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THE GENUS *WORONICHINIA* (CYANOBACTERIA) IN NATURAL LAKES OF DRAWA NATIONAL PARK (POLAND)

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Abstract. *Woronichinia* Elenkin is a cyanobacteria genus characteristic of lentic ecosystems. The type species, *W. naegeliana* (Unger) Elenkin, often blooms in the plankton of eutrophic reservoirs but this genus also contains species sensitive to high nutrient concentrations. The study analyzed the diversity and biomass of *Woronichinia* in lakes in a national park, isolated from the direct impact of human activity. The lakes were in various trophic states resulting from gradual and natural changes of trophy. Trophy was assessed with the use of the trophic diatom index, according to the classification we proposed for natural lakes. The relationship between the biomass and the trophic state of lakes was investigated with the use of multivariate unconstrained analysis with supplementary variables. Five species of *Woronichinia* were identified in all trophic types of lakes except for two oligotrophic ones: *W. compacta* (Lemmerm.) Komárek & Hindák, *W. delicatula* (Skuja) Komárek & Hindák, *W. karelica* Komárek & Komárk.-Legn., *W. obtusa* Joosten and *W. naegeliana* (Unger) Elenkin. The occurrence and biomass of the species were related to the trophic state of the lakes. The absence of *Woronichinia* in two oligotrophic lakes could be due to the high concentration of humic compounds in the sediments. The low nitrogen-to-phosphorus ratio characteristic of the oligo-mesotrophic lakes resulted in increased species diversity. The lakes' isolation from human activity fostered the development of rare and sensitive species such as *W. delicatula* and *W. karelica*.

Key words: Cyanobacteria, diversity, natural eutrophication, trophic status, natural lakes, *Woronichinia*

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INTRODUCTION

In times of expanding urbanization and industrialization, aquatic ecosystems unaffected or slightly affected by human impacts are extremely rare. Changes in nutrient levels in these ecosystems are gradual, and transformation of environmental conditions from oligotrophy to eutrophy is very slow (Kociolek & Stoermer 2009; Leng 2009). The diversity of cyanobacteria in naturally eutrophic ecosystems has been neglected by taxonomists, whose attention has been focused on cyanobacteria in anthropogenically changed ecosystems. Habitats that have maintained their natural character are important biodiversity sites due to their potential to host rare, sensitive, endangered and endemic species (Cantonati *et al.* 2012). Rising awareness of the threats to such ecosystems or habitats has led to their being placed under different forms of conservation (Kociolek & Stoermer 2009; Cantonati *et al.* 2012).

The genus *Woronichinia*, distinguished and described by Elenkin (1933), is a characteristic genus of cyanobacteria in standing-water ecosystems. The type species of the genus, *Woronichinia naegeliana* (Unger) Elenkin, previously known as *Coelospharium naegelianum* Unger, is widespread in ecosystems with high nutrient content. It often blooms in the plankton of meso-eutrophic to eutrophic reservoirs, and produces toxins (Scot 1991; Skulberg *et al.* 1994; Wilk-Woźniak & Mazurkiewicz-Boroń 2003; Wilk-Woźniak *et al.* 2006). Many *Woronichinia* species prefer oligo- and mesotrophic waters with low nutrient levels: for example, *W. ruzickae* Komárek & Hindák or *W. elorantae* Komárek & Komárk.-Legn. (Komárek & Hindák 1988; Komárek & Komárková-Legnerová 1992; Komárek & Anagnostidis 2008).

Woronichinia is one of six genera of the Coelosphaeriaceae family (Komárek *et al.* 2014).

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Seventeen species were described within *Woronichinia* (Komárek & Anagnostidis 2008; Joosten 2006; Komárek & Hauer 2013). Two, *Gomphosphaeria wichurae* (Hilse & Rabenhorst) Drouet & Daily and *W. hungarica* Hortobágyi, have an unclear status; probably they are morphotypes of *W. naegeliana* (Komárek & Anagnostidis 2008). For the genera, Joosten (2006) distinguishes three species that are new combinations from the genus *Coelomoron*: *W. pusilla* (A. C. J. van Goor) Joosten, *W. tropicalis* (Senna, Peres & Komárek) Joosten and *W. microcystoides* (Komárek) Joosten.

All *Woronichinia* species are limnophilic. The characteristic morphological structure of colonies allows *Woronichinia* to develop in habitats of lentic water ecosystems, such as the benthos, periphyton, metaphyton and plankton. New colonies develop from single cells released from old and disintegrated colonies in the form of expulsing cells. Longitudinal division of cells, perpendicular to one another in successive generations, and perpendicular to the colony surface, results in the formation of new colonies whose cells are arranged only at the peripheral layer. The cells are attached to a system of mucilaginous stalks, and the colonies are enveloped by hydrated mucilage often visible only after staining (Komárek & Hindák 1988; Komárek & Komárková-Legnerová 1992; Komárek & Anagnostidis 2008; Pliński & Komárek 2007). Such a structure of a colony allows it to float freely in the water column.

