Hydrobiologia (2010) 656:43–53
DOI 10.1007/s10750-010-0433-2

The influence of *Ceratophyllum demersum* L. and *Stratiotes aloides* L. on richness and diversity of aquatic vegetation in the lakes of mid-eastern Poland

Piotr Sugier · Bogdan Lorens · Stanisław Chmiel · Marek Turczyński

Published online: 14 September 2010

Abstract The aim of this study was to estimate the influence of *Ceratophyllum demersum* L. and *Stratiotes aloides* L. on the species richness and phytocoenotic diversity of aquatic vegetation in lakes. The study was based on field investigations in the Łęczna-Włodawa Lake District located in mid-eastern Poland. The studied lakes (32) included both polymictic and dimictic reservoirs. Both in the polymictic and dimictic lakes, statistically significant correlation coefficients were obtained between the parameters that characterize *Stratiotes aloides* (the frequency in the phytosociological relevés, the percent share of *Stratiotetum aloidis* association in the phytolittoral) and those characteristic for species richness (the total number of hydromacrophytes, the number of charophytes, elodeids, nymphaeids and lemnids), phytocoenotic richness (the mean number of species in the phytosociological relevés) and phytocoenotic diversity (the Shannon–Wiener Index). The communities with a share of *S. aloides* are characterized by higher species richness. However, not a single case of statistically significant dependency was reported between the parameters that describe *C. demersum* (the frequency in the phytosociological relevés, the percent share *Ceratophylletum demersi* association in the phytolittoral) and the vegetation traits in both lake groups. Common occurrence of *Stratiotes aloides* might be considered to be evidence for good status of an aquatic ecosystem and a very good indicator of species richness and diversity of aquatic vegetation.

Keywords *Ceratophyllum demersum* · *Stratiotes aloides* · Species richness · Diversity of aquatic vegetation

Guest editors: A. Pieterse, S. Hellsten, J. Newman, J. Caffrey, F. Ecke, T. Ferreira, B. Gopal, J. Haury, G. Janauer, T. Kairesalo, A. Kanninen, K. Karttunen, J. Sarvala, K. Szoszkiewicz, H. Toivonen, L. Triest, P. Uotila, N. Willby / Aquatic Invasions and Relation to Environmental Changes: Proceedings of the 12th International Symposium on Aquatic Weeds, European Weed Research Society

P. Sugier (✉) · B. Lorens
Department of Ecology, Faculty of Biology and Earth Sciences, Maria Curie-Skłodowska University, Akademicka 19 Str, 20-033 Lublin, Poland
e-mail: piotr.sugier@poczta.umcs.lublin.pl

S. Chmiel · M. Turczyński
Department of Hydrography, Faculty of Biology and Earth Sciences, Maria Curie-Skłodowska University, Akademicka 19 Str, 20-033 Lublin, Poland

Introduction

Macrophytes have an influence on nutrient dynamics, sedimentation and resuspension, and play an important role in natural and artificial reservoirs (Barko & James, 1998; Jeppesen et al., 1998a; Madsen et al., 2001; Coops, 2002; Horppila & Nurminen, 2003;

Strzałek & Koperski, 2009). They have a particularly strong effect on water transparency (Jeppesen et al., 1998a; Kufel & Kufel, 2002; van Donk & van de Bund, 2002; Gross et al., 2003) by providing a refuge for zooplankton (Jeppesen et al., 1998b) and by excreting allelopathic substances that inhibit phytoplankton growth (Gross et al., 2003; Smolders et al., 2003; Mulderij et al., 2005a, b, 2007). They also fix substantial amounts of nutrients in their biomass (Kufel & Ozimek, 1994; Van Donk & Van de Bund, 2002). This type of vegetation stabilizes the sediment and increases the level of oxygen in this environment (Barko & James, 1998; Vermaat et al., 2000; Horppila & Nurminen, 2001, 2003).

Aquatic macrophytes are used for environmental monitoring and water quality assessment (Kohler, 1982; Schneider & Melzer, 2003; Schamburg et al., 2004; Stelzer et al., 2005; Ciecierska, 2008; Penning et al., 2008a). Similarly to other groups of organisms, they can be used as indicators of pressures such as eutrophication of lakes (Murphy et al., 1990; Rørslett, 1991; Penning et al., 2008b). Presence or absence of certain macrophyte species in lakes can show good or bad water status (Moss et al., 2003; Penning et al., 2008b).

The phytocoenotic diversity of the littoral is one of the indicators determining the ecological status of lakes (Council of the European Communities, 2000). Several abiotic and biotic factors determine the aquatic macrophyte richness of lakes. The former group of factors includes, among others, latitude (Heino & Toivonen, 2008), water chemistry and the trophic state (Murphy et al., 1990; Rørslett, 1991; Vestergaard & Sand-Jensen, 2000; Bornette et al., 2001), water level fluctuation (Van Geest et al., 2005; Holm & Clausen, 2006; Maltchik et al., 2007) and the lake area and morphometry (Rørslett, 1991; Gasith & Hoyer, 1998; Vestergaard & Sand-Jensen, 2000; Murphy, 2002; Thomaz et al., 2003). Among the biotic factors, significant effect on the richness of plant species is exerted by dominant freshwater aquatic and wetland plant species (Gopal & Goel, 1993; Gough et al., 1994; Grace & Wetzel, 1998; Ervin & Wetzel, 2002). High above-ground growth rates in the case of these plant species are believed to contribute to their ability to out-compete other species for light by rapidly producing large quantities of photosynthetic tissues, relative to neighbouring species (Ervin & Wetzel, 2002).

The aim of this study was to estimate the influence of *Ceratophyllum demersum* L. and *Stratiotes aloides* L. on the species richness and phytocoenotic diversity of aquatic vegetation in lakes. *S. aloides* is a Eurasiatic species which grows mainly in shallow stagnant eu- and mesotrophic waters (Kornatowski, 1976; Cook & Urmi-König, 1983; Kłosowski & Kłosowski, 2001). This is a vigorously growing plant that will tend to swamp out other plants when grown in small ecosystems (Mulderij et al., 2005b). *C. demersum* belongs to circumpolar plants and is widespread in Eurasia and North America (Hultén & Fries, 1986). The species reduces mixing of the water column and may also contribute to an increase in water transparency by excretion of allelopathic substances that inhibit phytoplankton growth (Jasser, 1994, 1995; Mjelde & Faafeng, 1997; Smolders et al., 2000; Usenko et al., 2002; Gross et al., 2003; Mulderij et al., 2005a, b, 2007). *C. demersum* and *S. aloides* were noted in the list of "overall European tolerant species"—species occurring at increased frequency and abundance at higher eutrophication pressure (Penning et al., 2008b). Both these species are very common, often dominating in lakes, ponds, river-oxbows, channels, ditches, and other water bodies created by peat excavation in mid-eastern Poland (Kornatowski, 1976; Sugier & Lorens, 2000; Kłosowski & Kłosowski, 2001).

