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Impact of lake-catchment processes on phytoplankton community structure in temperate shallow lakes

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Abstract

Research on lake-catchment and biological processes is still innovative. Few reports on this topic exist in the scientific literature. This paper presents species richness, diversity, biomass composition of phytoplankton, and occurrence of cyanobacterial blooms in relation to complex lake-catchment processes in four shallow lakes. The results revealed that phytoplankton species richness increased with increasing lake trophic state, whereas the opposite relationship was observed for phytoplankton biodiversity. In less eutrophic and deeper lakes, the majority of dominant taxa were representatives of mixed, meso to eutrophic small- and medium-sized lakes. In highly eutrophic lakes, the dominant taxa were common representatives of shallow, very rich in nutrients, turbid, mix layers, and eu-hypertrophic environments. Redundancy analysis showed that lake depth, flushing time, and conductivity were the most significant factors for phytoplankton development and composition. The hypertrophic, polymictic, and flow-through Lake Syczyńskie was the most dynamic ecosystem among the lakes. Water mixing and high concentrations of P-PO₄ were beneficial for heavy blooms of the cyanobacterium *Planktothrix agardhii* observed in Lake Syczyńskie despite the high rate of water exchange. Contrary to the findings of some previous studies, *P. agardhii* seems to be resistant to flushing at very high loads and concentrations of nutrients (mostly of P-PO₄ and N-NO₃). Phytoplankton assemblages reflected the lakes' habitats, trophic status, and lake-catchment processes and revealed complex factors that influenced the lakes' functioning. The use of phytoplankton as an indicator of lake-catchment processes may help understand ecosystem dynamics, essential for the proper selection of management practices protecting aquatic systems against eutrophication.

KEYWORDS

cyanobacteria, diversity, eutrophication, flushing time, phytoplankton biomass, phytoplankton functional groups, *Planktothrix agardhii*

1 | INTRODUCTION

Lake-catchment areas are complex systems that include terrestrial and limnetic parts. The rate and intensity of in-lake processes are a derivative of local conditions of the lake catchment. Dissolved organic matter is transported within the catchment, and it may be accumulated in a lake basin, favouring or limiting the development of aquatic life

(Wantzen, Junk, & Rothhaupt, 2008). The quality of lake water results from many local factors, such as land use, soil type, surface geology, drainage area, topography, hydrology, and climate (Darcy & Carignan, 1997; Maberly et al., 2003; Nöges, 2009). Along with the water resources of the catchment and the fluvial dynamic, the rate and quantity of water exchange determine both physicochemical and biological in-lake processes (Lee, Hwang, Lee, Hwang, & Sung, 2009; Liu, Zhang,

& Liu, 2011). The quality of lake water is determined by nutrient loads from the watersheds (run-off and underground input). Surface inlets carry loads of domestic sewage and particles from agriculture and greatly influence the quality of water as well as the eutrophication process (Ravindra, Ameena, Monika, & Kaushik, 2003). However, most studies still treat lakes as isolated basins instead of studying them as complex ecosystems influenced by their catchments and surroundings. External factors such as allochthonous nutrient input, water inflow, and anthropogenic impacts as factors affecting the dynamics of organisms living within an ecosystem are often overlooked. At the same time, the hydrology of a lake is important for the stability of its ecosystem (Sujaul, Ismail, Muhammad Barzani, Sahibin, & Mohd Ekhwan, 2013).

Phytoplankton is a very important biotic element of aquatic ecosystems and plays a key role in the functioning of especially shallow, eutrophic waterbodies, in which planktonic algae and cyanobacteria are the main oxygen producers and component of food chains (Reynolds, 2006). In ecosystems receiving high nutrient and/or organic matter loads from catchments, water blooms of phytoplankton—especially of toxigenic cyanobacteria—are common negative phenomenon escalated by climate warming (Pearl et al., 2016). Cyanobacterial proliferation causes progressive degradation of surface freshwater quality, for example, by lowering water transparency, toxin production, and causing oxygen depletion during the bloom collapse phase (Chorus, 2012; Ferencz, Toporowska, Dawidek, & Sobolewski, 2017; Pearl & Huisman, 2008). Cyanobacterial blooms are of growing global concern (Kobos et al., 2013; Scholz, Esterhuizen-Londt, & Pflugmacher, 2017) because cyanotoxins pose a risk to aquatic ecosystems and their users (Chorus, 2012; World Health Organization, 2008). Hepatotoxic microcystin-LR was classified as contamination of freshwaters (World Health Organization, 2008). Cyanobacteria predominate at higher water temperature and high nutrient concentration (Pearl et al., 2016; Reynolds, 2006). In general, certain species and taxonomical groups of phytoplankton are more favoured than others under specific conditions; therefore, qualitative (taxonomic) and quantitative (abundance and biomass) compositions of phytoplankton communities vary across space and time (Reynolds, 2006). For example, in the temperate zone, diatoms (Bacillariophyceae) predominate at lower temperature in spring and autumn and during the water mixing, Chrysophyta in early summer, and Chlorococcales, Zygnematophyceae, and cyanobacteria in late summer. The taxonomical classification of phytoplankton species does not, however, adequately reflect their ecological function in freshwaters. Therefore, the classification of phytoplankton into functional groups was proposed (Padiśák, Borics, Grigorszky, & Soróczki-Pintér, 2006; Reynolds, Huszar, Kruk, Naselli-Flores, & Melo, 2002). This approach clusters species with similar traits, habitats, and common environmental sensitivities and tolerances and is an informative and increasingly used method in ecological studies of freshwater ecosystems.