The genus *Woronichinia* is closely related phylogenetically to the genus *Snowella* Elenkin (Rajaniemi-Wacklin *et al.* 2006). The resemblance is reflected in their high morphological similarity. The two genera occur in similar habitats and often co-occur in aquatic ecosystems, but there are some differences in colony structure as a result of differences in reproduction and colony growth. Longitudinal division of the usually oval *Woronichinia* cells initiates a split of the mucilaginous stalks along their entire length. Such division results in the formation of a colony whose cells are attached to radially orientated stalks. The cells are arranged more or less densely on the colony surface, though relatively evenly, along the peripheral layer. The mucilaginous stalks are wide, often as wide as the width of the cells, and transparent, visible only after staining. In contrast to *Woronichinia*, *Snowella* has mostly spherical cells, also attached to mucilaginous stalks, but after cell division the stalks do not split along their entire length. As a result, a system of thin, branched and usually visible stalks is formed. The partial split of the stalks causes the difference in the arrangement of the cells at the colony surface. *Snowella* cells are arranged unevenly, sometimes irregularly, and within different layers at the periphery of the colony (Komárek & Hindák 1988; Komárek & Komárková-Legnerová 1992; Komárek & Anagnostidis 2008).

This research addressed the diversity of the cyanobacteria genus *Woronichinia* in lakes characterized by various trophic states resulting from gradual and natural changes in trophy. The scope of the research included trophic status assessments of the lakes, taxonomic analyses of *Woronichinia* species, quantitative estimation of species based on their biomass, and analyses of the relationship between species occurrence (biomass) and environmental conditions (water pH, conductivity, oxygen content, trophic state).

STUDY AREA

The research was conducted in 12 lakes in Drawa National Park (DNP), Poland (Fig. 1). DNP was created in 1990 to protect the unique glacial landscape of the southern part of the Pomeranian Lake District. The lakes were formed during the last Pleistocene glaciation (Vistulian glaciation) (Kraska 1997; Pawlaczyk 1997). All the lakes are in the valley of the Płociczna River, except for Arkońskie Lake which is in the valley of Moczel Stream. The lakes are surrounded by a hard-to-reach forest area, and they differ due to the differences in the basins' morphometry, hydrology and land uses (Table 1).

The legal regulations stemming from conservation of the national park, and the lack of industry in the vicinity of the DNP, create an environment in which the lakes are isolated from direct human impacts. These aquatic ecosystems have not yet been transformed by humans and have maintained their

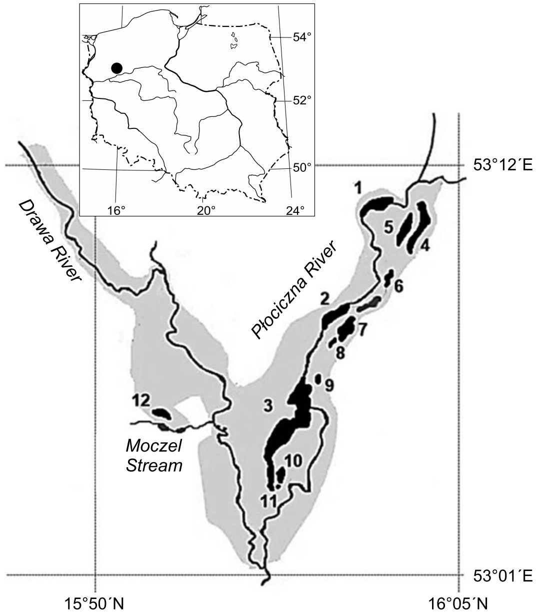

Fig. 1. Location of the studied lakes in Drawa National Park. 1 – Sitno, 2 – Płociczno, 3 – Ostrowieckie, 4 – Marta, 5 – Płociowe, 6 – Zdroje, 7 – Piaseczno Duże, 8 – Piaseczno Małe, 9 – Pustelnik, 10 – Czarne, 11 – Perkoz, 12 – Arkońske.

natural character. The annual inflow of biogenic compounds to these outflow-type and non-outflow-type lakes is low and moderate. The average nitrogen-to-phosphorus ratio (N:P) ranges between 30:1 and 35:1. The main source of nutrients is surface runoff from the forest area and precipitation. Higher biogenic loads are noted in lakes on the course of the Płociczna River. There the N:P ratio is *ca* 10:1, and these lakes are characterized by a higher trophic state (Szyper & Kraska 1997, unpubl.).

MATERIAL AND METHODS

ASSESSMENT OF THE ENVIRONMENTAL BACKGROUND

Basic physical and chemical properties of water such as pH, conductivity and dissolved oxygen were measured in May, June, July and September of 2013 with Elmetron CC-104, CP-401 and CO-401 field equipment.

