

Distribution, abundance and environmental conditions of the clonal aquatic fern *Salvinia natans* (L.) All. in the Vistula delta (Baltic Sea Region)

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Abstract: We examined the distribution, resources and environmental conditions of the clonal aquatic fern *Salvinia natans* (L.) All., expansive in the Vistula delta (N Poland). Before 2006, there were 7 stands of this species, while in the years 2006-2010 their number increased to 21. The most abundant populations were found in the rivers: Tuga (133.0 ± 37.6 indiv./ 0.1 m^2), Fiszewka (79.3 ± 6.0), Szkarpa (74.7 ± 5.0), Struga Orłowska (61.0 ± 2.0), Nogat (52.3 ± 2.5), Elbląg (40.3 ± 31.8), Wiślano-Zalewowy Canal (61.3 ± 3.2) and in the SW part of Lake Druzno (72.3 ± 2.5). *S. natans* did not colonise the weakly saline Vistula Lagoon and Elbląg Bay, which belong to the Baltic Sea. The plant under study occurred in shallow ($2.2 \pm 1.5 \text{ m}$), narrow ($17.9 \pm 13.6 \text{ m}$), slow-flowing ($0.11 \pm 0.12 \text{ m s}^{-1}$) and fertile ($4.7 \pm 4.2 \text{ mg TN dm}^{-3}$, $0.7 \pm 0.4 \text{ mg TP dm}^{-3}$) watercourses. The water in them had neutral or alkaline pH (7.2-9.2) and was weakly saline ($53.8 \pm 21.3 \text{ mg Cl dm}^{-3}$). A dense mat of *S. natans* significantly affected the environmental conditions in the watercourses: water oxygenation, PAR intensity and concentration of biogenic substances, especially phosphorus, decreased.

Key words: *Salvinia natans*, aquatic fern distribution, metapopulation abundance, Vistula delta, Poland

1. Introduction

Salvinia natans (L.) All. is an aquatic plant in the family Salviniaceae (Smith *et al.* 2006), which includes one genus with 32 taxa, 20 of them extinct (McFarland *et al.* 2004). It is a Eurosiberian and South Asian species that occurs in Southern, Eastern and Central Europe as well as South, Southeast and Southwest Asia (Meusel *et al.* 1965) within the suboceanic temperate, subtropical and tropical climate zones (Rothmaler *et al.* 1986). In Europe, *S. natans* grows in water bodies in the catchments of the Caspian, Black, Adriatic, Mediterranean and Baltic seas, and tributaries of rivers including the Po, Tiber, Arno, Danube, Dnieper, Dniester and Elbe (Casper & Krausch 1980). In Poland it occurs in the tributaries of the Vistula, Oder and San rivers (Fig. 1), predominantly in the south (65% of the stands), less often in the centre (24%) and least frequently in the north (11%) of the country. In the Vistula delta it is an expansive species (Szmeja *et al.* 2012) with an established phenology of its development cycle, reproductiveness and population mortality (Gałka & Szmeja 2012).

Salvinia natans (hereafter referred to as *Salvinia*) is an annual clonal plant, not a perennial, such as the majority of modern aquatic macrophytes (Szmeja 2006). A mature individual consists of similar structural units (modules). They are interconnected thanks to the shoot, to which the floating and submerged leaves are attached. The latter function as roots and a fin that prevents the plant from falling over. The hairs located on the upper surface of the leaf have a similar role. They trap air (Glimn-Lacy & Kaufman 2006), enable gaseous exchange and increase buoyancy (Tropepi & Ribecai 2000).

The aim of this work is to determine the number of *Salvinia natans* stands in the Vistula delta, their distribution, environmental conditions and co-occurring species and to investigate the phenomenon of expansion and the plant's effect on the watercourses.

2. Study area

The studies were conducted in the north of Poland in the entire area of the Vistula delta, which was formed

