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Tracking climate signals in lakes of northeastern Poland: modern sedimentation studies using chrysophyte cysts and diatoms

Poszukiwanie sygnału klimatycznego w jeziorach północno-wschodniej Polski: badania współczesnej sedymentacji z wykorzystaniem cyst złotowiciowców i okrzemek

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Contents

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The dissertation consists of three scientific publications, the leading author of which is a doctoral student. Two publications have been published in international journals with Impact Factor, and one is currently under review. In the subsequent parts of the doctoral dissertation, following numbering has been assigned to the publications:

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Abbreviations

AT	Air temperature
AT_SD	Standard Deviation of Air Temperature
BGA.PC	Phycocyanin
CF	To Confirm
Chl-*a*	Chlorophyll-*a*
DO	Dissolved Oxygen
SC	Specific Conductance
ESM	Electronic Supplementary Material
FM	Fall Mixing
NP.ratio	Total Nitrogen to Total Phosphorus Ratio
PZ	Photic Zone
PRCP	Precipitation
PRCP_SD	Standard Deviation of Precipitation Sum
RDA	Redundancy Analysis
RS	Reverse Stratification
S	Summer Stratification
SM	Spring Mixing
TN	Total Nitrogen
TP	Total Phosphorus
WS	Wind Speed
WS_SD	Standard Deviation of Wind Speed
WT	Water Temperature
VIF	Variance Inflation Factor

Streszczenie

Współczesna zmiana klimatu ma znaczący wpływ na ekosystemy wodne. Powoduje zmiany temperatury wody, reżimu termiczno-miktycznego oraz dostępności składników odżywczych, a co za tym idzie wpływa na florę i faunę jezior. Złożoność procesów zachodzących w środowisku nadal stanowi wyzwanie dla zrozumienia w jaki sposób zmiany klimatu, a w szczególności krótkookresowe zmiany warunków meteorologicznych, zapisują się w osadach jeziornych. W związku z powyższym, głównym celem niniejszej pracy doktorskiej była identyfikacja oraz wyjaśnienie zależności pomiędzy sezonową zmiennością warunków meteorologicznych a zbiorowiskami cyst złotowiciowców i okrzemek w słodkowodnych jeziorach strefy umiarkowanej. Tak wyznaczony cel pracy wymagał długookresowych badań trzech jezior zlokalizowanych w północno-wschodniej Polsce (Łazduny, Rzęśniki, Żabińskie) z wykorzystaniem wysokiej rozdzielczości monitoringu limnologicznego i hydrochemicznego, a także monitoringu współczesnej sedymentacji. Analizy statystyczne zebranych danych środowiskowych oraz danych meteorologicznych pozwoliły na prześledzenie zależności między zbiorowiskami cyst złotowiciowców i okrzemek a sezonowymi warunkami meteorologicznymi.

Przeprowadzone badania wykazały istotny wpływ warunków meteorologicznych na sezonowość oraz sukcesję gatunkową cyst złotowiciowców i okrzemek w badanych jeziorach. Oddziaływanie warunków meteorologicznych odbywa się za pośrednictwem reżimu termiczno-miktycznego i obiegu nutrientów, podkreślając znaczenie intensywności i czasu trwania okresów mieszania oraz stratyfikacji w kształtowaniu dynamiki rozwoju cyst złotowiciowców i okrzemek. Badania wykazały także różnice w reakcji cyst złotowiciowców i okrzemek na zmiany warunków meteorologicznych spowodowane specyficznymi dla poszczególnych jezior uwarunkowaniami lokalnymi. Statystycznie istotne reakcje cyst złotowiciowców i okrzemek na zmienność warunków meteorologicznych zostały zidentyfikowane w jeziorach Łazduny i Ręśniki, podczas gdy w eutroficznym Jeziorze Żabińskim zależności te były znacznie bardziej złożone. Szczegółowe analizy wykazały brak możliwości wskazania specyficznych morfotypów cyst złotowiciowców bądź gatunków okrzemek, których zmienność byłaby modelowana wyłącznie przez zmienne meteorologiczne. Niemniej jednak, rozpoznane zależności między badanymi wskaźnikami biologicznymi, w szczególności cystami złotowiciowców, a zmianami warunków meteorologicznych pokazały potencjał i ograniczenia ich wykorzystania w rekonstrukcjach paleoklimatycznych.

Abstract

Climate change has an adverse effect on aquatic ecosystems resulting in alterations in water temperature, lake mixing patterns, resource availability, and, in turn, lake biota. The complexity of processes occurring in the environment still pose a challenge in understanding how climate change and in particular meteorological conditions influence biotic signal formation in lake sediments. Therefore, this thesis aims to identify and explain the relationships between seasonal changes in meteorological conditions and composition of chrysophyte cyst and diatom communities in temperate freshwater lakes. Three lakes located in northeastern Poland (Łazduny, Rzęśniki, and Żabińskie) were studied for three and half years using high-resolution monitoring of limnological and hydrochemical properties of the water column as well as modern sedimentation. Statistical analyses of the collected data combined with the meteorological variables facilitated exploration of linkages between chrysophyte cyst and diatom assemblages and weather conditions.

A conducted study showed that the seasonality and species succession of chrysophyte cysts and diatoms were indirectly influenced by meteorological conditions acting through changes in the mixing regime and nutrient cycling of investigated lakes, and highlighted importance of timing and duration of mixing and stratification phases in shaping chrysophyte cyst and diatom dynamics. This study pointed out some differences in biota responses caused by site-specific conditions. Depending on the trophic status of the lake, the statistically significant responses to specific meteorological conditions could be detected in low-trophy lakes while in an eutrophic lake the relationships were much more complex. Detailed analyses showed that it was not possible to identify specific cyst morphotypes or diatom species whose variability was solely modeled by meteorological conditions. However, recognized links between studied biological proxies, especially chrysophyte cysts, and changes in meteorological conditions showed the potential and limitations of using them in paleoclimatic reconstructions.

Introduction

1. Introduction

1.1. Rationale

Ongoing climate change is among the most intensively explored research problems in Earth sciences as currently it is considered to be one of the most severe threats to ecosystems around the globe. However, monitoring and understanding the consequences of climate change pose challenges due to multitude of responses occurring within different ecosystems. Numerous studies demonstrate that lakes are highly sensitive to climate forcing that induce rapid response in physical, chemical, and biological lake properties (Adrian et al., 2009; Råman Vinnå et al., 2021). Worldwide distribution of lakes and the confirmed potential of lake sediments to act as excellent environmental archives, provide the opportunity to capture various aspects of climate change in many geographic locations and climatic regions. What is more, lake ecosystems integrate responses over time which further support their value as sentinels of climate change (Adrian et al., 2009). Studies concerning the response of lakes to global warming show profound effects on the thermodynamics of lake water and reveal rapid warming of inland waters throughout the world (Schneider and Hook, 2010; Woolway and Merchant, 2019). Documented climate-related changes include shorter duration of winter ice-cover, strengthening and extension of summer stratification, and changes in mixing patterns (Woolway and Merchant, 2019; Kraemer et al., 2021; Råman Vinnå et al., 2021; Pilla and Williamson, 2022). Through these alterations, climate exerts strong impacts on phytoplankton which forms the basis of aquatic food chains and has global importance for ecosystem functioning (Winder and Sommer, 2012).

Influence of meteorological conditions on the phytoplankton population has been explored for many years now, and its sensitivity to the occurring changes has been established (Reynolds, 2006; Winder and Hunter, 2008; Meis et al., 2009). The dynamics of phytoplankton is linked to annual fluctuations in temperature, water column stratification, light availability, and consumption by herbivores, which can be modified by climate-driven fluctuations. Changes in the mixing regime proved to be by far the most important, as they influence the nutrient cycling and light distribution in the water column, which are major factors shaping phytoplankton growth (Meis et al., 2009; Winder and Sommer, 2012). Nevertheless, the complexity of lake ecosystems still presents a challenge in understanding how changes in seasonal meteorological conditions are transferred into biotic signal preserved in sediments. This especially refers to the lakes of high trophy and high human impact, as in this case the climatic signal can be hindered by accompanying processes occurring in water column.

For reliable prediction of the effects of global warming on lake ecosystems, it is essential to disentangle different information recorded in lake sediments. This can be attained by modern process studies combining (i) meteorological conditions, (ii) limnological processes, (iii) physical and chemical characteristics of water column, and (iv) analyses of organisms with short generation times, strong seasonal replacement and excellent preservation in lake sediments, such as chrysophyte cysts and diatoms (Bonk et al., 2014; Kienel et al., 2017; Korkonen et al., 2017; Tylmann et al., 2017; Maier et al., 2018; Apolinarska et al., 2020; Żarczyński et al., 2022). Although studies of complex reactions of lake biota to changes in meteorological conditions have advanced considerably in recent years (Pla-Rabes and Catalan, 2011; Rühland et al., 2015; Maier et al., 2018, 2019), investigations based on high-resolution and long-term monitoring data are still scarce, albeit necessary. Additionally, as the seasonality and succession of chrysophyte cysts and diatoms have become an important issue in contemporary limnology due to increasing interest in environmental reconstructions (Köster and Pienitz, 2006; Hausmann and Pienitz, 2007; Kirilova et al., 2008; Zou et al., 2018) the need for high-resolution monitoring studies has become evident.

The issues outlined above indicate an important gap in our knowledge which motivated this research. The selected lakes: Lake Łazduny, Lake Rzęśniki, and Lake Żabińskie present exceptional value for paleoenvironmental reconstructions because they accumulate varved sediments (Tylmann et al., 2017). They are influenced by similar meteorological conditions due to their location in the same region, yet differ in terms of their trophic state and human impact, allowing analyses of the preservation and transformations of climate signals in sediments.

1.2. State of research

1.2.1. Lakes as sentinels of ongoing climate change

Lakes are characterized by great sensitivity to meteorological conditions, which is manifested in changes in the physical, chemical, and biological properties of lake water (Wetzel, 2001; Adrian et al., 2009). Effects of these changes are recorded in the sediments. To key variables that reflect either direct or indirect influence of meteorological conditions on lakes are: water temperature, ice phenology, water level, water transparency, and chemical composition.

Water temperature is one of the most important physical properties, as it affects the functioning of the whole lake ecosystem. Regional-scale air temperature directly influences surface waters in lakes making the epilimnion temperature a valuable indicator of climate change (Livingstone and Lotter, 1998; Hampton et al., 2015). Recent studies on lake water temperatures show global upward tendencies and inevitable alterations in physical properties of water bodies (Schneider and Hook, 2010). Stronger density gradients due to increasing water temperature have been proved to result in changes in the duration of stratification that shift the timing of spring and fall mixing, and changes in depth of thermocline (Boehrer and Schultze, 2008; Butcher et al., 2015; Woolway and Merchant, 2019; Råman Vinnå et al., 2021). Due to long-term climate-related changes in the thermal structure of lakes, observations of regime shifts from polymictic to dimictic, dimictic to monomictic, or monomictic to oligomictic, may become prevalent (Adrian et al., 2009). Beside its profound effect on the thermal structure of lakes, air temperature plays an important role in controlling ice phenology. Due to increasing air temperatures shortening of the periods with ice cover or even its disappearance, and shifts in timing of ice-off during the spring become more common (Marszelewski and Skowron, 2006; Sharma et al., 2021).

Climate change has also a great effect on limnological processes in the water column and on chemical properties of lake waters. All these changes in the temperature and thermal structure profoundly impact fluctuations of oxygen concentrations in the water column. Alterations in mixing patterns occurring as a result of global warming will therefore force changes in lakes' oxygenation (Jane et al., 2021). These, in turn, will affect the circulation of nutrients (release from sediments under anaerobic conditions) and other elements dependent on redox processes, e.g. Fe and Mn (Davison, 1993). Increasing supply of nutrients from catchments connected to weathering, precipitation, runoff, terrestrial primary productivity, and fire frequency, may significantly change the intensity of primary production. This, in turn, can affect water transparency, pH, chlorophyll-a content, precipitation of carbonates, and sedimentation rates. Furthermore, changes in the weathering rate and water balance play an important role in defining the levels of pH, ionic strength and composition in lake waters (Smol, 2008). Disentangling the roles of different stressors and processes poses a challenge, especially as additional factors such as eutrophication, atmospheric nitrogen deposition, and acidification simultaneously influence lake ecosystems, hindering the climate signal.

Complex interactions between meteorological conditions, lake physical and chemical characteristics, and human impact result in multiple stressors affecting sensitive lake organisms (Reynolds, 2006; Jäger et al., 2008; Winder and Sommer, 2012). Thus, using biological proxies as climate change indicators has some limitations. Nevertheless, several studies concerning widespread responses of lake biota to changing meteorological conditions emerged. Especially planktonic organisms have been in focus for many years (Jäger et al., 2008; Meis et al., 2009). It has been recognized that changes in spring and early summer phenology, growth rates, abundance, and species composition can provide a good reflection of meteorological conditions (Blenckner et al., 2007; Rühland et al., 2015; Kakouei et al., 2021). Nonetheless, changes in lake properties caused by ongoing global warming might change the responses of lake organisms that have already been identified and described.

1.2.2. Chrysophyte cysts and their indicative characteristics

Chrysophytes are the algae belonging to the classes Chrysophyceae and Synurophyceae (Sandgren, 1991). They are commonly called golden or golden-brown algae. Chrysophytes are mainly freshwater organisms, nevertheless some exceptions are found in marine environments and saline lakes (Sandgren, 1991). Chrysophytes often dominate the phytoplankton of oligotrophic lakes (Eloranta, 1995). Most of the chrysophytes are unicellular or colonial. They are diverse group producing siliceous vegetative cells, called cysts or stomatocysts. Cysts itself are hollow siliceous structures, usually spherical, with a single exit pore with or without a collar surrounding the pore (Sandgren, 1991; Duff et al., 1995). The surface ornamentation of chrysophyte cysts play an important role in their identification. Currently over 1000 morphotypes have been described (e.g. Duff et al. 1995; Pla 2001; Wilkinson et al. 2001). Similarly to diatoms, they are widely distributed and well preserved in lake sediments. Several studies show their strong sensitivity to changes in environmental conditions and distinct seasonality. Therefore, they can be considered as environmental indicators (Adam and Mahood, 1981; Sandgren, 1991; Cumming et al., 1993; Pla-Rabes and Catalan, 2011; Korkonen et al., 2017). Nevertheless, despite their high indicative potential, chrysophyte cysts are still an under investigated phytoplankton group in terms of paleoenvironmental applications and much less often used than other biological proxies.

Studies of chrysophyte cysts started to gain attention in the 1980s and 1990s. Since then, many paleolimnological works linked chrysophyte cysts with environmental variables, with some studies resulting in transfer function, which further enabled quantitative reconstructions. Several studies, showed that conductivity and salinity had a clear impact on the chrysophyte cysts (Cumming et al., 1993; Siver, 1993; Pienitz et al., 1992; Duff et al., 1995). The distribution of cysts was also attributed to changes in pH (Duff and Smol 1991; Facher and Schmidt 1996; Pla and Anderson 2005) and to water chemistry in general (Duff and Smol, 1991; Pla et al., 2003; Hernández-Almeida et al., 2015b). Only recently, the distinct seasonality of chrysophyte cysts and their associations with climate-related variables have come into focus. It has already been proved that cysts can serve as proxies for cold-season temperatures in the South Central Andes (Jong et al., 2016), Central and Eastern Pyrenees (Pla and Catalan, 2005), and the Alps (Kamenik and Schmidt, 2005). De Jong et al. (2013a; b) used a cyst-based transfer function to reconstruct cold-season temperatures throughout the course of the last millennium from the varved sediments of Lake Silvaplana in the Swiss Alps. Furthermore, Pla-Rabes and Catalan (2011) discovered a strong correlation between seasonal temperatures and chrysophyte cyst assemblages in the dimictic Lake Redo (Pyrenees), demonstrating that stomatocysts are excellent indicators of seasonal changes in air temperature. Also, in a study from Finnish lake Nautajärvi, Korkonen et al. (2017) revealed that spring chrysophyte assemblages are mainly controlled by spring discharge intensity, which was considered as a surrogate for spring weather conditions. In this study it also has been shown that summer cyst assemblages are influenced mainly by precipitation and air temperature. Hernández-Almeida et al. (2015a), who reconstructed winter severity from the varved sediments of Lake Żabińskie, further supported the ability of chrysophyte cysts to act as a climate proxy.

Overall, the available studies provide evidence that chrysophyte cysts have great potential as a powerful indicator of past environmental conditions. However, there is still a number of unknowns about these organisms. Even though cysts have been already studied in various locations around the world, the data concerning their modern sedimentation and seasonality are scarce.

1.2.3. Diatoms and their indicative characteristics

Diatoms (Bacillariophyceae) are single-celled, photosynthetic algae which can be found in almost every aquatic environment including both fresh and marine waters as well as aerial and soils habitats (Dixit et al., 1992). Diatoms are often the dominant primary producers in most freshwater lakes, sometimes covering the majority of phytoplankton biovolume (Rühland et al., 2015). They are characterized by siliceous cell walls and yellow-brown pigmentation. Each diatom cell consist of two valves held by girdle bands, which together form diatom frustule with characteristic intricate pattern, allowing fossil taxa to be identified at a species level (Battarbee et al., 2001). Diatoms constitute one of the most diverse groups of phytoplankton. Estimates of the number of diatom species range from 20,000–2 million, with currently over 75,000 named taxa in the group (Guiry and Guiry, 2022).

Due to excellent preservation of diatom silica shells and narrow optima and tolerances for several environmental variables, they are the most frequently used biological proxies in limnological and paleolimnological research (Battarbee et al., 2001). Diatoms, thanks to their short generation cycles can respond rapidly in a species-specific manner to changes in their environment, which further confirm their value as environmental indicators. In the last century, diatoms have been commonly used as bioindicators in lake ecosystems. A substantial body of research present applications of diatoms in studies describing shifts in salinity, pH, or trophic state in lakes (e.g. Birks et al., 1990; Dixit et al., 1992; Smol and Stoermer, 2010; Rzodkiewicz et al., 2017; Rzodkiewicz, 2018; Sienkiewicz et al., 2021). More recent research has shown the potential for using diatoms to track climate-induced changes (e.g. Rühland et al., 2015; Fritz 2008; Juggins 2013). Based on paleolimnological records, it has been recognized that shifts in diatom assemblage composition may be considered as a signal of climate change. For example, it has been suggested that changes in the duration of ice cover may have influenced the relative abundance shifts between planktonic and periphytic diatoms in Arctic lakes (Rühland et al., 2015; Smol and Douglas, 2007; Smol and Stoermer, 2010). Studies from deep lakes in subarctic regions also suggested that the recorded diatom assemblage shift from benthic to planktonic was associated indirectly with climate warming manifested through decreased ice-cover duration, prolonged growing season and increased thermal stability (Sorvari et al., 2002). This type of change is typically associated with an increase in small, cyclotelloid planktonic taxa and simultaneous decrease of small benthic fragilarioid taxa and/or large tychoplanktonic *Aulacoseira* species. Numerous studies from Europe and North America also emphasize that the recent diatom assemblage shift is not a direct response to changes in air temperature or/and ice cover, but rather reflects indirect interconnections between climatic variables and physical and chemical lake properties (Lotter and Bigler, 2000; Rühland et al., 2008; Winder and Hunter, 2008; Winder et al., 2009; Smol and Stoermer, 2010). As an example, Lotter and Bigler (2000) studied the response of diatom assemblages from alpine lakes to the duration of ice-cover and found that the ice cover period strongly inhibits plankton development. Their study also pointed out that the seasonal cycle of diatom blooms depends largely on the timing of the ice out, and is connected to increased light availability caused by thawing ice cover. Together with the mobilized nutrients from sediments, it acted as a trigger for productivity pulse. They also found a significant correlation between benthic *Fragilaria* Lygbye species and duration of ice cover. Also Rühland et al. (2008), in their comprehensive synthesis of over 200 diatom-based paleolimnological records from the Northern Hemisphere, indicated extraordinary similarities in taxon-specific shifts which occurred with the change in habitat structure and quality linked to hemispheric warming trends. In addition, Reavie et al. (2017) in 10 sediment cores recovered from the Laurentian Great Lakes, demonstrated that diatom assemblages have recently undergone a reorganization characterized by higher abundances of the species from *Cyclotella sensu lato* group, which was associated with increases in water and atmospheric temperatures. Changes in water column properties such as stratification depths, longer ice-free periods, and potential alterations in water quality resulting from climate warming may have led to these increases (Reavie et al., 2017).

More recent monitoring studies using sediment traps, water column sampling and surface sediments provided insightful information on the seasonal dynamics of diatom assemblages. These studies identified, similarly to paleolimnological findings, that changes in *Cyclotella–Fragilaria–Aulacoseira* diatom assemblages are connected to changes in climatic conditions, which refer to lake ice, thermal stratification, and mixing regimes seasonality, and changes in the depth of epilimnion (Kilham et al., 1996; Lotter and Bigler, 2000; Rautio et al., 2000; Ptacnik et al., 2003; Pannard et al., 2011). Species-specific diatom data collected from Lake Tahoe in USA over a 30-year period, provided evidence that the strengthening of thermal stratification resulting from climate warming favors small-celled *Cyclotella/Discotella* taxa (Winder and Hunter, 2008). Also, a study conducted in the Experimental Lakes Area in northwestern Ontario, Canada by Wiltse et al. (2016) showed that an increasing abundance of *Discostella* over time may be attributed to earlier ice-off and a longer spring turnover period, caused by higher winter and spring temperatures. Moreover, a number of studies using contemporary surface sediments point to temperature as important variable explaining the differences in diatom composition between lakes (e.g. Pienitz et al. 1995; Lotter et al. 1997; Weckström et al. 1997). What is more, seasonality and succession of diatom growth became a focus of contemporary limnology due to strong seasonal patterns of diatoms which are affected by meteorologic-related physical drivers such as temperature, light availability, mixing events, and thermal stratification. The established importance of temperature in diatom ecology presents thermal stratification as the main driver of diatom composition in three lakes in Maine, USA (Boeff et al., 2016). Zou et al. (2018) indicated that the water temperature was a major driver of the seasonal succession of diatom assemblages in Yunlong Lake in southwest China. Changes in the length and intensity of thermal stratification, which both affect the nutrients and light availability, also appeared to impact diatom fluxes (Huisman et al., 2004; Falkowski and Oliver, 2007; Winder and Sommer, 2012). Köster and Pienitz (2006), using year-long sediment trap study, showed that diatom seasonality in Bates Pond, Connecticut, USA is related to water column stratification and nitrogen cycling while Kienel et al. (2017) attributed changes in diatom assemblages in the Tiefer See located in northeast Germany to the availability of light and nutrients mainly correlated to the spring warming and the duration of water column mixing. A sediment trap study conducted by Hausmann and Pienitz (2007) in lakes in the Laurentian Mountains, Canada, showed the impact of ice break-up date on spring diatom composition. Also, Maier et al. (2019) demonstrated that conditions occurring in late winter, such as light and nutrient availability, under-ice stratification, timing of ice break-up, and lake turnover, play an important role in the formation of diatom sediment signal and indicated the significance of the processes occurring under the ice for lake ecology.

Although diatoms have been studied intensively for many years now, and it has been established that sedimentary record of lakes provide a valuable archive of past changes in community composition, the search for good indicators sensitive to changes in meteorological conditions and, in the long term, climatic conditions is still in progress, what created an obvious need for studies on modern sedimentation.

1.3. Hypotheses and aims

Lakes and their sediments are excellent natural archives as they collect and integrate global, regional and local environmental signals. Organisms living in lakes especially preserve the information about the environmental conditions due to their strong sensitivity to occurring changes. Attempts to relate the distributions and abundances of different species to the specific environmental conditions have become a central theme in ecology. Disentangling the effects of climate, human impact and other processes is challenging due to the large number of the environmental variables influencing species distribution as well as taxa themselves. However, comprehensive modern process studies which combine sediment trapping with systematic observations of lake and catchment properties seem to be a powerful tool for connecting species taxonomy and abundances to environmental variables. Only thorough recognition of the modern processes leading to biotic sediment signal formation can support better interpretation of specific biological indicators in sediment records. Based on this approach, the following hypotheses are addressed in this thesis:

Hypothesis 1: The influence of meteorological conditions on chrysophyte cyst and diatom assemblages in lakes is manifested mainly through changes in the lake mixing regime. The timing and duration of mixing and stratification phases control both the total fluxes and taxonomic composition of chrysophyte cysts and diatoms.

Hypothesis 2: In lakes of different trophic status, the response of lake biota to changes in meteorological conditions will be different. Direct relationships may be detected in low-trophy lakes. Under eutrophic conditions, these relationships are masked or modified by complex biogeochemical processes taking place in the water column.

Hypothesis 3: Long-term and high-resolution systematic observations of chrysophyte cyst and diatom variability should allow for finding precise indicators (cyst types or diatom species) of specific seasonal meteorological conditions.

The following objectives were set in order to test these hypotheses:

Objective 1: To determine seasonal patterns of variation in chrysophyte cyst and diatom assemblages from sediment traps in three lakes of different trophic status.

Objective 2: To explain the relationships between meteorological conditions and chrysophyte cyst and diatom assemblages in the investigated lakes.

Objective 3: To examine whether unusual meteorological conditions associated with ongoing climate change have a direct impact on seasonal patterns of chrysophyte cyst and diatom dynamics in temperate dimictic lakes.

Materials & methods

2. Materials and methods

2.1. The study framework

The presented study is based on three and half year-long, high-resolution monitoring records from three Polish lakes: Lake Łazduny, Lake Rzęśniki, and Lake Żabińskie. To meet the objectives of the study, the research strategy was based on three pillars (1) physical and chemical variables measured in the water column, (2) chrysophyte cyst and diatom assemblages collected from sediment traps, and (3) meteorological data (Fig. 1). The study design aimed to build a multiproxy dataset that could be used to analyze the relationships between different variables and provide the outcome in the form of three research papers. To do so, environmental data were first collected to obtain detailed information about limnological and hydrochemical conditions in investigated lakes. Simultaneously, sediment traps were installed at each lake to collect samples of chrysophyte cyst and diatom assemblages. Finally, daily meteorological data were obtained from the IMGW-PIB database. Three scientific publications were then prepared based on the gathered data (Fig. 1). In the first and second paper, chrysophyte cysts and diatoms combined with meteorological, limnological, and hydrochemical data, allowed to recognize the key processes responsible for shaping the fluxes and taxonomic composition dynamics in lakes Łazduny and Rzęśniki. Both papers present the links between meteorological conditions and biotic sediment signal in low-trophy lakes which have not been impacted by direct human activity. In the third paper, the response of chrysophyte cysts and diatoms to changing meteorological conditions is analyzed in Lake Żabińskie, a eutrophic lake with substantial human impact in the catchment.

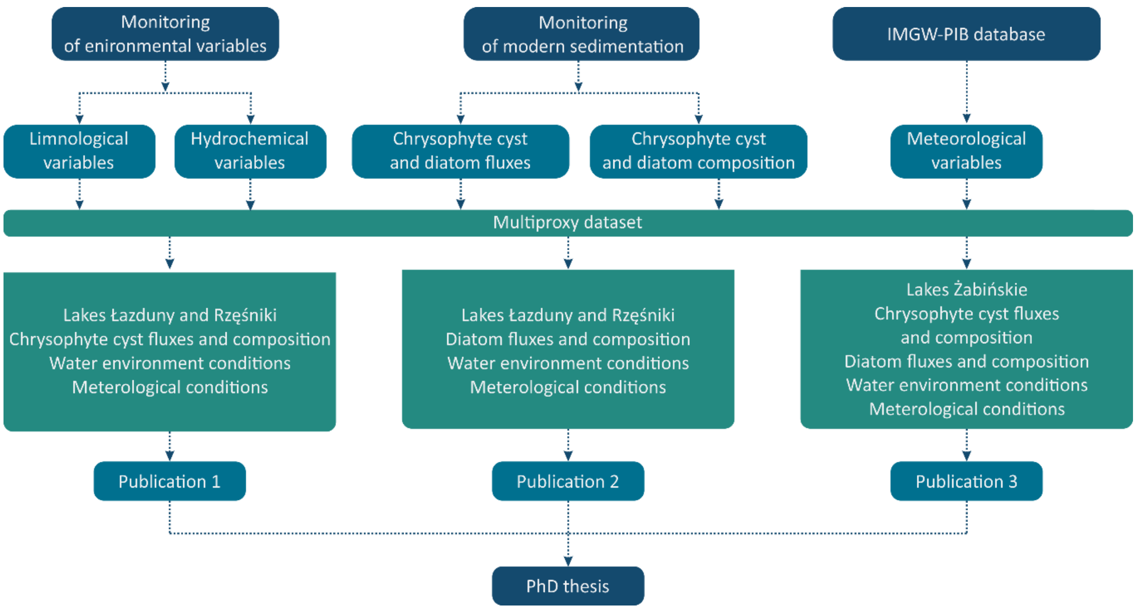

Figure 1. General workflow of the research process.

