequently, with lower PAR. C&RT analysis showed mineral concentration (Ca^{2+}, Cl^-, HCO_3^-) in the water, its conductivity, colour and flow to be the highest-ranking environmental factors affecting pondweeds.

Key words: *Potamogeton*, *Stuckenia*, pondweed, lakes, estuaries, watercourses, environmental factors

1. Introduction

The history of research concerning *Potamogeton* goes back to the turn of the 18th and 19th centuries. On the Polish territory, the research was conducted by Jan Fryderyk Wolfgang (1775-1859) and Stanisław Batyst Gorski (1802-1864). The first extensive monograph of the *Potamogeton* species was written by Hagström (1916) and was largely topical ever since (Zalewska-Gałosz 2008). In the 20th century, numerous scientists all over the world dealt with this group of plants, among them Fernald (1932), Ogden (1943), Haynes (1974), Reznicek & Bobbette (1976), Haynes & Hellquist (2000) in North America; Tur (1982) in South America; Miki (1937), Kadono (1982), Kaplan (2008), Wang *et al.* (2007) in Asia; Dandy (1937), Obermeyer (1966), Symoens *et al.* (1979), Kaplan & Symoens (2005) in Africa; Aston (1973) in Australia; Yuzepchuk (1934), Mäemets (1979, 1984), Tzvelev (1987), Kashina (1988), Volobaev (1993), Bobrov & Chemeris (2009) in Russia and Wiegleb (1983, 1984), Brux *et al.* (1988), Preston (1995), Kaplan (2005, 2010), Zalewska-Gałosz (2002, 2008) in Europe. Their research brought numerous studies of the kind; however, they were usually fragmentary. It was only Wiegleb and Kaplan (1998) who wrote a monograph covering 69 species and 50 hybrids existing today. Their occurrence all over continents shows their high adaptability to changing environmental conditions. Recently, however, most academic papers dealt with taxonomy and its verification, together with the distribution of species (Preston 1993; Preston & Stewart 1994; Afranowicz 2007; Chmara & Bociąg 2007; Kaplan 2008). As a result, subgenus *Coleogeton* was excluded from the *Potamogeton* genus and raised again to the rank of genus (Börner 1912; Holub 1984; Les & Haynes 1996; Haynes *et al.* 1998; Zang *et al.* 2008). However, knowledge of environmental conditions in which *Potamogeton* species occur is still insufficient.

This paper aims at the identification of environmental conditions of *Potamogeton* and *Stuckenia* taxa, which in Poland occur along southern Baltic coast (NW Poland). Conditions of *Potamogeton* and *Stuckenia* occurrence in lakes, watercourses and estuaries were compared, and main environmental factors influencing their appearance in this type of water bodies were identified. The paper discusses empirical and conceptual models of correlation of *Potamogeton* and *Stuckenia* environmental factors.

2. Material and methods

Field research was conducted between 2008-2017 in 32 lakes, 19 watercourses and 11 estuaries (NW Poland, Fig. 1). Each site underwent a single observation in July, in the afternoon, with the same methodology. Samples were collected at random by a diver in a transect of approximately 250 metres, at one-metre-interval depth zones down to the lowest zone of plant occurrence (Chmara *et al.* 2015). In the area of 0.1 m^2, coverage of individual taxa was identified, then all plants were collected and packed into sacks made of fine mesh (excluding samples of *P. polygonifolius* – noninvasive research at the Białogóra Nature Reserve). Altogether, 1474 samples with plants were collected. Plants were then segregated by taxa, dried and weighed. Samples which contained at least one taxon of *Potamogeton* or *Stuckenia* were used for further analysis (981 samples). 84 taxa altogether were identified in the samples, including 21 *Potamogeton* (17 species and 4 hybrids) and 2 *Stuckenia*. Key parts of specimens, like leaves, stems, stipules and inflorescence, were used to identify *Potamogeton* as described in the publications of Hagström (1916), Mądalski (1977), Wiegleb (1990), Zalewska-Gałosz (2008). Names of taxa were used in accordance with The Plant List (2013).

At the same depth zone of the transect where plant samples were collected, the diver collected sediment and water samples in order to describe the habitat of *Potamogeton* (212 water samples and 272 sediment samples). Water samples were put into polypropylene bottles (0.5 dm^3), while the sediment was collected in the form of a short core (1 dm^3) and then put into plastic ziplock bags. Measurements were taken in the water, for depth profiles of one metre. Temperature and oxygenation were measured with a WTW OXI 197i oxygen metre with the EOT 196 electrode. PAR at the sites where samples were collected was measured with LI-COR light metre with a flat sensor for incident radiation measurement LI-250 Light Meter, and the results were recalculated as a percentage of the light reaching water surface. Water flow was measured with Valeport flow meter, model 801 (flat) EM Flow Meter (the mean value three measurements for each depth zone where the plants occurred).

The research took into consideration aquatic environment factors generally recognised as important for the formation of plant communities, such as: depth, PAR intensity (van den Berg *et al.* 2003), oxygenation and temperature (Rooney & Kalff 2000), reaction (Srivasta *et al.* 1995), conductivity (Toivonen & Huttunen 1995), redox potential (in water and sediments), nutrient availa-

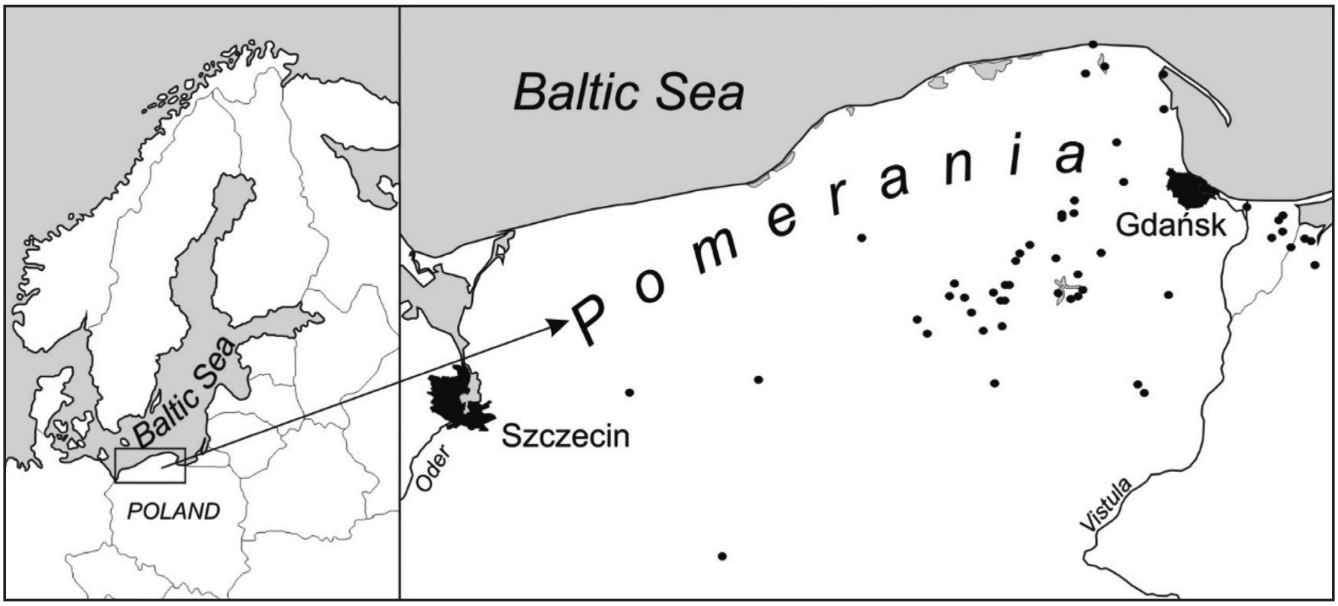

Fig. 1. Location of water bodies with pondweeds in north-western Poland

bility (C, N, P; Murphy *et al.* 2003), water colour, concentration of humic acids, calcium and chlorides, and water flow (Chambers *et al.* 1991; Madsen *et al.* 2001). In the sediment, the following factors were checked: hydration, organic and mineral matter contents, reaction, conductivity, contents of humic acid and calcium, non-carbonate mineral matter, and the proportions of various granulation fractions (Lehmann *et al.* 1997; Gafny & Gasith 1999).

