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PRIMARY RESEARCH PAPER

The influence of glucose and peat extract additions on the spring recruitment of *Gonyostomum semen* from the sediments

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Abstract The effect of two various forms of DOC on the *Gonyostomum semen* recruitment from sediments was conducted under experimental laboratory conditions. We tested the hypothesis that DOC is a factor enhancing spring recruitment of the species by exposing sediments from a humic lake with a 17-year bloom history, to three various DOC additions (two solutions of glucose and one solution of a peat extract). Sediments and lake water were incubated for 14 days at 16°C, in 14:10 h light:dark cycle, with germling and adult cell abundance ascertained in the water every third day, and water parameters every seventh day. Our important findings were that (1) *Gonyostomum* recruitment was uneven and the period of germination was relatively short; (2) all treatments significantly affected germling occurrence; however, sugar-derived DOC seemed to suppress the recruitment, whereas peat extract improved it. Due to the additional phosphorus load in peat treatment (against phosphorus-free sugar treatments), it is likely that it played a major role in the observed differences, however, our results did not exclude the potential role of peat-derived DOC forms. In conclusion, we proposed that *Gonyostomum* expansion is supported by enhanced recruitment from sediment seed banks related to water chemistry alterations, driven by the climate change.

Keywords *Gonyostomum semen* · Dissolved organic carbon · Recruitment · Cyst germination · Lake sediments

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Introduction

Gonyostomum semen (Ehr.) Diesing is a bloom-forming flagellate species that often occurs in humic lakes across Europe. During the last three decades, the number of reports on blooms of this alga in European freshwaters has increased (Cronberg et al., 1988; Lepistö et al., 1994; Noges & Laugaste, 2002; Willen, 2003; Rengefors et al., 2012; Pęczuła, 2013; Karosiene et al., 2014). The factors enabling the expansion and blooming of *Gonyostomum semen* are still under discussion. Among the hypothesized drivers for the observed increased distribution and abundance are eutrophication (Eloranta & Palomäki, 1986; Hongve et al., 1988; Laugaste, 1992; Lepistö & Saura, 1998), acidification (Cronberg et al., 1988; Korneva, 2000; Hansson, 2000), calcification of acid lakes (Hutorowicz, 1993), increased dissolved organic carbon (DOC), and fulvic acid concentrations (Findlay et al.,

2005; Rengefors et al., 2008), as well as the extension of the growing season related to the climate change (Rengefors et al., 2012), and the alternations in planktonic food webs (consisting of a fall in the abundance of filter-feeding Cladocera) (Hansson, 2000; Hehmann et al., 2001).

Like some other flagellate algae, *Gonyostomum semen* forms the resting cysts during autumn. These overwinter in sediments in seed banks, and after a dormancy period lasting at least 11 weeks, germinate and form a new generation in the water column (Figueroa & Rengefors, 2006; Rengefors et al., 2012). It is supposed that the benthic cyst formation in planktonic algae is an adaptation strategy enabling survival during unfavorable periods (Fryxell, 1983; Hansson, 2000), and the spring or summer encystment plays a crucial role in the bloom initiation or the seasonal succession (Anderson & Wall, 1978; Anderson & Rengefors, 2006). Although there are many studies about the factors which regulate algal cyst germination (Agrawal, 2009), the knowledge about *Gonyostomum semen* recruitment from sediments is poor. Yet, there is evidence that the cyst germination of this species is affected by temperature (Figueroa & Rengefors, 2006; Rengefors et al., 2012), phosphorus addition (Findlay et al., 2005), and the presence of Cladocera in the water column (Hansson, 1996).