2.2. Study sites

Lake Łazduny (53˚51'18.3"N, 21˚57'07.1"E, 128.8 m a.s.l.), Lake Rzęśniki (53˚50'30.0"N, 21˚58'35.9"E, 125.0 m a.s.l.), and Lake Żabińskie (54˚07'54.2"N, 21˚58'56.5"E, 117.0 m a.s.l.) are located in the Masurian Lake District in northeastern Poland (Figs 2, 3). This region represents a typical lowland postglacial landscape with diverse topography, a wide diversity of glacial landforms and common glaciofluvial deposits. Climatic conditions in the region are generally characterized by strong seasonality, with mean monthly air temperatures ranging from -3.3°C (January) to 18°C (July) (Tomczyk and Bednorz, 2022). Mean annual precipitation amounts to 600 mm with a maximum in July (ca. 80 mm). The predominant wind direction is west and southwest. A hydrographic network is rich in lakes of diverse dimensions and basin morphologies. The areal density of lakes locally exceeds 20% and values in the range of 5–10% are common for the entire area (Choiński, 2007). Typically, lakes are covered by ice between December and April (Marszelewski and Skowron, 2006).

Lakes Łazudny and Rzęśniki have similar maximum depths (22.4 m and 26 m, respectively) as well as surface areas (10.6 ha and 12 ha, respectively) (Figs 2, 4). The lake basins fill depressions along the NW-SE direction, which were formed by dead ice melting during the Late Glacial or the early Holocene (Sanchini et al., 2020). In the northern part of the catchment, elevations exceed around 153 m a.s.l. and decrease in a southerly direction with the minimum of 125 m a.s.l. (Fig. 2). The surface geology of their shared catchment (1.94 km^2) consists of glacial sands, gravels, and peat (Szumański and Laskowski 1990) (Fig. 2). The surroundings of both lakes are predominantly covered by dense forest with a dominance of coniferous trees (Fig. 2). Lake Łazduny has no surface inflows and one outflow in the southern part. Hence, it is supplied by groundwater and precipitation. Lake Rzęśniki has one inflow from the northwest and the outflow which drains into Lake Orzysz (Fig. 2). Primary measurements of hydrochemical variables from the years 2007-2010 indicated dimictic mixing regime and mesotrophic conditions in Lake Łazduny (Tylmann et al., 2013).

Of the three investigated lakes, Lake Żabińskie is the deepest (44.4 m) and has the largest surface area (41.6 ha) (Figs 3, 4). The lake basin is slightly elongated in the W-E direction and occupies a glacially eroded depression formed most likely during the Vistulian glaciation, but lacustrine sedimentation started as late as in early Holocene (ca. 11 ka BP) (Zander et al., 2021). The total catchment (24.79 km^2) is divided into three sub-catchments: Lake Łękuk (13.59 km^2), Lake Purwin (7.22 km^2), and the direct catchment of Lake Żabińskie (3.98 km^2). In the eastern part of the catchment elevations exceed 200 m a.s.l. and decrease generally in a westerly direction to a minimum of 117 m a.s.l. which is the water level of Lake Żabińskie (Fig. 3). The surface geology of the Lake Żabińskie catchment is composed mostly of glacial tills, sands, and gravels (Szumański, 1997; Pochocka-Szwarc and Lisicki, 2006) (Fig. 3). Lake surroundings are characterized by mixed land use. The northern and southwestern parts are covered by pine forests with spruce and birch trees. On the north of the lake basin, there is a recreation area established during the second half of 20th century. Fields and meadows dominate in the eastern and southeastern parts (Fig. 3). Lake Żabińskie has two permanent and one periodic inflow. The outflow drains westward into Lake Gołdopiwo (Fig. 3). Limnological monitoring of Lake Żabińskie from the years 2011-2014 indicates that it is primarily a dimictic and eutrophic water body, with periods of meromictic and monomictic mixing regime (Bonk et al., 2014).

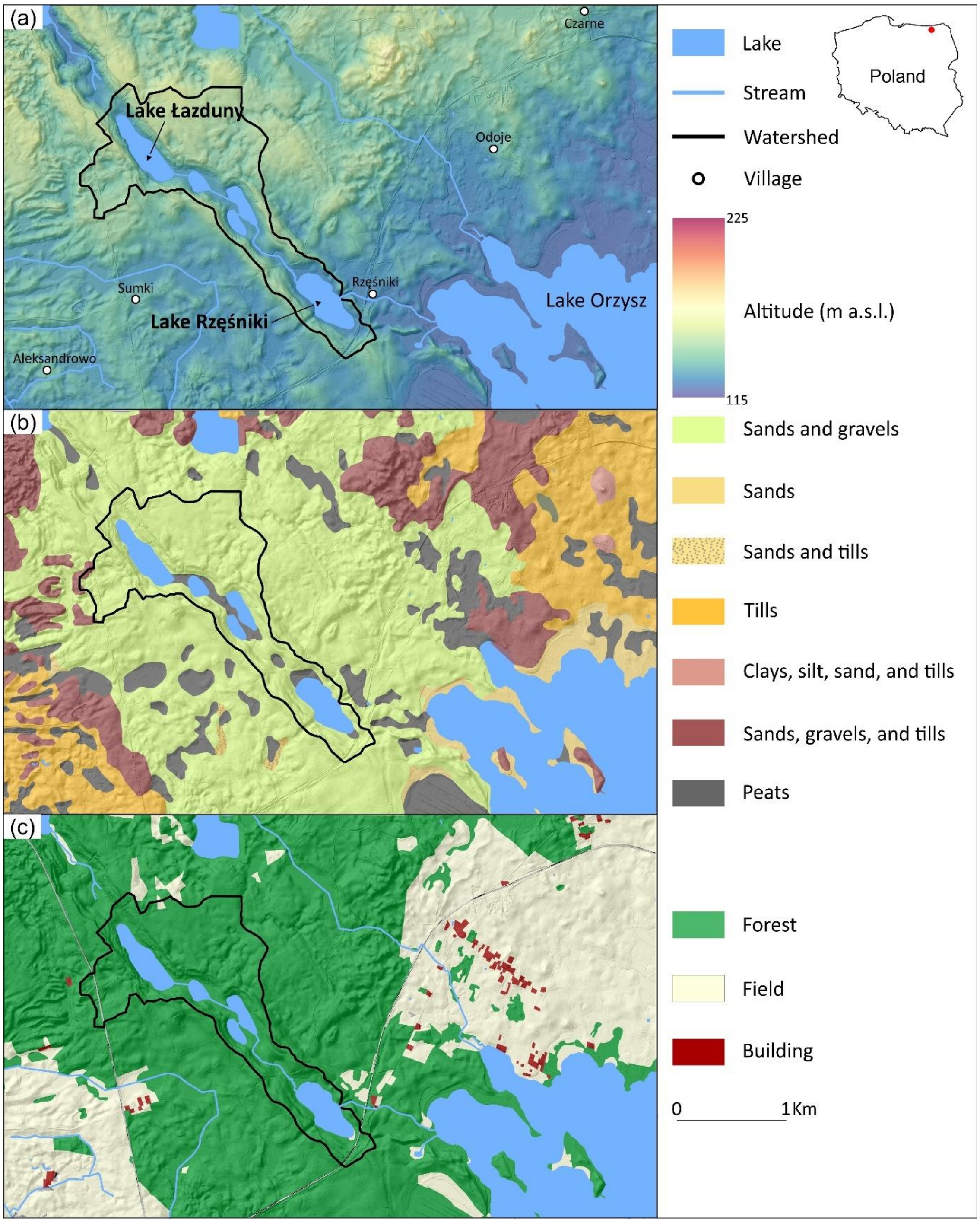

Figure 2. Catchment of lakes Łazduny and Rzęśniki and closest surroundings (a) topography, (b) surface geology, (c) land use.

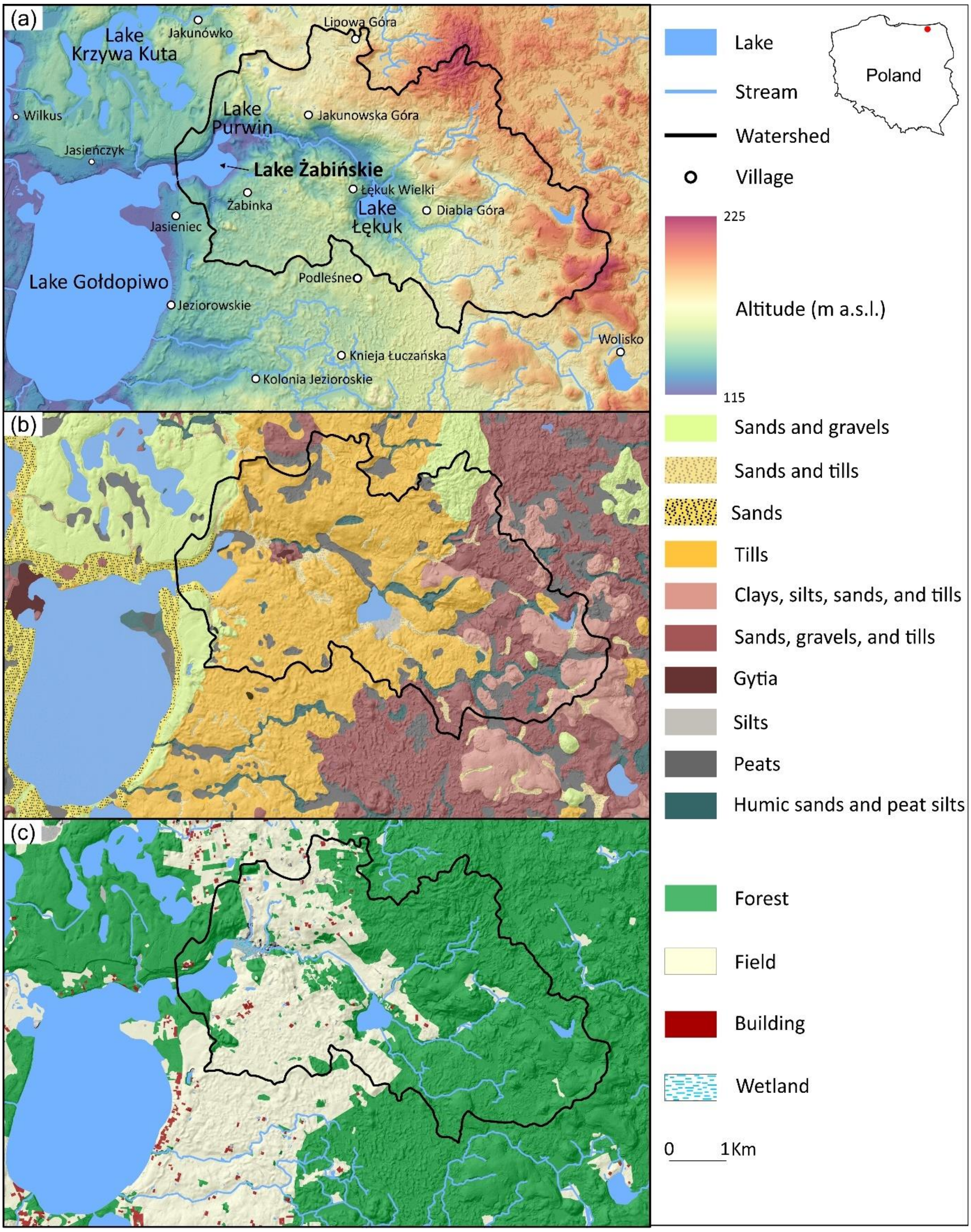

Figure 3. Catchment of Lake Żabińskie and closest surroundings (a) topography, (b) surface geology, (c) land use.

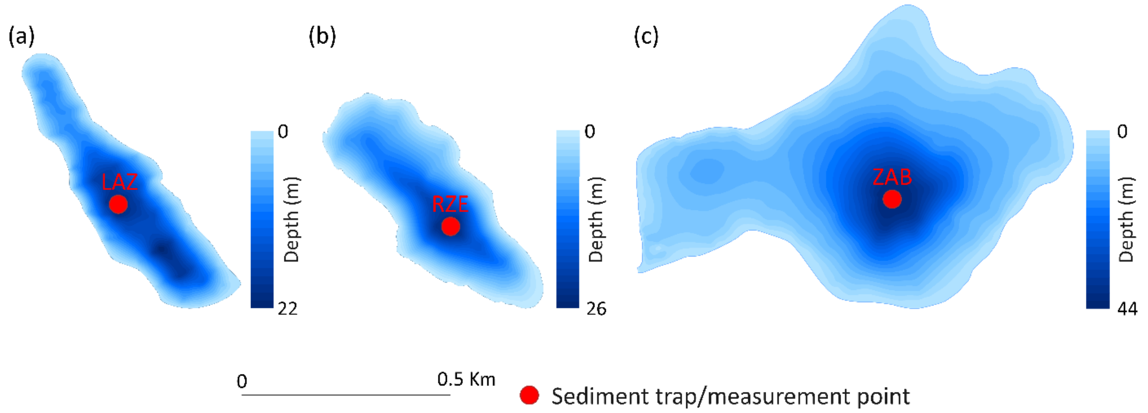

Figure 4. Bathymetry of lakes (a) Łazduny, (b) Rzęśniki, (c) Żabińskie, with location of the sediment trap / measurement point.

2.3. Methods overview

2.3.1. Environmental data

Meteorological data such as air temperature (AT), wind speed (WS), and precipitation (PRCP) for the closest meteorological stations – i.e., Mikołajki for lakes Łazudny and Rzęśniki, and Kętrzyn for Lake Żabińskie – were obtained from the Institute of Meteorology and Water Management–National Research Institute database (https://danepubliczne.imgw.pl/). Ice-cover dates were established based on field observations and satellite imagery.

Water column characteristics were monitored from December 2016 in lakes Łazduny and Żabińskie, and February 2017 in Lake Rzęśniki, until July 2020. Measurements of water temperature (WT), specific conductance (SC), pH, dissolved oxygen (DO), chlorophyll-a (Chl-*a*) and phycocyanin concentrations (BGA.PC) in the water column were conducted bi-weekly using EXO 2 Multiparameter Sonde (YSI, USA) at 1 m depth intervals. Additionally, in Lake Żabińskie WT was measured by HOBO Water Temperature Pro v2 loggers (ONSET) at depth of 1, 5, 10, 20, 30 and 40 meters. A Secchi disk was used to determine the transparency and the depth of the photic zone. Water samples were taken from three different depths in each lake (1 m, 10 m, 20 m in Lake Łazduny; 1 m, 10 m, 25 m in Lake Rzęśniki, 1 m, 10 m, 40 m in Lake Żabińskie). Total phosphorus (TP) and total nitrogen (TN) concentrations were measured using UV/VIS spectrophotometer (Spectroquant Prove 600 Spectrophotometer, Merck, Germany).

2.3.2. Modern sedimentation

To record the seasonal changes in chrysophyte cyst and diatom composition and fluxes, sediment samples were collected using sediment traps installed 1 m above the sediment surface in the deepest parts of lakes (Fig. 1). Each trap consisted of four 80-cm-long tubes with an inner diameter of 86 mm and a total active area of 232.4 cm^2. Sediment samples were collected approximately monthly during ice-free periods. Ice-cover period for each year is represented by one sample collected immediately after ice-out.

2.3.3. Chrysophyte cyst and diatom analyses

Sediment samples used for chrysophyte cysts and diatoms analyses were prepared using a standard method described by Battarbee et al. (2001). 50 mg of freeze-dried sediment was treated with 10% HCl to remove carbonates. Next, 30% H_2O_2 was used to eliminate organic matter. Samples were repeatedly washed with distilled water between each step. Following digestion all samples were mounted on microscope slides using the high refraction Naphrax® mounting medium. At least 100 chrysophyte cysts and 500 diatom valves were identified and counted per slide at 1000× magnification using a Nikon Eclipse E-200, Delta Optical Genetic Pro light, and Zeiss Axio Imager A2 light microscopes. Chrysophyte cyst identification followed Duff et al. (1995), Wilkinson et al. (2001), and Pla (2001). Due to difficulties with identification by light microscopy, the unornamented types were merged into 'collective groups' according to size: ≤5.9 µm (S001, S029, and S046); 6.0–8.9 µm (S009, S120, and S189); and ≥9.0 µm (S015, S042, and S150) (Fig. 5). In certain cases, the sizes of individual cysts were on the borderline between the two types. As a result, two additional groups were established (group 1–S001/S009, S029/S120, and S046/S189; group 2–S009/S015, S120/S042, and S189/S150). In addition, two ornamented types, D114 and D115, which can be easily confused under light microscopy, were merged into the 'collective group' D114/115 (Fig. 5). Diatom taxonomic identification was mainly based on Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b). The taxonomy was corrected to current conventional names based on recently accepted nomenclature (Guiry and Guiry, 2022). Chrysophyte cyst and diatom fluxes were calculated by adding divinylbenzene microscopic markers to samples (microspheres), which were then counted alongside chrysophyte cysts and diatoms (Battarbee and Kneen, 1982).

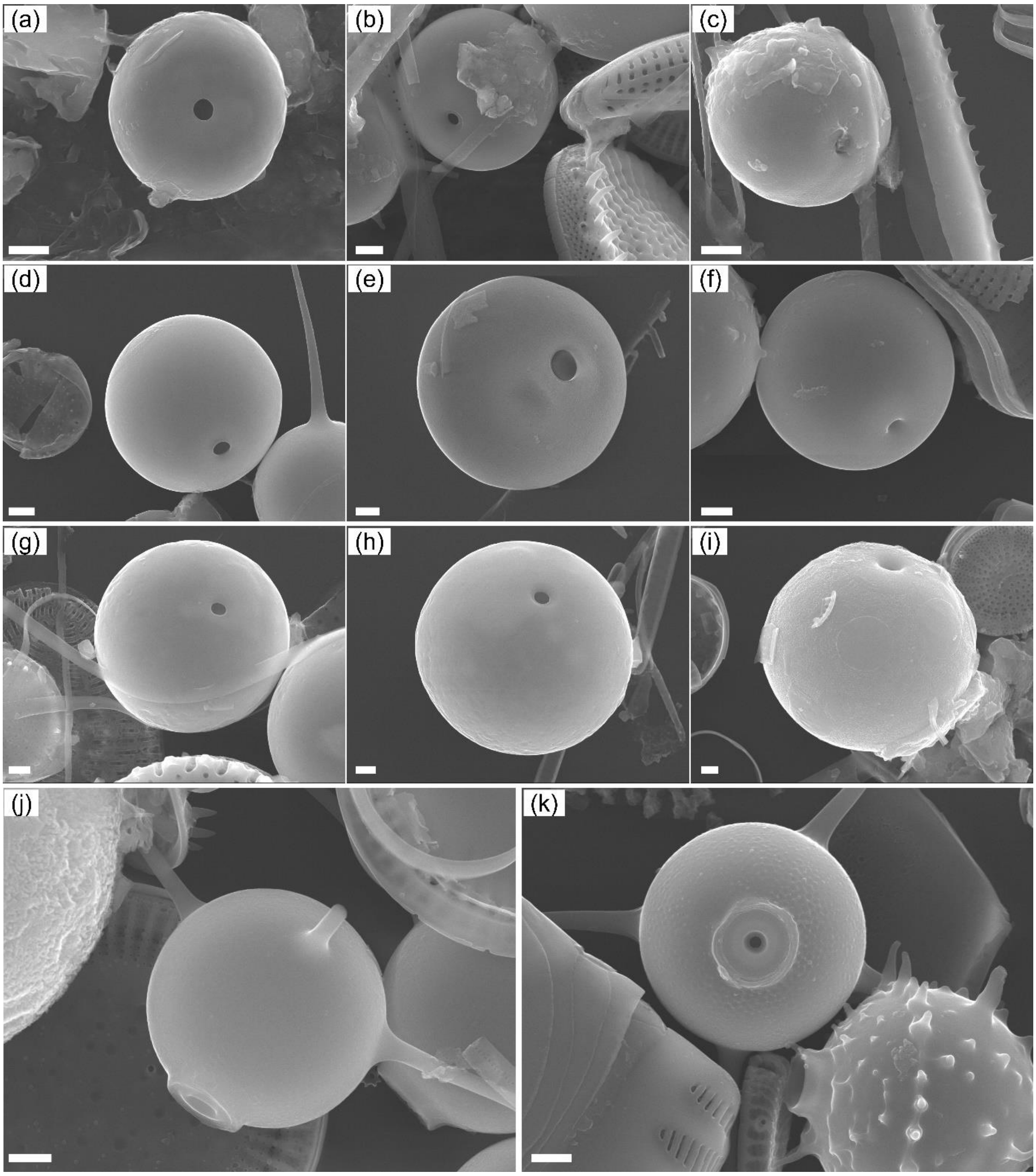

Figure 5. SEM micrographs of cyst morphotypes subjected to merging into ‘collective groups’ due to difficulties with identification under light microscope (scale bar – 1 μm); (a) S001, (b) S029, (c) S046, (d) S009, (e) S120, (f) S189, (g) S015, (h) S042, (i) S150, (j) D114, (k) D115.

2.3.4. Statistical analyses and data visualization

All statistical analyses and plotting were performed within the R environment (R Core Team, 2020). Firstly, to understand and familiarize with collected data, an exploratory data analysis was conducted. Environmental variables were prepared for further analysis as follows: for each measurement date, the Secchi disk depth was multiplied by 2.5 to determine the depth of the photic zone (Poikane, 2009), then measured parameters were averaged within this zone and for the periods of sediment trap exposure. Regarding chrysophyte cysts and diatoms, only taxa with an abundance of 2% or more in at least one sample were considered for further analyses.

Samples from ice-cover periods were excluded from analyses due to very low fluxes. To check which statistical approach will be most appropriate for the data analysis, Detrended Correspondence Analysis (DCA) was conducted. Then ordination methods (Redundancy Analysis – RDA) were performed on transformed data to explore relationships between the studied organisms and environmental conditions. Limnological (except pH), hydrochemical, and meteorological variables were log-transformed using natural logarithm - log(), whereas for chrysophyte cyst and diatom data log(x+1) was used. For each lake, three RDA runs were carried: the first one for the period of mixing, the second for stratification period, and the third for the combination of these two periods. Depending on the data manual selection and variance inflation factors (VIF) or forward selection were used to reduce the environmental variables and avoid over-fitting of the model. Additionally, with the assumption that response variables have a lagged reaction to explanatory variables (Duarte, 1990; Legendre and Legendre, 2012), we compared the chrysophyte cyst and diatom data with environmental variables from the same month, two weeks before, and one month before. To explore how much variation in taxonomic composition is explained by climatic and combined hydrochemical and limnological variables, variation partitioning was conducted. Chrysophyte cysts from lakes Łazduny and Rzęśniki were analyzed using Multilevel Pattern Analysis, to check for presence of indicator types (Cáceres et al., 2010).

All the maps were created with ArcGIS Pro 3.1.0 (Esri, United States of America). Digital terrain model was built from LIDAR data shared by Główny Urząd Geodezji i Kartografii. Geological maps were created based on Szczegółowa Mapa Geologiczna Polski 1: 50 000 – Portal GEOLOGIA (geologia.pgi.gov.pl). Data necessary to create land use maps of lakes catchments and theirs surroundings were obtained from Baza Danych Obiektów Topograficznych (BDOT10k - www.geoportal.gov.pl). Bathymetric maps of the lakes were created based on field measurements using an echosounder (Humminbird, USA).

Results

3. Results

3.1. Environmental conditions (Publications 1-3)

Monitoring of limnological and hydrochemical variables combined with the meteorological records enabled to recognize seasonal patterns in environmental conditions and mixing regimes in the investigated lakes. Over the observation period, diverse meteorological conditions were recorded – especially during the winter months. Between 2017 and 2019 temperatures below freezing point prevailed during the winter months and resulted in development of ice cover lasting from December/January till end of March (Fig. 6). In contrast, in winter 2019/2020 temperature records showed only around ten days with AT below 0°C, and the mean AT during that time reached around 5°C. Due to unexpectedly warm meteorological conditions, ice cover did not develop on the lakes (Fig. 6). Each year, during the spring, the increase in AT was observed and the highest increase rate and mean value (14.8°C) occurred in 2018, and the lowest mean AT in 2017 (8.1°C). Also summer of 2018 was the warmest from the observation period, with maximum AT recorded at that time reaching around 26°C, and mean value around 18°C. The highest WS values were observed during spring and fall, while the highest PRCP totals were observed in the summer months.

The diversity of meteorological conditions was accompanied by specific limnological processes. Between 2017 and 2018, the presence of the ice cover on each investigated lake was connected with development of reverse stratification. During the coldest winter 2017/2018, the lakes were covered with ice for >80 days. With the thawing of ice cover and increase of AT in spring, the water column mixing started which transported the oxygen to deeper water strata. The duration and depth of effective oxygen transport varied between years and between lakes (Tab. 1). Spring was followed by summer stratification, with oxygen present only in epilimnetic waters. An anoxic zone (DO <1 mg O_2 L^{-1}) developed below ca. 10 m depth in lakes Łazduny and Rzęśniki and ca. 5 m water depth in Lake Żabińskie (Fig. 6). Fall mixing started with deepening of the thermocline in late summer and was followed by oxygen transport to deeper waters. During the exceptional year 2020, the same pattern of deep and intense water column mixing developed in all three lakes. The longest period of homothermy and good oxygenation of the entire water column lasted from December 2019 in Łazduny and Rzęśniki and January 2020 in Lake Żabińskie till May 2020 (Tab. 1, Fig. 6).

Along with the changes in meteorological conditions and mixing regimes, alterations in nutrient concentrations in lake water were recorded. In general, observed seasonal variability showed that mixing periods were accompanied by increases in nutrient concentrations (Fig. 6). In Lake Łazduny the highest TP values was observed in fall 2017, in Lake Rzęśniki in spring 2017 and 2018, in Lake Żabińskie in spring 2018 and 2019. The turn of 2020 was characterized by the greatest values of TN in lakes Łazduny and Rzęśniki, while in Lake Żabińskie this happened in the spring of 2017 and 2019 (Fig. 6). Winters were generally characterized by elevated TN values. Along with nutrients concentrations, values of N:P ratio varied seasonally and interannually, with general increases in spring and fall. The highest N:P ratio values were recorded in spring 2017 and 2020 in lakes Łazduny and Rzęśniki, and spring of 2017 and 2018, and summer 2017 in Lake Żabińskie (Fig. 6). Chl-*a* peaks were observed in spring periods at the turn of April and

May. The greatest values of Chl-*a* concentrations from the entire observation period were recorded in spring of 2017 (Fig. 6).

Table 1. Summary of water column characteristics during the observation period in studied lakes.

