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Vertical distribution of expansive, bloom-forming algae *Gonyostomum semen vs.* plankton community and water chemistry in four small humic lakes

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Abstract – One of the features of *Gonyostomum semen*, a bloom-forming and expansive flagellate, is uneven distribution in the vertical water column often observed in humic lakes. In this paper, we analysed vertical distribution of the algae in four small (0.9–2.5 ha) and humic (DOC: 7.4–16.5 mg dm^{-3}) lakes with similar morphometric features with the aim to test the hypothesis that vertical distribution of *G. semen* may be shaped by zooplankton structure and abundance. In addition, we wanted to check whether high biomass of this flagellate has any influence on the chemical composition as well as on planktonic bacteria abundance of the water column. The results of the study showed that vertical distribution of the algae during the day varied among all studied lakes. Our most important finding was that (a) the abundance and structure of zooplankton community (especially in case of large bodied daphnids *Daphnia pulicaria, D. longispina* and copepod *Eudiaptomus graciloides*) may shape *G. semen* vertical distribution in studied lakes; (b) high *G. semen* biomass may decrease the content of ammonium ions in the water column by intense uptake, but has low effect on other water chemical parameters. The results of the study contribute to the understanding of the factors influencing this expansive algae behaviour as well as it shows interesting aspects of *G. semen* influence on some components of the lake ecosystem.

Keywords: *Gonyostomum semen* / vertical distribution / zooplankton / bacteria / humic lake

Résumé – Répartition verticale de l'algue invasive formant des fleurs d'eau *Gonyostomum semen* en relation avec communauté planctonique et la chimie de l'eau dans quatre petits lacs humiques. L'une des caractéristiques de *G. semen*, flagellé invasif à bloom, est une distribution inégale dans la colonne d'eau, souvent observée dans les lacs humiques. Dans cet article, nous avons analysé la distribution verticale de l'algue dans quatre petits lacs (0,9–2,5 ha) humiques (DOC: 7,4–16,5 mg dm^{-3}) avec des caractéristiques morphométriques similaires dans le but de tester l'hypothèse que la distribution verticale de *G. semen* peut être façonnée par la structure et l'abondance du zooplancton. De plus, nous voulions vérifier si la biomasse élevée de ce flagellé a une influence sur la composition chimique ainsi que sur l'abondance des bactéries planctoniques dans la colonne d'eau. Les résultats de l'étude ont montré que la distribution verticale de l'algue au cours de la journée variait d'un lac à l'autre. Notre constatation la plus importante est que a) l'abondance et la structure de la communauté zooplanctonique (en particulier dans le cas des grandes daphnies *Daphnia pulicaria*, *D. longispina* et du copépode *Eudiaptomus graciloides*) peuvent façonner la distribution verticale de *G. semen* dans les lacs étudiés; b) une biomasse élevée de *G. semen* peut diminuer la teneur en ions ammonium dans la colonne d'eau par une absorption intense, mais a un faible effet sur d'autres paramètres chimiques de l'eau. Les résultats de l'étude contribuent à la compréhension des facteurs influençant ce comportement

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invasif des algues ainsi que des aspects intéressants de l'influence de *G. semen* sur certaines composantes de l'écosystème du lac.

Mots clés : *Gonyostomum semen* / distribution verticale / zooplancton / bactérie / lac humique

1 Introduction

The problem of alien, invasive and expansive species is one of the most studied topics in ecology, notably in recent decades, with the appearance of global issues of increasing importance such as climate change, loss of biodiversity, habitat fragmentation or the introduction of genetically modified organisms (Lodge, 1993; Pociecha *et al.*, 2016). Apart from invertebrates, fish and macrophytes, invasions in aquatic habitats include planktonic cyanobacteria and algae, although the invasion of very small organisms is more cryptic than that of larger ones, and is therefore more difficult to detect (Sukenik *et al.*, 2012; Korneva, 2014). As a good example may serve *Gonyostomum semen*, a planktonic flagellate from Raphidophyceae group, which mass development was firstly described in small dystrophic pond in Massachusetts (United States) already in thirties of the 20th century (Drouet and Cohen, 1935). In last decades, at the turn of the 20th and 21st centuries it became widely studied and known as a bloom-forming species in humic lakes of Sweden, Norway, Finland, Estonia and northern Russia (Cronberg *et al.*, 1988; Hongve *et al.*, 1988; Lepistö *et al.*, 1994; Korneva, 2000; Laugaste and Nõges, 2005), then in Latvia, Lithuania and Poland (Hutorowicz *et al.*, 2006; Druvietis *et al.*, 2010; Karosiene *et al.*, 2014) and sporadically in other European locations (Le Cohu *et al.*, 1989; Negro *et al.*, 2000).

Gonyostomum semen in European lakes was sometimes described as an invasive species (Hongve *et al.*, 1988; Lepistö *et al.*, 1994; Lebret *et al.*, 2015), however, lack of historical records make the determination of its status very difficult. Recent studies aiming to detect resting cysts of the algae in Swedish lakes sediments with the use of PCR method, revealed that the species DNA was found in sediment depths corresponding to an age of 50 years, which suggest that the algae might be present in Swedish lakes many years before lake monitoring was started in this country (Johansson *et al.*, 2016a). Thus, it is rather assumed that the observed expansion of *G. semen* consists equally of the extension of its range, the colonization of new types of ecosystems and the increase in bloom frequency within sites already colonized (Laugaste and Nõges, 2005).