Materials and methods

Site description

This study is based on our own field investigation in the Łęczna-Włodawa Lake District located in mid-eastern Poland (51° 17′ 49″ N and 51° 35′ 56″ N; 22° 50′ 36″ E and 23° 42′ 17″ E). The area belongs to the sub-region of Polesie Zachodnie (Kondracki, 2002). The lakes constitute of a group of Polish lakes located outside the extent of the last glaciation (Wilgat, 1954). The processes of ground-ice melting (thermokarst) and karst phenomena contributed to the formation of lake basins (Harasimiuk & Wojtanowicz, 1998) The study lake group includes both polymictic and dimictic reservoirs. The polymictic lakes are eutrophic, while the dimictic ones are both eutrophic and mesotrophic. The maximum depth of the shallow lakes ranges from 1.1 to 6.5 m, and they cover an area of 1.4 to 136.7 ha. The dimictic lakes are from 6.5 to 38.8 m deep, and their area ranges from 8.5 to 256.3 ha (Radwan & Kornijów, 1998).

Sampling method

Thirty-two lakes were surveyed in this study. Field investigations were carried out in the summer seasons of 2005–2007. The occurrence of charophyte and aquatic vascular plants and plant communities was analyzed (reed swamp communities covering 3–10% of the phytolittoral were not considered). Macrophyte vegetation was studied with the use of the commonly applied mid-European phytosociological method, which is based on phytosociological data recorded from representative patches of vegetation by means of phytosociological relevés (Braun-Blanquet, 1964). Phytosociological relevés (1070) were made using an eleven-degree scale, with + symbol for the species coverage less than 5%, 1—for cover of 5–10%, 2—for 10–20%, …, 10—for 90–100%. In 180 of the relevés, *S. aloides* and/or *C. demersum* were noted. The number of phytosociological relevés (from 2 to 18) was correlated with the area of each phytocoenosis and their structure and species composition were presented. The range limits of macrophyte communities were established and phytosociological relevés were made along the transects using the Garmin GPS to record the location. The number of transects (from 8 to 28) was correlated with the area of a given lake and it depended on the degree of structural-spatial plant diversity. The macrophytes were searched from an anchored boat or pontoon.

For each lake, the following parameters were determined: the total number of hydromacrophytes (TNH), the number of charophytes (NC), the number of elodeids (NE), the number of nymphaeids (NN), the number of lemnids (NL), the mean number of species in the phytosociological relevés (MSR), the number of plant communities (NPC), the frequency of *C. demersum* in phytosociological relevés (FCR), the frequency of *S. aloides* in phytosociological relevés (FSR), the percent share of association *Ceratophylletum demersi* in the phytolittoral of the lake (SCP), the percent share of association *Stratiotetum aloidis* in the phytolittoral (SSP), and the Shannon–Wiener index (H). On the basis of the range of the distinguished plant communities in the transects, vegetation maps were prepared and their area was calculated; furthermore, the inventory of species and communities was estimated.

Analyses of water samples

Physical and chemical properties of the water of the 32 lakes were determined on the basis of analyses of water samples taken from the pelagic zone on one occasion in the summer of 2006–2007. At the site where each water sample was taken, its reaction and specific electrolytic conductivity (SEC) values were determined by means of the multiparametric probe YSI 600 XL, and the Secchi disk visibility (SD) was measured. The remaining analyses were carried out in the laboratory of the Hydrography Department of the Maria Curie-Skłodowska University in Lublin. Total nitrogen (TN) and total phosphorus (TP) were determined in non-filtered samples, acidified in the field to pH ∼2 with sulphuric acid. TP was determined according to the Hach 8190 method by means of the spectrophotometer Hach DR 2000. TN was determined in mineralized water samples (UV photolysis with the addition of H_2O_2) as the sum of all forms of nitrogen determined conductometrically with the use of an ion chromatograph (MIC 3 of Metrohm); in column Mtrosep C2 150, ammonium ion was determined, in column A SUPP 5 250—nitrates and nitrites. Chlorophyll *a* (Chl *a*) was analysed spectrophotometrically in samples extracted through the GF/C filter with hot alcohol (Nusch, 1980).

The trophic state of the lakes represented by the analysed water samples was specified with the help of the synthetic trophic state index (TSI) (Carlson, 1977; Kratzer & Brezonik, 1981). The TSI was calculated as the average value of: concentration of total phosphorus (in µg dm^{-3}) $TSI_{TP} = 14 \cdot \ln(TP) + 4.15$, visibility of the Secchi disk (in m) $TSI_{SD} = 60–14.41 \cdot \ln(SD)$, Chl *a* (in µg dm^{-3}) $TSI_{Chl\ a} = 9.81 \cdot \ln(Chl\ a) + 30.6$ (Carlson, 1977), and concentration of TN (in mg dm^{-3}) $TSI_{TN} = 14.43 \cdot \ln(TN) + 54.45$ (Kratzer & Brezonik, 1981). The TSI is generally applied in order to evaluate water fertility. It is assumed that values of the $TSI < 40$ indicate the oligotrophic state of the water, 40–50, mesotrophic; 50–70, eutrophic; over 70, hypertrophic.

Data analysis

Separate statistical analyses were performed for the polymictic and dimictic lakes. The Shannon–Wiener index (*H*) was calculated on the basis of the percentage share of the distinguished communities in the phytolittoral of each lake. The area of shallow water colonized by macrophytes is described by the term "phytolittoral" (the reed swamp species and communities were not considered). The percent share of each community in the phytolittoral was determined using the Arc-View program. The normality of the distribution of the data was analyzed using Shapiro–Wilk test. The relationships between the parameters were determined using Spearman's rank correlation coefficients. All data analyses were carried out in MVSP and Statistica version 5 programs.