Lake:	***Year***	***Łazduny***	***Rzęśniki***	***Żabińskie***
Ice cover length [days]:	*2017*	*74*	*74*	*75*
	2018	*87*	*87*	*88*
	2019	*77*	*77*	*77*
	2020	*7*	*7*	*2*
Spring mixing depth [m]:	*2017*	*15*	*13*	*28*
	2018	*13*	*10*	*28*
	2019	*13*	*9*	*24*
	2020	*22.4*	*26*	*44*
Fall mixing depth [m]:	*2017*	*14*	*13*	*30*
	2018	*22.4*	*17*	*17*
	2019	*22.4*	*20*	*36*

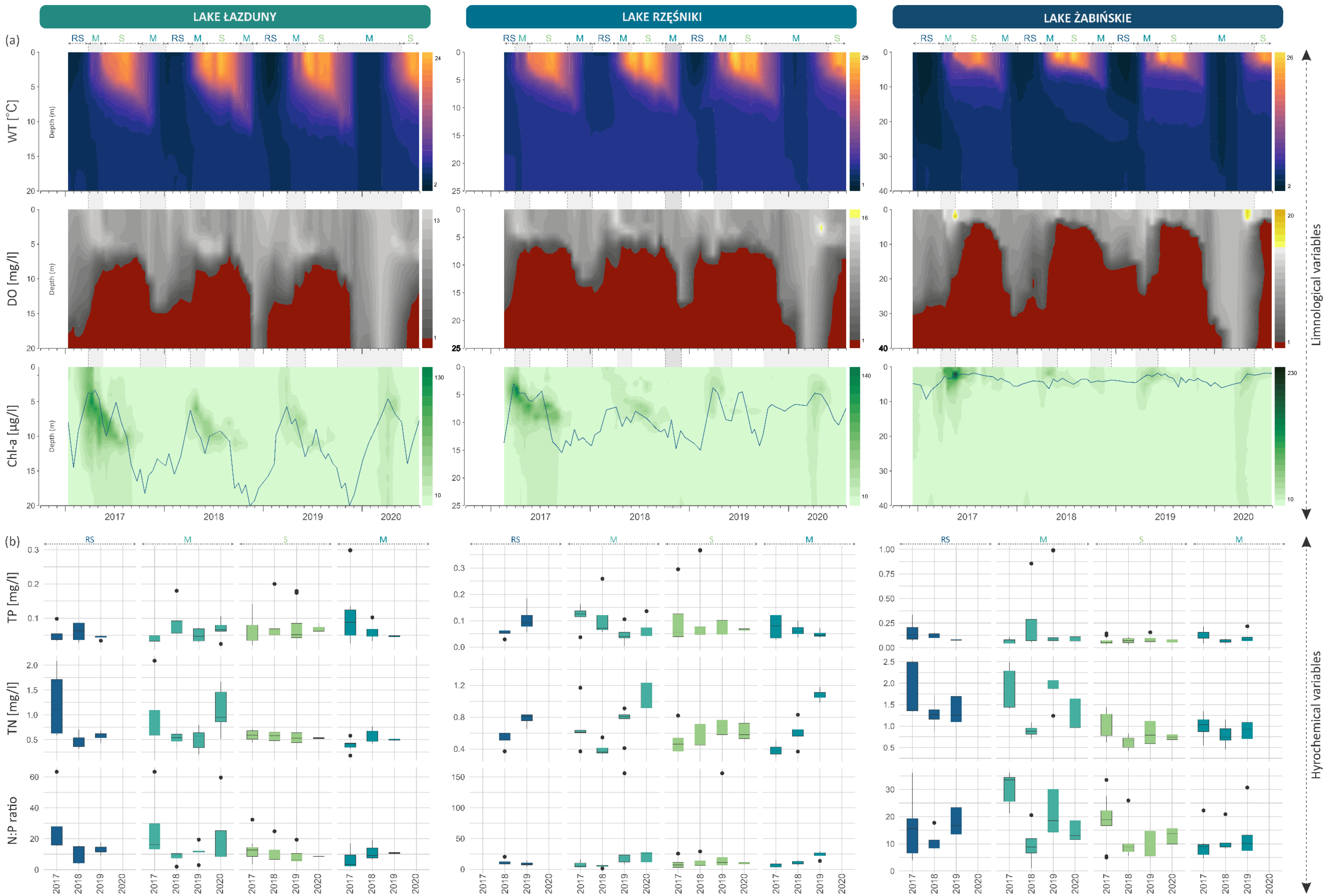

Figure 6. (a) Depth profiles of WT, DO, and Chl-a concentrations with depth of the photic zone (blue line), (b) boxplots of mean values of TP and TN for the depth of photic zone, and N:P ratio. "RS" stands for reverse stratification, "M" for mixing, and "S" for summer stratification.

3.2. Chrysophyte cysts and diatoms in lakes Łazduny and Rzęśniki (Publications 1, 2)

Although cysts and diatoms presented similar pattern of the total fluxes pulses, diatoms dominated over chrysophyte cysts. Additionally, lakes Łazduny and Rzęśniki were characterized by much higher fluxes of chrysophyte cysts, ca. 1 magnitude higher than Lake Żabińskie (Fig. 7). This is connected to the trophic status and promotion of the phytoplankton growth in lower-trophy lakes. In lakes Łazduny and Rzęśniki the total fluxes of both chrysophyte cysts and diatoms between 2017 and 2019 peaked in the spring and fall samples, following the pattern characteristic for dimictic lakes. Additionally, in Lake Rzęśniki two diatom fluxes peaks occurred each spring: first immediately after the ice out and second in the early summer. The magnitude of peaks varied between years with those from 2017 as the greatest, and general decreasing trend. The fluxes of chrysophyte cysts and diatoms in exceptional year 2020 were diverse. Chrysophyte cyst fluxes did not show any distinct peaks at that time and had generally low values, while increase in diatom fluxes was observed in March and was followed by quite an even distribution of diatom fluxes till the end of June.

The initial composition of diatom and chrysophyte cyst assemblages varied between investigated lakes (Fig. 7). Due to similar physical and chemical properties of lakes Łazduny and Rzęśniki, similarities were recorded in terms of taxonomic composition of chrysophyte cysts and diatoms. In Lake Łazduny, 127 cyst morphotypes in 34 samples were identified, 51 of which had a minimum occurrence of over 2% in at least one sample. The dominant ones were D114/115 (23.41%), unornamented 6–8.9 µm (12.9%), S033 (6.4%), unornamented ≤ 5.9 µm (5.8%), and S118 (4.6%), which accounted for more than half of the identified cysts (Figs 5, 7, 8). In Lake Rzęśniki, 160 cyst morphotypes in 33 samples were recognized, with 54 reaching an abundance of over 2% in at least one sample. The most common cysts included S041 (12.7%), D114/115 (12.6%), unornamented 6–8.9 µm (11.3%), S118 (8.1%), D317CF (4.8%), D116 (4.7%), and S033 (4.4%), which accounted for more than half of all the identified cysts (Fig. 7). In Lake Łazduny, of 176 diatom species, 31 reached a relative abundance at least 2% in one sample. The most common species were *Pantocsekiella comensis* (33.2% of all counted valves), *Pantocsekiella ocellata* (14%), *Lindavia radiosa* (7.9%), *Staurosira construens* (7%), *Asterionella formosa* (6.2%), *Stephanodiscus parvus* (4.2%), *Achnanthidium minutissimum* (3.7%), *Cyclotella cretica* var. *cyclopuncta* (2.7%), *Stephanodiscus neoastraea* (2.4%), *Staurosirella pinnata* (2.4%), *Staurosirella lapponica* (2%), *Pantocsekiella schumannii* (1%) (Fig. 7). They accounted for 86.7% of all counted valves. In 33 samples from Lake Rzęśniki, 124 diatom species were identified. 29 of them reached at least 2% in one sample, and the most abundant were *Pantocsekiella comensis* (38%), *Stephanodiscus parvus* (10.7%), *Staurosira construens*, *Lindavia radiosa* (5.8%), *Stephanodiscus neoastraea* (4.5%), *Stephanodiscus minutulus* (4.2%), *Pantocsekiella ocellata* (4.1%), *Fragilaria crotonensis* (4%), *Stephanodiscus hantzschi* (3.8%), *Staurosirella pinnata* (3.7%), *Achnanthidium minutissimum* (1.5%), *Stephanodiscus medius* (0.3%) (Fig. 7). They represented 89.8% of all valves counted.

RDA was conducted to assess the relationships between chrysophyte cysts (Publication 1), diatoms (Publication 2), and environmental variables. RDA results showed that cyst taxonomy was mainly modeled by SC, Chl-*a*, AT, AT_SD, pH and TN variability. Although multiple variables influenced seasonal and interannual changes in cyst taxonomic composition, RDA with variation partitioning provided the evidence of the direct influence of AT on the cyst composition. Among the most important variables influencing taxonomic composition of diatoms were AT, WS, WT, SC, TN, and BGA.PC. The response of diatoms to changes in environmental variables and meteorological conditions proved to be highly complex, and the recognized influence of AT and WS on diatom composition was not direct. Since the AT increase determine the strength and duration of the spring overturn, AT was more significant during the mixing periods. In contrast, WS had its greatest impact on diatoms during the stratification periods when the impact of increasing wind strength on the deepening of the epilimnion is noticeable.

Multi-level pattern analysis (Publication 1) showed that in Lake Łazduny cyst type D257 was associated with the period of fall mixing, S031 to spring and fall mixing, S159 to fall, spring mixing and the stratification period, and S404 to fall mixing and reverse stratification. In Lake Rzęśniki, types S130 and S180 were associated with spring and fall mixing, S161 with spring and fall mixing and stratification, and S159 with spring and fall mixing and reverse stratification. Examples of the cysts are shown in Fig. 8.

The obtained results show that both chrysophyte cyst and diatom seasonality indirectly corresponds to meteorological conditions acting through changes in the mixing regimes, which in turn influences nutrient and light availability in the lakes. Statistical analyses revealed that the taxonomic composition of studied organisms is dependent on multiple variables. Nevertheless, air temperature and wind speed are the most important meteorological variables influencing cyst and diatom assemblages. Additionally, specific cyst types were indicative of different periods of physical lake structure.

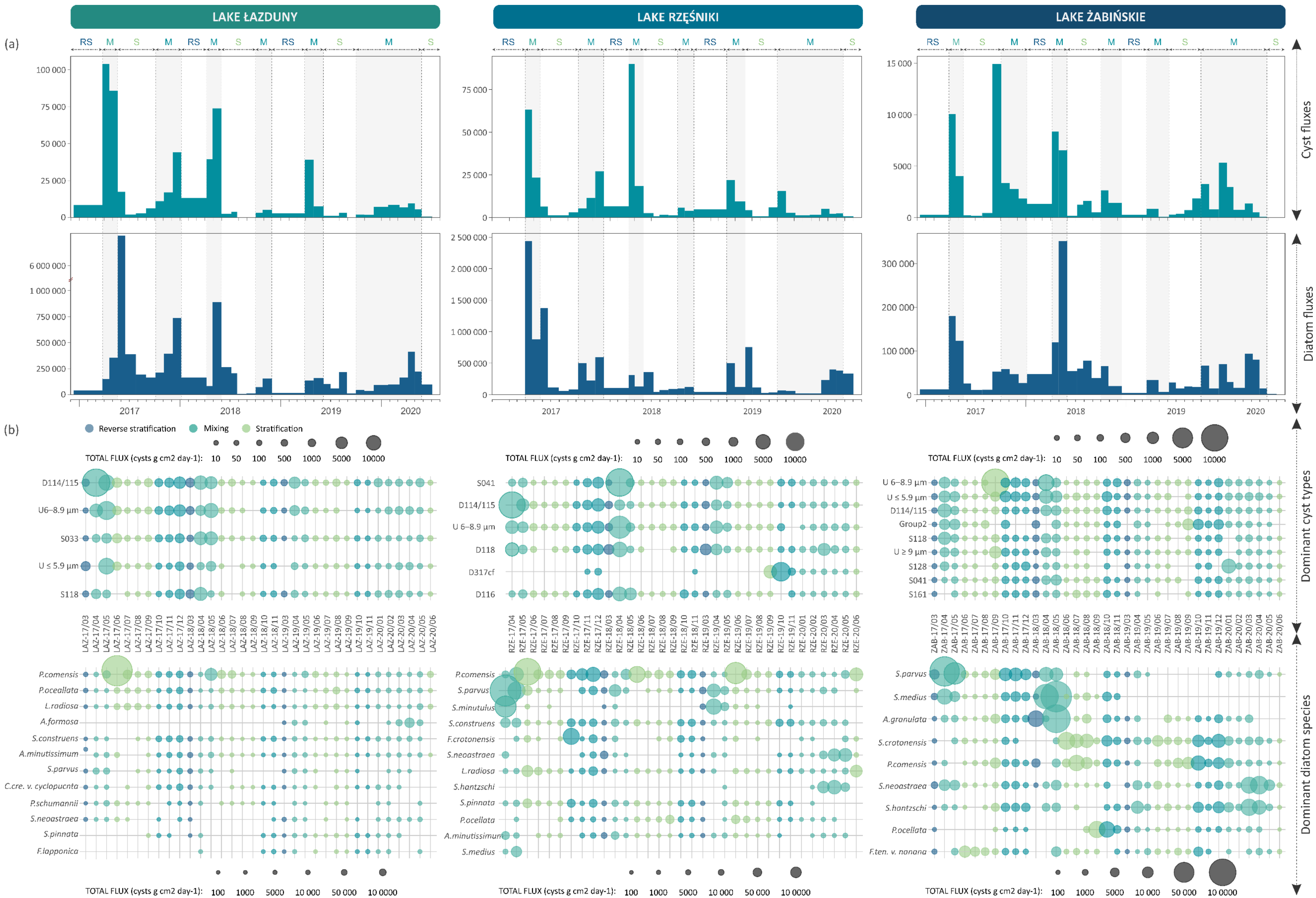

Figure 7. (a) Chrysophyte cyst and diatom total fluxes, and (b) bubble matrix of dominant chrysophyte cyst and diatom taxa. "RS" stands for reverse stratification, "M" for mixing, and "S" for summer stratification.

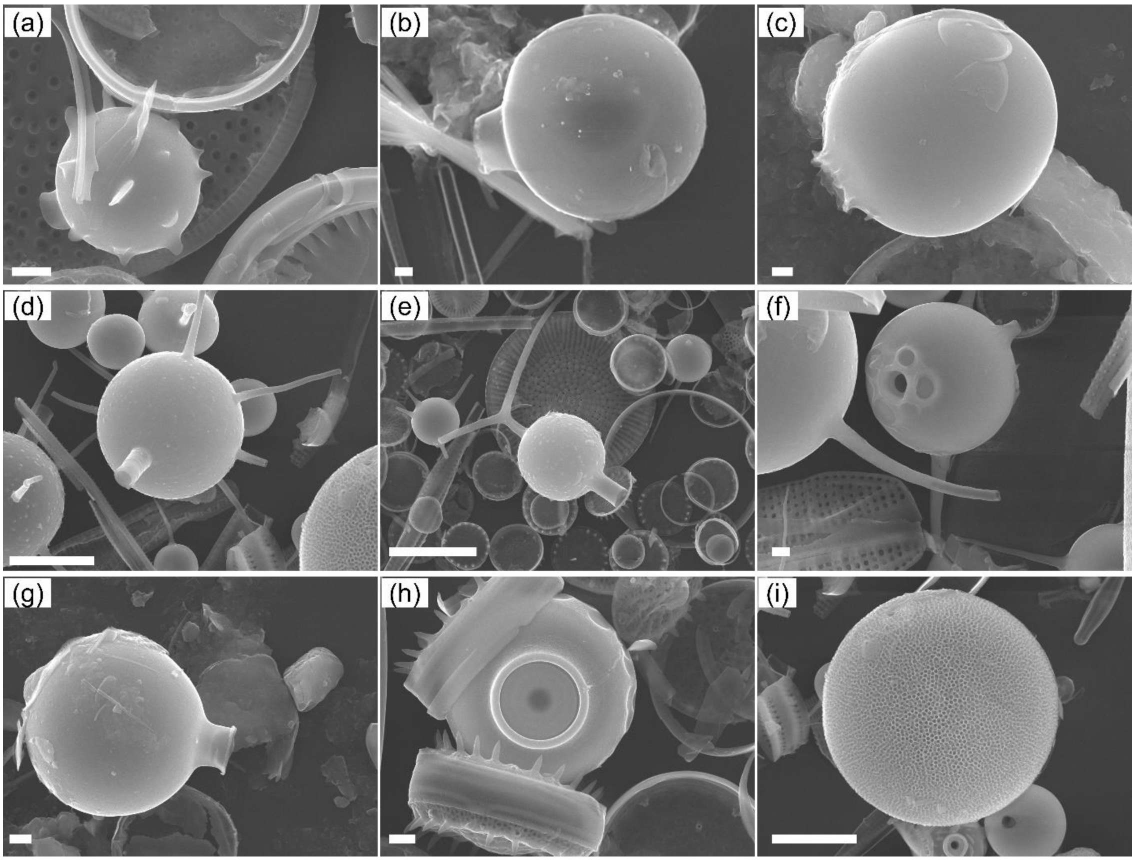

Figure 8. SEM micrographs of selected cyst morphotypes (scale bar – 1 µm); (a) S033, (b) S041, (c) S118, (d) S128, (e) S130, (f) S159, (g) S161, (h) S180, (i) S404.

3.2. Chrysophyte cysts and diatoms in Lake Żabińskie (Publication 3)

Chrysophyte cyst and diatom total fluxes in Lake Żabińskie followed a seasonal pattern, with maximum during the transition between winter and spring, and the greatest values recorded in spring of 2017. A notable exception occurred during the summer 2017 when chrysophyte cyst fluxes reached the highest overall value. A lack of ice cover during the winter of 2020 resulted in an increase in fluxes in January, followed by a decline in February, and a subsequent increase in March and April. In May and June 2020, fluxes decreased. Even though chrysophyte cysts and diatoms presented similar patterns of flux pulses, diatoms dominated during the study period, with fluxes featuring an order of magnitude approximately greater than the chrysophyte cysts (Fig. 7).

In terms of taxonomic composition, Lake Żabińskie substantially differed from lakes Łazduny and Rzęśniki. In eutrophic Lake Żabińskie the number of identified chrysophyte cyst types and diatom species was much lower. Of the 109 cyst morphotypes or "collective categories" found in Lake Żabińskie, 39 had an abundance of equal to or greater than 2% in at least one sample. Dominant morphotypes or 'collective groups' were unornamented 6–8.9 µm (14.3%), unornamented ≤ 5.9 µm (11%), group 2 (8.4%), D114/115 (6%), S128 (5.3%), S118 (3.9%), S041 (3.6%), S161 (3.2%), unornamented ≥ 9 µm (3.1%) (Fig. 7, 8). They accounted for more than 50% of all identified cysts.

In 35 analyzed samples, 123 diatom species were identified, with dominant *Fragilaria crotonensis* (7.8%), *Stephanodiscus parvus* (7.3%), *Pantocsekiella comensis* (7%), *Stephanodiscus neoastraea* (5.9%), *Stephanodiscus hantzschi* (5.7%), *Fragilaria tenera* var. *nanana* (4.4%), *Stephanodiscus medius* (4%), *Aulacoseira granulata* (3.9%), and *Pantoseckiella oceallata* (3.2%) which accounted for approximately half of the recognized species (Fig. 7).

According to the results, under eutrophic conditions, direct influences of meteorological conditions on lake biota are masked by complex relationships with physical and chemical conditions. This was confirmed by statistical analyses which did not show any significant and strong relationships. Nevertheless, careful investigation of processes occurring in the water column, allow to assume that ice cover and mixing regime influenced by air temperature and wind speed are the main factors affecting both chrysophyte cyst and diatom seasonal succession patterns. Additionally, it has been recognized that changes in meteorological conditions caused species turnover of both chrysophyte cysts and diatoms, further confirming sensitivity of studied organism to changing weather conditions. The biotic response in Lake Żabińskie to unusual meteorological conditions that occurred in 2020 differed from "typical" years in terms of diatom and chrysophyte cyst bloom phenology, and resulted in flux peaks during winter months. This response, not as pronounced as in lakes with lower productivity, can be attributed to the already turbid and nutrient-high conditions, which modify the threshold for noticeable changes to occur.

Conclusions & outlook

4. Conclusions and outlook

The results of high-resolution monitoring of environmental variables, modern sedimentation, and meteorological records enabled the research hypotheses addressed in this thesis to be verified. The results confirm that the influence of meteorological conditions on chrysophyte cyst and diatom assemblages is manifested through changes in lake mixing regime. It has been also established that the timing and duration of mixing and stratification phases determine the dynamics of chrysophyte cyst and diatom fluxes to a large extent, as well as their taxonomic composition. Additionally, this study validates the hypothesis that biota in lakes of different trophic status respond differently to the same meteorological conditions. In spite of observations of both stronger and weaker relationships between chrysophyte cysts and diatoms and meteorological conditions, the results suggest that it is not possible to identify specific cyst morphotypes or diatom species whose variability is solely modeled by meteorological conditions, thus negating the third hypothesis.

The assumed scientific goals of this thesis were achieved. The seasonal pattern of variation in chrysophyte cyst and diatom assemblages in lakes Łazduny, Rzęśniki, and Żabińskie has been determined which allowed the following conclusions to be drawn:

- The seasonal pattern observed in each lake showed characteristic peaks occurring during spring and fall mixing and substantial decrease of fluxes during summer stratification and ice cover periods.
- While the general seasonal pattern was comparable between all lakes, the site-specific variability referring to differences in the seasonal succession of specific diatom taxa, the occurrence of the peaks of total fluxes, and differences in taxonomic composition was also observed.

The relationships between meteorological conditions and chrysophyte cyst and diatom assemblages in the investigated lakes were explained, and following findings emerged:

- Changes in meteorological conditions and mixing regime in the investigated lakes were found to be directly related. Air temperature and wind speed were the variables that had the greatest impact on the mixing regime of the lakes.
- The mixing regime was identified as the primary factor influencing nutrient cycling in the investigated lakes, thereby playing a key role in the seasonal and interannual variations of chrysophyte cyst and diatom fluxes.
- The taxonomic composition of both chrysophyte cysts and diatoms is influenced by multiple stressors that often act simultaneously. Meteorologic-driven changes in the water column were found to be complex, making it difficult to establish direct relationships between specific taxa and environmental variables. While RDA analysis indicated a correlation between cyst and diatom assemblages with air temperature (AT) and wind speed (WS) in lakes Łazduny and Rzęśniki, it was ineffective for the Lake Żabińskie dataset.
- Meteorological conditions can have a significant impact on chrysophyte cysts and diatom assemblages in low trophy lakes whereas they are less apparent in eutrophic lakes.

Additionally, the impact of unusual meteorological conditions that occurred in 2020 (no ice cover) on seasonal patterns of chrysophyte cyst and diatom dynamics in temperate dimictic lakes were examined, and the following inferences were made:

-The same response in a form of a prolonged period of whole water column mixing from fall 2019 to mid-spring 2020 was recorded in all investigated lakes.

- The response of chrysophyte cysts and diatoms to the lack of ice cover in 2020 varied between the lakes, and was more pronounced in lower trophy lakes. Nevertheless, in each lake changes in phenology and species turnover were observed. In low trophy lakes Łazduny and Rzęśniki, chrysophyte cyst fluxes decreased substantially and no distinctive peaks were recorded, while diatom fluxes increased in spring 2020 and generated low peak in Łazduny and equally spread flux in spring and early summer in Rzęśniki. In Lake Żabińskie, both chrysophyte cyst and diatom peaks occurred earlier than in other years (i.e. during the winter months).

- Recorded differences in the response to lack of ice cover in 2020 may be attributed to the initial biota composition, where eutrophic species are more tolerant to the prevailing high-nutrient, turbid, and low-light conditions of eutrophic lakes.

The results of this study suggest possible directions for future research. Recognized links between studied biological proxies, especially chrysophyte cysts, and changes in meteorological conditions imply that they may be used in paleoclimatic reconstructions. Therefore, investigation of short sediment cores and comparison with instrumental meteorological data could be a subsequent step. Future studies should also focus on examining the impact of extreme years on longer-term trends in paleolimnological records, what can be attained by studies of cores with high temporal resolution and associated meteorological data. An exciting scientific opportunity to reveal meteorological conditions in the past may be possible using annually laminated sediment records. Future research could also focus on expanding observation period to build decadal datasets of monitoring data that could be invaluable for a better understanding of environment-proxy relationships. Also, incorporation of long-term observational data to models can improve our ability to make accurate predictions about the future dynamics of lake ecosystems. Based on this study, it is also advised that future studies should focus on expanding this type of monitoring observations along environmental gradients, to observe the driving mechanisms of chrysophyte cyst, diatom, and other biota seasonality and species succession across different lake types and climatic regions.

References

References

Adam, D.P., Mahood, A.D., 1981. Chrysophyte cysts as potential environmental indicators. Geol. Soc. Am. Bull. 92, 839–844.

Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W., Livingstone, D.M., Sommaruga, R., Straile, D., Donk, E.V., Weyhenmeyer, G.A., Winder, M., 2009. Lakes as sentinels of climate change. Limnol. Oceanogr. 54, 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283

Apolinarska, K., Pleskot, K., Pełechata, A., Migdałek, M., Siepak, M., Pełechaty, M., 2020. The recent deposition of laminated sediments in highly eutrophic Lake Kierskie, western Poland: 1 year pilot study of limnological monitoring and sediment traps. J. Paleolimnol. 63, 283–304. https://doi.org/10.1007/s10933-020-00116-2

Battarbee, R.W., Jones, V.J., Flower, R.J., Cameron, N.G., Bennion, H., Carvalho, L., Juggins, S., 2001. Diatoms, in: Smol, J.P., Birks, H.J.B., Last, W.M., Bradley, R.S., Alverson, K. (Eds.), Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators, Developments in Paleoenvironmental Research. Springer Netherlands, Dordrecht, pp. 155–202. https://doi.org/10.1007/0-306-47668-1_8

Battarbee, R.W., Kneen, M.J., 1982. The use of electronically counted microspheres in absolute diatom analysis. Limnol. Oceanogr. 27, 184–188. https://doi.org/10.4319/lo.1982.27.1.0184

Baza Danych Obiektów Topograficznych BDOT10k [WWW Document]. URL www.geoportal.gov.pl.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C., Braak, C.J.F. Ter, 1990. Diatom and pH reconstruction. Philos. Trans. R. Soc. 327, 263–278. https://doi.org/10.1017/CBO9781107415324.004

Blenckner, T., Adrian, R., Livingstone, D.M., Jennings, E., Weyhenmeyer, G.A., George, D.G., Jankowski, T., Järvinen, M., Aonghusa, C.N., Nõges, T., Straile, D., Teubner, K., 2007. Large-scale climatic signatures in lakes across Europe: a meta-analysis. Glob Chang Biol 13, 1314–1326. https://doi.org/10.1111/j.1365-2486.2007.01364.x

Boeff, K.A., Strock, K.E., Saros, J.E., 2016. Evaluating planktonic diatom response to climate change across three lakes with differing morphometry. J. Paleolimnol. 56, 33–47. https://doi.org/10.1007/s10933-016-9889-z

Boehrer, B., Schultze, M., 2008. Stratification of lakes. Rev. Geophys. 46. https://doi.org/10.1029/2006RG000210

Bonk, A., Tylmann, W., Amann, B., Enters, D., Grosjean, M., 2014. Modern limnology, sediment accumulation and varve formation processes in Lake Żabińskie, northeastern Poland: comprehensive process studies as a key to understand the sediment record. J. Limnol. 73. http://dx.doi.org/10.4081/jlimnol.2014.1117

Butcher, J.B., Nover, D., Johnson, T.E., Clark, C.M., 2015. Sensitivity of lake thermal and mixing dynamics to climate change. Clim. Change 129, 295–305. https://doi.org/10.1007/s10584-015-1326-1

Cáceres, M.D., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x

Choiński, A., 2007. Limnologia fizyczna Polski. Wydawnictwo Naukowe Uniwersytetu im. Adama Mickiewicza, Poznań.

Cumming, B.F., Wilson, S.E., Smol, J.P., 1993. Paleolimnological potential of chrysophyte cysts and scales and of sponge spicules as indicators of lake salinity. Int. J. Salt Lake Res. 2, 87–92. https://doi.org/10.1007/BF02905055

Davison, W., 1993. Iron and manganese in lakes. Earth Sci Rev. 34, 119–163. https://doi.org/10.1016/0012-8252(93)90029-7

De Jong, R., Kamenik, C., Grosjean, M., 2013. Cold-season temperatures in the European Alps during the past millennium: variability, seasonality and recent trends. Quat. Sci. Rev. 82, 1–12. https://doi.org/10.1016/j.quascirev.2013.10.007

De Jong, R., Kamenik, C., Westover, K., Grosjean, M., 2013. A chrysophyte stomatocyst-based reconstruction of cold-season air temperature from Alpine Lake Silvaplana (AD 1500–2003); methods and concepts for quantitative inferences. J. Paleolimnol. 50, 519–533. https://doi.org/10.1007/s10933-013-9743-5

Dixit, S.S., Smol, J.P., Kingston, J.C., Charles, D.F., 1992. Diatoms: powerful indicators of environmental change. Environ. Sci. Technol. 26, 22–33. https://doi.org/10.1021/es00025a002

Duarte, C.M., 1990. Time lags in algal growth: generality, causes and consequences. J. Plankton Res. 12, 873–883. https://doi.org/10.1093/plankt/12.4.873

Duff, K., Zeeb, B.A., Smol, J.P., 1995. Atlas of Chrysophycean Cysts, Developments in Hydrobiology. Springer Netherlands, Dordrecht.

Duff, K.E., Smol, J.P., 1991. Morphological descriptions and stratigraphic distributions of the chrysophycean stomatocysts from a recently acidified lake (Adirondack Park, N.Y.). J. Paleolimnol. 5, 73–113. https://doi.org/10.1007/BF00226558

Eloranta, P., 1995. Biogeography of chrysophytes in Finnish lakes, in: Chrysophyte Algae: Ecology, Phylogeny and Development. Cambridge University Press, Cambridge, pp. 214–231.

Facher, E., Schmidt, R., 1996. A siliceous chrysophycean cyst-based pH transfer function for Central European lakes. J. Paleolimnol. 16, 275–321. https://doi.org/10.1007/BF00207575

Falkowski, P.G., Oliver, M.J., 2007. Mix and match: how climate selects phytoplankton. Nat Rev Microbiol 5, 813–819. https://doi.org/10.1038/nrmicro1751

Fritz, S.C., 2008. Deciphering climatic history from lake sediments. J Paleolimnol 39, 5–16. https://doi.org/10.1007/s10933-007-9134-x

Guiry, M.D., Guiry, G.M., 2022. AlgaeBase. World-wide electronic publication, National University of Ireland.