An increased DOC concentration is supposed to promote *Gonyostomum semen* development in lakes, as the species probably uptakes organic compounds by osmotrophy—directly as fulvic acids or by cell lysis of other microorganisms (Rengefors et al., 2008). A large fraction of DOC in lakes is colored and composed of fulvic and humic acids of allochthonous origin (Schindler et al., 1992; Wetzel, 1992). The load of this matter results in worsened light climate in lakes (Nürnberg & Shaw, 1998; Pace & Cole, 2002), which is also proposed as a factor favoring *Gonyostomum semen* domination, due to the species sensitivity to excessive insolation (Findlay et al., 2005). The DOC concentration and its structure in humic lakes are related to various factors. Among these are: the area of lake catchment, the land cover in the catchment, the area of the lake, winter and summer precipitation, the time of snowmelt, and other climatic factors. Hence, there is no common pattern in seasonal changes in DOC concentration in humic lakes (Pace & Cole, 2002; Vuorenmaa et al., 2006). Nevertheless, some evidence from central Europe showed that the maximal DOC concentration in any lake may be reached in May or June (Górniak et al., 2002). In small humic lakes in central-eastern Poland, the water color values in May are often higher than in July or September, indicating a high load of colored allochthonous DOC derived from snowmelt and spring rainfall (Pęczuła, unpublished). Spring *Gonyostomum* recruitment may be, therefore, affected by a DOC pulse from the catchment, particularly because the month of May is supposed as the period in which the species cysts have the best encystment ability after 6–7 months of dormancy (Rengefors et al., 2012).

We have put forward the hypothesis that the dissolved organic carbon can be one of the factors enhancing *Gonyostomum semen* spring recruitment from the sediments. We aimed to test it in laboratory conditions by exposing sediments from a humic lake in which *Gonyostomum* blooms are observed, to various glucose and peat extract additions.

Methods

In April 2013, a laboratory experiment was conducted to stimulate the appearance of *Gonyostomum* from lake sediments, by adding various organic carbon additions: glucose and peat extract. We had decided to use the carbohydrate as it is a colorless, nitrogen- and phosphorus-free form of DOC, and it was previously applied in other experimental studies concerning DOC addition to lake ecosystem (Blomqvist et al., 2001).

Sediment samples were collected in late April, from Lake Płotycze (eastern Poland, N51°23′34.9″, E23°37′03.8″). This lake is significant in that the algae form a high biomass and dominate the phytoplankton structure since the end of the last century (Pęczuła, 2007, 2013). Detailed limnological characteristics of the lake can be found in Pęczuła & Szczurowska (2013). The sampling was conducted during the ice-melting period, in the ice-free littoral area (2 m of depth), when the central part of the lake was still covered with a thin ($\sim$1 cm) layer of ice. A total of 12 sediment cores with above-sediment water were taken using a Uwitec gravity core sampler (diameter 6 cm). Additionally, 20 dm^3 of lake water was sampled by way of a Ruttner sampler, from the depth 0.5 m above the sediments. All samples were kept in the dark and protected against heating (by

covering with foamed polystyrene insulation) during the 2 h transportation to the laboratory.

In the laboratory, 20 dm^3 of sampled lake water was filtered through a GF/C fiber-glass filter. The initial DOC concentration in this water was 23.0 ± 0.2 mg dm^{-3}, pH 6.4, electrolytic conductivity 30 μS cm^{-1}, and phosphate concentration 0.014 ± 0.005 mg dm^{-3}. The water above the sediments from the core tubes was carefully removed by way of a thin pipe, and replaced by 1.2 dm^3 of the filtered lake water that had incorporated the various treatment additions. The experimental design consisted of three replicated controls (marked as C) and three types of treatments (in three replications each). The first two treatments included two various solutions of glucose: 15 mg (marked as G5) and 30 mg (marked as G10) dissolved in 1.2 dm^3 of filtered lake water, giving an assumed addition of 5 and 10 mg C dm^{-3}. The actual addition of glucose-derived DOC to the lake water was then analytically verified at 4.6 ± 0.8 and 7.5 ± 0.7 mg dm^{-3}, respectively. The third treatment consisted of one solution of a peat extract (84 mg DOC dm^{-3}), marked as P. The extract was obtained by boiling 0.3 dm^3 of filtered lake water with 3 g of fresh peat, sampled from the transitional fen surrounding the lake, and filtering this through a GF/C fiber-glass filter. Mixing 300 ml of this extract with 0.9 dm^3 of lake water gave an addition of 4.0 ± 0.7 DOC dm^{-3} to the lake water.

