



Impact of *Nitellopsis obtusa* (Desv.) J. Groves, a regionally alien and invasive charophyte, on macrophyte diversity in the species native range

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Abstract This study aimed to determine the relationships between the abundance of *Nitellopsis obtusa*, a controversial charophyte, locally red-listed in its native Eurasian range but invasive in North America, and the species diversity of macrophyte stands dominated by *N. obtusa*. Three lakes of different morphology, productivity and catchment were surveyed in the species native range. In each lake, the species composition and cover of three *N. obtusa*-dominated stands were determined monthly from spring to autumn and illustrated by the Shannon–Wiener diversity index. Water chemistry supplemented vegetation study. The species diversity turned out to be lake-specific and declined with the increasing share of *N. obtusa*, which developed mass occurrence

in less mineralised and less fertile waters, leaving no space and limiting light and nutrient availability for large and branchy macrophytes. We postulate that this mechanism makes *N. obtusa* a superior competitor in less fertile waters and seems common to both native and invaded territories, as is the pool of macrophyte species most frequently co-occurring with *N. obtusa*.

Keywords *Chara*-lakes · Biodiversity · Aquatic plants · Macroalgae · Inter-species relationships

Introduction

Wetland vegetation constitutes an integral functional component of aquatic ecosystems and a particularly important role is assigned to submerged macrophytes, i.e. macroscopic algae and higher plants. By creating vast communities of submerged aquatic vegetation

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(SAV), macrophytes significantly affect the physical and chemical water characteristics. Through multiple feedback mechanisms, including interactions between species within a macrophyte community, abundant SAV generates and maintains the clear-water state in a given body of water (Jeppesen et al., 1997; Scheffer & Jeppesen, 2007; Schubert et al., 2018). However, the role of SAV in the network of feedback mechanisms varies and significant differences were found between angiosperms and macroscopic algae from a group of charophytes (Blindow et al., 2014). Despite the above, the dominance of single taxa at the expense of the overall SAV species diversity can occur along with water eutrophication, ultimately followed by the complete disappearance of submerged vegetation (Zhang et al., 2017).

Charophytes (Charophyta, Characeae), also referred to as stoneworts, are a group of mainly freshwater submerged macrophytes which are particularly sensitive to an increase in water trophy and turbidity (Schubert et al., 2018). Therefore, these macroscopic green algae are used as bioindicators of good water quality (Schneider et al., 2015). Charophytes are considered a particularly effective functional component of aquatic ecosystems which through biological interactions and influence on the physical and chemical water properties, contribute to the induction and maintenance of the clear-water state in lakes (van den Berg et al., 1998; Kufel & Kufel, 2002; Blindow et al., 2014). In less productive transparent waters, charophytes develop mass occurrence and create extensive communities, referred to as beds, mats or stands, or more vividly charophyte meadows, which depending on the dominant species, can hibernate in mild winters (Pelechaty et al., 2017; Schubert et al., 2018).

Although many charophytes are susceptible to water quality deterioration, not all species are geographically limited and rare (Schubert et al., 2018). It is also possible that a species that is locally of conservation concern may colonize a new territory, where it spreads rapidly, gaining the status of an invasive alien species (Escobar et al., 2016). Such a charophyte is *Nitellopsis obtusa* (Desv.) J. Groves, commonly referred to as starry stonewort thanks to a feature typical of this species, namely white star-like (stellate) bulbils, numerous formed from the thalli nodes (Krause, 1997; Kabus, 2016; Larkin et al., 2018). In addition to freshwater environments, as an

oligohaline halotolerant species, *N. obtusa* can also occur in brackish waters (Urbaniak, 2003; Kabus, 2016; Bučas et al., 2019). In freshwater, the species occurs frequently in mesotrophic to meso-eutrophic lakes, less frequently in rivers (Wood & Imahori, 1965; Larkin et al., 2018).

Nitellopsis obtusa is one of three extant species of *Nitellopsis* mentioned in the literature (Alix et al., 2017). Contrary to *N. bulbilifera* Dontberg, recorded from Argentina and New Mexico (Tindall et al., 1965; Alix et al., 2017), and *N. sarcularis* Zanevaled, only reported from its type locality on the Indonesian island of Lombok (Alix et al., 2017), *N. obtusa* is characterised by a wide distribution across the northern hemisphere (Korsch, 2018). Within its native range from Europe to Japan the species is regionally red-listed as near threatened in Switzerland (Auderset Joy & Schwarzer, 2012), vulnerable in Finland (Koistinen, 2010), Sweden (Johansson et al., 2010) and Great Britain (Stewart and Church, 1992), and threatened in Japan (Kato et al., 2014). In Central and Eastern Europe, however, *N. obtusa* is a common charophyte (Urbaniak & Gąbka, 2014; Kabus, 2016). In Poland, where the study reported was conducted, *N. obtusa* currently occurs in numerous lakes (Styperek et al., 2014), despite the status of an endangered alga assigned to this species at the beginning of the 21st century (Siemińska et al., 2006). By creating compact mats that dominate the submerged vegetation of some lakes, *N. obtusa* can be considered nuisance. With climate warming, the spread of *N. obtusa* in European waters and the change in the species conservation status has been noted. Moreover, in recent four decades *N. obtusa* has expanded its range to North America where propagating only vegetatively, it has become an invasive alien species that poses a real threat to local biodiversity (Alix et al., 2017; Karol & Sleith, 2017; Larkin et al., 2018; Harrow-Lyle & Kirkwood, 2021). Hence, in the study performed in four lakes in central New York (USA), Brainard & Schulz (2017) revealed a decrease in species richness and biomass of native macrophytes along with an increase in *N. obtusa* abundance.

Therefore, it is important to recognize the potential ecological impact of *N. obtusa* on other macrophytes in the species native range, especially in SAV communities where *N. obtusa* occurs abundantly. This study aimed to assess the relationships between native plant species richness and diversity within *N. obtusa*-

dominated macrophyte stands. In particular, we aimed to identify native species which could potentially be strong competitors with *N. obtusa*, and those which could be outcompeted. Environmental conditions driving these macrophyte communities were also assessed to ascertain the most important factors. Our research included three lakes located in the part of *N. obtusa* native range, where the species is not endangered. As the lakes are differentiated in terms of morphology, catchment land use and water chemistry, an attempt was made to find out whether the structure of *N. obtusa*-dominated macrophyte stands were site- or lake-specific.