Hampton, S.E., Moore, M.V., Ozersky, T., Stanley, E.H., Polashenski, C.M., Galloway, A.W.E., 2015. Heating up a cold subject: prospects for under-ice plankton research in lakes. J. Plankton Res. 37, 277–284. https://doi.org/10.1093/plankt/fbv002

Hausmann, S., Pienitz, R., 2007. Seasonal climate inferences from high-resolution modern diatom data along a climate gradient: a case study. J. Paleolimnol. 38, 73–96. https://doi.org/10.1007/s10933-006-9061-2

Hernández-Almeida, I., Grosjean, M., Przybylak, R., Tylmann, W., 2015a. A chrysophyte-based quantitative reconstruction of winter severity from varved lake sediments in NE Poland during the past millennium and its relationship to natural climate variability. Quat. Sci. Rev. 122, 74–88. https://doi.org/10.1016/j.quascirev.2015.05.029

Hernández-Almeida, I., Grosjean, M., Tylmann, W., Bonk, A., 2015b. Chrysophyte cyst-inferred variability of warm season lake water chemistry and climate in northern Poland: training set and downcore reconstruction. J. Paleolimnol. 53, 123–138. https://doi.org/10.1007/s10933-014-9812-4

Huisman, J., Sharples, J., Stroom, J.M., Visser, P.M., Kardinaal, W.E.A., Verspagen, J.M.H., Sommeijer, B., 2004. Changes in Turbulent Mixing Shift Competition for Light Between Phytoplankton Species. Ecology 85, 2960–2970. https://doi.org/10.1890/03-0763

Institute of Meteorology and Water Management-National Research Institute, [WWW Document]. Public data of IMWR-NRI. URL https://danepubliczne.imgw.pl/.

Jäger, C.G., Diehl, S., Schmidt, G.M., 2008. Influence of water-column depth and mixing on phytoplankton biomass, community composition, and nutrients. Limnol. Oceanogr. 53, 2361–2373. https://doi.org/10.4319/lo.2008.53.6.2361

Jane, S.F., Hansen, G.J.A., Kraemer, B.M., Leavitt, P.R., Mincer, J.L., North, R.L., Pilla, R.M., Stetler, J.T., Williamson, C.E., Woolway, R.I., Arvola, L., Chandra, S., DeGasperi, C.L., Diemer, L., Dunalska, J., Erina, O., Flaim, G., Grossart, H.-P., Hambright, K.D., Hein, C., Hejzlar, J., Janus, L.L., Jenny, J.-P., Jones, J.R., Knoll, L.B., Leoni, B., Mackay, E., Matsuzaki, S.-I.S., McBride, C., Müller-Navarra, D.C., Paterson, A.M., Pierson, D., Rogora, M., Rusak, J.A., Sadro, S., Saulnier-Talbot, E., Schmid, M., Sommaruga, R., Thiery, W., Verburg, P., Weathers, K.C., Weyhenmeyer, G.A., Yokota, K., Rose, K.C., 2021. Widespread deoxygenation of temperate lakes. Nature 594, 66–70. https://doi.org/10.1038/s41586-021-03550-y

Jong, R.D., Schneider, T., Hernández-Almeida, I., Grosjean, M., 2016. Recent temperature trends in the South Central Andes reconstructed from sedimentary chrysophyte stomatocysts in Laguna Escondida (1742ma.s.l., 38°28S, Chile). Glob Planet Change 137, 24–34. https://doi.org/10.1016/j.gloplacha.2015.12.006

Juggins, S., 2013. Quantitative reconstructions in palaeolimnology: new paradigm or sick science? Quat. Sci. Rev. 64, 20–32. https://doi.org/10.1016/j.quascirev.2012.12.014

Kakouei, K., Kraemer, B.M., Anneville, O., Carvalho, L., Feuchtmayr, H., Graham, J.L., Higgins, S., Pomati, F., Rudstam, L.G., Stockwell, J.D., Thackeray, S.J., Vanni, M.J., Adrian, R., 2021. Phytoplankton and cyanobacteria abundances in mid-21st century lakes depend strongly on future land use and climate projections. Glob Change Biol 27, 6409–6422. https://doi.org/10.1111/gcb.15866

Kamenik, C., Schmidt, R., 2005. Chrysophyte resting stages: a tool for reconstructing winter/spring climate from Alpine lake sediments. Boreas 34, 477–489. https://doi.org/10.1080/03009480500231468

Kienel, U., Kirillin, G., Brademann, B., Plessen, B., Lampe, R., Brauer, A., 2017. Effects of spring warming and mixing duration on diatom deposition in deep Tiefer See, NE Germany. J. Paleolimnol. 57, 37–49. https://doi.org/10.1007/s10933-016-9925-z

Kilham, S.S., Theriot, E.C., Fritz, S.C., 1996. Linking planktonic diatoms and climate change in the large lakes of the Yellowstone ecosystem using resource theory. Limnol. Oceanogr. 41, 1052–1062. https://doi.org/10.4319/lo.1996.41.5.1052

Kirilova, E.P., Bluszcz, P., Heiri, O., Cremer, H., Ohlendorf, C., Lotter, A.F., Zolitschka, B., 2008. Seasonal and interannual dynamics of diatom assemblages in Sacrower See (NE Germany): a sediment trap study. Hydrobiologia 614, 159–170. https://doi.org/10.1007/s10750-008-9504-z

Korkonen, S.T., Ojala, A.E.K., Kosonen, E., Weckström, J., 2017. Seasonality of chrysophyte cyst and diatom assemblages in varved Lake Nautajärvi – implications for palaeolimnological studies. J. Limnol. 76. https://doi.org/10.4081/jlimnol.2017.1473

Köster, D., Pienitz, R., 2006. Seasonal diatom variability and paleolimnological inferences - a case study. J. Paleolimnol. 35, 395–416. https://doi.org/10.1007/s10933-005-1334-7

Kraemer, B.M., Pilla, R.M., Woolway, R.I., Anneville, O., Ban, S., Colom-Montero, W., Devlin, S.P., Dokulil, M.T., Gaiser, E.E., Hambright, K.D., Hessen, D.O., Higgins, S.N., Jöhnk, K.D., Keller, W., Knoll, L.B., Leavitt, P.R., Lepori, F., Luger, M.S., Maberly, S.C., Müller-Navarra, D.C., Paterson, A.M., Pierson, D.C., Richardson, D.C., Rogora, M., Rusak, J.A., Sadro, S., Salmaso, N., Schmid, M., Silow, E.A., Sommaruga, R., Stelzer, J.A.A., Straile, D., Thiery, W., Timofeyev, M.A., Verburg, P., Weyhenmeyer, G.A., Adrian, R., 2021. Climate change drives widespread shifts in lake thermal habitat. Nat. Clim. Chang. 11, 521–529. https://doi.org/10.1038/s41558-021-01060-3

Krammer, K., Lange-Bertalot, H., 1986. Bacillariophyceae 1. Teil: Naviculaceae, in: Ettl, H., Gerlof, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora von Mitteleuropa Band 2/1. Jena, p. 876.

Krammer, K., Lange-Bertalot, H., 1988. Bacillariophyceae 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae, in: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora von Mitteleuropa, Band 2/2. Gustav Fischer Verlag, Stuttgart, p. 596.

Krammer, K., Lange-Bertalot, H., 1991a. Bacillariophyceae 3. Teil: Centrales, Fragilariaceae, Eunotiaceae, in: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora von Mitteleuropa Band 2/3. Gustav Fischer Verlag, Stuttgart, p. 576.

Krammer, K., Lange-Bertalot, H., 1991b. Bacillariophyceae 4. Teil: Achnanthaceae., in: Ettl, H., Gärtner, G., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora von Mitteleuropa, Band 2/4. Gustav Fischer Verlag, Stuttgart, p. 437.

Legendre, P., Legendre, L., 2012. Numerical Ecology, Volume 24 - 3rd Edition. Elsevier Science.

Lisicki, S., Rychel, J., 2003. Szczegółowa mapa geologiczna Polski. Arkusz Wydminy (144). URL https://geologia.pgi.gov.pl

Livingstone, D.M., Lotter, A.F., 1998. The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. J. Paleolimnol. 19, 181–198. https://doi.org/10.1023/A:1007904817619

Lotter, A.F., Bigler, C., 2000. Do diatoms in the Swiss Alps reflect the length of ice-cover? Aquat. sci. 62, 125–141. https://doi.org/10.1007/s000270050002

Lotter, A.F., Birks, H.J.B., Hofmann, W., Marchetto, A., 1997. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. J. Paleolimnol. 18, 395–420. https://doi.org/10.1023/A:1007982008956

Maier, D.B., Diehl, S., Bigler, C., 2019. Interannual variation in seasonal diatom sedimentation reveals the importance of late winter processes and their timing for sediment signal formation. Limnol. Oceanogr. 64, 1186–1199. https://doi.org/10.1002/lno.11106

Maier, D.B., Gälman, V., Renberg, I., Bigler, C., 2018. Using a decadal diatom sediment trap record to unravel seasonal processes important for the formation of the sedimentary diatom signal. J. Paleolimnol. 60, 133–152. https://doi.org/10.1007/s10933-018-0020-5

Marszelewski, W., Skowron, R., 2006. Ice cover as an indicator of winter air temperature changes: Case study of the Polish Lowland lakes. Hydrol Sci J 51, 336–349. https://doi.org/10.1623/hysj.51.2.336

Meis, S., Thackeray, S.J., Jones, I.D., 2009. Effects of recent climate change on phytoplankton phenology in a temperate lake. Freshwater Biol. 54, 1888–1898. https://doi.org/10.1111/j.1365-2427.2009.02240.x

Pannard, A., Bormans, M., Lagadeuc, Y., 2011. Phytoplankton species turnover controlled by physical forcing at different time scales. Can. J. Fish. Aquat. Sci. https://doi.org/10.1139/f07-149

Pienitz, R., Smol, J.P., Birks, H.J.B., 1995. Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. J. Paleolimnol. 13, 21–49. https://doi.org/10.1007/BF00678109

Pienitz, R., Walker, I.R., Zeeb, B.A., Smol, J.P., Leavitt, P.R., 1992. Biomonitoring past salinity changes in an athalassic subarctic lake. Int. J. Salt Lake Res. 1, 91–123. https://doi.org/10.1007/BF02904364

Pilla, R.M., Williamson, C.E., 2022. Earlier ice breakup induces changepoint responses in duration and variability of spring mixing and summer stratification in dimictic lakes. Limnol. Oceanogr. 67, S173–S183. https://doi.org/10.1002/lno.11888

Pla, S., 2001. Chrysophycean cysts from the Pyrenees. Schweizerbart Science Publishers, Stuttgart, Germany.

Pla, S., Anderson, N.J., 2005. Environmental factors correlated with chrysophyte cyst assemblages in low arctic lakes of southwest Greenland. J. Phycol. 41, 957–974. https://doi.org/10.1111/j.1529-8817.2005.00131.x

Pla, S., Camarero, L., Catalan, J., 2003. Chrysophyte cyst relationships to water chemistry in Pyrenean lakes (NE Spain) and their potential for environmental reconstruction. J. Paleolimnol. 30, 21–34. https://doi.org/10.1023/A:1024771619977

Pla, S., Catalan, J., 2005. Chrysophyte cysts from lake sediments reveal the submillennial winter/spring climate variability in the northwestern Mediterranean region throughout the Holocene. Clim. Dyn. 24, 263–278. https://doi.org/10.1007/s00382-004-0482-1

Pla-Rabes, S., Catalan, J., 2011. Deciphering chrysophyte responses to climate seasonality. J. Paleolimnol. 46, 139–150. https://doi.org/10.1007/s10933-011-9529-6

Pochocka-Szwarc, K., Lisicki, S., 2006. Szczegółowa mapa geologiczna Polski. Arkusz Orłowo (105). URL https://geologia.pgi.gov.pl.

Poikane, S., 2009. Water Framework Directive intercalibration technical report. Part 2: Lakes. OPOCE, Luxembourg.

Ptacnik, R., Diehl, S., Berger, S., 2003. Performance of sinking and nonsinking phytoplankton taxa in a gradient of mixing depths. Limnol. Oceanogr. 48, 1903–1912. https://doi.org/10.4319/lo.2003.48.5.1903

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [WWW Document]. URL https://www.R-project.org/

Råman Vinnå, L., Medhaug, I., Schmid, M., Bouffard, D., 2021. The vulnerability of lakes to climate change along an altitudinal gradient. Commun. Earth Environ 2, 1–10. https://doi.org/10.1038/s43247-021-00106-w

Rautio, M., Sorvari, S., Korhola, A., 2000. Diatom and crustacean zooplankton communities, their seasonal variability and representation in the sediments of subarctic Lake Saanajärvi. J. Limnol. 59, 81–96. https://doi.org/10.4081/jlimnol.2000.s1.81

Reavie, E.D., Sgro, G.V., Estepp, L.R., Bramburger, A.J., Chraïbi, V.L.S., Pillsbury, R.W., Cai, M., Stow, C.A., Dove, A., 2017. Climate warming and changes in Cyclotella sensu lato in the Laurentian Great Lakes. Limnol. Oceanogr. 62, 768–783. https://doi.org/10.1002/lno.10459

Reynolds, C.S., 2006. The Ecology of Phytoplankton, Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge.

Rühland, K., Paterson, A.M., Smol, J.P., 2008. Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. Glob Chang Biol 14, 2740–2754. https://doi.org/10.1111/j.1365-2486.2008.01670.x

Rühland, K.M., Paterson, A.M., Smol, J.P., 2015. Lake diatom responses to warming: reviewing the evidence. J. Paleolimnol. 54, 1–35. https://doi.org/10.1007/s10933-015-9837-3

Rzodkiewicz, M., 2018. Wykorzystanie współczesnych zespołów okrzemkowych w rekonstrukcjach paleośrodowisk jezior przybrzeżnych. Studia i prace z geografii nr 65. Bogucki Wydawnictwo Naukowe, Poznań.

Rzodkiewicz, M., Gąbka, M., Szpikowska, G., Woszczyk, M., 2017. Diatom assemblages as indicators of salinity gradients: a case study from a coastal lake. Oceanol. Hydrobiol. Stud. 46, 325–339. https://doi.org/10.1515/ohs-2017-0034

Sanchini, A., Szidat, S., Tylmann, W., Vogel, H., Wacnik, A., Grosjean, M., 2020. A Holocene high-resolution record of aquatic productivity, seasonal anoxia and meromixis from varved sediments of Lake Łazduny, North-Eastern Poland: insight from a novel multi-proxy approach. J Quat Sci 35, 1070–1080. https://doi.org/10.1002/jqs.3242

Sandgren, C.D., 1991. Chrysophyte reproduction and resting cysts: A paleolimnologist's primer. J. Paleolimnol. 5, 1–9. https://doi.org/10.1007/BF00226555

Schneider, P., Hook, S.J., 2010. Space observations of inland water bodies show rapid surface warming since 1985. Geophys. Res. Lett. 37. https://doi.org/10.1029/2010GL045059

Sharma, S., Richardson, D.C., Woolway, R.I., Imrit, M.A., Bouffard, D., Blagrave, K., Daly, J., Filazzola, A., Granin, N., Korhonen, J., Magnuson, J., Marszelewski, W., Matsuzaki, S.-I.S., Perry, W., Robertson, D.M., Rudstam, L.G., Weyhenmeyer, G.A., Yao, H., 2021. Loss of Ice Cover, Shifting Phenology, and More Extreme Events in Northern Hemisphere Lakes. J. Geophys. Res. Biogeosci. 126, e2021JG006348. https://doi.org/10.1029/2021JG006348

Sienkiewicz, E., Gąsiorowski, M., Hamerlík, L., Bitušík, P., Stańczak, J., 2021. A new diatom training set for the reconstruction of past water pH in the Tatra Mountain lakes. J. Paleolimnol. 65, 445–459. https://doi.org/10.1007/s10933-021-00182-0

Siver, P.A., 1993. Inferring the specific conductivity of lake water with scaled chrysophytes. Limnol. Oceanogr. 38, 1480–1492. https://doi.org/10.4319/lo.1993.38.7.1480

Smol, J.P., 2008. Pollution of Lakes and Rivers: A Paleoenvironmental Perspective. 2nd Edition. Wiley-Blackwell Publishing, Oxford.

Smol, J.P., Douglas, M.S., 2007. From controversy to consensus: making the case for recent climate change in the Arctic using lake sediments. Front Ecol Environ 5, 466–474. https://doi.org/10.1890/060162

Smol, J.P., Stoermer, E.F., 2010. The diatoms: application for the environmental and earth sciences, Cambridge University Press. https://doi.org/10.1016/S0022-0981(01)00239-8

Sorvari, S., Korhola, A., Thompson, R., 2002. Lake diatom response to recent Arctic warming in Finnish Lapland. Glob Change Biol 8, 171–181. https://doi.org/10.1046/j.1365-2486.2002.00463.x

Szumański, A., 1997. Szczegółowa mapa geologiczna Polski. Arkusz Giżycko (104). URL https://geologia.pgi.gov.pl.

Szumański, A., K. Laskowski, 1990. Szczegółowa mapa geologiczna Polski. Arkusz Miłki (143). URL https://geologia.pgi.gov.pl.

Tomczyk, A., Bednorz, E., 2022. Atlas klimatu Polski (1991–2020). Bogucki Wydawnictwo Naukowe, Poznań.

Tylmann, W., Enters, D., Kinder, M., Moska, P., Ohlendorf, C., Poręba, G., Zolitschka, B., 2013. Multiple dating of varved sediments from Lake Łazduny, northern Poland: Toward an improved chronology for the last 150 years. Quat. Geochronol. 15, 98–107. https://doi.org/10.1016/j.quageo.2012.10.001

Tylmann, W., Głowacka, P., Szczerba, A., 2017. Tracking climate signals in varved lake sediments: research strategy and key sites for comprehensive process studies in the Masurian Lakeland. Limnol. Rev. 17, 159–166. https://doi.org/10.1515/limre-2017-0015

Weckström, J., Korhola, A., Blom, T., 1997. The Relationship between Diatoms and Water Temperature in Thirty Subarctic Fennoscandian Lakes. AAAR 29, 75–92.

Wetzel, R., 2001. Limnology. Lake and River Ecosystems, 3rd ed. Academic Press, San Diego.

Wilkinson, A.N., Zeeb, B.A., Smol, J.P., 2001. Atlas of Chrysophycean Cysts: Volume II, Developments in Hydrobiology. Springer Netherlands, Dordrecht.

Wiltse, B., Paterson, A.M., Findlay, D.L., Cumming, B.F., 2016. Seasonal and decadal patterns in Discostella (Bacillariophyceae) species from bi-weekly records of two boreal lakes (Experimental Lakes Area, Ontario, Canada). J. Phycol. 52, 817–826. https://doi.org/10.1111/jpy.12443

Winder, M., Hunter, D.A., 2008. Temporal organization of phytoplankton communities linked to physical forcing. Oecologia 156, 179–192. https://doi.org/10.1007/s00442-008-0964-7

Winder, M., Reuter, J.E., Schladow, S.G., 2009. Lake warming favours small-sized planktonic diatom species. Proc. Royal Soc. B 276, 427–435. https://doi.org/10.1098/rspb.2008.1200

Winder, M., Sommer, U., 2012. Phytoplankton response to a changing climate. Hydrobiologia 698, 5–16. https://doi.org/10.1007/s10750-012-1149-2

Woolway, R.I., Merchant, C.J., 2019. Worldwide alteration of lake mixing regimes in response to climate change. Nat. Geosci. 12, 271–276. https://doi.org/10.1038/s41561-019-0322-x

Zander, P.D., Żarczyński, M., Vogel, H., Tylmann, W., Wacnik, A., Sanchini, A., Grosjean, M., 2021. A high-resolution record of Holocene primary productivity and water-column mixing from the varved sediments of Lake Żabińskie, Poland. Sci. Total Environ. 755, 143713. https://doi.org/10.1016/j.scitotenv.2020.143713

Żarczyński, M., Zander, P.D., Grosjean, M., Tylmann, W., 2022. Linking the formation of varves in a eutrophic temperate lake to meteorological conditions and water column dynamics. Sci. Total Environ. 842, 156787. https://doi.org/10.1016/j.scitotenv.2022.156787

Zou, Y., Wang, L., Zhang, L., Liu, Y., Li, P., Peng, Z., Yan, Y., Zhang, J., Lu, H., 2018. Seasonal diatom variability of Yunlong Lake, southwest China–a case study based on sediment trap records. Diatom Research 33, 381–396. https://doi.org/10.1080/0269249X.2018.1541823

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Original Articles

The relationship between chrysophyte cyst assemblages and meteorological conditions: Evidence from a sediment-trap study in northeast Poland

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ABSTRACT

Climate change causes alterations in lake systems, thus influencing lake biota. Studies of phytoplankton with short generation times and seasonal replacement provide an opportunity for assessing how aquatic organisms respond to changes in environmental conditions. This study explores the potential of chrysophyte cysts as indicators of seasonal and interannual changes in meteorological conditions in Lakes Łazduny and Rzęśniki, located in northern Poland. Monthly chrysophyte cyst data from sediment traps, biweekly limnological and hydrochemical data, and daily meteorological data were used to find and explain the relationships between chrysophyte cysts and changes in meteorological conditions. We showed that cyst seasonality indirectly corresponds to meteorological conditions acting through changes in the mixing regimes, which in turn influences nutrient and light availability. Statistical analyses revealed that the taxonomic structure and interannual variability of chrysophyte cysts are dependent on multiple variables. Nevertheless, air temperature was the most important meteorological variable influencing cyst assemblages. Cysts were indicative of different periods of lake physical structure, suggesting the potential of chrysophyte cysts in paleoclimatic studies.

1. Introduction

Ongoing climate change causes disturbances that alter freshwater ecosystems. Due to the sensitivity of lakes to changes in the atmosphere and the surrounding landscape, they are considered to be valuable archives of environmental conditions (Catalan et al., 2013; Williamson et al., 2009; Zolitschka et al., 2015). Although meteorological conditions influence physical, chemical, and biological processes in lakes, the interpretation of climate signals in lake sediments is not straightforward. This is because interactions between lake biota and environmental conditions are highly complex, which is attributed to various biotic and abiotic factors controlling the distribution, size, and abundance of lake organisms, such as resource availability and partitioning, density-dependent predation, and storage effects (Adrian et al., 2009, 2006; Chesson, 2000; Zufiaurre et al., 2021). However, the role of meteorological conditions is increasing as ongoing climate change has a significant impact on lakes. This is exemplified by changes in the duration of ice cover, strengthening of summer stratification, and changes in mixing patterns (Råman Vinnå et al., 2021).

To understand the impact of environmental change on aquatic ecosystems, it is crucial to understand the factors that control species composition and dynamics. An analysis of communities that exhibit strong seasonal replacement and short generation times provides an opportunity to understand how changes in environmental conditions influence the dynamics of biotic proxies (Reynolds, 2006). For example, phytoplankton is sensitive to annual fluctuations of temperature, water column stratification, and light availability (Berger et al., 2010; Diehl et al., 2002). In particular, the mixing regime is the primary factor affecting phytoplankton growth and competition. The period of water mixing is usually accompanied by changes in nutrient and light availability. Strong mixing and weak stratification result in high-nutrient fluxes into the water column, while climate warming-induced weak mixing with strong stratification promotes low-nutrient fluxes. This exacerbates stress on aquatic organisms by giving a competitive advantage to specific algal cell types that are better competitors for nutrients (Catalan and Fee, 1994; Wilhelm and Adrian, 2008; Winder and Sommer, 2012). Moreover, the stratification period favors smaller and buoyant species (Reynolds et al., 1987). Other variables influencing phytoplankton assemblages, such as pH, water ionic composition, and conductivity are also subject to climate-induced modifications in

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weathering rates (Catalan et al., 2014) and water balance (Adrian et al., 2009; Battarbee, 2000).

Chrysophytes are a diverse group of freshwater algae that produce siliceous vegetative cells, called cysts or stomatocysts, with over 1000 morphotypes currently described (Duff et al., 1995; Pla, 2001; Wilkinson et al., 2001). They are widely distributed and often very well preserved in lake sediments (Korkonen et al., 2020, 2017; Pla-Rabes and Catalan, 2011; Duff et al., 1995; Wilkinson et al., 2001). Given their sensitivity to changes in physicochemical conditions and distinct seasonality, chrysophyte cysts can be considered environmental indicators. For example, they have been used to infer changes in nutrient concentration and pH (Duff and Smol, 1991; Facher and Schmidt, 1996; Korkonen et al., 2020; Pang and Wang, 2014; Pla et al., 2003; Smol, 1985). Cysts have also been shown to respond robustly to changes in ionic composition and electrical conductivity (Hernández-Almeida et al., 2015b; Pla and Anderson, 2005; Siver, 1993). Most recent studies suggest that cysts are potential proxies for cold-season temperatures (De Jong et al., 2016; De Jong and Kamenik, 2011; Kamenik and Schmidt, 2005; Pla and Catalan, 2005; Pla-Rabes and Catalan, 2011). De Jong et al. (2013a, b) applied a cyst-based transfer function to the varved sediments of Lake Silvaplana (Swiss Alps) and reconstructed cold-season temperatures during the last millennium. Also, Pla-Rabes and Catalan (2011) found a close link between seasonal temperatures and chrysophyte cyst assemblages in the dimictic Lake Redo (Pyrenees), and showed that stomatocysts are excellent proxies of seasonal changes in air temperature. The potential of chrysophyte cysts to serve as temperature proxies was further confirmed by Hernández-Almeida et al. (2015a), who reconstructed winter severity from the varved sediments of Lake Żabińskie in northeast Poland for the last millennium.

Even though chrysophyte cysts are commonly found in lakes and their potential for paleoclimatology is recognized, the seasonality and succession of chrysophyte cysts growth have only recently become the focus of contemporary research (Korkonen et al., 2020, 2017; Pla-Rabes and Catalan, 2011). Consequently, long-term observations are needed to better understand the importance of each environmental variable in controlling the occurrence and distribution of different cyst types. High-resolution monitoring of lake properties and meteorological conditions combined with the collection of sediment samples accumulated over the same time interval provides an opportunity to investigate the relationships between chrysophyte cysts and their seasonality and changing environmental conditions. Such approach is crucial for a reliable interpretation of paleolimnological records (Bonk et al., 2015; Maier et al., 2018; Pla-Rabes and Catalan, 2011).

In this study, we investigated stomatocyst variability in sediment samples from Lakes Łazduny and Rzęśniki to determine whether changes in their fluxes and taxonomy can be explained by meteorological conditions. We hypothesized that indirect influence of meteorological conditions on the mixing regime and the biogeochemical properties of lake water was a major driver of changes in chrysophyte cyst production in different seasons. We also checked whether chrysophyte cysts can directly respond to specific meteorological variables. To evaluate these hypotheses, we selected lakes with no direct human impact, sampled sediment traps at monthly intervals, and linked chrysophyte cyst analysis to meteorological, limnological, and hydrochemical variables. We used statistical tools to identify the most influential factors controlling cyst assemblages. In the last step, we searched for potential indicator cyst types for mixing/stratification periods.

2. Materials and methods

2.1. Study site

A detailed characterization of the studied lakes and their catchments was provided by Tylmann et al. (2017). Here, we only present a short description that focuses on the most important points.

The Łazduny (53°51′18.3″N, 21°57′07.1″E, 128.8 m a.s.l.) and Rzęśniki (53°50′30.0″N, 21°58′35.9″E, 125.0 m a.s.l.) lakes are located in the Masurian Lake District in northeastern Poland (Fig. 1). Climatic conditions in the region are characterized by strong seasonality (cold winters and warm summers) and continentality. According to available data (Institute of Meteorology and Water Management–National Research Institute, 2021), mean monthly air temperatures at the meteorological station in Mikołajki, located around 30 km from the lakes, range from −3.3 °C in January to 18 °C in July. The mean annual precipitation is 600 mm with a peak in July (ca. 80 mm). The predominant wind direction is westerly and southwesterly. Typically, lakes in this region are covered by ice between December and April (Marszelewski and Skowron, 2006).

The Łazduny and Rzęśniki basins fill NW–SE-oriented tunnel valleys which were formed during the Late Glacial or the early Holocene (Sanchini et al., 2020). The surface geology of their catchment (1.94 km^2) consists of glacial sands, gravels, and peats (Lisicki and Krzywicki, 2013). Both lakes are surrounded by dense, mostly coniferous forests. Both have similar maximum depth (22.4 m and 26.0 m, respectively) and surface area (10.6 ha and 12.0 ha, respectively). Łazduny has no surface inflows, but it has one outflow in the southern part. Thus, it is supplied by groundwater and precipitation. In contrast, Rzęśniki has one inflow from the NW and an outflow into Lake Orzysz (Fig. 1).