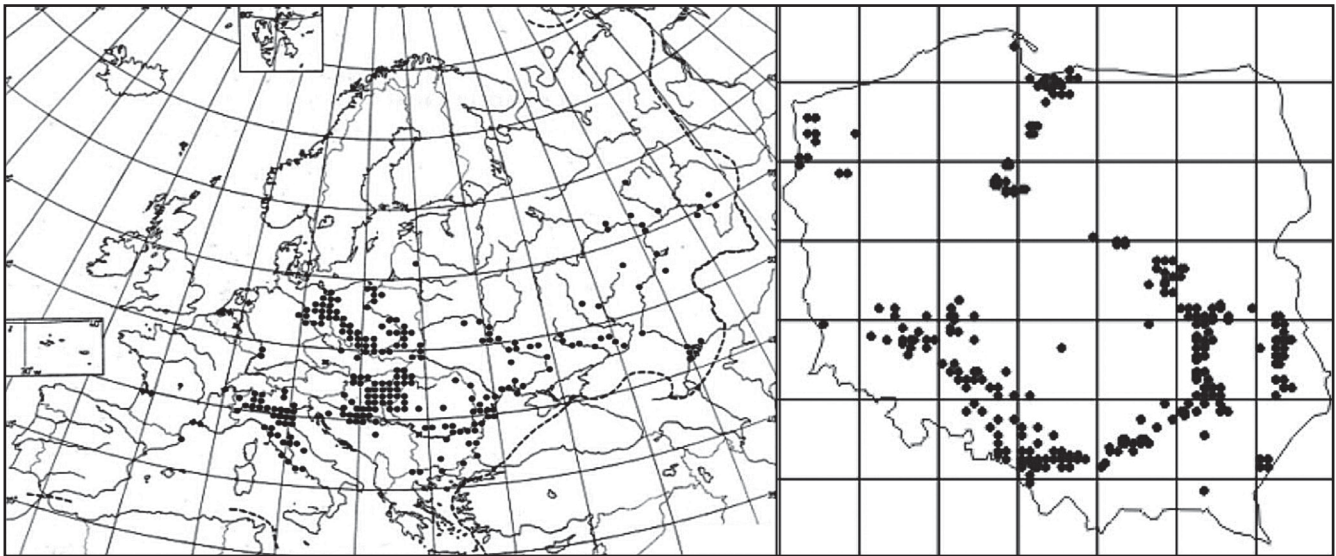


Fig. 1. Distribution of *Salvinia natans* in Europe (left; acc. to Jalas & Suominen 1972) and Poland (right; acc. to Zajac & Zajac 2001, modified)

towards the end of the Pleistocene. In the Holocene, its morphology and hydrology changed significantly. Today it is a wedge-shaped area covering 1,700 km², cut by a dense network of polders, canals and drainage ditches. Their construction began in the 13th century. Since then, the system has been gradually extended. The fertile soils of this area have long been extensively exploited for agriculture. The delta's hydrological system relies on its proximity to the Baltic Sea and on the Vistula and its tributaries.

In the study area, *Salvinia* has occurred at least since the climatic optimum of the Holocene, as in the valleys of the lower Oder (Latałowa & Święta 2003) and the lower Rhine (Zandstra 1966). In the area of Gdańsk, which is situated at the western border of the delta, *Salvinia* was sparse in the 5th and 6th centuries A.D., while in the 7th and 8th centuries it occurred on a massive scale (Święta-Musznicka *et al.* 2011). This means that in the latter period there were favourable hydrological, thermal and trophic conditions enabling the population to develop rapidly, which might be due to the air (and water) temperature rise along the south coast of the Baltic Sea (Seppä & Poska 2004; Sillasoo *et al.* 2009). Since the 9th century, the population size gradually decreased and, consequently, the plant was very rarely found in Gdańsk or the Vistula delta until the 15th century. There is no evidence of its presence in this area from the second half of the 16th to the 18th century (Święta-Musznicka *et al.* 2011).

The first botanical paper about the occurrence of *Salvinia* in the Vistula delta and Elbląg and Fiszewka rivers was published in the mid-19th century (Klinggraeff 1858). An analysis of several publications which appeared between the mid-19th and the end of the 20th

century indicates that the plant grew in the same seven watercourses and formed very small populations. At that time, many botanists from Gdańsk and Königsberg (Kaliningrad since 1946) associated in the organisations such as the Gdańsk Natural Society (das Naturforschende Gesellschaft) and the Prussian Botanical Association (das Preussische Botanische Verein) visited the delta. The contemporary researchers have been assisted in their work by amateur botanists, especially teachers, pharmacists and doctors. The area has been regularly visited by botanists from Gdańsk, Olsztyn and other research centres in Poland since the mid-20th century. In 2000-2003, the abundance and density of the local populations rapidly increased (Markowski *et al.* 2004), whereas in 2006-2010 the population abundance in many watercourses, especially near Elbląg and Malbork, as well as in the depression around Lake Druzno, was already so high that the vast hydrological regulation system, established in the 14th century and extended over the next centuries, was threatened with blockage.