Materials and methods

Studied lakes

Monthly field surveys and sampling were carried out in the growing season 2008 in three lakes of western Poland. Two lakes, Lake Niesłysz (52°13'27.9" N, 15°23'37.0" E) and Lake Złoty Potok (52°12'58.4" N, 15°22'21.8" E) are located in Lubusz Land, whilst the third one, Lake Lednica (52°31'57.5" N, 17°22'33.8" E), in Greater Poland. The lakes detailed description and location was presented in previous works (Pełechaty et al., 2015; Pełechata et al., 2016, 2020). The most important differences between the lakes are area, depth and shape of the lakes basin. Further differences relate to the main land use of the catchment area, hence the water bodies studied also vary in terms of water productivity and clarity. The largest and deepest is Lake Niesłysz (surface area and depth of 486.2 ha and 34.7 m, respectively). This fully stratified and dimictic body of water is characterised by a low Carlson (1977) Trophic State Index (TSI = 44.3) and high water transparency (average Secchi depth visibility in the study period reached 4.08 m), indicating mesotrophic state of this lake. Lake Złoty Potok, though classified as a dimictic lake, is much smaller and shallower (32.8 ha and 13.7 m). It is also a mesotrophic lake (TSI = 45.2) with a high Secchi depth visibility (4.79 m). Lake Lednica (341.4 ha and 15.1 m), the second largest lake in this study, is, compared to other lakes, highly enriched in dissolved substances and nitrogen. This lake is characterised by the highest productivity reflected in the highest TSI value (49.3) and the lowest Secchi depth visibility

(3.57 m), that allows for the lake classification as a slightly eutrophic body of water. This results from the main land use type of the catchment area which sharply differs Lake Lednica, which catchment area is used agriculturally in 75%, from lakes Niesłysz and Złoty Potok, characterised by the dominance of forest in their catchments.

The diversified shape of lakes Niesłysz and Lednica compared to the uniformly oval Lake Złoty Potok (Pełechaty et al., 2015) is reflected in the lakes vegetation structure. Therefore, the widest vegetated zone (the phytolittoral) was described in Lake Niesłysz, followed by lakes Lednica and Złoty Potok (Pełechata et al. 2020). The latter lake, was also characterised by the lowest per cent of lake area occupied by vegetation, whilst the highest share of vegetation was estimated in Lake Lednica. High water clarity favours the development of stable and diversified vegetation in all the lakes, particularly when the SAV is considered. The phytolittoral of all the lakes studied was dominated by charophytes, which formed extensive underwater meadows. In Lake Niesłysz, the SAV was dominated by *N. obtusa*, *Chara tomentosa* L. and *C. aspera* (Deth.) Willd. In Lake Złoty Potok, the charophyte meadows were also abundantly developed in the form of compact stands with the dominance of *C. aspera* and *N. obtusa*. A smaller share of other species was also observed. In Lake Lednica, in turn, the vegetation structure was more varied and patchy. In addition to *N. obtusa* and *C. tomentosa*, two other charophytes, *C. contraria* Kütz and *C. globularis* Thuill. were also recorded amongst the dominants. The macrophyte stands, however, were usually composed of multiple species. In all the lakes studied, vascular plants and mosses contributed to a lesser extent to the SAV structure. The detailed description of the lakes vegetation was presented by Pełechata et al. (2020).

Study design

The samples were collected monthly between May (in lakes Niesłysz and Złoty Potok) or June (in Lake Lednica) and October 2008. In each lake, three permanent study sites of 25 m² were randomly selected (L1, L2, L3 in Lake Lednica, ZP1, ZP2, ZP3 in Lake Złoty Potok and N1, N2, N3 in Lake Niesłysz) in the submerged macrophyte stands dominated by *N. obtusa*. The depths of the sites ranged

from 1.7 to 3.5 m (2.2 m on average). In each stand, due to the commonly applied mid-European phytosociological method of Braun-Blanquet (1964), all species were listed and the per cent area covered by each species was estimated according to the following scale: r, single individuals, negligible cover; +, a few individuals or clusters (< 5%); 1, 5%; 2, 5–25%; 3, 25–50%; 4, 50–75%; and 5, 75–100%.

In addition to the species composition and cover, the macrophyte height was determined as the difference between the depth of the stand and the distance between the water surface and the top of the plants measured in the central part of the stand. This helped to calculate the per cent volume of water inhabited by plants (PVI). This index was calculated for each stand and month of study as the product of the per cent cover of the stand and the macrophyte height divided by the stand depth. This parameter reflects the abundance of macrophyte stands in relation to water column (i.e., 0% = no macrophytes and 100% = the water column overgrown from the lake bottom to the surface) and indicates its potential significance for the stands structure. All the submerged vegetation measurements were performed by snorkelling or from the boat, using a small anchor with a calibrated rope.

Prior to macrophyte surveys the measurements of physical and chemical parameters and sampling of surface water in the central point of each *N. obtusa*-dominated stand were performed. The temperature and oxygen concentration were measured with Elmetron CX-401 m (Elmetron Sp. J, Zabrze, Poland). The electrolytic conductivity and pH were measured using CyberScan 200 and CyberScan 20, respectively (Eutech Instruments Europe BV, Nijkerk, The Netherlands). The samples for further chemical analyses were collected with a 3-L water sampler (Uwitec, Mondsee, Austria) from a depth of 0.5 m and poured into 1-L bottles. The samples were fixed with chloroform, transported in a portable refrigerator and kept at 4 °C until the remaining chemical analyses were performed. Water clarity was determined as the Secchi disc visibility in the macrophyte-free pelagic region of the lakes studied.

