Phytoplankton response to the massive expansion of Elodea nuttallii (Planch.) H.St.John, 1920 in a floodplain lake of the Vistula River (Poland)

Ewa A. Dembowska¹*, Dariusz Kamiński² and Anna Wojciechowska²

¹Chair of Microbiology and Immunobiology, Faculty of Biological Sciences, Kazimierz Wielki University, Powstańców Wielkopolskich 10, 85-090 Bydgoszcz, Poland
²Chair of Geobotany and Landscape Planning, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University, Lwowska 1, 87-100 Toruń, Poland

Author e-mails: dembow@ukw.edu.pl (ED), daro@umk.pl (DK), ankawoj@umk.pl (AW)

*Corresponding author

Abstract

The spread of invasive non-native species, one of the greatest threats to biodiversity and the economy, affects the structure and functions of ecosystems at all levels. At the beginning of the 21st century a rapid expansion of the submerged macrophyte Elodea nuttallii was observed in southern and eastern Europe. However, this plant, native to North America, was already recorded in Europe in the first half of the 20th century. Our study aimed to evaluate changes in phytoplankton communities caused by the presence of this new invader. The research was conducted in a large floodplain lake in the Vistula valley (north-central Poland) and involved regular monitoring of the lake’s ecological status using phytoplankton-based methods. Long-term observations enabled us to track the impact of this invasive plant on phytoplankton and to compare the conditions of the phytoplankton community before and after Elodea nuttallii invasion. In the first stage of the research (2007–09) massive phytoplankton growth (max. biomass over 90 mg/L) and Cyanobacteria blooms (mainly of Aphanizomenon flos-aquae) were noted. Submerged vegetation along the shore was sparse and its development was inhibited by phytoplankton shading. Elodea nuttallii was first reported in this lake in 2009, together with native macrophyte species. The second stage of the research was carried out in the years 2013–15, when E. nuttallii had already colonised the lake, in some parts occupying the entire bottom surface and almost completely outcompeting native species of submerged macrophytes. As a consequence, the abundance and biomass of phytoplankton decreased. The highest biomass recorded in summer 2013–15 was approximately 4 mg/L. Secchi depth increased from 0.5 m in 2007–08 to 1.6 m in 2015. Elodea nuttallii expansion caused a shift from the turbid-water to clear-water state with higher water transparency. Phytoplankton blooms did not develop. The massive growth of E. nuttallii seems to have caused positive changes in the lake ecological status. However, E. nuttallii is considered to be a highly invasive species, threatening native hydrobionts at various levels of organisation.

Key words: invasive species, Cyanobacteria, functional groups of phytoplankton, water bloom, RDA

Introduction

Invasive, non-native plants have negative impacts on the ecosystems into which they are introduced: they threaten biodiversity and cause changes in...
the structure of plant communities, and in extreme cases lead to the extinction of native species (Catford et al. 2012). They owe their success to a number of adaptations, including reproductive characteristics such as the production of a large number of seeds, effective dispersal, easy shoot multiplication (Stiers et al. 2011b), high growth rate (Erhard and Gross 2006), wide tolerance range (Angelstein and Schubert 2008) and allelopathic interactions (van Kleunen et al. 2015; Gao et al. 2017). In recent years the invasion of non-native plant species has intensified due to climate change and globalisation. Once these non-natives are established outside their natural habitat, they can quickly colonise a new area (Pyšek et al. 2009). Invasive species can be more resistant than native species to human impacts and ecosystem degradation. Any disruptions to a given ecosystem and the emergence of new ecological conditions may promote their spread (Lonsdale 1999).

Due to the inability to predict the timing of establishment of new populations of a non-native, it is difficult to assess their environmental impacts, with documented status before and after the invasion. Lake Port Drzewny has been investigated since 2007 (Dembowska et al. 2012). During our long-term phytoplankton research, the presence of *Elodea nuttallii* (Planch.) H.St.John, 1920, a non-native submerged macrophyte, was recorded in the lake. Its appearance was accompanied by rapid quantitative and qualitative changes in the phytoplankton community, and these deviated from previously observed patterns.