3. Methods

The studies were conducted in 2006-2010 in the entire area of the delta. We assume that an individual watercourse represents a single stand, not any of its sections as it has been reported in the literature so far. This is due to the fact that the location of stands changes in time. We considered only these stands which were in the same place of a given watercourse for the whole growth season. Transit (in the Vistula) and deposit (in the Baltic Sea, i.e. in the Vistula Lagoon and Elbląg Bay) populations were not included. The deposit popu-

lations emerged only in autumn and consisted of senile individuals which had flowed from the watercourses to the sea.

The evaluation of the watercourses was based on the measurements of their depth, width, flow speed and analyses of the physico-chemical surface water properties. Three 0.5 dm³ water samples were collected from each stand. In total, 63 water samples were taken to determine the following: pH, conductivity (µS cm), total phosphorus (mg TP dm⁻³), total nitrogen (mg TN dm⁻³), calcium (mg Ca²⁺ dm⁻³), chlorides (mg Cl⁻ dm⁻³) and dissolved organic carbon (mg DOC dm⁻³) according to the methods described by Eaton *et al.* (2005) and Szmeja (2006). The flow speed in the watercourses [m s⁻¹] was measured using a hydrometric current meter. We also examined the sediments in the watercourses, i.e., the organic matter content (%), pH, redox (mV)

and hydration (%). The measurements were performed by methods presented in the work by Szmeja (2006). The effect of *Salvinia* on the aquatic environment was analysed in the River Tuga in two site variants: under a dense mat of this plant (100% cover) and without this cover. In both types of sites, flow speed (m s⁻¹), PAR irradiance (Li-250 meter; µmol m⁻²), temperature (°C) and oxygen saturation of the water (WTW 96 oximeter) were measured along the depth gradient every 0.1 m according to the methods described by Szmeja (2006).

4. Results

4.1. Distribution and abundance

In the Vistula delta, 21 stands of *Salvinia* were recorded, including 20 in watercourses (11 rivers and 9 irrigation) and one in a lake (Fig. 2). The majority of the