The tubes were then put in a growth cabinet at 16°C (which is regarded as the best for germling viability, Figueroa & Rengefors, 2006), with a light: dark cycle of 14:10 h, at a light intensity of 1.0 μmol m^{-2} s^{-1} at the surface of the sediments. The experiment lasted for 14 days. At day 1, 7, and 14, samples of 0.13 dm^3 were taken from the middle depth of the water column in each tube and the loss of water was replaced by the same amount of filtered lake water stored in darkness at 4°C. Due to the low oxygen conditions observed at the seventh day sampling, the above-sediment water in all experimental tubes was aerated using a standard aquarium pump for 5 min. This was done to improve oxygen content, as anoxic or very low oxygen conditions are known to inhibit or prevent germination of algal cysts (Anderson et al., 1987; Ishikawa & Taniguchi, 1994; Kremp & Anderson, 2000), and these conditions would disrupt the experiment. Another rationale for this manipulation was the attempt of mimicking the mixing conditions in temperate lakes occurring in spring after ice melting. Dissolved oxygen concentration, pH, and conductivity were measured in the samples using a YSI556 Multi Probe (MPS). In addition, phosphates concentration was measured using a molybdate method (Hermanowicz et al., 1976), while dissolved organic carbon was determined using a TOC-V_{CSH} Schimadzu analyzer. Beyond this work, a subsample of 0.02 dm^3 was fixed with a Lugol solution and, subsequently, examined for *Gonyostomum* abundance using an inverted microscope and the Utermöhl method (Vollenweider, 1969). Two additional samples (0.02 dm^3) for *Gonyostomum* analyses were taken at day 4 and 11. During microscopic examination, we have counted small cells (width: 16.2 ± 2.1 μm, length: 20.2 ± 3.2 μm) and large cells (width: 28.3 ± 6.1 μm, length: 45.1 ± 9.2 μm) separately. Small forms were classified as germlings (being up to 24 h after germination) and the others, as mature cells (Figueroa & Rengefors, 2006).

In order to determine the significance of differences between chemical compounds in the control and experimental tubes, one-way ANOVA analysis with Tukey's test was performed. As the two factors showed significant differences (DOC and P-PO_4), the influence of these on the number of germs was verified using main effect analysis of variance (ANOVA). The test of Kołmogorow–Smirnow was used to verify the normal distribution of the collected data. Both analyses were performed in STATISTICA 7.0.

Results

The initial DOC concentration in the control tubes amounted to 22.3 ± 0.9 mg dm^{-3}. What is more, the addition of glucose in treatments resulted in significantly higher values of the parameter (27.6 ± 0.9 mg dm^{-3} in G5, $F = 52.5$, $P < 0.01$, ANOVA; 29.5 ± 2.0 mg dm^{-3} in G10, $F = 4.56$, $P < 0.01$, ANOVA). In the P and G5 tubes comparable DOC concentrations were obtained (27.1 ± 1.1 mg dm^{-3} in P tanks). During the experiment, a decrease in DOC content was observed in all treatment tubes, reaching on the last day, a level similar to that of the control tubes, which was ± constant throughout the study (Fig. 1a). The addition of DOC in the experimental tanks was reflected in an increase of the water color only in the P tanks (48.9 ± 1.4–53.2 ± 1.2 mg Pt