*Elodea nuttallii* is considered to be a highly invasive plant species (Anđelković et al. 2016). This plant is rapidly spreading in Central and Eastern Europe (Table 1). This submerged macrophyte was first recorded in Europe in 1914 in the Royal Botanic Gardens in Kew (Cook and Urmia-König 1985). Over the next 80 years it spread to many countries in Central and Western Europe (Josefsson 2011). At the turn of the 21st century, having overcome environmental barriers, the species moved further eastward, to locations partly outside its optimal sub-Atlantic climate (Chorna et al. 2006), and beyond its forecasted range (Steen et al. 2019). In Poland it was first recorded in the Vistula River in 2007 (Kamiński 2010).

*Elodea nuttallii* owes its success to a number of adaptations that facilitate its competition with native species of submerged macrophytes. As a neophyte, it has no natural enemies in Europe. Moreover, it has a wide tolerance range and can survive in different trophic conditions (from eutrophic to meso-oligotrophic) (Zehnsdorf et al. 2015), easily adapting even to the low salinity of some salt marshes and brackish waters (Thouvenot and Thiébaut 2018). In comparison with native species it is more resistant to anthropogenic nutrient inputs that cause eutrophication. Further, temporary nutrient shortage does not slow its growth (Thiébaut 2005). The plant, which tolerates shading and strong sunlight, is also resilient
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Table 1. The range and spread of *E. nuttallii* in Europe.

<table>
<thead>
<tr>
<th>First known occurrence: Year</th>
<th>Country</th>
<th>Literature</th>
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<tbody>
<tr>
<td>1914</td>
<td>England</td>
<td>Cook and Urmi-König 1985</td>
</tr>
<tr>
<td>1939</td>
<td>Belgium</td>
<td>Verloove 2006</td>
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<tr>
<td>1941</td>
<td>the Netherlands</td>
<td>Simpson 1990</td>
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<tr>
<td>1950</td>
<td>France</td>
<td>Greulich and Trémolières 2006</td>
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<tr>
<td>1953</td>
<td>Germany</td>
<td>Casper and Krausch 1980</td>
</tr>
<tr>
<td>1960</td>
<td>Ireland</td>
<td>Simpson 1984</td>
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<tr>
<td>1964</td>
<td>Belarus</td>
<td>Panasenko and Shcherbakov 2018</td>
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<tr>
<td>1970</td>
<td>Austria</td>
<td>Steen et al. 2019</td>
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<tr>
<td>1974</td>
<td>Denmark</td>
<td>Steen et al. 2019</td>
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<tr>
<td>1980s</td>
<td>Switzerland</td>
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<td>1980</td>
<td>Luxembourg</td>
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<tr>
<td>1986</td>
<td>Slovakia</td>
<td>Hrníček et al. 2019</td>
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<td>1988</td>
<td>the Czech Republic</td>
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<td>1991</td>
<td>Sweden</td>
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<td>Hungary</td>
<td>Kiraly et al. 2007b</td>
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<td>1997</td>
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<td>2001</td>
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<td>Prokopuk and Zub 2019</td>
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<td>2007</td>
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<td>2006</td>
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<td>Kocic et al. 2014</td>
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<td>2002</td>
<td>Bulgaria</td>
<td>Georgiev et al. 2019</td>
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<tr>
<td>2006</td>
<td>Norway</td>
<td>Steen et al. 2019</td>
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<td>2007</td>
<td>Poland</td>
<td>Kamiński 2010</td>
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<td>2017</td>
<td>Albania</td>
<td>Mesterházy 2017</td>
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<tr>
<td>2017</td>
<td>Russia</td>
<td>Panasenko and Shcherbakov 2018</td>
</tr>
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to temporary desiccation (Barrat-Segretain and Cellot 2007). In spring, it starts to grow earlier (at 4 °C) than native plant species and produces strongly branched shoots that shade the lake bottom (Zehnsdorf et al. 2015), thus limiting the development of native species (Stiers et al. 2011a). It is classified as a fast growing, rapidly spread macrophyte (Hilt et al. 2006) that reproduces vegetatively by the fragmentation of stems (Barrat-Segretain et al. 2002; Barrat-Segretain and Elger 2004; James et al. 2006). *Elodea nuttallii* contains chemical compounds that limit its consumption by herbivores (Erhard et al. 2007), protect the plant against epiphytic algae (Erhard and Gross 2006; Hilt 2008; Hilt and Gross 2008) and inhibit the growth of planktonic algae, including Cyanobacteria (Vanderstukken et al. 2014), responsible for blooms, e.g., *Microcystis areuginosa* (Wu et al. 2009). Of the allelochemical substances, *E. nuttallii* produces numerous organic compounds such as polyphenols, organic (e.g., fatty) acids, alkaloids, terpenoids and ketones (Gao et al. 2017). Considering its negative impact on the natural environment and economy, *E. nuttallii* has been identified as an invasive species posing a threat to the EU environment (EU 2017).