Results

The water of the studied lakes had a weak alkaline reaction (Tables 1, 2). Values in the range 7.6–8.1 were noted in polymictic lakes, and values in the range 7.7–8.2 in dimictic ones. The specific electrolytic conductivity of water was varied. Measured values ranged from 83 to 471 µS cm^{-1}, with the average value for the entire data set at the level of 251 µS cm^{-1}. In polymictic lakes, the SEC ranged from 94 to 471 µS cm^{-1}, and in dimictic lakes from 83 to 362 µS cm^{-1}. The Secchi disk visibility in polymictic lakes (0.6–2.3 m deep, 1.2 m on average) was less than in dimictic lakes (0.5–5.1 m deep, 2.1 m on average). In the case of Chl *a*, in polymictic lakes the concentration ranged from 10 to 84 µg dm^{-3} (average 23 µg dm^{-3}), and in dimictic lakes from 4 to 65 µg dm^{-3} (average 16 µg dm^{-3}). Total nitrogen in the studied waters ranged from 0.8 to 4.6 mg dm^{-3}. The average TN concentration amounted to 1.9 mg dm^{-3} in polymictic lakes, and 1.5 mg dm^{-3} in dimictic lakes. Total phosphorus occurred in the studied samples on the average level of 0.046 mg dm^{-3} (from 0.02 to 0.15 mg dm^{-3}). The average TP concentration amounted to 0.05 mg dm^{-3} in polymictic lakes, and to 0.04 mg dm^{-3} in dimictic ones.

Based on the TSI, the contemporary trophic state of the studied water samples was the following: mesotrophy (TSI < 50) was determined only in reference to the water taken from the Lake Piaseczno. Eutrophic state (TSI 50–70) was determined for the water samples taken from 28 lakes; in this group, water from nine lakes had index values suggesting little-advanced eutrophication processes—the TSI ranged from 50 to 55 (lakes: Kleszczów, Łukie, Rotcze, Bialskie, Białe

Table 1 Selected physical and chemical parameters of water from polymictic lakes of the Łęczna-Włodawa Lake District

Lakes	pH	SEC (µS cm^{-1})	TP (mg dm^{-3})	TN (mg dm^{-3})	Chl *a* (µg dm^{-3})	SD (m)	TSI
Cycowe	7.8	360	0.12	4.3	63	0.6	71.8
Długie	7.7	143	0.03	1.9	13	1.2	57.5
Gumienko	7.9	317	0.05	1.8	45	0.7	64.1
Karaśne	7.6	250	0.03	1.3	15	1.1	56.8
Kleszczów	7.9	139	0.03	0.9	12	2.0	51.1
Koseniec	7.6	226	0.04	2.0	15	0.8	60.5
Lubowierz	7.8	285	0.03	1.4	12	1.4	55.7
Łukie	8.0	266	0.03	1.5	12	2.3	54.1
Miejskie	7.9	148	0.06	2.2	21	0.7	64.0
Moszne	7.9	150	0.03	1.2	11	1.1	55.8
Perespilno	7.6	94	0.05	1.4	16	0.9	59.8
Płotycze	7.8	341	0.05	1.6	18	2.3	58.5
Pniówno	8.1	382	0.05	1.9	14	1.4	59.2
Rotcze	7.9	207	0.03	1.1	10	1.3	52.7
Wereszczyńskie	7.7	471	0.03	1.5	18	2.2	57.8
Wspólne	7.6	275	0.04	1.8	17	1.1	60.5
Zienkowskie	7.6	404	0.15	4.6	84	0.8	75.0

SEC specific electric conductivity, *TP* total phosphorus, *TN* total nitrogen, *Chl a* chlorophyll *a*, *SD* Secchi disk visibility, *TSI* trophic state index

Table 2 Selected physical and chemical parameters of water from dimictic lakes of the Łęczna-Włodawa Lake District

Lakes	pH	SEC (µS cm^{-1})	TP (mg dm^{-3})	TN (mg dm^{-3})	Chl *a* (µg dm^{-3})	SD (m)	TSI
Bialskie	8.2	273	0.03	1.0	9	3.2	50.8
Białe W	8.0	174	0.03	1.1	8	3.6	50.1
Czarne S	7.9	332	0.04	1.8	13	1.3	58.1
Czarne W	7.7	205	0.04	1.4	17	1.1	58.4
Glinki	7.8	269	0.09	2.8	65	0.5	70.1
Głębokie U	8.0	217	0.08	2.2	14	1.4	61.2
Gumienek	7.9	301	0.04	1.1	13	1.6	55.5
Krasne	8.1	289	0.03	1.2	10	2.8	52.2
Łukcze	7.9	247	0.04	1.8	18	1.1	59.5
Maśluchowskie	7.9	139	0.04	1.2	10	1.7	55.0
Piaseczno	7.8	83	0.02	0.8	4	5.1	44.8
Rogóźno	8.1	247	0.03	1.2	8	2.5	51.3
Sumin	8.2	362	0.05	2.0	29	0.6	64.0
Uściwierz	8.0	241	0.03	1.6	13	2.0	55.1
Zagłębocze	8.0	185	0.03	1.1	7	3.6	50.1

Explanations of the abbreviations as in Table 1)

Włodawskie, Krasne, Maśluchowskie, Rogóźno, Zagłębocze). Advanced eutrophy (hypereutrophy) was determined in the case of the water of 3 lakes: Cycowe, Zienkowskie and Glinki. The water from these lakes showed the TSI above 70.

Several reservoirs out of the polymictic lake group (Łukie, Płotycze) are characterized by a clear water state with high frequency of *S. aloides* (FSR) and *C. demersum* (FCR) in the phytocoenoses and a high share of the association *S. aloidis* in the phytolittoral (Tables 1, 3). These lakes display a relatively high number of hydromacrophytes and a great variety of species in plant communities (Fig. 1). A reverse observation was made in the group of highly eutrophied reservoirs (Miejskie, Pniówno, Wspólne), where there occurred frequent episodes of algal blooms. These lakes are characterized by low *S. aloides* frequency in the phytocoenoses, an insignificant share of association *S. aloidis* in the phytolittoral, and by scarcity of species and a low number of taxa in phytocoenoses (Table 3).

Slightly lower values of FSR were noted in the group of the dimictic reservoirs (Table 4). As in the case of the polymictic reservoirs, the lakes with the highest FSR and SSP values (Bialskie, Uściwierz, Zagłębocze, Łukcze) had the largest number of hydromacrophytes (Fig. 2). The lakes with a high frequency of *C. demersum* in the phytocoenosis and a great share of the association *C. demersi* in the phytolittoral (Czarne Włodawskie, Maśluchowskie, Gumienek) displayed a low number of hydromacrophytes, but these relations were not confirmed statistically.