The analytical procedures applied in the laboratory analyses of water were described in details in Pelechaty et al. (2010) and Pelechaty et al. (2013). Water colour determinations were performed based on the visual method against a platinum scale. Anions (NO_3^- , PO_4^{3-}) and cations (NH_4^+ , Ca^{2+} , Mg^{2+}) were

determined using an 881 Compact IC Pro model Metrohm ion chromatograph (Metrohm, Switzerland). Total alkalinity was determined by titration of a 0.1 mol/l HCl-acidified water sample against methyl orange as an indicator. Determination of total hardness was performed by the versenate method. The concentration of total nitrogen (TN) was analysed by Kjeldahl's method and that of total phosphorus (TP) by the colorimetric molybdenate method with ascorbic acid as a reducer with a Merck Spectroquant® Pharo 100 apparatus (Merck KGaA, Darmstadt, Germany).

Data processing and statistical approach

For each *N. obtusa* stand studied, species richness was expressed as the number of species which occurred at least once over the study period, whilst the species diversity was determined as the Shannon–Wiener diversity index (H') (Shannon, 1948), calculated from the species cover. For H' index calculation and for further statistical data analysis, the Braun-Blanquet scale (range from r to 5) was transformed into the numerical van der Maarel (1979) scale (range from 1 to 9), as follows: $r = 1$, $+ = 2$, $1 = 3$, $2 = 5$, $3 = 7$, $4 = 8$, $5 = 9$.

The normality of distributions of the analysed variables and the homoscedasticity of variances were tested with the Shapiro–Wilk and Levene tests, respectively. One-way ANOVA and post hoc Scheffe test were used to determine lake-to-lake differences in H' index, whereas for site-to-site and lake-to-lake comparisons of the water properties and PVI a non-parametric ANOVA by Kruskal–Wallis H-test and a post hoc multiple comparison test were applied. In order to determine the relationships between the cover of *N. obtusa* and other macrophytes and the H' index, PVI, and water properties, Pearson correlation (r , where parametric test was allowed) or Spearman rank correlation (R , where non-parametric test was required) were calculated. In all tests $P < 0.05$ was accepted as being statistically sound. Principal Component Analysis (PCA) was applied to reflect the site-to-site and lake-to-lake differences in the structure of the studied *N. obtusa*-dominated stands. Three species were found at one site only and, thus, were excluded from this analysis. For all statistical analyses STATISTICA 12 package (StatSoft Inc., Tulsa, OK, USA) was applied.

Results

The structure and species diversity of macrophyte stands dominated by *Nitellopsis obtusa*

In all the studied macrophyte stands, *N. obtusa* was the primary component in terms of occurrence and cover. Nevertheless, other macrophytes, namely charophytes, angiosperms and a moss species, contributed to the community structure and the total number of species per a single stand ranged from 4 to 9 (Table 1). The stands studied in Lake Niesłysz were averagely less rich in species as compared to stands in other lakes.

According to the data on species richness presented in Table 1, the stands studied were rich mainly in charophytes and in some vascular plants, this being also reflected in the species frequencies (Fig. 1). In addition to *N. obtusa* that obviously occurred at each site studied, *C. contraria* was the most frequently noted species amongst charophytes and *Stuckenia*

pectinata (L.) Börner amongst angiosperms. Three species were found at one site only (Table 1; Fig. 1). As demonstrated by the PCA analysis (Fig. 2), *C. aspera*, out of charophytes, was recorded in all stands studied in lakes Złoty Potok and Niesłysz, whilst this species did not occur in Lake Lednica. Out of angiosperms, *Myriophyllum spicatum* L., was also not recorded in Lake Lednica, whilst by contrast, *Utricularia vulgaris* L. occurred exclusively in this lake. Lake Lednica stands were also preferred by *Najas marina* L., less frequent in other lakes. The stands studied in Lake Niesłysz were characterised by a low frequency of angiosperms in favour of charophytes, mainly *C. aspera* and *C. filiformis*, which is emphasized by the central position of the stands studied in this lake in the PCA ordination space (Fig. 2B) and by the fact that in none of the study sites in this lake a common angiosperm, namely *Ceratophyllum demersum* L., was found (Table 1; Fig. 2). Figure 2A reflects the relationships between species in the studied *N. obtusa*-dominated stands. The same

Table 1 Species composition in submerged macrophyte stands dominated by *Nitellopsis obtusa* studied in three lakes of western Poland

Lakes	Species acronyms	Family	Lake Lednica			Lake Złoty Potok			Lake Niesłysz		
			L1	L2	L3	ZP1	ZP2	ZP3	N1	N2	N3
Charophytes											
<i>Nitellopsis obtusa</i> (N.A. Desvaux) J. Groves	<i>Nio</i>	Characeae	+	+	+	+	+	+	+	+	+
<i>Chara aspera</i> Willd	<i>Cha</i>	Characeae	–	–	–	+	+	+	+	+	+
<i>Chara contraria</i> A.Braun ex Kützing	<i>Chc</i>	Characeae	+	+	+	+	+	–	+	+	+
<i>Chara tomentosa</i> L	<i>Cht</i>	Characeae	+	+	+	–	–	+	–	+	–
<i>Chara filiformis</i> Hertzsch	<i>Chf</i>	Characeae	+	–	–	+	+	+	–	+	+
<i>Chara globularis</i> Thuiller	<i>Chg</i>	Characeae	+	+	+	+	–	–	–	–	+
Mosses and angiosperms											
<i>Najas marina</i> L	<i>Nam</i>	Hydrocharitaceae	+	+	+	+	+	–	–	–	+
<i>Stuckenia pectinata</i> (L.) Börner	<i>Stp</i>	Potamogetonaceae	+	–	+	+	+	+	+	+	+
<i>Ceratophyllum demersum</i> L	<i>Ced</i>	Ceratophyllaceae	+	–	–	+	+	+	–	–	–
<i>Utricularia vulgaris</i> L	<i>Utv</i>	Lentibulariaceae	+	+	+	–	–	–	–	–	–
<i>Myriophyllum spicatum</i> L	<i>Mys</i>	Haloragaceae	–	–	–	+	–	+	–	–	+
<i>Potamogeton compressus</i> L	<i>Poc</i>	Potamogetonaceae	–	+	–	–	–	–	–	–	–
<i>Batrachium circinatum</i> Sibth	<i>Bac</i>	Ranunculaceae	–	–	–	–	–	+	–	–	–
<i>Fontinalis antipyretica</i> Hedw	<i>Fna</i>	Fontinalaceae	–	–	–	–	–	–	–	–	+
Total			9	7	7	9	7	8	4	6	9