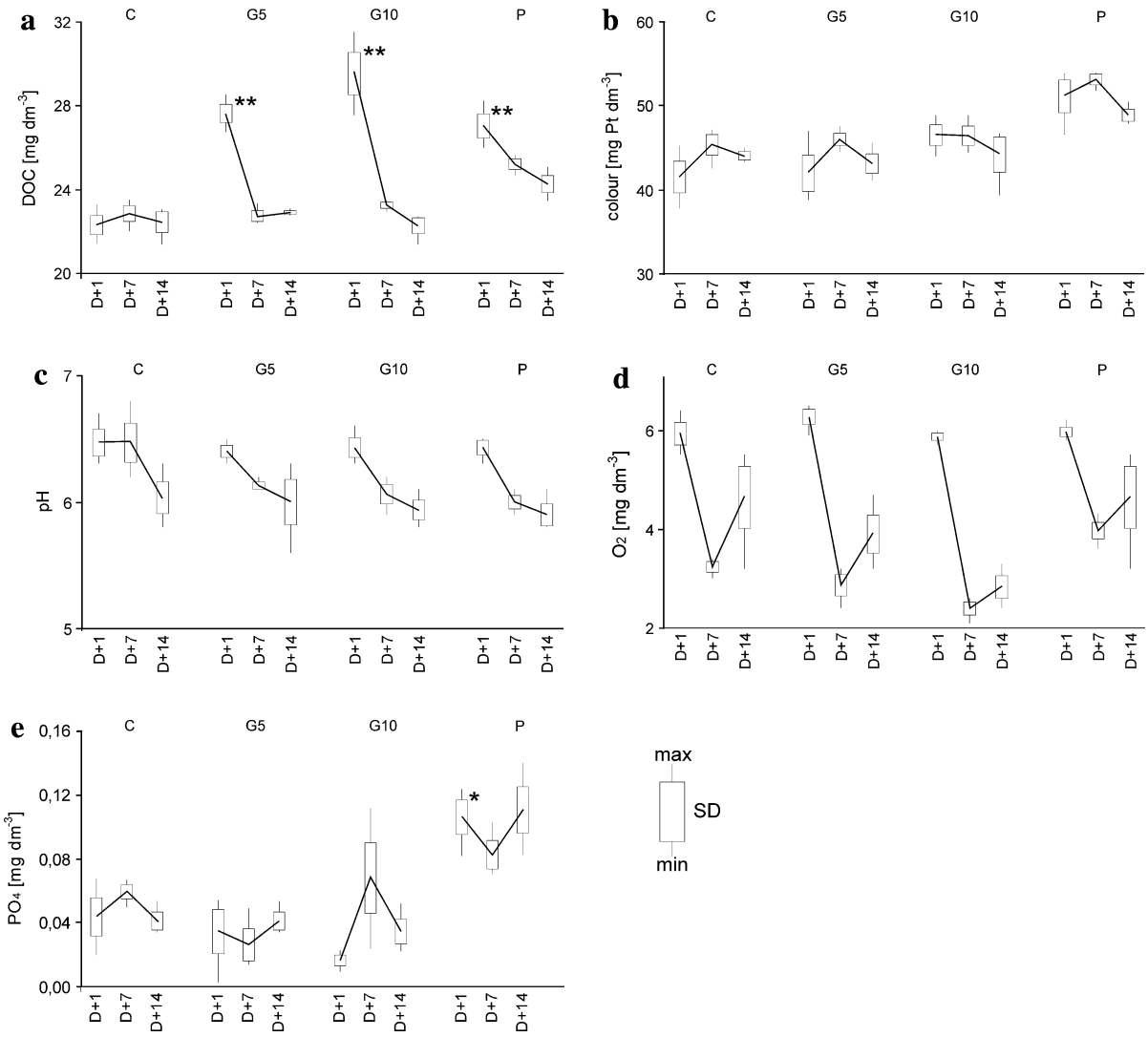

Fig. 1 Changes of **a** dissolved organic carbon, **b** water color, **c** pH, **d** dissolved oxygen, and **e** phosphates in control and experimental tanks (*C* control, *G5* 5 mg of glucose addition, *G10* 10 mg of glucose addition, *P* peat extract addition; $D + 1$, $D + 7$, and $D + 14$—consecutive days of the experiment; *single asterisk* $P < 0.05$, *double asterisk* $P < 0.01$, differences against controls at D + 1, one-way ANOVA)