Over the last few decades, some studies have shown that water level fluctuations (WLFs), water flushing time (T_f), and flow rate may explicitly or implicitly influence the abundance and composition of phytoplankton (Bailey-Watts, Kirika, May, & Jones, 1990; Leira & Cantonati, 2008, and references therein), including the cyanobacteria

community (Carvalho et al., 2011; Padiśák, Köhler, & Hoeg, 1999; Pawlik-Skowronska & Toporowska, 2016; Romo, Soria, Fernández, Ouahid, & Barón-Solá, 2013). A few reports (Leira & Cantonati, 2008, and references therein) have revealed that WLFs affect phytoplankton abundance, biomass, size structure, taxonomic composition, species diversity, and rate of community compositional change. However, the studies were primarily focused on floodplain lakes. An 18-year study focused on the shallow Loch Leven (Bailey-Watts et al., 1990) showed that variation in flushing rate had a considerable effect on temperature regimes and the supplies and in-lake dynamics of nutrients. Through such changes, flushing rate may control major features of phytoplankton succession such as the temporal predominance of diatoms, as well as detailed sequences of events related to the development and collapse of particular phytoplankton species and, as a consequence, in some cases, of the zooplankton preying on them. A fast rate of lake flushing may be associated with the fast removal of large amounts of nutrients from the lake (Piotrowicz, Kraska, Klimaszuk, Szyper, & Joniak, 2006), which can lower the phytoplankton biomass and determine its dynamics. However, the decrease in biomass of some cyanobacteria (e.g., those belonging to *Aphanizomenon*) may result from cyanobacterial intolerance to sudden environmental changes rather than the dilution effect (Padiśák et al., 1999). Statistically elaborated data from 134 lakes (Carvalho et al., 2011) showed that water retention time is one of the most important factors influencing cyanobacterial mass development.

Because planktonic algae and cyanobacteria may quickly respond to changing environmental factors (Brettum & Andersen, 2005; Laplace-Treytore & Feret, 2016; Napiórkowska-Krzewietke, Stawecki, Pyka, Zdanowski, & Zebek, 2016; Padiśák et al., 2006; Reynolds et al., 2002), phytoplankton is an important element of the ecological monitoring of aquatic ecosystems and is included in the EU Water Framework Directive (WFD 2000/60/EC; EC Parliament Council, 2000). The similarity in composition of phytoplankton assemblages in similar lakes and at similar times is easier to explain than the differences in assemblage structure in lakes of different types, hydromorphology, or catchments (Reynolds, 2006). Thus, an innovative approach using phytoplankton as an indicator of complex lake-catchment processes is required. Until now, it has been used only fragmentarily in a few studies (Ferencz, Dawidek, & Toporowska, 2014; Paul et al., 2012). For example, Paul et al. (2012) showed direct links between some phytoplankton groups and land use shaping trophic state in Rotorua lakes (New Zealand). According to Ferencz et al. (2014), the quantitative and qualitative structures of phytoplankton in three shallow Polish lakes were shaped by base flow, catchment land use, ionic load, and the hydrochemical influence of the streams.

Modern limnological studies and current ecological problems arising out of water eutrophication and global warming require both hydromorphological and biological analyses with the use of informative ecological tools. Therefore, we hypothesized that a lake's phytoplankton assemblages reflect very well the complex lake-catchment processes in the shallow lakes studied, and phytoplankton may be a key indicator of lake functioning. The aims of our study were to (a) determine the hydromorphological factors shaping the phytoplankton assemblages and development of cyanobacterial blooms, (b) analyse species richness, diversity, and biomass composition of phytoplankton

in four different lakes, and (c) analyse how complex lake-catchment processes shaped the phytoplankton assemblages in the lakes studied.

2 | METHODS

2.1 | Study area

The study was conducted in four lakes: Chuteckie, Tarnowskie, Pniówno, and Syczyńskie located in eastern Poland (Europe), between 51°17'12"–51°24'58"N and 23°14'16"–23°21'55"E (Figure 1). The lakes belong to the group of so-called łączna–Włodawa Lakes. All the lakes studied are small (between 2.8 and 8.2 ha), shallow (between 1.2 and 4.3 m average depth), and have extensive catchment areas, which taken together with their small basins, higher the eutrophication risk (Table 1). Both the Ohle and Schindler indices showing the eutrophication risk (Ohle, 1953; Schindler, 1974) amounted to higher values for dimictic Lakes Chuteckie and Tarnowskie, being at a better trophic status (slight eutrophy) than for polymictic, highly eutrophic Lakes Pniówno and Syczyńskie. The land use in catchments varies from one to another. Lakes Syczyńskie and Tarnowskie have typical agriculture-dominated catchments with over 70% of the area covered by arable lands. The catchments of Lakes Chuteckie and Pniówno are more diverse, comprising 35% wetlands and 20% forests, respectively. All the lakes, except Lake Pniówno, are flow-through water bodies.

2.2 | Territorial research

The water levels of both lakes and their streams (inflows and outflows) were observed daily. The flow rates were measured bimonthly using the OTT Nautilus 2000 flow meter. The number of cross sections was determined according to the European ISO EN Rule 748 (1997). Daily flow rate values were calculated by using a rating curve.

Calculations of the basin volumes and bathymetric maps were prepared using geographic information system software ArcView 3.2

(Razavi, 2001), via the inverse distance weighted method. Bathymetric lake and catchment data were calculated using Golden Software Didger 3.0 (Didger User's Guide, 2013) and Surfer 8.0 (Surfer User's Guide, 2002). The volume of the water storage of the lakes was obtained by calculating the difference between the degree of basin repletion, at the beginning and at the end of the study period, as converted into water volume:

$$S = V_e - V_b, \quad (1)$$

where S is the storage, V_e the lake volume on the last day of the water year (period from November 1 to October 31), and V_b the lake volume on the first day of the water year (Dawidek & Ferencz, 2014).

The flushing time was calculated using the following equation:

$$T_f = V \times Q^{-1}, \quad (2)$$

where T_f is the flushing time, Q discharge of the outlet, and V the lake volume (Dawidek & Ferencz, 2014).

WLFs were calculated as follows:

$$WLF = \frac{\Delta H}{Z} \quad (3)$$

where ΔH is the amplitude of water levels (m) and Z is the mean depth (m; Kutyla, 2014).

2.3 | Sample collection and physicochemical analyses of water

Water samples for the analysis of chemical parameters were collected once a season (from spring to autumn) from the uppermost (0–0.5 m) layer of water in the pelagic zone of each lake. Water transparency (Secchi disk depth), pH, and conductivity were measured in situ. $N-NH_4$, $N-NO_3$, $P-PO_4$, and total phosphorus (TP) concentrations in the water were analysed by a high-performance liquid chromatography–photodiode array detection system (Shimadzu).