The trophic status of the DNP lakes was assessed on the basis of indicator benthic diatoms. Benthic water samples for qualitative and quantitative analysis of diatom assemblages were collected in May, June, July and September 2013. Diatoms were extracted from the samples according to the procedure of Żelazna-Wieczorek (2011), embedded in Naphrax® resin, and analyzed on the basis of cell wall morphology. The quantitative shares of diatoms were estimated from each permanent slide by counting 400 diatom valves (Cholnoky 1968). The trophic diatom index (TDI) was calculated with the use of OMNIDIA 4.1 software, based on the qualitative and quantitative analyses. The trophic status of the ecosystems was classified according to the TDI value and the trophic classification following

Table 1. Characteristics of the studied lakes in Drawa National Park, according to Czerniawski *et al.* (2010) and Szyper and Kraska (1999, unpublished).

No.	Lake	Type	Area [ha]	Mean / max. depth [m]	Capacity [km^3]	Nutrient input [kg/year]		Main source of nutrients
						N	P	
1	Sitno	on flow	74.2	4.0 / 7.0	2666.7	87608	8975	Płociczna River
2	Płociczno	on flow	56.2	2.7 / 5.3	1530.9	103267	9483	Płociczna River
3	Ostrowieckie	on flow	387.6	9.4 / 28.5	36433.1	111736	6657	Płociczna river
4	Marta	no outflow	66.1	7.7 / 25.0	5111.4	9949	318	Forest
5	Płociowe	no outflow	35.3	10.3 / 25.0	3620.0	2467	74	Forest, precipitation
6	Zdroje	outflow	21.3	2.9 / 4.8	612.1	3287	105	Forest
7	Piaseczno Duże	no outflow	58.7	7.6 / 25.9	4519.2	3030	87	Forest, precipitation
8	Piaseczno Małe	no outflow	8.0	3.2 / 6.8	258.4	418	12	Forest, precipitation
9	Pustelnik	outflow	2.7	2.4 / 5.1	65.76	686	22	Forest
10	Czarne	no ouflow	19.1	11.5 / 29.0	2196.5	846	24	Forest, precipitation
11	Perkoz	no ouflow	1.3	2.07 / 4.6	27.7	68	2	Forest, precipitation
12	Arkońskie	ouflow	13.1	2.7 / 3.8	n.d.	n.d.	n.d.	Forest, precipitation

Table 2. Physical and chemical properties of water, TDI values and trophic state of lakes in Drawa National Park.

No.	Lake	Water pH	Conductivity (mean) [µS/cm]	Oxygen content (mean) [mg/l]	TDI (mean)	Trophic state
1	Sitno	7.6	327	5.7	47.9	Oligo-highly mesotrophic
2	Płociczno	7.8	312	8.1	67.7	Eutrophic
3	Ostrowieckie	8.2	328	7.4	65.1	Eutrophic
4	Marta	7.8	220	7.9	42.5	Oligo-mesotrophic
5	Płociowe	8.1	236	8.2	40.1	Oligo-mesotrophic
6	Zdroje	7.8	270	7.6	48.6	Oligo-highly mesotrophic
7	Piaseczno Duże	8.3	303	8.1	37.1	Oligo-slightly mesotrophic
8	Piaseczno Małe	7.9	85	6.6	33.8	Oligotrophic
9	Pustelnik	7.6	39	5.3	31.7	Oligotrophic
10	Czarne	8.3	271	7.4	39.4	Oligo-slightly mesotrophic
11	Perkoz	8.1	331	6.4	35.2	Oligo-slightly mesotrophic
12	Arkońskie	7.8	102	7.8	33.9	Oligotrophic

Żelazowski *et al.* (2004). For the purpose of this research we proposed a division of the oligo-mesotrophic class according to Żelazowski *et al.* (2004) into three classes: oligo-slightly mesotrophic, oligo-mesotrophic, and oligo-highly mesotrophic, as follows: oligotrophy ($TDI \leq 35$), oligo-slight mesotrophy ($35 < TDI \leq 40$), oligo-mesotrophy ($40 < TDI \leq 45$), oligo-high mesotrophy ($45 < TDI \leq 50$), mesotrophy ($50 < TDI \leq 60$), eutrophy ($60 < TDI \leq 75$) and hypereutrophy ($TDI > 75$).

CYANOBACTERIA ANALYSIS

Benthic and metaphytic samples for cyanobacteria analysis were collected in May, June, July and September of 2013. Samples were collected live with a pipette aspirator into 125 ml containers and maintained at 4°C during transport to the laboratory. Then every sample was preserved with 2% solution of formaldehyde. Qualitative analysis was based on cell and colony morphology following Komárek and Hindák (1988), Komárek and Komárková-Legnerová (1992), Komárek and Anagnostidis (2008), Joosten (2006) and Rajaniemi-Wacklin *et al.* (2006). Species diversity was studied by LM at 400× and 1000×. Observations were documented with photographs taken with a Nikon E540 camera and scaled with Corel Photo-Paint X7 software at 1000×1 and 750×1.