The main objective of this study was to examine phytoplankton in Lake Port Drzewny during Cyanobacteria blooms (pre-invasion period) and to assess the influence of *E. nuttallii* on the phytoplankton structure (invasion period). We observed Cyanobacteria bloom termination and higher water transparency followed by the shift from turbid- to clear-water state.
Specific objectives included the following: 1) qualitative analysis of the phytoplankton community (phytoplankton species composition) and quantitative analysis of the phytoplankton (abundance and biomass); 2) evaluation of changes in phytoplankton functional groups and biodiversity; 3) assessment of the impact of *E. nuttallii* on water quality parameters (e.g. water transparency, oxygenation, chlorophyll *a* content). We hypothesised that in the turbid state (prior to *E. nuttallii* invasion), phytoplankton would be characterised by higher biological diversity, and that *E. nuttallii* invasion would cause dramatic changes in the phytoplankton community, including in the structure and biomass of Cyanobacteria.

**Materials and methods**

*Description of the study area*

The study was conducted in a floodplain lake located in the lower Vistula River valley (Poland). With a length of 1,068 km, the Vistula River is the longest river in Poland, and has a catchment area of 194,000 km². It has all the characteristics of a lowland river over most of its course. The flow rate in the study period ranged from 232 to 6190 m³/s and a slope is approx. 0.18‰.

Lake Port Drzewny (53°01′N; 18°30′E) lies on the right-hand Vistula River bank in Toruń and is connected to the river via a channel at 744.5 km. Formed in the 17th century, at the beginning of the 20th century it was used for timber floating. The construction of the port, which began in 1906, involved deepening the lake in the west and east. The lake served as a Vistula river port even without a shore reinforcement system or freight facilities. In 1934, based on Decision No. 18/34 of January 10, 1934 issued by the Pomeranian Voivode, this water body was declared a protected spawning ground for the Vistula population of pike-perch (*Sander lucioperca* Linnaeus, 1758). The port basin has a length of 1,800 m and a width of 350–390 m. The entry channel is 1,500 m long and 60–70 m wide. The lake surface at the average water level is 59.4 ha in the port basin and 11.4 ha in the entry channel (the total of 70.8 ha). The average depth is 2 m. In the eastern part there are two pits with a depth of approx. 11 m, formed by gravel mining.

*Phytoplankton sampling and analysis*

Phytoplankton was collected during the growing season, i.e. from April to October, with the following frequency: bimonthly in the years 2007–09, and monthly in the years 2013–15. The sampling site was located at the north-eastern edge of the lake (Supplementary material Figure S1). Samples for the analysis of the phytoplankton species composition were collected with a 10-μm-mesh plankton net in vertical and horizontal hauls and preserved with formalin. For quantitative analysis, non-concentrated samples were
Phytoplankton abundance was determined under inverted microscope using Utermöhl’s method (1958). Phytoplankton biomass (TPB) was determined volumetrically by comparing single cells’ or colonies’ shapes to geometric solids (Hillebrand et al. 1999; Sun and Liu 2003; Napiórkowska-Krzebietke and Kobos 2016). It was assumed that 1 mm³ of algae is equal to 1 mg (Holmes et al. 1969; Elser and Carpenter 1988). Biovolume is presented as biomass (wet weight) per litre (B; mg/L).