The species has some features which might impede its detection in lake samples, thus making its invasion/expansion more "cryptic". This is, among others: cell sensitivity, which effects in its deformation in fixed samples and frequent occurrence only in deeper water layers. Although several studies showed that *G. semen* tends to be unevenly distributed in the vertical column of water and can change its vertical location (Cowles and Brambel, 1936; Cronberg *et al.*, 1988; Le Cohu *et al.*, 1989, Eloranta and Räike, 1995; Pithart *et al.*, 1997; Negro *et al.*, 2000; Salonen and Rosenberg, 2000; Grabowska and Górniak, 2004, Pęczuła *et al.*, 2013), there is no general agreement about the causes and mechanisms of the phenomenon. Some studies (Cronberg *et al.*, 1988; Salonen and Rosenberg, 2000) pointed the importance of epilimnetic phosphorus depletion as a driver of the algae behavior; Eloranta and Räike (1995) stated that *G. semen* diel migrations are particularly related to the species light avoidance, while Pęczuła *et al.* (2013) suggested that the role of zooplankton grazers may be crucial as well. Trophic relations between *G. semen* and zooplankton species have been studied recently, mainly testing the algae as a food source, sometimes with contradictory results (Williamson *et al.*, 1996; Lebret *et al.*, 2012; Johansson *et al.*, 2013; Björnerås, 2014). There are also few studies on the impact of *G. semen* blooms on plankton communities, benthic invertebrates or fishes in the ecosystem scale (Trigal *et al.*, 2011; Angeler and Johnson, 2013; Karosiene *et al.*, 2014) or in the laboratory studies (Pęczuła *et al.*, 2017). Nevertheless, the knowledge on biotic and abiotic relations with *G. semen* in the context of its vertical distribution is still scarce.

Our study aimed to test the hypothesis that vertical distribution of *G. semen* in small humic lakes may be shaped by zooplankton structure and abundance. In addition, we wanted to check whether high biomass of this flagellate, unevenly distributed in the vertical profile has any influence on the chemical composition as well as on the planktonic bacteria abundance of the water column.

2 Material and methods

We conducted the study in four seepage, dimictic lakes (Suchar I, Suchar II, Wądołek and Widne) in the Suwałki Lakeland region (Wigierski National Park, north-eastern Poland). The lakes are situated close to each other and have small surface area (0.9–2.5 ha) but high relative depth (3.5–12.7%; Tab. 1). All of them are humic (water colour: 43.7–133.1 mg Pt dm^{-3}, DOC: 7.4–16.5 mg dm^{-3}; Tab. 2) with moderate or high total phosphorus content (0.052–0.368 mg dm^{-3}) and circumneutral or slightly acidic pH (Tab. 2). Samples were collected once in mid-July 2015 in the central part of each lake, in the early afternoon during semi-cloudy weather. The water for biological and chemical analyses was sampled using a Ruttner sampler (volume of 2 dm^3), from every one meter of the depth, except for zooplankton. For the latter analysis we sampled a total 10 dm^3 of water from three layers: epilimnion, metalimnion and hypolimnion (Fig. 1) from one, two or three depths of each, depending on the lake and layer thickness. Then water was poured together in one sample, filtered with plankton net of 55 μm mesh and reduced to the volume of 0.1 dm^3.

In biological samples, *G. semen* fresh biomass was determined using an inverted microscope according to Utermöhl's method (Vollenweider, 1969). As there is no generally accepted formula for *Gonyostomum* biovolume calculation in the published data, we have chosen an ellipsoid as a geometric model (Hillebrand *et al.*, 1999) and then recalculated the biovolume to fresh biomass, with an

Table 1. Morphometric parameters of studied lakes (after: Górniak 2006).

	Suchar I	Suchar II	Wądołek	Widne
Area [ha]	0.96	2.52	1.09	2.04
Maximum depth [m]	4.0	10.0	15.0	5.7
Mean depth [m]	2.3	4.6	8.9	2.8
Relative depth [%]	3.6	5.6	12.7	3.5
Z_{epi} [m][1]	1.8	2.2	1.7	2.0

[1] Theoretical epilimnion thickness; $Z_{epi} = 4.4\sqrt{D}$, where D is the maximum effective length of lake (Patalas, 1960).

assumption that the volumetric mass density of algal cells equals 1 g cm^{-3} (cell volume of 10^9 μm^3 is considered as equal to 1 mg of biomass). Zooplankton was determined using light microscope (Olympus BX53, Japan). Mean values of the animal length were used to estimate the wet weight of planktonic crustaceans by applying the equations after Błędzki and Rybak (2016), while fresh biomass of rotifers was established following Ejsmont-Karabin (1998) method. Bacterial abundance in biological samples has been determined by standard epifluorescence microscopy (Olympus BX61, Japan) with Porter and Feig (1980) method. Bacterial cells were stained with fluorochrome 4′,6-diamidino-2-phenylindole (DAPI) and collected on a Nuclepore filter (pore size, 0.2 mm) and then counted. Bacterial biomass has been estimated on a base of carbon conversion factors for a single bacterial cell (Lee and Fuhrman, 1987).

