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The influence of drought on diatom assemblages in a temperate climate zone: A case study from the Carpathian Mountains, Poland

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A R T I C L E I N F O

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A B S T R A C T

The aim of our research was to trace changes in the composition and structure of diatom communities and diatom ecological traits under the influence of drought. We also examined the impact of drought on the results of the Polish Diatom Index (IO) and the Indice de Polluo-Sensibilité Spécifique (IPS), which is the most commonly used diatom index in European countries, as a preliminary assessment of how changes in watercourses during climate-change related drought affect environmental quality assessments. The studies were conducted on watercourses in an area devoid of significant anthropogenic pressures, i.e., the protected area of Magura National Park in the Carpathian Mountains, Poland. The chemical parameters and ecological condition based on diatom analysis permitted classifying the watercourses as having good and very good status. Drought periods had a significant impact on some water parameters such as electrolytic conductivity, pH, nitrogen compounds, chlorides, and sulfates. Changes in the composition and structure of diatom communities were observed; however, in larger watercourses they were much smaller than those in smaller watercourses of a higher order. During drought periods, the share of diatoms from the motile guild and terrestrial species increased significantly in the streams. Drought had positive effects on the increased biodiversity of benthic diatom communities. Diatom index values showed statistically significant differences between drought-free and drought periods. In the present study, the differences observed were small enough to not affect the final ecological status classification. However, given the significant increase in the abundance of motile species, which are often classified as indicators of pollution, we believe that in watercourses with lower ecological statuses the occurrence of motile taxa related to drought symptoms (e.g., low water current, formation of depository habitats) could have had an impact on lowering statuses during ecological water assessments.

1. Introduction

Diatoms are a commonly used element in the assessment of the status of the aquatic environment in monitoring conducted by the Member States of the European Union since they meet assessment requirements of the phytobenthos element referred to in the Water Framework Directive (Directive 2000/60/EC) (Almeida, 2001; Ács et al., 2009; Kelly et al., 2009a, 2009b; Van Dam et al., 2007; Vilbaste et al., 2004; Charles et al., 2020). In the United States, methods to assess water environment disturbances based on diatoms are also under continual

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development (Kireta et al., 2012; Ponader et al., 2007; Potapova and Charles, 2007; Charles et al., 2020). This is because diatoms largely respond directly to most physical, chemical, and biological variables in river ecosystems, and their environmental preferences are well documented (Kelly et al., 1998; Stevennson, 2014). Each species has specific environmental requirements for many factors, and this is the basis on which diatom classification systems were developed (e.g., Van Dam et al., 1994; Coste and Ayphassorho, 1991). Not only diatom indices, but also functional groups, namely ecological guilds, provide valuable information about water quality and changes in aquatic environments (Rimet and Bouchez, 2012). Ecological guilds are groups of species that live in the same environment or belong to the same taxonomic group and exploit the same resources (Passy, 2007; Berthon et al., 2011). In this paper we used the ecological guilds concept to track changes caused by drought that were linked closely to low water levels and changes in physico-chemical parameters.

The increase in the number of extreme weather events such as drought is linked to climate change (IPCC 2014). Global-scale studies show the remarkable shifts in climate zone borders (Belda et al., 2014). According to IPCC (2014), the frequency of heat waves has increased in large parts of Europe, Asia, and Australia, which significantly reduces the amount of surface waters. Usually, reduced reservoir water volumes contribute to increasing nutrient and pollution concentrations during drought. The changes observed indicate the increasing frequency, duration, and intensity of drought in large parts of Europe, which includes Poland (Spinoni et al., 2016). The results of simulations conducted for the Carpathian basin (Bartholy and Pongracz, 2005; Bartholy et al., 2014) showed a significant warming tendency, especially in summers. The frequency of cold temperatures extremes has decreased, while warm extremes are predicted to occur more often in the coming decades. Changes in precipitation levels are also predicted, and significant seasonal precipitation amounts are likely to decrease. At the same time, the probability of drought is predicted to increase, especially in the summer months. Predictions for Poland indicate an increase in summer temperatures, especially in the southern part of the country. Climate models do not show clearly in which direction precipitation changes will go, but all of the models indicate an increase of the maximum volume of one-off rainfall (i.e., maximum precipitation values over 24 h) (Christensen and Christensen, 2003; Christensen et al., 2007). This will result in longer periods of water deficits in summer interrupted by short periods of heavy rainfall (Christensen and Christensen, 2003). Increased rainfall variability could lead to reduced river runoff and decreased soil moisture in summer months during precipitation deficits. Additionally, increased water temperatures will affect aquatic ecosystems by increasing the risk of eutrophication, reducing dissolved oxygen and leading to decay processes (Christensen et al., 2007).

Climate change has led to changes in water regimes including the drying up of formerly permanent watercourses in late summer. To effectively conserve biodiversity and properly assess the water ecological status of streams and rivers, it is crucial to understand the biodiversity dynamics induced by low water levels during drought (Steward et al., 2012).

On a local scale, temporary streams are considered to be low biodiversity ecosystems during both drying and flowing phases (Tornés and Ruhí, 2013; Acuña et al., 2014; Stubbington et al., 2017). Permanent streams are dominated by lotic taxa, whereas lentic and terrestrial species are also present in communities in temporary watercourses. Therefore, temporary watercourses globally can be more diverse then perennial ones (Stubbington et al., 2017). Benthic diatoms are especially important in small streams because they are the prevailing primary producer component (Kireta et al., 2012); therefore, changes in the structure and functioning of diatom communities affect entire ecosystems.

Studies focusing on the influence of drought on aquatic ecosystems and intermittent streams are increasingly numerous (Barthès et al., 2015; Boix et al., 2010; Delgado et al., 2012; Tornés and Ruhí, 2013; Calapez et al., 2014; Falasco et al., 2016; Piano et al., 2017; Stubbington et al., 2019; Cantonati et al., 2020; Novais et al., 2020; Várbiró et al., 2020). However, these focus mostly on typical intermittent streams in the Mediterranean region. There is sparse data about the influence of periods of low water levels on phytobenthos, and consequently on the ecological assessment of water status, in mountain streams in temperate regions (B-Béres et al., 2019; Várbiró et al., 2020). Most publications from temperate highlands and mountain regions focus on general biodiversity (e.g., Kawecka, 2003, 2012; Vasiljević et al., 2014).

The area in which our study was conducted is unique with regard to its land use history. As a result of renaturation lasting over 60 years, forests now cover over 90% of the area, and this special region was designated as Magura National Park (MNP) in 1995. The data we collected allowed us to trace the impact of drought on the richness and diversity of diatom communities in streams with waters of high ecological status that corresponded to reference conditions.

In this paper we present the results of analyses of the composition and structure of diatom communities and diatom ecological guilds during drought induced by climate change. To trace the impact of drought on the ecological status of waters based on diatom indices, we used the Polish diatom index (IO) and the Indice de Polluo-Sensibilité Spécifique (IPS) (Coste and Ayphassorho, 1991), which is the most widely applied index in EU member countries. Thus, it was possible to trace the impact of drought on diatom indices in waters of high ecological status and on final assessments of ecological status. All the results we present are a unique addition to the literature on this topic.

2. Study area

The study was conducted in the headwaters of the Wisłoka River and selected tributaries in Magura National Park and its protective buffer zone (southeast Poland) (Fig. 1). The Wisłoka River is a right-bank tributary of the Vistula River that is in the Baltic Sea catchment area. The sources of the Wisłoka River are located in the Lower Beskid Mountains at an altitude of 664 m a.s.l. The river is 164 km long. The upper and middle parts of the catchment area are mainly composed of Cretaceous and Tertiary flysch strata. All watercourses were subjected to high water level fluctuations that are typical of mountain rivers. In rain-free periods, the flows in these watercourses are very low, and in summer the water temperature in the shallow, wide channels is high and can exceed 20 °C (Soja, 2009). The area where the study was conducted is covered mostly by forest (93.8%), while the rest of the area is used largely for agriculture. Until 1947, this area was densely populated, and forestation was below 40%. In 1947, as a result of the "Operation Vistula", the area's inhabitants were forced to resettle, which resulted in its depopulation. The significant reduction of human pressure resulted in a substantial increase in forested areas and ecological restoration, which also had a considerable impact on surface waters.

