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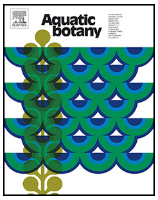

Winter temperature and shifts in phytoplankton assemblages in a small *Chara*-lake

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ABSTRACT

The structure of phytoplankton was analyzed along four successive growing seasons in relation to environmental conditions following contrasting winters in a shallow, mesotrophic *Chara*-lake (Lake Jasne, western Poland). The 2008 and 2009 growing seasons followed mild winters, whilst these of 2010 and 2011, had severe winters. After mild winters, despite higher availability of nutrients in the lake water, phytoplankton was less numerous than after severe winters, as reflected in the total abundance and the abundance and biomass of Chrysophyceae. Moreover, water clarity was higher after mild than after severe winters (5.2 m versus 3.8 m, mean Secchi depths). Contrary to abundance, total phytoplankton biomass showed no differences between the studied periods. However, a greater biomass of Cyanoprokaryota, particularly *Dolichospermum lemmermannii* (Richter) Wacklin, Hoffmann et Komárek and *Aphanothece clathrata* W. et G.S. West., was observed after mild winters, possibly in response to greater nutrient availability. *A. clathrata* also had higher abundance after mild winters. Nutrient budget and solute content as well as color, clarity, and, to a lesser extent, temperature of water were explanatory variables. We postulate that extensive charophyte meadows may be a crucial factor to control the phytoplankton dynamics in *Chara*-lakes. Overwintering charophytes may reduce phytoplankton densities by modifying phytoplankton responses to nutrient concentrations, which are higher due to shorter and warmer winters induced by climate change.

1. Introduction

Shallow lakes may occur in two alternative stable states: with clear or turbid water and poorly or abundantly developed phytoplankton, respectively (e.g., Scheffer et al., 1993; Jeppesen, 1998; Scheffer and van Nes, 2007). One state can shift to the other even between years and, in addition to a number of driving forces related to nutrient concentration, climate change and related winter severity are postulated in recent literature to affect ecosystem relationships resulting in shifts between states (Hargeby et al., 2006; Bayley et al., 2007).

Shallow lakes are more strongly affected by stochastic meteorological events (Köhler and Hoeg, 2000) than deep lakes. Hence, the mechanisms responsible for the functioning of shallow clear water ecosystems are probably sensitive to seasonal weather conditions and long-term climatic changes (Scheffer et al., 2001; Mooij et al., 2005). Massive occurrence of submerged vegetation is a key factor responsible for the stabilization of clear water conditions (Blindow, 1992a; Scheffer, 1999; Scheffer and van Nes, 2007; Bayley et al., 2007). Particular ecological importance in an ecosystem is attributed to charophytes, due to their high colonization capacity (Blindow and Hootsmans, 1991) and their positive impact on water clarity (e.g., Scheffer et al., 1993; Van den Berg et al., 1998; Blindow et al., 2002; Apolinarska et al., 2011; Pełechaty et al., 2015). Any internal or external alterations of environmental conditions (e.g., an increase of nutrient load or high magnitude of weather conditions) or rapid disturbances, which lead to the destruction of submerged vegetation, may trigger an increase of phytoplankton density and a related decrease in water clarity (Blindow, 1992b; Scheffer et al., 1993; Hargeby et al., 2006).

The quality of winters and in particular the duration of ice cover may significantly affect the functioning of lakes, especially clear water shallow lakes (Bayley et al., 2007). As a result of climate warming, seasonal ice cover is observed to decline (Dokulil et al., 2010). Thus, the symptoms of eutrophication are thought to be enhanced, including macrophyte loss and related increased

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Table 1
The weather conditions in four successive winters (December–February) in the studied period 2007–2011.

Winters	Thermal condition in particular winters[b]	Mean air temperature in winters (°C)[a]	Total precipitation in winters (mm)[a]	Maximum length of snow cover period (days)[a]	The maximum snow depth (mm)[a]
2007/2008	Anomalously warm	3.4	268.4	2	10
2008/2009	Thermally normal	0.2	176.2	31	220
2009/2010	Very cold	−2.1	205.9	70	250
2010/2011	Very cold	−1.6	274.2	52	340

[a] Based on the data of the Institute of Meteorology and Water Management (IMGW) in Poznań.
[b] Based on Miętus et al. (2010, 2011),).

development of phytoplankton as an effect of elevated release of phosphorus from sediments (Moss et al., 2009; Dokulil and Teubner, 2011) or greater loads from the catchment area (Rip et al., 2007). Ecosystem state at the end of winter can be treated as the starting point for the initial stages of plankton succession in a new growing season (Sommer et al., 2012). Thus, winter weather and all anomalies resulting from climatic changes may be significant for the development and domination of different autotrophic groups (Gerten and Adrian, 2000; Bayley et al., 2007). The precise outline however is still under debate since some authors predict an increase in phytoplankton (particularly Cyanoprokaryota) biomass as a result of climatic change (Jeppesen et al., 2003; Kosten et al., 2012), whereas others do not see such threats (Hamilton et al., 2002).