Submerged macrophytes observations

At the same times, yearly observations of submerged macrophytes were carried out. Species distributions in designated transects between the northern and southern shores of the lake were evaluated during the vegetative optimum (the first half of August) in accordance with the ESMI (Ecological State Macrophyte Index) methods (Ciecierska and Kolada 2014) for assessing water quality in inland water bodies.

Measurement of physical and chemical parameters

The following variables were measured in situ using a portable probe (WTW MultiLine P4): water temperature (WT; °C), pH, dissolved oxygen concentration (DO; mg/L), oxygen saturation (DO; %), electric conductivity (EC; μS/cm) and water transparency (SD; m) using a Secchi disc. Water for chlorophyll a (Chl-a) content analysis was collected with each phytoplankton sampling. Chlorophyll a content was determined using the Nusch (1980) method. For Chl-a content (Chl-a; µg/L), water was filtered through a Whatman GF/C glass-fibre filter and extracted with 90% ethanol. Absorbance was measured using a Jasco UV/VIS V-530 spectrophotometer.

Data analysis

The trophic level of the lake was assessed on the basis of Trophic State Index (TSI) (Carlson 1977; Carlson and Simpson 1996). TSI was calculated based on Secchi disc visibility and chlorophyll a content.

The Shannon Biodiversity Index (H’) was calculated based on the phytoplankton abundance using Past 4.02 software (Hammer et al. 2001).

The dominant species described in this paper, with biomass exceeding 10%, were classified into functional groups (Fgs), which were marked with alphanumeric codes based on Reynolds (2006) and Padisák et al. (2009). The assumption of the functional classification of phytoplankton was to determine the adaptive characteristics of species, not related to phylogenetic similarity. The number of functional groups was determined in all samples.

The results from all years were compared using the Kruskal-Wallis test and Dunn test (a post-hoc test). The analyses were performed using Past 4.02.
The results were then correlated with the measured environmental variables (EC, pH, DO, SD) and RDA (redundancy analysis) was performed as a direct ordination method (ter Braak and Šmilauer 2012). At the same time, a Monte Carlo permutation test and forward selection of variables were performed to determine which of the environmental variables significantly affected the variability of the examined community. These analyses were performed using the Canoco 5.0 package. In an ordination diagram, the vectors represent environmental variables and functional groups of species, and geometric figures represent samples collected in successive years of the research.

**Results**

**Habitat conditions**

In the first stage of the research (2007–09) water transparency was low, ranging from 0.3 m to 2.0 m. (Table S1, Figure 1), with the average value being 0.67 m (N = 32). The lowest water transparency was recorded in summer (Jun–Jul) while the highest, in autumn (Sept–Oct) 2009, i.e. at the end of the growing season. In the second stage of the research (2013–15), water transparency was considerably higher, ranging from 0.4 m to 2.8 m. The average value was almost twice as high and amounted to 1.13 m (N = 23). The lowest water transparency was noted in summer (Jul and Aug) 2013, and the highest in August 2013. The average pH, EC, WT and DO were similar in both study periods.

Carlson TSI calculated from Secchi depth was 67 (50–77) in the pre-invasion period and indicated an advanced eutrophic state (Table S1). The lowest TSI SD values were recorded at the end of October, i.e. at the end of the phytoplankton growing season. The highest values, indicating hypertrophy, were recorded in summer (Jul–Aug) during phytoplankton blooms. During the *E. nuttallii* invasion, the average TSI SD was lower (60), indicating a moderate eutrophic state (Table S1). The highest TSI was recorded in 2013, during the early stages of *E. nuttallii* invasion. In August 2015, marked by very intensive growth of this macrophyte, the TSI SD was...
lowest (45), which is typical of mesotrophic water bodies. The average TSI values calculated from Chl-a content were slightly lower and in both study periods indicated moderate eutrophic conditions. TSI values indicating advanced hypertrophy were recorded in summer of 2008 during intense blooms. The lowest value, indicating mesotrophic conditions, was recorded in October 2014 during *E. nuttallii* invasion.