Measurements of temperature, electrolytic conductivity (EC), pH and dissolved oxygen concentration were carried out in the field using a HQ40D Multi Meter (Hach-Lange GmbH) as well as water transparency with the use of standard Secchi disc. Other hydrochemical parameters were determined in the laboratory within 24 h of sampling using standard methods described by APHA (2001). Iron ion (Fe^{3+}) concentration was measured spectrophotometrically with the 1,10-phenanthroline method. Total hardness (Ca + Mg), and calcium were measured by EDTA titration method. Magnesium concentration was calculated as the difference between total hardness and Ca concentration. Sulphate concentration was measured with turbidity spectrophotometric method. Two phosphorus (P) forms were determined: soluble reactive P (SRP) in less than 0.45 μm fraction and total P (TP) by peroxodisulphate UV digestion of unfiltered sample. Both SRP and TP fractions were analysed spectrophotometrically with the phosphormolybdenum blue method of Murphy and Riley (1962), as modified by Neal *et al.* (2000). Nitrogen (N) forms were analysed spectrophotometrically, using reagents by Riedel de Häen, according to the following methods: NH_4^+ – indofenol blue method, NO_2^- with sulfanilic acid by the chromotropic acid method and NO_3^- with N-(1-naphthyl)-ethylenediamine with the zinc catalyst method. The analyses of dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and total nitrogen (TN) concentrations were carried out using the high temperature catalytic combustion method with a Shimadzu carbon analyser (TOC-L, Japan). Water samples for DOC determinations were filtered through a 0.45 μm filter, acidified with 2 M HCl to ~pH 2 and rinsed with synthetic air CO_2 free to remove traces of inorganic carbon. Chlorophyll-*a* concentration was determined by the spectrophotometric method with ethanol extraction (ISO, 1992).

Relationship between *G. semen* biomass and chemical factors was searched with the use of Pearson correlation coefficients. Analysis was performed using Gnumeric spreadsheet ver. 1.10.13 software.

3 Results

3.1 *Gonyostomum semen* biomass, chlorophyll-a and bacterial abundance

In three (Suchar I, Suchar II and Wądołek) out of four studied lakes, the mean biomass of *G. semen* in vertical water column was >1.0 mg dm^{-3}, with the highest value in lake Suchar I (3.9 mg fresh weight dm^{-3}). In lake Widne, mean biomass of the algae was much smaller and equals 0.09 mg FW dm^{-3}. In three mentioned lakes the distribution of studied flagellate was clearly uneven with at least two various patterns which appeared in the vertical water column (Fig. 1). In lake Suchar I, the algae population was very sparse at representing thick epilimnion depth of 1 m (0.08 mg FW dm^{-3}), increasing significantly with the increasing depth, reaching the highest biomass (7.4 mg FW dm^{-3}) at the near-bottom, poorly oxygenated ($O_2 = 1.5$ mg dm^{-3}) and dark (Secchi depth = 1.2 m) layer of 4 m. The opposite pattern was found in lake Suchar II, where the highest algae biomass was noted in the epilimnetic depths of 1 and 2 m (4.7 mg FW dm^{-3} and 3.1 mg FW dm^{-3}, respectively). In metalimnion (3–5 m) the biomass was several-fold lower (0.5–1.0 mg FW dm^{-3}) as well as in the nearly anoxic ($O_2 = 0.6$–0.8 mg dm^{-3}) hypolimnetic layer (6–8 m) at which the population was very sparse (fresh weight: 0.1–0.3 mg dm^{-3}). Similar (to a certain extent) pattern was observed in the deepest (12 m) lake Wądołek. We found the highest *Gonyostomum* biomass (1.5–2.2 mg FW dm^{-3}) in the upper three meters, although this layers of water represented both well oxygenated and light-saturated epilimnion (1 m) and weakly oxygenated (O_2 at 2 m = 2.7 mg dm^{-3}, below 3 m < 1 mg dm^{-3}) and dark (water transparency = 0.8 m) upper metalimnion (2–3 m). At subsequent depths (4–6 m) the biomass of the flagellate was two-fold lower (0.9–1.2 mg FW dm^{-3}) and below 7 m had the values <0.3 mg FW dm^{-3} (Fig. 1).

The concentration of chlorophyll-*a* in the water column of studied lakes reflected the vertical distribution of *G. semen* only in two lakes (Fig. 1, Tab. 2). It was the most clear in Suchar I, where we noted very low concentration (6.5 μg dm^{-3}) in epilimnetic layer and several hundred higher in meta- and hypolimnion (241.2±165 μg dm^{-3} and 470.9 μg dm^{-3}, respectively). It was also visible in lake Wądołek, where the highest values of this parameter were noted in metalimnetic layer. In lake Suchar II chlorophyll-*a* concentrations did not reflect *Gonyostomum* biomass vertical distribution: we found that chlorophyll-*a* values increased with the increasing depth (Tab. 2). Although we had no biomass data concerning other than *G. semen* planktonic algae, microscopic examination (without counting) showed that in Suchar I other species was on negligible biomass level, while in Suchar II and Wądołek there were scarce populations of small cryptomonads and chlorophytes. In lake Widne at all depths, the advantage of

Table 2. Biological, physical and chemical parameters in vertical water column of studied lakes (epi = epilimnion, meta = metalimnion, hypo = hypolimnion; chl-*a* = chlorophyll-*a*, GB = *G. semen* biomass, zoo = total zooplankton biomass, BA = bacterial abundance, C = water colour).