In this paper, physical and chemical factors of the aquatic environment were assayed in the laboratory, following the works of Hermanowicz *et al.* (1999), and Eaton *et al.* (2005). Water and sediment conductivity was measured with LF 96 conductivity meter with a TETRACON 96 electrode, and the redox potential and pH – with a WTW 320/SET1 pH meter with respective glass METTLER electrode and SENTIX 97T electrode. Water colour was identified by comparative method according to platinum-cobalt scale. The concentration of dissolved forms of inorganic carbon (DIC; CO_2, HCO_3^- and CO_3^{2-}) in water was assessed by titration, concentration of calcium in water – by complexometric EDTA method, and in sediments after Ca^{2+} extraction – with hydrochloric acid (1:1). Humic acids concentration was measured with UV-VIS spectrophotometer at the wave length of 330 nm according to Moore (1985, 1987) and Górniak (1996), while in the sediment after earlier extraction – in 0.5n NaOH. Total nitrogen, total phosphorus and chlorides were estimated with a MERCK Spectroquant cuvette test on the UV-VIS spectrophotometer. Samples for phosphorus assays were earlier mineralised in the environment of sulphuric and nitric acids in Microwave Digestion System – Start D (Milestone). Hydration was measured on the basis of the difference between fresh and dry sediment, after drying it at 105°C to dry solids. Organic matter content was calculated from the difference between the sediment weight before and after combustion at 550°C in the Thermolyne 62700 muffle furnace. Non-carbonate matter content (SiO_2) in the sediment was estimated after previous dissolution of a weighed portion of the incinerated sediment in 1:1 HCl solution. The share of sediment fractions of different granulations: <0.1mm, 0.1-0.25 mm, 0.25-0.5 mm, 0.5-1 mm, 1-2 mm and >2mm was calculated as weight percentage of dry sediment after sifting through sieves with specified mesh size.

The database was constructed as a matrix in which each of the species was entered into a separate column (84) and each line represented a single sample (981 samples of *Potamogeton*). Individual fields of the matrix were filled in a binary way (yes – 1, no – 0). Next, the occurrence of individual types of *Potamogeton* was calculated.

Another matrix with the same structure was produced for 981 samples in terms of 14 water properties and 10 sediment properties, where – like in the previous database – the line represents the next sample and the column – the identified environmental feature.

The STATISTICA 12.0 software was used for data analysis to calculate arithmetic average, standard deviation, minimum and maximum value for each of the studied features, for each species, and type of water body. In order to establish the length of the distribution gradient, CANOCO 4.5 software was used for detrended correspondence analysis (DCA, gradient length = 1.304). In order to identify main factors affecting species and genus distribution (*Potamogeto* and *Stuckenia*) in the water bodies studied, the *principal component analysis* (PCA) was conducted on the basis of calculations made by Canoco 4.5 (Hastie *et al.* 2001; Ter Braak & Šmilauer 2002). Before analyses, the scaling was focused on inter-species correlations, samples were cantered and standardised, but the data were not transformed. The selection of environmental variables was automatic.

The analysis of relationships between the occurrence of *Potamogeton* and *Stuckenia* and environmental factors in the water bodies was performed by means of the Classification and Regression Tree (C&RT) with Gini impurity (I_G(f) in the Statistica 12.0 software, in accordance with the recommendations given by Bell (1999); Austin (2007) and Olden *et al.* (2008). Predictive validity of environmental factors was determined according to the value of the validity coefficient.

3. Results

3.1. Pondweeds in the study area

21 pondweed taxa were found in the lakes, 13 in the watercourses and 10 in the estuaries (Table 1). *Stuckenia pectinata*, *Potamogeton perfoliatus*, *P. obtusifolius*, *P. crispus*, *P. natans*, *P. lucens* and *P. compressus* occurred in each of the waterbody categories. *Stuckenia filiformis*, *P. gramineus*, *P. polygonifolius*, *P. ×nitens*, *P. ×salicifolius* and *P. ×angustifolius*, inhabited only lakes, while the occurrence of *P. nodosus* and *P. ×sparganifolius* was confined to the watercourses.

Most pondweeds occurred at the depths of up to two metres. The water in such places was slightly alkaline (pH 7.5-8.5), rich in nitrogen, phosphorus, carbon (DIC) and calcium, and slightly coloured (Table 2). Chloride concentration varied significantly, from 0.5 mg $Cl^- dm^{-3}$ in the lakes, 116.3 mg $Cl^- dm^{-3}$ in the estuary section of the River Vistula up to 5121,4 mg $Cl^- dm^{-3}$ in the Bay of Puck. The water was well oxygenated, but the photosynthetic irradiation was low. The sediment was pH-neutral, poorly hydrated, with a low redox. It contained little organic matter but was rich in SiO_2 and calcium (Table 3).

Table 1. Number of pondweed samples in the studied waterbodies by category

Species	Number of samples			
	lakes	watercourses	estuaries	total
S. pectinata (L.) Börner	161	51	54	266
P. perfoliatus L.	97	47	34	178
P. obtusifolius Mert. & W. D. J. Koch	70	46	18	134
P. friesii Rupr.	114	6	-	118
P. crispus L.	48	28	32	108
P. natans L.	79	8	16	103
P. lucens L.	29	26	18	73
P. gramineus L.	62	-	-	62
P. compressus L.	31	16	3	50
P. trichoides Cham. & Schltdl.	17	-	23	40
P. praelongus Wulfen	29	-	4	33
P. alpinus Balb.	8	23	-	31
P. berchtoldii Fieber	16	2	-	18
P. pusillus L.	13	-	2	15
P. ×nitens Weber	14	-	-	14
P. ×salicifolius Wolfg.	13	-	-	13
P. rutilus Wolfg.	7	4	-	11
S. filiformis (Pers.) Börner	10	-	-	10
P. polygonifolius Pourr.	6	-	-	6
P. nodosus Poir.	-	5	-	5
P. ×angustifolius J. Presl	5	-	-	5
P. ×sparganifolius Laest. ex Fr.	-	3	-	3
P. acutifolius Link ex Roem. & Schult.	1	-	-	1

Table 2. Water traits in the studied pondweed habitats

Species	pH	Conductivity [µS cm^{-1}]	Water colour [mg Pt dm^{-3}]	Ca^{2+} [mg dm^{-3}]	$N_{tot.}$ [mg dm^{-3}]	$P_{tot.}$ [mg dm^{-3}]	Cl^- [mg dm^{-3}]	PAR [%]	Oxygenation [%]
S. pectinata	8.02±0.44	384±309	22±18	55.3±28.0	1.5±1.1	0.3±0.2	259.2±910.1	30.0±20.2	107.2±107.2
P. perfoliatus	7.96±0.40	371±273	28±22	53.4±23.4	1.5±1.2	0.4±0.2	21.8±33.0	30.7±21.5	110.7±19.6
P. obtusifolius	8.10±0.33	331±233	25±22	51.1±17.4	2.4±1.7	0.4±0.2	16.3±21.5	29.1±22.0	102.5±32.4
P. friesii	7.96±0.29	223±35.9	12±6	42.9±8.3	1.3±0.7	0.2±0.1	4.6±2.5	27.4±22.8	110.8±22.6
P. crispus	8.01±0.38	394±305	29±33	56.7±29.3	1.7±1.3	0.4±0.2	52.5±265.3	28.4±24.5	96.9±38.7
P. natans	7.75±0.70	258±240	27±28	36.6±28.2	1.5±0.8	0.3±0.2	16.3±27.3	34.0±22.2	96.0±28.9
P. lucens	7.81±0.32	466±332	31±26	59.4±24.0	1.5±0.8	0.4±0.2	25.2±28.1	17.5±15.6	83.7±34.6
P. gramineus	7.85±0.24	160±44.1	10±6	28.1±7.4	1.2±0.6	0.2±0.1	4.4±1.8	49.8±25.1	114.8±9.7
P. compressus	8.09±0.35	345±303	31±10	46.5±16.3	2.6±1.2	0.4±0.1	17.4±20.9	15.2±12.3	96.1±22.8
P. trichoides	7.87±0.41	559±319	34±16	76.6±37.4	2.3±0.7	0.4±0.1	37.9±26.7	14.5±12.8	83.3±27.9
P. praelongus	8.01±0.23	209±288	22±10	29.1±21.4	2.1±1.5	0.7±0.5	10.7±22.4	18.7±7.7	102.8±23.0
P. alpinus	7.80±0.33	244±40.3	15±5	46.1±9.3	1.8±1.5	0.3±0.2	4.0±1.9	40.6±22.7	105.5±21.7
P. berchtoldii	8.16±0.35	249±76.2	12±6	42.1±10.8	1.0±0.8	0.2±0.1	10.2±8.4	23.7±17.0	113.3±22.0
P. pusillus	8.06±0.56	237±186	17±10	43.7±35.4	2.3±1.5	0.3±0.2	9.8±15.6	26.2±9.5	108.1±14.6
P. ×nitens	7.9±0.19	189±13.7	9±5	31.9±2.8	0.8±0.7	0.2±0.1	5.2±1.9	28.0±11.2	122.6±6.4
P. ×salicifolius	8.09±0.34	196±22.7	6±4	35.0±3.1	1.1±0.5	0.1±0.1	4.8±6.2	17.4±1.6	105.9±0.3
P. rutilus	7.71±0.13	165±93.0	11±3	32.3±22.6	2.3±2.0	0.3±0.2	3.3±0.3	30.9±22.8	110.8±30.2
S. filiformis	7.98±0.19	206±0.7	10±3	39.5±8.6	0.9±0.1	0.1±0.1	5.3±0.3	39.5±6.2	121.4±3.9
P. poligonifolius	4.89±0.1	48.8±5.4	275±137	1.2±0.1	0.8±0.1	0.2±0.1	8.7±2.2	12.8±8.3	48.9± 3.7
P. nodosus	7.67±0.03	367±0.0	25±2	62.2±0.3	0.9±0.1	0.2±0.1	9.2±0.4	45.4±3.0	65.1±0.0
P. ×angustifolius	7.78±0.0	155±0.0	12±0	27.7±0.0	1.7±0.0	0.1±0.0	1.6±0.0	19.2±0.0	111.7±0.0
P. ×sparganifolius	8.27±0.0	189±0.0	15±0	44.9±0.0	0.9±0.0	0.4±0.0	6.7±0.0	43.3±0.0	147.5±0.0
P. acutifolius	8.16	240.0	35	41.04	3.6	0.34	9.44	6.57	106.1