**Submerged macrophytes cover**

In the years 2007–09, submerged macrophyte vegetation was poorly developed, covering less than 10% of the bottom (Figure 2). In the designated transects, the presence of *Elodea canadiensis* Michx, 1803, *Potamogeton pectinatus* L, 1753, *Potamogeton crispus* L, 1753, *Potamogeton perfoliatus* L, 1753, *Potamogeton natans* L, 1753, *Ceratophyllum demersum* L, 1753, *Myriophyllum spicatum* L, 1753 was confirmed, while *E. nuttallii* was not encountered. However, in the years 2013–15 the expansion of *E. nuttallii* was obvious. The plant occupied 50 to 80% of the lake surface, forming thick clusters on the bottom and dense mats floating below the surface in the central part of Port Drzewny. Native species of submerged macrophytes were reported sporadically.
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Dembowska et al. (2021), Aquatic Invasions 16(4): 601–616, https://doi.org/10.3391/ai.2021.16.4.02

Figure 3. Box plots showing min/max phytoplankton biomass (TPB) and Cyanobacteria biomass (TCB) in Lake Port Drzewny during pre-invasion (dark boxes) and during E. nuttallii invasion (light boxes); whiskers – min/max, box – Q1–Q3, line – median, x – mean value, dots – outliers.

Phytoplankton development

Despite differences between the two research stages, the phytoplankton biomass was always indicative of highly eutrophic water bodies. In the pre-invasion period, the average phytoplankton biomass was approximately 25 mg/L (Figure 3). The analysis confirmed the dominance of functional groups H1, J, Lo and P (Tables S1, S2). In summer, harmful algae blooms were noted, mainly of Nostocales (Fg H1, Cyanobacteria), e.g. Aphanizomenon flos-aquae Ralfs ex Bornet & Flahault, 1886, Dolichospermum planctonicum (Brunnthaler) Wacklin, Hoffmann et Komárek, 2009, D. flos-aquae (Brébisson ex Bornet et Flahault) Wacklin, Hoffmann et Komárek, 2009. Cyanobacteria constituted 25% of the total phytoplankton biomass on average. Biodiversity measured as Shannon index in the pre-invasion period was 1.233, and the evenness index was 0.669 (Table S1).

In the subsequent stage, i.e. during E. nuttallii invasion, the average phytoplankton biomass was four times lower (approx. 6 mg/L). Although Cyanobacteria constituted almost 37% of the total phytoplankton biomass, they did not form blooms. Their average biomass was 2 mg/L (Tables S1, S2, Figure 3), while the highest, approximately 17 mg/L, was recorded in July 2013, at the early stage of E. nuttallii development. With the presence of E. nuttallii, the share of algae from functional groups B, C, H1, X3 and Y increased considerably. Functional group Y, which includes large Cryptomonadales, had a similar average biomass before and during E. nuttallii invasion, i.e. 1.73 mg/L and 1.76 mg/L, respectively. The Shannon index value was lower during E. nuttallii invasion and amounted to 0.888 (although
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Figure 4. Number of functional groups (± SE) in subsequent years. Differences between years are statistically significant ($p < 0.05$, Kruskal-Wallis test, $H = 12.9$, df = 5). Letters above bars represent groups that differ from each other according to the post-hoc test (Dunn’s test). Dark boxes indicate the years before the invasion, the light boxes the period during *E. nuttallii* invasion; whiskers – min/max, box – Q1–Q3, line – median, x – mean value, dots – outliers.

The results were not statistically significant), but evenness index was almost the same (0.646) as in the previous period (Table S1).