L1-3, ZP1-3 and N1-3 are three sites studied in lakes Lednica, Złoty Potok and Niesłysz, respectively; +, species occurred; –, species did not occur. Species acronyms refer to those used in Fig. 2

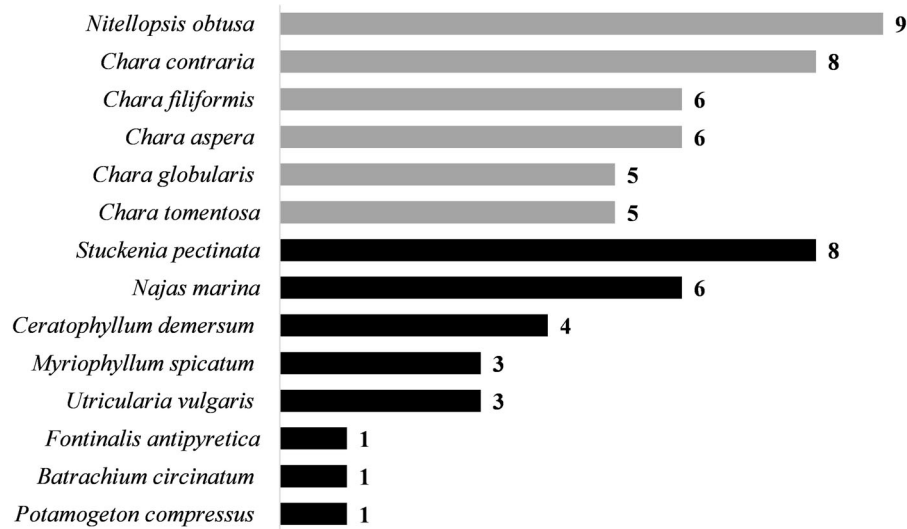


Fig. 1 The number of occurrences of macrophytes in *Nitellopsis obtusa* stands studied in western Poland. Gray bars, charophytes; black bars, vascular plant and moss species

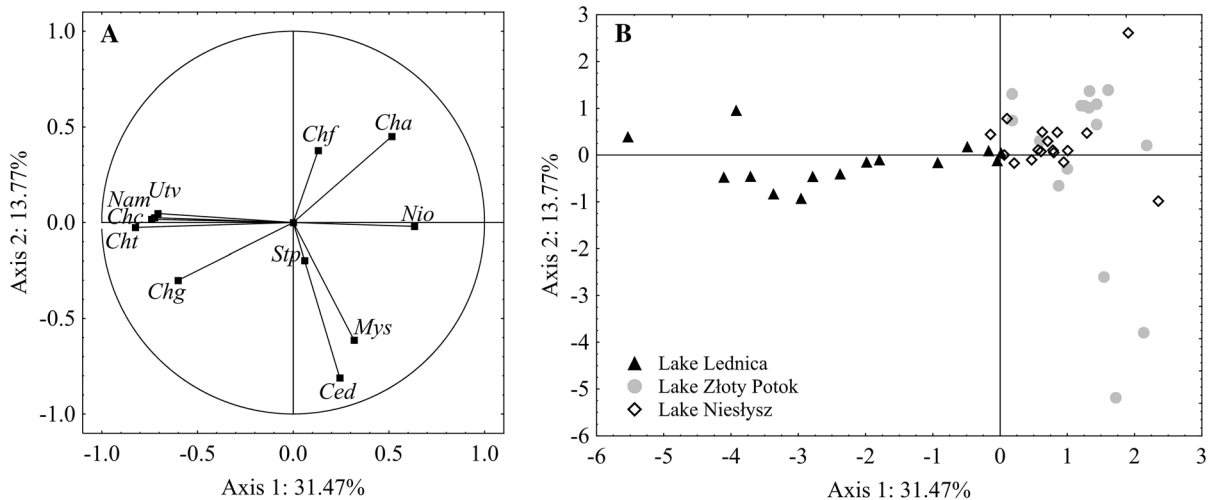


Fig. 2 PCA output for the macrophyte species composition and cover in nine *Nitellopsis obtusa* stands studied monthly along growing season in three lakes of western Poland. **A** relationships

direction of the species marker lines indicates positive correlations, whilst the opposite direction indicates negative relationships. As shown in Fig. 2B, the species composition of the studied stands clearly distinguished Lake Lednica (Fig. 2B, left panels) from the other two lakes (Fig. 2B, right panels) in the PCA ordination space defined by the first and second principal components, which together accounted for more than 45% of the variance observed in the structure of *N. obtusa*-dominated stands.

between species in the studied stands; **B** lake-to-lake differences in the structure of the studied *N. obtusa* stands. Species acronyms as in Table 1

All the stands were very compact and characterised by a 100% macrophyte coverage. *Nitellopsis obtusa* had the highest cover in all stands studied, whilst other macrophytes were less important or occurred as accompanying species (Supplementary Fig. S1). Despite higher fertility in comparison to other lakes, Lake Lednica was characterised by the lowest *N. obtusa* proportion, within 40%, whilst the highest *N. obtusa* cover was evidenced in Lake Niesłysz, where the species accounted for more than 60% of the total

macrophyte coverage (Supplementary Fig. S1). Therefore, the Shannon–Wiener diversity index showed a clear downward trend from the highest values in Lake Lednica, through intermediate values characterising the study sites in Lake Złoty Potok, to the lowest diversity evidenced in Lake Niesłysz (Supplementary Fig. S1) and the Pearson correlation evidenced a very strong and highly statistically significant negative dependency between H' and the cover of *N. obtusa* ($r = -0.96$, $r^2 = 0.92$, $P < 0.001$, Fig. 3). The lake-to-lake differences in H' index turned out to be statistically sound in light of ANOVA ($F_{(2,6)} = 7.9162$, $P < 0.05$) and species diversity of *N. obtusa*-dominated stands in Lake Lednica was significantly higher compared to those studied in Lake Niesłysz (Fig. 4). To conclude, despite some minor site-to-site dissimilarities, the structure of *N. obtusa*-dominated macrophyte stands turned out to be lake-specific.