Both in the polymictic and dimictic lakes (Tables 5, 6), statistically significant correlation coefficients were obtained between the parameters that characterize *S. aloides* (SSP, FSR) and those characteristic for species richness (TNH, NC, NN, NE), phytocoenotic richness (MSR) and phytocoenotic diversity (*H*). However, not a single case of statistically significant dependency was reported between the parameters that describe *C. demersi* (SCP, FCR) and the vegetation traits in both lake groups.

In the polymictic lake group (Table 5), positive correlations were observed between SSP and TNH and between SSP and NC. Statistically significant correlations were also observed between FSR and NN and FSR and MSR.

In the case of the dimictic lakes (Table 6), there were many more statistically significant dependencies between the analyzed parameters. They were positive only and involved the relations between the parameters that characterize *Stratiotes* and those typical of species richness and diversity. The percent share of *S. aloidis* in the phytolittoral was highly positively correlated with TNH, and very highly with NE. A positive correlation was also found between SSP and the number of plant communities (NPC) in the phytolittoral.

Table 3 Vegetation characteristics of polymictic lakes of the Łęczna-Włodawa Lake District

Lakes	MSR	NPC	*H*	FCR	SCP	FSR	SSP
Cycowe	3.8	5	1.34	33	5.0	42	5.0
Długie	3.0	3	0.50	4	0.1	24	0.3
Gumienko	5.2	3	1.20	93	11.0	100	68.0
Karaśne	4.5	3	0.76	4	1.0	4	1.0
Kleszczów	1.5	6	0.72	5	1.0	5	1.0
Koseniec	2.7	2	0.82	3	1.0	100	21.0
Lubowierz	5.6	8	1.80	3	0.4	86	1.1
Łukie	4.9	7	0.62	82	11.0	100	87.6
Miejskie	1.2	2	0.01	4	0.1	4	0
Moszne	4.8	3	0.57	60	0.1	45	3.0
Perespilno	2.0	1	0	22	0	0	0
Płotycze	5.8	3	1.53	88	0.1	100	46.2
Pniówno	2.4	3	1.56	80	25.0	5	0.1
Rotcze	2.0	10	2.25	26	6.8	53	47.3
Wereszczyńskie	4.2	3	1.32	5	0.1	5	0.1
Wspólne	3.5	4	0.76	30	10.0	14	5.0
Zienkowskie	4.1	3	0.83	50	5.0	8	1.0

MSR the mean number of species in the phytosociological relevés, *NPC* the number of plant communities, *H* the Shannon–Wiener index, *FCR* the frequency of *Ceratophyllum demersum* in the phytosociological relevés, *SCP* the percent share of association *Ceratophylletum demersi* in the phytolittoral of the lake, *FSR* the frequency of *Stratiotes aloides* in the phytosociological relevés, *SSP* the percent share of association *Stratiotetum aloidis* in the phytolittoral

Table 4 Vegetation characteristics of dimictic lakes of the Łęczna-Włodawa Lake District

Lakes	MSR	NPC	*H*	FCR	SCP	FSR	SSP
Bialskie	3.2	5	1.42	50	12.4	43	9.4
Białe W	2.5	5	1.25	90	65.0	5	0.5
Czarne S	2.2	7	2.35	30	20.7	5	0.5
Czarne W	2.0	2	1.10	100	48.0	4	1.5
Glinki	2.9	2	0.19	50	0.5	29	2.0
Głębokie U	3.2	4	1.37	32	3.4	0	0.0
Gumienek	2.1	3	1.37	87	19.1	5	0.5
Krasne	2.9	4	1.38	81	55.4	24	7.3
Łukcze	2.1	8	2.25	22	2.4	49	49.7
Maśluchowskie	1.0	1	0	100	100.0	0	0.0
Piaseczno	1.5	3	1.33	23	6.7	2	1.0
Rogóźno	2.2	4	1.13	3	1.0	3	1.0
Sumin	1.5	3	1.47	2	1.0	2	3.3
Uściwierz	4.8	8	1.99	34	1.0	43	35.0
Zagłębocze	3.8	6	2.02	66	53.2	49	14.0

Explanations of the abbreviations as in Table 3

Moreover, the frequent occurrence of *S. aloides* in the macrophyte communities had an influence on species richness and diversity (Table 6). The species frequency was positively correlated with TNH, NC and NE. Positive dependencies were also reported between the frequency of *S. aloides* and the number of the communities in the lake.

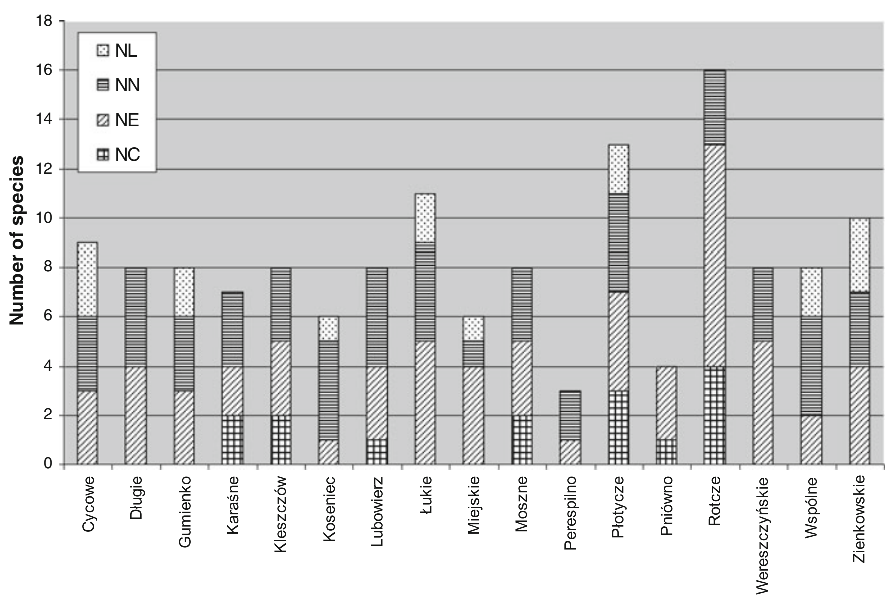

Fig. 1 Species richness of polymictic lakes of the Łęczna-Włodawa Lake District; *NC* the number of charophytes, *NE* the number of elodeids, *NN* the number of nymphaeids, *NL* the number of lemnids