dm^{-3}). However, in all tubes, a similar pattern of changes during the experiment appeared: an initial increase followed by a decrease (Fig. 1b). Initial water pH in all tanks was nearly the same (ca. 6.4), and, consequently, decreased to 5.9–6.0 (Fig. 1c). Dissolved oxygen concentrations measured on the first day in all tubes were comparable (5.9 ± 0.1 –6.3 ± 0.3 mg dm^{-3}), and after seven days, we have observed their substantial decrease to 2.4 ± 0.3–4.0 ± 0.4 mg dm^{-3}. The performed aeration improved the oxygen conditions, nevertheless, by the last day, the oxygen concentrations were lower in comparison to the initial, and in one case, they reached a very low level (2.8 ± 0.4 mg dm^{-3} in G10, Fig. 1d). Base phosphate concentrations in C, G5, and G10 tubes ranged from 0.017 ± 0.007 to 0.044 ± 0.024 mg dm^{-3} and fluctuated slightly (increased or decreased) throughout the study period. Distinctively higher values ($F = 11.4$, $P < 0.05$) occurred in the tubes enriched with the peat extract (Fig. 1e). Electrolytic conductivity oscillated in all tubes—between 31.0 and 33.0 µS cm^{-1}.

On the day following the setting up of the experiment, we found *Gonyostomum* germlings in all

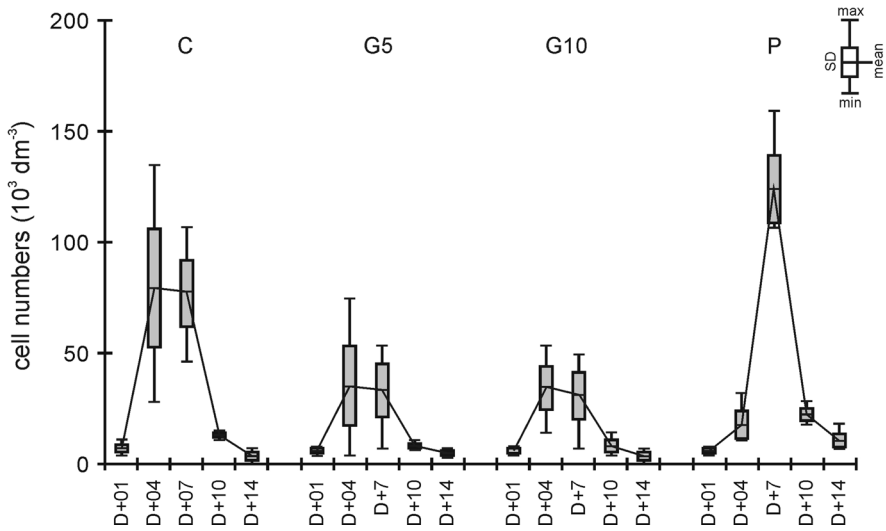

Fig. 2 Changes in *Gonyostomum semen* germling cell numbers in control and experimental tanks (*C* control, *G5* 5 mg of glucose addition, *G10* 10 mg of glucose addition, *P* peat extract addition; *D* + 1, *D* + 7, and *D* + 14—consecutive days of the experiment)

Table 1 Results of main effects ANOVA on number of germlings, testing for the effect of DOC and P-PO_4

	df	SS	MS	*F*	*P*
Number of germlings					
Intercept	1	2.43	2.43	98.30	**<0.001****
DOC	3	6.61	2.20	8.91	**<0.001****
P-PO_4	2	2.92	1.45	58.70	**<0.001****
DOC × P-PO_4	6	1.09	1.82	7.36	**0.004****