Explanations: see Fig. 2

Table 3. Sediment traits in the studied pondweed habitats

Species	Depth [m]	Organic matter [%]	Hydration [%]	pH	Redox potential [mV]	Ca^{2+} [mg g^{-1} d.w.]
S. pectinata	1.3±0.9	6.2±8.5	34.9±25.1	7.19±0.3	-242±104	57.8±96.5
P. perfoliatus	1.1±0.9	4.5±6.7	30.6±22.6	7.18±0.37	-248±101	46.9±85.0
P. obtusifolius	1.3±1.1	9.6±11.9	37.8±27.4	7.22±0.32	-245±121	55.6±87.0
P. friesii	1.9±1.2	10.9±9.8	37.0±30.0	7.18±0.23	-244±70	152.8±131.0
P. crispus	1.7±1.6	12.1±14.9	39.1±27.0	7.15±0.34	-243±116	45.0±80.0
P. natans	1.0±0.6	15.5±25.4	42.2±31.7	6.94±0.39	-156±143	36.3±77.1
P. lucens	1.6±0.7	10.8±12.1	53.9±27.5	7.13±0.38	-258±111	31.8±42.1
P. gramineus	0.8±1.1	1.4±2.2	18.3±12.8	6.99±0.29	-131±185	2.7±2.7
P. compressus	1.3±0.5	4.5±5.4	42.1±19.7	7.21±0.32	-288±76	88.3±94.7
P. trichoides	1.1±0.5	10.4±13.2	48.3±25.5	6.96±0.32	-322±56	40.8±76.4
P. praelongus	2.1±0.7	33.2±22.0	76.2±34.0	6.91±0.21	-225±104	14.0±21.8
P. alpinus	1.0±1.0	6.0±11.9	25.8±27.0	7.22±0.21	-147±130	8.8±6.7
P. berchtoldii	2.3±1.5	3.0±5.6	17.0±27.1	7.21±0.16	-251±91	31.5±73.4
P. pusillus	1.4±1.0	5.5±6.4	45.3±31.0	6.89±0.39	-192±133	22.8±46.9
P. ×nitens	2.1±1.0	1.4±1.0	23.7±19.3	7.14±0.35	-211±93	5.5±5.6
P. ×salicifolius	4.2±0.3	2.2±3.4	36.4±11.8	7.25±0.18	-199±38	3.0±1.2
P. rutilus	2.2±1.4	2.9±1.0	15.6±11.5	6.99±0.34	-121±175	1.7±0.8
S. filiformis	0.5±0.4	3.9±10.9	15.8±27.1	7.21±0.31	-41±96	13.2±36.6
P. poligonifolius	0.3±0.1	29.4±25.6	76.8±18.1	5.34±0.29	-187±79	4.9±4.5
P. nodosus	0.5±0.1	2.6±3.6	30.1±14.2	7.23±0.29	-573±173	6.0±0.1
P. ×angustifolius	1.9±0.3	2.0±0	26.8±0	6.8±0	-144±0	0.9±0
P. ×sparganifolius	1.1±0.2	38.8±0	16.1±0	7.45±0	-259±0	6.5±0
P. acutifolius	1.6	4.28	58.04	7.24	-308	232.15

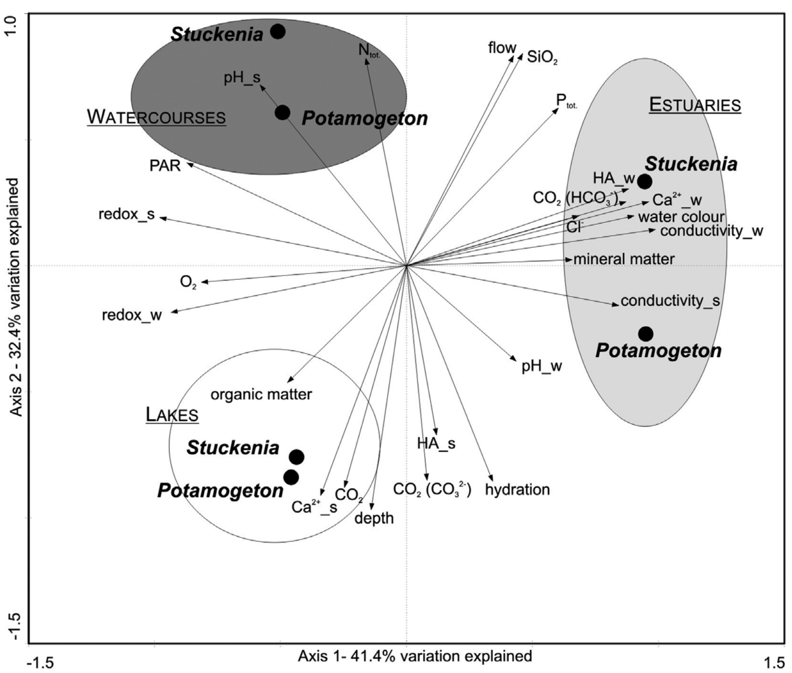

Fig. 2. Model of the relationship between pondweed distribution and PCA-ranked environmental factors in the studied lakes, watercourses and estuaries
Explanations: HA – humic acids, $N_{tot.}$ – total nitrogen, $P_{tot.}$ – total phosphorus, PAR – photosynthetically active radiation

Summary of PCA analysis					
Axes	1	2	3	4	Total inertia
Eigenvalues:	0.414	0.324	0.175	0.071	1.000
Cumulative percentage variance of species data:	41.4	73.8	91.3	98.4	
Sum of all eigenvalues					1.000

Table 4. Environmental factors and differences in water and sediment traits for the studied waterbody types