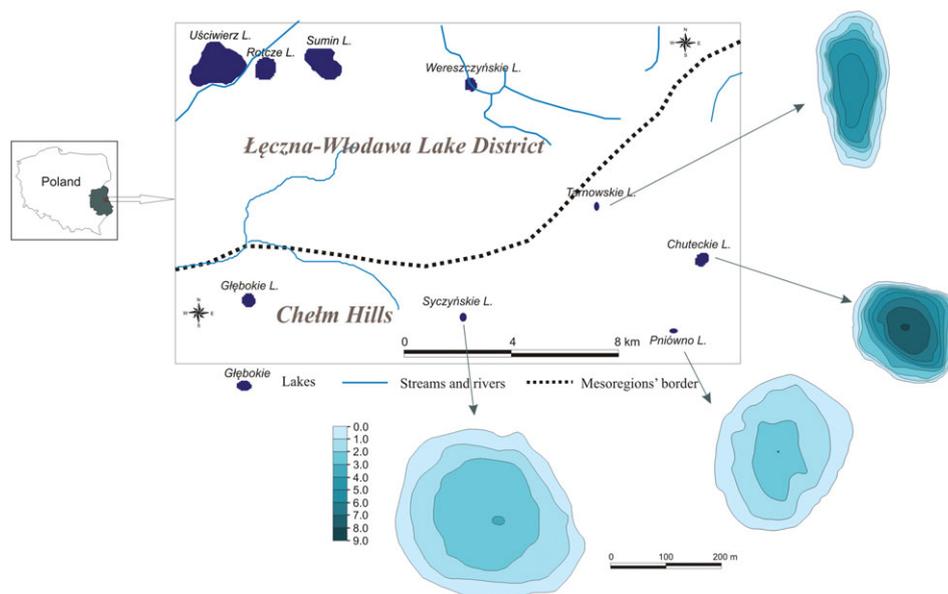


FIGURE 1 Location of the lakes studied and their bathymetry

TABLE 1 Hydromorphological features of the lakes, properties of the lakes' catchments, and their impact on the lakes studied

Parameters	Lake Chuteckie	Lake Tarnowskie	Lake Pniówno	Lake Syczyńskie
Lake area (ha)	2.81	2.78	5.25	8.15
Volume (m ³)	120,030	99,480	63,150	125,610
Average depth (m)	4.27	3.58	1.20	1.54
Catchment area (ha)	552	482	169	266
Land use (%)				
Arable lands	53.9	73.8	49.5	78.7
Meadows	6.5	19.1	12.4	4.1
Orchards	1.3	3.2	6.0	
Forests and shrubs	1.1	1.67	18.1	10.9
Water bodies	0.5	0.6	3.1	3.1
Wetlands	34.3		1.7	
Buildings	1.9	1.7	8.8	2.2
Others	0.4		0.5	1.1
Schindler coefficient (category of degradation susceptibility)	46.0 (II)	48.5 (II)	26.7 (II)	21.8 (II)
Ohle coefficient	196.3	173.4	32.2	32.6
Lake type	Flow-through	Flow-through	Lake with an outlet	Flow-through
Mixing type	Dimictic	Dimictic	Polimictic	Polimictic

Total suspended solids (TSS) and total organic carbon (TOC) were determined using the PASTEL UV spectrophotometer. The molar ratio of dissolved inorganic nitrogen to dissolved inorganic phosphorus was also calculated. Carlson trophic state index (TSI), based on water transparency and TP concentration in water, was calculated in accordance with Carlson (1977). TSI values lower than 40 indicated oligotrophic state of the lake, from 40 to 50 mesotrophic state, from 50 to 70 eutrophic state, and over 70—hypertrophic state (Carlson & Simpson, 1996).

2.4 | Phytoplankton collection and analyses

Quantitative (100 ml of water) and qualitative (concentrated by using 25- μ m phytoplankton net) phytoplankton samples were collected from the surface (0.5 m) layer of water in the central part of the lakes once a season (from spring to autumn). Quantitative samples were preserved with a Lugol's solution and then with a formalin/glycerine mixture (3:1). Phytoplankton identification was performed on fresh material with a light microscope, in accordance with manuals (Cox, 1996; Komárek, 2013; Komárek & Anagnostidis, 1999, 2000, 2005; Komárek & Fott, 1983; Starmach, 1989). Phytoplankton taxa were counted by using light microscopy in a 1-ml Sedgwick–Rafter counting chamber. One colony of coccoid or 100 μ m of filamentous taxa were recognized as individuals. Species with contribution in the total phytoplankton biomass higher than 50% were considered as dominants; those with contribution from 25% to 49% as subdominants; and with contribution from 10 to 24% as accompanying taxa. Phytoplankton of Lake Syczyńskie was analysed based on published data (Toporowska & Pawlik-Skowrońska, 2011, 2014). The phytoplankton composition was categorized in terms of phytoplankton “functional” assemblages (Padisák et al., 2006; Reynolds et al., 2002). The biomass of particular phytoplankton taxa was estimated by measuring cell

volume (Hillebrand, Dürselen, Kirschtel, Pollinger, & Zohary, 1999). The Shannon–Wiener diversity index and the Duffy dominance index for phytoplankton communities were calculated based on the number of taxa and their biomass (Duffy, 1968; Shannon & Weaver, 1949).

2.5 | Statistical analyses

Differences in four hydrological factors (Tf, mean depth Z, volume of water, and water level), 10 physicochemical parameters (transparency, pH, conductivity, concentrations of N-NH₄, N-NO₃, P-PO₄, TP, TSS, TOC, and dissolved inorganic nitrogen/dissolved inorganic phosphorus ratio), and phytoplankton biomass among the lakes were analysed using series of one-way analysis of variance (Statsoft Statistica package for Windows). Ordination techniques were used to describe the relationships among the phytoplankton assemblages and all the environmental variables studied. The indirect multivariate method, detrended correspondence analysis, was used to measure and illustrate gradients of phytoplankton communities. Because the length of the gradient was lower than three standard deviations (SD), we used redundancy analysis (RDA) to explore the relationships among the abundance of particular taxonomic groups of phytoplankton and environmental variables. Before running the analysis, correlation coefficients among the environmental variables were evaluated, and forward selection was used to detect and remove from the analysis any variables that were highly correlated. The final set of hydrological and limnological variables considered were Tf, Z, pH, conductivity, and concentrations of N-NH₄, N-NO₃, P-PO₄, TSS, and TOC. RDA was based on normalized, log-transformed data. A Monte Carlo analysis with 499 permutations was used to determine the most important variables. The ordination analyses were performed in CANOCO 4.5 software for Windows (Ter Braak & Šmilauer, 2002).