2.2. Environmental variables

Environmental data were collected regularly to evaluate the relationships between environmental conditions and chrysophyte cyst fluxes. To estimate the variability of physical, chemical, and biological parameters, the lakes were monitored biweekly from December 2016 (Łazduny) or February 2017 (Rzęśniki) to July 2020. Water temperature (WT), specific conductivity (EC), pH, dissolved oxygen (DO), and chlorophyll-a (Chl-a) concentrations in the water column were measured at 1-m depth intervals using an EXO 2 Multiparameter Sonde (YSI, USA). At the same time, water transparency was measured using a Secchi disc. Concentrations of total phosphorus (TP) and total nitrogen (TN) were measured in water samples collected from the depths of 1 m and 10 m, and 1 m above the lake bottom. TP and TN were measured under laboratory conditions by the colorimetric method using a Spectroquant Prove 600 spectrophotometer (Merck, Germany). Meteorological data for the meteorological station in Mikołajki were obtained from the database of the Institute of Meteorology and Water Management–National Research Institute (2021). The data include daily values of air temperature, wind speed, and precipitation sums.

2.3. Sediment traps

Sediment traps were installed in the studied lakes 1 m above the sediment surface (Fig. 1). Each sediment trap consisted of four 80-cm-long tubes with an inner diameter of 86 mm and a total active area of 232.4 cm^2. Sediment samples were collected monthly during the ice-free period to record changes in taxonomical structure and the flux of chrysophyte cysts. Period with ice cover for each year is represented by one sample collected immediately after ice-out.

2.4. Chrysophyte cysts analysis

Chrysophyte cyst samples were prepared using a standard method (Battarbee, 1986). Fifty milligrams of freeze-dried sediment was treated with 10% HCl to remove carbonates and 30% H_2O_2 to oxidize organic matter. A known number of divinylbenzene microspheres were added to the chrysophyte cysts suspension (Battarbee and Kneen, 1982), and slides were prepared using the Naphrax® mounting medium. A minimum of 100 cysts were counted along random transects at 1000 × magnification, using the Zeiss Axio Imager A2 light microscope. Cyst identification followed Duff et al. (1995), Wilkinson et al. (2001), and Pla (2001). Microspheres were counted alongside the cysts to determine

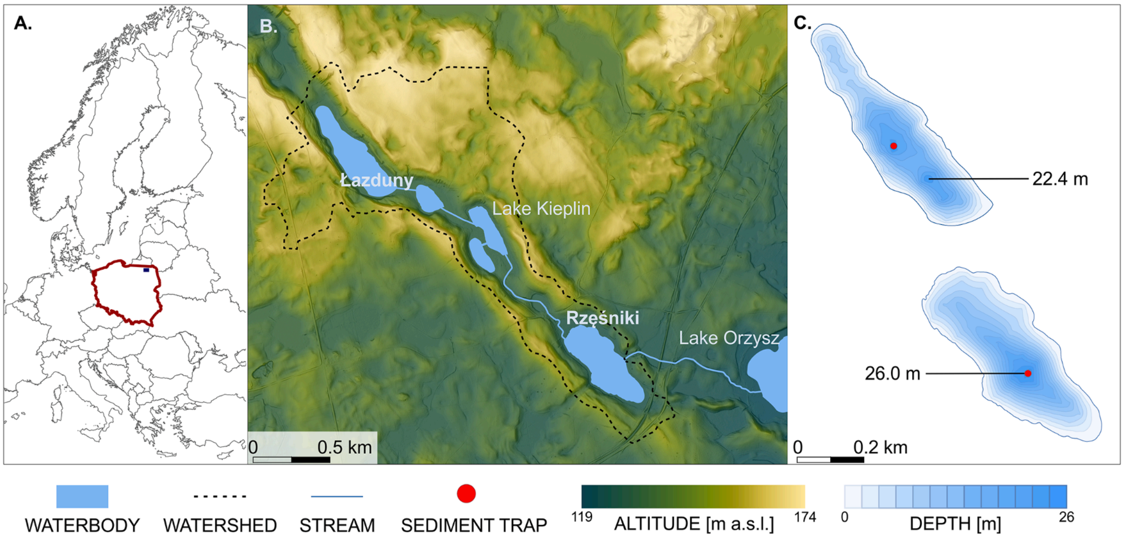

Fig. 1. Location of the studied lakes in Europe and Poland (A), topography and hydrography of the catchment (B), and bathymetric maps with the location of sediment traps (C).

cyst fluxes (Battarbee and Kneen, 1982).

2.5. Numerical analysis

For statistical analyses, we averaged biweekly hydrochemical and limnological data from the photic zone covering the same time as the monthly sediment trap data. The depth of the photic zone was estimated for each measurement date by multiplying the Secchi disk depth by 2.5 (Poikane, 2009) (Electronic supplementary material (ESM), Fig. S1). Daily meteorological data were also calculated as a mean or standard deviation value for the exposure period of the sediment traps. In total, 13 environmental variables were considered for statistical analysis, including TP, TN, EC, Chl-a, DO, WT, pH, mean air temperature, standard deviation of air temperature (AT_SD), the sum of precipitation (PRCP), standard deviation of precipitation sum (PRCP_SD), mean wind speed, and standard deviation of wind speed (WS_SD).

Cyst assemblages are shown as fluxes. To count the total flux, we used all of the counted cysts, including unknown types. However, we excluded unknown types for further statistical analyses to avoid random noise. Due to difficulties with identification by light microscopy, the unornamented types were merged into 'collective groups' according to size: $\leq$ 5.9 μm (S1, S29, and S46); 6.0–8.9 μm (S9, S120, and S189); and $\geq$ 9.0 μm (S15, S42, and S150). In some cases, the sizes of individual cysts were on the border between the two types; therefore, we distinguished two additional groups (group 1–S1/S9, S29/S120, and S046/S189; group 2–S9/15, S120/42, and S189/150). Also, two ornamented types, D114 and D115, which can be easily confused under light microscopy, were merged into the 'collective group' D114/115. Only cyst taxa reaching abundances of 2% or more in at least one sample were included in further analyses. Based on temperature and oxygen concentration measurements in the water column, we divided the study period into three characteristic phases: reverse stratification (wintertime with ice cover), mixing (spring and fall isothermy), and stratification (ice-free period except mixing); we classified the samples according to these phases (Figs. 2 and 3). Samples from the periods of reverse stratification were excluded from numerical analyses due to very low values of cyst fluxes.

Statistical analyses were performed in the R environment, version 4.1.0 (R Core Team, 2020). Prior to analyses, environmental data (except for pH) and cyst fluxes were log-transformed (log() and log(x + 1), respectively). To check for the presence of indicator cyst types, we conducted a multi-level pattern analysis (multipatt() function within the "indicspecies" package version 1.7.9) with the physical structure periods of the lakes as groups (Cáceres et al., 2010). The relationships between cysts communities and environmental variables were explored using ordination analyses. Firstly, cyst data were analyzed using Detrended Correspondence Analysis (DCA) to determine the gradient length of cysts composition. DCA showed that data had gradient lengths below 4 SD in both lakes. Therefore, to correlate cyst data with environmental variables, we selected a linear model (Redundancy Analysis, RDA) (Legendre and Legendre, 1998). Using the "vegan" package (version 2.5–7), we carried out three RDA runs: the first one for the period of mixing, the second for stratification, and the third for the combination of these two periods. Splitting the data into two periods allowed us to study interannual variability for each of these periods, which circumvent the effect of the strong seasonality of cyst assemblages. Manual selection and variance inflation factors (VIF) were used to reduce the environmental variables and avoid over-fitting (ESM, Table S1). Assuming a lagged reaction of the response variables to explanatory variables (Duarte, 1990; Legendre and Legendre, 1998) in the RDA, we compared chrysophyte cyst data with environmental variables from the same month, two weeks before and one month before. We tested the significance of variables using the Monte Carlo permutation test with N = 999 permutations. To explore how much variation in species composition is explained by climatic and combined hydrochemical and limnological variables, we conducted variation partitioning (varpart() in "vegan") (Borcard et al., 1992).

3. Results

3.1. Environmental variables

The monthly mean values of meteorological parameters varied intra- and inter-annually. The highest values of spring and summer air temperatures were recorded in 2018. The winter of 2019–2020 was exceptional as it was the warmest winter in the last 200 years in Poland. The summer seasons of 2017 and 2018 were characterized by the highest PRCP values, while the lowest values were observed each year in the spring. Increased wind speed values occurred during winter, spring and fall compared to the summer months, with the highest values observed from November 2019 to February 2020 (Figs. 2 and 3).

Limnological measurements in both lakes show different mixing regime patterns throughout the observation period. From 2017 to 2019, we observed reverse stratification in the water columns during winter, while normal stratification was noted in the summer. In these periods, much of the water column was anoxic (Figs. 2 and 3). In both lakes,

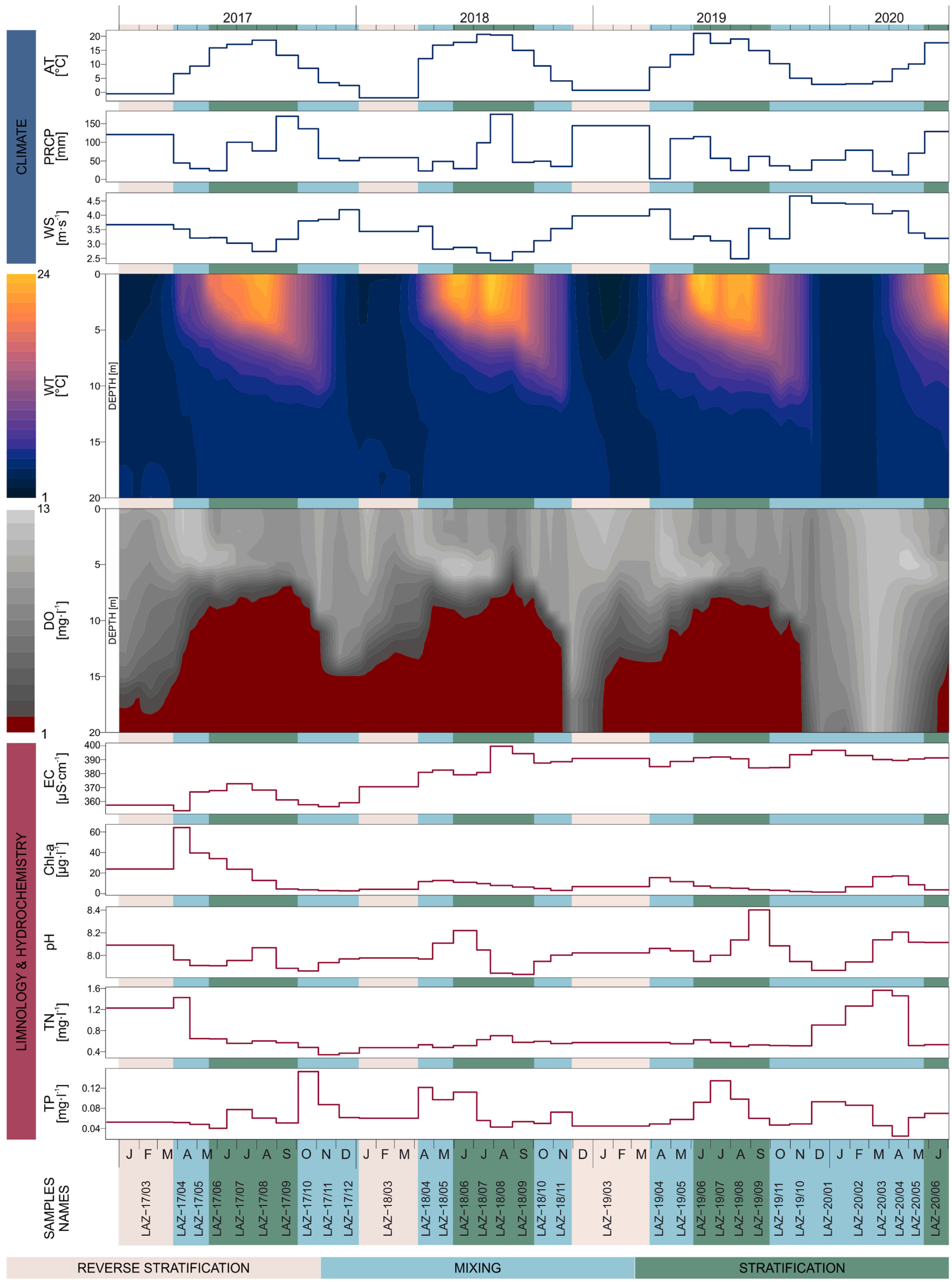

Fig. 2. Mean values of climatic, limnological, and hydrochemical parameters with depth profiles of WT and DO concentrations in Lake Łazduny (reverse stratification mean value for the entire winter period).

spring mixing was incomplete, which can be deduced from oxygen distributions showing anoxic conditions (DO < 1 mg l^{-1}) below 13–15 m in Łazduny and below 9–13 m in Rzęśniki. Periods of fall mixing were longer, which resulted in more effective transport of oxygen to deep waters. In Łazduny, a complete overturn occurred in 2018 and 2019, while in 2017, oxygen was only recorded to 15 m depth (Fig. 2). In Rzęśniki, fall mixing was also more intense than during the spring as we observed DO concentrations above 1 mg l^{-1} up to depths of 13, 17, and 20 m (Fig. 3). The winter of 2019–2020 was an exception characterized by ice-free conditions, allowing for prolonged water column mixing and good oxygenation of the whole water column lasting until the end of May or mid-June in Rzęśniki and Łazduny, respectively (Figs. 2 and 3).

In both lakes, we recorded an increase of EC values in 2018. Chl-a concentrations showed higher values during the spring and early

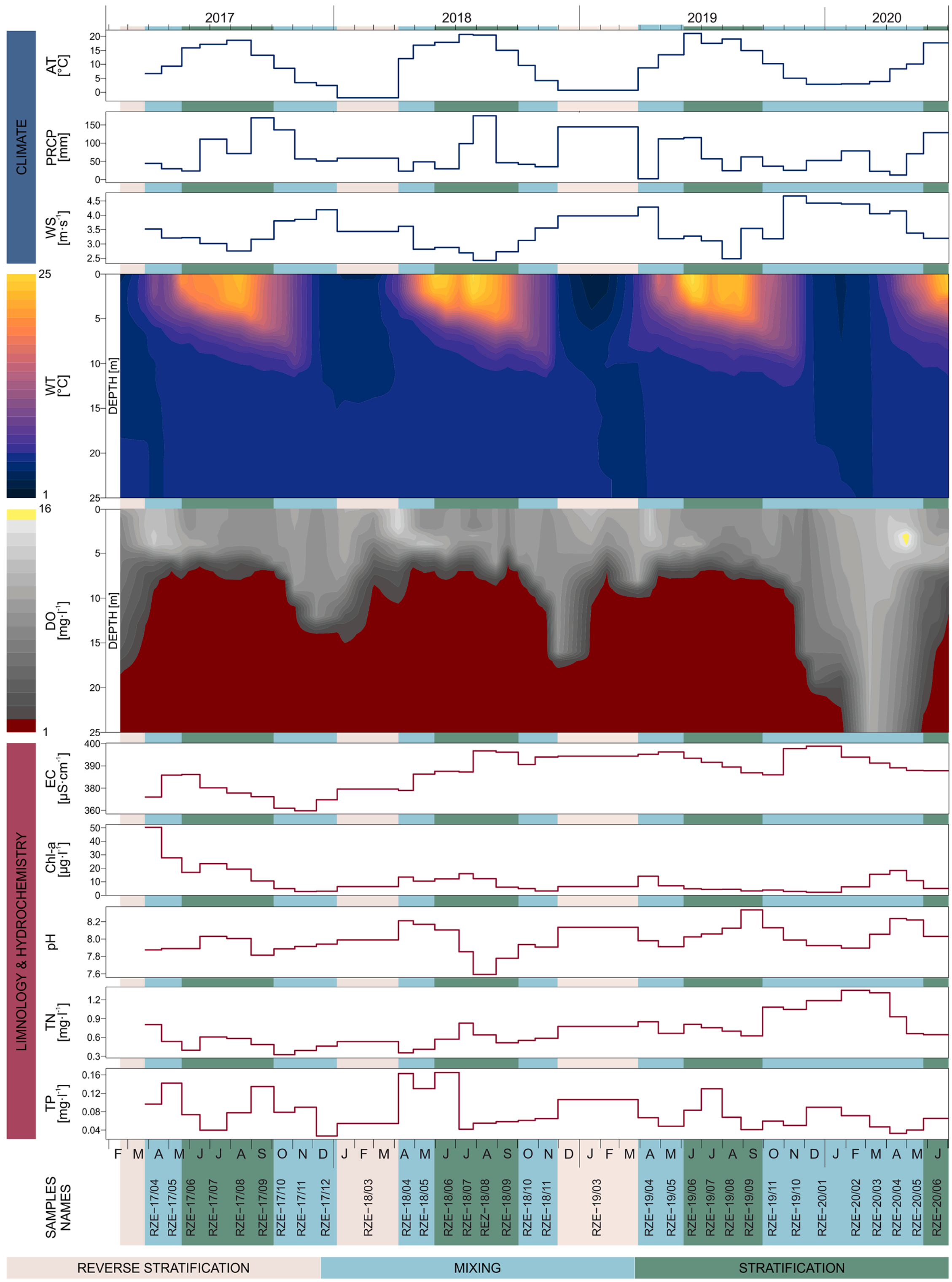

Fig. 3. Mean values of climatic, limnological, and hydrochemical parameters with depth profiles of WT and DO concentrations in Lake Rzęśniki (reverse stratification mean value for the entire winter period).

summer months, with the highest peak in April 2017. The pH values were generally higher during stratification periods, while the concentrations of TN and TP during mixing periods. The highest concentrations of TN were observed in both lakes during deep and intense mixing in fall 2019–spring 2020.

3.2. *Chrysophyte cyst composition and total fluxes*

Values of R^2 obtained for RDAs conducted with no lagged, two-weeks lagged and one month lagged data showed that in most cases environmental data from one month before explained the highest percent of variation in cyst assemblages (ESM, Table S2). Therefore, we present and interpret the results derived from RDA conducted with one month lag.

In Łazduny, we identified 127 cyst morphotypes in 34 samples, 51 of which had a minimum occurrence of over 2% in at least one sample (ESM, Fig. S2). Dominant morphotypes or 'collective groups' were D114/115 (23.41%), unornamented 6–8.9 μm (12.9%), S033 (6.4%), unornamented less than or equal to 5.9 μm (5.8%), and S118 (4.6%), which accounted for more than half of the identified cysts (Fig. 4). In Rzęśniki, we found 160 cyst morphotypes in 33 samples. Fifty-four of them reached abundances of over 2% in at least one sample (ESM, Fig. S3). The most common cysts were S041 (12.7%), D114/115 (12.6%), unornamented 6–8.9 μm (11.3%), S118 (8.1%), D317CF (4.8%), D116 (4.7%), and S033 (4.4%), which accounted for more than half of all the identified cysts (Fig. 5). Both the total fluxes and fluxes of individual cysts in both lakes showed the highest values in spring (April–May) and fall (October–December) (Figs. 4 and 5). It was only in 2020 that stomatocyst fluxes did not show any distinctive peaks. Additionally, some morphotypes (D239 and D339 in Łazduny, D78 and S202 in Rzęśniki) showed the highest flux values during the summer (ESM,

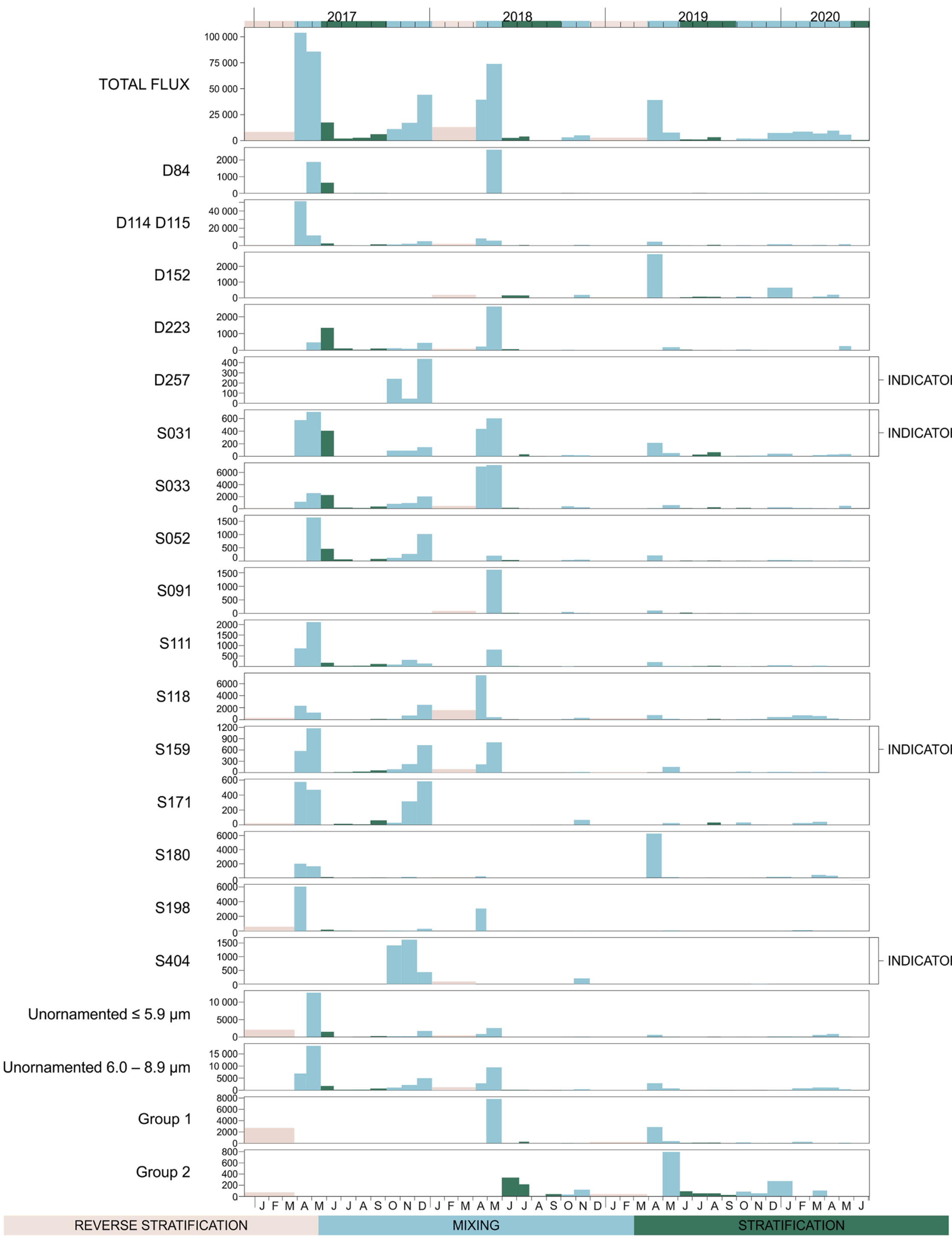

Fig. 4. Total fluxes and the fluxes of selected dominant chrysophyte cysts [cysts g × cm^{-2} × day^{-1}] (the width of the bars represents the length of the exposure period of sediment traps) in Lake Łazduny; INDICATOR-types pointed by multi-level pattern analysis as significantly associated with different periods of lake physical structure.

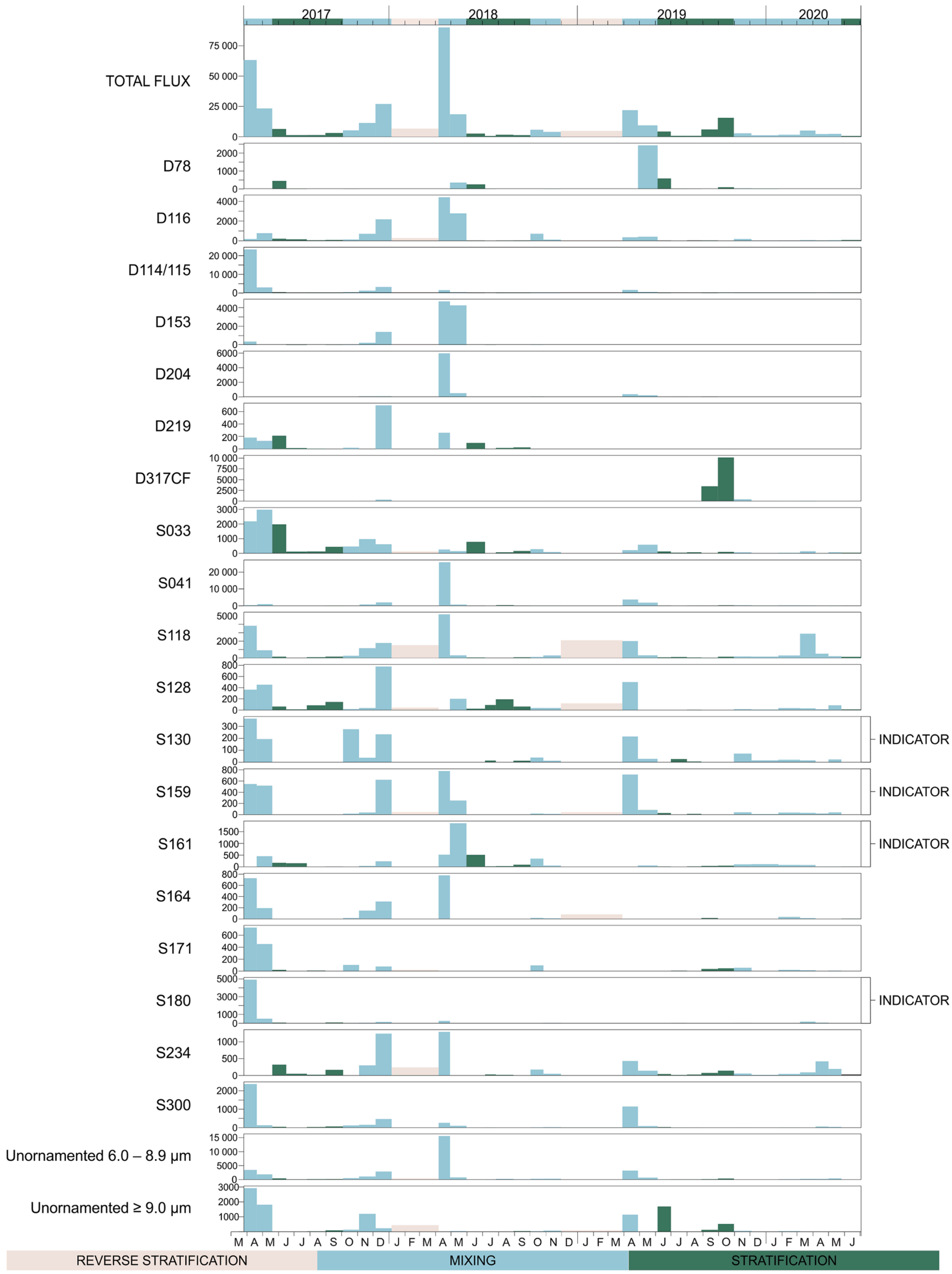

Fig. 5. Total fluxes and the fluxes of selected dominant chrysophyte cysts [cysts g × cm^{-2} × day^{-1}] (the width of the bars represents the length of the exposure period of sediment traps) in Lake Rzęśniki; INDICATOR-types pointed by multi-level pattern analysis as significantly associated with different periods of lake physical structure.

Figs. S2 and S3).

Multi-level pattern analysis indicated four statistically significant cyst types associated with different periods of lake physical structure and their combinations in Łazduny, with the S031 stomatocysts linked to spring and fall mixing, S159 to fall and spring mixing and the stratification period, D257 linked only to the period of fall mixing, and S404 to fall mixing and reverse stratification (Table 1, Fig. 4). Also, four morphotypes were identified as significantly related to lake physical structure periods in Rzęśniki, with morphotypes S130 and S180 associated with spring and fall mixing, S161 with spring and fall mixing and stratification, and S159 with spring and fall mixing and reverse stratification (Table 1, Fig. 5).

Table 1
Results of multi-level pattern analysis (stat represents the association between the type and the group).

Group	ŁAZDUNY Cyst type	Stat	*p* value	RZĘŚNIKI Cyst type	Stat	*p* value
Spring mixing + fall mixing	S031	0.892	0.003	S130	0.831	0.006
				S180	0.761	0.036
Spring mixing + fall mixing + stratification				S161	0.933	0.034
Spring mixing + fall mixing + reverse stratification	S159	0.804	0.040	S159	0.956	0.001
Fall mixing	D257	0.612	0.027			
Fall mixing + reverse stratification	S404	0.739	0.004			

3.3. Relationship between chrysophyte cysts and environmental variables

RDA conducted for the combined periods of mixing and stratification explained 52.0% and 54.6% of the variance in cyst data at Łazduny and Rzęśniki, respectively (ESM, Fig. S4). Air temperature and wind speed proved to be important variables driving seasonal changes and differentiating samples from the observation period into two general groups: the first group characterized by high air temperature values (stratification) and the second by higher wind speed values (mixing). Based on these findings, we provide a detailed description of the results obtained from RDA conducted for each season separately.