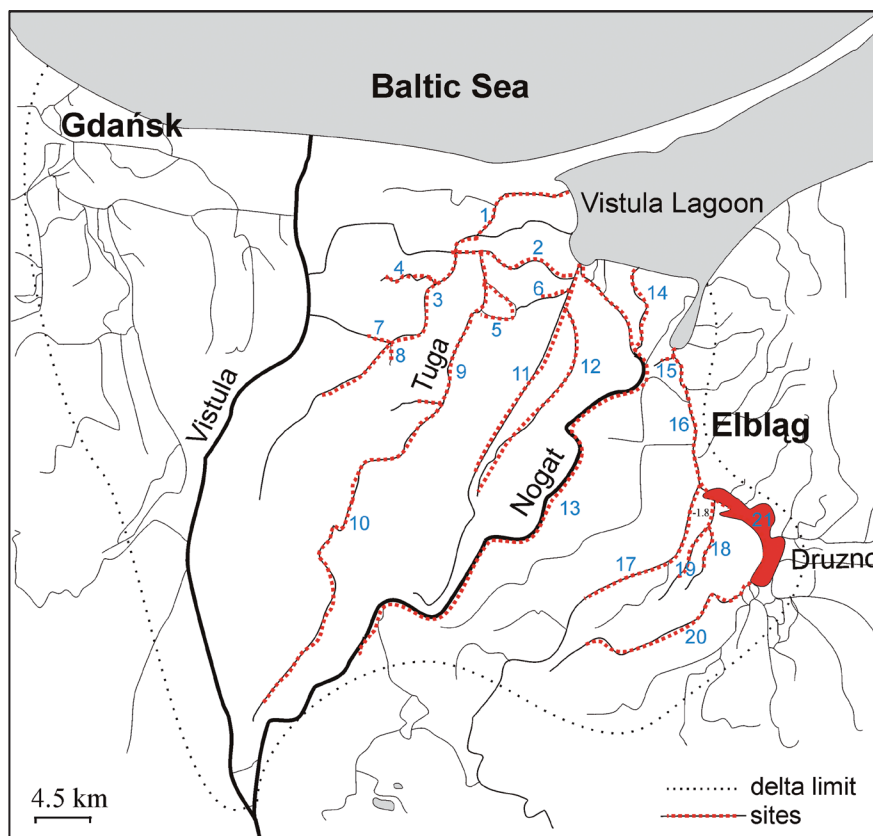


Fig. 2. Distribution of *Salvinia natans* sites (1-21) in the Vistula delta

Explanations: 1 – Wisła Królewiecka River: Rybina (54°17'09"N, 19°07'03"E), 2 – Szarpawa River: from Broniewo through Rybina (54°17'03"N, 19°07'05"E) and Chelmek (54.274°N, 19.178°E) to the Vistula Lagoon, 3 – Linawa River: from Stawiec through Nowotna (54°16'00"N, 19°06'11"E) to the mouth into Szarpawa, 4 – Tributary canal to Linawa River: 54°15'34"N, 19°04'17"E, 5 – Stara Tuga River: in Stobiec (54.266 N, 19.170E), 6 – Drzewny Canal: from Marzęcino to the mouth into the Panieński Canal (54.259 N, 19.239 E), 7 – Wiślano-Zalewowy Canal: 2 km to the NW of Stare Babki (54°13'57"N, 19°02'29"E) to the mouth into the Linawa River, 8 – Struga Orłowska River: 1 km to the SW of Stare Babki, 2 km to the NW of Orłowo (54°13'28"N, 19°03'23"E), 9 – Tuga River: from Nowy Staw through Nowy Dwór Gdański (54°12'35"N, 19°07'08"E) to Tujsk, 10 – Święta River: from Nowy Staw through Marynowy (54°10'33"N, 19°05'14"E) to the mouth into the Tuga River, 11 – Panieński Canal: to the N of Solnica through Marzęcino (54°14'01"N, 19°14'10"E) to the mouth into the Vistula Lagoon, 12 – Izbowa Łacha Canal (Stary Nogat): Stobna (54°12'07"N, 19°16'52"E), 13 – Nogat River: from Malbork (54°01'37"N, 19°02'31"E) to the Elbląg Bay, 14 – Cieplicówka Canal: 2 km to the SW of Batorowo and 1.5 km to the E of Kępiny Wielkie (54°13'51"N, 19°19'56"E), 15 – Canal in Nowakowo, 4 km to the N of Elbląg (54°13'28"N, 19°21'13"E), 16 – Elbląg River: from Druzno Lake, Nowakowo (54°13'07"N, 19°21'44"E) to the mouth into the Elbląg Bay, 17 – Fiszewka River: from Fiszewo, through Gronowo Elbląskie (54°06'00"N, 19°18'18"E) to the mouth into the Elbląg River, 18 – Dolna Tina River: from Różany (54°04'02"N, 19°19'15"E) to the mouth into the Górna Tina River, 19 – Górna Tina River: 2 km to the N of Różany (54°04'21"N, 19°19'19"E), to the mouth into the Elbląg River, 20 – Bawleka River: at the road bridge from Wiśniewo to Krzewsk (54°02'55"N, 19°25'43"E), 21 – Druzno Lake: mainly its W and SW parts



Fig. 3. *Salvinia natans* in Druzno Lake (1), Wisła Królewiecka River (2), Tuga River (3), Nogat River (4), Tina River (5) and Drzewny Canal (6). Photographs by K. Banaś (September 2005)

stands were located in the eastern part of the delta, where depressions are found. This part is situated slightly lower in relation to the sea level than the western part. The most abundant populations (>60 individuals/0.1 m²) occurred in the rivers Fiszewka, Tuga, Szkarpa and their tributaries, as well as the watercourses in the depressions along the western and, particularly, south-western shores of Lake Druzno. Slightly less numerous populations (30-60 indiv./0.1 m²) were found in the rivers Nogat and Święta, canals Cieplicówka and Panieński and their tributaries. The plant under study did not grow in the weakly saline waters of the Vistula Lagoon. Also, it was not recorded in the watercourses flowing down the Elbląg Elevation situated to the east of Lake Druzno, either. Its periodic presence in the shallow and largely fresh waters of the Elbląg Bay cannot be ruled out.

The plant under study occurred in watercourses of different sizes and formed populations of varied density in them (Fig. 3). In the study years, the most abundant populations were recorded in the widest rivers (about 20 m), that is, in the Tuga (133.0±37.6 indiv./0.1 m²), Fiszewka (79.3±6.0), Szkarpa (74.7±5.0), Struga Orłowska (61.0±2.0), Nogat (52.3±2.5) and Elbląg (40.3±31.8), and in Wiślano-Zalewowy (61.3±3.2). Lake Druzno was characterised by population of fairly high density. Populations of lower density were found in slightly narrower watercourses (up to 12 m), e.g. in the Panieński Canal (37.7±2.5), Drzewny Canal (35.0±5.0) and the Święta River (31.0±3.6), whereas the lowest density was observed in the narrowest (up to 10 m), that is, in the Dolna Tina (29.3±3.1), Cieplicówka (13.0±3.6) and Górna Tina (7.3±1.5).