3 | RESULTS

3.1 | Hydromorphological features of the lakes and physicochemical parameters of the lakes' water

The lakes studied differed significantly primarily in hydrological parameters such as mean depth ($F = 513.636$, $df = 3$, $P < 0.0156$), water volume ($F = 11.15$, $df = 3$, $P = 0.003$), Tf ($F = 6.856$, $df = 3$, $P = 0.025$), and water levels ($F = 8.601$, $df = 3$, $P = 0.016$). For example, although in all lakes (except Lake Pniówno) the fastest flushing occurred in spring (Table 2), in general, the water exchange was the highest in Lake Syczyńskie and the lowest in Lake Pniówno. WLFs were a few times higher in Lakes Pniówno and Syczyńskie than in Lakes Chuteckie and Tarnowskie. Among physicochemical parameters, water transparency ($F = 49.305$, $df = 3$, $P < 0.000$) and TP ($F = 24.517$, $df = 3$, $P = 0.002$) and P-PO₄ ($F = 5.156$, $df = 3$, $P = 0.028$) concentrations were significantly different.

Despite the high nutrient load in Lake Chuteckie (Table 3), concentration of nutrients in the lake water was several times lower than in Lakes Pniówno and Syczyńskie (Table 4). For example, in the first two lakes, mean annual concentrations of TP in water were equal to 0.029 and 0.047 mg L⁻¹, respectively, whereas in the other two water bodies, they amounted to 0.163 and 0.252 mg L⁻¹, respectively. Generally, the lake's waters were slightly alkaline (7.2–8.2 pH) and abundant in dissolved solids, reflected in high conductivity values (485–607 μS cm⁻¹). Water transparency, one of the main trophic parameters, which differed significantly among the lakes, was the highest in Lake Chuteckie (2.53 m) and the lowest in Lake Syczyńskie (0.59 m). The differences in TP concentrations and water transparency among the lakes were reflected in the trophic state of the lakes indicated by the TSI_{SD + TP} index. The values amounted to 63 in Lake Pniówno and 76 in Lake Syczyńskie and indicated the highly eutrophic

TABLE 2 The rate of flushing time (Tf) and water level fluctuations (WLFs) in the lakes studied (seasonal mean values)

Seasons	Lake Chuteckie	Lake Tarnowskie	Lake Pniówno	Lake Syczyńskie
Tf (days)				
Spring	71	246	10,652	52
Summer	220	440	5,397	151
Autumn	132	272	1,053	155
WLFs				
Spring	5.1	3.0	12.1	12.6
Summer	5.0	3.1	11.6	32.9
Autumn	5.3	3.8	10.6	21.8

TABLE 3 Total nutrient load for the study period (kg per year)

Nutrients	Lake Chuteckie	Lake Tarnowskie	Lake Pniówno	Lake Syczyńskie
N-NH ₄	361.03	22.68	37.34	236.71
N-NO ₃	271.82	14.37	11.40	341.36
P-PO ₄	30.27	3.51	8.33	203.90
TP	139.99	12.54	38.16	212.08

and hypertrophic state of the lakes, respectively (Table 4). The TSI_{SD + TP} values were much lower in Lakes Chuteckie and Tarnowskie (52 and 50, respectively), showing eutrophic and meso-eutrophic state of the lakes, respectively.

3.2 | Characteristics of phytoplankton species richness and biomass composition

Phytoplankton species richness (Figure 2) increased with worsening trophic state of the lakes (Table 4). It was the lowest in Lake Tarnowskie (32–40 taxa) and the highest in Lake Syczyńskie (29–69 taxa; Figure 2), in which, in general, the contribution of Euglenophyceae was higher whereas that of Cryptophyceae was lower in comparison with other lakes (Figure 3).

The phytoplankton structure and biomass (Figure 3) differed among the lakes studied ($F = 5.688$, $df = 3$, $P = 0.022$) and reflected their trophic and ecological status (Tables 1 and 4) very well. The total phytoplankton biomass (Figure 3) was much higher in the highly eutrophic Lakes Pniówno and Syczyńskie (4.25–14.14 and 11.54–37.09 mg L⁻¹, respectively) than in the slightly eutrophic Lakes Tarnowskie and Chuteckie (0.32–0.41 and 0.44–2.04 mg L⁻¹, respectively). In particular seasons, in Lakes Chuteckie and Tarnowskie, the composition of phytoplankton biomass (Figure 3a) was more diverse than in the other two lakes, affected by cyanobacterial blooms. Depending on the season, in Lake Chuteckie, Bacillariophyceae, Dinophyceae, and Euglenophyceae reached over 25% of the total phytoplankton biomass. Chlorophyceae and Cryptophyceae were accompanying taxa. In Lake Tarnowskie, the predominance of diatoms (in all seasons)—accompanied by Dinophyceae, Cryptophyceae, and Chlorophyceae—was noted. In Lake Pniówno, in spring and autumn, cryptophytes reached a high percentage in the total phytoplankton biomass, whereas in Lake Syczyńskie, in autumn, the predominance of small centric diatoms was noted. In Lake Pniówno, in summer (Figure 3b), and in Lake Syczyńskie, in spring and summer, a distinct predominance of cyanobacteria with filamentous *Planktothrix aghardii* (Table 5) was observed. This species was also observed during the study period in Lakes Chuteckie and Tarnowskie but never exceeded 5% of the total phytoplankton abundance, and its biomass reached only up to 0.003 mg L⁻¹ (data not shown).

Species diversity (Figure 4) of phytoplankton (expressed as the Shannon–Wiener index) decreased with increasing TSI values (Table 4), whereas the Duffy dominance index (Figure 4) showed an inverse relationship and was the highest in Lake Syczyńskie, affected by long-lasting cyanobacterial blooms (Figure 3).

