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Factors affecting occurrence and bloom formation of the nuisance flagellate *Gonyostomum semen* in boreal lakes☆

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ABSTRACT

We examined changes in *G. semen* occurrence and bloom incidence in 146 boreal lakes in Sweden sampled at least once between 1992 and 2010, and used a time-by-space model to assess the environmental variables that best explain patterns in *G. semen* distribution and bloom formation.

We showed that *G. semen* has become more common, although there were no significant shifts in its geographical distribution during the study period. In particular, *G. semen* was spreading into new lakes in the Central Plains ecoregion (southern Sweden), whereas its occurrence and biomass usually remained low in the Borealic Upland and Fennoscandian Shield ecoregions.

G. semen biomass and the incidence of blooms did not increase significantly during the study period, but fluctuated among years and reached a maximum in 2003. The occurrence of *G. semen* was mainly explained by temperature and the length of the growing season, whilst local-scale variables, such as pH and water color, were the best predictors of blooms.

Analysis of bloom formation at three different levels of *G. semen* dominance: *G. semen* >50%, >75%, and >90% of total phytoplankton biomass revealed a wide range of responses to environmental variation. For example, pH, water color and to a lesser extent temperature explained bloom formation at the 50% level, whereas lake morphometry was important at the 90% level.

These results suggest that with ongoing brownification and climate warming boreal systems will likely become more susceptible to invasions of *G. semen*.

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1. Introduction

Gonyostomum semen (Ehrenberg) Diesing is a noxious mixotrophic phytoflagellate with an expanding distribution in northern European countries (Lepistö et al., 1994). The species is often referred to as invasive (Hansson, 2000; Litchman, 2010; Rengefors et al., 2012) and can potentially alter ecosystem food webs (Johansson et al., 2013; Lebret et al., 2012). *G. semen* possesses several traits that give the flagellate a competitive advantage over other phytoplankton species. For example, it has the capability of migrating vertically from the epilimnion, where it photosynthesizes during the day, to the cold and nutrient-rich hypolimnion at night, resulting in a reduction of metabolic losses and avoidance of potential grazers (Zaret and Suffern, 1976). Furthermore, formation of benthic cysts provides resistance to adverse conditions (Figueroa and Rengefors, 2006; Hansson, 1996, 2000), and large cell size (length > 55 μm on average) in combination with potential defense mechanisms (trichocysts) can make *G. semen* less susceptible to zooplankton grazing (Lebret et al., 2012).

High biomass of *G. semen* may result in a reduction in biomass of small edible phytoplankton species (Rengefors et al., 2008), which may have negative implications for zooplankton and fish assemblages. The recreational use of lake ecosystems can also be negatively affected by *G. semen* blooms, since the discharge of mucilaginous strands (trichocysts) upon contact may cause skin irritation to swimmers (Sörensen, 1954).

Seasonal maxima of *G. semen* usually occur in August (Willen, 2003) and blooms last for up to three months from late June until late September (Peltomaa and Ojala, 2010). During blooms *G. semen* biomass may dominate the phytoplankton community by >95% (Pithart et al., 1997). Although annual blooms are common once *G. semen* has established in a lake (Hehmann et al., 2001), the incidence and dynamics of the blooms are poorly understood (Angeler et al., 2010). Laboratory experiments have shown that higher temperatures may promote larger biomasses of *G. semen*;

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growth of *G. semen* starts at temperatures above 6 °C, is optimal at temperatures between 9 and 12 °C and decreases rapidly with increasing temperatures above 19 °C (Rengefors et al., 2012). In addition to temperature, other factors have been suggested to explain the occurrence and bloom incidence of *G. semen*. *G. semen* occurs most often in forested lakes with high phosphorous concentrations, high levels of dissolved organic carbon (DOC) and low pH values (Hehmann et al., 2001; Willen, 2003). Shallow depths and longer stratification periods could also promote the size of *G. semen* populations because the cells are recruited from resting cysts at depths less than 4 m (Figueroa and Rengefors, 2006; Hansson, 1996) and because *G. semen* can regulate its position in the water column, thus benefiting from stable stratification (Salonen and Rosenberg, 2000).

In this study, we address factors that affect the spatial distribution and bloom incidence of *G. semen* in boreal lakes. We analyzed trends in detection and bloom incidence of *G. semen* during a 19-year period, and tested the hypothesis of Rengefors et al. (2012) that changes in temperature and water color (a generally accepted proxy for dissolved organic carbon) are good predictors of the increased occurrence of *G. semen* in lakes within the same climatic region.