The diameter of the *Woronichinia* colonies was measured ($n = 20$ for each species), and the average volume of the colonies was estimated from their diameter. Colonies were counted in a 0.05 ml volume of precisely mixed, non-concentrated material for each sample. The average volume of the colonies (Vc_i [mm^3]) and the number of colonies (Nc_i) was used for biomass estimation (B_i [mm^3/ml]) of each species in 1 ml of sample, as follows:

$$B_i = \frac{Vc_i \times Nc_i}{0.05}$$

The relationship between the biomass of the *Woronichinia* species and the basic properties of the water was assessed using multivariate constrained analysis – redundancy analysis (RDA). The trophic state of the lakes was determined using multivariate unconstrained analysis – principal component analysis (PCA) with supplementary variables. Both analyses employed CANOCO for Windows 5.1 (Lepš & Šmilauer 2003).

RESULTS

ENVIRONMENTAL BACKGROUND OF THE LAKES

The water of the studied lakes was slightly alkaline. Water pH ranged from 7.6 in Pustelnik and Sitno Lake to 8.3 in Piaseczno Duże Lake and Czarne Lake. Conductivity ranged from 39 µS/cm in Pustelnik Lake to 331 µS/cm in Perkoz Lake. The lowest oxygen concentration (5.3 mg/l) was recorded in Pustelnik Lake, and the highest (8.2 mg/l) in Płociowe Lake.

The trophic diatom index ranged from 31.7 to 67.7. The highest TDI was noted in the lakes on the Płociczna River: Płociczno Lake and Ostrowieckie Lake. The lowest TDI was noted in two small lakes isolated from the Płociczna River (Piaseczno Małe Lake, Perkoz Lake) and in one larger lake in the Moczel stream valley (Arkońskie Lake). Following the trophic state classification proposed for the research, three lakes were oligotrophic, three oligo-slightly mesotrophic, two oligo-mestrophic, two oligo-highly mesotrophic and two eutrophic. Data on the chemical properties of the water and the trophic status of the studied lakes are compiled in Table 2.

CYANOBACTERIA ANALYSIS

Five *Woronichinia* species were noted in the lakes of Drawa National Park: *W. karelica* Komárek & Komárk.-Legn. (Fig. 2A), *W. delicatula* (Skuja) Komárek & Hindák (= *Gomphosphaeria delicatula* Skuja) (Fig. 2B), *W. obtusa* Joosten [= *W. compacta* auct., non *W. compacta* (Lemm.) Komárek & Hindák) (Fig. 2C), *W. compacta* (Lemmerm.) Komárek & Hindák [= *Gomphosphaeria lacustris* var. *compacta* Lemm.; *G. compacta* (Lemm.) Ström] (Fig. 3A) and *W. naegeliana* (Unger) Elenkin [*Coelosphaerium naegelianum* Unger; *Gomphosphaeria naegeliana* (Unger) Lemm.] (Fig. 3B). The diagnostic characters of the identified species were in accordance with taxonomic references; data on the important morphological characters are compiled in Table 3. The morphologically similar species *Snowella litoralis* (Häyrén) Komárek & Hindák (Fig. 3C) was present together with the *Woronichinia* species.

Species of *Woronichinia* were noted in all trophic types of lakes except for two oligotrophic ones: Piaseczno Małe Lake and Pustelnik Lake. Most of the species were present in the metaphyton. Only *W. naegeliana* was present exclusively in the

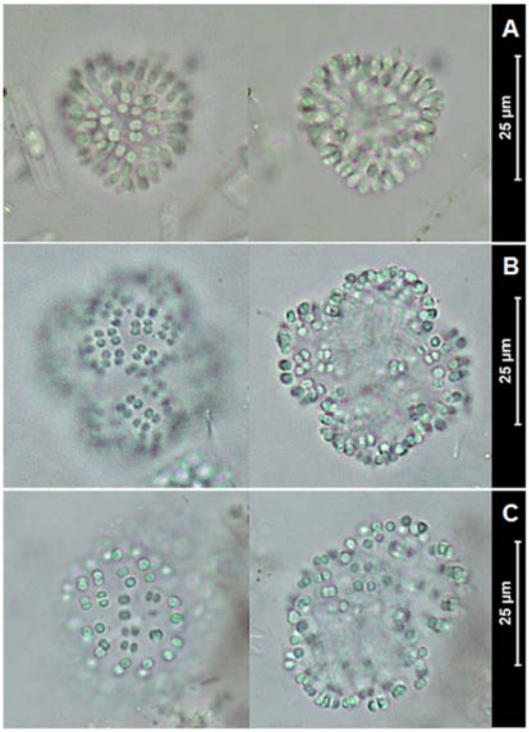

Fig. 2. Rare species of *Woronichinia* Elenkin identified in lakes of Drawa National Park. A – *Woronichinia karelica* Komárek & Komárk.-Legn., B – *Woronichinia delicatula* (Skuja) Komárek & Hindák, C – *Woronichinia obtusa* Joosten. Images present two planes of the colony.