Water properties and PVI in *N. obtusa*-dominated stands

Physical and chemical properties of water and PVI in *N. obtusa* stands are presented in Table 2. Water characteristics evidenced greater differences amongst the three lakes studied than amongst the macrophyte stands investigated within a single lake. Water mineralisation appeared to be the primary differentiating factor, reflected in the electrolytic conductivity values which were sharply higher in macrophyte stands

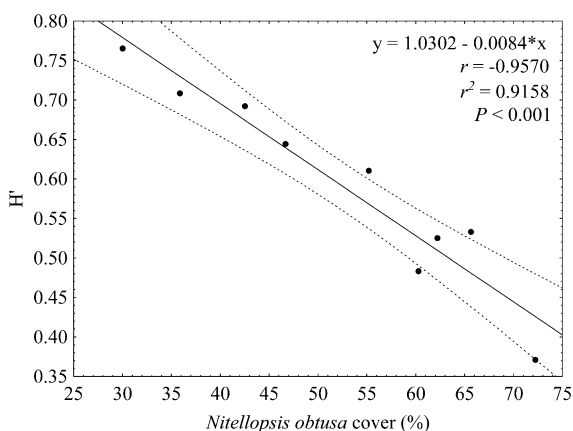


Fig. 3 The dependence of the Shannon–Wiener diversity index (H') on the coverage of *Nitellopsis obtusa* in the studied *N. obtusa* stands. The dashed lines indicate the 95% confidence interval

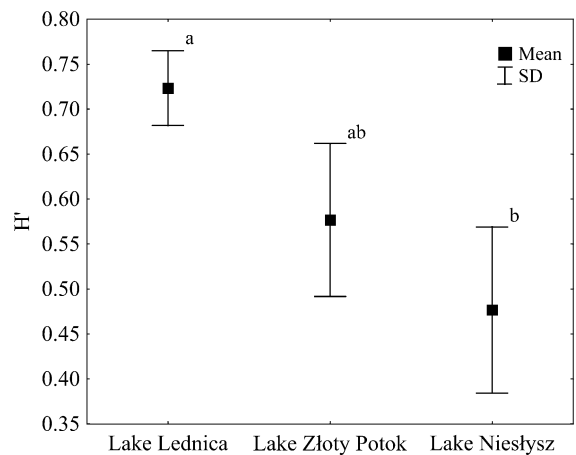


Fig. 4 Differences in the Shannon–Wiener diversity index (H') between *Nitellopsis obtusa* stands studied in three lakes of western Poland. Mean values \pm standard deviations are presented. Different letters indicate statistically significant differences at $P < 0.05$

studied in Lake Lednica compared to stands in other lakes (Table 2). Also, visibly higher water hardness and related calcium and magnesium concentrations distinguished Lake Lednica from lakes Złoty Potok and Niesłysz. Total and mineral forms of nitrogen constituted another group of water properties with values remarkably higher in Lake Lednica than in other lakes under study. Lakes Złoty Potok and Niesłysz were rather similar in terms of water chemistry but the latter one was characterised by a lower alkalinity, hardness and mineralisation of water as well as the total phosphorus and nitrogen concentrations (Table 2).

In contrast to water characteristics, the lowest PVI values of the stands studied were evidenced in Lake Lednica, whilst the highest values were recorded in Lake Niesłysz (Table 2). Nevertheless, the differences between the lakes studied turned out to be rather minor and site-to-site differences in PVI values were more pronounced in lakes Złoty Potok and Niesłysz than in Lake Lednica. (Table 2).

Water temperature, pH, TP concentration and PVI did not differentiate amongst the studied sites and lakes (Kruskall–Wallis H-test, $P > 0.05$). All other properties except Mg^{2+} and NH_4^+ concentrations significantly (H and post hoc tests, $P < 0.05$) differed between Lake Lednica and Lake Niesłysz, whilst the aforementioned concentrations of magnesium and ammonium differed Lake Lednica from Lake Złoty

Table 2 Environmental variables in submerged macrophyte stands dominated by *Najasopsis obtusa* studied in three lakes of western Poland