4.2. Co-occurring species

In the watercourses of the delta, *Salvinia* occurred in a fairly stable set of aquatic plants. It was accompanied by indigenous pleustophytes, nympheids and elodeids, as well as helophytes, especially *Phragmites australis* (Cav.) Trin. ex Steud. (the frequency of the reed in the *Salvinia* clusters expressed as the proportion of cover ranging from 0 to 1 was 0.8) in the bank zones of the watercourses. In these zones, where the majority of *Salvinia* aggregations were located, *Hydrocharis morsus-ranae* L. (0.6), *Nymphaea alba* L., *Numphar lutea* (L.) Sibth & Sm. (0.4), *Stratiotes aloides* L. (0.3) and *Sagittaria sagittifolia* L. (0.3) were frequent. In the river current, the examined plant was found with *Lemna minor* L. (0.6), *Spirodella polyrrhiza* (L.) Schleid. (0.6) and *Ceratophyllum demersum* L. (0.4), and, less frequently, *Ricciocarpus natans* (L.) Corda (0.2) and *Lemna trisulca* L. (0.1).

The set of co-occurring species changed within a year. In spring, the spores of the plant under study were effectively trapped in the clusters of *Phragmites*;

in summer, *Salvinia*'s young development stages moved with the river current and were caught by the floating leaves of *N. alba*, *N. lutea* and *H. morsus-ranae*; in autumn, it was accompanied by *Lemna minor* and *S. polyrrhiza* (the frequency of each of these species was higher than 0.5 in general), and less frequently *N. alba*, *N. lutea* and *H. morsus-ranae* (<0.5), which facilitated the flowing of the spores to the lower sections of rivers and to the watercourses situated in depressions.

4.3. Environmental conditions

Salvinia occurred in shallow (0.5-7.0 m; 2.2±1.5 m) and fairly narrow (6-60 m; 17.9±13.6 m) watercourses. They were mainly characterised by a slow flow (0.01-0.4 m s⁻¹; 0.11±0.12 m s⁻¹) and considerable fertility (0.3-16.2 mg TN dm⁻³; 4.7±4.2 mg TN dm⁻³, 0.1-1.4 mg TP dm⁻³; 0.7±0.4 mg TP dm⁻³) (Table 1). The water had neutral or alkaline pH (7.2- 9.2) and was slightly saline (53.8±21.3 mg Cl dm⁻³). The salinity of the watercourses was caused by intrusions of water from the Vistula Lagoon. Marked fluctuations of the water level are an important feature of the watercourses, which are integrated into the hydrological regulation system of the delta. The only lake habitat (Druzno) is shallow, eutrophic and, similarly like the watercourses, characterised by highly variable water levels.

The substrate in the watercourses was varied, ranging from mineral, in places where the current was fast, to organic, where the water flowed slowly. Strongly reduced sediment (-195.3±-179.3 mV), which was fairly well hydrated (59.3±24.5%), rich in organic matter (1.8±1.1%) and generally had neutral or alkaline pH (6.9-7.8), was deposited close to the banks, particularly near rushes. The substrate did not freeze over in the study years.

4.4. Impact on watercourses

The watercourse sections free from *Salvinia* were usually occupied by *Spirodella polyrrhiza*, *Lemna minor*, *Hydrocharis morsus-ranae*, *Potamogeton pectinatus* L., *P. lucens* L., *Myriophyllum spicatum* L., *Elodea canadensis* Michx. or *Ceratophyllum demersum* L. s.s. Only sparse pleustophytes, nympheids or hydrocharids remained in the dense *Salvinia* mat. Under its surface, however, the submerged macrophytes were almost completely eliminated. This means that the presence of compact aggregations of *Salvinia* leads to a decrease in plant species diversity in a river.

In the Tuga River, in the places free from *Salvinia*, the water flow speed was 0.3±0.01 m s⁻¹, while in the sections covered with a dense mat made up of this plant, the flow was visibly disturbed. On the water surface the flow stopped, and about 0.2 m below the mat it increased to decrease again at a greater depth (Fig. 4). The *Salvinia* mat immobilised the surface water layer in the river.

