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Factors promoting persistence of the bloom-forming *Gonyostomum semen* in temperate lakes

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ABSTRACT

The nuisance large flagellate *Gonyostomum semen* (Raphidophyceae) is typical for brown-water lakes in temperate and boreal regions. This study is focused on two annual cycles of *G. semen* in shallow temperate lakes (one of which stratifies) with a particular emphasis on the species' ecology and its potential impact on the alternation of phytoplankton assemblages. Temperature and phosphorus were the main forces driving seasonal growth of the raphidophyte. *G. semen* occurred at a broad temperature range and prevailed for the extended period from spring to late autumn at maximum biovolume and forming up to 98.7% of total phytoplankton in June–July and/or September. The species exclusively dominated under phosphate-replete conditions and caused heavy blooms in the stratified lake. The species outcompeted other flagellates in the lakes; considerable fluctuations in phytoplankton species composition occurred during the periods at low *G. semen* biovolume.

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1. Introduction

Ongoing climate change, eutrophication and acidification/brownification of lakes impact on integrity of aquatic ecosystems, alter the composition of phytoplankton communities, lead to biodiversity loss and often promote the establishment of hazardous bloom-forming species in new habitats, resulting in many adverse changes to the ecosystem (Sala et al., 2000; Strecker et al., 2004; Vuorenmaa et al., 2014). When nuisance blooms occur, in nutrient-rich freshwaters they typically consist of cyanobacteria (O'Neil et al., 2012), whereas in brown-coloured lakes the large flagellate *Gonyostomum semen* may cause blooms (Hagman et al., 2015; Rengefors et al., 2012).

The raphidophyte *G. semen* is reported to be a common nuisance species in many temperate and boreal lakes, especially in Scandinavia. During recent decades, it has increased in biovolume and bloom frequency in ecosystems typical for this species and continues to expand into new habitats (Hagman et al., 2015; Hongve et al., 1988; Pęczuła et al., 2013; Rengefors et al., 2012). The successful establishment of *G. semen* has been shown to be favoured by increase of temperature, concentrations of nutrients and dissolved organic carbon (Findlay et al., 2005; Hehmann et al., 2001; Rengefors et al., 2008, 2012; Trigal et al., 2011), and by decrease the grazing pressure (Johansson et al., 2013; Lebret et al., 2012).

The ability of *G. semen* to form a dense population may affect the ecosystem of a lake by disturbing the food-web. Its large cells and the ejection of mucilaginous threads by trichocysts render it inedible to most grazers. It may thus disturb energy transfer to higher trophic levels (Johansson et al., 2013; Lebret et al., 2012; Trigal et al., 2011). *G. semen* is capable of totally dominating the phytoplankton flora by as much as 98% for extended periods (Figueroa and Rengefors, 2006; Havens, 1989). In this way, the raphidophyte alters phytoplankton communities by reducing species richness (Angeler et al., 2010; Cronberg et al., 1988) or by causing shifts in dominant taxa even in the absence of blooms (Hagman et al., 2015). Furthermore, *G. semen* blooms can cause human health problems by inducing an allergic skin reaction, thus reducing the recreational use of lakes (Cronberg et al., 1988), and it can also obstruct filters used for water treatment (Berge, 1991).

Phytoplankton in *Gonyostomum* lakes consists mainly of flagellate algae (chrysophytes, cryptophytes, dinoflagellates) which are adapted to grow in particularly unstable environments (Lepistö and Saura, 1998; Peltomaa et al., 2013; Poniewozik et al., 2011; Trigal et al., 2011). Their capacity for mixotrophic nutrition and vertical migration confer competitive advantages over other algae for major nutritional resources in acidic, usually nutrient-poor humic lakes

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(Arvola et al., 1999; Jones, 1992; Salonen and Rosenberg, 2000). In such ecosystems, light penetration is limited due to high concentrations of humic substances and anoxic hypolimnia often occur (Arvola, 1984; Salonen et al., 1984).

In Lithuania, *G. semen* was detected in a relatively large number of small humic and clear-water lakes (Koreivienė et al., 2012). However, occurrence of the species has frequently been reported only at a late stage, as water blooms became visible, and it then had a noticeable impact on the phytoplankton community, habitat and ecosystem function (Karosienė et al., 2014). The timing and magnitude of occurrence, prediction of *G. semen* succession patterns in the lakes of temperate zone have not been quite understood yet. The aim of this study was to assess the development patterns of *G. semen* over the growth season in two humic temperate lakes in relation to environmental variables.

2. Study area

The study was performed in two shallow lakes with recurring blooms of the raphidophyte *G. semen.* Lake Pabezninkai (54°21′40 N, 24°33′55 E) is a polymictic lake (max depth 3.0 m and area 61.4 ha), having moderate biovolume of *G. semen* of < 10 $mm^3 L^{-1}$. The species occasionally causes blooms at this site. Lake Slabada (55°08′15 N, 25°42′30 E) is a small thermally stratified lake (max depth 5.2 m and area <1 ha) and suffers from annual *G. semen* blooms (>10 $mm^3 L^{-1}$). Thermal and oxygen stratification developed in late May and continued until September, and anoxic conditions occurred in the hypolimnion (2–3 m depth).