Variable	Unit	Lake Lednica			Lake Zloty Potok			Lake Nieslysz		
		L1	L2	L3	ZP1	ZP2	ZP3	N1	N2	N3
Site depth	m	2.0	3.5	3.0	2.0	1.8	2.2	2.0	1.9	1.7
Water temp	°C	17.48 ± 6.04	17.62 ± 6.14	17.58 ± 6.14	18.07 ± 4.03	17.76 ± 4.15	17.76 ± 4.13	17.80 ± 3.84	17.68 ± 3.82	18.05 ± 4.12
		9.0–24.5	9.0–24.9	9.1–11.3	11.9–21.7	12.0–21.2	12.1–21.1	11.9–20.9	11.9–20.5	11.8–21.4
Oxygen	mg l ⁻¹	10.66 ± 0.78	10.66 ± 1.15	10.59 ± 0.73	9.25 ± 0.57	8.99 ± 0.85	9.06 ± 0.85	10.16 ± 1.10	10.89 ± 1.02	10.91 ± 1.49
		9.8–11.7	9.1–11.7	9.8–11.3	8.6–9.9	7.9–10.2	7.7–9.9	9.0–11.6	9.4–12.3	8.8–12.4
pH	-	8.48 ± 0.19	8.52 ± 0.24	8.54 ± 0.23	8.39 ± 0.27	8.06 ± 0.56	8.08 ± 0.67	8.58 ± 0.20	8.62 ± 0.22	8.58 ± 0.19
		8.2–8.7	8.2–8.7	8.2–8.8	7.9–8.7	7.1–8.6	6.9–8.7	8.4–8.9	8.3–9.0	8.3–8.9
Electrolytic conductivity	µS cm ⁻¹	771.8 ± 51.7	769.6 ± 51.2	768.4 ± 52.9	321.8 ± 18.7	314.2 ± 23.1	313.0 ± 23.3	285.3 ± 34.2	287.7 ± 29.3	280.7 ± 37.5
		685–823	684–822	681–820	296–346	277–340	279–343	239–333	252–332	222–333
Alkalinity	mval l ⁻¹	2.68 ± 0.19	2.70 ± 0.23	2.70 ± 0.28	2.28 ± 0.19	2.22 ± 0.16	2.28 ± 0.18	1.92 ± 0.15	1.88 ± 0.12	1.90 ± 0.17
		2.4–2.9	2.3–2.9	2.2–2.9	2.0–2.5	2.0–2.4	2.1–2.5	1.7–2.1	1.7–2.0	1.7–2.1
Hardness	°dH	20.68 ± 0.6	20.63 ± 0.75	20.71 ± 0.83	8.93 ± 0.72	8.83 ± 0.70	8.86 ± 0.71	8.13 ± 0.42	8.14 ± 0.49	8.20 ± 0.65
		19.6–21.1	19.3–21.1	19.3–21.3	7.9–9.7	7.9–9.7	7.9–9.8	7.46–8.59	7.44–8.60	7.36–8.81
Water colour	Pt	12.9 ± 0.22	12.9 ± 0.22	13.1 ± 0.65	10.4 ± 1.20	11.0 ± 0.00	10.9 ± 0.55	10.33 ± 0.41	10.42 ± 0.49	10.42 ± 0.92
		12.5–13.0	12.5–13.0	12.5–14.0	8.0–11.0	11.0–11.0	10.0–11.5	10.0–11.0	10.0–11.0	9.0–11.5
TP	mg l ⁻¹	0.13 ± 0.14	0.08 ± 0.11	0.09 ± 0.10	0.10 ± 0.04	0.09 ± 0.05	0.11 ± 0.05	0.05 ± 0.02	0.06 ± 0.02	0.07 ± 0.02
TN	mg l ⁻¹	0.03–0.30	0.02–0.28	0.03–0.27	0.05–0.15	0.05–0.16	0.07–0.18	0.03–0.08	0.03–0.08	0.04–0.09
		13.47 ± 5.91	13.67 ± 5.97	14.49 ± 5.52	1.81 ± 0.17	1.87 ± 0.32	2.05 ± 0.34	1.37 ± 0.24	1.30 ± 0.25	1.43 ± 0.36
PO ₄ ³⁻	mg l ⁻¹	10.11–23.91	10.22–24.22	10.73–24.19	1.57–2.05	1.54–2.27	1.54–2.36	1.12–1.72	1.07–1.72	1.02–1.95
		0.06 ± 0.03	0.06 ± 0.02	0.10 ± 0.07	0.18 ± 0.08	0.17 ± 0.11	0.21 ± 0.13	0.08 ± 0.02	0.09 ± 0.04	0.11 ± 0.05
NH ₄ ⁺	mg l ⁻¹	0.03–0.09	0.03–0.08	0.05–0.23	0.08–0.30	0.08–0.33	0.10–0.41	0.04–0.10	0.04–0.14	0.06–0.20
		0.41 ± 0.10	0.38 ± 0.14	0.39 ± 0.15	0.08 ± 0.03	0.08 ± 0.03	0.06 ± 0.05	0.16 ± 0.04	0.15 ± 0.10	0.14 ± 0.09
NO ₃ ⁻	mg l ⁻¹	0.30–0.53	0.22–0.51	0.17–0.52	0.04–0.11	0.04–0.11	0.02–0.14	0.11–0.23	0.02–0.32	0.01–0.21
		5.62 ± 2.78	5.74 ± 2.71	6.08 ± 2.72	0.17 ± 0.08	0.19 ± 0.14	0.24 ± 0.09	0.04 ± 0.05	0.05 ± 0.06	0.04 ± 0.05
Mg ²⁺	mg l ⁻¹	3.91–10.50	3.99–10.50	3.87–10.70	0.10–0.32	0.10–0.43	0.17–0.40	0.01–0.12	0.01–0.14	0.01–0.12
		22.93 ± 0.28	22.89 ± 0.26	22.98 ± 0.36	4.69 ± 0.08	4.71 ± 0.04	4.71 ± 0.06	5.70 ± 0.14	5.72 ± 0.15	5.74 ± 0.17
Ca ²⁺	mg l ⁻¹	22.5–23.2	22.5–23.1	22.5–23.5	4.5–4.7	4.7–4.8	4.64–4.78	5.42–5.80	5.41–5.82	5.41–5.88
		109.84 ± 4.45	109.62 ± 5.40	109.82 ± 45.90	57.43 ± 3.72	56.78 ± 3.47	57.10 ± 3.39	48.45 ± 3.08	48.20 ± 3.00	48.44 ± 4.07
PVI	%	102.2–113.2	100.2–113.3	99.5–113.4	52.3–61.8	53.2–61.8	53.5–62.3	43.7–51.8	43.6–51.2	43.1–53.2
		8.70 ± 7.14	7.80 ± 7.05	8.50 ± 6.64	16.58 ± 11.14	6.28 ± 4.60	13.18 ± 7.26	12.46 ± 11.27	11.62 ± 8.74	20.40 ± 16.71

Table 2 continued

Variable	Unit	Lake Lednica			Lake Złoty Potok			Lake Niesłysz		
		L1	L2	L3	ZP1	ZP2	ZP3	N1	N2	N3
		1.0–20.0	0.4–15.4	0.5–13.3	3.0–30.0	1.4–11.1	2.3–18.2	0.8–30.0	1.3–21.1	0.5–35.3

Means \pm standard deviations and minimum – maximum ranges are presented

L1-3, ZP1-3 and N1-3 three sites studied in lakes Lednica, Złoty Potok and Niesłysz, respectively; TP total phosphorus, TN total nitrogen, PVI per cent volume of water inhabited by plants

Potok. Out of all macrophytes identified in the stands studied, the cover of *N. obtusa* revealed strong and statistically highly significant positive correlation with PVI ($R = 0.67$, $P < 0.001$) and negative correlations with electrolytic conductivity ($R = -0.72$, $P < 0.001$), water hardness ($R = -0.63$, $P < 0.001$), Ca^{2+} concentration ($R = -0.63$, $P < 0.001$) and TN concentration ($R = -0.62$, $P < 0.001$).