Statistical analysis demonstrated that the number of functional groups decreased significantly in the years 2013–15 compared to previous years (Figure 4): while in 2007–09 there were 12.5 functional groups on average, in 2014–15 there were only 9.5. This was associated with the emergence of *E. nuttallii*, which soon outcompeted other species. As a consequence, water transparency (SD) increased. This was the only statistically significant variable in the RDA analysis. Higher water transparency explains 6% of the variability of the examined dataset. The vast majority of functional groups were recorded only in the initial part of the research; with the mass development of *E. nuttallii* the number diminished to four groups, namely B, X2, X3 and $X_{pH}$ (Figure 5).

Discussion

Conducted over nearly ten years, our observations in Port Drzewny were aimed at assessing phytoplankton growth under various environmental conditions. Massive development of the non-native submerged plant *E. nuttallii* was a major influencing factor on phytoplankton composition. Many studies from the turn of the 21st century addressed the issue of two alternative stable equilibria and their impact on shallow eutrophic ecosystems (Scheffer and Jeppesen 1998; Perrow et al. 1999; Asaeda et al. 2002; Kelly et al. 2015). In our research we also observed two alternative regimes: turbid- and clear-water state. In the first stage of the research (2007–09), Port Drzewny had characteristics of a shallow turbid lake with phytoplankton...
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Figure 5. RDA for functional groups identified in the studied dataset and for measured environmental parameters. Only one environmental variable (SD) was significantly important for the variability within the dataset (red vector). It explains 6% of total variability of the dataset. Geometrical figures represent samples from subsequent years (2007, 2008, 2009 – pre-invasion period; 2013, 2014, 2015 during invasion).

...dominance, Cyanobacteria blooms, high chlorophyll *a* content and low water transparency (approx. 0.5 m).

The year 2008 was marked by particularly poor water quality (Dembowska et al. 2012), including a large contribution of the potentially toxic Cyanobacteria *A. flos-aquae* to the high phytoplankton biomass. In 2009, *E. nuttallii* was first reported in the lake, although still as an element of previously identified plant communities (Kamiński 2010). However, submerged vegetation covered only a small part of the bottom near the shores.

In 2010, catastrophic floods swept through Central Europe, causing changes in water quality in many aquatic ecosystems. In the studied floodplain lake (Dembowska 2017), water transparency increased suddenly, while submerged macrophyte communities vanished almost completely. Only single, short shoots of *E. nuttallii* were encountered. Initially, the changes were associated exclusively with mechanical turbulences. Nostocales (mainly *A. flos-aquae*), abundant in 2007–09 but very sensitive to water mixing, nearly disappeared. It is also possible that Cyanobacteria that had accumulated in the upper layer of bottom sediments were washed out by flood waters, and that this limited the blooms considerably.

During the second stage of the research (2013–15), symptoms indicating a change to the so-called clear-water alternative stable equilibrium with...
elodeid dominance were observed. For example, a fourfold decrease in phytoplankton biomass was observed, and the chlorophyll a content decreased threefold, with an associated significant increase in water transparency. We assume that the conditions for clear-water state were created by the 2010 flood. The flood distributed existing propagules and also provided new vegetative dispersal units of macrophytes (Cellot et al. 1998). This may have resulted both in invasions of non-native macrophyte species and to subsequent periodic changes in the structure and function of phytoplankton (Mihaljević et al. 2009, 2010). Due to climate change, the frequency of extreme floods is increasing. Therefore, higher dynamics between the dominance of macrophytes (including invasive species such as *E. nuttallii*) and the dominance of phytoplankton can be expected.

In 2013, a large share of Cyanobacteria in the phytoplankton was still reported, but in subsequent years both the total phytoplankton biomass and Cyanobacteria biomass decreased dramatically. In the last year of the research, Cyanobacteria were virtually absent from the phytoplankton. At the same time, *E. nuttallii* dominated in the lake, covering the bottom and forming dense clusters in many places. Due to the bottom flatness and shallowness of the lake, the plant easily reached the surface, filling the entire open-water zone.