3. Material and methods

The 15 sampling sites were located in Magura National Park (49°31′07″N, 21°28′27″E) – 5 on the Wisłoka River, and 10 on its tributaries (Świerzówka, Rzeszówka, Krempna, Baranie, Zima Woda, a small unnamed tributary of the Wisłoka River, and a tributary of Zimna Woda stream) (Fig. 1). The sites in the Wisłoka River were exposed to sunlight (sites 1–5), while trees and shrubs growing on watercourse banks reduced light penetration at the sites located in the tributaries (sites 6–15).

The studies were conducted in April, July, August, and October 2013, and in April and October 2014. In spring 2013 (April), the water levels in the watercourses examined were elevated from late snow-cover melting (Fig. 2). In late summer and fall (August and October 2013), the water levels were very low because of low rainfall and high air temperature (Figs. 3 and 4). The water level in the smaller watercourses (sites 6–15) was very low. During this period, one of the watercourses

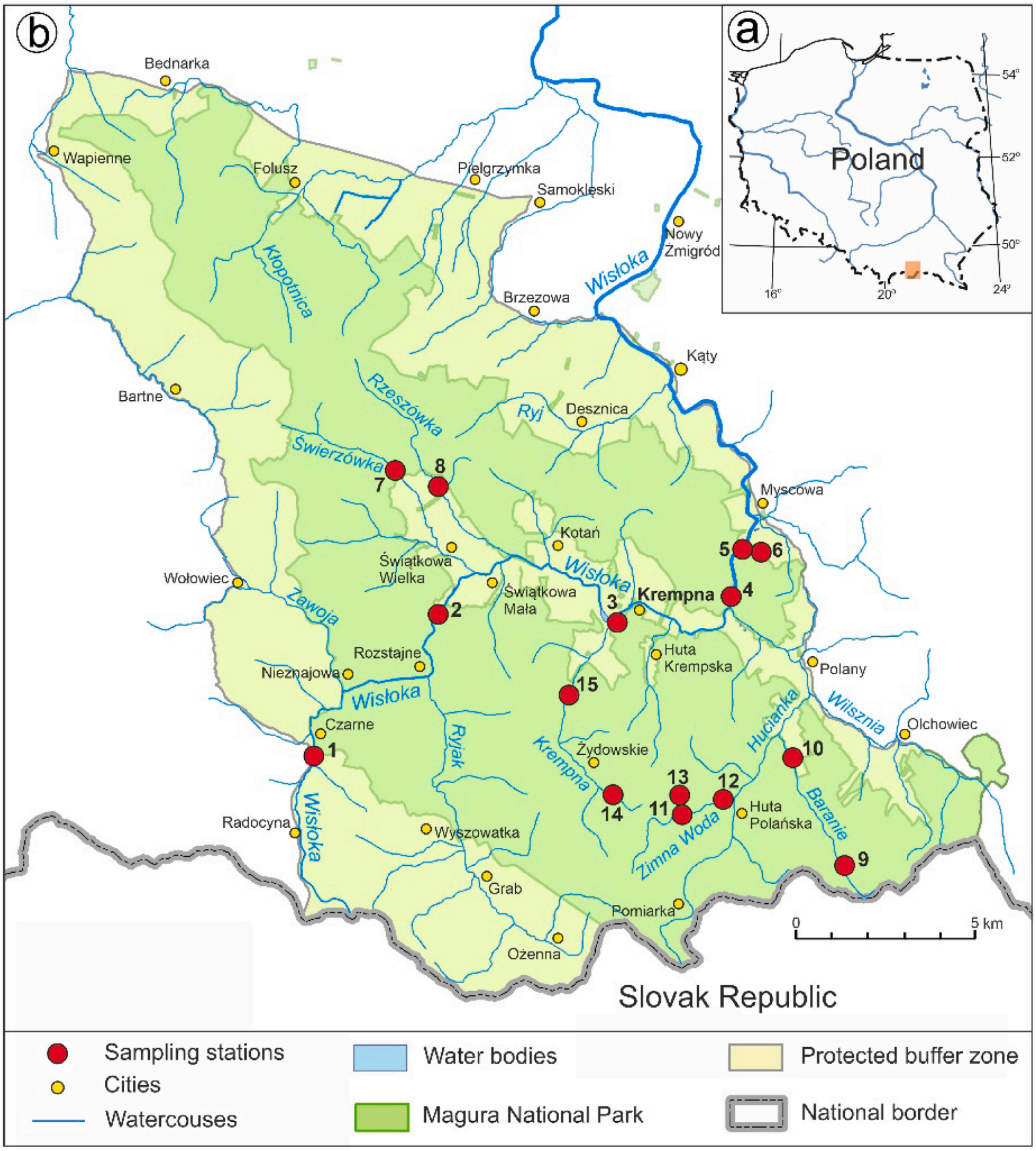

Fig. 1. The study area: a. location of Magura National Park, b. location of sampling sites: 1–5 - Wisłoka, 6 - Wisłoka tributary, 7 - Świerzówka, 8 - Rzeszówka, 9–10 - Baranie, 11–12 - Zimna Woda, 13 - Zimna Woda tributary, 14–15 - Krempna.

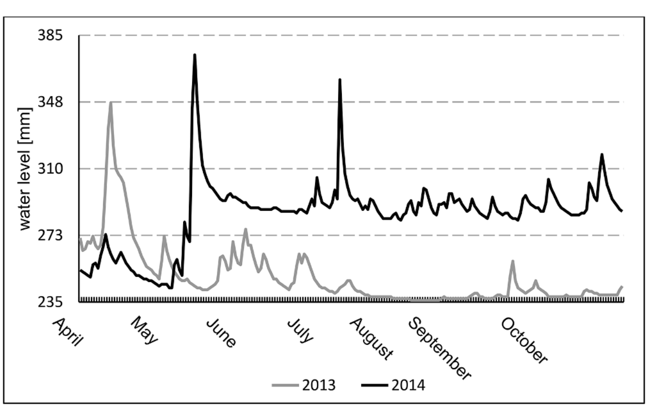

Fig. 2. Relative water level [mm] in the Wisłoka River at site 3 during the sampling periods in 2013 and 2014 (source: National Institute of Meteorology and Water Management – IMGW; https://danepubliczne.imgw.pl).

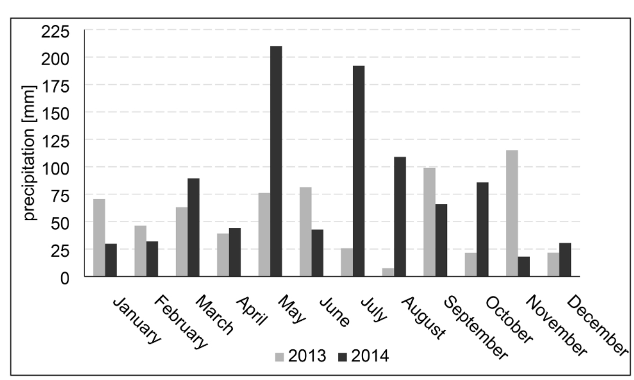

Fig. 3. Precipitation [mm] in the Wisłoka River at site 3 during 2013 and 2014 (source: National Institute of Meteorology and Water Management – IMGW, https://danepubliczne.imgw.pl).