Discussion

Lake-related species diversity decline in *N. obtusa*-dominated stands

The study reported evidenced lake-to-lake differentiation in the structure of *N. obtusa*-dominated stands. These lake-specific varied proportions of individual species proved to be more significant than those between sites within one lake, contrary to our earlier study of macrophyte stands dominated by another common charophyte species, *Chara tomentosa* (Pełechaty et al., 2015). The structure of *C. tomentosa* stands proved to be site-specific in four lakes of western Poland, three of which were included in this study. In turn, *N. obtusa* tended to develop mass occurrence and create stands of simple structure in lakes with less mineralized and less fertile, but clearer water. This result is in line with the common opinion on the requirements of *N. obtusa* (Urbaniak, 2003; Kabus, 2016) and charophytes in general (Krause, 1981; Schubert et al., 2018), which is also reflected in the definition of the formed by charophytes European Natura 2000 habitat 3140 “Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp.” The share of non-charophyte species decreased from the most mineralised and fertile water of Lake Lednica, through a minor share in less productive water of Lake Złoty Potok, to be negligible in Lake Niesłysz, which is characterised by the lowest solute and total nitrogen concentrations in water amongst the lakes surveyed. In a result, the Shannon–Wiener diversity index significantly decreased with increasing coverage of *N. obtusa* from Lake Lednica to Lake Niesłysz, although an opposed trend can be expected with a decrease in water fertility and an improvement in water quality. Thus, our study documented a kind of trade-off in the structure of *N. obtusa* stands, a drop in general

macrophyte species diversity in favour of the increasing share of charophytes and of *N. obtusa* in particular.

All the *N. obtusa* stands investigated were very compact and characterised by a 100% macrophyte coverage. Hence, the PVI values neither significantly differentiated between the sites and lakes nor showed clear relationship with the stands depth. Nevertheless, the lowest PVI values were recorded in Lake Lednica, whilst the highest were noted in Lake Niesłysz. This could have resulted from the size and growth form of the dominant species, *N. obtusa*, positively and significantly correlated with the PVI values, as its thalli can be up to 200 cm tall (Urbaniak, 2003). This was the case of Lake Niesłysz, where specimens of *N. obtusa* both produced very large thalli and formed very dense carpets. In our opinion this rather than the relationship with water fertility alone may explain the significantly lower share of angiosperms and the lowered species diversity of *N. obtusa* stands in Lake Niesłysz compared to those investigated in Lake Lednica. We postulate that the species composition and quantitative share of *N. obtusa* stands depend on the growth form of *N. obtusa*, which makes the species a superior competitor to large macrophytes in less fertile waters where it develops mass occurrence and forms extensive, compact and often monospecific carpets. Whilst small charophyte species, such as *C. aspera*, *C. filiformis* and *C. contraria*, or the most frequent in our study angiosperm of a slender habitus, *S. pectinata*, can survive in tight *N. obtusa* beds, tall and branchy angiosperms, such as *N. marina*, and robust charophytes, such as *C. tomentosa* or *C. globularis*, find adequate space in less compact stands where nutrient uptake is less restricted. The possibility that large beds of *N. obtusa* might reduce nutrients availability to other aquatic plants was also indicated by Larkin et al. (2018) as a possible mechanisms of the species spread in its invaded range in North America. In our opinion, this also applies to photosynthesis, as light may be more accessible in sparser communities of more fertile lakes than in compact stands of less fertile and more clear bodies of water.

Our study showed a significant negative impact of high *N. obtusa* coverage on the Shannon–Wiener diversity index in the species native range, where the species is common and not subject to any threat. This decline in the diversity of aquatic macrophytes corresponds to the results obtained by Brainard & Schulz (2017) in the invaded range of *N. obtusa*, where

the species richness and biomass of native macrophytes decreased along with an increase in *N. obtusa* abundance. As it emerges from our study and research of other authors (Dąbbska, 1964; Urbaniak & Gąbka, 2014), *N. obtusa* reveals a tendency to create expansive monospecific stands not only in the invaded territory but also within the native range, where a decrease in species diversity in dense communities dominated by *N. obtusa* is in most cases natural. Our results indicate a potential mechanism of the negative relationships between the abundance of *N. obtusa* and the biodiversity of aquatic macrophytes, which however, is not easily associated with an increase in water trophy. On the contrary, as shown in the study in Lake Constance, abundant recovery of *N. obtusa* was observed along with re-oligotrophication of water (Murphy et al., 2018). Our research in Lake Kuźnickie (W Poland), in which *N. obtusa* is one of co-dominants of the lake submerged vegetation (Brzozowski et al., 2018), also revealed that the increasing share of *N. obtusa* in submerged vegetation and the spread of this macroalga in the form of monospecific beds coincided with a decrease in total phosphorus concentration and water quality improvement (Brzozowski et al., 2021).

Co-occurrence of *N. obtusa* with aquatic macrophytes across environmental conditions and the native and invaded geographical range

Taking into account the predictability and unpredictability of threats to local biodiversity resulting from the expansion of *N. obtusa* in the area where it is an invasive alien species, and changes in its distribution within the native range (Alix et al., 2017; Karol & Sleith, 2017; Larkin et al., 2018), it seems important to recognize which species may and most often coexist with the charophyte studied under certain environmental conditions. The ecological plasticity of *N. obtusa* is wide as the species can be found in a variety of environments, from freshwater lakes, through rivers, gravel pits and rice fields to brackish waters (Krause, 1997; Kabus, 2016; Larkin et al., 2018). Such a wide distribution of *N. obtusa* is related to the tolerance of high nutrient levels, hence it can occur in eutrophic and even highly eutrophic waters, and changeable salinity as the species is known from oligohaline waters (Urbaniak, 2003; Bučas et al., 2019) but is able to survive salinity fluctuation up to 17 PSU (Winter et al., 1999). Also, the adaptation to light

conditions (Pokrzywiński et al., 2020) and depth range indicate the eurytopic nature of starry stonewort, reported from 0.5 to > 14 m deep sites in its native range and between 0.5 and 7 m in the invaded range (Larkin et al., 2018). Nevertheless, based on our results combined with the results of previous investigations of 50 *N. obtusa*-dominated stands in 15 lakes of western Poland (Styperek et al. 2014), as well as the environmental data from the above-cited works from the species invaded range, it can be concluded that *N. obtusa*-dominated stands prefer mesotrophic to moderately eutrophic lakes. The present study demonstrate that in addition to the concentration of nutrients, and more specifically total and ammoniacal nitrogen, the mineralisation of water, reflected in the values of electrolytic conductivity and related variables, such as water hardness, alkalinity and the concentrations of calcium and magnesium, was the factor significantly differentiating Lake Lednica from lakes Złoty Potok and Niesłysz. Such a wide range of electrolytic conductivity values falls within the tolerance range of *N. obtusa*, following the above-mentioned adaptation to both freshwater and more mineralized brackish waters (Martin et al., 2003; Urbaniak, 2003). Note-worthy, the values of electrolytic conductivity of lakes Złoty Potok and Niesłysz, in which low species diversity was revealed with mass occurrence of *N. obtusa*, were comparable to those reported from the

invaded territory (Larkin et al., 2018 and references therein).