3.3 | Relationships among the hydromorphological features of the lakes, physicochemical water parameters, and structure of phytoplankton communities

According to the functional phytoplankton classification (Table 5), the phytoplankton assemblages reflected the observed hydromorphological features of the lakes and hydrological processes very well. In Lakes Chuteckie and Tarnowskie, the majority of dominant and subdominant taxa belonged to the functional groups B/C, D, Y,

TABLE 4 Physicochemical parameters of water of the lakes studied (mean and range of values for vegetation seasons) and their trophic state

Parameters	Lake Chuteckie	Lake Tarnowskie	Lake Pniówno	Lake Syczyńskie
Water transparency (m)	2.53 (2.33–2.68)	1.65 (1.47–1.82)	1.20 (1.05–1.50)	0.59 (0.41–0.76)
pH	7.8 (7.2–8.1)	7.9 (7.8–8.1)	7.7 (7.2–8.1)	7.5 (7.2–8.2)
Conductivity ($\mu\text{S cm}^{-1}$)	552 (529–607)	533 (492–563)	566 (529–607)	528 (485–587)
N-NH ₄ (mg L ⁻¹)	0.121 (0.073–0.213)	0.160 (0.009–0.336)	0.384 (0.022–0.854)	0.360 (0.199–0.468)
N-NO ₃ (mg L ⁻¹)	0.292 (0.011–0.694)	0.039 (0.016–0.083)	0.070 (0.025–0.143)	0.079 (0.059–0.089)
P-PO ₄ (mg L ⁻¹)	0.010 (0.009–0.014)	0.024 (0.011–0.037)	0.106 (0.050–0.214)	0.158 (0.101–0.195)
DIN/DIP ratio	104.7 (13.5–237.8)	17.5 (13.9–21.2)	18.8 (0.5–37.5)	6.2 (5.9–6.3)
PT (mg L ⁻¹)	0.029 (0.017–0.047)	0.068 (0.007–0.112)	0.163 (0.133–0.208)	0.252 (0.217–0.282)
TSS (mg L ⁻¹)	3.23 (2.5–4.7)	8.13 (2.5–15.1)	10.25 (2.5–19.4)	29.13 (6.8–60.7)
TOC (mg L ⁻¹)	11.6 (6.0–17.8)	8.9 (7.7–12.5)	10.5 (5.8–13.3)	6.5 (6.3–6.8)
TSI _{SD} + TP ^a	52 Eutrophic	50 Meso-eutrophic	63 Highly eutrophic	76 Hypertrophic

Note. DIN: dissolved inorganic nitrogen; DIP: dissolved inorganic phosphorus; TOC: total organic carbon; TSI: trophic state index; TSS: total suspended solids; TP: total phosphorus; SD, standard deviation.

^aClassification of lake's trophic state was based on TSI index according to Carlson and Simpson (1996).

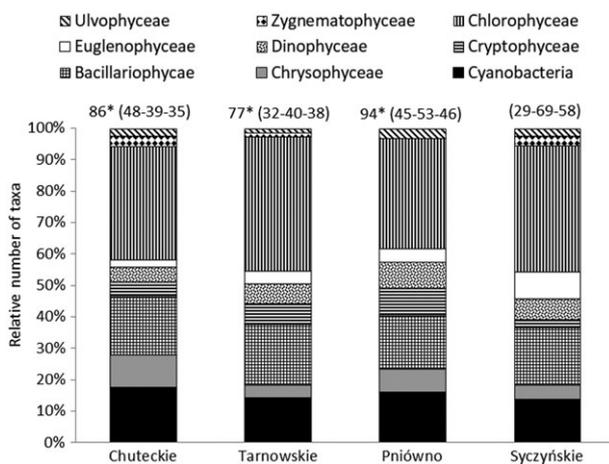


FIGURE 2 Species richness of phytoplankton assemblages in the lakes: *total number of taxa (except Lake Syczyńskie due to lack of data) and range of values in the period studied (in brackets: spring–summer–autumn, respectively). Chart with Lake Syczyńskie on the basis of data from Toporowska and Pawlik-Skowrońska (2011, 2014)

and X2 and was typical for mixed, meso to eutrophic small- and medium-sized lakes. In Lakes Pniówno and Syczyńskie, taxa belonging to groups S1, D, and X1 prevailed, as these are representatives of shallow, very rich in nutrients, turbid, mix layers, and eu-hypertrophic environments. It seems that in more eutrophic and shallower lakes, *P. agardhii* was the most important indicator, showing a tolerance to light deficiency and a preference for high nutrient concentration and water mixing.

RDA (Figure 5a) showed that all the environmental variables accounted for 61.2% of the total variance in the composition of phytoplankton communities. However, the variables that most significantly explained the variance in the communities were mean depth of the lake ($\lambda = 0.20$; $F = 2.43$; $P = 0.032$), flushing time ($\lambda = 0.16$; $F = 2.36$; $P = 0.048$), and conductivity ($\lambda = 0.13$; $F = 2.62$; $P = 0.048$). P-PO₄ concentration also seemed to be important

($\lambda = 0.13$; $F = 1.99$; $P = 0.086$). Lake depth correlated positively with abundance of Zygnematophyceae and negatively with abundance of Chlorophyceae, Euglenophyceae, and Dinophyceae. Longer flushing time correlated positively with Cryptophyceae and negatively with Chrysophyceae. Conductivity and TOC correlated positively with Cryptophyceae, P-PO₄ with cyanobacteria and N-NH₄ with Dinophyceae and Chlorophyceae abundance. RDA biplot (Figure 5b) showed that the spring sample from Lake Pniówno was separated from the rest of the sites primarily because of longer flushing time. The other samples could be divided into three groups. One of them was primarily composed of samples collected from Lake Syczyńskie and was characterized by high P-PO₄ concentrations. The second group was composed of most samples collected from the deeper and less eutrophic Lakes Chuteckie and Tarnowskie and was associated with the mean depth of these lakes. The last group was most heterogeneous and composed of summer and autumn samples from Lake Tarnowskie and autumn sample from Lake Pniówno.

4 | DISCUSSION

Our study revealed that variation in lake-catchment processes shaping hydrochemical and physical parameters in lakes resulted in differentiation of phytoplankton assemblages among the waterbodies studied. We show that phytoplankton is a very good indicator of the processes observed. Among hydromorphological factors influencing phytoplankton composition and lake functioning, the depth of the lake, shaping the mixing type of lake, and flushing time were the most important. Among physicochemical variables, conductivity and concentration of P-PO₄, being a result of ionic loads and balance, as well as of some properties of lakes' catchments, were the most significant. Our work completes some previous field (e.g., Padisák et al., 1999; Reynolds & Lund, 1988; Toporowska & Pawlik-Skowrońska, 2014) and modelling (Carvalho et al., 2011) studies, which were, however, often focused on a single hydrological process. Therefore, our holistic work is still an innovative approach in limnological and hydrobiological research.