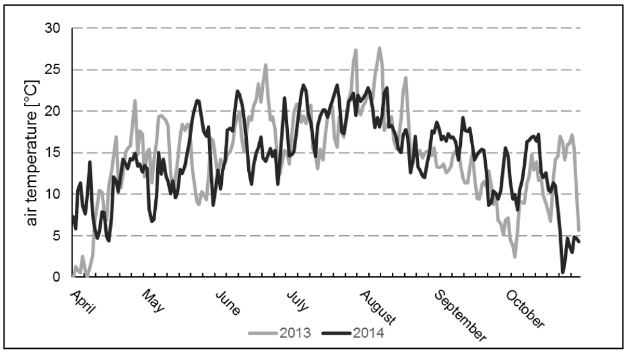

Fig. 4. Average daily air temperature from a weather site nearest to the study area (source: National Institute of Meteorology and Water Management – IMGW; https://danepubliczne.imgw.pl).

completely dried up (site 6). In this paper, August and October 2013 were considered months of drought.

3.1. Chemical analysis

Electrolytic conductivity (EC), pH, water temperature, and dissolved oxygen were measured *in situ* using the following equipment: MARTINI EC59, MARTINI pH56, and METTLER TOLEDO SevenGo pro. Detailed chemical analyses of the water samples were performed in a laboratory. The ion content (Cl^-, SO_4^{2-}, NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}) of the samples was analyzed with chromatography with a Thermo Scientific DIONEX ICS–5000 + DC device (PN-EN ISO, 2009).

3.2. Diatom analysis

Sampling was conducted according to the standard method used in Polish diatom monitoring studies (Picińska-Fałtynowic and Błachuta, 2010; Zgrundo et al., 2018), which meets the requirements of EN-PN 13946:2014-05. The diatoms were collected by brushing submerged stones and rocks with a toothbrush. In August and October 2013, the site on the unnamed Wisłoka tributary (site 6) had completely dried up, so no samples were taken. In total 88 samples were collected during field trips.

Diatom samples were processed in a chromic mixture (a mixture of sulfuric acid and potassium dichromate) to remove organic matter, then washed five times using a centrifuge at 2,500 rpm. Permanent diatom slides were mounted in Pleurax resin (refractive index 1.75). A Carl Zeiss Axio Imager A2 light microscope equipped with Nomarski differential interference contrast optics was used to identify and count diatoms at a magnification of 1000×. At least 400 valves were counted on each slide. Taxa were identified to the species level using the following keys: Krammer and Lange-Bertalot (1986), Krammer and Lange-Bertalot (1988), Krammer and Lange-Bertalot (1991a), Krammer and Lange-Bertalot (1991b), Lange-Bertalot (1993), Lange-Bertalot (2001), Lange-Bertalot and Metzeltin (1996), Reichardt (1999), Krammer (2002), Krammer (2003), Werum and Lange-Bertalot (2004), Levkov et al. (2016), Lange-Bertalot et al. (2011), Lange-Bertalot et al. (2017). The relative abundance of the taxa was used for statistical analysis. Taxa with shares of assemblages of at least 5% were identified as dominants.

All diatoms identified were assigned to function groups termed ecological guilds. These are groups of organisms that inhabit the same habitat, but which adapt in different ways to prevailing abiotic conditions. The low-profile guild consisted of species of short stature, including prostrate, adnate, small erect, solitary centric, and slow-moving species that are resistant to physical disturbances (water turbulence) and do not tolerate nutrient enrichment. The high-profile guild was comprised of large stalked species or those that form colonies, including filamentous, branched, chain-forming, and tube-forming diatoms that cannot resist turbulence in the environment. The motile guild consisted of fast moving species adapted to depositional habitats (Hudon and Legendre, 1987; Passy, 2007; Berthon et al., 2011; Rimet and Bouchez, 2012). Additionally, pioneer taxa were distinguished according to Berthon et al. (2011). Pioneer diatoms are able to colonize bare substrates faster than other species and are generally of a small size. In our study, *Achnanthidium minutissimum* and its varieties, *Amphora inariensis* and *A. pediculus*, were classified as pioneers. Furthermore, terrestrial taxa and those able to live in temporarily dry sites were identified according to Van Dam et al. (1994) and Barragán et al. (2018) to investigate whether their share in assemblages increased during drought.

The IO index (Picińska-Fałtynowicz et al., 2006) was calculated using the formats of the national monitoring body (http://www.gios.gov.pl; access date: 12.05.2020). The IPS (Coste and Ayphassorho, 1991) index was calculated using OMNIDIA 4.2 (Lecointe et al., 1993, database 2015). The scores yielded by the IO index were interpreted using class limit values following the Regulations of the Minister of Maritime Economy and Inland Navigation of 11 October 2019 (Journal of Laws 2019, item 2149) and by those of the IPS index the recommendations of Eloranta and Soinien (2002) (Table S1).

3.3. Statistical analysis

Student's *t*-test was used to analyze the impact of drought on the physico-chemical water parameters, the richness of diatom communities, and diatom indices. Values at $p < 0.05$ were considered statistically significant. All calculations were performed with Statistica 13.3.

Detrended Correspondence Analysis (DCA) was performed to determine the similarity of diatom communities. Prior to analysis, diatom data were $\log_{10}(x + 1)$ transformed, centered, and standardized by species. The percentage abundance of all identified diatoms were used in the DCA analysis. The gradient length was 3.2. The first ordination axis explained 40.02% of the variation, the second 18.92%, and the third 14.52%. Redundancy analysis (RDA) was applied to analyze the influence of environmental factors on diatom communities. Species with at least a 5% of share in the assemblage in a sample were included in the analysis. Prior to RDA analysis, diatom data were $\log_{10}(x + 1)$ transformed, centered, and standardized by species. In addition to measurements of water physico-chemical parameters, water level and shading were included. Water levels were measured using a hydrological rod. The shading at sites was analyzed on orthophotomaps and the percentages of high plant cover were assigned to one of four classes (class 1: 0–20%, class 2: >20–50%, class 3: >50–80%, class 4: >80% shading). The gradient length for the RDA was 2.6. The eigenvalue for the first axis was 0.168, for the second 0.059, and for the third 0.051. The statistical significance test performed for RDA analysis showed the statistical significance of the model ($p = 0.002$, $F = 7.9$). All variables explained 66.4% of variability (41% of variation plus 24.4% of adjusted variation). The share of individual parameters was as follows: water level (9.6%), shading level 4 (9.3%), chlorides (7.6%), shading level 1 (7.0%), nitrates (6.0%), temperature (5.6%), sulphates (4.7%), nitrites (4.1%), ammonium (4.1%), and conductivity (3.8%).

All analyses (DCA, RDA) were performed using Canoco 5 (Ter Braak and Šmilauer, 2012).

4. Results

4.1. Water chemistry

The variability of physico-chemical water parameters during field work is presented in Fig. 5. The water temperature ranged from 8.1 °C to 21.4 °C and fluctuated in an annual cycle according to season and the shading level of the watercourses. The pH of waters was usually close to neutral and alkaline and periodically, mostly in fall 2013, it decreased to around 6.5 (with the exception of site 6, where pH was always over 7).