In Łazduny, RDA conducted for the mixing and stratification periods showed that the selected environmental variables explained 72.6% and 76.0% of the variance in cysts composition, respectively. For the mixing period, EC, Chl, and air temperature (34.9%, $p < 0.05$) were the most important variables. The RDA 1 axis mainly represented the gradient of EC, while the RDA 2 was correlated to air temperature. Morphotypes D152, S171, D404, and D257 were associated with RDA 1, while S091, group 1, and S198 were correlated with RDA 2. Samples from 2017 had the lowest EC values and the highest fluxes of cyst types present (Fig. 6). For the stratification period, EC was the only significant variable explaining 22.3% of the variance in cysts taxonomy. EC and air temperature were closely related to RDA 1, which was mainly associated with the distribution of the unornamented 6–8.9 µm, D84, D223, and S052 cysts. RDA 2 was represented by the gradient of TP and AT_SD, and was correlated to D152, group 1, and group 2 cysts. 'Collective groups' (group 1 and group 2) reached the highest accumulation rates in the samples from June and July 2018 and 2019, which were characterized by high TP values (Fig. 6).

RDA conducted for the mixing and stratification periods in Rzęśniki explained 75.4% and 73.2% of the variance in cyst data, respectively. For the mixing period, air temperature, TN, and EC were significant variables explaining 40.8% of the variance. RDA1 was correlated to EC, TN, and TP and to the distribution of the S180, S153, S159, and S164 cysts. Cysts D204, S234, S171, and S130 showed the highest correlation

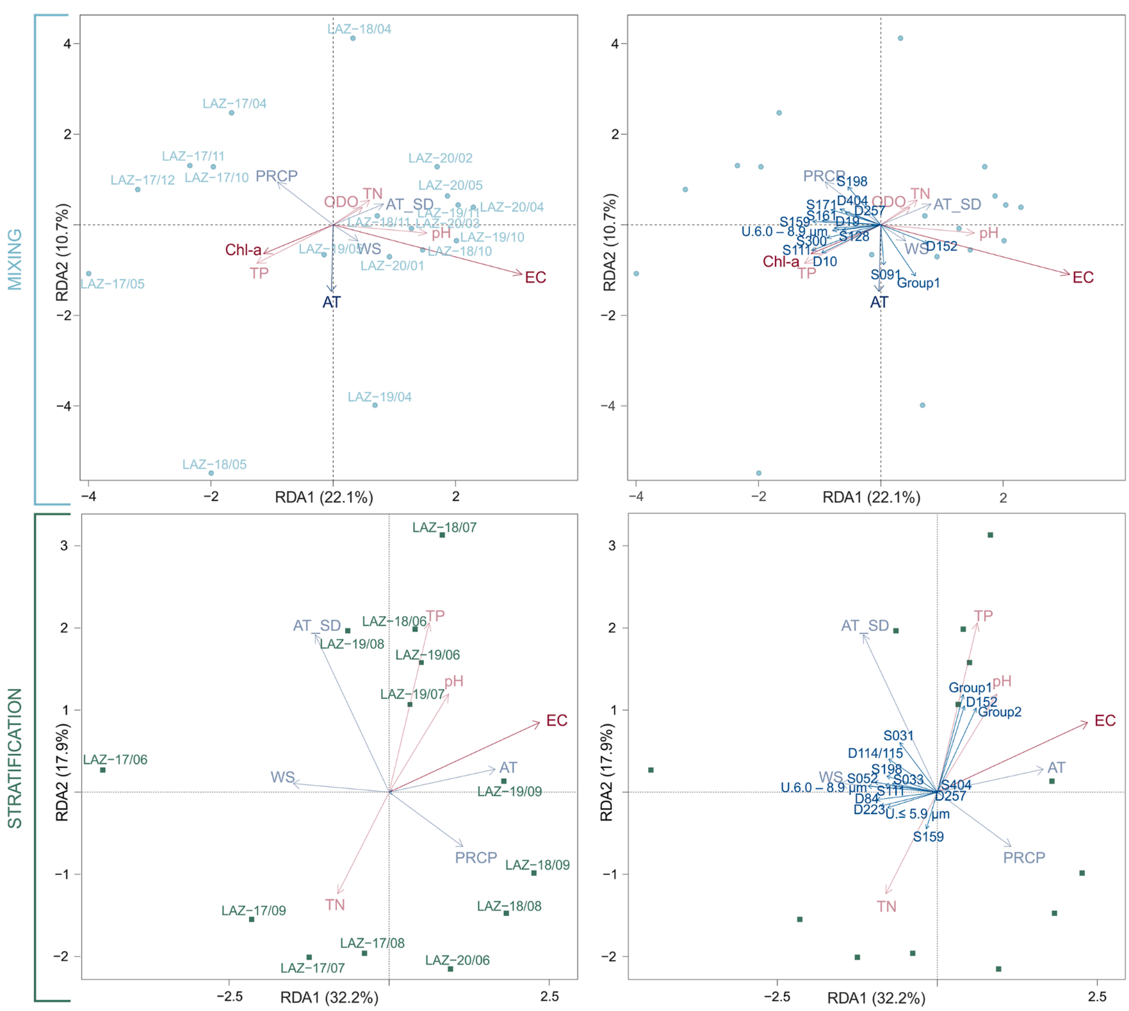

Fig. 6. RDA biplots of samples (left) and cysts morphotypes and 'collective groups' (right) with explanatory variables for the periods of mixing and stratification in Lake Łazduny (significant variables are highlighted with more intense colors; "U" stands for unornamented, "AT" for air temperature, "WS" for wind speed).

to RDA 2, represented by the gradient of AT_SD. The fall 2019 samples had the highest EC values and TN concentrations (Fig. 7). For the stratification period, AT_SD, EC, and pH were the most important variables, explaining 31.6% of the variation in cysts composition. RDA 1 was strongly correlated with air temperature, AT_SD, and wind speed. Morphotypes S300 and D78 showed major correlation with RDA 1. Cysts S128, D219, unornamented $\geq$ 9.0 μm, and D317CF were associated to RDA 2, which represented the gradient of EC, pH, and TN. Samples from August and October 2019 were characterized by high EC values and dominated by cyst D317CF (Fig. 7).

4. Discussion

4.1. Chrysophyte cyst seasonality

In Lakes Łazduny and Rzęśniki, chrysophyte cysts exhibit a seasonal succession characterized by different fluxes and assemblage composition during the periods of mixing and stratification. The fluxes correspond to the major seasonal changes in physical environment described for dimictic lakes (Sandgren, 1988). The effects of changes in meteorological conditions on cyst assemblages are very likely mediated by changes in thermal stratification patterns, which alter the length of the growing season and vertical mixing processes (Pla-Rabes and Catalan, 2011; Smol et al., 2005).

In our study, from 2017 to 2019, we observed the highest peaks in stomatocyst abundance after the ice-out. Depending on the intensity of spring mixing, we also recorded increased values in the fall, with the highest value noted in the fall of 2017, when spring mixing was characterized by the highest intensity and depth as well as nutrient input. In the exceptional year of 2020 (with no ice cover), the cyst composition changed, and no distinctive peaks were recorded in the spring (Figs. 3 and 4).

The seasonal changes in cyst fluxes observed in Lakes Łazduny and Rzęśniki are consistent with the findings of Pla and Catalan (2011), who indicated the relationship between chrysophyte cysts and ice cover length is a result of the impact of winter/spring air temperature on the onset and strength of the spring mixing period. They demonstrated that the spring mixing period is the most important determinant of nutrient availability during the growing season, and emphasized the importance of the onset, length, and intensity of the spring mixing period on the seasonal replacement of chrysophytes. A short mixing phase caused by a long ice-cover period can result in incomplete cycling and uptake of nutrients in the lake, which could be used during fall mixing and thus cause a second peak in phytoplankton production (Pla-Rabes and Catalan, 2011). Rising air temperatures can also cause an absence of ice cover during the winter period and result in a longer mixing period and thus a longer period of nutrient availability, inducing changes in cyst composition (Catalan and Fee, 1994; Sharma et al., 2019). Also, studies from Austria (Kamenik and Schmidt, 2005), the Pyrenees (Pla and Catalan, 2005), and the Swiss Alps (De Jong et al., 2013; De Jong and Kamenik, 2011) showed that stomatocyst composition is closely related to winter/spring temperatures.

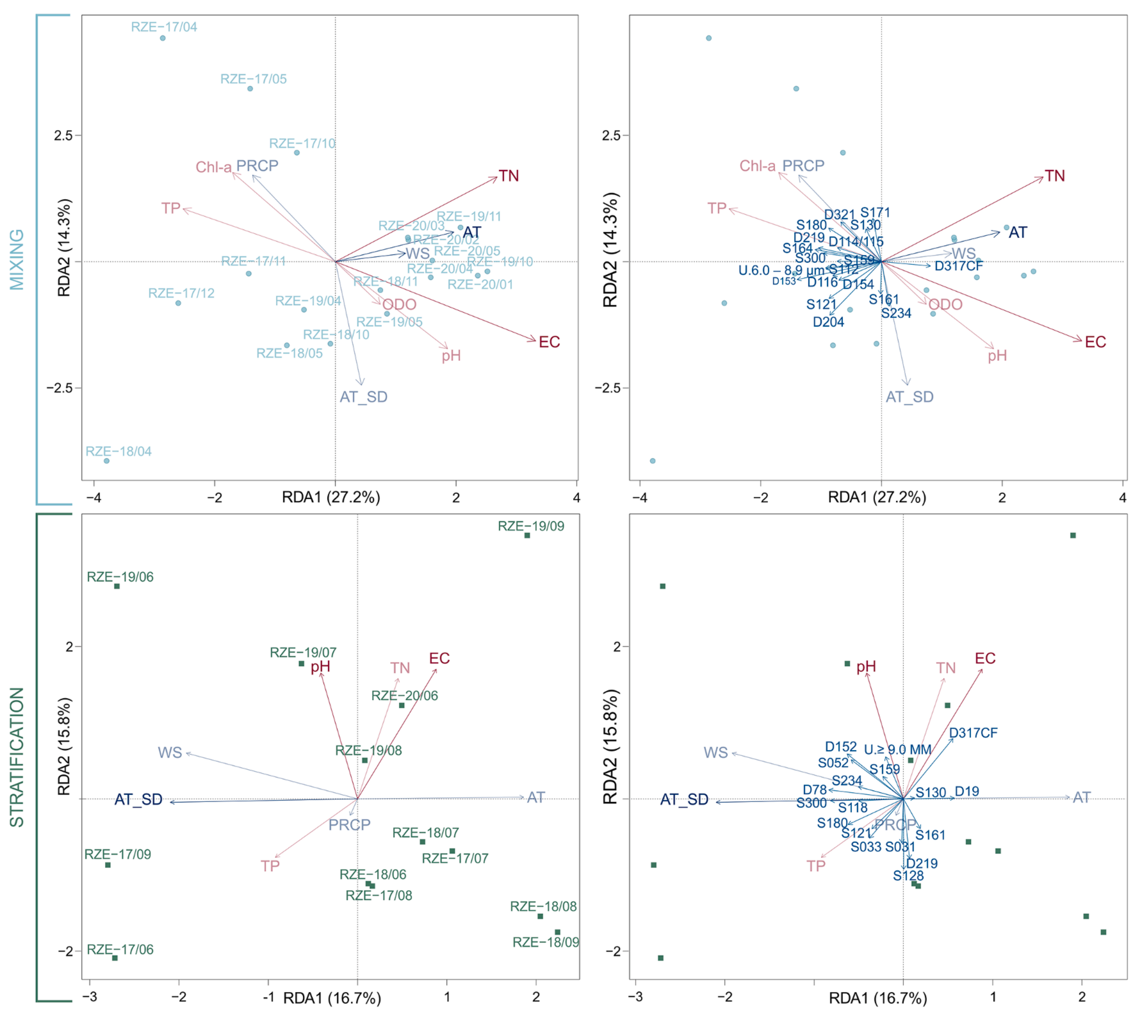

Fig. 7. RDA biplots of samples (left) and cysts morphotypes and 'collective groups' (right) with explanatory variables for the periods of mixing and stratification in Lake Rzęśniki (significant variables are highlighted with more intense colors; "U" stands for unornamented. "AT" for air temperature, "WS" for wind speed).

In our interpretation, the main reason of the decrease in cyst fluxes in 2020 was limited phosphorus and light availability as well as low WT. This prolonged overturn period increased deep-water oxygen concentrations and, consequently, reduced phosphorus recycling, which minimized spring phosphorus availability for algal growth (Catalan and Fee, 1994). During the spring overturn period with high TN, phosphorus would be a limiting factor which would determine chrysophyte assemblages throughout the growing season (Pla-Rabes and Catalan, 2011). Moreover, during the winter season in Poland, mean relative sunshine duration is the lowest (Bartoszek et al., 2020), ranging from seven to nine daylight hours. This period was also characterized by lowest Secchi disc values from all the mixing periods, ranging between 1.85 and 4.4 m and 1.9–3.8 m at Łazduny and Rzęśniki, respectively. Light intensity is the fundamental driver of ecosystem processes, as it affects the rate of photosynthesis and primary production. As light is essential for photosynthesis, a decrease in photosynthetic active radiation (PAR) transmission in turbid waters reduces primary production, including chrysophytes (Wetzel, 2001). Furthermore, maximum abundance of chrysophytes is noted in water temperature between 10 °C and 20 °C (Sandgren, 1988). The WT during that period was below this optimal interval (4.0–8.5 °C in Łazduny, 3.8–9.4 °C in Rzęśniki, with a dominance of lower temperatures), thus further limiting cyst development.

4.2. Environmental factors influencing cyst distribution

Changes in environmental conditions influence phytoplankton assemblages; nevertheless, little is known about time lags in their response. Studies conducted by Duarte (1990) revealed that the lag time between growth stimuli and algal growth response for lakes is around three weeks. Additionally, phytoplankton cells have different sinking velocity that is determined by multiple factors, including conditions within the lake. Therefore, the time it takes for cells to reach the sediment trap should also be considered, especially during summer stratification, when the water column is divided into compartments and temperature and density gradients create a natural barrier for sinking organisms and particles (Wetzel, 2001). According to our findings, a one-month lag in the RDA environmental dataset provides better understanding of stomatocysts response to changing environmental conditions. Therefore, we suggest that when examining chrysophyte cysts and their relationships with the environmental conditions, this time lag should be considered and carefully studied in statistical analysis.

With the above assumptions, we identified multiple environmental variables influencing chrysophyte cyst assemblages in the studied lakes. EC was one of the most important variables during the mixing and stratification periods in both lakes. Most of the cysts, including the dominant types (such as unornamented cysts with a size of 6.0–8.9 μm in Łazduny, S033 and S180 in Rzęśniki, or D114/115 in both lakes) preferred conditions with low EC values. Moreover, according to our data, EC increased over the observation period was negatively correlated with total cyst fluxes (Figs. 6 and 7). The influence of EC on cyst assemblages has been already recognized in correlation-based studies (Cumming et al., 1993; Duff et al., 1997; Hernández-Almeida et al., 2015b; Pla and Anderson, 2005); nevertheless, the mechanism itself is not well understood. It is generally believed that the effect of conductivity on algal species is related to the ability of algal cells to adjust to changes in external osmotic pressure (Cumming et al., 1993). In addition, increasing concentrations of selected ions, such as potassium, may be toxic to some chrysophyte species (Cumming et al., 1993; Sandgren, 1988). It has also been suggested that changes in conductivity induce alterations in lake water alkalinity and zooplankton composition, which may be another cause of the decrease in chrysophyte cyst fluxes (Duff et al., 1997).

Air temperature itself proved to be an important climate-related variable explaining a major part of the variation in cyst data, especially during the mixing period. We identified a clear pattern of relationships between air temperature and the occurrence of specific cyst types. The effect of air temperature is most likely mediated through changes in WT. Studies conducted in Swiss lakes by Livingstone and Lotter (1998) and in Lake Superior by Piccolroaz et al. (2015) show that water and air temperature are strongly correlated. This is especially true during the main growing season in the summer when short-time variability in air temperature is reflected in the temperature of the uppermost parts of water column (Livingstone and Lotter, 1998). Individual species and subspecific taxa of chrysophytes tend to be restricted along the temperature gradient, but chrysophytes are often considered the most important group at low water temperatures. Sandgren (1988) showed that the maximum abundance of chrysophytes occurs between 10 °C and 20 °C, with a decline at higher temperatures; their maximum biomass was observed in the spring when the temperature is lower than 12 °C (Sandgren et al., 1995). The influence of surface water temperature on cyst assemblages was also shown in studies from northwestern Canada, where authors recognized different cyst morphotypes preferring different temperatures (Brown et al., 1997). Cyst types in Łazduny and Rzęśniki generally preferred lower values of air temperature and therefore lower WT, which supports the previous findings. Additionally, for the stratification period in Rzęśniki, AT_SD proved to be more significant than air temperature and explained around 10% of variance in cyst data, which suggests that temperature variability and rate of change is perhaps more important than the actual temperature values. We observed that with the higher variability in air temperature fluxes of cyst types such as D78, S300 and S118 increased, while fluxes of type D19 decreased. Environmental variability may promote coexistence of planktonic species (Zufiaurre et al., 2021), and thus determine changes in chrysophyte assemblages.

During the mixing period, Chl-a and TN also proved to be important variables for cyst assemblages in the Łazduny and Rzęśniki lakes, respectively. Chl-a is frequently used as a measure of lake productivity, that is a biological indicator of lake trophic status in environmental assessments. The response of cyst assemblages to nutrients has been demonstrated in studies conducted in mountain lakes (Kamenik et al., 2001; Pla et al., 2003). Multiple studies show that increasing trophy causes a drop in the contribution of chrysophytes to the total algae biomass (Sandgren, 1988; Smol, 1985). Chrysophytes can outcompete other algae in low-nutrient environments (e.g. Eloranta, 1995), but may be excluded under eutrophic conditions because of their relatively slow growth rates or inability to secrete alkaline phosphatase under alkaline conditions (Duff et al., 1997). The fluxes of cyst types found in our study showed a mostly negative correlation to TN, suggesting that the chrysophyte species from Łazduny and Rzęśniki prefer low-nutrient conditions.

Cysts are also well known to respond to changes in pH (Duff et al., 1997; Facher and Schmidt, 1996; Pla et al., 2003). During stratification, intense photosynthesis can lead to increased pH values in the epilimnion and new habitat conditions, at least in circumneutral lakes (Pla-Rabés and Catalan, 2018). Generally, chrysophytes are tolerant of a wide pH range (4.5–8.5) (Sandgren, 1988). Therefore, pH would not be a limiting factor for cyst development in Łazduny and Rzęśniki, as the recorded values do not exceed the optimum, although it would determine their occurrence and the final chrysophyte assemblages.

The covariation between the environmental variables used in the RDA makes it difficult to point out a single variable as the main factor controlling changes in cyst composition and interannual variability. To answer the question of the extent to which meteorological variables drive alterations in cyst assemblages, we conducted variation partitioning analysis. It showed that meteorological variables explained 12.8% and 16.0% of the variation in the cyst data during the mixing period and 10.1% and 19.2% during stratification in Łazduny and Rzęśniki, respectively (Fig. 8). Those results suggest a direct influence of specific meteorological variables on chrysophyte cysts. However, the analysis did not show shared variance between meteorological parameters and limnological/hydrochemical variables. It is clear that changing meteorological conditions drive long-term seasonal limnological

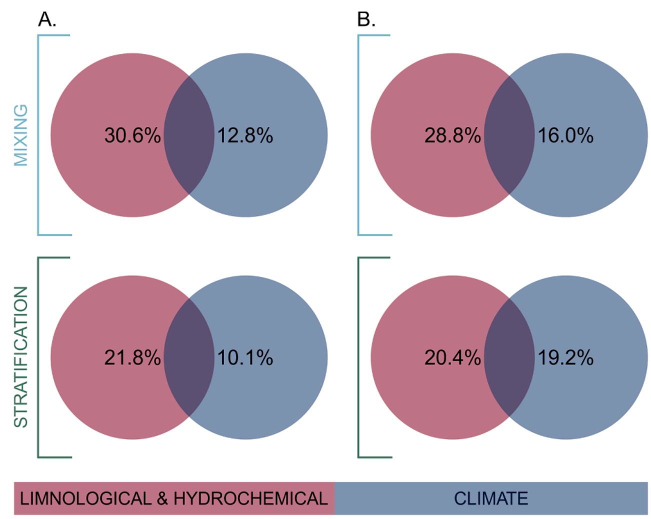

Fig. 8. Venn diagram representing the percent of variance in cyst data explained by limnological and hydrochemical, and climate variables in Łazduny (A) and Rzęśniki (B) (no shared variance recorded).

processes such as mixing regime and resource availability (Catalan and Fee, 1994; Livingstone et al., 2010; Sánchez-López et al., 2015) and that their indirect influence on chrysophyte cysts may be much higher.

Although investigated lakes are characterized by very similar environmental conditions, we observed the differences between present cyst assemblages and the main factors influencing the taxonomic structure. From seventy-two cyst types with abundance > 2% in at least one sample, thirty-three were present in both lakes (ESM, Fig S2). In the case of types present in both lakes we observed that the temporal changes in their fluxes are very similar between lakes with slight differences in their values. However, we noted differences between cysts types present only in one lake both for mixing and stratifications periods (ESM, Fig. S3). Also environmental variables driving cyst composition varied slightly between lakes especially during the stratification period (Figs. 6 and 7). Those differences may be attributed to multiple factors such as dissimilarities in the hydrological type or catchment properties. However, pointing out a single factor that is playing a major role in differentiating the investigated lakes is difficult at this stage of research.

4.3. Cysts as indicators of specific environmental conditions

Based on the analyses, we identified types that respond to certain environmental conditions. Cyst types S031 and S130, S159, and S180 were singled out as promising indicators for both mixing periods, while the D257 and S404 types were solely for fall mixing. However, two of these types, S159 and S404, were indicated as characteristic of both the mixing and the reverse stratification periods. The low deposition in the winter samples likely results from fall mixing, so they can be treated as indicators of the mixing period. In a previous study from Finland, cyst S031, which was also found in Łazduny, was pointed out as a cold-tolerant type that prefers a short ice-free period (Korkonen et al., 2020). Type S130, recorded in Rzęśniki, is a widespread taxon with an affinity for cold waters. Additionally, in a study from Lake Redon, it was also indicated as a type characteristic of both spring and fall mixing (Pla-Rabes and Catalan, 2011). Morphotype S159, which was present in both lakes, was previously found in shallow, highly alkaline (pH > 8.5) lakes in Canada (Duff et al., 1997), but no information is available on its affinity for temperature. S180 is known to be produced by the chrysophyte species *Spiniferomonas bourrellyi*, which is considered a cold-water indicator, and was most prevalent in cool, deep, and oligotrophic mountain lakes (Duff et al., 1995). S404 and D257 were previously found only in Lake Redo (Spain) and Santa Isabel Lake, Costa Rica, respectively, but their ecological requirements and biological affinity are still unknown (Pla, 2001; Wilkinson et al., 2001).

There are many possible consequences of ongoing climate warming and rising air temperatures for lake ecosystems. It is believed that mixing regime patterns will be altered by the shortening or even disappearance of the ice cover phase and strengthening and lengthening of summer stratification (Woolway and Merchant, 2019). Those changes in aquatic ecosystem processes will undoubtedly directly and indirectly affect phytoplankton communities, including chrysophytes (Rühland et al., 2015). Loss of snow and ice cover induces changes in the underwater irradiance regime and influences lakes productivity. Therefore, climate change will contribute to the eutrophication of lake waters (Råman Vinnå et al., 2021; Winder and Sommer, 2012). During the observation period, we recorded cyst responses to the lack of ice cover, which was manifested by a decrease in their fluxes and changes in their taxonomic structure (i.e., the presence of cyst types that were absent in previous years (ESM, Figs. S2 and S3). We therefore think that further climate-induced changes in the lake ecosystem will increase the abundance of organisms that are more tolerant to eutrophic and warm conditions and will decrease the abundance of organisms such as chrysophytes that prefer more oligotrophic environments.

5. Conclusions

In this study, we sought to find and explain the relationships between changes in meteorological conditions and both chrysophyte cyst fluxes and taxonomic structure. We also tested whether cysts directly respond to meteorological variables and assessed the potential of specific cyst types as indicators of mixing or stratification periods. The study of Lakes Łazduny and Rzęśniki revealed that chrysophyte cysts react both directly and indirectly to changes in meteorological conditions. It has been shown that their seasonality is strongly dependent on the physical properties of lakes, which are altered by changing meteorological conditions. Ice cover and mixing intensity, controlling the availability of light and nutrients, are the major drivers of changes in cyst seasonality. The analyses also showed that multiple environmental variables influence cyst taxonomic structure and interannual variability. Nevertheless, both the mean and standard deviation values of air temperature proved to be vital variables for the development of individual cyst types, which confirms the direct impact of meteorological conditions.

We believe that, due to their strong seasonality, chrysophyte cysts have a great potential to be useful indicators of changes in past meteorological conditions. Therefore, studies combining high resolution monitoring of in-lake conditions and chrysophyte cyst data may provide ecological information that will support future applications of cysts in modern and seasonal paleoclimatic studies (e.g., monitoring programs) that can be used to test seasonal climate models.

CRediT authorship contribution statement

Agnieszka Szczerba : Investigation, Writing – original draft, Funding acquisition. **Sergi Pla-Rabes:** Investigation, Writing – review & editing. **Maurycy Żarczyński:** Investigation, Writing – review & editing. **Wojciech Tylmann:** Investigation, Writing – review & editing, Funding acquisition.

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.2021.108395.

References

Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W., Livingstone, D.M., Sommaruga, R., Straile, D., Van Donk, E., Weyhenmeyer, G.A., Winder, M., 2009. Lakes as sentinels of climate change. Limnol. Oceanogr. 54 (6part2), 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283.

Adrian, R., Wilhelm, S., Gerten, D., 2006. Life-history traits of lake plankton species may govern their phenological response to climate warming. Glob. Change Biol. 12, 652–661. https://doi.org/10.1111/j.1365-2486.2006.01125.x.

Bartoszek, K., Matuszko, D., Soroka, J., 2020. Relationships between cloudiness, aerosol optical thickness, and sunshine duration in Poland. Atmospheric Res. 245, 105097. https://doi.org/10.1016/j.atmosres.2020.105097.

Battarbee, R.W., 2000. Palaeolimnological approaches to climate change, with special regard to the biological record. Quat. Sci. Rev. 19 (1-5), 107–124. https://doi.org/10.1016/S0277-3791(99)00057-8.

Battarbee, R.W., 1986. Diatom analysis. In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. John Wiley and Sons, Chichester, pp. 527–570.

Battarbee, R.W., Kneen, M.J., 1982. The use of electronically counted microspheres in absolute diatom analysis. Limnol. Oceanogr. 27 (1), 184–188. https://doi.org/10.4319/lo.1982.27.1.0184.

Berger, S.A., Diehl, S., Stibor, H., Trommer, G., 2010. Water temperature and stratification depth independently shift cardinal events during plankton spring succession. Glob. Change Biol. 16, 1954–1965. https://doi.org/10.1111/ecog.04895.

Bonk, A., Tylmann, W., Amann, B., Enters, D., Grosjean, M., 2015. Modern limnology and varve-formation processes in Lake Żabińskie, northeastern Poland: comprehensive process studies as a key to understand the sediment record. J. Limnol. 74 https://doi.org/10.4081/jlimnol.2014.1117.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the Spatial Component of Ecological Variation. Ecology 73, 1045–1055. https://doi.org/10.2307/1940179.

Brown, K.M., Zeeb, B.A., Smol, J.P., Pienitz, R., 1997. Taxonomic and ecological characterization of chrysophyte stomatocysts from northwestern Canada. Can. J. Bot. 75 (5), 842–863. https://doi.org/10.1139/b97-094.

De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119 (10), 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x.

Catalan, J., Fee, E.J., 1994. Interannual variability in limnic ecosystems: origin, patterns, and predictability. In: Limnology Now: A Paradigm of Planetary Problems. Elsevier Science, New York, pp. 81–97.

Catalan, J., Pla-Rabés, S., García, J., Camarero, L., 2014. Air temperature-driven CO2 consumption by rock weathering at short timescales: Evidence from a Holocene lake sediment record. Geochim. Cosmochim. Acta 136, 67–79. https://doi.org/10.1016/j.gca.2014.04.005.

Catalan, J., Pla-Rabés, S., Wolfe, A.P., Smol, J.P., Rühland, K.M., Anderson, N.J., Kopáček, J., Stuchlík, E., Schmidt, R., Koinig, K.A., Camarero, L., Flower, R.J., Heiri, O., Kamenik, C., Korhola, A., Leavitt, P.R., Psenner, R., Renberg, I., 2013. Global change revealed by palaeolimnological records from remote lakes: a review. J. Paleolimnol. 49 (3), 513–535. https://doi.org/10.1007/s10933-013-9681-2.