Fig. 2 Species richness of dimictic lakes of the Łęczna-Włodawa Lake District; explanations of the abbreviations as in Fig. 1

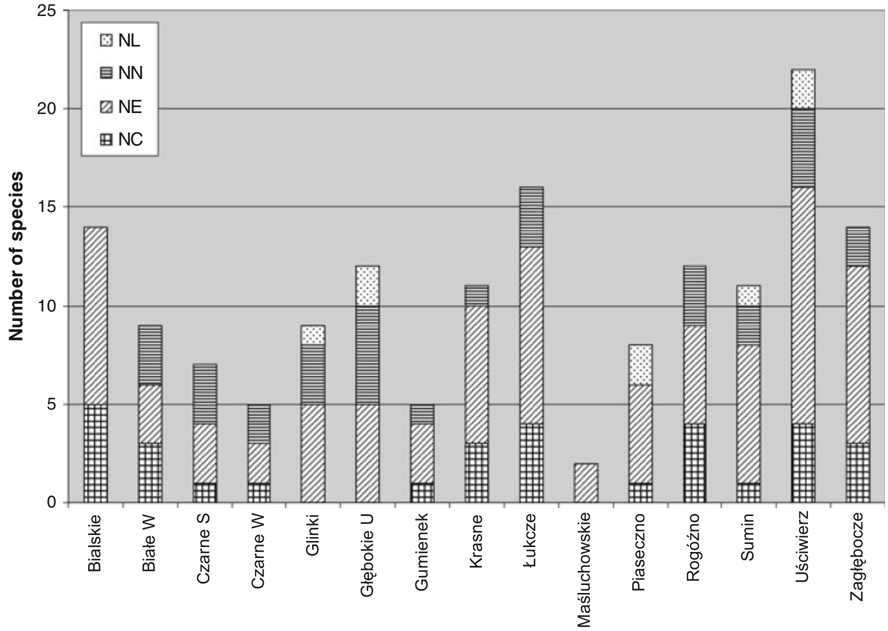

Table 5 Correlation coefficients between vegetation parameters in the polymictic lakes

Parameters	FCR	SCP	FSR	SSP
TNH	0.43	0.09	0.47	0.59*
NC	0.32	−0.15	0.29	0.77*
NE	0.24	−0.14	0.05	−0.01
NN	−0.03	0.09	0.59*	0.40
NL	0.46	0.35	−0.12	−0.04
MSR	0.38	−0.08	0.53*	0.44
NPC	0.13	0.38	0.22	0.40
H	0.20	0.31	0.29	0.25

TNH the total number of hydromacrophytes; other explanations of the abbreviations as in Fig. 1 and Table 3

* $0.01 < P \leq 0.05$, ** $0.001 < P \leq 0.01$, *** $P \leq 0.001$

Table 6 Correlation coefficients between vegetation parameters in the dimictic lakes

Parameters	FCR	SCP	FSR	SSP
TNH	−0.45	−0.41	0.62**	0.86***
NC	−0.10	−0.18	0.63*	0.60*
NE	−0.46	−0.42	0.62*	0.90***
NN	−0.38	−0.43	0.24	0.13
NL	0.00	0.74	0.24	0.00
MSR	0.05	−0.18	0.69**	0.50
NPC	−0.31	−0.03	0.62**	0.54*
H	−0.42	−0.05	0.45	0.54*

Explanations of the abbreviations as in Fig. 1 and Tables 3 and 5

* $0.01 < P \leq 0.05$, ** $0.001 < P \leq 0.01$, *** $P \leq 0.001$

The communities with a share of *S. aloides* are characterized by higher species richness (Table 6), as confirmed by positive correlations between FSR and MSR and between SSP and Shannon–Wiener index (*H*).

Discussion

Trophic status and the size of a reservoir are important factors that determine its richness and diversity (Murphy et al., 1990; Rørslett, 1991; Vestergaard & Sand-Jensen, 2000; Bornette et al., 2001; Lougheed et al., 2001). The present analysis focuses mainly on the role of the macrophytes commonly growing in water reservoirs and their importance for estimating richness and diversity.

The relations between SCP, FCR and the other parameters of richness and diversity were not statistically significant either in the polymictic or dimictic lakes. The frequency of *C. demersum* and *S. aloides* in macrophyte communities is not related to the presence of phytocoenoses with its share. These species produce and release allelopathically active compounds and may inhibit phytoplankton growth, thus contributing to water transparency (Jasser, 1994; Mjelde & Faafeng, 1997; Gross et al., 2003) and providing favourable habitat conditions for other macrophytes. However, in a few of the investigated lakes, a fairly high trophic level and cyanobacteria blooms was observed. *C. demersum* is a species of highly eutrophic and highly turbid habitats, where it copes successfully (Hutchinson, 1975). It belongs to the species of the "turbidity tolerant" flora (Nurminen, 2003), which grow rapidly, tolerate disturbance and stress and are successful competitors (Nichols & Shaw, 1986). Only elodeids are able to survive in high trophic levels and turbid water conditions. This is illustrated by the analyzed Koseniec and Perespilno lakes and by other examples of *C. demersum* being the only hydromacrophyte reported from turbid and eutrophied reservoirs (Kornijów et al., 2002; Lorens, 2006).

S. aloides, which was abundant in the analyzed lakes, plays a crucial role in stabilizing the clear water state similarly to other aquatic macrophytes (Scheffer & Jeppesen, 1998; Jeppesen et al., 1998a). Many authors claimed that the absence of phytoplankton in the presence of *Stratiotes* is caused by nutrient limitation rather than allelopathy (Brammer & Wetzel, 1984). Waterbodies dominated by *S. aloides* are, however, usually very clear despite the moderately high nutrient concentrations (Mulderij et al., 2005a). For this reason, competition for nutrients may be less significant in the relations between *S. aloides* and other photoautotrophs. In this study, the positive relations between *S. aloides* frequency in the study phytocoenoses, or the *S. aloidis* share, and species richness and diversity are clearly visible. Especially during the submerged phase, *S. aloides* might be favoured by the ability to produce allelopathic compounds that inhibit phytoplankton growth and may affect its biomass and composition (Mulderij et al., 2007). Thus, hydromacrophytes are provided with favourable living conditions. Hence, higher species richness, and especially a bigger number of elodeids and charophytes was noted in the dimictic lakes with a high share of *S. aloidis* in the phytolittoral and with a high frequency of this species in the phytocoenosis.