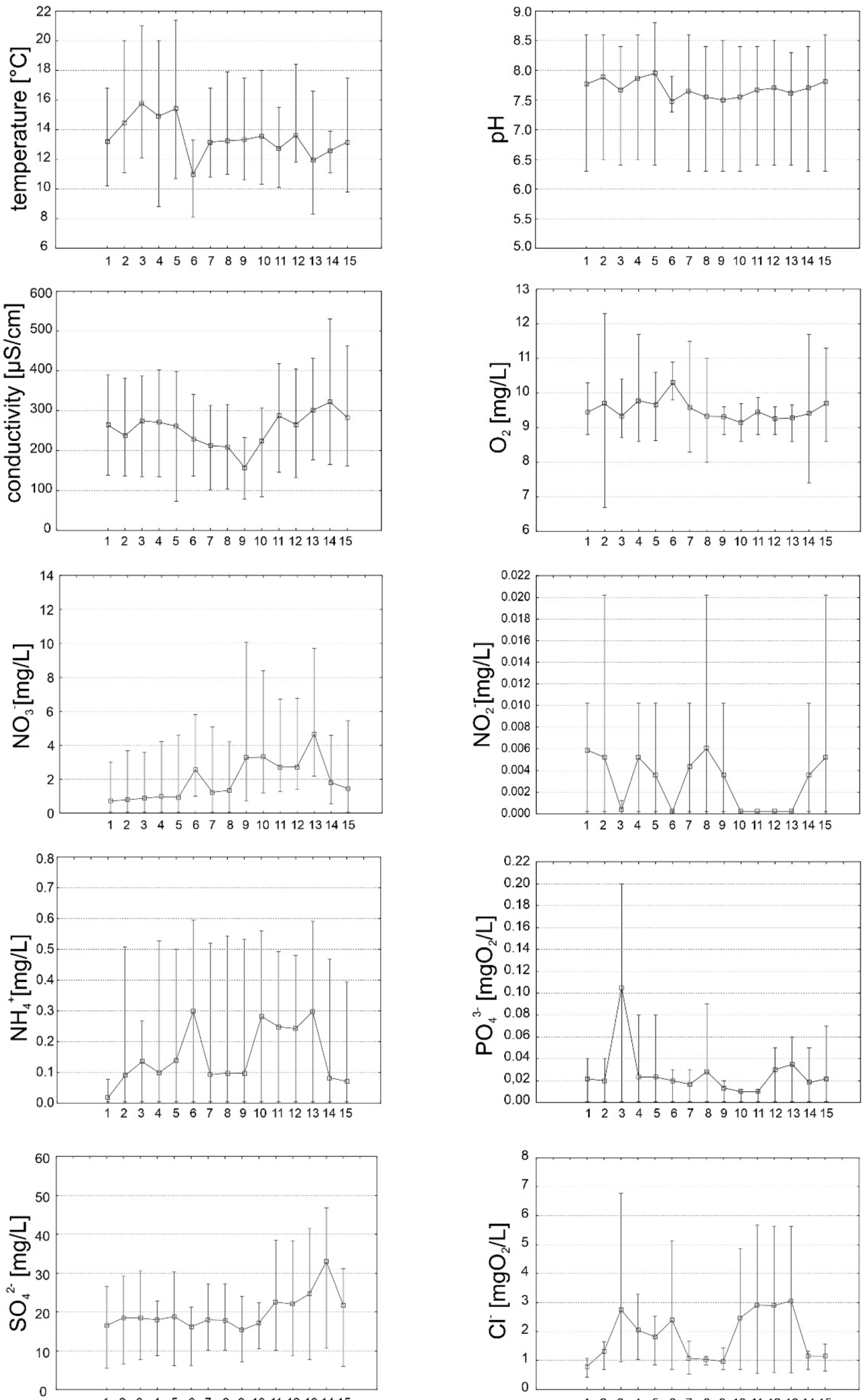

Fig. 5. Variability of physico-chemical water parameters at sampling sites (1–15). Box indicates the mean, whiskers indicate the minimum and maximum values.

The conductivity values (EC) varied from 73 μS cm^{-1} to 530 μS cm^{-1}. In each sampling period the lowest EC values were recorded at site 9, while the highest were at sites 14 and 15. The oxygen content was always high, but in the summer months the lowest values of about 7 mg l^{-1} were recorded at sites 2 and 14. The concentration of nutrients was variable. The content of nitrates ranged from below the limit of detection (<0.01 mg L^{-1}) to 10.1 mg L^{-1}. The lowest values were measured mostly at sites 1–5, 8, and 9 in August and October 2013. The highest values were recorded in April 2013, especially at sites 9–13.

Concentrations of nitrites, ammonium nitrogen, and phosphates were generally low, and were often below the limit of detection. An increase in phosphate content (0.20 mg L^{-1}) was recorded at site 3 in December 2014. The content of sulphates was between 5.5 mg L^{-1} and 46.8 mg/L, and the highest was recorded in October 2013, especially at sites 12–15. Chloride content varied from 0.42 mg L^{-1} to 6.77 mg L^{-1}. The highest chloride values were recorded in October 2013 at sites 3 and 11–13 and the lowest in April 2014 at sites 1, 7–9, and 14–15.

Among the parameters analyzed, 7 changed statistically significantly when values were compared for drought-free and drought periods. During drought, conductivity, chloride and sulphate concentrations increased, whereas pH and nitrogen form concentrations (nitrates, nitrites, and ammonium) decreased (Table 1).

4.2. Diatom richness

Altogether, 549 diatom taxa from 80 genera were recorded. In the smallest, highly shaded streams (e.g., sites 6 and 12–14) the number of taxa was lower than in the larger, fully sunlit streams (e.g., sites 1–5) (Fig. 6). The number of taxa was significantly higher ($p < 0.05$) in summer (average number of taxa = 97) and fall (average number of taxa = 95) than in spring (average number of taxa = 81), but no statistically significant differences were detected between summer and fall ($p > 0.05$). During the drought period (August and October 2013), the number of taxa was not statistically different from that during the rest of the sampling campaign.

4.3. Diatom domination structure

The most frequently observed taxa and also the dominant ones were *Achnanthidium pyrenaicum* (Hustedt) Kobayasi and *A. minutissimum* s.s. (Kützing) Czarnecki. The taxa reached at least a 5% share in the assemblage, in 52 and 42 samples of 88, respectively. Both taxa also formed very abundant populations with a maximum of 72.4% (site 2, April 2014) for *A. pyrenaicum* and 50.8% for *A. minutissimum* s.s (site 3, October 2014), but *A. pyrenaicum* was much less abundant in the smallest streams (sites 6 and 13) where reached a maximum of 12.8%. The average share in samples was 24.5% for *A. pyranaicum* and 14.7% for *A. minutissimum* s.s. throughout the study period. During the drought period compared to the drought-free period, the average share of each taxa decreased from 15.7% to 14.2% for *A. pyrenaicum*, and from 25.9% to 21.3% for *A. minutissimum.*

Encyonopsis subminuta Krammer & E. Reichardt was a taxon that dominated only during drought (up to 53.7%). Species such as *Cymbella excisa* Kützing (abundance up to 14.3%), *C. parva* (W.Smith) Kirchner (abundance up to 15.9%), *Diatoma moniliformis* Kützing (abundance up to 27.9%), *D. vulgaris* (abundance up to 7.8%), and *Fragilaria gracilis* Østrup (abundance up to 47.2%) were observed much more frequently in the drought period (sites 1–5). At sites 6–15 during drought periods, increased abundance was noted for *Nitzschia dissipata* (Kützing) Rabenhorst, *Nitzschia fonticola* (Grunow) Grunow, and *Cocconeis* spp., while that of *Gomphonema olivaceum* (Hornemann) Brébisson, *Meridion circulare* (Greville) Agardh, and *Gomphonema pumilum* (Grunow) E. Reichardt & Lange-Bertalot decreased. Species of the genera *Gomphonema* and *Meridion* developed numerously mainly in spring when high currents and cold water were present. On the other hand, in spring the share of *Achnanthidium minutissimum* in communities was lower than in the other seasons. Detailed changes in the diatom domination structure during drought-free and drought periods are presented in Supplementary material (Fig. S1–S3).

Table 1
Results of Student's *t*-test for water parameters during drought-free (April 2013, July 2013, April 2014, October 2014) and drought (July and October 2013) periods; SD – standard deviation, n – number of samples. Data statistically significant for p-value < 0.05 are marked in bold.