Table 1. Water features at the *Salvinia natans* sites (1-21, cf. Fig. 1) in the Vistula delta

Feature	pH	Conductivity	Cl ⁻	DOC	Ca ²⁺	TN	TP	V
Sites	min.-max.	[$\mu\text{s cm}^{-1}$] x \pm s.d.	[mg l ⁻¹] x \pm s.d.	[mg dm ⁻³] x \pm s.d.	[mg dm ⁻³] x \pm s.d.	[mg dm ⁻³] x \pm s.d.	[mg dm ⁻³] x \pm s.d.	[ms ⁻¹] x \pm s.d.
1	7.6-7.9	988 \pm 13.1	65.1 \pm 0.05	2.6 \pm 0.01	83.3 \pm 1.2	1.5 \pm 0.4	0.8 \pm 0.1	0.03 \pm 0.004
2	7.7-7.8	991 \pm 9	65.1 \pm 0.1	2.8 \pm 0.05	81.1 \pm 2.3	9.4 \pm 0.7	0.7 \pm 0.1	0.08 \pm 0.01
3	7.4-7.5	1012 \pm 6	61.5 \pm 0.4	8.5 \pm 0.8	108.3 \pm 25.6	2.2 \pm 1.6	0.6 \pm 0.2	0.02 \pm 0.004
4	7.2-7.3	1037 \pm 2	62.0 \pm 2.6	8.5 \pm 0.9	96.3 \pm 15.8	0.3 \pm 0.2	-	0.3 \pm 0.02
5	8.2-8.3	855 \pm 10	49.7 \pm 5.5	-	82.0 \pm 4.0	5.5 \pm 0.1	-	0
6	8.1-8.6	899 \pm 11	88.3 \pm 1.5	-	81.5 \pm 3.1	3.2 \pm 0.1	-	0.1 \pm 0.05
7	7.4-7.5	1345 \pm 14	67.1 \pm 0.1	7.8 \pm 0.05	125.6 \pm 7.9	3.3 \pm 0.6	-	0.13 \pm 0.05
8	7.6-7.7	870 \pm 5	60.8 \pm 0.2	3.1 \pm 0.1	96.2 \pm 6.3	1.7 \pm 0.6	-	0
9	7.3-7.4	749 \pm 9	49.4 \pm 0.07	1.7 \pm 0.05	87.5 \pm 0.3	10.6 \pm 1.0	0.8 \pm 0.01	0.3 \pm 0.3
10	7.4-7.6	731 \pm 6	50.6 \pm 1.02	1.6 \pm 0.04	80.4 \pm 16.4	3.0 \pm 1.1	0.1 \pm 0.07	0.05 \pm 0.01
11	8.3-8.5	884 \pm 5	99.5 \pm 1.3	-	88.5 \pm 0.2	3.2 \pm 0.1	0.2 \pm 0.01	0.03 \pm 0.003
12	7.8-7.9	711 \pm 10	38.7 \pm 0.6	3.2 \pm 0.03	119.2 \pm 2.3	3.0 \pm 0.4	-	0
13	7.5-7.6	681 \pm 12	39.9 \pm 3.8	2.4 \pm 0.02	93.2 \pm 11.6	8.8 \pm 1.3	0.3 \pm 0.001	0.12 \pm 0.03
14	7.7-7.8	609 \pm 9	51.2 \pm 0.3	1.7 \pm 0.15	67.8 \pm 7.4	6.9 \pm 1.0	0.9 \pm 0.1	0.02 \pm 0.01
15	7.5-7.6	887 \pm 6	55.6 \pm 1.5	2.4 \pm 0.04	137.4 \pm 1.2	1.8 \pm 0.1	0.7 \pm 0.2	0.09 \pm 0.03
16	7.9-8.3	740 \pm 12	69.0 \pm 0.1	3.5 \pm 0.04	92.8 \pm 0.9	1.6 \pm 0.3	0.5 \pm 0.05	0.2 \pm 0.06
17	7.6-9.2	1125 \pm 5	67.5 \pm 0.3	4.0 \pm 0.1	88.7 \pm 19.4	1.2 \pm 0.4	1.1 \pm 0.01	0.4 \pm 0.04
18	7.8-7.9	555 \pm 38	14.0 \pm 0.7	2.4 \pm 0.4	83.1 \pm 1.4	1.8 \pm 0.2	-	0.01 \pm 0.01
19	7.2-7.3	702 \pm 6	29.2 \pm 0.2	5.2 \pm 0.15	124.1 \pm 2.9	16.2 \pm 1.2	1.2 \pm 0.1	0.02 \pm 0.003
20	7.6-7.7	511 \pm 2	33.5 \pm 0.1	-	117.0 \pm 2.0	10.8 \pm 0.2	0.4 \pm 0.03	0.01 \pm 0.002
21	7.5-7.6	505 \pm 4	13.1 \pm 0.8	2.9 \pm 0.1	101.1 \pm 2.7	2.5 \pm 0.2	1.4 \pm 0.01	0