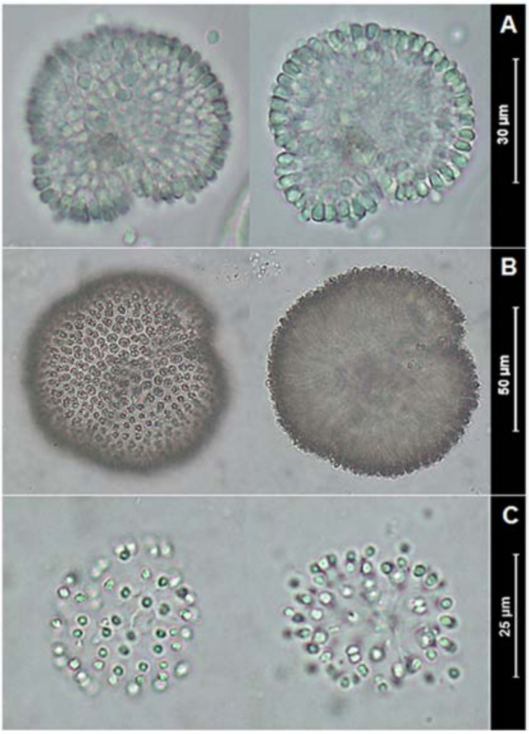

Fig. 3. Common species of *Woronichinia* Elenkin and *Snowella* Elenkin identified in lakes of Drawa National Park. A – *Woronichinia compacta* (Lemmerm.) Komárek & Hindák. B – *Woronichinia naegeliana* (Unger) Elenkin. C – *Snowella litoralis* (Häyrén) Komárek & Hindák. Images present two planes of the colony.

Table 3. Comparison of morphological characters of *Woronichinia* species identified in lakes of Drawa National Park, with taxonomical comments.

		W. karelica	*W. delicatula*	*W. obtusa*	*W. compacta*	*W. naegeliana*
Colonies	shape and dimensions	spherical, 25–28 µm (up to 30 µm)[a], cells moderately densely packed, distance between cells 1.0–2.5 µm	spherical or composed of subcolonies, 30–35 µm (20–75 µm)[a], cells moderately densely packed, distance between cells 1.4–2.9 µm	spherical or composed of subcolonies, 32–40 µm (30–60 µm)[a], cells loosely packed, distance between cells 1.5–3.8 µm	spherical or composed of subcolonies, 52–57 µm (to 80 µm)[a], cells very densely packed, often without gaps	spherical, oval, irregular, composed of subcolonies, 70–85 µm (to 180 µm)[a], cells loosely or densely packed, high variability
	Av (SD) volume [mm^3]	0.9 (± 0.09) × 10^{-5}	1.8 (± 0.3) × 10^{-5}	2.6 (± 0.5) × 10^{-5}	8.4 (± 0.7) × 10^{-5}	25.3 (± 4.2) × 10^{-5}
Cell	shape	narrow, elongated	spherical	initially spherical, becoming obovoid	oval, often obovoid, narrowed at base	ellipsoidal
	length × width [µm]	4.8–5.2 × 1.8–2.0 (3–6 × 1.5–2.0)[a]	1.3–1.7 (1.0–1.5)[a]	2.8–3.3 × 2.4–2.8 (2.8–4.2 × 2.0–3.6)[a]	4.0–4.8 × 3.0–3.4 (3–6 × 1.5–3.5)[a]	5–7 × 3.8–4.0 [(3) 5–7 × 1.5–5.0][a]
	content	homogenous (sometimes with small gas vesicles)[1]	homogenous	homogenous	homogenous	with many aerotopes
Av. biomass [mm^3/ml]		0.5 × 10^{-3}	2 × 10^{-3}	11 × 10^{-3}	20 × 10^{-3}	108 × 10^{-3}
Ecological niche		metaphyton	metaphyton	benthos and metaphyton	metaphyton	benthos
Similar species		*W. kuselae* with smaller, pale olive–green cells: 2.4–3.0 × 1.0–1.5 µm, occurs outside Europe in the Himalayan region	*W. tenera* with larger cells: 2.0–2.5 µm, occurs often in moorland waters and *Sphagnum* pools	*W. elorantae* with smaller cells: 2.5–3 × 1.6–2.0 µm, forms smaller colonies, to 20 and rarely 38 µm	*W. botrys* with larger and wider cells: 5–6 × 3.5–5.0 µm, and finely granulated blue– or olive–green content	*W. fremyi* with smaller cells: 3.0–4.5 × 2.2–3.8 µm, with point-like aerotopes, occurs outside Europe in tropical regions

[a] according to Komárek & Anagnostidis (2008) and Joosten (2006)

benthos. Together with *Woronichinia, Snowella litoralis* was present in all oligo-mesotrophic lakes (TDI: 35–50 according to Żelazowski *et al.*'s 2004 classification).