Parameter	Drought-free period (n = 60)		Drought period (n = 28)		p-value
	Mean	SD	Mean	SD	
Temperature	13.662	3.067	13.243	2.594	0.34200
pH	7.928	0.485	7.496	0.802	**0.00376**
Conductivity	198.667	69.747	372.000	72.840	**0.00000**
O_2	9.691	0.900	9.300	1.165	0.15313
NO_3^-	2.276	2.4355	0.676	0.943	**0.00305**
NO_2^-	0.005	0.006	0.001	0.003	**0.02025**
NH_4^+	0.215	0.251	0.023	0.069	0.00264
PO_4^{3-}	0.110	0.599	0.009	0.011	0.47717
SO_4^{2-}	16.748	6.682	28.336	8.271	**0.00000**
Cl^-	1.551	1.201	2.387	1.809	**0.01659**

4.4. Similarity of diatom assemblages

DCA analysis revealed considerable variability in the diatom data (Fig. 7). The diatom communities from sites on the large watercourse (sites 1–5) with good light conditions grouped on the left side of the graph, while communities from small watercourses with poor light conditions grouped on the right. Concurrently, the communities at sites in the largest stream were most similar to each other regarding composition and structure regardless of season. It is noteworthy, however, that the communities from these sites during drought periods were grouped close together in the canonical space on the far left side of the diagram and exhibited only slight change from the typical communities. At sites on small watercourses with poor light conditions, the composition and structure of communities differed depending on season; in spring and early summer the communities were grouped in the lower right part of the graph and from fall in the upper right. In many cases, the communities at the same sites during the drought periods in 2013 were not significantly different from those in fall 2014. Significantly greater differences were noted between the fall (including during the drought periods) and spring communities at the same sites.

4.5. Effect of environmental parameters on diatom communities

Water level and shading were the most important factors for differentiating diatom assemblages at sampling sites (Fig. 8). The high shading class, which was created for the needs of this analysis, had the most significant influence. High water level, high temperature, and high insolation were the most important factors influencing the development of communities in the large watercourse (manly sites 1–5), whereas low water level and higher nutrient concentrations determined the development of diatom assemblages in the smallest watercourses (sites 6 and 11–15). Our analysis showed that the high water level had the most important impact on abundant species from the genera *Encyonema, Diatoma*, *Gomphonema*, and *Meridion.* On the other hand, high shading favored the development of *Cocconeis* spp. and *Fragilaria perminuta*. The most abundant and frequent species, i.e., *A pyrenaicum* and *A. minutssimum* s.s, did not exhibit strong correlations with the environmental variables studied. However, the abundant terrestrial taxon *Humidophila perpusilla* reacted positively to decreased water levels and negatively to increased conductivity and nutrients (see Fig. S4 in Supplementary material).

4.6. Diatom guilds

Changes in the percentage shares of individual guilds are shown in the graphs in Figs. 9–11. The representatives of pioneer diatoms were included in the charts as a group within the low-profile guild because all pioneer diatoms identified were part of this guild. Low-profile diatoms were the most numerous group (on average made up 66.5% in a sample) in the communities. High-profile diatoms constituted 19.8% and motile forms 11.2%, on average. During drought, the abundance of the motile guild increased twofold with a statistically significant difference in comparison with the drought-free periods (Table 2). The increase in

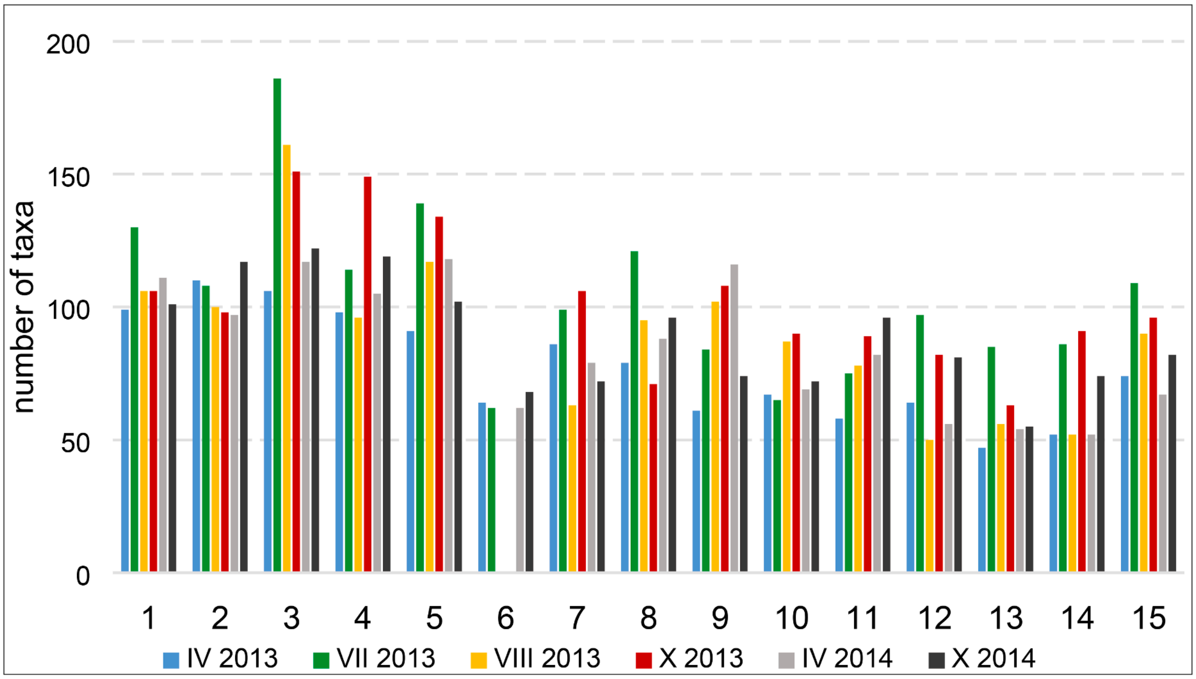

Fig. 6. Number of taxa at each sampling sites (1–15).

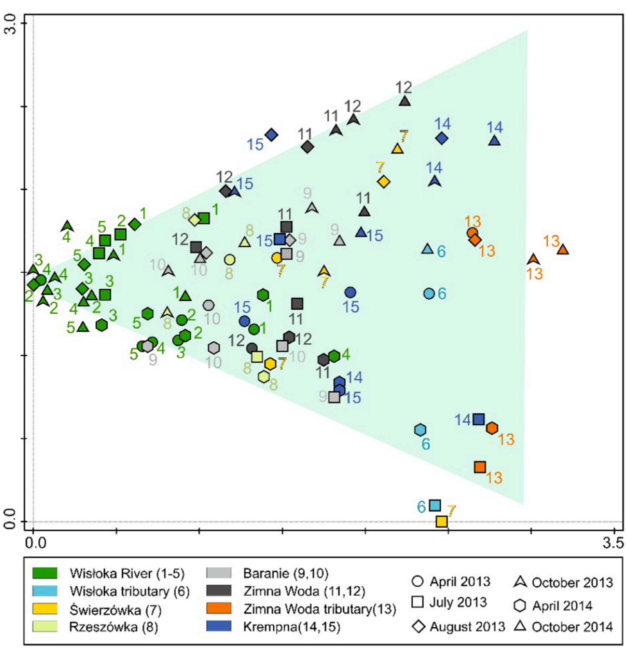

Fig. 7. DCA ordination plot for diatom data. The light green triangle in the background represents decreasing similarity in diatom assemblages at sites in the large watercourse to little ones along environmental gradients associated with watercourse orders and light regimes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

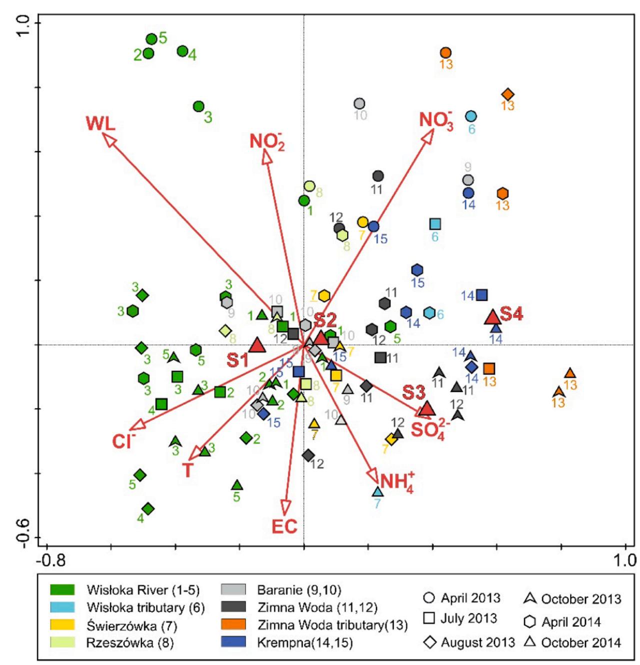

Fig. 8. Redundancy analysis (RDA) graph of statistically significant environmental variables and their influence on diatom assemblages: Cl^- – chlorides, EC – electrolytic conductivity, NO_3^- – nitrates, NO_2^- – nitrites, S1–S4 – shading degree, T – temperature, WL – water level.

abundance of the low-profile group was relatively smaller (by 10%), but the change was statically significant.