Water oxygenation decreased directly under the mat. Such conditions existed down to the river bed, mainly due to limited oxygen permeation from the atmosphere to the water and the use of remaining oxygen by massively developing zooplankton. In addition, the dense *Salvinia* mat limited light transmission to the deeper river layers. Only 10% of the PAR light permeated through the layer of *Salvinia*, which magnified the negative effect of the mat. However, the mat hardly affected the water temperature in the river (Fig. 4).

The *Salvinia* mat collected a considerable amount of biogenic substances from the water, especially phosphorus. In the Tuga River, in places where the plant occurred in great numbers, the total phosphorus concentration was 0.7 \pm 0.3 mg TP dm⁻³, whereas directly under the mat its concentration fell below 0.01 mg TP dm⁻³. This means that the *Salvinia* mat can be effectively used for eliminating phosphorus from watercourses.

5. Discussion

Scattered and occasionally forming extremely small populations, *Salvinia natans* occurred in the same seven watercourses in the Vistula Delta from the mid-19th to the end of the 20th century (Markowski *et al.* 2004). In the years 2000-2010, the number of stands increased from 7 to 21. Between 2006 and 2010, in half of them (10 stands) populations were very abundant. Such a rapid increase in the number of stands, which had not been recorded in the area of the delta for at least 150 years, is the evidence of the expansion of this species. A similar phenomenon was observed in Rhineland-

Palatinate (Wolff & Schwarzer 2005) and Baden-Württemberg (Sebald *et al.* 1990) between 1990 and 2004, that is, at the same time as in the Vistula delta. The expansion of *Salvinia* in the Vistula delta can be attributed to an increase in the mean March and April temperatures after 1989 and a decrease in the interannual temperature variation in these months (Szymeja *et al.* 2012).

According to climatologists, including Hurrell (1995, 1996) and Marsz & Styszyńska (2010), after 1989, warm humid air has more often flowed from above the Atlantic to the north-western part of Europe, Scandinavia and the Baltic Sea region, especially in the cold seasons. Galka and Szymeja's (2012) studies indicate that the massive occurrence of *Salvinia* in the delta was caused by a low gametophyte mortality in early spring and high intensity of vegetative propagation in summer. The latter is highly correlated to the water temperature ($r=0.91$).

Salvinia does not generally go beyond the occupied hydrological systems, which was confirmed by Zutshi & Vass (1971), Spalek (2008) and the results of our work. However, this does not apply during expansion. A rapid increase in the number of *Salvinia* stands was possible thanks to the ease with which the plant moved throughout the hydrological system of the delta.

Species of the genus *Salvinia* grow in fertile waters (Pieterse & Murphy 1990). In the study area, they were rich in phosphorus, as in Rhineland-Palatinate and Baden-Württemberg (Wolff & Schwarzer 2005) or irrigation canals in Kashmir (Zutshi & Vass 1971). The water had high electrolytic conductivity, was weakly