	Lakes n=629		Watercourses n=196		Estuaries n=156		Statistical significance		
Trait	mean±SD	min-max	mean±SD	min-max	mean±SD	min-max	a	b	c
Depth [m]	1.8±1.3	0.0-6.3	0.7±0.6	0.1-2.4	1.1±0.6	0.3-2.5	***	***	**
water traits									
pH	7.9±0.5	4.8-8.9	7.8±0.4	7.3-8.4	8.0±0.5	6.9-8.9	**	-	**
Conductivity [μS cm^{-1}]	193.8±66.1	34.5-336	278.2±66.2	189.1-575	905.1±164.6	451-1136	***	***	***
Redox [mV]	60±82	-120-395	53±89	-86-322	17±132	-276-255	-	***	***
Colour [mg Pt dm^{-3}]	17±31	2-400	22±11	8-45	52±32	15-160	-	***	***
HA [mg dm^{-3}]	2.7±4.1	0.3-45.1	3.8±1.7	1.2-8.3	6.3±3.6	2.2-17.1	**	***	***
CO_2 [mg dm^{-3}]	8.0±6.4	0.1-41.4	5.4±4.2	1.3-24.2	5.1±3.2	0.7-11.4	***	***	-
CO_3^{2-} [mg CO_2 dm^{-3}]	9.5±10.3	0.0-62.9	4.9±5.2	0.0-26.4	8.7±6.4	0.0-18.5	***	-	***
HCO_3^- [mg CO_2 dm^{-3}]	61.0±26.4	7.0-140.8	107.8±42.6	59.0-286.0	180.9±58.9	92.4-311.1	***	***	***
Ca^{2+} [mg dm^{-3}]	35.2±13.1	1.0-69.2	51.5±11.0	41.0-94.5	96.6±16.9	78.8-131.5	***	***	***
$N_{tot.}$ [mg N dm^{-3}]	1.3±0.9	0.3-4.0	1.9±1.6	0.3-5.3	1.5±0.9	0.5-4.8	***	-	**
$P_{tot.}$ [mg P dm^{-3}]	0.2±0.2	0.0-1.3	0.4±0.2	0.1-0.8	0.5±0.2	0.1-1.5	***	***	**
Cl^- [mg dm^{-3}]	6.0±5.8	0.5-50.3	6.1±2.7	2.0-16.3	495.1±1156.2	47.6-5121.4	-	***	***
PAR [%]	28.7±20.1	1.5-100.0	42.0±22.2	0.4-100.0	18.0±21.8	0.1-100.0	***	***	***
O_2 [%]	111.2±19.0	12.3-161.2	101.7±30.6	35.9-147.5	71.1±30.3	7.6-117.9	***	***	***
Flow [ms^{-1}]	0	0	0.2±0.1	0-0.5	0.1±0.2	0-0.6	***	***	***
sediment traits									
pH	7.1±0.4	5.1-8.2	7.3±0.3	6.7-8.0	7.1±0.3	6.5-7.5	***	-	***
Conductivity [μS cm^{-1}]	281.2±229	41.1-2150	349±439	42.3-1435	636.3±355.4	40.0-1428	*	***	***
Redox [mV]	-210±118	-352-256	-195±1270	-650-267	-329±105	-460-33	-	***	***
Ca^{2+} [mg g^{-1} d.w.]	73.0±109.8	0.4-376.9	17.9±35.6	1.0-188.4	23.7±31.1	0.7-153.0	***	***	-
HA [mg g^{-1} d.w.]	8.1±13.5	0.1-135.1	5.9±13.3	0.2-60.4	9.1±9.9	0.0-33.1	-	-	-
Hydration [%]	39.1±31.4	0.4-99.9	29.2±20.5	0.8-83.2	43.0±25.7	13.1-92.7	**	-	***
Organic matter [%]	10.8±16.1	0.3-92.8	8.0±12.9	0.3-38.9	7.7±8.2	0.2-28.2	-	-	-
Mineral matter [%]	89.2±16.1	7.2-99.7	89.6±19.2	38.1-99.7	92.3±8.2	71.9-99.8	-	-	-
SiO_2 [%]	66.1±35.8	0.2-100.3	78.7±24.1	32.4-98.4	78.9±18.4	29.8-98.6	***	**	-
Fraction >2mm [%]	5.6±12.2	0.0-76.8	10.2±15.2	0.0-62.4	2.0±5.3	0.0-19.6	***	*	***
1-2 mm [%]	3.3±4.3	0.0-20.2	4.8±4.2	0.0-14.8	2.4±3.9	0.0-13.5	**	-	***
0.5-1 mm [%]	8.7±10.0	0.0-37.3	16.8±12.9	0.0-57.4	7.8±12.1	0.0-43.6	***	-	***
0.25-0.5mm [%]	22.4±17.6	0.0-62.3	31.1±17.2	0.0-65.2	16.3±20.4	0.0-64.4	***	*	***
0.1-0.25 mm [%]	29.4±19.4	0.0-83.4	26.7±19.7	0.0-84.5	24.5±19.5	0.0-68.8	-	*	***
<0.1 mm [%]	30.3±34.5	0.0-100.0	10.0±20.0	0.1-100.0	46.2±37.4	0.1-100.0	***	***	***

Explanations: statistically significant differences between the studied lakes and watercourses (a), lakes and estuaries (b), watercourses and estuaries (c); - no difference, *p≤0.05, **p≤0.01, ***p≤0.001 (post-hoc Tukey's test), n – number of samples, HA – humic acids, $N_{tot.}$ – total nitrogen, $P_{tot.}$ – total phosphorus, PAR – photosynthetically active radiation

The environmental factors affecting pondweeds in the selected categories of water bodies differed significantly in all their traits, except for the content of organic and mineral matter and of humic acid content in the sediment (Table 4). Furthermore, there was a significant difference between environmental factors at the sites of *Potamogeton* species and *Stuckenia* species, respectively (Table 5).

The heterogeneity of environmental conditions for pondweeds in the studied water bodies is presented in Fig. 2. The strongest positive correlation with the first PCA ordination axis is shown mainly by calcium concentration, water colour, water and sediment conductivity. Negative correlation with the first axis is demonstrated by water and sediment redox, and slightly weaker by oxygenation. The strongest correlation with the second axis is shown by water depth, and slightly less by sediment hydration, CO_2 content, flow, content of SiO_2 and $N_{tot.}$

The occurrence of pondweeds in the lakes strongly correlated with the second PCA ordination axis. Positive correlation was shown by water depth, content of CO_2, sediment Ca and organic matter, while negative correlation was demonstrated, primarily, by the flow and SiO_2 content. Environmental factors for *Potamogeton* and *Stuckenia* in the lakes were similar.

Table 5. Environmental factors for *Potamogeton* and *Stuckenia* in the waterbodies studied. Statistically significant differences at p<0.05 are presented in bold type

	Potamogeton n=836				*Stuckenia* n=276				Mann-Whitney U test	
Trait	mean	SD	min	max	mean	SD	min	max	Z	p
Depth [m]	1.5	1.2	0	6.3	1.3	0.9	0.1	4.6	1.419	0.156
water traits										
pH	7.90	0.48	4.79	8.87	8.01	0.43	6.31	8.85	**-3.380**	**<0.001**
Conductivity [µS cm^{-1}]	314	257	34.5	1136	378	305	41.9	1136	**-3.734**	**<0.001**
Redox [mV]	47	97	-276	395	53	94	-276	254	**-2.601**	**0.009**
Colour [mg Pt dm^{-3}]	24	33	2	400	22	18	2	80	0.290	0.772
HA [mg dm^{-3}]	3.6	4.1	0.3	45.1	3.3	2.1	0.7	9.4	-1.678	0.093
CO_2 [mg dm^{-3}]	7.0	5.8	0.1	41.4	6.2	4.6	0.7	19.4	1.499	0.134
CO_3^{2-} [mg CO_2 dm^{-3}]	8.8	9.2	0	62.9	7.0	7.6	0	28.6	**2.795**	**0.005**
HCO_3^- [mg CO_2 dm^{-3}]	91.5	60.5	7.0	311.1	89.3	46.0	7.0	311.1	-1.631	0.103
Ca^{2+} [mg dm^{-3}]	46.9	24.6	1.0	131.5	54.8	27.6	3.4	131.5	**-4.322**	**<0.001**
$N_{tot.}$ [mg N dm^{-3}]	1.56	1.16	0.30	5.27	1.44	1.08	0.38	5.27	1.933	0.053
$P_{tot.}$ [mg P dm^{-3}]	0.34	0.23	0.02	1.47	0.29	0.19	0.03	1.22	**2.574**	**0.010**
Cl^- [mg dm^{-3}]	19.6	98.3	0.5	2757	250.0	894.6	0.5	5121	**-2.930**	**0.003**
PAR [%]	29.1	22.3	0.1	100	30.4	20.0	0.5	100	-1.589	0.112
O_2 [%]	102.0	29.2	7.6	161.2	107.7	17.8	12.3	147.5	-1.684	0.092
Flow [ms^{-1}]	0.06	0.13	0	0.64	0.07	0.15	0	0.64	0.381	0.703
sediment traits										
pH	7.10	0.37	5.10	8.24	7.19	0.30	6.49	7.98	**-2.782**	**0.005**
Conductivity [µS cm^{-1}]	358.7	345.3	40.0	2150	291.2	186.0	41.9	879	0.603	0.547
Redox [mV]	-226	127	-650	267	-235	110	-457	256	1.357	0.175
Ca^{2+} [mg g^{-1} d.w.]	52.9	91.8	0.4	376.9	56.2	95.3	0.7	354.0	-0.625	0.532
HA [mg g^{-1} d.w.]	8.5	13.8	0.05	135.1	4.7	7.9	0.05	43.9	**5.265**	**<0.001**
Hydration [%]	38.6	29.5	0.5	99.9	34.2	25.4	0.4	92.3	1.213	0.225
Organic matter [%]	10.3	15.2	0.2	92.8	6.1	8.6	0.3	38.9	**3.826**	**<0.001**
Mineral matter [%]	89.3	16.3	7.2	99.8	93.2	11.5	38.1	99.7	**-3.755**	**<0.001**
SiO_2 [%]	71.0	31.6	0.2	100	72.1	32.6	0.2	100	0.349	0.727
Fraction >2mm [%]	6.4	12.8	0.0	76.8	4.6	10.8	0.0	66.4	1.384	0.166
1-2 mm [%]	3.6	4.3	0.0	20.2	2.9	4.1	0.0	20.2	1.788	0.074
0.5-1 mm [%]	10.5	11.6	0.0	57.4	9.1	10.1	0.0	57.4	0.898	0.369
0.25-0.5mm [%]	23.5	18.4	0.0	65.2	24.7	20.2	0.0	65.2	-0.891	0.373
0.1-0.25 mm [%]	26.4	18.3	0.0	80.7	35.3	21.8	0.0	84.5	**-5.613**	**<0.001**
<0.1 mm [%]	29.2	35.4	0.05	100	23.2	28.2	0.04	100	1.524	0.127

Explanations: see Fig. 2

The occurrence of pondweeds in watercourses closely correlateed with the second ordination axis factors. Positive correlation was found with flow, SiO_2 and $N_{tot.}$ content, sediment pH and the >0.25 mm fraction, and negative correlation with <0.1 mm, sediment hydration and depth. Compared with *Potamogeton*, *Stuckenia* occurred in shallower, faster-flowing waters, on less hydrated sediment of medium or large grain size with a small proportion of the smallest fraction (<0.1 mm).