	Suchar I			Suchar II			Wądołek			Widne	
	epi	meta	hypo	epi	meta	hypo	epi	meta	hypo	epi	meta
GB [mg dm^{-3}]	0.08	4.08±1.5	7.39	3.90±1.1	0.70±0.2	0.22±0.1	1.47	1.69±0.6	0.47±0.4	0.09	0.12 ±0.11
chl-*a* [µg dm^{-3}]	6.5	241.2±165	470.9	47.4±19.6	63.1±53.3	71.6±50.5	39.1	153.5±54.5	50.5	13.4±2.8	134.8
zoo [mg dm^{-3}]	0.71	0.52	0.31	1.32	0.45	0.05	2.62	2.44	0.18	0.82	0.37
BA [10^6 cells ml^{-1}]	2.61	3.82±1.2	7.83	3.32	1.27±3.5	2.73±1.0	4.65	8.15±8.1	6.52±4.1	2.64 ±1.4	7.18
pH	7.8	6.2–7.1	6.0	6.7–8.1	5.9–6.2	6.1–6.2	6.1	5.8–5.9	5.8–5.9	6.9–7.2	6.3
EC [µS cm^{-1}]	24.1	29.2±8.8	39.7	27.9±9.5	24.0±2.3	31.2±0.6	54.2	32.8±3.7	40.5±10.3	64.6±47.9	41.3
DOC [mg dm^{-3}]	9.9	10.3±0.5	11.3	7.7±0.9	6.8±0.1	7.4±0.3	16.4	13.3±0.3	13.3±0.5	14.1±6.5	9.8
DIC [mg dm^{-3}]	3.2	3.4±0.3	4.2	3.5±0.1	3.3±0.6	4.1±0.4	3.2	3.6±0.2	4.1±0.4	4.2±0.8	4.0
C [mg Pt dm^{-3}]	87.8	85.9±8.4	141.5	72.5±2.1	87.3±10.6	117.1±59.8	133.0	158.8±14.5	160.4±10.2	43.6±10.3	36.2
TP [µg dm^{-3}]	49.2	89.7±5.7	98.3	331.8±28.0	463.5±21.6	153.5±74.0	52.3	64.2±26.1	87.8±96.5	53.0±30.3	111.6
SRP [µg dm^{-3}]	14.6	19.7±4.2	40.2	27.8±0.5	18.1±2.2	30.7±3.0	34.3	8.1±2.9	38.7±49.6	21.2±9.8	16.3
TN [mg dm^{-3}]	0.761	0.823±0.01	0.824	0.610±0.04	0.988±0.183	1.5±0.06	0.850	0.869±0.16	1.482±0.92	0.764±0.02	0.796
NH_4-N [µg dm^{-3}]	228.3	170.7±11.2	142.7	179.1±12.6	240.8±43.8	263.2±13.4	178.1	169.4±17.2	353.7±266	250.3±19.5	206.5
NO_3-N [µg dm^{-3}]	49.7	75.3±8.7	90.5	123.2±65.8	276.5±334.0	93.8±13.2	83.5	93.6±13.4	94.9±11.9	40.6±3.5	50.7
Ca [mg dm^{-3}]	9.4	9.5±0.1	9.5	7.3±1.8	7.7±0.8	8.1±0.6	9.2	9.1±0.1	9.6±0.3	12.2±1.4	11.7
Mg [mg dm^{-3}]	0.851	0.881±0.04	0.668	0.456±0.45	1.742±0.33	2.043±2.54	0.790	0.972±0.18	1.114±0.26	1.722±1.30	1.337
SO_4 [mg dm^{-3}]	11.1	15.2±2.8	13.1	13.8±2.5	14.0±4.2	13.5±2.4	13.2	14.1±0.3	14.7±0.5	10.9±1.2	10.3
Fe [mg dm^{-3}]	2.32	2.67±0.5	3.4	1.65±0.2	1.96 ±0.07	2.52±0.35	2.12	1.74±1.10	1.82±1.35	1.47±0.88	2.32

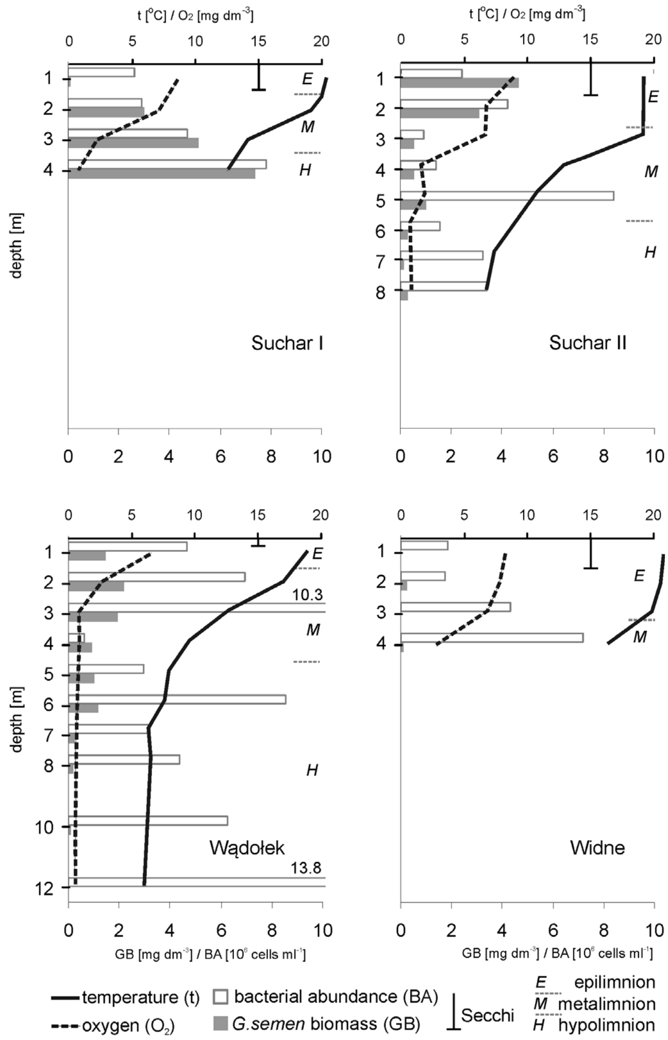

Fig. 1. *Gonyostomum semen* biomass, bacterial abundance, temperature and oxygen content in the vertical column of four studied lakes.

representatives of other algae groups over raphidophytes was recorded. The highest biomass reached zygnematophytes (1 m), dinoflagellates (2 m and 3 m) and cryptomonads (4 m).