The average volumes of colonies for the *Woronichinia* species (measured for the purpose of determining species biomass) and the average biomass of species are compiled in Table 3. The biomass estimates of the *Woronichinia* species showed differences in the quantity of species between lakes of various trophic states. The least abundant species (Nc_i = 60/ml), with the lowest biomass ($B_i = 0.5\times10^{-3} \pm 0.05 \times 10^{-3}$ mm^3/ml), was *W. karelica*. It was recorded in only one, oligo-slightly mesotrophic Czarne Lake. *Woronichinia compacta* was also noted in oligo-slightly mesotrophic lakes but at slightly higher abundance and high biomass (Czarne Lake: Nc_i = 160/ml; $B_i = 13.4\times10^{-3} \pm 1.1 \times 10^{-3}$ mm^3/ml; Perkoz Lake: Nc_i = 80/ml; $B_i = 6.7\times10^{-3} \pm 0.5 \times 10^{-3}$ mm^3/ml). *Woronichinia delicatula* was recorded in only one, oligo-mesotrophic Marta Lake. The abundance and biomass of this species were low (Nc_i = 120/ml; $B_i = 2.2\times10^{-3} \pm 0.3 \times 10^{-3}$ mm^3/ml).

Woronichinia obtusa was the most common species and had the highest number of colonies. It was present in all trophic types of lakes with the exception of oligotrophic. The number of colonies increased along the trophic state gradient, reaching maximum in oligo-highly mesotrophic Zdroje Lake (in the benthos Nc_i = 200/ml; $B_i = 5.2\times10^{-3} \pm 1.0 \times 10^{-3}$ mm^3/ml; in the metaphyton Nc_i = 320/ml; $B_i = 8.3\times10^{-3} \pm 1.7 \times 10^{-3}$ mm^3/ml).

Woronichinia naegeliana was present only in the benthos of two lakes with extreme trophic states (oligo- and eutrophic). It occurred with 560 colonies per ml and biomass $141.6\times10^{-3} \pm 23.8 \times 10^{-3}$ mm^3/ml in oligotrophic Arkońskie Lake, while in eutrophic Płociczno Lake it occurred with 300 colonies per ml and biomass $75.9\times10^{-3} \pm 12.7 \times 10^{-3}$ mm^3/ml.

The standard deviation of the variables in the multivariate constrained analysis was 6.5; therefore RDA was used to summarize part of the variation of species composition explained by environmental variables. The adjusted explained variation was 44%. The analysis showed that the pH, conductivity and TDI vectors were the most significant ones in arranging taxa in the ordination space. *Woronichinia obtusa* showed a positive correlation with conductivity and TDI, and *W. compacta* and *W. karelica* with pH (Fig. 4).

The standard deviation of variables in the multivariate unconstrained analysis was 0.6; therefore PCA with supplementary variables was used to summarize the variation of species composition and to interpret this summary with the help of environmental variables. The adjusted explained variation was 52.8%, while the supplementary variables accounted for 59.6%. Vertical axes divided the ordination plot due to trophic state into oligo- and close to oligotrophic, where environmental vectors had a high multiple correlation with the ordination axes; and into oligo-meso to eutrophic, where environmental vectors showed a low correlation with the ordination axes (Fig. 5). The PCA biplot revealed a relationship between the biomass of the *Woronichinia* species and the trophic state of the lakes. A strong positive relationship with oligotrophic state was recorded among *W. delicatula* and *W. naegeliana*, and with oligo-slightly mesotrophic

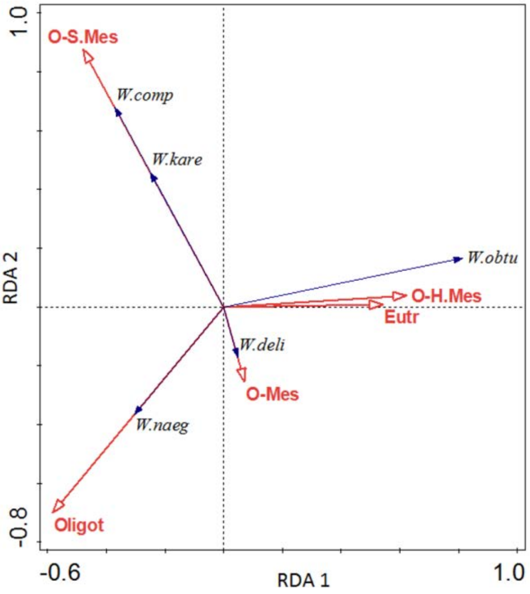

Fig. 4. RDA biplot of the relationship between *Woronichinia* species biomass and the basic properties of water in the lakes of Drawa National Park.