** significant at the level $P < 0.01$

tanks, but at low numbers ($6.2 \pm 2.2 \times 10^3$ dm^{-3}, mean for all samples). On the fourth and the seventh day, elevated germling counts were noted in both controls and the two glucose treatments. In the controls, these values amounted $79.1 \pm 53.3 \times 10^3$ and $76.7 \pm 30.1 \times 10^3$ dm^{-3} respectively, while in the G tanks, they were two-fold lower (30.7×10^3 – 35.4×10^3 dm^{-3}; Fig. 2). On the consecutive day sampling, the values were low, comparable to the first day. A different pattern was evident with respect to the peat tubes. These showed a distinctively higher abundance only on the seventh day. Furthermore, their mean value ($124.0 \pm 30.7 \times 10^3$ dm^{-3}) was almost twice as high as in the control on the corresponding day of sampling. On the directly preceding and following days (fourth and tenth), germling cell numbers amounted to $17.7 \pm 12.2 \times 10^3$ and $22.4 \pm 5.4 \times 10^3$ dm^{-3}, respectively (Fig. 2). Finally, main effect analysis of variance reveals that DOC and phosphates (each one separately as well as both together) significantly affected germling occurrence in the water above the sediments (Table 1).

Mature cell numbers showed a different pattern of changes (Fig. 3). In the control tubes, during the experiment, we observed two subsequent periods of population change, an increase (to $73.2 \pm 28.8 \times 10^3$ –$74.4 \pm 7.1 \times 10^3$ dm^{-3}) and a decrease (to $20.1 \pm 10.8 \times 10^3$–$21.2 \pm 12.7 \times 10^3$ dm^{-3}) between the first and the seventh day, as well as between the seventh and the last day. Similar dynamics were noted in the glucose treatments, although the peak values were lower (Fig. 3). Interestingly, in the tubes with peak extract addition, the mature cell numbers increased continuously until the tenth day, reaching $114.5 \pm 44.8 \times 10^3$ dm^{-3}. Afterwards, the values declined to $38.9 \pm 19.7 \times 10^3$ dm^{-3} by the last day.

Discussion

Our first important finding (although unintended with respect to the main goal of the research) was that *Gonyostomum semen* recruitment was uneven during the experiment. The maximal abundance of cells observed at the fourth and the seventh day indicates that the period of germination of the species at 16°C is relatively short. Moreover, the mean numbers of cells in the water column above the sediments in controls

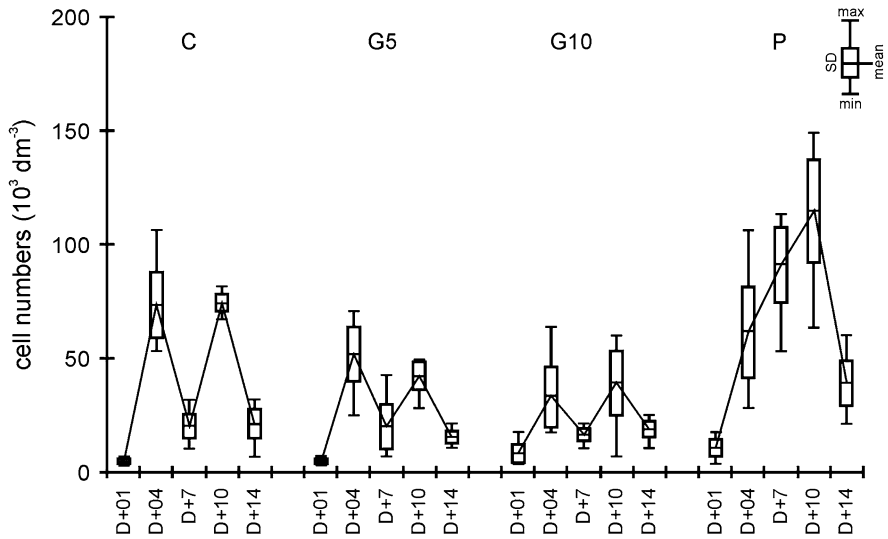

Fig. 3 Changes in *Gonyostomum semen* adult cell numbers in control and experimental tanks (*C* control, *G5* 5 mg of glucose addition, *G10* 10 mg of glucose addition, *P* peat extract addition; $D + 1$, $D + 7$, and $D + 14$—consecutive days of the experiment)