The occurrence of pondweeds in estuaries correlated with the factors from the first PCA ordination axis. Environmental factors for *Stuckenia* correlated positively with calcium concentration, water colour, water conductivity and humic acid content, while showing negative correlation with water redox. Environmental

Table 6. Environmental factors for *Potamogeton* and *Stuckenia* in the studied lakes. Statistically significant differences at p<0.05 are presented in bold type

	Potamogeton				*Stuckenia*				Mann-Whitney U test	
Trait	mean	SD	min	max	mean	SD	min	max	Z	p
Depth [m]	1.81	1.3	0.00	6.30	1.57	1.1	0.10	4.60	1.299	0.194
water traits										
pH	7.94	0.5	4.79	8.87	8.04	0.3	6.31	8.72	**-2.008**	**0.045**
Conductivity [$\mu S\ cm^{-1}$]	191	67	35	336	218	52	42	336	**-4098**	**<0.001**
Redox [mV]	54	84	-120	395	73	76	-81	254	**-3.846**	**<0.001**
Colour [mg Pt dm^{-3}]	18	33	2	400	13	9	2	35	**2.058**	**0.040**
HA [mg dm^{-3}]	2.8	4.3	0.3	45.1	2.4	1.4	0.7	7.2	-1.200	0.230
CO_2 [mg dm^{-3}]	7.9	6.6	0.1	41.4	7.6	5.3	2.0	19.4	-1.225	0.221
CO_3^{2-} [mg CO_2 dm^{-3}]	9.6	10.3	0.0	62.9	8.7	8.8	0.0	28.6	0.983	0.326
HCO_3^- [mg CO_2 dm^{-3}]	60.8	26.8	7.0	140.8	69.2	24.6	7.0	140.8	**-4.235**	**<0.001**
Ca^{2+} [mg dm^{-3}]	34.4	13.4	1.0	69.2	40.2	8.9	3.4	68.1	**-5.297**	**<0.001**
$N_{tot.}$ [mg N dm^{-3}]	1.40	0.9	0.29	4.0	1.31	0.9	0.38	3.79	1.857	0.063
$P_{tot.}$ [mg P dm^{-3}]	0.25	0.2	0.02	1.34	0.20	0.1	0.03	1.22	**2.705**	**0.007**
Cl^- [mg dm^{-3}]	5.9	5.7	0.5	50.3	7.3	6.7	0.5	50.3	**-2.806**	**0.005**
PAR [%]	27.9	20.9	1.5	100.0	31.3	17.6	4.7	100.0	**-3.596**	**<0.001**
O_2 [%]	110.8	20.1	12.3	161.2	112.2	11.8	12.3	136.1	0.077	0.938
Flow [ms^{-1}]	0.00	0.0	0.00	0.00	0.00	0.0	0.00	0.00	0.000	1.000
sediment traits										
pH	7.04	0.4	5.10	8.24	7.16	0.3	6.46	7.76	**-3.459**	**0.001**
Conductivity [$\mu S\ cm^{-1}$]	280	235	41	2150	278	168	42	879	-0.896	0.370
Redox [mV]	-212	117	-352	256	-223	105	-352	256	1.388	0.165
Ca^{2+} [mg g^{-1} d.w.]	69.5	107.7	0.4	376.9	84.7	111.2	0.8	354.0	**-3.567**	**<0.001**
HA [mg g^{-1} d.w.]	8.7	14.3	0.1	135.1	6.1	9.4	0.1	43.9	**3.157**	**0.002**
Hydration [%]	39.8	31.4	0.5	99.9	38.8	30.5	0.4	92.3	0.727	0.467
Organic matter [%]	11.3	16.9	0.3	92.8	6.9	7.5	0.3	35.0	1.927	0.054
Mineral matter [%]	88.7	16.9	7.2	99.7	93.1	7.5	65.0	99.7	-1.893	0.058
SiO_2 [%]	67.4	35.2	0.2	100.0	62.7	36.5	0.2	100.0	**2.181**	**0.029**
Fraction >2mm [%]	5.8	12.5	0.0	76.8	5.0	11.9	0.0	66.4	0.841	0.400
1-2 mm [%]	3.4	4.3	0.0	20.2	3.0	4.6	0.0	20.2	1.239	0.215
0.5-1 mm [%]	8.7	9.9	0.0	37.3	7.8	9.7	0.0	36.2	0.870	0.384
0.25-0.5mm [%]	22.5	17.8	0.0	62.3	22.0	17.5	0.0	62.3	0.041	0.967
0.1-0.25 mm [%]	28.4	18.8	0.0	80.7	35.3	21.5	0.0	83.4	**-3.238**	**0.001**
<0.1 mm [%]	30.9	35.5	0.1	100.0	26.7	30.2	0.0	100.0	0.711	0.477

Explanations: see Fig. 2

factors for *Potamogeton* positively correlated mainly with sediment conductivity and the share of the <0.1mm fraction, while showing negative correlation with PAR and sediment redox (Fig. 2).

3.2. Environmental factors in the lakes

The lakes in which *Potamogeton* genus species occurred were diversified in terms of their hydrochemical properties (Table 6). Plants grew at a depth range from 0 to 6.3 metres (1.8±1.3 m) and a broad spectrum of water pH (4.8-8.9), conductivity (34.5-336.0 $\mu S\ cm^{-1}$), and redox (-120-395 mV). Water was usually well oxygenated, but poorly photosynthetically irradiated, with a low concentration of humic acids, inorganic carbon, calcium and chlorides, but a fairly high concentration of nitrogen and phosphorus. Sediment was moderately hydrated; it contained little organic matter, but considerable amounts of inorganic matter 88.7±16.9% (66% of silica, the rest being mostly calcium) and was chiefly composed of small fractions <0.5 mm (>80%). Sediment pH (5.1-8.2), conductivity (41.1-2150 $\mu S/cm^{-1}$) and redox (-352-256 mV) showed significant variability.

Stuckenia species, compared with *Potamogeton,* grew in lakes of slightly higher reaction (p=0.045), conductivity (p<0.001) and redox (p<0.001). Concentrations of bicarbonates, calcium (p<0.001) and chlorides were also higher (p=0.005; Table 6), as was the PAR reaching plants (p<0.001). Total phosphorus

Table 7. Environmental factors for *Potamogeton* and *Stuckenia* in the studied watercourses. Statistically significant differences at p<0.05 are presented in bold type

	Potamogeton				*Stuckenia*				Mann-Whitney U test	
Trait	mean	SD	min	max	mean	SD	min	max	Z	p
Depth [m]	0.8	0.6	0.1	2.4	0.6	0.2	0.2	1.4	-1.104	0.270
water traits										
pH	7.82	0.4	7.26	8.42	7.75	0.4	7.44	8.42	1.802	0.072
Conductivity [µS cm^{-1}]	289	104	189	870	272	37	189	308	-1.460	0.144
Redox [mV]	52	91	-86	322	59	71	-7	241	**-2.437**	**0.015**
Colour [mg Pt dm^{-3}]	20	10	8	45	28	11	12	40	**-4.894**	**<0.001**
HA [mg dm^{-3}]	3.8	1.8	1.2	8.3	4.1	1.3	2.0	6.5	-0.823	0.411
CO_2 [mg dm^{-3}]	5.8	4.3	0.7	24.2	2.8	1.3	1.3	5.7	**6.078**	**<0.001**
CO_3^{2-} [mg CO_2 dm^{-3}]	5.1	5.5	0.0	26.4	4.7	2.9	0.0	10.1	-1.438	0.150
HCO_3^- [mg CO_2 dm^{-3}]	111.7	45.3	59.0	286	95.1	21.3	59.0	118.8	1.797	0.072
Ca^{2+} [mg dm^{-3}]	52.4	12.4	41.0	94.5	48.9	5.2	42.2	62.1	1.044	0.296
$N_{tot.}$ [mg N dm^{-3}]	2.00	1.7	0.31	5.27	1.79	1.5	0.60	5.27	-0.178	0.859
$P_{tot.}$ [mg P dm^{-3}]	0.43	0.2	0.07	0.76	0.44	0.1	0.30	0.76	0.548	0.584
Cl^- [mg dm^{-3}]	7.4	8.9	2.0	70.0	5.4	1.2	2.9	9.0	**3.129**	**0.002**
PAR [%]	42.4	23.2	0.4	100.0	36.8	14.4	13.2	74.0	**2.160**	**0.038**
O_2 [%]	100.2	32.0	35.9	147.5	107.2	25.6	58.6	147.5	**-2.712**	**0.007**
Flow [ms^{-1}]	0.20	0.1	0.01	0.46	0.14	0.1	0.07	0.34	**2.437**	**0.015**
sediment traits										
pH	7.32	0.3	6.66	7.98	7.49	0.3	7.05	7.98	**-3.370**	**0.001**
Conductivity [µS cm^{-1}]	390	462	42	1435	132	87	52	364	**4.153**	**<0.001**
Redox [mV]	-195	131	-650	267	-182	91	-337	116	-0.242	0.809
Ca^{2+} [mg g^{-1} d.w.]	20.0	37.8	1.0	188.4	3.9	1.9	1.0	6.7	**2.946**	**0.003**
HA [mg g^{-1} d.w.]	6.5	14.2	0.2	60.4	2.0	3.0	0.2	8.5	**2.766**	**0.006**
Hydration [%]	30.3	21.9	0.8	83.2	21.9	7.0	8.8	34.1	1.186	0.236
Organic matter [%]	7.9	12.5	0.3	38.9	7.1	13.9	0.3	38.9	**2.245**	**0.025**
Mineral matter [%]	89.9	18.4	38.1	99.7	89.3	22.3	38.1	99.7	**-2.245**	**0.025**
SiO_2 [%]	78.1	24.3	32.4	98.4	85.4	21.4	37.3	98.3	**-2.404**	**0.016**
Fraction >2mm [%]	11.3	15.9	0.0	62.4	5.5	11.2	0.00	62.4	**2.681**	**0.007**
1-2 mm [%]	5.3	4.2	0.0	14.9	2.5	2.8	0.1	10.0	**4.640**	**<0.001**
0.5-1 mm [%]	17.3	13.0	0.0	57.4	14.8	11.2	1.0	57.4	1.629	0.103
0.25-0.5mm [%]	29.9	16.2	0.0	65.2	39.5	20.9	5.3	65.2	**-2.909**	**0.004**
0.1-0.25 mm [%]	24.4	16.3	0.0	52.9	33.8	26.0	3.7	84.5	**-2.766**	**0.006**
<0.1 mm [%]	11.5	21.7	0.1	100.0	3.4	3.7	0.3	8.9	**2.828**	**0.005**