In shallow lakes, *S. aloides* colonizes a large area and very often emerges as early as in the middle of the vegetation period forming dense patches and thus hindering access to light, which in most lakes is the key factor that limits colonization by submerged macrophytes (Chambers & Kalff, 1985; Van den Berg et al., 2003). *Stratiotes* has an allelopathic effect on the phytoplankton; yet, when the plants start to become partly emergent, allelopathy may be less important, and alternative processes, e.g. the shading effect of *S. aloides* on phytoplankton may become more important (Mulderij et al., 2005a, 2007). Light limitation may suppress the occurrence of other submerged plants. On that account, the relations between SSP, FSR and the remaining parameters of richness and diversity are less visible in shallow lakes than in dimictic lakes.

In deep lakes, *S. aloides* becomes emergent rarely or much later than in shallow lakes, because it inhabits greater depths. The shading effect is much less and better access to light in the water column, compared to that in shallow lakes, facilitates the colonization and existence of a bigger number of species, mainly elodeids, which is suggested by the statistical analyses performed here. The study lakes are characterized by a relatively big share of *S. aloidis* in the phytolittoral and high frequency of this species in phytosociological relevés. Sometimes these reservoirs host a great share of charophytes which just as *S. aloides,* have an allelopathic effect (Van Donk & Van de Bund, 2002), and influence the transparency of water (Wium-Andersen et al., 1982; Van den Berg 1999; Van Donk & Van de Bund, 2002).

In some of the study lakes, *S. aloidis* has covered more than 50% of the whole lake area. During summer time this species creates a dense homogenous bed (Sugier & Lorens, 2000; Tarkowska-Kukuryk, 2006; Strzałek & Koperski, 2009), which determines the clear water state (Sugier & Lorens, 2000). *S. aloides* is the most available substratum for macroinvertebrate colonization (Tarkowska-Kukuryk, 2006), and could be used as an indicator of a valuable habitat in terms of macroarthropod diversity and species richness (Suutari et al., 2009).

During the last decades, *S. aloides* has declined considerably in Europe, where it grows in its northern limits (Cook & Urmi-König, 1983), especially due to eutrophication, iron limitation, and sulphide and ammonium toxicity (Toivonen, 1985; Toivonen & Bäck, 1989; Smolders et al., 1996; Smolders et al., 2003). Its common occurrence might be considered to be evidence for good status of an aquatic ecosystem

(Tarkowska-Kukuryk, 2006). The influence of *S. aloides* on richness and diversity of macrophytes is especially distinct in stratified lakes. Water soldier is a very good indicator of species richness and diversity of aquatic vegetation.

Acknowledgments The results presented in this article were financially support by Polish Ministry of Science and Higher Education and Polish State Committee for Scientific Research as grant number 2P04E 00927. The authors would like to thank Dr Arnold Pieterse and two anonymous reviewers for discussion and comments.

References

Barko, J. W. & W. F. James, 1998. Effects of submerged aquatic macrophytes on nutrient dynamics, sedimentation and resuspension. In Jeppesen, E., M. Søndergaard, M. Søndergaard & K. Christoffersen (eds), The Structuring Role of Submerged Macrophytes in Lakes. Ecological Studies, Vol. 131. Springer, New York: 197–214.

Bornette, G. H., A. Piegay, A. Citterio, C. Amoros & V. Godreau, 2001. Aquatic plant diversity in four river floodplains: a comparison at two hierarchical levels. Biodiversity and Conservation 10: 1683–1701.

Brammer, E. S. & R. G. Wetzel, 1984. Uptake and release of K^+, Na^+ and Ca^{2+} by the water soldier, *Stratiotes aloides* L. Aquatic Botany 19: 119–130.

Braun-Blanquet, J., 1964. Pflanzensoziologie, Gründzügeder der Vegetationskunde. 3Aufl. Springer Verlag, Wien.

Carlson, R. E., 1977. A trophic state index for lakes. Limnology and Oceanography 22: 361–369.

Chambers, P. A. & J. Kalff, 1985. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. Canadian Journal of Fisheries & Aquatic Sciences 42: 701–709.

Ciecierska, H., 2008. Makrofity jako wskaźniki stanu ekologicznego jezior. Monografie i Rozprawy, Uniwersytet Warmińsko-Mazurski, Olsztyn.

Cook, C. D. K. & K. Urmi-König, 1983. A revision of the genus *Stratiotes* (Hydrocharitaceae). Aquatic Botany 16: 213–249.

Coops, H., 2002. Ecology of charophytes: an introduction. Aquatic Botany 72: 205–208.

Council of the European Communities, 2000. Directive of the European Parliament and of the Council establishing a framework for community action in the field of Water Policy (2000/60/EC). Official Journal of the European Communities 43: 1–73.

Ervin, G. N. & R. G. Wetzel, 2002. Influence of a dominant macrophyte, *Juncus effusus*, on wetland plant species richness, diversity, and community composition. Oecologia 130: 626–636.

Gasith, A. & M. V. Hoyer, 1998. Structuring role of macrophytes in lakes: changing influence along lake size and depth gradients. In Jeppesen, E., M. Søndergaard, M. Søndergaard & K. Christoffersen (eds), The Structuring Role of Submerged Macrophytes in Lakes. Ecological Studies, Vol. 131. Springer, New York: 381–392.

Gopal, B. & U. Goel, 1993. Competition and allelopathy in aquatic plant communities. Botanical Review 59: 155–210.

Gough, L., J. B. Grace & K. L. Taylor, 1994. The relationship between species richness and community biomass: the importance of environmental variables. Oikos 70: 271–279.

Grace, J. B. & R. G. Wetzel, 1998. Long-term dynamics of *Typha* populations. Aquatic Botany 61: 137–146.

Gross, E. M., D. Erhard & E. Iványi, 2003. Allelopathic activity of *Ceratophyllum demersum* L. and *Najas marina* ssp. *intermedia* (Wolfgang) Casper. Hydrobiologia 506–509: 583–589.

Harasimiuk, M. & J. Wojtanowicz, 1998. Budowa geologiczna i rzeźba terenu Pojezierza Łęczyńsko-Włodawskiego. In Harasimiuk, M., Z. Michalczyk & M. Turczyński (eds), Jeziora Łęczyńsko-Włodawskie, Lublin: 41–53 (in Polish).