Chesson, P., 2000. Mechanisms of Maintenance of Species Diversity. Annu. Rev. Ecol. Syst. 31 (1), 343–366. https://doi.org/10.1146/ecolsys.2000.31.issue-110.1146/annurev.ecolsys.31.1.343.

Cumming, B.F., Wilson, S.E., Smol, J.P., 1993. Paleolimnological potential of chrysophyte cysts and scales and of sponge spicules as indicators of lake salinity. Int. J. Salt Lake Res. 2 (1), 87–92. https://doi.org/10.1007/BF02905055.

De Jong, R., Kamenik, C., 2011. Validation of a chrysophyte stomatocyst-based cold-season climate reconstruction from high-Alpine Lake Silvaplana. Switzerland. J. Quat. Sci. 26 (3), 268–275. https://doi.org/10.1002/jqs.v26.310.1002/jqs.1451.

De Jong, R., Kamenik, C., Grosjean, M., 2013. Cold-season temperatures in the European Alps during the past millennium: variability, seasonality and recent trends. Quat. Sci. Rev. 82, 1–12. https://doi.org/10.1016/j.quascirev.2013.10.007.

De Jong, R., Schneider, T., Hernández-Almeida, I., Grosjean, M., 2016. Recent temperature trends in the South Central Andes reconstructed from sedimentary chrysophyte stomatocysts in Laguna Escondida (1742ma.s.l., 38°28S, Chile). Glob. Planet. Change 137, 24–34. https://doi.org/10.1016/j.gloplacha.2015.12.006.

Diehl, S., Berger, S., Ptacnik, R., Wild, A., 2002. Phytoplankton, Light, and Nutrients in a Gradient of Mixing Depths: Field Experiments. Ecology 83, 399–411. https://doi.org/10.1890/0012-9658(2002)083[0399:PLANIA]2.0.CO;2.

Duarte, C.M., 1990. Time lags in algal growth: generality, causes and consequences. J. Plankton Res. 12 (4), 873–883. https://doi.org/10.1093/plankt/12.4.873.

Duff, K.E., Zeeb, B.A., Smol, J.P. (Eds.), 1995. Atlas of Chrysophycean Cysts. Springer Netherlands, Dordrecht.

Duff, K.E., Smol, J.P., 1991. Morphological descriptions and stratigraphic distributions of the chrysophycean stomatocysts from a recently acidified lake (Adirondack Park, N. Y.). J. Paleolimnol. 5, 73–113. https://doi.org/10.1007/BF00226558.

Duff, K.E., Zeeb, B.A., Smol, J.P., 1997. Chrysophyte cyst biogeographical and ecological distributions: a synthesis. J. Biogeogr. 24, 791–812. https://doi.org/10.1046/j.1365-2699.1997.00122.x.

Eloranta, P., 1995. In: Chrysophyte Algae: Ecology, Phylogeny and Development. Cambridge University Press, pp. 214–231. https://doi.org/10.1017/CBO9780511752292.011.

Facher, E., Schmidt, R., 1996. A siliceous chrysophycean cyst-based pH transfer function for Central European lakes. J. Paleolimnol. 16, 275–321. https://doi.org/10.1007/BF00207575.

Hernández-Almeida, I., Grosjean, M., Przybylak, R., Tylmann, W., 2015a. A chrysophyte-based quantitative reconstruction of winter severity from varved lake sediments in NE Poland during the past millennium and its relationship to natural climate variability. Quat. Sci. Rev. 122, 74–88. https://doi.org/10.1016/j.quascirev.2015.05.029.

Hernández-Almeida, I., Grosjean, M., Tylmann, W., Bonk, A., 2015b. Chrysophyte cyst-inferred variability of warm season lake water chemistry and climate in northern Poland: training set and downcore reconstruction. J. Paleolimnol. 53 (1), 123–138. https://doi.org/10.1007/s10933-014-9812-4.

Institute of Meteorology and Water Management - National Research Institute, 2021. https://danepubliczne.imgw.pl/ [WWW Document] (accessed 5.10.21).

Kamenik, C., Schmidt, R., 2005. Chrysophyte resting stages: a tool for reconstructing winter/spring climate from Alpine lake sediments. Boreas 34, 477–489. https://doi.org/10.1080/03009480500231468.

Kamenik, C., Schmidt, R., Kum, G., Psenner, R., 2001. The Influence of Catchment Characteristics on the Water Chemistry of Mountain Lakes. Arct. Antarct. Alp. Res. 33 (4), 404–409. https://doi.org/10.1080/15230430.2001.12003448.

Korkonen, S., Weckström, J., Korhola, A., 2020. Biogeography and ecology of freshwater chrysophyte cysts in Finland. Hydrobiologia 847 (2), 487–499. https://doi.org/10.1007/s10750-019-04112-0.

Korkonen, S.T., Ojala, A.E.K., Kosonen, E., Weckström, J., 2017. Seasonality of chrysophyte cyst and diatom assemblages in varved Lake Nautajärvi – implications for palaeolimnological studies. J. Limnol. 76 https://doi.org/10.4081/jlimnol.2017.1473.

Legendre, P., Legendre, L., 1998. Numerical Ecology, Volume, 24–2nd Edition. Elsevier Science.

Lisicki, S., Krzywicki, T., 2013. Szczegółowa mapa geologiczna Polski. Arkusz Miłki (143). [Book in Polish].

Livingstone, D.M., Adrian, R., Blenckner, T., George, G., Weyhenmeyer, G.A., 2010. In: The Impact of Climate Change on European Lakes. Springer Netherlands, Dordrecht, pp. 51–61. https://doi.org/10.1007/978-90-481-2945-4_4.

Livingstone, D.M., Lotter, A.F., 1998. The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palæolimnological implications. J. Paleolimnol. 19, 181–198. https://doi.org/10.1023/A:1007904817619.

Maier, D.B., Gälman, V., Renberg, I., Bigler, C., 2018. Using a decadal diatom sediment trap record to unravel seasonal processes important for the formation of the sedimentary diatom signal. J. Paleolimnol. 60 (2), 133–152. https://doi.org/10.1007/s10933-018-0020-5.

Marszelewski, Włodzimierz, Skowron, Rajmund, 2006. Ice cover as an indicator of winter air temperature changes: Case study of the Polish Lowland lakes. Hydrol. Sci. J. 51 (2), 336–349. https://doi.org/10.1623/hysj.51.2.336.

Pang, W., Wang, Q., 2014. Chrysophycean stomatocysts from the Aershan Geological Park (Inner Mongolia). China. Phytotaxa 187 (1), 1. https://doi.org/10.11646/phytotaxa.187.110.11646/phytotaxa.187.1.1.

Piccolroaz, S., Toffolon, M., Majone, B., 2015. The role of stratification on lakes' thermal response: The case of Lake Superior. Water Resour. Res. 51, 7878–7894. https://doi.org/10.1002/2014WR016555.

Pla, S., 2001. Chrysophycean cysts from the Pyrenees. Bibliotheca Phycologica.

Pla, S., Anderson, N.J., 2005. Environmental factors correlated with chrysophyte cyst assemblages in low arctic lakes of southwest Greenland. J. Phycol. 41, 957–974. https://doi.org/10.1111/j.1529-8817.2005.00131.x.

Pla, S., Camarero, L., Catalan, J., 2003. Chrysophyte cyst relationships to water chemistry in Pyrenean lakes (NE Spain) and their potential for environmental reconstruction. J. Paleolimnol. 30, 21–34. https://doi.org/10.1023/A:1024771619977.

Pla, S., Catalan, J., 2005. Chrysophyte cysts from lake sediments reveal the submillennial winter/spring climate variability in the northwestern Mediterranean region throughout the Holocene. Clim. Dyn. 24 (2-3), 263–278. https://doi.org/10.1007/s00382-004-0482-1.

Pla-Rabés, S., Catalan, J., 2018. Diatom species variation between lake habitats: implications for interpretation of paleolimnological records. J. Paleolimnol. 60 (2), 169–187. https://doi.org/10.1007/s10933-018-0017-0.

Pla-Rabes, S., Catalan, J., 2011. Deciphering chrysophyte responses to climate seasonality. J. Paleolimnol. 46 (1), 139–150. https://doi.org/10.1007/s10933-011-9529-6.

Poikane, S., 2009. Water Framework Directive intercalibration technical report. Part 2: Lakes. OPOCE, Luxembourg.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Råman Vinnå, L., Medhaug, I., Schmid, M., Bouffard, D., 2021. The vulnerability of lakes to climate change along an altitudinal gradient. Commun. Earth Environ. 2, 1–10. https://doi.org/10.1038/s43247-021-00106-w.

Reynolds, C.S., 2006. The Ecology of Phytoplankton, Ecology. Cambridge University Press, Cambridge, Biodiversity and Conservation.

Reynolds, C.S., Oliver, R.L., Walsby, A.E., 1987. Cyanobacterial dominance: The role of buoyancy regulation in dynamic lake environments. N. Z. J. Mar. Freshw. Res. 21 (3), 379–390. https://doi.org/10.1080/00288330.1987.9516234.
Rühland, K.M., Paterson, A.M., Smol, J.P., 2015. Lake diatom responses to warming: reviewing the evidence. J. Paleolimnol. 54 (1), 1–35. https://doi.org/10.1007/s10933-015-9837-3.
Sánchez-López, G., Hernández, A., Pla-Rabes, S., Toro, M., Granados, I., Sigró, J., Trigo, R.M., Rubio-Inglés, M.J., Camarero, L., Valero-Garcés, B., Giralt, S., 2015. The effects of the NAO on the ice phenology of Spanish alpine lakes. Clim. Change 130 (2), 101–113. https://doi.org/10.1007/s10584-015-1353-y.
Sanchini, A., Szidat, S., Tylmann, W., Vogel, H., Wacnik, A., Grosjean, M., 2020. A Holocene high-resolution record of aquatic productivity, seasonal anoxia and meromixis from varved sediments of Lake Łazduny, North-Eastern Poland: insight from a novel multi-proxy approach. J. Quat. Sci. 35 (8), 1070–1080. https://doi.org/10.1002/jqs.v35.810.1002/jqs.3242.
Sandgren, C.D. (Ed.), 1988. Growth and reproductive strategies of freshwater phytoplankton. Presented at the International Phycological Symposium, Cambridge University Press, Cambridge.
Sandgren, C.D., Smol, J.P., Kristiansen, J. (Eds.), 1995. Chrysophyte Algae: Ecology, Phylogeny and Development. Cambridge University Press, Cambridge.
Sharma, S., Blagrave, K., Magnuson, J.J., O'Reilly, C.M., Oliver, S., Batt, R.D., Magee, M. R., Straile, D., Weyhenmeyer, G.A., Winslow, L., Woolway, R.I., 2019. Widespread loss of lake ice around the Northern Hemisphere in a warming world. Nat. Clim. Change 9 (3), 227–231. https://doi.org/10.1038/s41558-018-0393-5.
Siver, P.A., 1993. Inferring the specific conductivity of lake water with scaled chrysophytes. Limnol. Oceanogr. 38 (7), 1480–1492. https://doi.org/10.4319/lo.1993.38.7.1480.
Smol, J.P., 1985. The ratio of diatom frustules to chrysophycean statospores: A useful paleolimnological index. Hydrobiologia 123 (3), 199–208. https://doi.org/10.1007/BF00034378.
Smol, J.P., Wolfe, A.P., Birks, H.J.B., Douglas, M.S.V., Jones, V.J., Korhola, A., Pienitz, R., Ruhland, K., Sorvari, S., Antoniades, D., Brooks, S.J., Fallu, M.-A., Hughes, M., Keatley, B.E., Laing, T.E., Michelutti, N., Nazarova, L., Nyman, M., Paterson, A.M., Perren, B., Quinlan, R., Rautio, M., Saulnier-Talbot, E., Siitonen, S., Solovieva, N., Weckstrom, J., 2005. Climate-driven regime shifts in the biological communities of arctic lakes. Proc. Natl. Acad. Sci. 102 (12), 4397–4402. https://doi.org/10.1073/pnas.0500245102.
Tylmann, W., Głowacka, P., Szczerba, A., 2017. Tracking climate signals in varved lake sediments: research strategy and key sites for comprehensive process studies in the Masurian Lakeland. Limnol. Rev. 17, 159–166. https://doi.org/10.1515/limre-2017-0015.
Wetzel, R., 2001. Limnology. Lake and River Ecosystems, 3rd ed. Academic Press, San Diego.
Wilhelm, S., Adrian, R., 2008. Impact of summer warming on the thermal characteristics of a polymictic lake and consequences for oxygen, nutrients and phytoplankton. Freshw. Biol. 53, 226–237. https://doi.org/10.1111/j.1365-2427.2007.01887.x.
Wilkinson, A.N., Zeeb, B.A., Smol, J.P., 2001. Atlas of Chrysophycean Cysts:, Volume II. Developments in Hydrobiology, Springer, Netherlands, Dordrecht.
Williamson, C.E., Saros, J.E., Vincent, W.F., Smol, J.P., 2009. Lakes and reservoirs as sentinels, integrators, and regulators of climate change. Limnol. Oceanogr. 54 (6part2), 2273–2282. https://doi.org/10.4319/lo.2009.54.6_part_2.2273.
Winder, M., Sommer, U., 2012. Phytoplankton response to a changing climate. Hydrobiologia 698 (1), 5–16. https://doi.org/10.1007/s10750-012-1149-2.
Woolway, R.I., Merchant, C.J., 2019. Worldwide alteration of lake mixing regimes in response to climate change. Nat. Geosci. 12 (4), 271–276. https://doi.org/10.1038/s41561-019-0322-x.
Zolitschka, B., Francus, P., Ojala, A.E.K., Schimmelmann, A., 2015. Varves in lake sediments – a review. Quat. Sci. Rev. 117, 1–41. https://doi.org/10.1016/j.quascirev.2015.03.019.
Zufiaurre, A., Felip, M., Giménez-Grau, P., Pla-Rabès, S., Camarero, L., Catalan, J., Saros, J., 2021. Episodic nutrient enrichments stabilise protist coexistence in planktonic oligotrophic conditions. J. Ecol. 109 (4), 1717–1729. https://doi.org/10.1111/jec.v109.410.1111/1365-2745.13591.

Supplementary materials – Publication 1

Table S1. Variables selected for RDA (WS – wind speed, AT – air temperature).

VARIABLES	ŁAZDUNY			RZĘŚNIKI		
REGIME PHASE	MIXING	STRATIFICATION	MIXING + STRATIFICATION	MIXING	STRATIFICATION	MIXING + STRATIFICATION
TP	+	+	+	+	+	+
TN	+	+	+	+	+	+
SC	+	+	+	+	+	+
ODO	+	-	+	+	-	+
pH	+	+	+	+	+	+
Chl-a	+	-	+	+	-	+
WT	-	-	-	-	-	-
AT	+	+	+	+	+	+
AT_SD	+	+	-	+	+	+
WS	+	+	+	+	+	+
WS_SD	-	-	-	-	-	-
PRCP	+	+	+	+	+	+
PRCP_SD	-	-	-	-	-	-

Table S2 Values of R^2 for RDAs conducted with no lagged, two-weeks lagged, and one month lagged data.

	MIXING			STRATIFICATION			MIXING + STRATIFICATION		
	NO LAG	2 WEEKS	1 MONTH	NO LAG	2 WEEKS	1 MONTH	NO LAG	2 WEEKS	1 MONTH
ŁAZDUNY	66.9	69.4	75.6	67.6	74.7	76.0	48.0	50.7	52.0
RZĘŚNIKI	71.0	75.7	75.4	75.3	68.3	73.2	50.0	53.0	54.5

Fig. S1. Depth of the photic zone in Łazduny (A) and Rzęśniki (B).

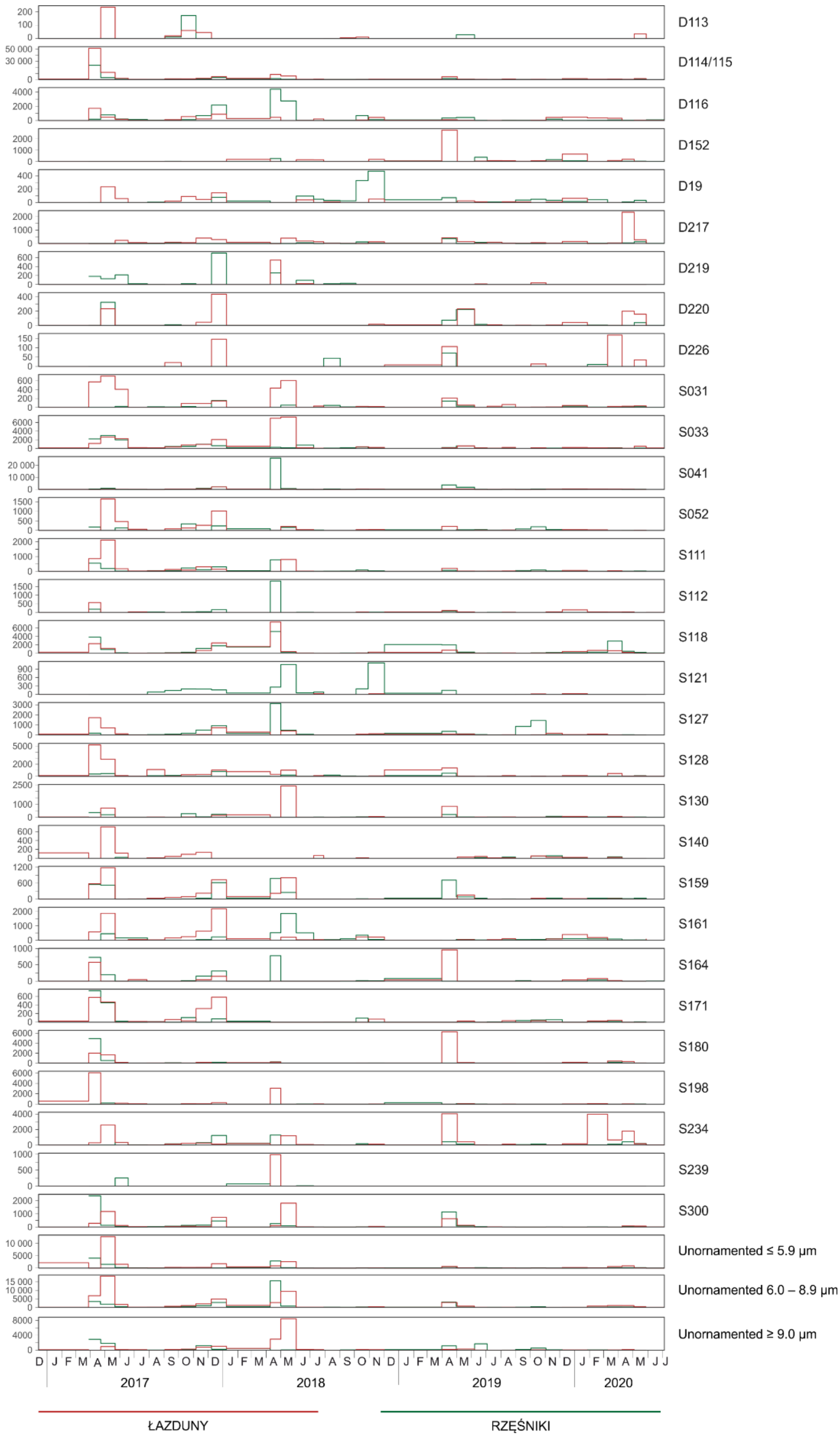

Fig. S2. Fluxes of chrysophyte cysts [cysts d^{-1} cm^2^{-1}] with an abundance of ≥2% in at least one sample present both in Lake Łazduny and Lake Rzęśniki (where CYST 1, CYST 2, and CYST 3 are possible new morphotypes; however, confirmation of this fact requires further research).

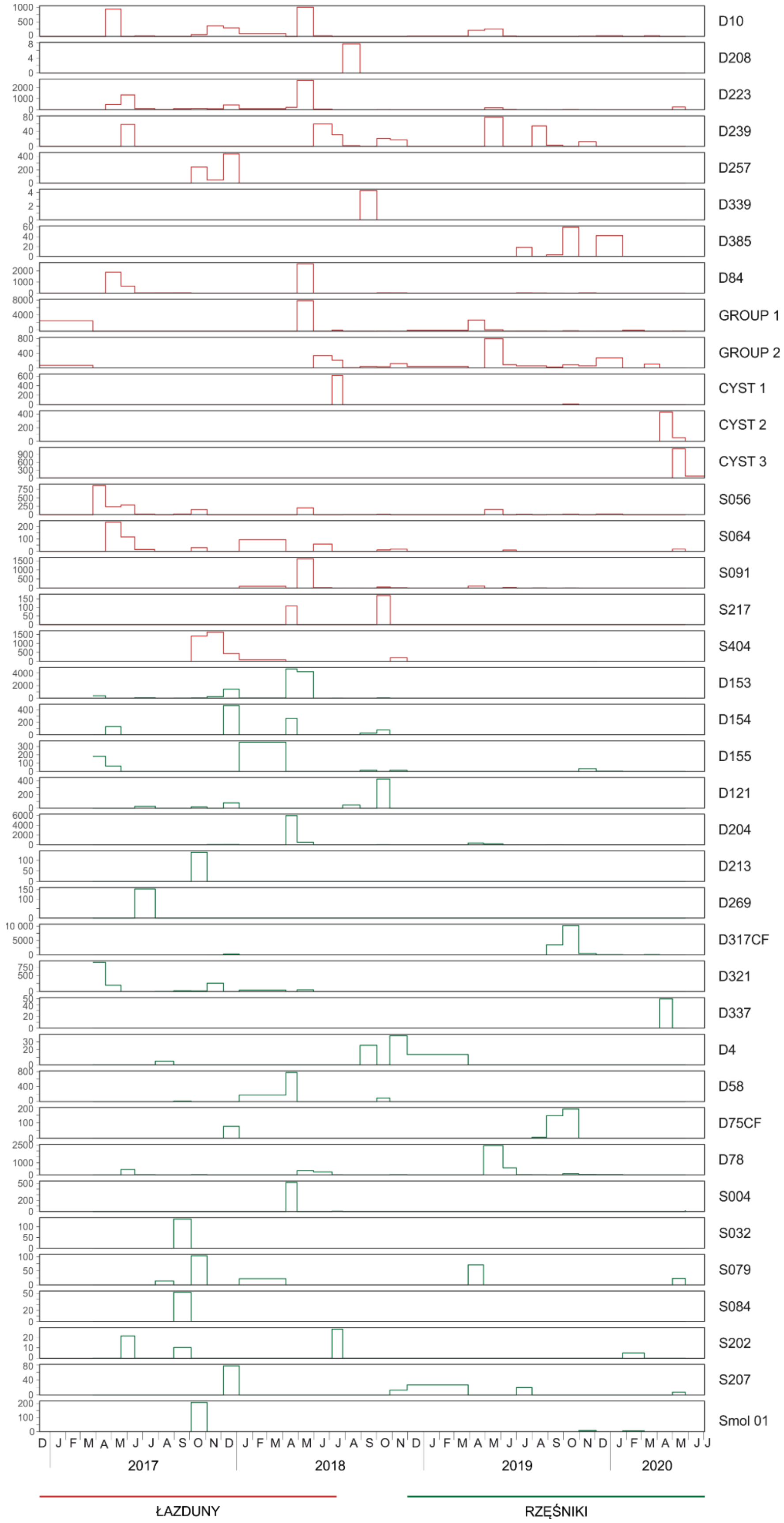

Fig. S3. Fluxes of chrysophyte cysts [cysts d^{-1} $cm^{\wedge}2^{-1}$] with an abundance of ≥2% in at least one sample present either in Lake Łazduny or in Lake Rzęśniki.

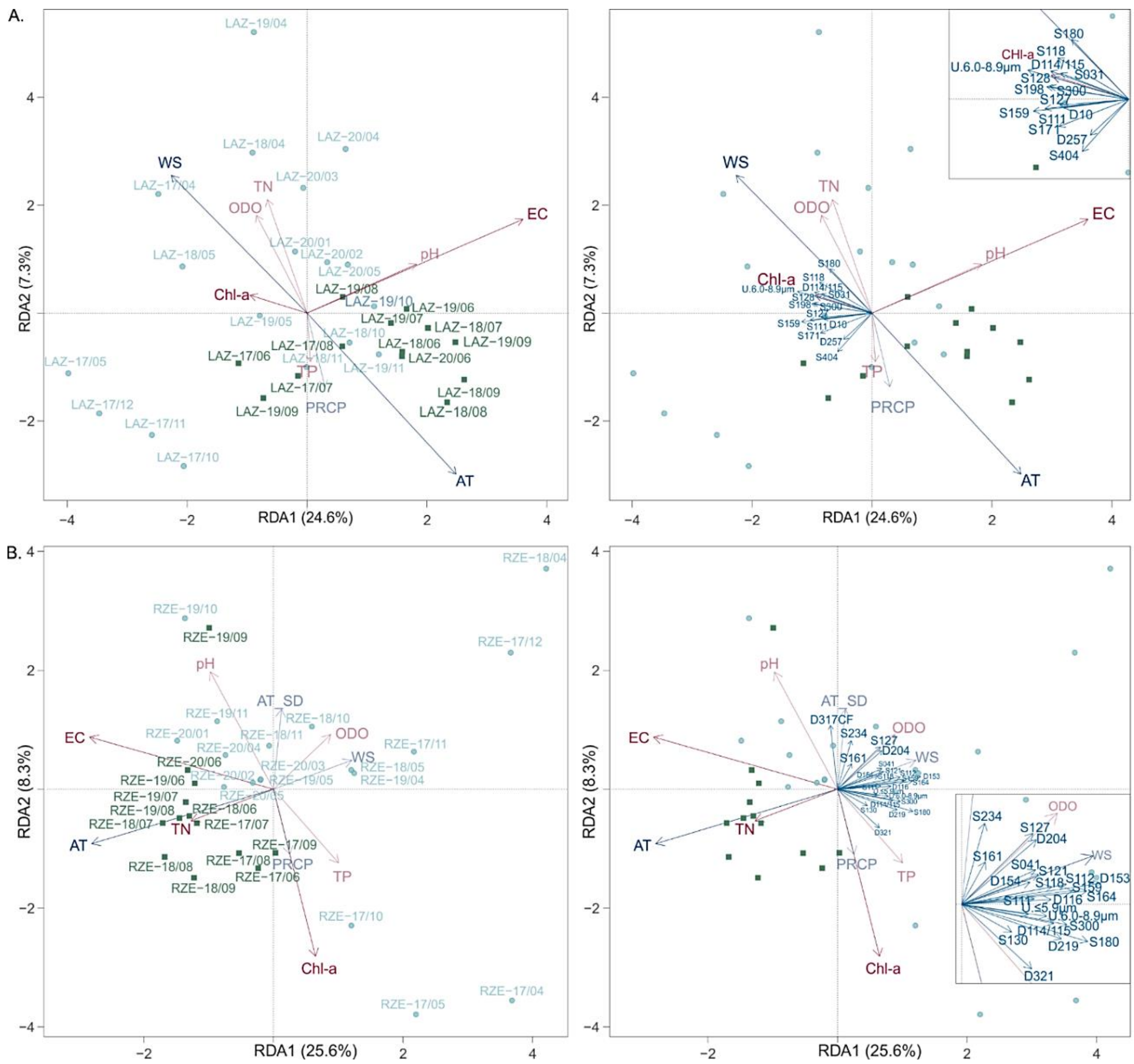

Fig. S4. RDA biplots of samples (left) and cyst morphotypes and ‘collective groups’ (right) with explanatory variables for mixing combined with stratification in Łazduny (A) and Rzęśniki (B) (significant variables are highlighted with more intense colors).

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I hereby confirm my contribution to the scientific paper: "The relationship between chrysophyte cyst assemblages and meteorological conditions: Evidence from a sediment-trap study in northeast Poland" (Ecological Indicators, 2021, 133, 108395) being a part of the doctoral dissertation "Tracking climate signals in lakes of northeastern Poland: modern sedimentation studies using chrysophyte cysts and diatoms".

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Publication 2

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Modern diatom assemblages and their association with meteorological conditions in two lakes in northeastern Poland

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ABSTRACT

The population dynamics of diatoms are affected by a variety of environmental variables. Due to their short generation times and high sensitivity to changes in physicochemical conditions, diatoms are considered good environmental indicators. The main goal of our study was to find and explain the relationships between changes in meteorological conditions and diatom fluxes and taxonomic composition based on the example of two small lakes: Łazduny and Rzęśniki. Using meteorological data, sediment traps, and regular measurements of limnological and hydrochemical properties of the water column, we collected a three-year-long, high-resolution series of observations. The results show that total diatom fluxes are indirectly influenced by changes in meteorological conditions, acting through changes in the mixing regimes that determine the nutrient and light availability in lakes. Statistical analyses showed that the variability of the diatom data is correlated with air temperature and wind speed. Nevertheless, their influence on diatom assemblages is most likely the surrogate for the complex changes in the physical structure of the investigated lakes. Despite many similarities between the studied lakes such as mixing regime patterns, dominant diatom taxa, and seasonal dynamics of diatom fluxes, we recorded differences in both the seasonal succession of specific diatom taxa and the occurrence of the peaks of total fluxes, and differences in taxonomic composition referring to less dominant taxa. We attribute these dissimilarities to the local conditions, such as the hydrological types of the lakes, the extent of the littoral zone, and exposure to the sunlight connected to the position in the catchment.