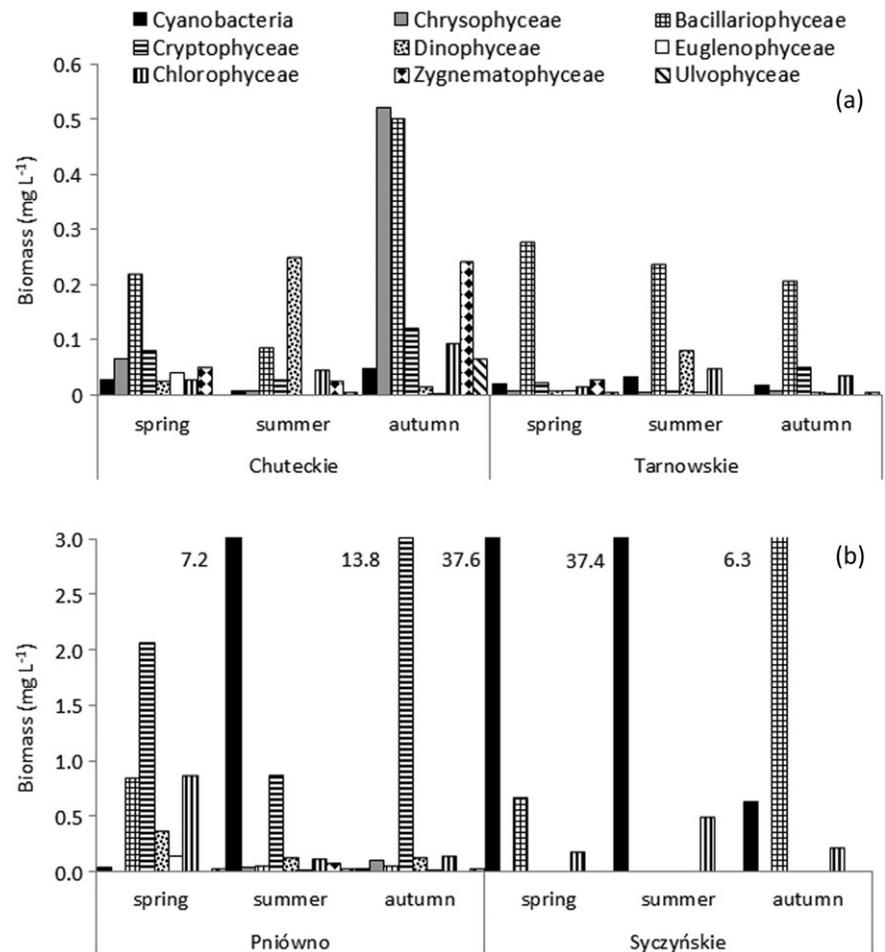


FIGURE 3 Phytoplankton biomass and its structure in Lakes (a) Chuteckie and Tarnowskie and (b) Pniówno and Syczyńskie. Chart with Lake Syczyńskie on the basis of data from Toporowska and Pawlik-Skowrońska (2014)

Diversity patterns of phytoplankton changed between the four lakes studied. Ecological theory predicts that diverse ecosystems are more stable, that is, more resistant to stressors, than less diverse ecosystems (Hooper et al., 2005). Our study showed that phytoplankton biomass was much lower, whereas its composition was more diverse in the less eutrophic, deeper, and dimictic Lakes Chuteckie and Tarnowskie than in the highly eutrophic, shallower, and polymictic Lakes Pniówno and Syczyńskie. Previous studies on phytoplankton and lake trophic state (Brettum & Andersen, 2005; Napiórkowska-Krzebietke & Dunalska, 2015; Paul et al., 2012) showed similar results. The mixed phytoplankton assemblage of Lake Chuteckie, together with the high (over 10% in the total phytoplankton biomass) seasonal contribution of some chrysophytes, was typical for mesotrophic, macrophyte-dominated lakes of good ecological status (Moss et al., 2003). Similar results of low and diverse phytoplankton biomass, but of slightly lower species diversity, were found in Lake Tarnowskie, which was characterized by a lower nutrient load but longer flushing time in comparison with Lake Chuteckie. The general decrease found for chrysophytes along the trophic gradient in the lakes studied is a well-known ecological feature of this class of species prevailing in oligotrophic lakes (Lyche, 1990). In general, in Lakes Chuteckie and Tarnowskie, phytoplankton assemblages and their most abundant taxa belonging to certain phytoplankton functional groups (Reynolds, 2006) were indicators of mixed, meso to eutrophic small- and medium-sized lakes. The predominant taxa of Lake Tarnowskie belonged primarily to small chlorophytes and centric diatoms characteristic of moderate

eutrophication (Reynolds, 2006). In the highly eutrophic Lakes Pniówno and Syczyńskie, the dominant taxa, belonging primarily to cryptophytes and cyanobacteria, respectively, were indicators of shallow, very rich in nutrients, turbid, mix layers, and eu-hypertrophic environments (Reynolds et al., 2002). Increasing species richness and decreasing phytoplankton biodiversity observed with increasing lake trophic state are, in general, consistent with studies on phytoplankton ecology (Reynolds, 2006). A 4-year study by Toporowska and Pawlik-Skowrońska (2014), however, showed that in Lake Syczyńskie, phytoplankton species richness decreased in periods of strong cyanobacterial blooms, deteriorating the trophic state of the lake. We found that the high phytoplankton biomass and cyanobacterial blooms driven by the eutrophication of Lakes Pniówno and Syczyńskie resulted from very specific and very complex lake-catchment processes. Ionic retention in both lakes was positive for each measured nutrient (Ferencz et al., 2017), which may suggest that advanced eutrophication was a consequence of high loads of nutrient input. As a result, very high concentrations of nutrients in lake's waters were observed. However, statistically significant differences among nutrient concentrations in all the lakes studied were found only for P-PO₄ and TP. As RDA showed, P-PO₄ was the main chemical factor favouring cyanobacterial development. Run-off and groundwater recharge influence hydrochemistry in the catchment scale (Smart et al., 2001; Soulsby, Tetzlaff, Rodgers, Dunn, & Waldon, 2006). However, this pattern has not been confirmed in the lakes studied, among which the highest groundwater recharge occurred in Lake Syczyńskie,

TABLE 5 Classification of the most abundant phytoplankton taxa to phytoplankton functional groups explaining in-lake processes and habitat type of the lakes studied