Explanations: see Fig. 2

was lower (p=0.007), but highly variable (0.03–1.22 mg dm^{-3}). Sediment was rich in mineral matter, with the pH slightly higher than in the case of *Potamogeton* (p=0.001). The proportion of humic acids and silica was generally lower (p=0.002 and p=0.029, respectively), the prevailing fraction being 0.1-0.25 mm, while calcium content was higher (p<0.001; Table 6).

3.3. Environmental factors in watercourses

In the watercourses with *Potamogeton*, water was slightly alkaline (pH 7.8±0.4), with moderately high conductivity and positive redox (Table 7). It was also well oxygenated, slightly coloured, relatively well photosynthetically irradiated, rich in nitrogen, phosphorus and inorganic carbon (HCO_3^- and CO_2), but poor in chloride ions. The flow rate was moderate (0.20±0.1 m s^{-1}), with a broad variation range (0.01-0.46 m s^{-1}). Sediment was rich in mineral matter, with a high proportion of silica and the prevailing fraction was fine grain, mostly 0.5-0.25mm. Calcium and humic acid concentration varied considerably (1.0-188.4 mg Ca^{2+} g^{-1} d.w.; 0.2-60.4 mg C g^{-1} d.w. respectively).

At the sites with *Stuckenia*, water was more strongly coloured (p<0.001) than at the sites with *Potamogeton*; it was also poorer in carbon dioxide (p<0.001) and in chlorides (p=0.002; Table 7). Oxygen concentration in water was higher (p=0.007), while insolation and flow rate were lower (p=0.038 and p=0.015, respectively).

Table 8. Environmental factors for *Potamogeton* and *Stuckenia* in the studied estuaries. Statistically significant differences at p<0.05 are presented in bold type

	Potamogeton				*Stuckenia*				Mann-Whitney U test	
Trait	mean	SD	min	max	mean	SD	min	max	Z	p
Depth [m]	1.11	0.6	2.50	0.30	0.96	0.4	1.60	0.30	1.319	0.187
water traits										
pH	7.85	0.5	6.91	8.74	8.19	0.6	6.91	8.85	**-4.547**	**<0.001**
Conductivity [µS cm^{-1}]	874	162	451	1136	970	130	666	1136	**-3.802**	**<0.001**
Redox [mV]	13	141	-276	255	-12	129	-276	178	1.004	0.315
Colour [mg Pt dm^{-3}]	58	32	15	160	42	24	15	80	**3.230**	**0.001**
HA [mg dm^{-3}]	6.8	3.7	2.3	17.1	5.4	2.4	2.2	9.4	1.789	0.074
CO_2 [mg dm^{-3}]	5.3	3.4	0.7	11.4	4.7	1.6	0.7	8.4	0.648	0.517
CO_3^{2-} [mg CO_2 dm^{-3}]	10.4	5.9	0.0	18.5	4.2	4.9	0.0	17.6	**6.269**	**<0.001**
HCO_3^- [mg CO_2 dm^{-3}]	197.2	52.0	92.4	311.1	145.4	63.5	92.4	311.1	**6.166**	**<0.001**
Ca^{2+} [mg dm^{-3}]	93.1	14.2	78.8	131.5	105.1	18.6	82.4	131.5	**-4.818**	**<0.001**
$N_{tot.}$ [mg N dm^{-3}]	1.61	0.9	0.51	4.82	1.50	1.1	0.51	3.80	1.468	0.142
$P_{tot.}$ [mg P dm^{-3}]	0.55	0.2	0.16	1.47	0.43	0.2	0.13	0.78	**2.824**	**0.005**
Cl^- [mg dm^{-3}]	95.2	240	47.6	2757	1227	1692	47.6	5121	**-6.496**	**<0.001**
PAR [%]	16.3	17.4	0.1	100.0	21.7	27.3	0.5	100.0	-1.240	0.215
O_2 [%]	66.4	30.8	7.6	117.9	94.5	18.1	45.6	117.9	**-5.742**	**<0.001**
Flow [ms^{-1}]	0.11	0.2	0.00	0.64	0.22	0.3	0.00	0.64	0.077	0.939
sediment traits										
pH	7.08	0.3	6.47	7.52	7.03	0.2	6.54	7.44	0.514	0.608
Conductivity [µS cm^{-1}]	653	393	40	1428	479	141	192	640	**2.321**	**0.020**
Redox [mV]	-326	115	-460	33	-316	101	-457	-33	-1.038	0.299
Ca^{2+} [mg g^{-1} d.w.]	26.5	32.5	1.4	153.0	15.2	23.5	0.7	67.7	**3.814**	**<0.001**
HA [mg g^{-1} d.w.]	10.4	10.4	0.1	33.1	2.5	3.5	0.2	16.0	**3.944**	**<0.001**
Hydration [%]	44.8	27.9	13.1	92.7	30.7	10.1	14.7	49.7	1.858	0.063
Organic matter [%]	8.8	8.7	0.2	28.2	2.4	2.2	0.3	10.4	**3.564**	**<0.001**
Mineral matter [%]	91.2	8.7	71.9	99.8	97.6	2.2	89.6	99.7	**-3.564**	**<0.001**
SiO_2 [%]	76.7	19.7	29.8	98.6	89.5	6.4	77.7	98.1	**-3.330**	**<0.001**
Fraction >2mm [%]	2.0	5.2	0.0	19.6	2.3	5.3	0.0	18.7	**-2.023**	**0.043**
1-2 mm [%]	2.5	4.0	0.0	13.5	2.9	3.6	0.0	11.7	**-2.229**	**0.026**
0.5-1 mm [%]	9.0	13.0	0.0	43.6	7.5	8.4	0.2	29.4	-1.815	0.069
0.25-0.5mm [%]	19.0	21.6	0.0	64.5	19.1	20.9	0.4	64.5	-1.470	0.142
0.1-0.25 mm [%]	20.5	17.1	0.0	61.5	37.2	19.6	15.4	68.9	**-5.464**	**<0.001**
<0.1 mm [%]	46.0	40.0	0.1	100.0	30.4	26.3	0.3	81.0	**2.081**	**0.037**

Explanations: see Fig. 2

Sediment was mostly mineralised, with a higher proportion of silica (p=0.016), medium- or fine grained (0.5-0.25 and 0.25-0.1 mm) and very low content of calcium (p=0.003) and of humic acids (p=0.006). The reaction was higher (pH 7.5±0.3; p=0.001) and conductivity was much lower (p<0.001; Table 7).

3.4. Environmental factors in estuaries

In the estuaries with *Potamogeton*, water was alkaline, strongly coloured, with high conductivity caused by the considerable concentration of chlorides, carbonates, bicarbonates and calcium (Table 8). Water was rich in phosphorus, but poorly photosynthetically irradiated and oxygenated. Sediment was mineralised, with a high silica content and the prevalence of fine and very fine grain (<0.1 mm and 0.1-0.25 mm). Calcium compound content was relatively low, while humic acid content exhibited great variability (0.1-33.1 mg C g^{-1} d.w.).