Heino, J. & H. Toivonen, 2008. Aquatic plant biodiversity at high latitudes: patterns of richness and rarity in Finnish freshwater macrophytes. Boreal Environment Research 13: 1–14.

Holm, T. E. & P. Clausen, 2006. Effects of water level management on autumn staging waterbird and macrophyte diversity in three Danish coastal lagoons. Biodiversity and Conservation 15: 4399–4423.

Horppila, J. & L. Nurminen, 2001. The effect of an emergent macrophyte (*Typha angustifolia*) on sediment resuspension in a shallow north temperate lake. Freshwater Biology 46: 1447–1455.

Horppila, J. & L. Nurminen, 2003. Effects of submerged macrophytes on sediment resuspension and internal phosphorus loading in Lake Hiidenvesi (southern Finland). Water Research 37: 4468–4474.

Hultén, E. & M. Fries, 1986. Atlas of North European vascular plants. North of the Tropic of Cancer, Vol. 1. Koeltz Scientific Books, Königstein.

Hutchinson, G. E., 1975. A Treatise on Limnology. Vol. III. Limnological Botany. Wiley, New York.

Jasser, I., 1994. Influence of *Ceratophyllum demersum* on phytoplankton community in experimental conditions. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 25: 2291–2295.

Jasser, I., 1995. The influence of macrophytes on a phytoplankton community in experimental conditions. Hydrobiologia 306: 21–32.

Jeppesen, E., M. Søndergaard, M. Søndergaard & K. Christoffersen, 1998a. The Structuring Role of Submerged Macrophytes in Lakes. Ecological Studies, Vol. 131. Springer, New York.

Jeppesen, E., M. Søndergaard, J. P. Jensen, E. Mortensen & T. Jørgensen, 1998b. Cascading trophic interactions from fish to bacteria and nutrients after reduced sewage loading: an 18 year study of a shallow hypertrophic lake. Ecosystems 1: 250–267.

Kłosowski, S. & G. Kłosowski, 2001. Flora Polski. Rośliny wodne i bagienne. Multico Press, Warszawa (in Polish).

Kohler, A., 1982. Wasserpflanzen als Belastungsindikatoren. Decheniana – Beihefte. Bonn 26: 31–42.

Kondracki, J., 2002. Geografia regionalna Polski. Wyd. Naukowe PWN, Warszawa. (in Polish).

Kornatowski, J., 1976. Dynamics of *Stratiotes aloides* L. development. Polskie Archiwum Hydrobiologii 23: 365–376.

Kornijów, R., H. Smal, W. Pęczuła, B. Lorens, J. Rechulicz, P. Sugier, P. A. Paleolog-Demetraki, S. Ligęza, M. Tarkowska-Kukuryk, D. Kowalczyk, K. Szafran & A. Halkiewicz, 2002. Hypertrophication of Lake Syczyńskie (Eastern Poland). Limnological Review 2: 209–215.

Kratzer, C. R. & P. L. Brezonik, 1981. A Carlson-type trophic state index for nitrogen in Florida lakes. Water Resources Bulletin 17: 713–715.

Kufel, L. & I. Kufel, 2002. Chara beds acting as nutrient sinks in shallow lakes—a review. Aquatic Botany 72: 249–260.

Kufel, L. & T. Ozimek, 1994. Can *Chara* control phosphorus cycling in Lake Luknajno (Poland)? Hydrobiologia 275(276): 277–283.

Lorens, B., 2006. Szata roślinna jezior rzecznych oraz ich różnorodność fitocenotyczna i gatunkowa. In Wojciechowska, W. (ed.), Jeziora rzeczne Doliny Środkowego Bugu. Różnorodność biologiczna i krajobrazowa. Wydawnictwo KUL: 55–94 (in Polish).

Lougheed, V. L., B. Crosbie & P. Chow-Fraser, 2001. Primary determinants of macrophyte community structure in 62 marshes across the Great Lakes basin: latitude, land use, and water quality effects. Canadian Journal of Fisheries & Aquatic Sciences 58: 1603–1612.

Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch & D. F. Westlake, 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia 444: 71–84.

Maltchik, L., A. S. Rolon & P. Schott, 2007. Effects of hydrological variation on the aquatic plant community in a floodplain palustrine wetland of southern Brazil. Limnology 8: 23–28.

Mjelde, M. & B. A. Faafeng, 1997. *Ceratophyllum demersum* hampers phytoplankton development in some small Norwegian lakes over a wide range of phosphorus concentrations and geographical latitude. Freshwater Biology 37: 355–365.

Moss, B., D. Stephen, C. Alvarezn, E. Becares, W. Van der Bund, S. E. Collings, et al., 2003. The determination of ecological status in shallow lakes—a tested system (ECOFRAME) for implementation of the European Water Framework Directive. Aquatic Conservation: Marine and Freshwater Ecosystems 13: 507–549.

Mulderij, G., W. M. Mooij, A. J. P. Smolders & E. Van Donk, 2005a. Allelopathic inhibition of phytoplankton by exudates from *Stratiotes aloides*. Aquatic Botany 82: 284–296.

Mulderij, G., W. M. Mooij & E. Van Donk, 2005b. Allelopathic growth inhibition and colony formation of the green alga *Scenedesmus obliquus* by the aquatic macrophyte *Stratiotes aloides*. Aquatic Ecology 39: 11–21.

Mulderij, G., B. Mau, E. Van Donk & E. M. Gross, 2007. Allelopathic activity of *Stratiotes aloides* on phytoplankton—towards identification of allelopathic substances. Hydrobiologia 584: 89–100.

Murphy, K. J., 2002. Plant communities and plant diversity in softwater lakes of Northern Europe. Aquatic Botany 73: 287–324.

Murphy, K. J., B. Rørslett & I. Springuel, 1990. Strategy analysis of submerged lake macrophyte communities: an international example. Aquatic Botany 36: 303–323.

Nichols, S. A. & B. H. Shaw, 1986. Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum*, *Potamogeton crispus*, and *Elodea canadensis*. Hydrobiologia 131: 3–21.

Nurminen, L., 2003. Macrophyte species composition reflecting water quality changes in adjacent water bodies of Lake Hiidenvesi, SW Finland. Annales Botanici Fennici 40: 199–208.

Nusch, E. A., 1980. Comparison of different methods for chlorophyll and phaeopigments determination. Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie 14: 14–36.