The average share of pioneer taxa was 17.0% in the samples (Figs. 9–11). At some sites (1–5 and 13–15) the abundance of pioneer diatoms increased from spring to fall. The highest number of pioneer diatoms was recorded at site 6 in spring 2014 after the period related to the complete drying of the watercourse and at sites 10 and 15 in October 2014. Pioneer diatoms were practically absent at sites 9–15 periodically mainly in spring 2013 and/or during the drought in 2013.

Terrestrial diatoms did not reach significant percentage abundances in the communities studied. In most of the samples, terrestrial diatoms occurred only as individual valves, and higher abundances were only noted for *Humidophila perpusilla* (Grunow) Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová. This species was the most abundant terrestrial diatom (up to 8.6% of total abundance) in October 2013. Other taxa such as *Stauroneis parathermicola* Lange-

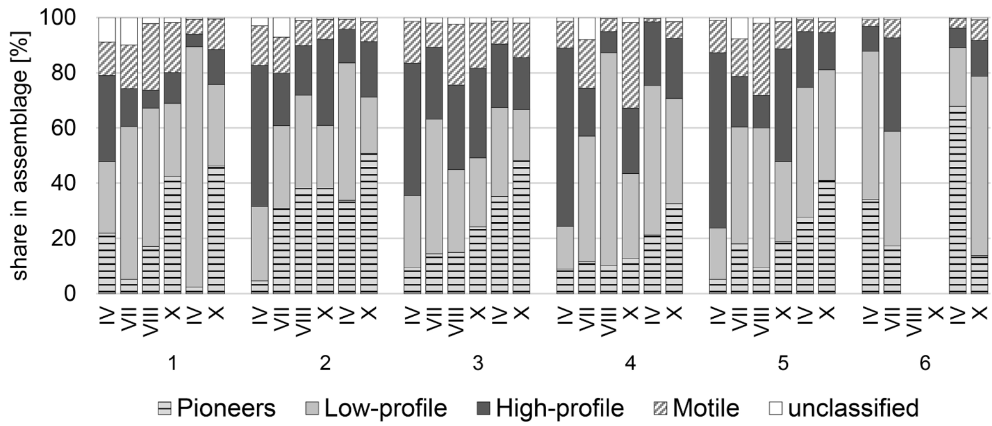

Fig. 9. Percentage shares of ecological guilds and pioneer taxa at each sampling site (1–6) in subsequent sampling campaigns.

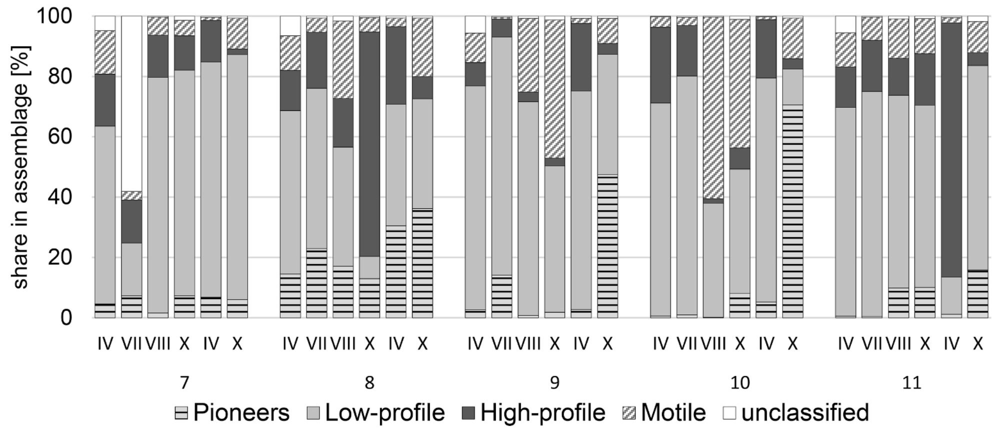

Fig. 10. Percentage shares of ecological guilds and pioneer taxa at each sampling site (7–11) in subsequent sampling campaigns.

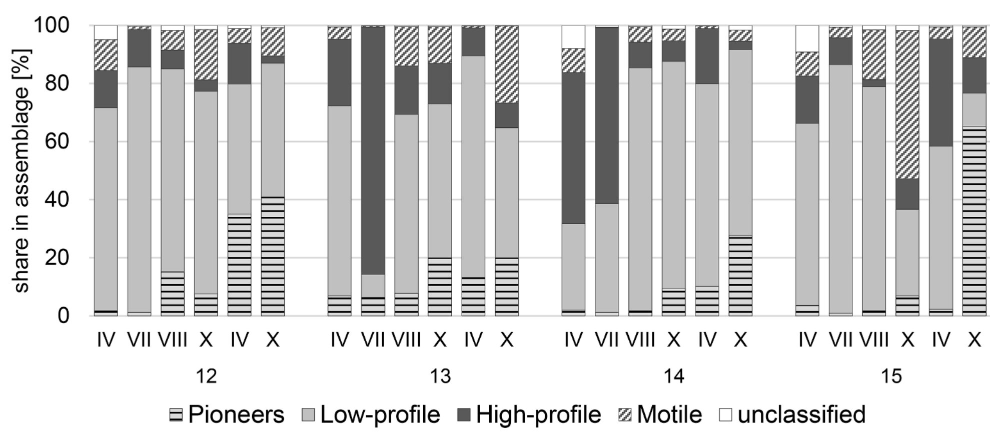

Fig. 11. Percentage shares of ecological guilds and pioneer taxa at each sampling site (12–15) in subsequent sampling campaigns.

Bertalot, *Gomphonema productum* (Grunow) Lange-Bertalot & Reichardt, *Humidophila contenta* (Grunow) Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová, *Stauroneis thermicola* (Petersen) Lund, and *Nitzschia pusilla* Grunow contributed a maximum of 1.4% of the total abundance. The average share of terrestrial taxa was very low, but it was distinctly significantly higher in drought periods. Their abundance increased from an average share of 0.24% in samples during the drought-free periods to an average of 0.94% during drought.

4.7. *Diatom indices*

The values of the IO index ranged from 0.49 to 0.81, (Fig. 12a) and according to current interpretations used in monitoring in Poland (Journal of Laws 2019, item 2149), this indicates waters of good and high ecological statuses. The lowest value was recorded in fall 2013 at site 11, while the highest (0.80 and 0.81) was recorded at sites 9 and 10 during spring 2013 and 2014. The mean values of the index were almost identical for samples collected in smaller watercourses (0.67) and in the largest watercourse (sites 1–5) (0.66). In all sampling periods the highest

Table 2
Results of Student's *t*-test for percentage shares of taxa in each ecological guild during drought-free and drought periods; SD – standard deviation, n – number of samples. Data statistically significant at p-value < 0.05 are marked in bold.