after the fourth day were 79.1×10^3 dm^{-3}, which corresponds to the germination rate of 8.47×10^6 m^{-2} day^{-1}. The value is lower than that noted by Hansson (1996), which showed the germination rate of ca. 28×10^6 m^{-2} day^{-1} after five days of an experiment examining the impact of grazers on *Gonyostomum* recruitment, but at a temperature of 18°C. Previous research (Figueroa & Rengefors, 2006; Rengefors et al., 2012) have shown that higher temperatures promote the germination of cysts out of dormancy, therefore, the 2°C lower temperature in our experiment may explain the observed difference in the germination rate.

The present study was designed primarily to determine the effect of various forms of DOC addition on *G. semen* recruitment. Statistical analyses revealed that DOC significantly affected germling occurrence in water. However, DOC addition in the form of sugar (without phosphates), regardless of its dose, seemed to suppress germling appearance, whereas, when added as a peat extract (which resulted also in increased phosphate content), an improvement came about. Moreover, peat extract delayed the time of the largest recruitment by about 3 days. The fact that the elevated sugar-derived DOC (with zero phosphorus increase) led to the decrease of the alga recruitment could suggest, that it was the increased phosphorus concentrations in the peat treatment that played a major role in the observed differences.

These findings are consistent with those of Findlay et al. (2005), who found that phosphorus addition of 0.05 mg dm^{-3} gave ten times higher biomass in the water above sediments after 8–11 days of the recruitment experiment. However, the authors counted all *Gonyostomum* cells (both germling and mature), so it is hard to distinguish whether phosphorus addition enhanced the germination or the growth rate of the species. Nevertheless, a number of studies reported the positive role of phosphorus in the germination of resting forms of various algal species. This effect was revealed for cysts of two dinoflagellates: *Ceratium hirundinella* (Rengefors & Anderson, 1998) and *Gymnodinium catenatum* (Figueroa et al., 2006), zoospores of *Cladophora glomerata* and *Rhizoclonium hieroglyphicum* (Agrawal & Misra, 2002), akinetes of various cyanobacteria species (Hüber, 1985; van Dok & Hart, 1997; Agrawal & Misra, 2002) or *Enteromorpha* sp. spores (Sousa et al., 2007). The influence of phosphorus on germination success is explained by the ability of cysts to uptake nutrients, as it was suggested by Rengefors et al. (1996) in regard to dinoflagellate *Scrippsiella trochoidea*. According to Agrawal (2009), the lack of phosphorus, which decreases spore or cyst germination in algae, indicates the synthesis of fresh nucleic acids during this process. Nevertheless, there are also reports revealing the lack of the effect of nutrients (including phosphorus) on the algal cyst germination (Sako et al., 1985; Binder & Anderson, 1987; Cannon, 1993). Moreover, the research we have conducted prior to this experiment, concerning long-term changes in phytoplankton community of Lake Płotycze (the same lake from which

the sediments had been used in this experiment) reveals that, after the rising of the water level, the community had been dominated by *Gonyostomum semen*, which was accompanied with DOC increase, but phosphorus decrease (Pęczuła & Szczurowska, 2013).

Other possible explanation of our findings may be related to the content of dissolved organic compounds in the peat extract. It is known, that the growth rate of *Gonyostomum* is supported by fulvic acids (Rengefors et al., 2008), which may explain the continuous increase of adult cell numbers in our experimental peat tanks, in contrast to controls and glucose treatments. Humic substances have been also shown to positively affect the growth rate of some dinoflagellates (Prakash & Rashid, 1968; Doblin et al., 1999; Gagnon et al., 2005); however, there is no single study concerning the impact of humic substances on any algal cyst germination.