The number of dominant phytoplankton functional groups during the invasion period decreased. Cryptophytes, classified as Fg Y, turned out to be the most resistant to *E. nuttallii* dominance. The success of *Cryptomonas* sp. div. is based on their ability to use different sources of energy and carbon (mixotrophy) and their ability to move, which facilitates their adaptation to dynamically changing conditions in floodplain lakes. Small flagellates are probably the most representative group of the phytoplankton of floodplain lakes (Görgényi et al. 2019) and the dominant Fg in the invaded ponds (Stiers and Triest 2017).

The decrease in the abundance, biomass, biodiversity and number of functional groups of phytoplankton caused by the massive growth of elodeids has been extensively studied and is well documented in the literature. In our study, the emergence and development of *E. nuttallii* were quite rapid and led to a complete transformation of the phytoplankton structure. The most important effect was inhibited growth of Cyanobacteria, which, prior to *E. nuttallii* invasion, caused harmful blooms (mainly *A. flos-aquae*). Due to their ability to produce cyanotoxins, these Cyanobacteria are undesirable components of phytoplankton communities.

Dense stands of macrophytes can affect phytoplankton abundance directly and indirectly. The direct effects of *E. nuttallii* on phytoplankton include competition and allelopathy (described in the Introduction), which is a well-known area of active research in ecology (e.g. Gao et al. 2017). The competition for nutrients between submerged macrophytes and phytoplankton
is also well documented (e.g. van Donk et al. 1993; van Donk and van de Bund 2002; Erhard and Gross 2006; Celewicz-Goldyn 2010; Hilt and Lombardo 2010; Haroon and Abdel-Aal 2016; Dembowska et al. 2018).

In addition, there is a wide range of indirect effects of *E. nuttallii* on the environment. Densely growing elodeids provide a perfect habitat for many organisms, and for zooplankton in particular (Perrow et al. 1999; Semenchenco 2008; Kuczyńska-Kippen and Joniak 2016). During *E. nuttallii* invasion, the phytoplankton biomass decreased significantly and community structure changed as well. Small flagellates (Fgs Y, X2, X3) and diatoms (Fgs B, C) had a greater relative share in the phytoplankton biomass. These algae represent R strategists and are good food for zooplankton. Small algae replaced large Dinoflagellata (Fg Lo), colonial Cyanobacteria (Fg H1), and planktonic diatoms and Chlorophyta (Fgs P, J) with branched shapes that prevented them from being consumed by zooplankton.

In conclusion, *E. nuttallii* invasion had a significant effect on the entire biotic community of the lake, in particular on the phytoplankton and native submerged macrophytes. Long-term research on phytoplankton species composition (with a well-documented state before and after the invasion) supports the conclusion that the observed quantitative and qualitative changes in algae species composition are directly related to the invasion of *E. nuttallii*.

Clear-water state is highly desired in eutrophic ecosystems, but the simplification of the community structure caused by the dominance of one macrophyte species has many disadvantages and reduces ecosystem resilience to disturbances. The invasion of *E. nuttallii* also resulted in unfavourable changes in the structure and function of phytoplankton communities. Therefore, the positive effects, such as increased water transparency and the termination of Cyanobacteria blooms, are deceptive.

There are several controversies regarding the assessment of the environmental impact of *E. nuttallii* and durability of the changes. However, it is important to remember that *E. nuttallii* is a non-native plant that grows quickly and outcompetes native species, which might lead to the impoverishment of diversity, simplification of communities, and a threat to the stability of the ecosystem.

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Authors contribution

ED: research conceptualisation; sample design and methodology; investigation and data collection; data interpretation; funding provision; and writing – original draft and editing; DK: research conceptualisation; sample design and methodology; investigation and data collection; data interpretation; writing – original draft and editing; AW: data analysis.

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References
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**Supplementary material**

The following supplementary material is available for this article:

**Table S1.** Main morphological, biological and physico-chemical characteristics of the studied floodplain lake.

**Table S2.** Percentage share of functional groups in total phytoplankton biomass in 2007–09 and 2013–15.

**Figure S1.** Location of the investigated floodplain lake in Vistula River valley.

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