The bacterial abundance in studied lakes varied between 3.28×10^6 cells ml^{-1} and 6.82×10^6 cells ml^{-1} (mean values for the water column). In lake Suchar I bacterial number in the water column was higher with the increasing depth, reaching the highest values at 4 m (11.84×10^6 cells ml^{-1}), which reflected the pattern of *G. semen* vertical distribution (Fig. 1). Increased bacterial abundance at depths where *Gonyostomum* formed higher biomass was also noted in two other lakes but only in upper layers (1–4 m in Suchar II and 1–5 m in Wądołek). This pattern could not be seen at deeper layers, for example in lake Suchar II, at 5 m the peak of bacterial abundance (8.37×10^6 cells ml^{-1}) was observed, while flagellate biomass was on relatively low level. Similar case was observed in lake Wądołek at depth of 6 m (Fig. 1). In lake Widne, where *Gonyostomum* biomass in the water column was very low, bacterial abundance shown similar pattern to lake Suchar I, when increased values occurred with the increasing depth (Fig. 1).

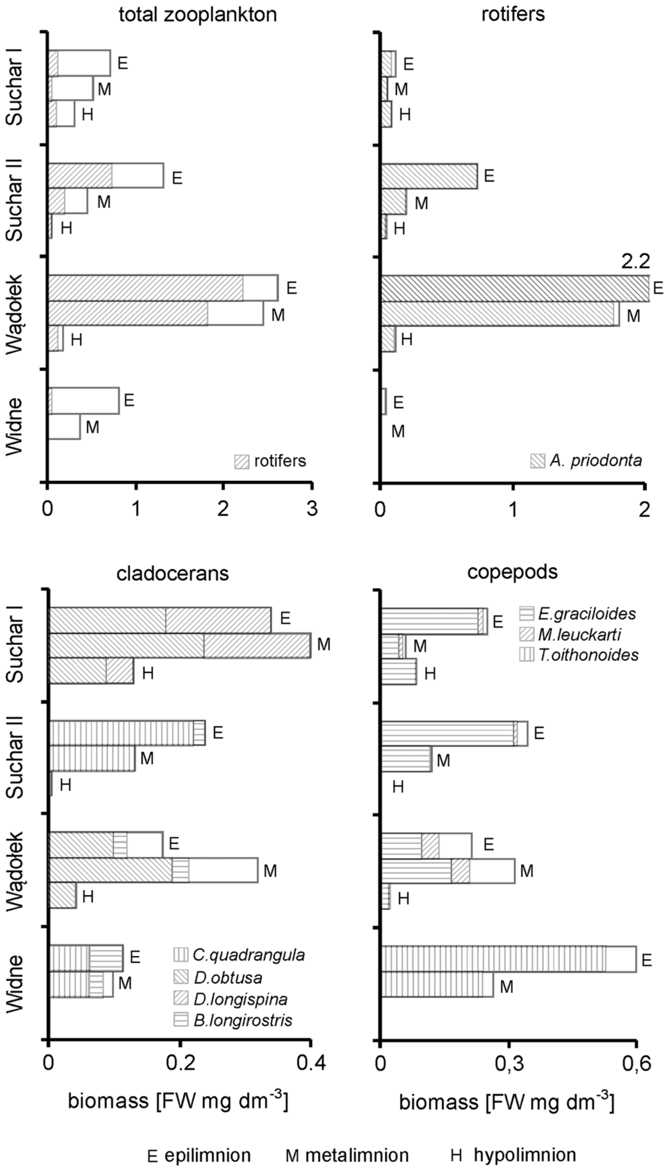

Fig. 2. Biomass of total zooplankton, rotifers, cladocerans and copepods with dominant species in three thermal layers of studied lakes.

3.2 Zooplankton

The total biomass of zooplankton (crustaceans and rotifers) was clearly the highest in Wądołek lake (1.74 mg FW dm^{-3}, mean for the water column). In three other lakes the values of this parameter was more or less similar and range between 0.51 mg FW dm^{-3} and 0.60 mg FW dm^{-3} (means for the water column). Vertical distribution of zooplankton in studied lakes was analysed in the water column in three layers (epilimnion, metalimnion and hypolimnion, Fig. 2). In all lakes the highest zooplankton biomass was found in epilimnion, although in two of them (Suchar I and Wądołek) the metalimnetic zooplankton communities were likewise abundant (epi *vs.* meta: 0.70 *vs.* 0.52 mg FW dm^{-3}; 2.61 *vs.* 2.44 mg FW dm^{-3}, respectively). Interestingly, in lake Suchar I total zooplankton biomass in near-bottom, poorly oxygenated layer of 4 m was on moderate level and amounted 0.30 mg FW dm^{-3}. In other lakes with high *Gonyostomum* biomass (Suchar II, Wądołek) the hypolimnetic zooplankton was scarce (0.05 mg FW dm^{-3} and 0.17 mg FW dm^{-3}, respectively).

Clear differences in zooplankton structure among studied lakes was found (Fig. 2). Rotifers dominated the biomass in lake Wądołek (in epilimnion – 85%, in metalimnion – 74% of the total biomass) and Suchar II (55% and 44%, respectively) while in lake Suchar I cladocerans prevailed (49% and 79%, respectively) with small share of rotifers (10–16%). In epilimnion and metalimnion of this lake we found the highest biomass of cladocerans among all studied lakes. What is interesting, in all mentioned lakes one species dominated the rotifer community – *Asplanchna priodonta*, which comprised 76–99% of the group biomass. In lake Widne (where *G. semen* formed very small biomass) rotifers had insignificant share in the total zooplankton biomass. Cladocerans in lake Suchar I were dominated by two large-bodied *Daphnia* species (*D. longispina*, *D. obtusa*); the latter one being also a dominant in lake Wądołek. Clearly different cladoceran structure was found in lake Suchar II, where small-bodied *Ceriodaphnia quadrangula* together with *Bosmina longirostris* comprised 100% of the cladoceran biomass. Copepods in lakes with high *Gonyostomum* biomass was dominated by *Eudiaptomus graciloides*, while in lake Widne the most numerous species was *Thermocyclops oithonoides* (which did not occur in other lakes).