Lake Pabezninkai is characterized by slightly acidic water, high water colour and TOC concentration (Table 1). In Lake Slabada, pH was neutral, the conductivity and the concentrations of ammonium, phosphate and total phosphorus (TP) were as much as two-fold greater than in Lake Pabezninkai. The amount of total nitrogen (TN) was similar for both lakes (mean values from 1.49 to 1.64 mg L^{-1}, respectively).

3. Materials and methods

Sampling was performed monthly during the ice-free period from May to November in 2012 and 2013. A Ruttner sampler was used to collect water samples at 1 m vertical intervals in the deepest part of the lakes. Phytoplankton was preserved in Lugol's solution for the counting of *G. semen* and in 4% (v/v) formaldehyde solution (final concentration in the sample) for the remaining species. Algae were identified and enumerated in a Nageotte chamber using a light microscope. At least 600 counting units per sample were estimated (Olenina et al., 2006). Biovolume was calculated based on cell numbers and mean cell volumes of individual species (Olenina et al., 2006; Olrik et al., 1998). Cell volume was calculated from measurements obtained for up to 25 cells per species. The cell size of *G. semen* was determined using live material.

Water temperature, pH and conductivity were measured *in situ* using a MultiLine F/Set-3 portable universal meter. Water transparency was determined using a Secchi disc. Dissolved oxygen was measured using the Winkler method. Water colour was assessed by means of a photometer HI 96727 following the removal of particulate matter involving filtering lake water through a 0.45 μm pore filter. Light intensity was measured using a LI-250A light meter and underwater sensor. Total organic carbon (TOC), TP and TN were determined in accordance with standard methods (LST EN ISO 10304; LST EN ISO 14911; ISO 8245:2003).

Differences in abiotic characteristics of the studied lakes and in the biovolume of phytoplankton communities between studied years were determined using the non-parametric Mann-Whitney *U* test (at $p < 0.05$). The relationships between environmental parameters and phytoplankton data as response variables were evaluated by applying multivariate redundancy analysis (RDA) and the Pearson correlation coefficient (at $p < 0.05$). The data of response and explanatory variables were square-root transformed. Statistical analysis was performed using Statistica 7.0 and BRODGAR 2.7.2 software programmes.

4. Results

4.1. Seasonal changes in Gonyostomum semen and phytoplankton biovolume

In both studied lakes, *G. semen* was found at the beginning of May (when surface water temperature exceeded 12.7 °C) and persisted until November, when surface water temperature fell to 5 °C (Fig. 1). The species displayed a similar seasonal growth pattern in both lakes with no significant differences between years (Mann-Whitney *U* test, $p > 0.05$). However, in Lake Pabezninkai the biovolume of *G. semen* was rather low with maximum values of

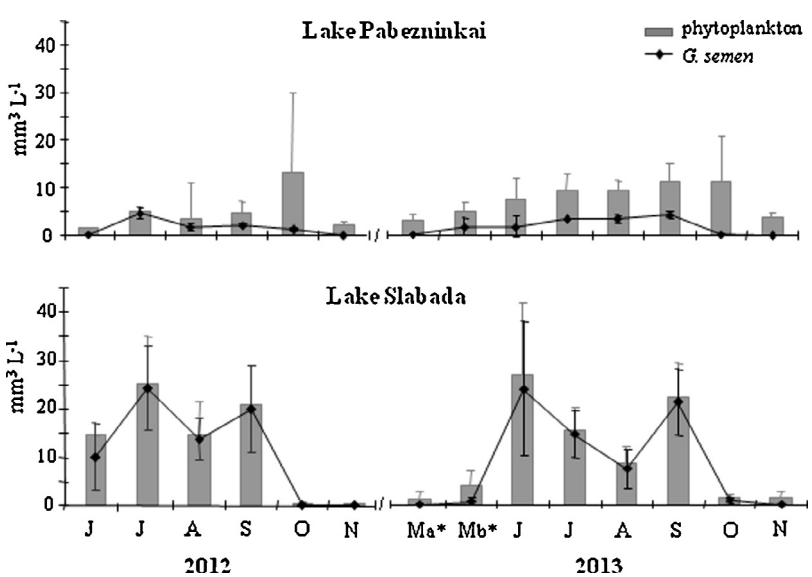

Fig. 1. Seasonal variations in total phytoplankton and *Gonyostomum semen* biovolume in the lakes in 2012–2013. Data represent mean values ± SD in the water column. Abbreviations: Ma*—2nd of May, soon after ice-break; Mb*—16th of May.

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