Diatom life form	Drought-free period (n = 60)		Drought period (n = 28)		p-value
	Mean	SD	Mean	SD	
Pioneers	18.89	18.50	13.11	11.23	0.131129
Low-profile	39.35	23.96	50.73	21.42	**0.034842**
Low-profile (with pioneers)	67.77	20.24	63.84	17.68	0.380250
High-profile	21.64	18.86	15.81	15.24	0.156129
Motile forms	7.56	5.52	19.15	15.08	**0.000001**

IO index values were recorded at sites 8–10. The IO index values were significantly lower during drought in comparison with drought-free periods (Table 3).

The IPS index values ranged from 15.2 (site 3) to 18.9 (site 9) (Fig. 12b), and, according to Eloranta and Soinien (2002), this indicated the good and high ecological statuses of the waters. The highest values were recorded in spring 2014, while the lowest were noted in fall 2013. The mean value for sites 1–5 was 16.6, but for smaller watercourses the mean values was higher at 17.09. As in the case of the IO index, the values of the IPS index were significantly lower during drought. The results of Student's *t*-test showed statistically significant differences between index scores during drought in comparison with drought-free periods (Table 3).

Table 3
The results of the Student's *t*-test for IO and IPS diatom indices in drought-free and drought periods; SD – standard deviation, n – the number of samples. Data statistically significant at p-value < 0.05 are marked in bold.

Index	Drought-free period (n = 60)		Drought period (n = 28)		p-value
	Mean	SD	Mean	SD	
IO	0.695	0.075	0.636	0.077	**0.00093**
IPS	17.168	0.919	16.332	0.814	**0.00008**

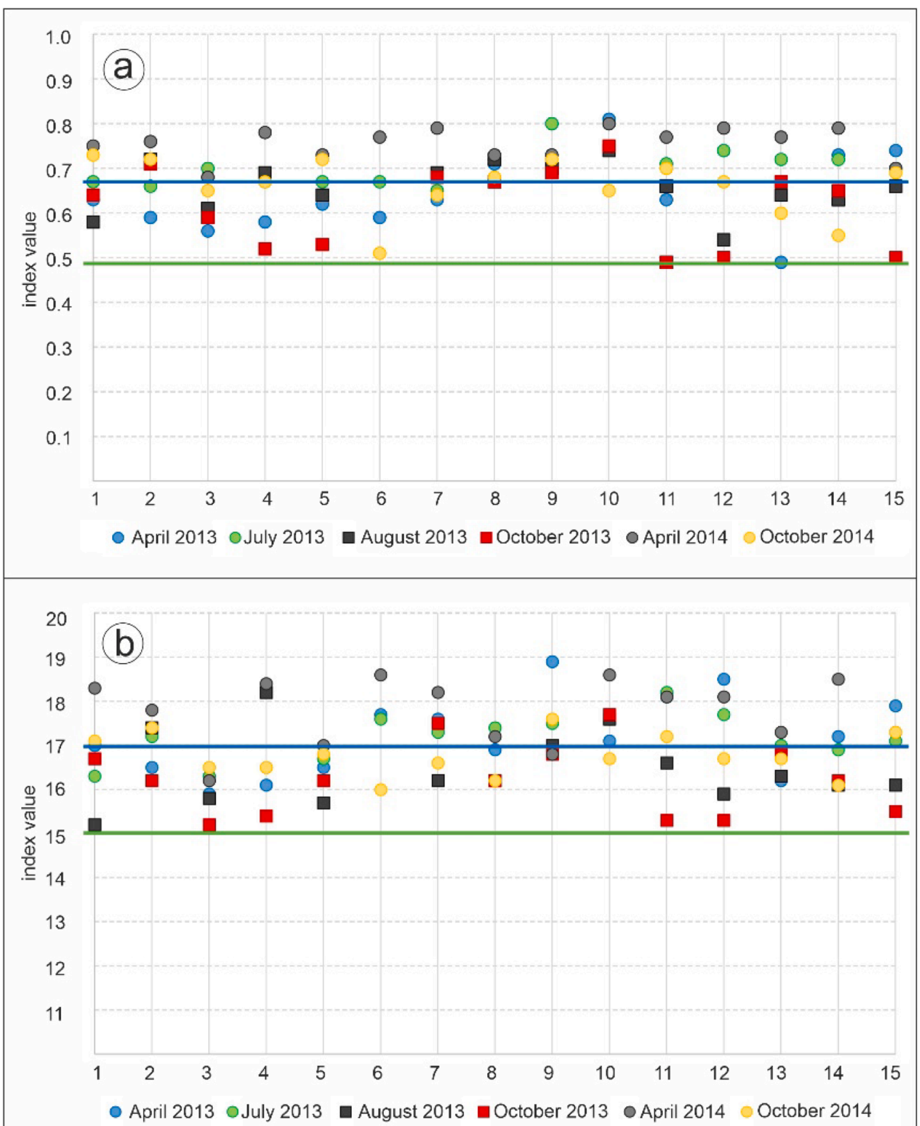

Fig. 12. Values of the IO (a) and IPS (b) indices calculated for all samples. Drought is marked with a square. Blue horizontal line represent the boundary between the good and high ecological statuses, and the green line between the moderate and good statuses. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Discussion

The water parameters measured at sampling sites were typical for Carpathian flysch streams and small flysch rivers. The nutrient levels in the waters studied were low, and the values measured were within the ranges reported by other authors who conducted research in Magura National Park under drought-free conditions (Szczęsny, 2005; Bors and Koszelnik, 2009; Kalda and Liszka, 2013). Nitrate values increased only in spring 2013 from intensive snow melt, which is a natural process in mountain streams (Campbell et al., 2000a, 2000b; Ohte et al., 2004). Although drought had a statistically significant effect on increases (conductivity, chlorides, sulphates) or decreases (pH, nitrogen compounds) of the values of the parameters measured, these values remained low in comparison with drought-free periods. As previously mentioned, these values themselves are still considered to be typical of Carpathian flysch streams and rivers. Decreased nutrient concentrations during drought was explained by the uptake by primary producers with no nutrient influx associated with surface runoff (Stubbington et al., 2019).

Water temperatures in the large, well-sunlit watercourse (sites 1–5) varied to a greater extent than those in smaller watercourses constantly influenced by underground exudate water, but their seasonal fluctuations were typical in relation to stream order and the degree of shading (Studinski et al., 2012). Despite this, no statistically significant differences in water temperature between the drought and drought-free periods were observed.

The total number of diatom taxa identified in our study in comparison with other studies conducted in the region in small rivers and streams (Noga et al., 2012, 2014, 2016; Żelazna-Wieczorek, 2012) was higher, but the taxonomic composition was regarded as typical for the Lower Beskid region (Carpathians). The highest number of taxa was identified at sites 1–5 in the large watercourse. The lowest number of taxa was recorded in the smallest (site 13 and 14) and shaded streams (site 9, 11, and 12) with high water fluctuations, which was confirmed in other studies (Hill and Knight, 1988; Rout and Gaur, 1994; Stevenson, et al., 1991). Some previous studies clearly demonstrated that the number of taxa correlated inversely with stream order as understood in the classical approach, i.e., the smaller the watercourse, the higher the order (Stenger-Kovács et al., 2014; Szabó et al., 2004). We showed, like Douglas (1958) and Cambra and Gomà (1997), that during high water levels (April 2013) the number of diatom taxa decreased, because high-speed water currents washed away species not adapted to turbulent waters (e.g., motile and high-profile taxa), leaving those that were firmly attached to substrate (low-profile taxa). On the other hand, later in the summer at lower water flow rates the number of taxa increased from the succession of diatom communities. Our observations of changes in diatom communities during summer periods of low precipitation and fall drought were also examples of disturbances in aquatic ecosystems that prevent the domination of one species and support increased diversity (Peterson, 1987; Huston, 1979; Calapez et al., 2014).