3.3 Hydrochemical parameters

All the investigated lakes have represented water quality typical for humic lakes with low pH (less than 7 pH) except the Suchar I in the epilimnion layer. The lowest pH value has been recorded in the Suchar II metalimnion layer. Investigated lakes were characterized by a small content of mineral substances in water, as shown by EC values ranging from 24 µS cm^{-1} (metalimnion layer in Suchar II) to 64.6 µS cm^{-1} (epilimnion of Widne Lake). This is confirmed with the results obtained for such parameters as Ca^{2+}, Mg^{2+}, $SO_4^{3-}$and $Fe^{2+/3+}$ significantly affecting EC values (Tab. 2).

An important indicator of dystrophy advance is the DIC to DOC ratio, which in any lake case is less than 1 (Tab. 2). TP concentrations in the individual water layers are on average in the range of up to 50 µg dm^{-3} to 110 µg dm^{-3} except for Suchar II, where TP values were much higher (Tab. 2). This pattern was not observed for SRP, whose concentrations in all investigated lakes were close to each other with the maximum values of soluble reactive phosphorus at the bottom water layer (Tab. 2). Total nitrogen in all tested lakes had similar values, and a gradual increase of this element along with depth was observed; however, the concentration of ammonium ions was usually two to three times higher as compared to the concentration of nitrate ions in all sampled depths. The smallest concentrations of NO_3-N were recorded in Widne Lake and the highest in Suchar II. The vertical changes of this parameter in Suchar II were characterized with maximum concentration in the metalimnion (Tab. 2). Concentrations of ammonium ions ranged from about 140 µg dm^{-3} in the hypolimnion of Suchar I to about 350 µg dm^{-3} in the hypolimnion of Wądołek Lake. In case of NH_4-N, the concentration changes of this parameter with the depth were described in two patterns: gradual decrease of concentration (Suchar I and Widne) and gradual increase (Suchar II and Wądołek) (Tab. 2). There was a significant negative correlation between *Gonyostomum* biomass and NH_4-N concentration in all lakes ($r^2 = 0.65$, $p < 0.001$). However, no significant correlation was found between the flagellate biomass and SRP concentration or NO_3-N content (Fig. 3), as well as in the case of the other hydrochemical parameters.

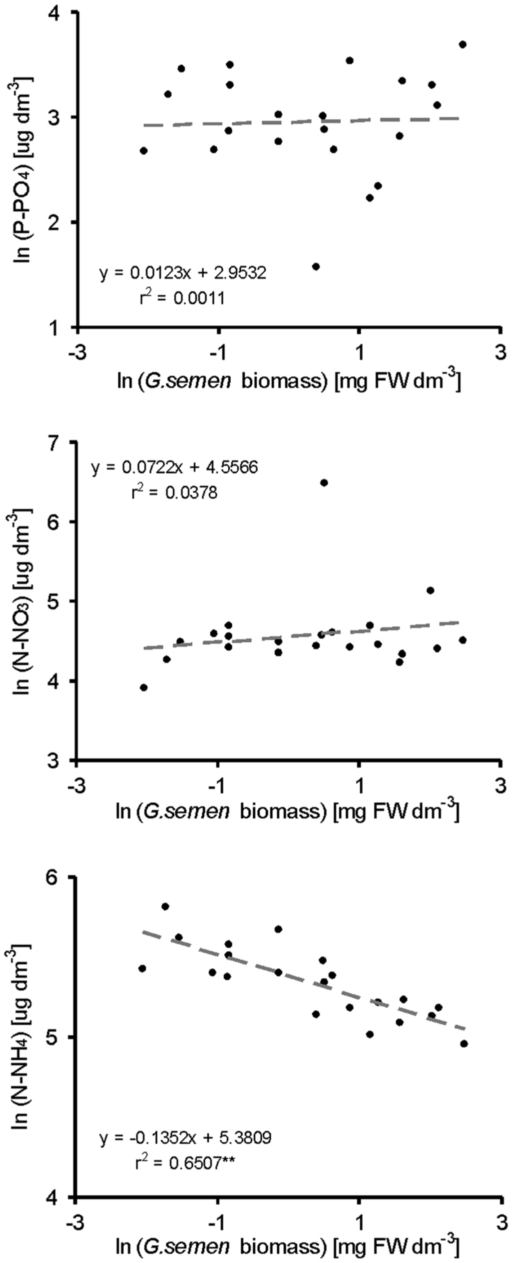

Fig. 3. Relationships between *Gonyostomum semen* fresh biomass (ln) and concentration of nutrient mineral forms (ln) (Pearson correlation coefficients with *t*-Student tests, two asterisks show statistical significance $p < 0.001$).

4 Discussion

The results of our study showed that *G. semen* daytime vertical distribution in the water column clearly varied among three small and stratified lakes with similar morphometric and chemical features. Diverse patterns of *G. semen* distribution was reflected in various ways in the bacterial, rotifer and crustacean vertical distribution, as well as in the taxonomic structure of zooplankton communities. Moreover, we found, that during a daytime, high *G. semen* biomass might influence the mineral content of the vertical water column, as can be seen in the case of ammonium ions.