Phytoplankton taxa	Functional groups ^a	Habitat ^a	Chut.	Tarn.	Pn.	Sycz.
Cyanobacteria						
<i>Aphanocapsa holsatica</i>	K	Shallow, nutrient rich columns	+ (a)			
<i>Snowella lacustris</i>	Lo	Deep and shallow, oligo- to eutrophic lakes		+ (a)		
<i>Planktothrix agardhii</i>	S1	Very rich in nutrients turbid, mix layers			++++ (sr)	+++ (s) ++++(sr)
Bacillariophyceae						
<i>Aulacoseira</i> sp.	P	Meso-eutrophic epilimnia	++ (a)			
<i>Cyclotella</i> sp.	B	Mesotrophic, vertically mixed, small-medium lakes	+ (a)			
<i>Cylindrotheca closterium</i> <i>Nitzschia</i> cf. <i>subacicularis</i> <i>Nitzschia</i> sp. <i>Stephanodiscus hantzschii</i>	D	Shallow, enriched turbid waters	+ (s) + (s)		+ (s)	
<i>S. minutulus</i>	B/C	Mixed, meso- to eutrophic small- and medium-sized lakes		++++(sr)		++ (s) ++++ (a)
<i>Stephanodiscus</i> spp.			++ (sr)			
<i>Ulnaria ulna</i>	D					++ (a)
Chrysophyceae						
<i>Dinobryon sociale</i>	E	Usually small, shallow, base poor lakes	++ (a)			
<i>Kephyrion planktonicum</i> <i>K. cf. rubri-claustrii</i>	X2	Shallow, meso-eutrophic environments	+ (s) + (a)			
Cryptophyceae						
<i>Chroomonas acuta</i> <i>C. nordstedti</i> <i>Cryptomonas erosa</i> <i>C. cf. rostratiformis</i> <i>Cryptomonas</i> sp.	Y	Usually small, enriched lakes	+++ (s) + (a)	+++ (a)	+++ (s) ++ (a) + (sr) +++ (a)	
Chlorophyceae						
<i>Chlamydomonas</i> cf. <i>gloeophila</i> <i>C. kuteinikowii</i> <i>Chlamydomonas</i> sp.	X2		++ (s)		+++ (a)	
<i>Chlorella</i> spp.	X1	Shallow, mixed, eu-hypertrophic environments	++ (sr) + (a)		+++ (s)	+ (sr)
<i>Crucigenia tetrapedia</i>	J	Shallow, enriched lakes	++ (sr)			
<i>Dictyosphaerium subsolitarium</i> <i>Kirchneriella contorta</i> <i>Tetrachlorella incerta</i>	F	Clear, deeply mixed meso-eutrophic lakes		++ (s) + (a) + (a)		
Small coccoid taxa	X1		+ (s) ++ (a)		+ (sr)	++ (sr)

Note. +++++: dominant taxa (contribution >50% in the total phytoplankton abundance); +++: subdominant taxa (25–49%); ++: accompanying taxa (10–24%); +: 5–9%; s: spring, sr: summer; a: autumn. Tarn.: Tarnowski; Chut.: Chuteckie; Pn.: Pniówno; Sycz.: Syczyńskie. Data for Lake Syczyńskie on the basis of Toporowska and Pawlik-Skowrońska (2014).

^aAccording to Reynolds et al. (2002) and Padišák et al. (2006).

favoured by a high share of carbonate sediments (Ferencz & Dawidek, 2014), whereas the ecological state of the lake was poor (Ferencz et al., 2017). This suggests that the role of catchment area in shaping phytoplankton assemblages, water quality, and lake functioning is more important than catchment geology. Around 80% of the catchment of Lake Syczyńskie has been used as arable land. Our study also confirmed a previous finding (Taranu et al., 2010) that shallow lakes had higher TP concentrations than deeper lakes under equivalent agricultural development.

Our finding that flushing can be decisive in phytoplankton development is in agreement with previous studies (Padišák et al., 1999;

Reynolds & Lund, 1988). However, we show that some additional factors may change the response of phytoplankton to flushing. For example, long flushing time, observed in Lake Pniówno, increases the growth potential of some phytoplankton species belonging to cyanobacteria and cryptophytes (Padišák et al., 1999; Pawlik-Skowronska & Toporowska, 2016). These phytoplankton groups also have the ability to respond quickly to the availability of environmental resources because of potentially high growth rates. On the other hand, we did not observe a positive relationship between short flushing time and water quality in Lake Syczyńskie, affected by a heavy and long-lasting *P. agardhii* bloom due to high nutrient loads and, consequently,

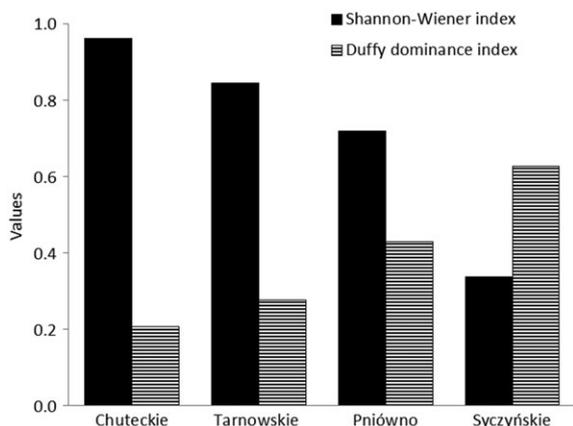


FIGURE 4 Indices of phytoplankton biodiversity in the lakes studied (chart with Lake Syczyńskie on the basis of data from Toporowska & Pawlik-Skowrońska, 2014)

high nutrient concentrations in water. Our results are in opposition to the report of Mantzouki, Visser, Bormans, and Ibelings (2016) classifying *P. agardhii* as a species sensitive to intensive flushing. Pawlik-Skowrońska and Toporowska (2016) showed that intensive and frequent flushing increased cyanobacteria species richness and biodiversity and lowered the biomass of *Microcystis* and *Aphanizomenon* in two hydrologically modified lakes despite their periodical supply with nutrient-rich river waters. In the case of deeper, dimictic Lakes Chuteckie and Tarnowskie, favoured in terms of groundwater input, longer flushing time increased the time of interaction between groundwater and sediments, leading to increment of leaching of carbonates rocks and, hence, improve water quality (Venohr et al., 2005). We also found that lakes with lower water level amplitude (lowest values of index of WLFs) had lower and more diverse phytoplankton biomass than lakes with high water level dynamics. The aforementioned findings indicate that the hydrology of the lake determines the stability of the lake ecosystem (Sujaul et al., 2013) and, consequently, of the phytoplankton assemblage. In areas in which

the dominant land-use type is agricultural, nutrient loading is often so high that large quantities of nitrate leach into groundwater, which discharges into streams as seepage or subsurface run-off (Decamps et al., 2004). A high water quality and stable and diverse phytoplankton assemblage in Lake Chuteckie result from many of the aforementioned factors, as well as the fact that the lake basin is surrounded by peatbog, which is a system with high potential for nutrient retention (Verhoeven, Arheimer, Yin, & Hefting, 2006). Our study confirmed that catchment-wide land use is a better predictor of nutrient levels than other catchment features (Castillo, 2010; Quilbe et al., 2008).