Estuaries with *Stuckenia* were characterised, primarily, by a very high chloride content (p<0.001) and its great variability (47.6-5121.4 mg Cl^- dm^{-3}). The reaction was higher than in the case of *Potamogeton* (p<0.001), so was conductivity (p<0.001) and calcium concentration (p<0.001), while phosphorus concentration was lower (p=0.005). Water was very strongly oxygenated and slightly coloured (p=0.001; Table 8) allowing more light to reach plants (p<0.001) than in the water bodies with *Potamogeton*. Sediment was mineralised and, as

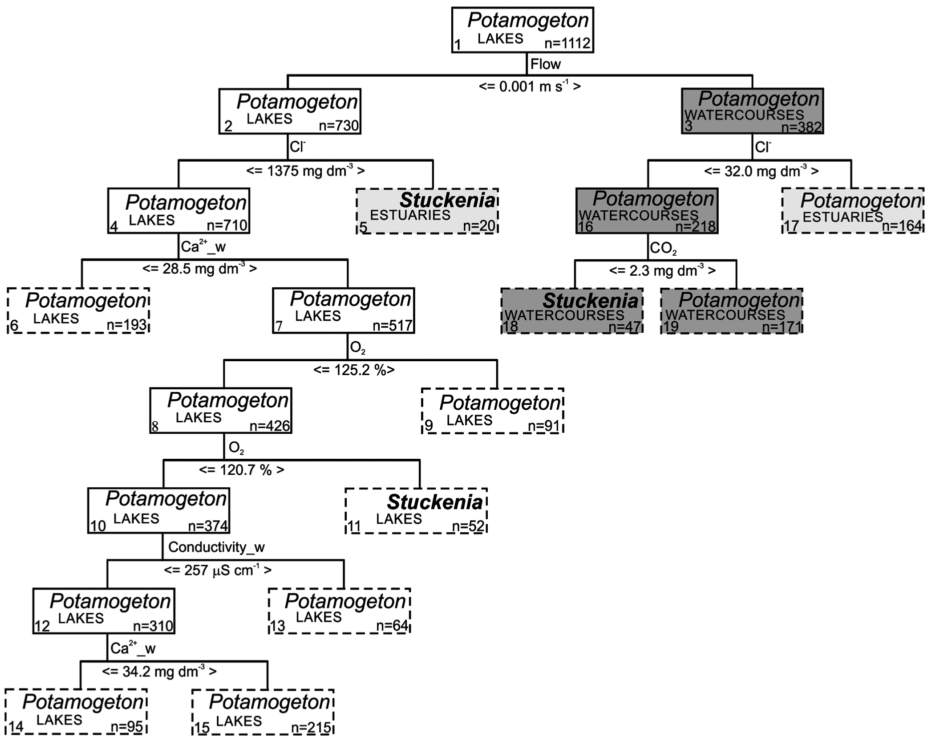

Fig. 3. Empirical model of *Potamogeton* and *Stuckenia* dependence on C&RT-ranked environmental factors in the studied lakes, watercourses and estuaries

in the case of sites with *Potamogeton*, fine and very fine grain fractions prevailed, with a slightly higher share of silica ($p<0.001$). Sediment conductivity was lower ($p=0.02$) as was the case with calcium and humic acid content ($p<0.001$; Table 8).

3.5. The rank of environmental factors

The dependence of *Potamogeton* and *Stuckenia* distribution on environmental factors in particular waterbody types is presented in an empirical model (Fig. 3), designed according to the Classification and Regression Trees (C&RT) method. Two main branches of the model are shaped by water flow.

The left branch of the empirical model (Fig. 3) illustrates the environmental factors in the lakes, with low chloride concentration in water. This is where mainly *Potamogeton* communities developed. Differences within this group of water bodies were chiefly related to calcium and chloride concentration in water as well as its conductivity and oxygenation. *Stuckenia* communities were mainly associated with chloride-rich waters in estuaries (above 1375 mg dm^{-3}) and with lakes in which water was well oxygenated (120.7-125.2%).

The right branch of the model (Fig. 3) shows the environmental factors in water bodies of considerable flow rate, i.e., in watercourses, but also in some of the estuaries, where chloride concentration was higher than 32 mg dm^{-3}. Here, it was mainly communities with *Potamogeton* which developed. Where chloride concentration was lower than 32 mg dm^{-3}, and free carbon dioxide was below 2.3 mg dm^{-3}, communities with *Stuckenia pectinata* developed.

The C&RT model indicates that calcium concentration in water was the main environmental feature (validity coefficient =1) controlling pondweed distribution in the water bodies studied and affecting the mineral content of water. Predictive validity of environmental factors in this model indicates that equally important were: water conductivity (validity coefficient =0.98), concentration of Cl^- (0.93) and CO_2 (0.83), water colour and flow (0.69 and 0.68 respectively; Fig. 4). It should be noted that the traits connected with water oxygenation and sediment redox are statistically significant in the model. The results may indicate that with the plant group of such diversity, other traits of environment may affect the distribution of particular species. The rank of other environmental factors in the model is much lower (<0.5).

4. Discussion

Most of the pondweeds (Potamogetonaceae) in Pomerania are found in neutral or slightly alkaline water rich in calcium and bicarbonates. Similar observations have been made in North America (Ogden 1943; Moyle 1945; Hellquist 1980; Pip 1987), Japan (Kadono 1982) and elsewhere in Europe (Wiegleb 1984). The conducted studies demonstrated concentration of Ca, water

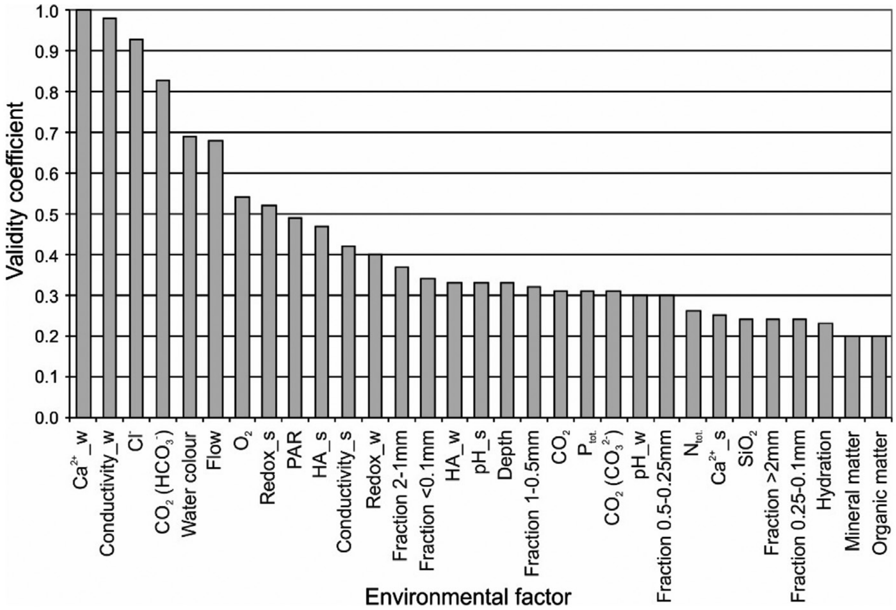

Fig. 4. Predictive validity of environmental factors in C&RT model

conductivity, concentration of Cl^- and CO_2, water colour and flow to be the highest rank environmental factors for pondweeds (see Fig. 4). It should be stressed that the empirical model presented with the Classification and Regression Tree (C&RT; Cf. Fig. 3) identifies water flow as the main factor determining pondweed occurrence in particular kinds of water bodies (lakes, watercourses and estuaries), making them the main branches of the classification tree. The remaining characteristics related to water mineral content, like the concentration of calcium, chlorides and carbonates, have an impact on waterbody differentiation within the particular branches of the tree.