Early studies on *G. semen* vertical distribution stated that the alga forms its density peak in the surface layer (Salonen and Rosenberg, 2000) or that its distribution is strictly dependent on the weather conditions (Eloranta and Räike, 1995). However, Cronberg *et al.* (1988) showed that *G. semen* could be vertically distributed in various ways in the same lake during summer period. This was later confirmed by Pęczuła *et al.* (2014), who suggested that a pattern of *G. semen* vertical distribution in the water column is not universal, but rather depends on particular lake conditions, including phosphate content, light climate and zooplankton. It is also well-established from a variety of studies (Cowles and Brambel, 1936; Cronberg *et al.*, 1988; Pithart *et al.*, 1997; Salonen and Rosenberg, 2000) that *Gonyostomum* migrates in the vertical water column (moves upward in the morning and downward in the afternoon); however, some studies showed that the species could stay in deep, anoxic and dark layers of the water column through most of the diurnal cycle (Pęczuła *et al.*, 2014). Such pattern might occur in the case of lake Suchar I, where the density peak in the near-bottom layer with very sparse population in the epilimnion was found. In other studied lakes, *G. semen* distribution in the vertical profile was: reversed (decreased biomass with increasing depth in Suchar II), non-linear (the density peak in the metalimnion in Wądołek) or the algae population was very sparse or virtually absent (Widne). All studied lakes had common morphometric and chemical characteristics, which are known to support *Gonyostomum* high biomass development: small surface area with high relative depth which enables sharp thermal stratification to develop, slightly acidic or circumneutral pH, low level of calcium, moderate/high humic and phosphorus content (Rosén, 1981; Lepistö *et al.*, 1994; Reynolds *et al.*, 2002; Rengefors *et al.*, 2012; Pęczuła, 2013; Pęczuła *et al.*, 2013; Karosiene *et al.*, 2014). The similarity of water quality parameters in studied lakes (both among them and within their water columns) taken together with diverse patterns of *G. semen* vertical distribution, points to a zooplankton as a potential factor influencing this diversity.

Flagellate algae can migrate at a rate of 1 m h^{-1} and are able to move through big temperature gradients which enables them to change their position in the vertical water column during a day (Salonen *et al.*, 1984; Jones, 1988). It was suggested that, among others, grazing pressure by zooplankton may influence these changes (Arvola *et al.*, 1992). Parallel to *G. semen*, migrations maintained by rotifers (*Polyartha vulgaris*, *A. priodonta*) and crustaceans (*C. quadrangula*, *E. graciloides*) were observed in some studies (Salonen and Rosenberg, 2000; Pęczuła *et al.*, 2014), which suggested that zooplankton has a potential role in shaping the algae vertical distribution in lakes. However, the role of zooplankton control of *G. semen* by grazing is still discussed. The alga was previously considered inedible due to its large dimensions which are above the preferred size range for many filter-feeding zooplankton as well as the presence of trichocysts, which eject threads of mucilage in a mechanical stress (Cronberg *et al.*, 1988; Havens, 1989). Nevertheless, recent studies had showed that *G. semen* mucilage is not harmful for *Daphnia magna*; moreover, disintegrated cells of the alga may serve as nutritive component enhancing daphnids body growth (Pęczuła *et al.*, 2017). Also, many recent experimental studies revealed that *Gonyostomum* may be directly grazed by zooplankton, including rotifers (*A. priodonta*), cladocerans (*Daphnia magna*, *Daphnia pulicaria*, *Holopedium gibberum*) or copepods (*Diaptomus oregonensis*, *Eudiaptomus gracilis*) (Williamson *et al.*, 1996; Lebret *et al.*, 2012; Johansson *et al.*, 2013; Björnerås, 2014).

In lake Suchar, where *G. semen* population was virtually absent in epilimnion and increased with the increasing depth, we found large bodied daphnids (*D. pulicaria*, *D. longispina*) and copepod *E. graciloides* as dominating in the water column, with their density peak in epilimnion and metalimnion. Rotifer *A. priodonta*, which dominates in other two lakes with high *Gonyostomum* biomass (especially in lake Wądołek) had very small abundances there. It is a well-known pattern, that communities of large-bodied zooplankton, *i.e. Daphnia* can graze more intensively on phytoplankton than communities dominated by rotifers or small-bodied cladocerans like *Bosmina* (Agasild and Nõges, 2005). It was also confirmed by a series of laboratory feeding experiments on *G. semen*. *A. priodonta*, which is a common zooplankter in *Gonyostomum*-dominated lakes (Cronberg *et al.*, 1988) showed an average ingestion rate of the algae at 680 cells d^{-1} (Björnerås, 2014). Large-bodied crustaceans fed on *G. semen* with higher rate – for *Daphnia magna* it was 696–1922 cells d^{-1} (Lebret *et al.*, 2012), for *H. gibberum* – 2160 cells d^{-1} and for *E. gracilis* – 1872 cells d^{-1} (Johansson *et al.*, 2013). Thus, we can suppose, that in lake Suchar I the specific vertical pattern of *G. semen* (the most abundant population in anoxic hypolimnion) is strongly shaped by the presence of large-bodied effective feeders in the upper layer. Grazer-avoidance behaviour in *G. semen* was revealed experimentally by Hansson (2000), which showed that cyst recruitment of this alga is inhibited by the presence of Cladocera and hypothesised the existence of some chemical cues which might be received by *Gonyostomum*. Similar pattern of *G. semen* vertical distribution was described by Pęczuła *et al.* (2014) in small humic lake of 5 m depth, where dense algae population stayed most of the diurnal cycle in near-bottom layers moving at noon upwards only to the bottom of the euphotic zone, dominated by crustaceans. Different patterns of *G. semen* vertical distribution in lake Suchar II (with algae population as dense as in Suchar I, but concentrated in epilimnion) may be influenced by a smaller grazing pressure. It seems that small-bodied cladocerans (*C. quadrangula* and *B. longirostris*) with rotifer *A. priodonta* were not able to control *Gonyostomum* population effectively there, thus the algae may develop in high biomass in surface layers. Very poor grazing ability of *Ceriodaphnia* ssp. when fed on *Gonyostomum* was showed by Johansson *et al.* (2013)