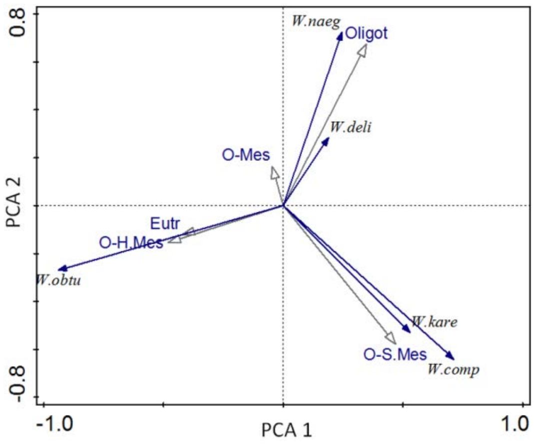

Fig. 5. PCA biplot of the relationship between *Woronichinia* species biomass and the trophic state of the studied lakes of Drawa National Park; oligotrophy (Oligot); oligo-slight mesotrophy (O-S Mes); oligo-mesotrophy (O-Mes); oligo-high mesotrophy (O-H Mes); eutrophy (Eutr).

state among *W. karelica* and *W. compacta*. The presence of *W. obtusa* was highly related to ecosystems with elevated nutrient content.

Discussion

We found the genus *Woronichinia* to be taxonomically diverse in natural lakes of Drawa National Park (DNP). The lakes are isolated from direct human impacts, which reduces the rate of their natural eutrophication. The factors that cause changes of trophy in natural ecosystems are associated mainly with basin morphology, biological processes in the ecosystem (e.g., mineralization rate) and external sources of nutrients (Leng 2009). All lakes in DNP were formed during the Vistulian glaciation but they are at different stages of natural eutrophication, as confirmed by diatom bio-assays using the trophic diatom index (TDI). The trophy of lakes isolated from the river course is elevated mainly by nutrient inflow from the forest area and from precipitation. Depending on basin morphology and the intensity of biological processes in the ecosystem, lakes are more or less susceptible to acceleration of eutrophication. In shallow lakes like Zdroje Lake, mixing of water results in the release of nutrients from sediments and increasing eutrophication, but if the bottom of the lake is covered with vegetation, as in Arkońskie Lake, the vegetation binds the sediments and prevents it from releasing nutrients into the water. Lakes located on the river course are supplied with nutrients mainly through river inflow. The share of this source of nutrients may even reach 94%, as in Sitno Lake (Czerniawski & Piasecki 2004; Szyper & Kraska 1999, unpubl.; Kraska 1998, unpubl.; Kraska & Piotrowicz 1998, unpubl.). Most of the lakes of DNP are oligo-mesotrophic. This trophic state promoted the diversity of the *Woronichinia* species, because many species of this genus prefer oligo-mesotrophic conditions. In eutrophic reservoirs, especially in those transformed by human activity, the diversity of *Woronichinia* is low, and such reservoirs generally include *W. naegeliana* and its morphotypes (Komárek & Komárková-Legnerová 1992; Komárek & Anagnostidis 2008; Pliński & Komárek 2007). However, a study of the cyanobacteria microflora in the Netherlands (Joosten 2006) revealed *Woronichinia* diversity in eutrophic reservoirs. These reservoirs were classified as eutrophic but were characterized by low human impacts. They could in fact be closer to moderately eutrophic, because the species diversity of *Woronichinia* in such conditions is higher than in anthropogenically transformed reservoirs with a disturbed ratio of nitrogen to phosphorus (Santos *et al.* 2012).

The low N : P ratio characteristic for the oligo-mesotrophic lakes isolated from the river in DNP resulted in increased *Woronichinia* species diversity. In general, the biomass and abundance of cyanobacteria are higher in ecosystems with a high N : P ratio than in those with a low N : P ratio (Havens *et al.* 2003); in the case of the *Woronichinia* genus, which prefers waters with moderate fertility, a low ratio of these nutrients favors its species diversity.