Phytoplankton (particularly cyanobacterial) blooms observed in Lakes Syczyńskie and Pniówno both strongly reflected and influenced lake functioning. The dominant *P. agardhii* is a common cyanobacterium in temperate, eutrophic freshwaters and may form long-lasting water blooms primarily in shallow, well-mixed water bodies (Reynolds et al., 2002; Rohrlack et al., 2008). Under nutrient-rich conditions, this species by its proliferation promotes the conditions for its own growth by creating appropriate light-limiting circumstances. This was confirmed by our studies, which showed very low water transparency (~0.5 m) in Lake Syczyńskie during the strongest *P. agardhii* boom. At low P concentrations, slower flushing, and lower WLFs in Lakes Chuteckie and Tarnowskie, *P. agardhii* reached low biomasses; however, its occurrence was observed during the entire study period. There is a risk that with increasing eutrophication of these lakes, the conditions for *P. agardhii* growth will gradually improve. Until the critical phosphorus value, the mixed phytoplankton assemblage may collapse, and the cyanobacterium may dominate, deteriorating water quality and changing the alternative state of the lakes. Next to the lowering of water quality, production of cyanotoxins and many other biologically active compounds is another negative effect of cyanobacterial blooms (Welker & Döhren, 2006). *P. agardhii* is a common producer of hepatotoxic microcystins and, as was recently shown, many other bioactive oligopeptides (Grabowska, Kobos, Toruńska-Sitarz, & Mazur-Marzec, 2014; Rohrlack et al., 2008). This creates risks for both ecosystems and humans as cyanotoxins are

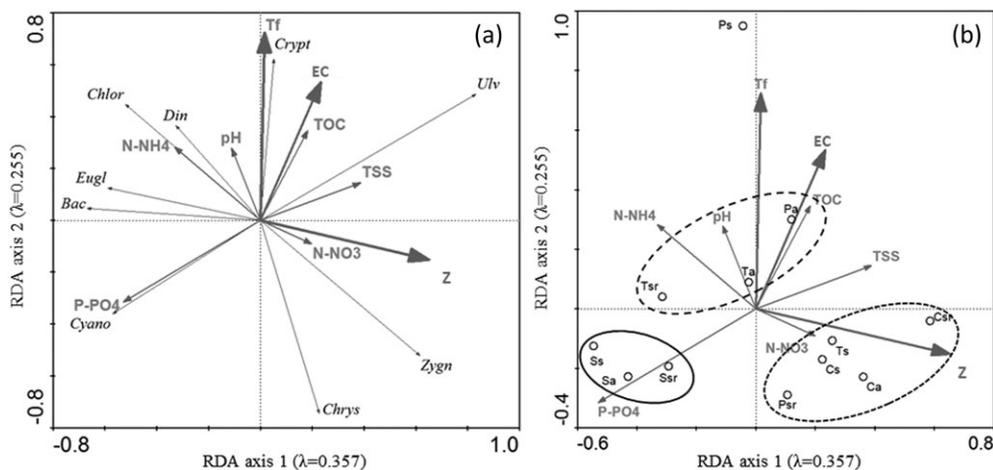


FIGURE 5 Redundancy analysis (RDA) biplots of environmental variables and particular phytoplankton groups (a) and phytoplankton samples collected in particular lakes and seasons (b). Bolded arrows indicate significant variables based on Monte Carlo permutation test ($P < 0.05$). Cyano: Cyanobacteria; Chlor: Chlorophyceae; Bac: Bacillariophyceae; Din: Dinophyceae; Eugl: Euglenophyceae; Crypt: Cryptophyceae; Ulv: Ulvophyceae; pH; EC: electrical conductivity; Tf: flushing time; Z: mean depth; TOC: total suspended solids; TOC: total organic carbon; C: Lake Chuteckie; T: Lake Tarnowskie; P: Lake Pniówno; S: Lake Syczyńskie; s: spring; sr: summer; a: autumn

harmful to lake biocenoses and living organisms and may, for example, accumulate in the trophic chain that includes fish (Pawlik-Skowrońska, Toporowska, & Rechulicz, 2012). Therefore, understanding how complex ecosystem dynamics work is highly important especially in the light of climate warming and water eutrophication.

5 | CONCLUSIONS

Our study shows that phytoplankton assemblage is a good, sensitive, and very important indicator of complex lake-catchment processes shaping the trophic and ecological status of freshwater ecosystems. Lake depth and flushing time, together with conductivity and P-PO₄ concentration being a result of nutrient loads and balance, were the main factors shaping the composition of phytoplankton communities. Among the catchment factors, land use played a far more important role than catchment geology. Lower phytoplankton biomass and higher biodiversity were characteristic of less eutrophic and deeper lakes, whereas high biomass predominated by a few species, including potentially toxigenic cyanobacterium *P. agardhii*, was found in highly eutrophic and shallower lakes. Chrysophytes were favoured by higher depth, longer flushing time, and lower P-PO₄ concentrations, Cyanobacteria primarily by higher P-PO₄ concentrations, Cryptophyceae by longer flushing time, and Chlorophyceae, Dinophyceae, and Euglenophyceae by higher N-NH₄ concentrations and smaller lake depth. The study also showed that the bloom-forming *P. agardhii* reached low biomass at low P concentrations, slow flushing, and low WLFs. But there is a risk that with the increasing eutrophication of lakes, the conditions for *P. agardhii* growth will gradually improve, and until the critical phosphorus value, the mixed phytoplankton community may collapse, and the cyanobacterium may dominate, deteriorating water quality and changing the alternative state of the lakes. With regard to the aforementioned findings, use of phytoplankton as an indicator of lake-catchment processes may help understand ecosystem dynamics, essential for the proper selection of management practices for protecting aquatic systems against eutrophication.

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CONFLICT OF INTEREST

There is no conflict of interest.

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