The high similarity of the composition and structure of communities developing in the large watercourse (sites 1–5) suggested that in the period from spring to fall large streams offer stable environmental conditions facilitating the full development of communities adapted to local climatic and geographic conditions. On the other hand, the diatom communities in the smaller watercourses were characterized by greater diversity in composition and structure stemming from unstable environmental conditions caused by the seasons and extreme phenomena such as spring floods or summer/fall drought. The influence of disturbances such as drought on the increase of species richness and diversity in river diatom communities during the annual cycle was reported by, among others, Peterson (1987), Huston (1979), and Calapez et al. (2014). Stubbington et al. (2017) also mentioned drought from a broader perspective that globally affected increased biodiversity by contributing to the growth of diversity in small watercourses. Diversity patterns can be related to transitions between lotic, lentic, and terrestrial instream conditions particularly when differences are considered among sites in larger regions and over longer time spans (Stubbington et al., 2017). In a recent study conducted in perennial and intermittent streams on Cyprus, Cantonati et al. (2020) suggested that the co-presence of several species of the same genus increased the resistance of diatom communities to changes in environmental conditions. A shift in environmental conditions, on the one hand, caused a decrease in the number of genera comprising communities, while, on the other hand, this affected increases in the number of species from the same genus. This qualitative change in the community was not accompanied by a quantitative change, hence traditional diversity indices did not indicate significant changes in community composition or structure (Cantonati et al., (2020). Data from temporary streams indicated that, even after stream channels dry completely, shortly after water returns to channels most communities were not significantly different from those typical of the region before drought (Elias et al., 2015). With these facts in mind, it is not surprising that diatom assemblages in the waters studied were not drastically different, particularly in the low order larger watercourse. Furthermore, the results of our studies confirmed observations reported in the literature that stream size and shading level directly influence the amount of waters carried, and, together with current speed, that nutrient availability impacts the development of diatom assemblages in mountain running water ecosystems (Artmann et al., 2003; Plenković-Moraj et al., 2008; Rout and Gaur, 1994).

At most of the study sites, the diatom communities were dominated by low-profile taxa that are regarded as tolerant to physical disturbances (e.g., strong currents) (Passy, 2007; Rimet and Bouchez, 2012; Novais et al., 2020). Our results showing the dominance of low-profile taxa during high water levels in spring also confirmed the observations of Novais et al. (2020) conducted in intermittent streams that ceased flowing in very dry periods. Furthermore, under the eurhenic conditions (continuous water flow with riffles) prevailing in mountain streams, low-profile diatoms are best adapted to survive and resist strong water currents (Ács and Kiss, 1993; Novais et al., 2020). The significant increase in the abundance of motile species during drought suggests the occurrence in watercourses of conditions of low water current and the formation of depository habitats and increasing siltation (Passy, 2007; Falasco et al., 2016). According to some authors (Fairchild et al., 1985; Van der Grinten et al., 2004), the motile guild is comparatively free of both resource limitation because it has the physical capability of selecting the most suitable habitat and that is why, the motile guild can be observed to increases with decreases in nutrient availability (both phosphates and nitrates), which was also observed in our studies. This phenomenon is explained as a reaction to stress and the search for resource-rich microhabitats (Johnson et al., 1997). Furthermore, during drought at the same sites we observed a slight increase in pollution-tolerant taxa, such as those of the genera *Navicula* (e.g., *N. tripunctata*, *N. cryptotenella*, *N. radiosa*) and *Nitzschia* (e.g., *N. dissipata* ssp. *dissipta*, *N. fonticola*, *N. recta*, *N. sociabilis*) (Lange-Bertalot et al., 2017). Representatives of the genera *Navicula* and *Nitzschia* are included in the motile guild (e.g., Passy, 2007), and increases in their abundance, in our opinion, were not associated with increased organic pollution but with factors such as reduced water current and the formation of depository habitats, which were mentioned previously.

Pioneer taxa are considered to be diatoms that disperse rapidly (Passy, 2007; Novais et al., 2020). In the current material studied, the main pioneer taxa was *A. minutissimum* s.s., which occurred regularly, although it was less frequent in spring. It is regarded as an "early colonizer" and pioneer (Berthon et al., 2011), and it is expected to develop in high numbers in spring. In studies by Kelly et al. (2008) and Cantonati et al. (2020), *A. minutissimum* was considered to be part of "reference" assemblages and an indicator of unpolluted sites (Stubbington et al., 2019) together with other *Achnanthidium* spp. Additionally, it is considered to be an indicator of high ecological status in the IPS index (Lecointe et al., 1993). Conditions for the co-occurrence of species from lentic and lotic environments can form during non-flowing cycles as isolated ponds in highly dynamic streams, like those in our study in a mountain region. Thus taxa considered as pioneers, like *A. minutissimum*, can occur regularly in high numbers. The *A. minutissimum* complex is observed across various water status categories, but it is particularly abundant in high-status habitats (Stubbington et al., 2019). Furthermore, the *A. minutissimum* complex is an example of diatoms that span terrestrial and freshwater habitats that can also inhabit terrestrial soils (Blanco et al., 2017).

In our samples from smaller watercourses the number and abundance of terrestrial taxa significantly increased in drought periods, but the increase was imperceptible on the scale of entire communities. Studies from Cyprus (Cantonati et al., 2020) also showed a lower number of these species than was anticipated. These authors suggested that, since knowledge about the autecology of pseudaerial and euaerial species remains poor, these species go undetected. Nevertheless, we agree with the opinions of Falasco et al. (2016) and B-Béres et al. (2019) who stated that terrestrial taxa are strong indicators of drought.

Although the diatom indices showed statistically significant differences between drought and drought-free periods, decreased values during drought did not influence the classification of water ecological status. Studies from Mediterranean regions revealed similar results with regard to both diatom indices and changes in community abundance and taxonomic structure (Boix et al., 2010; Calapez et al., 2014).

The analysis of diatom ecological groups (guilds, pioneer and terrestrial taxa) provided additional information about changes in the microphytobenthos caused by drought that supplement information on diatom indices interpretation. For example, increases in the abundance of motile taxa, e.g., from the genera *Nitzschia* and *Navicula*, which are considered to prefer waters with high trophic levels and electrolyte contents (Van Dam et al., 1994; Lange-Bertalot et al., 2017), can lead to decreased diatom indices values and consequently classified as poorer status aquatic habitats. This threat is also emphasized by Stubbington et al. (2019), who postulate that existing indices require further evaluation to establish their potential for use in biomonitoring during dry-phase periods and that their potential might vary over time in relation to dry-phase durations and space.

6. Conclusions

1. During drought in the watercourses studied, significant changes in water chemistry variables were observed (increased conductivity and sulphate concentration, and reduced pH and nitrate, nitrite, and ammonium concentrations).
2. During periods of the highest water levels, the number of taxa observed was the lowest, but this number increased during summer and drought periods.
3. Diatom community composition did not change significantly with regard to the dominant taxa when drought periods were compared with drought-free periods. The differences in assemblage structure were related to watercourse size – the smaller the watercourse, the more pronounced the differences.
4. The low-profile guild was the most abundant. During drought, the abundance of motile and low-profile diatoms increased significantly. The share of terrestrial diatoms was small throughout the research period, but their number increased significantly during drought.
5. During drought periods, diatom indices values in watercourses with good ecological and high trophic statuses were significantly lower in comparison with drought free periods, but decreases in values did not affect the final classifications of water ecological status.

CRediT authorship contribution statement

Łukasz Peszek: Writing - original draft, Conceptualization, Investigation, Software, Validation, Writing - review & editing. **Aleksandra Zgrundo:** Conceptualization, Writing - original draft, Validation, Writing - review & editing. **Teresa Noga:** Methodology, Supervision. **Natalia Kochman-Kędziora:** Investigation, Writing - review & editing. **Anita Poradowska:** Investigation. **Mateusz Rybak:** Investigation. **Czesław Puchalski:** Funding acquisition, Resources. **Janina Lee:** Methodology, Supervision, Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107579.

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