The division of the oligo-mesotrophic class into three classes of increasing mesotrophic conditions allowed us to examine the relations between the occurrence of certain species and the trophic state of the lakes. The least abundant species were *W. karelica* and *W. delicatula*. Both species occur in oligotrophic and oligo-mesotrophic reservoirs of Europe (Komárek & Anagnostidis 2008) but until now they had not been recorded in the water ecosystems of Poland. Pliński and Komárek (2007) mentioned the potential occurrence of *W. karelica* in the Baltic Bay, as it is present in the Eastern Baltic region (Hällfors 2004), but until now the presence of this species in Poland had not been noted. The results of our study in DNP confirm the ecological preferences of both species regarding trophy state, and suggest that the presence of *W. karelica* may be related to high water pH.

The presence of *W. compacta* was noted in two ecosystems of oligo-slightly mesotrophic type with high water pH. This species is commonly recorded in Poland in various trophic conditions, especially in the Baltic region (Pliński & Komárek 2007). Its presence only in oligo-slightly mesotrophic lakes in DNP is puzzling, as it has a wide tolerance to trophy and from time to time is a dominant species in eutrophic ecosystems (Krevs *et al.* 2007).

Woronichinia obtusa, distinguished by Joosten (2006) from the *W. compacta* complex, was predominant, occurring in the highest numbers in DNP. This species preferred oligo-mesotrophic to eutrophic waters with high conductivity. Its biomass gradually increased with increasing trophy, reaching the highest biomass in oligo-highly mesotrophic conditions. In eutrophic waters, where the ratio of N:P was higher, its biomass decreased. Joosten (2006) noted that in the cyanobacteria microflora of the Netherlands it is often present in eutrophic reservoirs. Our study in DNP showed different trophic state preferences. The reservoirs in the Netherlands may be closer to moderately eutrophic, as mentioned above. Moreover, the character of the water ecosystems in Joosten's (2006) studies and at the DNP differ due to latitude and geology; this might account for the divergence of findings. Until now this species had not been recorded in Poland, but it may have been identified as *W. compacta* or under the former name *Gomphosphaeria compacta* (Siemińska & Wołowski 2003).

Woronichinia naegeliana was present both in eutrophic and in oligotrophic lakes of DNP. It occurred with higher biomass in the oligotrophic lake than in the eutrophic one. This may not be surprising, since Brettum (1989) classified this species as characteristic for oligo-mesotrophic waters; however, later studies revealed the presence of *W. naegeliana* in meso-eutrophic and eutrophic reservoirs (Wilk-Woźniak & Mazurkiewicz-Boroń 2003; Wilk-Woźniak *et al.* 2006; Joosten 2006). This suggests that *W. naegeliana* may have a wide tolerance to trophy. Its wide occurrence and potentially wide tolerance to trophy may explain why this species has high morphological variability (Komárek & Komárková-Legnerová 1992).

A study of cyanobacteria in 1997 by Szeląg-Wasilewska and Gołdyn (1998, unpubl.) in DNP mentions only the presence of *Gomphosphaeria* species, which were transferred in 1988 to the genus *Snowella* by Komárek and Hindák (1988). The authors did not mention the presence of *Woronichinia* species in the lakes. They identified only *Gomphosphaeria rosea* (Snow) Lemmerm. *G. rosea* sensu Lemmermann (1907–1910) was transferred to *Snowella* (Elenkin 1938), but the typical *Snowella rosea* (Snow) Elenkin occurs only outside Europe, in waterbodies of North America (Smith 1920; Komárek & Anagnostidis 2008). Most likely, *G. rosea* sensu Komárek (Komárek 1958) was recorded at the DNP. This species was transferred to *Snowella* in 1988 as *Snowella litoralis* (Komárek & Hindák 1988). We recorded *S. litoralis*; it co-occurred with *Woronichinia* species in oligo-mesotrophic lakes. The ecological preferences of *S. litoralis* are in line with the references (Komárek & Hindák 1988; Komárek & Anagnostidis 2008).

Woronichinia species were absent in two oligotrophic lakes: Piaseczno Małe and Pustelnik. Both lakes had high concentrations of humic compounds in the sediment and low levels of dissolved oxygen during the study period. The low concentrations of nutrients and oxygen, and the lower water pH than in the other studied lakes, may together have created unfavorable conditions for the development and growth of *Woronichinia* species.

As compared with Joosten's (2006) findings, the taxonomical diversity of the genus *Woronichinia* in Drawa National Park can be considered high. Such diversity is a result of the nature of these ecosystems: natural, undisturbed by direct human impacts, and with different trophy resulting from natural processes of ecosystem transformation. Rare and sensitive species such as *W. karelica* and *W. delicatula* have developed in these ecosystems. The fact that these habitats are inside a national park, are protected from the direct effects of human activity and are isolated from anthropogenic processes of ecosystem transformation is very important. This isolation has permitted gradual, natural changes in the trophy of these lakes. In view of previous studies (Szeląg-Wasilewska & Gołdyn 1998, unpubl.), we infer that the conservation of these ecosystems has led to an increase in the species diversity of the studied genus. Protection of unique ecosystems is essential for maintaining species diversity.

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