A comparison of the number of species co-occurring with *N. obtusa* in Europe and North America allows for the following summary based on our own study and the available literature data (Dąmbska, 1964; Schloesser et al., 1986; Bailly & Schaefer, 2010; Styperek et al., 2014; Urbaniak & Gąbka, 2014; Midwood et al., 2016; Alix et al., 2017; Brainard & Schulz, 2017; Boissezon et al., 2017; Larkin et al., 2018). The total number of aquatic plants co-occurring with *N. obtusa* in Europe reaches 27, including 11 charophyte species and 16 non-charophyte macrophytes. For North America these numbers are quite similar and amount to 36, 11 and 25, respectively. In total, 53 identified species can be given for both territories, including 18 charophytes and 35 non-charophyte species. The list of all species is included in the supplementary Table S1. The most common species co-occurring with *N. obtusa* in Europe and North America are presented in Table 3. With a few exceptions, the spectrum of species identified in the study reported is consistent with that in Table 3.

Worldwide distribution versus propagation mode of *N. obtusa*

Nitellopsis obtusa is widely distributed in Europe and Asia. In Europe, the species has been recorded from

Table 3 Species most frequently co-occurring with *Nitellopsis obtusa*, based on literature sources: (Dąmbska, 1964; Schloesser et al., 1986; Bailly & Schaefer, 2010; Urbaniak & Gąbka, 2014; Styperek et al., 2014; Midwood et al., 2016; Alix et al.,

2017; Brainard & Schulz, 2017; Boissezon et al., 2017; Larkin et al., 2018; this study and own unpublished data from western Poland)

Species	Continent
<i>Chara contraria</i> A.Braun ex Kützing	Europe and North America
<i>Nitella flexilis</i> (L.) C. Agardh	Europe and North America
<i>Myriophyllum spicatum</i> L.	Europe and North America
<i>Najas marina</i> L.	Europe and North America
<i>Stuckenia pectinata</i> (L.) Börner	Europe and North America
<i>Utricularia vulgaris</i> (L.)	Europe and North America
<i>Elodea canadensis</i> Michaux	mainly in North America
<i>Chara globularis</i> Thuiller	mainly in Europe
<i>Ceratophyllum demersum</i> L.	mainly in Europe
<i>Vallisneria americana</i> Michx	North America
<i>Chara tomentosa</i> L.	Europe
<i>Fontinalis antipyretica</i> Hedw	Europe

the Baltic Sea and Scandinavia southward to Spain, southern France, Italy, the Balkans and eastward to Russia (Urbaniak, 2003; Kabus, 2016; Vesić, 2016; Romanov et al., 2018). In Asia, *N. obtusa* is known from Turkestan, India, Myanmar, China and Japan (Ling et al., 2000; Urbaniak, 2003; Kato et al., 2005, 2014). Although the species is locally red-listed within its native range, it is common in Western, through Central and Eastern European countries. As revised by Larkin et al. (2018), the species has been reported from new sites in Europe and its conservation status has locally been lowered. In 2003, *N. obtusa* was rediscovered in Japan (Kato et al., 2005), after which new populations were found in five lakes, although the species was considered threatened (Kato et al., 2014). The concern was aroused by the fact that the species expanded its range to North America, where for four decades, it has been colonizing new sites bringing the risk of local biodiversity decline (Geist et al., 1981; Escobar et al., 2016; Midwood et al., 2016; Alix et al. 2017; Karol & Sleith, 2017).

Such a wide and increasing range must raise the question of the role of reproduction in the expansion of *N. obtusa*. Amongst charophytes, two groups of species are distinguished, monoecious species with male and female gametangia on the same individuals, and dioecious species represented by separate male and female individuals. In addition to generative reproduction, both categories commonly reproduce vegetatively by special bulbils or by fragmentation of their morphologically complex thalli. Whilst vegetative reproduction allows charophytes to gain dominance in a colonized environment and to survive unfavourable conditions, e.g. overwintering, in a result of sexual reproduction charophytes create oospore banks which renew populations and communities in the same place even after long time. In addition, oospores can also be transported over long distances, e.g. by birds, contributing to the expansion of charophytes (Schubert et al., 2018 and references therein). Due to Proctor (1980) monoecious species tend to be cosmopolitan, whilst dioecious species are restricted to smaller areas. Noteworthy, the expansion of *N. obtusa* contradicts this hypothesis as the species is a dioecious macroalga. Moreover, *N. obtusa* propagates vegetatively, primarily by means of numerous produced bulbils, rarely producing male gametangia, antheridia, and, even more rarely, female oogonia, and the co-occurrence of fertile male and female

individuals of starry stonewort is rarely observed and related to environmental instability, such as droughts (Boissezon et al., 2017 and references therein). In this regard, questions arise and further study is needed about the actual importance of vegetative propagation in changing climate as well as the contribution of man to the spread and expansion of *N. obtusa*.

Conclusions

The species diversity of *N. obtusa* stands studied in three lakes of the species native range, turned out to be lake-specific and sharply declined with an increase in the species cover. The starry stonewort developed mass occurrence in less mineralised and less fertile waters, leaving no space and limiting light and nutrient availability for large and branchy macrophytes. We postulate that this mechanism makes *N. obtusa* a superior competitor in less fertile waters and seems common to both native and invaded territories, as is the pool of macrophyte species most frequently co-occurring with *N. obtusa*. The obtained results fill in the gaps in knowledge on the influence of *N. obtusa* on native species diversity. Therefore, this study may be used for conservation purposes in *N. obtusa* native range and act as comparative data for the research conducted on the invaded territory.

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