2. Methods

Our data set contained phytoplankton samples from 146 lakes uniformly distributed across Sweden and sampled at least once during the period 1992–2010 (i.e. 1309 samples) as part of the Swedish national lake survey (Fig. 1). Forty-five lakes were sampled annually between 1995 and 2010 and had a complete time series of 16 years. The studied area covers three ecoregions in Sweden (the Borealic Uplands (north-west), Fennoscandian Shield (north-east) and the Central Plains (south) ecoregions (Illies, 1978)) and a broad climatic range. The surrounding landscape consists mainly of coniferous forests but also deciduous forests and agricultural land, particularly in the south. More information is available in Table 1.

Table 1
Variables used as predictors in the random forest analysis.

	Mean	SD	Range
pH	6.4	0.73	4.1–9.7
Ca (meq L^{-1})	0.24	0.34	0.005–3.9
Mg (meq L^{-1})	0.09	0.09	0.001–1.5
SO_4 (meq L^{-1})	0.12	0.17	0.004–3.2
NH_4 (μg L^{-1})	25.9	44.6	1–1115
NO_3 (μg L^{-1})	64.1	132	1–5072
TN (μg L^{-1})	438	236	24–6440
PO_4 (μg L^{-1})	2.93	3.75	0–128
TP (μg L^{-1})	11.4	11.8	1–351
Absorbance 420 nm	0.97	29.7	0–1164
TOC (mg L^{-1})	9.16	4.84	0.1–42.2
Temperature perc90 (°C)	19	3.5	11–27
Growing season	63.9	15.8	0–98
Temperature April (°C)	3.8	3.0	−10.7–9.5
Temperature May (°C)	9.0	2.8	−4.7–13.8
Temperature June (°C)	13	2.2	1.1–17
Temperature July (°C)	16	2.2	5.2–20
Temperature August (°C)	14.7	2.6	2.5–21
Mean depth (m)	4.37	1.53	1.60–11.3
Surface area (km^2)	1.19	2.22	0.027–14
Catchment area	25	57	0.15–37
Coniferous forest (%)	0.51	0.19	0–0.81
Wetlands (%)	0.09	0.10	0–0.65
Water bodies (%)	0.14	0.08	0.02–0.35

2.1. Sampling

Phytoplankton samples were collected between 15 July and 15 September, i.e. in conjunction with the seasonal maximum of the *G. semen* blooms in Sweden (Angeler et al., 2010; Willen, 2003). In general, lakes located in northern Sweden were sampled in late August to early September, whereas in the south samples were collected in late July to early August. In lakes with a surface area > 1 km^2 an epilimnetic (0–4 m) water sample was collected at the deepest part of the lake using an acrylic plastic tube sampler (30 mm diameter). In lakes with a surface area < 1 km^2 five

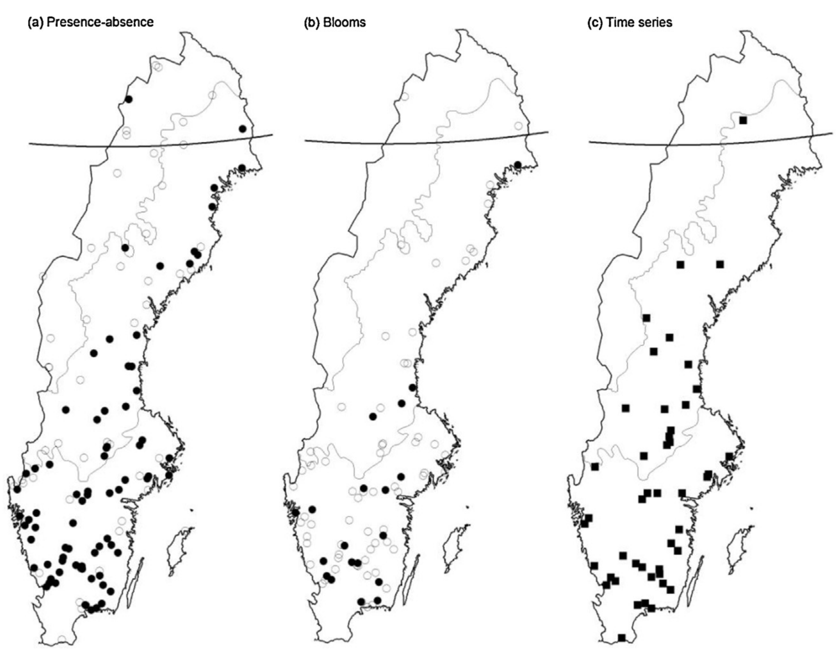

Fig. 1. Maps showing the location of the study lakes. (a) The 124 lakes used in the detection model. Filled circles represent lakes with *G. semen*. (b) The 83 lakes used in the bloom model. Filled circles represent lakes with blooms. (c) The 45 lakes sampled annually between 1995 and 2010 and used to assess trends in prevalence, bloom incidences and geographical distribution. The thick black line marks the Arctic Circle (latitude 66°33′44″N). Thin black lines mark the Borealic Uplands (north-west), Fennoscandian Shield (north-east) and the Central Plains (south) ecoregions.

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