The *Potamogeton* occurrence model, accounting for flow and Ca concentration only, is a source of new, detailed information (Fig. 5). Pondweed environmental factors in lakes, compared with other water bodies, are low concentration of calcium and the absence of water flow. In watercourses, pondweeds occurred in waters of considerable flow rate and only slightly higher calcium concentration than in lakes. In estuaries, pondweeds preferred waters with the highest calcium concentration and

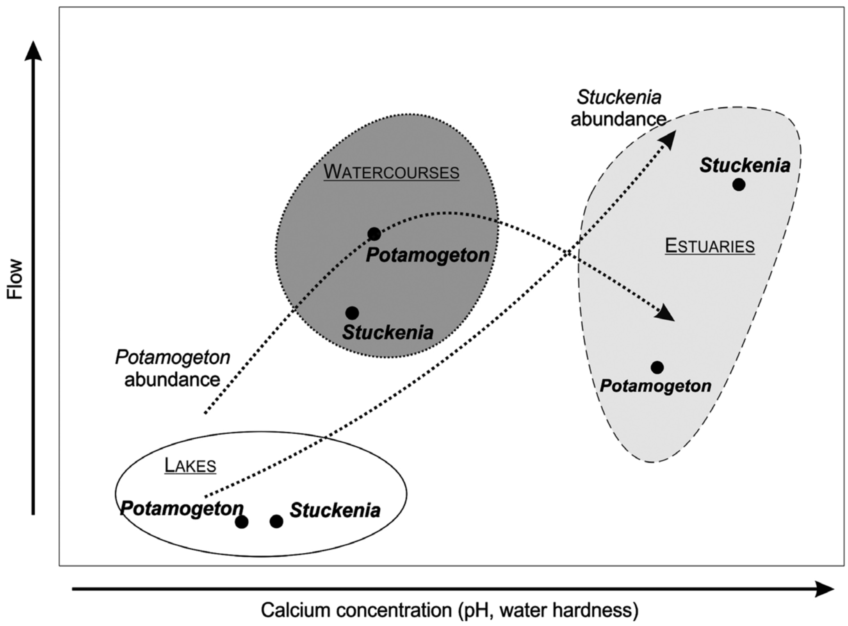

Fig. 5. Conceptual model for *Potamogeton* and *Stuckenia* in the studied lakes, watercourses and estuaries

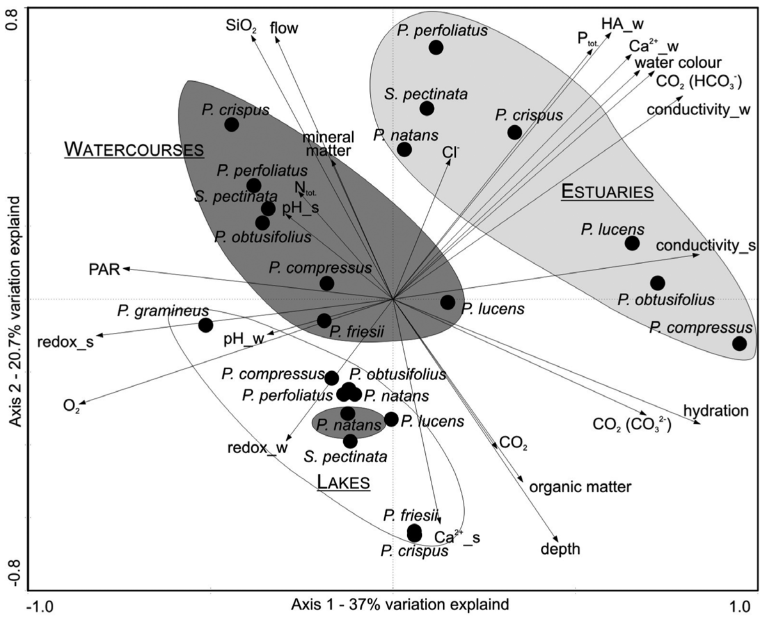

Fig. 6. Model of the relationship between the occurrence of most common pondweed species and PCA-ranked environmental factors in the studied lakes, watercourses and estuaries
Explanations: see Fig. 2

Summary of PCA analysis					
Axes	1	2	3	4	Total inertia
Eigenvalues:	0.370	0.207	0.081	0.074	1.000
Cumulative percentage variance of species data:	37.0	57.7	65.8	73.2	
Sum of all eigenvalues					1.000

varying flow. In lakes, *Potamogeton* showed a preference for lower calcium concentration than *Stuckenia*, in watercourses were connected with faster flow, while in estuaries – occurred in lower flow waters than *Stuckenia*. In lakes and watercourses, species of the *Potamogeton* genus were more abundant than *Stuckenia*, contrary to estuaries in which *Stuckenia* were more plentiful than *Potamogeton*. The model demonstrates the growing abundance of *Stuckenia* as water flow and calcium concentration grow (Fig. 5). It should be remembered that in the water bodies under examination, *Stuckenia* genus is represented only by *Stuckenia pectinata*; in lakes – also by *Stuckenia filiformis*. *S. pectinata* is a species of a broad range of environmental factors and is present in all kinds of water bodies. In their studies, both Hellquist (1980) and Kadono (1982) found the species to be distinctive and made it to be a separate group marked by high alkalinity and high content of bicarbonates and calcium. Chloride concentration in water bodies studied by Kadono (1982) in Japan varied from 16.9 to 4830 mg dm^{-3}. The variability was even higher in Pomerania, ranging between 0.48 and 5121 mg dm^{-3}. Such great environmental adaptability is the result of high phenotypic plasticity of *S. pectinata* (Kaplan 2002; Pilon & Santamaria 2002; Santamaria *et al.* 2003).

Environmental factors affecting pondweeds in water bodies were diverse, mainly because of the large number of *Potamogeton* genus species and their different habitat requirements. They were also affected by a multitude of water and sediment traits (Fig. 6) in particular kinds of the water body.

In lakes, the heterogeneity of pondweed environmental conditions was largely dependent on water depth and the resulting water and sediment traits, with a lesser impact of water and sediment oxygenation and redox potential (Cf. Fig. 6). *P. gramineus* could be found in shallow and well photosynthetically irradiated lake areas. It only occurred in non-running waters and showed a preference for water bodies of moderate alkalinity and mineral content. Similar regularities were observed by researchers in the USA (Moyle 1945; Spence 1967; Hellquist 1980), Japan (Kadono 1982) and Estonia (Mäemets *et al.* 2010). Like in the area studied here, the species showed a preference for shallow zone of lake areas. Consequently, it can also survive periods outside the water body when the water table is low. A similar adaptability was shown by another species – *P. polygonifolius*. It also occurred in shallow lake areas, but of completely different physico-chemical properties than *P. gramineus*. It was recorded in only one site in Pomerania, in a humic lake situated in the coastal strip. Its water was highly acidic (pH 4.79) and extremely poor in minerals (48.9 µS cm^{-1}). In other sites in Poland (Lower Silesia) and in Germany (Saxony), the species occurred also in low pH peatbogs, but of considerably higher conductivity and calcium content (Zalewska-Gałosz *et al.* 2012). Spence (1972) placed the species in the macrophyte group, incapable of using bicarbonate ions for photosynthesis. A similar observation was made by Kadono (1980) concerning *P. fryeri*, which requires free CO_2 in the water to grow. *P. crispus* and *P. perfoliatus*, on the other hand, are adapted to use carbon from bicarbonates for photosynthesis, so they can be found in many water bodies, particularly when water is highly alkaline and rich in bicarbonates and calcium. In the lakes studied here, *P. crispus* like *P. friesii* occurred in deep zones on the sediments rich in calcium and organic matter.

Pondweed environmental factors in watercourses were diversified, primarily, by high flow rate, resulting in high silica content and a significant proportion of coarse and medium grain sediment size. Preference for fast-flowing watercourses rich in silica was shown by *P. crispus*, while slow-flowing ones were preferred by *P. compressus*, *P. friesii* and *P. lucens*. *P. natans* deserves special attention, as it was the only species to occupy habitats of nearly identical properties, both in watercourses and in lakes (Cf. Fig. 6). Very rare species occurring in watercourses only comprised *P. nodosus* and *P.* ×*sparganifolius*. The former can be found in water bodies of high and low alkalinity alike and is regarded as highly adaptable (New England: Hellquist 1980). However, the specimens from waters poor in bicarbonates were infertile. The observations were confirmed by Moor & Clarkson (1967) and by Moyle (1945) in a different part of the United States and by Clapham *et al.* (1962) on the British Isles. In Pomerania, the species occurred in one highly-alkaline watercourse only and its specimens were fertile.

Pondweed environmental factors in estuaries may differ according to flow, sediment hydration, the amount of humic acids and sediment fraction of less than 0.1 mm, but to a certain degree, also to the presence of minerals in water (conductivity, calcium concentration, chlorides and others). Estuaries of considerable flow rate and rich in chlorides, calcium and humic acids were dominated by *Potamogeton perfoliatus* and *Stuckenia pectinata*, while estuaries with highly hydrated sediment, rich in humic acids and fraction of less than 0.1 mm were preferred by *P. lucens* and *P. obtusifolius*, and, especially, by *P. compressus* (Fig. 6). *P. crispus*, in Pomerania and in Japan alike (Kadono 1982), shows a preference for waters rich in calcium and bicarbonates and for saltwater bodies. Moreover, Hellquist (1980) in New England as well as Moyle (1945) and McCombie & Wile (1971) observed a significant correlation between the presence of the species and high biogenic content.

This was not observed in water bodies of northwestern Poland; however, the species was found to occupy waters of considerable flow rate – both in rivers and estuaries – which indicates its great adaptability.

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Autor Contributions

Research concept and desing: Marek Merdalski, Krzysztof Banaś

Acquisition and/or assembly of data: Marek Merdalski, Krzysztof Banaś

Data analysis and interpretation: Marek Merdalski, Krzysztof Banaś

Drafting the article: Marek Merdalski, Krzysztof Banaś, Rafał Ronowski

Critical revision: Marek Merdalski, Krzysztof Banaś, Rafał Ronowski

Final approval: Marek Merdalski, Krzysztof Banaś, Rafał Ronowski

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