In this study, the structure of a phytoplankton assemblage was studied in relation to environmental conditions following contrasting winters in a shallow charophyte-dominated lake. We hypothesized that submerged vegetation, dominated by extensive and overwintering charophyte meadows, changes the response of phytoplankton to higher nutrient availability following warm winters, preventing an increase in phytoplankton abundance and biomass during the growing season.

Our four-year study period does not reflect long-term climate changes but avoids the possible covariance of a range of potentially confounding external and internal factors and adaptive phytoplankton community change.

2. Material and methods

2.1. Study area

The study object, Lake Jasne (15.1 ha), is a shallow (9.5 m maximum and 4.3 m mean depth), charophyte-dominated lake. The lake (52°17′7″N, 15°03′6″E) is located in the southern part of a tunnel-valley, near the town of Torzym, in mid-western Poland (Pojezierze Lubuskie Lake District). Over 90% of the drainage basin is covered by pine and beech forests and the lake is used for recreation to a limited extent. Based on Carlson's (1997) trophic state index Lake Jasne is considered a clear water mesotrophic lake of low phytoplankton biomass (Pełechaty et al., 2015). Submerged vegetation covers almost 70% of the lake bottom and charophyte meadows composed of 10 species of *Characeae* predominate, reaching a maximum depth of 7.9 m (Pełechaty et al., 2010; Pukacz and Pełechaty, 2013). *Chara rudis* A. Br., *C. tomentosa* L. and *Nitellopsis obtusa* (Desvaux) J. Groves are dominants and the thickness of carbonate sediments allows for the conclusion that charophytes are a constant element with no structural changes for longer than the last eight years, i.e., from the beginning of our research in the lake.

2.2. Field survey

The study was performed monthly during the growing seasons 2008–2011 (06–10/2008, 04–10/2009, 04–10/2010, 05–10/2011). Water samples were collected using a 3 L watersampler (Uwitec, Mondsee, Austria) and distributed to 1 L bottles. Samples were preserved with Lugol's solution for phytoplankton and with chloroform for hydrochemical analyzes. Additionally, live phytoplankton was also sampled using a plankton net of 10 μm mesh size. Basic physicochemical analyzes of surface lake water, including water temperature, oxygen concentration, conductivity and pH, were performed by means of portable field measurement equipment: Elmetron CX-401 (Elmetron Sp. j., Zabrze, Poland), CyberScan 200 and CyberScan 20 (Eutech Instruments Europe BV, Nijkerk, The Netherlands), respectively. Additionally, water clarity was measured by Secchi disk. Field measurements and water sampling were performed at the depth of 0.5 m in the macrophyte-free central, deepest part of the lake.

2.3. Laboratory analyzes

Anions (Cl^-, $NO_3{}^-$, $NO_2{}^-$, $SO_4{}^{2-}$, $PO_4{}^{3-}$), cations ($NH_4{}^+$, Ca^{2+}, Mg^{2+}), water color, total hardness and alkalinity, total nitrogen (TN) and total phosphorus (TP) were determined from the 1 L water sample. The analytical procedures and laboratory equipment applied were presented in detail elsewhere (Pełechaty et al., 2010).

Water samples for phytoplankton analyzes were subjected to sedimentation, condensed to a volume of 15 mL and then additionally preserved with formaldehyde. Qualitative (the number of taxa and species composition) and quantitative (abundance and biomass, reported as number of individuals ml^{-1} and $mg\ L^{-1}$) analyzes of phytoplankton were performed using a Zeiss Primo Star microscope with phase contrast (Carl Zeiss, Oberkochen, Germany). Phytoplankton individuals were determined and counted in 100 fields of a Fuchs-Rosenthal counting chamber (height: 0.2 mm, area: 0.0625 mm^2). The counted individuals were cells, colonies or trichomes with a length of 100 μm. To calculate the biomass, the species were approximated with simple geometric or combined forms (Wetzel and Likens, 1991). The measurements necessary to calculate the biomass were carried out separately for each sample by measuring 30 individuals and determining the mean size for each species. Phytoplankton taxonomy followed Van den Hoek et al. (1995). For both abundance and biomass, the Shannon diversity index (H') was calculated (Shannon, 1948).

2.4. Meteorological characteristics of winters preceding the studied growing seasons

The study covered the growing seasons following winters 2007/2008, 2008/2009, 2009/2010 and 2010/2011. Winters 2007/2008 and 2008/2009 were characterized by much higher air temperatures than the next two winters and much shorter maximum length of snow cover period (Table 1). According to the Polish Climate Monitoring Newsletters (Miętus et al., 2010, 2011) the winters were classified as anomalously warm (2007/2008) and thermally normal (2008/2009). The winters of 2009/2010 and 2010/2011, in turn, were classified as very strong. Out of the four winters, the winters 2007/2008 and 2009/2010 were characterized as contrasting relative to each other. Considering the above differences in weather conditions as well as other characteristics presented in Table 1, the four studied growing seasons were