in experimental laboratory conditions (ingestion rate ca. 30 cells d^{-1}). In lake Wądołek, where total zooplankton biomass was two- to three-fold higher than in the other lakes, *G. semen* biomass was twice lower than in lakes Suchar I and Suchar II. There was also a population of large-bodied *D. obtusa* there, which taken together led to the conclusion that *G. semen* population is effectively controlled in this lake. In lake Widne with very scarce *G. semen* population we observed the most different zooplankton community, with lack of *A. priodonta* and copepod *T. oithonoides* instead of *E. graciloides* which dominated in the other lakes. Lack of this species might suggest that they prefer only these humic lakes, which suffer with high *G. semen* biomass; however, we cannot deliver any evidences as our data set is too small.

The grazing pressure of zooplankton on *Gonyostomum* was probably decreased also by the presence of other algae as well as bacteria in the water column. The concentration of chlorophyll-*a* in the water column strictly followed the biomass of *G. semen* only in lake Suchar I. In other lakes, phytoplankton community consisted also with small flagellates – mainly cryptomonads as well as with small coccoid. As it was showed by Gladyshev *et al.* (1999), *Cryptomonas erosa* was the most preferable algal species during feeding experiments with *C. quadrangula*, which appeared to be a selective grazer. *Cryptomonas* spp. is considered as a very valuable food source also for other zooplankton species (Brett *et al.*, 2009). This fact may decrease zooplankton grazing pressure on *Gonyostomum* in those of studied lakes in which there was more diverse phytoplankton community (Suchar II and Wądołek). Bacterial abundance in water column of studied lakes appeared to be diversified as well. We noted some interesting pattern in which bacterial abundance reflected (in various degree depending on the lake) the pattern of *G. semen* vertical distribution (in whole water column in lake Suchar I, 1–4 m in Suchar II and 1–5 m in Wądołek). We can hypothesize that extended bacterial growth may occur on the disintegrated algal biomass, which is a known phenomenon at the end of algal bloom (Van Boekel *et al.*, 1992). Kamiyama *et al.* (2000) noted the increase of bacteria numbers at the end of other raphidophyte species (*Heterosigma akashiwo*) bloom. Moreover, Johansson *et al.* (2016b) found that in lakes with higher *G. semen* biomass, cladoceran species contained more bacterial fatty acids than those of algal origin which points to suggestion that during *Gonyostomum* bloom an increased utilization of bacterial resources by zooplankton take place. However, the high abundance of bacteria (increasing with depth) was noted also in lake Widne, where *Gonyostomum* biomass was very low, thus making the explanation of the observed patterns more complicated.

Although total nitrogen in all studied lakes had similar values, we observed the two- to three-fold higher concentration of ammonium over the nitrate form. Nitrate ions are sensitive to the low-redox conditions which occurs in humic stratified lakes experiencing high biochemical oxygen demand as a result of higher DOC concentration. Under these conditions the nitrate reduction to ammonium and gaseous nitrogen is accelerated through microbial oxidation of organic matter. The principal forms of nitrogen available to algae are nitrate, nitrite and ammonium ions (Reynolds, 2006), however natural populations of phytoplankton usually appear to exhibit preferential uptake of NH_4^+ over NO_3^- (Berman *et al.*, 1984). Thus, high concentration of ammonium ions in studied lakes created good conditions for development of phytoplankton, especially *G. semen*. According to Domingues *et al.* (2011) preference for ammonium are group-specific and it was observed mainly in green algae and cyanobacteria. Probably *G. semen* may be one of the species better adapted to ammonium rather than nitrate uptake, especially that such preferences were described in other raphidophytes, like *H. akashiwo* (Herndon and Cochlan, 2007). Moreover, the negative and significant correlation between *G. semen* biomass and NH_4-N concentration which was observed in our lakes suggests that during the day, the alga intense ammonium uptake may significantly change the mineral content of the water column. Such phenomenon is observed inside blooms of other species, when ambient concentrations of inorganic nutrient forms may be reduced or even depleted due to algal incorporation into its biomass (Heisler *et al.*, 2008). Thus, our results may serve as further example of the influence of *G. semen* on the lake ecosystem, as it was earlier revealed or suggested in case of plankton, benthic invertebrates or fish (Trigal *et al.*, 2011; Angeler and Johnson, 2013; Karosiene *et al.*, 2014; Pęczuła *et al.*, 2017). Further research including laboratory tests as well as day/night nutrient dynamics within the lake ecosystems dominated by the species may make this topic more clear.

The present study enhanced the understanding of the ecology of the expanding flagellate alga *G. semen*, particularly in terms of its vertical distribution and its influence on lake ecosystem. Our study confirms some previous findings but also contributes additional evidence suggesting that vertical distribution of this alga in humic lakes may be shaped by zooplankton structure and abundance. We also suppose that high *G. semen* biomass may modify some parameters of the water column, as it was showed in case of ammonium ions. However, with a small sample size caution must be applied in extrapolation of the results to other humic lake ecosystems; thus our study should be considered as a preliminary one and additional further research on this topic is strongly recommended.

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