Unfortunately, we cannot distinguish the effects of peat-derived DOC and phosphorus on the enhanced germination in the treatments with peat extract. Moreover, a combined effect of both factors is very likely, as the peat extract certainly contained an extra amount of phosphorus, present in the form of humic-metal ion complexes (Petrovic & Kastelan-Macan, 1996; Gerke, 2010). Utilization of DOC by bacteria, which are subsequently grazed by heterotrophic flagellates, leads to phosphorus regeneration and its renewed availability for phytoplankton (Granéli et al., 1999). The possible enhanced bacterial growth during our experiment was visible in changes of chemical parameters (a substantial decrease of DOC and oxygen content in the treatments).

In contrast to our use of peat extract within the experiment, the addition of glucose seemed to inhibit the recruitment of *Gonyostomum*, which was a rather unexpected finding. It is difficult to explain this result, but it might be related to an oxygen decline which occurred in all the tanks, but was most evident in the G5 and G10 treatments, as anoxic or very low oxygen conditions are known to inhibit or prevent germination of various protistan cysts, such as in the dinoflagellates (Anderson et al., 1987; Ishikawa & Taniguchi, 1994; Kremp & Anderson, 2000). Although in our experimental tanks we did not observed such severe conditions (the oxygen level never dropped below 2 mg dm^{-3}, mainly due to the aeration within the experiment), we cannot exclude this factor, as knowledge of the impact of oxygen conditions on *Gonyostomum* cyst germination is lacking. The performed aeration certainly rearranged the environmental conditions, which might have disrupted germination trends. This may be regarded as a limitation of our study design, but the manipulation was applied to all treatments (including controls), so the conclusions based on observed differences between tubes seem to be valid.

Another possible, although speculative, explanation for lower recruitment in sugar treatments is that glucose addition might bring about the enhanced growth of the bacteria and heterotrophic nannoflagellates (as we have concluded above, on the basis of changes in DOC and O_2 content). The same phenomenon was observed during a whole-lake experiment with sucrose addition (Blomqvist et al., 2001). What is more, previous research has realized that some bacteria may produce a variety of compounds, including toxic proteins, polyanionic polymers, substituted alkaloids, and cyclic peptides, which showed inhibitory activity on some algal spores germination (review in: Agrawal, 2009).

Although we cannot differentiate the effects of DOC and phosphorus, our findings revealed that some peat-derived compounds enhanced the recruitment of *G. semen* cysts from sediments. Thus, we have shown that germination of *Gonyostomum* cysts may be regulated not only by the temperature (Figueroa & Rengefors, 2006) or the presence of the grazers (Hansson, 1996, 2000), but also by the allochthonous chemicals derived from peat. What are the ecological implications of our finding? The amount of compounds reaching the lake from peatland catchments is regulated by hydrometeorological factors (Schindler & Curtis, 1997; Hudson et al, 2003), which are significantly impacted by recent climate change (Whitehead et al., 2009). For example, since the end of the last century, various reports have shown considerable DOC increase in the freshwaters of Northern and Central Europe (Hejzlar et al., 2003; Worrall et al., 2004; Evans et al., 2005; Monteith et al., 2007). These observed changes have been linked to such factors as increase of air temperature, rainfall intensity and atmospheric carbon dioxide, or a decline in acid deposition, although their detailed role are still under debate (Delpla et al., 2009). Recent scientific developments in freshwater ecology have highlighted the actual and predicted impact of climate change also

on the increase of phosphorus loadings to lakes (Jeppesen et al., 2009). In the light of our findings, we can propose that one of the mechanisms of *Gonyostomum semen* expansion throughout European freshwaters in the last decades is related to the enhanced recruitment of the species from sediment seed banks, and this has been influenced by climate change-driven water chemistry. This hypothesis stays in agreement with suggestions proposed by Rengefors et al. (2012) that global warming supports *Gonyostomum* expansion and blooms in Europe, not only by the increase of the temperature, but, indirectly, also by the increase of DOC concentrations in freshwaters. Further studies concerning the role of oxygen, phosphorus and humic acids, as well as the role of bacteria in *Gonyostomum semen* cyst germination, will be of great help in our understanding of this invasive and bloom-forming raphidophyte ecology within European freshwaters.

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