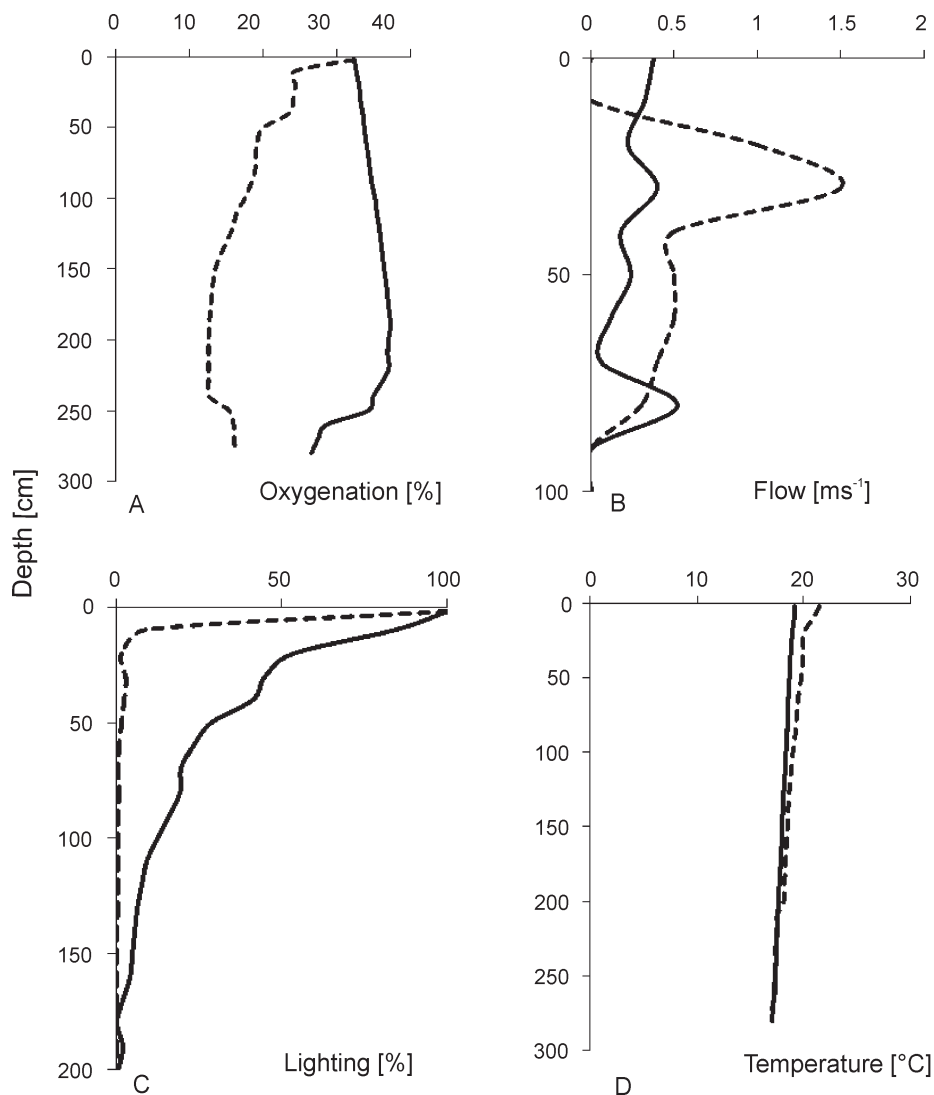


Fig. 4. Oxygenation (A), flow speed (B), lighting (C) and temperature (D) in the vertical profile of the Tuga River with a dense *Salvinia* mat on the water surface (broken line) and without such a mat (solid line)

saline (Table 1) and contained much organic carbon (3.8 ± 2.3 mg OC dm⁻³), which came from fertile soils and decomposing plants. This might be due to the fact that the watercourses, especially the small ones, had not been cleaned (dredged) frequently enough.

Dense mats of *Salvinia* floating on the water surface strongly disturbed the environmental conditions in the watercourses (cf. Fig. 4). The flow of the surface water layer was blocked, and the water under the mat shaded and anoxic, which adversely affected the majority of aquatic organisms in the watercourses, particularly rhizophytes, phytoplankton, zooplankton and ichthyofauna, mainly fry. The oxygen deficit under the mat results from its limited permeation from the atmosphere to the water (Cordo & Center 2000). The portion of oxygen which passes through the dense *Salvinia* mat is intercepted by animals, especially zooplankton, for

which the mat represents a new habitat (Battle & Mi-huc 2000; Kaenel *et al.* 2000). In addition, the mat of *Salvinia*, similarly like other pleustophytes (Perna & Burrows 2005), inhibits the water flow in the watercourses and shades them, which leads to the elimination of almost all submerged plants (Schlettwein & Bethune 1992; Howard & Harley 1998).

6. Conclusions

The rapid increase in the number of *Salvinia natans* stands in the Vistula delta, from seven in the years 2000-2003 to 21 in 2006-2010, is the consequence of this species' expansion. The phenomenon might be due to the mean March and April temperature rise which happened after 1989 and the decrease in the interannual temperature variation in these months in the delta area,

which can be associated with the higher activity of the positive phase of the North Atlantic Oscillation (NAO⁺) in the Baltic Sea region at that time. The expansion of the studied plant is limited to the watercourses of the delta and one lake (Druzno). *Salvinia* does not spread to the water bodies of the southern Baltic Sea. The massive occurrence of *S. natans* causes reduction of water oxygenation, PAR intensity and concentration

of biogenic substances, especially phosphorus, in the watercourses.

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