Penning, W. E., B. Dudley, M. Mjelde, S. Hellsten, J. Hanganu, A. Kolada, M. Van den Berg, S. Poikane, G. Phillips, N. Willby & F. Ecke, 2008a. Using aquatic macrophyte community indices to define the ecological status of European lakes. Aquatic Ecology 42: 253–264.

Penning, W. E., M. Mjelde, B. Dudley, S. Hellsten, J. Hanganu, A. Kolada, M. Van den Berg, S. Poikane, G. Phillips, N. Willby & F. Ecke, 2008b. Classifying aquatic macrophytes as indicators of eutrophication in European lakes. Aquatic Ecology 42: 237–251.

Radwan, S. & R. Kornijów, 1998. Hydrobiologiczne cechy jezior – stan aktualny i kierunki zmian. In Harasimiuk M., Z. Michalczyk & M. Turczyński (eds), Jeziora Łęczyńsko-Włodawskie, Lublin: 129–144 (in Polish).

Rørslett, B., 1991. Principal determinants of aquatic macrophyte richness in northern European lakes. Aquatic Botany 39: 173–193.

Schamburg, J., C. H. Schranz, G. Hofmann, D. Stelzer, S. Schneider & U. Schmedtje, 2004. Macrophytes and phytobenthos as indicators of ecological status in German lakes—a contribution to the implementation of the Water Framework Directive. Limnologica 34: 302–314.

Scheffer, M. & E. Jeppesen, 1998. Alternative stable states. In Jeppesen, E., M. Søndergaard, M. Søndergaard & K. Christoffersen (eds), The Structuring Role of Submerged Macrophytes in Lakes. Ecological Studies, Vol. 131. Springer, New York: 397–406.

Schneider, S. & A. Melzer, 2003. The trophic index of macrophytes (TIM)—a new tool for indicating the trophic state of running waters. International Review of Hydrobiology 88: 49–67.

Smolders, A. J. P., J. G. M. Roelofs & C. den Hartog, 1996. Possible causes for the decline of the water soldier (*Stratiotes aloides* L.) in the Netherlands. Archiv für Hydrobiologie 136: 327–342.

Smolders, A. J. P., L. H. T. Vergeer, G. van der Velde & J. G. M. Roelofs, 2000. Phenolic contents of submerged, emergent, and floating leaves of aquatic and semi-aquatic macrophyte species: why do they differ? Oikos 91: 307–310.

Smolders, A. J. P., L. P. M. Lamers, C. den Hartog & J. G. M. Roelofs, 2003. Mechanisms involved in the decline of

Stratiotes aloides L. in the Netherlands: sulphate as a key variable. Hydrobiologia 506–509: 603–610.

Stelzer, D., S. Schneider & A. Melzer, 2005. Macrophyte-based assessment of lakes—a contribution to the implementation of the European water framework directive in Germany. International Review of Hydrobiology 90: 223–237.

Strzałek, M. & P. Koperski, 2009. The *Stratiotes aloides* L. stand as a habitat in oxbow lake Bużysko. Aquatic Botany 90: 1–6.

Sugier, P. & B. Lorens, 2000. Zbiorowiska roślinne jeziora Łukie w Poleskim Parku Narodowym. Parki Narodowe i Rezerwaty Przyrody 19: 3–18. (in Polish).

Suutari, E., J. Salmela, L. Paasivirta, M. J. Rantala, K. Tynkkynen, M. Luojumäki & J. Suhonen, 2009. Macroarthropod species richness and conservation priorities in *Stratiotes aloides* (L.) lakes. Journal of Insect Conservation 13: 413–419.

Tarkowska-Kukuryk, M., 2006. Water soldier *Stratiotes aloides* L. (Hydrocharitaceae) as a substratum for macroinvertebrates in a shallow eutrophic lake. Polish Journal of Ecology 54: 441–451.

Toivonen, H., 1985. Changes in the pleustic macrophyte flora of 54 small Finnish lakes in 30 years. Annales Botanici Fennici 22: 37–44.

Toivonen, H. & S. Bäck, 1989. Changes in aquatic vegetation of a small eutrophicated and lowered lake (Southern Finland). Annales Botanici Fennici 26: 27–38.

Usenko, O. M., A. I. Sakevich & V. D. Palamarchuk, 2002. Influence of phenol acids of hydrophytes on the development of plankton algae. International Journal on Algae 4: 20–28.

Thomaz, S. M., D. C. Souza & L. M. Bini, 2003. Species richness and beta diversity of aquatic macrophytes in a large subtropical reservoir (Itaipu Reservoir, Brazil): the influence of limnology and morphometry. Hydrobiologia 505: 119–128.

Van den Berg, M. S., 1999. Charophyte colonization in shallow lakes—processes, ecological effects and implications for lake management. PhD Dissertation, University of Amsterdam, Amsterdam, The Netherlands: 138 pp.

Van den Berg, M. S., W. Joosse & H. Coops, 2003. A statistical model predicting the occurrence and dynamics of submerged macrophytes in shallow lakes in the Netherlands. Hydrobiologia 506–509: 611–623.

Van Donk, E. & W. J. Van de Bund, 2002. Impact of submerged macrophytes including charophytes on phyto- and zooplankton communities: allelopathy versus other mechanisms. Aquatic Botany 72: 261–274.

Van Geest, G. J., H. Wolters, F. C. J. M. Roozen, H. Coops, R. M. M. Roijackers, A. D. Buijse & M. Scheffer, 2005. Water-level fluctuations affect macrophyte richness in floodplain lakes. Hydrobiologia 539: 239–248.

Vermaat, J. E., L. Santamaria & P. J. Roos, 2000. Water flow across and sediment trapping in submerged macrophyte beds of contrasting growth form. Archiv für Hydrobiologie 148: 549–562.

Vestergaard, O. & K. Sand-Jensen, 2000. Aquatic macrophyte richness in Danish lakes in relation to alkalinity, transparency, and lake area. Canadian Journal of Fisheries & Aquatic Sciences 57: 2022–2031.

Wilgat, T., 1954. Jeziora Łęczyńsko-Włodawskie. Annales Universitatis Mariae Curie-Skłodowska, sectio B, 8: 37–122.

Wium-Andersen, S., U. Anthoni, C. Christophersen & G. Houen, 1982. Allelopathic effects on phytoplankton by substances isolated from aquatic macrophytes (Charales). Oikos 39: 187–190.