1. Introduction

Along with the growing interest in the functioning of ecosystems under ongoing climate change, the need for a long-term perspective for reliable interpretation of the observed variability has become clear. Among environmental archives of environmental changes, lakes are exceptional because their sediments provide high-resolution records over different time scales (Zolitschka et al., 2015). The physical, chemical and biological characteristics of lakes are sensitive to changes in climate, and the sedimentary record of lakes provides a valuable archive of past changes in the community composition of diatoms. These records can be difficult to interpret without knowledge of present-day diatom dynamics over seasons (Smol, 2008; Adrian et al., 2009). Therefore, a thorough understanding of direct and indirect relationships between the climate, the water column, and the sediment archive, is needed to fully exploit the potential of lake sediments as recorders of environmental conditions variability (Leavitt et al., 2009). These complex relationships include multiple variables and processes, e.g. the water temperature, mixing and stratification patterns, light availability, nutrient cycling, pH and ionic composition, primary production, and sediment re-distribution (Battarbee, 2000; Smol, 2008).

Due to the complexity of lake ecosystems, understanding how changes in meteorological conditions influence the dynamics of biological proxies is a major challenge. To address this issue, analysis of lake biota communities, such as diatoms (Bacillariophyceae), exhibiting strong seasonal replacement and short generation times, can be used (Reynolds, 2006). Diatoms are common in lake sediment records and provide an adequate long-term perspective to understand ecosystem responses to changes in environmental conditions (Dixit et al., 1992; Smol and Cumming, 2000). Good preservation of diatom silica valves and specific ecological optima and tolerances to important physical and chemical limnological variables of different species make diatoms the most frequently used biological proxies in limnological and paleolimnological research (Battarbee et al., 2001). During the last century,

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diatoms have been commonly used in studies describing, among others, shifts in acidification, salinization, pH, heavy metal pollution, nutrient conditions, trophic state, and water transparency in lake bodies (Birks et al., 1990; Gasse, 2002; Stenger-Kovács et al., 2007; Cantonati et al., 2009; Smol and Stoermer, 2010; Luoto et al., 2012; Bennion et al., 2014; Gautam et al., 2017). However, with the increasing interest in high-resolution environmental reconstructions, the seasonality and succession of diatom growth have become an important issue in contemporary limnology (Köster and Pienitz, 2006; Hausmann and Pienitz, 2007; Kirilova et al., 2008; Korkonen et al., 2017; Zou et al., 2018).

There is considerable potential for using diatom assemblages to track climate-induced changes (Fritz, 2008; Juggins, 2013). Recent findings indicate temperature as one of the most important aspects of diatom ecology (Hausmann and Lotter, 2001; Bigler and Hall, 2003; Thompson et al., 2005; Rühland et al., 2008; Winder et al., 2009) and point to mixing regime as the main driver of changes in the diatom composition (Interlandi et al., 1999; Weckström and Korhola, 2001; Köster and Pienitz, 2006; Wiltse et al., 2016). Kienel et al., (2017) attribute changes in diatom assemblages to the availability of light and nutrients strongly correlated to spring warming and the duration of water column mixing. The response of diatoms to a length of ice-cover was investigated in alpine lakes by Lotter and Bigler (2000), who suggested a strong inhibition of plankton development under the ice and pointed out a correlation between ice-cover duration and the relative abundance of different species. A recent study by Maier et al. (2019) demonstrated the importance of late winter conditions (e.g., light and nutrient availability, under-ice stratification, timing of ice break-up and lake turnover) on the formation of the diatom signal in sediments. They indicated a much greater than previously expected importance of processes under the ice on lake ecology. However, different patterns of diatom response indicate that the relationships between diatom assemblages and changes in meteorological conditions are still not sufficiently explained.

In this study, we aimed to test the hypothesis about the direct influence of meteorological conditions as drivers of changes in the taxonomical composition of diatoms. To verify this hypothesis, we investigated two lakes located in northeastern Poland: Łazduny and Rzęśniki, which are influenced by the same meteorological conditions and are not subjected to direct human influence. Specifically, our goals were 1) to assess the diatom total fluxes and taxonomic structure composition changes, 2) to explain the relationships between environmental conditions and diatom assemblages, and 3) to determine seasonal patterns of variation in diatom assemblages from sediment traps, in relation to measured physical, chemical, and meteorological variables in two small, but deep lakes from Poland. Our study showed that the combination of limnological measurements, sediment trapping, and meteorological data led to an explanation of diatom assemblage dynamics in the investigated lakes and their relationship with environmental variables.

2. Methods and materials

2.1. Study sites

The studied lakes – Łazduny (53°51′18.3″N, 21°57′07.1″E, 128.8 m a.s.l.) and Rzęśniki (53°50′30.0″N, 21°58′35.9″E, 125.0 m a.s.l.) – are located in the Masurian Lake District in northeastern Poland (Fig. 1). Climatic conditions within the study region are characterized by strong continentality and seasonality, with cold winters and warm summers. Typically, the lakes are covered by ice between late December and early April (Institute of Meteorology and Water Management, 2022).

Lakes Łazduny and Rzęśniki are situated in small depressions (with a surface area of 10.6 and 12 ha, respectively) in a NW-SE elongated

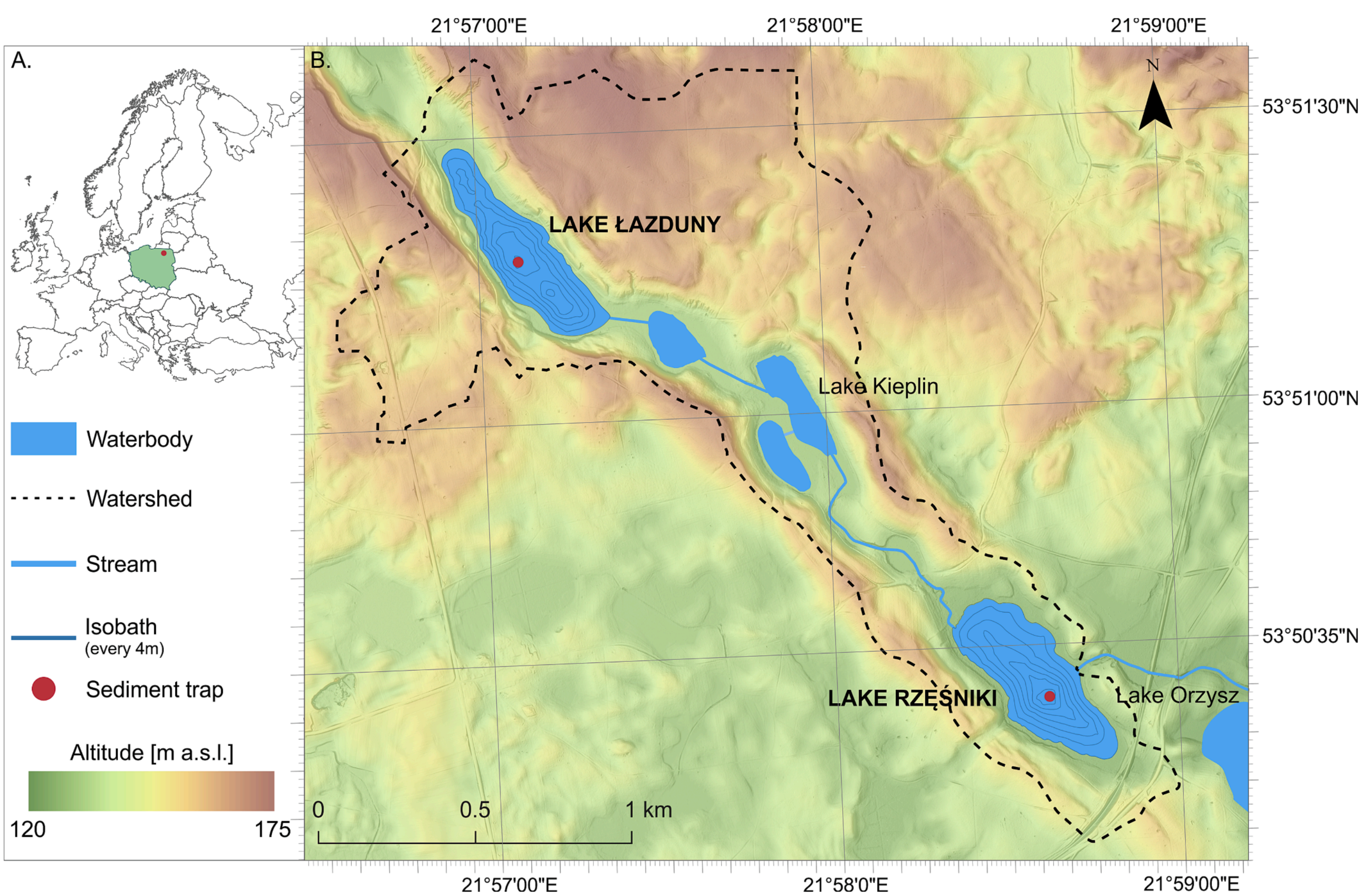

Fig. 1. Localization in Europe (A) and catchment topography (B) of lakes Łazduny and Rzęśniki. Bathymetric maps are embedded (isobaths every 4 m).

tunnel valley (Fig. 1). The maximum water depths reach 22.4 m and 26 m in Łazduny and Rzęśniki, respectively. The lakes share a homogenous catchment of 1.94 km^2 that lies within an outwash plain built of glaciofluvial sand and gravel deposits. A chain of lakes is located in a deep subglacial channel, the bottom of which is covered by peat deposits. About 85 % of the catchment is covered by woodland communities, with coniferous trees predominating. Small and uncovered areas are found in the northern part. There is no settlement in the catchment. Lakes Łazduny and Rzęśniki are hydrologically connected to Lake Orzysz by a small stream. Chemical data show that these are slightly alkaline and hardwater lakes. Lake Łazduny is currently mesotrophic, while Rzęśniki is eutrophic (Table 1). More details about both lakes are provided by Tylmann et al. (2017).

2.2. Data collection

The studied lakes were monitored bi-weekly, starting from December 2016 in Łazduny and February 2017 in Rzęśniki, until July 2020. Measurements of the water temperature (WT), specific conductance (SC), pH, dissolved oxygen (DO), chlorophyll-a (Chl-a) and phycocyanin (BGA.PC) concentrations in the water column were conducted with EXO 2 Multiparameter Sonde (YSI, USA) at a 1 m depth interval (starting at the 1st meter to the 20th meter in Łazduny, and to the 25th meter in Rzęśniki). A Secchi disc was used to estimate water transparency. Water samples were taken from water depths of 1, 10, 20 (Łazduny) and 25 (Rzęśniki) meters. Total phosphorus (TP) and total nitrogen (TN) concentrations were measured with a UV/VIS spectrophotometer (Spectroquant Prove 600 Spectrophotometer, Merck, Germany).

Meteorological data such as daily air temperature (AT), wind speed (WS), and precipitation (PRCP) for the closest meteorological station, Mikołajki (around 25 km from the studied lakes), were obtained from the database of the Institute of Meteorology and Water Management–National Research Institute (https://danepubliczne.imgw.pl/).

To record seasonal changes in the diatom composition and total fluxes, we installed sediment traps (four 80 cm long tubes with an inner diameter of 86 mm and total active area of 234 cm^2) one meter above the sediment surface in the deepest parts of the lakes. Sediment traps were emptied with monthly resolution except for the periods of ice cover. Freeze-dried sediment samples were prepared for diatom analysis according to the method described by Battarbee et al. (2001). To remove carbonates, 50 mg of material was treated with 10 % HCl, then with 30 % H_2O_2 to eliminate organic matter, and repeatedly washed with distilled water. Slides were made with the Naphrax® mounting medium. At least 500 valves were counted in random transects at 1000x magnification using Nikon Eclipse E-200 and Delta Optical Genetic Pro light microscopes (numerical aperture of objectives and condenser top lens – 1.25). Counts were made continuously along transects until sufficient amount of valves were counted. The diatom fluxes were estimated using counted alongside divinylbenzene microspheres (mean diameter of 8.3 μm) (Battarbee and Kneen, 1982). Diatom identification followed mainly Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b). Names were updated according to AlgaeBase (Guiry and Guiry, 2022).

2.3. Data analysis

In the first step, limnological and hydrochemical data measured during periods of sediment trap exposure were averaged for the photic zone estimated as the Secchi disc visibility multiplied by 2.5 (Poikane, 2009). Further for each variable we counted a mean value for the period of sediment trap exposure (in most cases it covered 3 measurements). Next, all environmental variables except pH (i.e. TP, TN, EC, BGA-PC, DO, WT, pH, mean AT, standard deviation of AT, sum of PRCP, standard deviation of PRCP, mean WS, standard deviation of WS) were log-transformed, centered and standardized before further analysis. Based on water temperature and oxygen concentrations, we divided the observational period and classified each sample into one of three phases, i.e., reverse stratification (winter with ice cover, usually recorded between December and March), mixing (spring and fall isothermy, recorded between April–May, and October–November, respectively) and stratification (ice-free period except mixing, recorded between June–September).

Only species with an abundance of 2 % or more in at least one sample and present in both lakes were included in the statistical analyses. Diatom fluxes data served as the basis for all statistical analyses. Due to low diatom fluxes during the reverse stratification period, these samples were removed from further statistical analysis. Prior to the analyses, flux values were log transformed ($\log(x + 1)$), since the species data contained many zeros and this transformation enabled the use of linear methods (Legendre and Legendre, 2012).

Statistical analyses were carried out using R version 4.2.1 (R Core Team, 2022). In the first step we conducted detrended correspondence analysis (DCA) to compare diatom assemblages of the studied lakes. Next, we assessed correlation between variables (Electronical Supplementary Materials Fig. S1.) and used forward selection to reduce the number of environmental variables in the ordination analysis (Borcard et al., 1992). Further, the linear model (Redundancy Analysis, RDA) was used to show the relationship between diatom fluxes and environmental variables (Legendre and Legendre, 2012). This method was used for the whole period as well as for the mixing and stratification phases separately for both lakes jointly using the 'vegan' package. Next, the statistical significance of each variable added was assessed by a Monte Carlo permutation test (999 unrestricted permutations) (Electronical Supplementary Materials Table S1.). Finally, we conducted variation partitioning to analyze to what extent changes in diatom fluxes and composition are explained by meteorological variables and combined hydrochemical and limnological variables (Borcard et al., 1992).

3. Results

3.1. Environmental variables

A summary of the measured limnological and hydrochemical variables is presented in Table 1. Winter seasons, apart from the one of 2020, had the coldest air and water temperatures, and for around three month the lakes were covered with ice (Figs. 2, 3). In both lakes between 2016 and 2019 during winter we observed the development of winter

Table 1
Minimal and maximal values of limnological and hydrochemical variables obtained from all conducted measurements, with an explanation of all used abbreviations.

Abbreviation:	*Explanation:*	*Unit*	*Min. Łazduny*	*Max. Łazduny*	*Min. Rzęśniki*	*Max. Rzęśniki*
BGA.PC	Phycocyanin	$\mu g\ l^{-1}$	0.00	12.58	0.00	10.72
Chl-a	Chlorophyll-a	$\mu g\ l^{-1}$	0.00	138.19	0.00	143.09
DO	Dissolved oxygen	$mg\ l^{-1}$	0.00	13.81	0.00	16.95
SC	Specific conductance	$\mu S\ cm^{-1}$	310.60	453.30	346.5	454.3
pH	pH		7.09	8.73	7.08	8.76
TN	Total nitrogen	$mg\ l^{-1}$	0.036	4.23	0.056	2.02
TP	Total phosphorus	$mg\ l^{-1}$	0.005	0.64	0.005	0.64
WT	Water temperature	°C	1.24	24.95	0.86	25.47

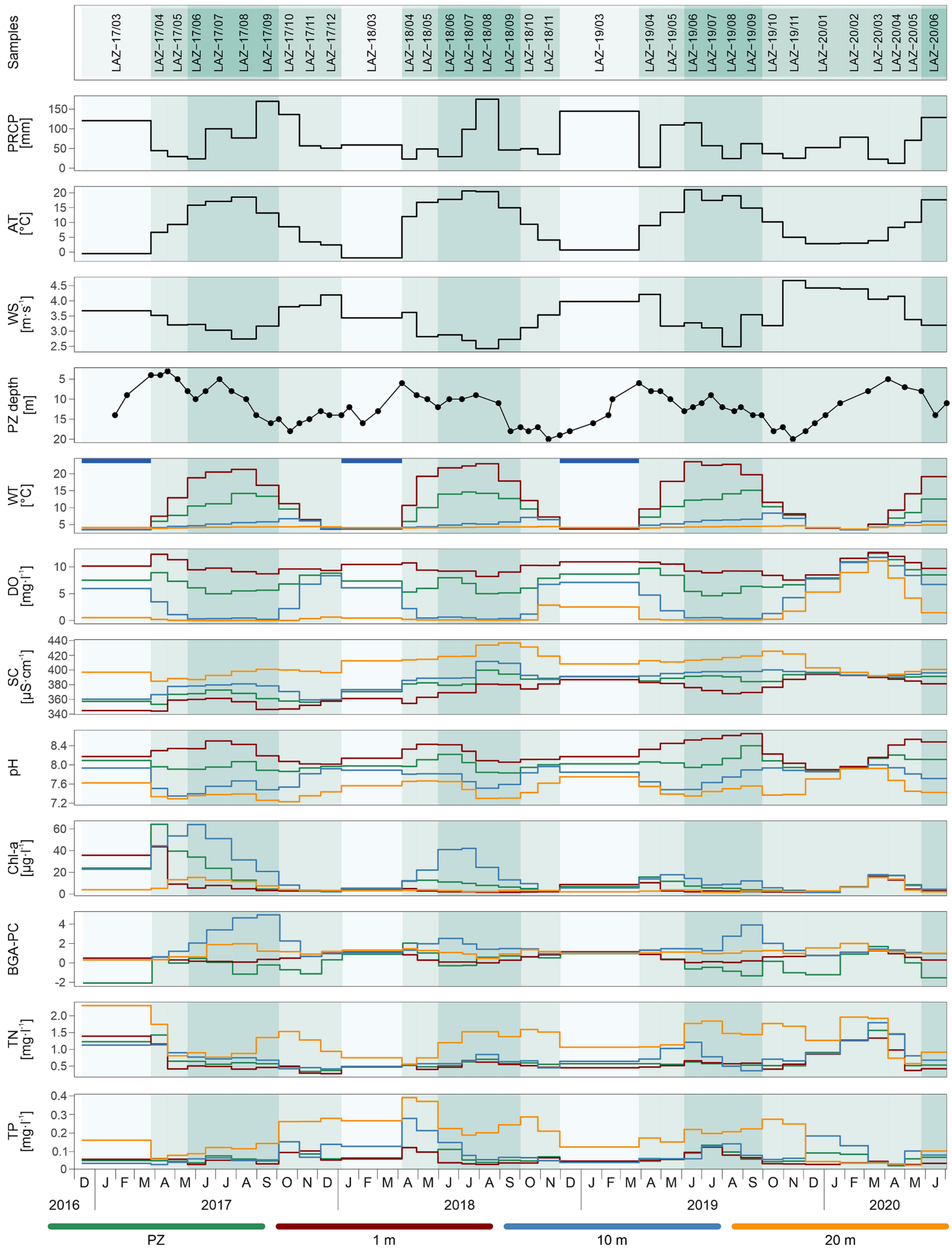

Fig. 2. Mean values of AT, WS, sum of PRCP, and mean values of environmental variables for different water depths and photic zone (PZ) in Lake Łazduny. Mean values and sum were calculated for each exposure time of the sediment trap. Blue bars indicate ice cover while background colors indicate characteristic phases: white – reverse stratification (wintertime with ice cover), light green – mixing (spring and fall isothermy), green – stratification (ice-free period except for mixing). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

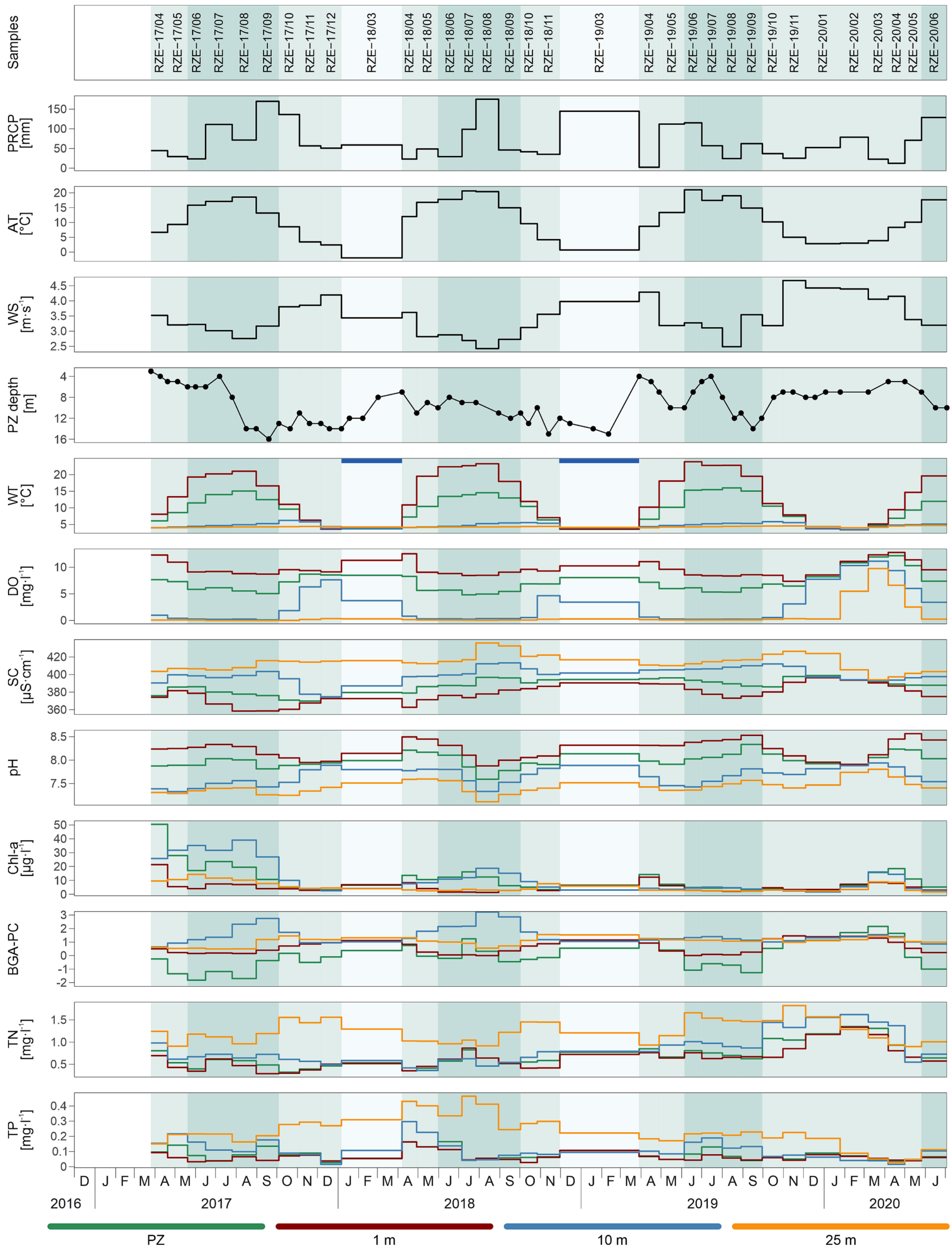

Fig. 3. Mean values of AT, WS, sum of PRCP, and nean values of environmental variables for different water depths and photic zone depth (PZ) in Lake Rzęśniki. Mean values and sum were calculated for each exposure time of the sediment trap. Colors of background as explained in Fig. 2.

stratification and noted anoxic conditions (DO < 1 mg l^{-1}) in large parts of the water columns. The values of TP and TN as well as SC had their highest values in near-bottom waters during that season. Soon after the ice-off, we observed incomplete mixing reaching the depths of 13–18 m in Łazduny, and 9–18 m in Rzęśniki. These seasons were generally characterized by increased values of WS and a quick increase of AT. We also observed elevated concentrations of TN, and TP in the surface waters. Chl-a concentrations were highest during the spring mixing with the exception of 2018, when we observed raised values in the summer. After the spring mixing period with the increase of AT, we noted the development of strong summer stratification and the highest values of pH. BGA-PC showed higher values during the whole summer in Rzęśniki, while in Łazduny showed higher values only in the late summer. A fall decrease of AT and increase of WS initiated the period of fall mixing starting around October each year. In Łazduny, a complete overturn with a well-oxygenated water column occurred in 2018 and in 2019, while in 2017 we recorded oxygen down to around 18 m. In Rzęśniki, fall mixing reached the depths of 13, 17 and 20 m. In both lakes during fall we noted increasing values of TN and TP with increasing depth.

The winter of 2020 was the warmest, with AT above 5 °C. During that period we observed complete mixing of the water column and the highest concentrations of DO from the observation period in the whole water column. It was also the longest period of mixing, starting in November 2019 and lasting to May 2020, with the highest concentrations of TN (Figs. 2, 3).

3.2. Diatoms

Over the observation period in both lakes we observed increased values of total diatom fluxes in spring and fall (Fig. 4). In Łazduny, single peaks were recorded in late spring, while in Rzęśniki two characteristic peaks were observed: first immediately after the ice-out and second in the early summer. In both lakes, a much smaller fall peak was generally present at the end of year, with the exception of fall 2017, when in Rzęśniki we recorded two peaks at the beginning and end of the season. In both lakes in spring and early summer 2017 we recorded the highest diatom fluxes from the entire observation period, up to five times higher than in other years. Also the highest fall fluxes values were recorded in 2017. The winter and summer periods, however, were characterized by rather low total fluxes in both lakes (Fig. 4).

In Lake Łazduny, of 176 diatom taxa, 31 reached a relative abundance at least 2 % in one sample (Figs. 5, 6). The most common species were: *Pantocsekiella comensis* (Grunow) K.T.Kiss & E.Ács (33.2 % of all counted valves), *Pantocsekiella ocellata* (Pantocsek) K.T.Kiss & Ács (14 %), *Lindavia radiosa* (Grunow) De Toni & Forti (7.9 %), *Staurosira construens* Ehrenberg (7 %), *Asterionella formosa* Hassall (6.2 %), *Stephanodiscus parvus* Stoermer & Håkansson (4.2 %), *Achnanthidium minutissimum* (Kützing) Czarnecki (3.7 %), *Cyclotella cretica* var. *cyclopuncta* (Håkansson & J.R.Carter) R.Schmidt (2.7 %), *Stephanodiscus neoastraea* Håkansson & Hickel (2.4 %), *Staurosirella pinnata* (Ehrenberg) D.M.Williams & Round (2.4 %), *Staurosirella lapponica* (Grunow) D.M.Williams & Round (2 %), *Pantocsekiella schumannii* (Grunow) K.T. Kiss & E.Ács (1 %) (Figs. 5, 6). These dominant taxa accounted for 86.7 % of all the valves counted.

In Lake Rzęśniki, 29 of 124 diatom taxa reached a relative abundance at least 2 % in one sample (Figs. 5, 6), and most abundant among them were: *Pantocsekiella comensis* (Grunow) K.T.Kiss & E.Ács (38 %), *Stephanodiscus parvus* Stoermer & Håkansson (10.7 %), *Staurosira construens* Ehrenberg (9.2 %), *Lindavia radiosa* (Grunow) De Toni & Forti (5.8 %), *Stephanodiscus neoastraea* Håkansson & Hickel (4.5 %), *Stephanodiscus minutulus* Hajós (4.2 %), *Pantocsekiella ocellata* (Pantocsek) K.T.Kiss & E.Ács (4.1 %), *Fragilaria crotonensis* Kitton (4 %), *Stephanodiscus hantzschi* Grunow (3.8 %), *Staurosirella pinnata* (Ehrenberg) D.M.Williams & Round (3.7 %), *Achnanthidium minutissimum* (Kützing) Czarnecki (1.5 %), *Stephanodiscus medius* Håkansson (0.3 %) (Figs. 5, 6). They accounted for 89.8 % of all the counted valves.

The general taxonomic composition was similar in both lakes. From 37 species with an abundance of 2 % or more, 23 occurred as the most

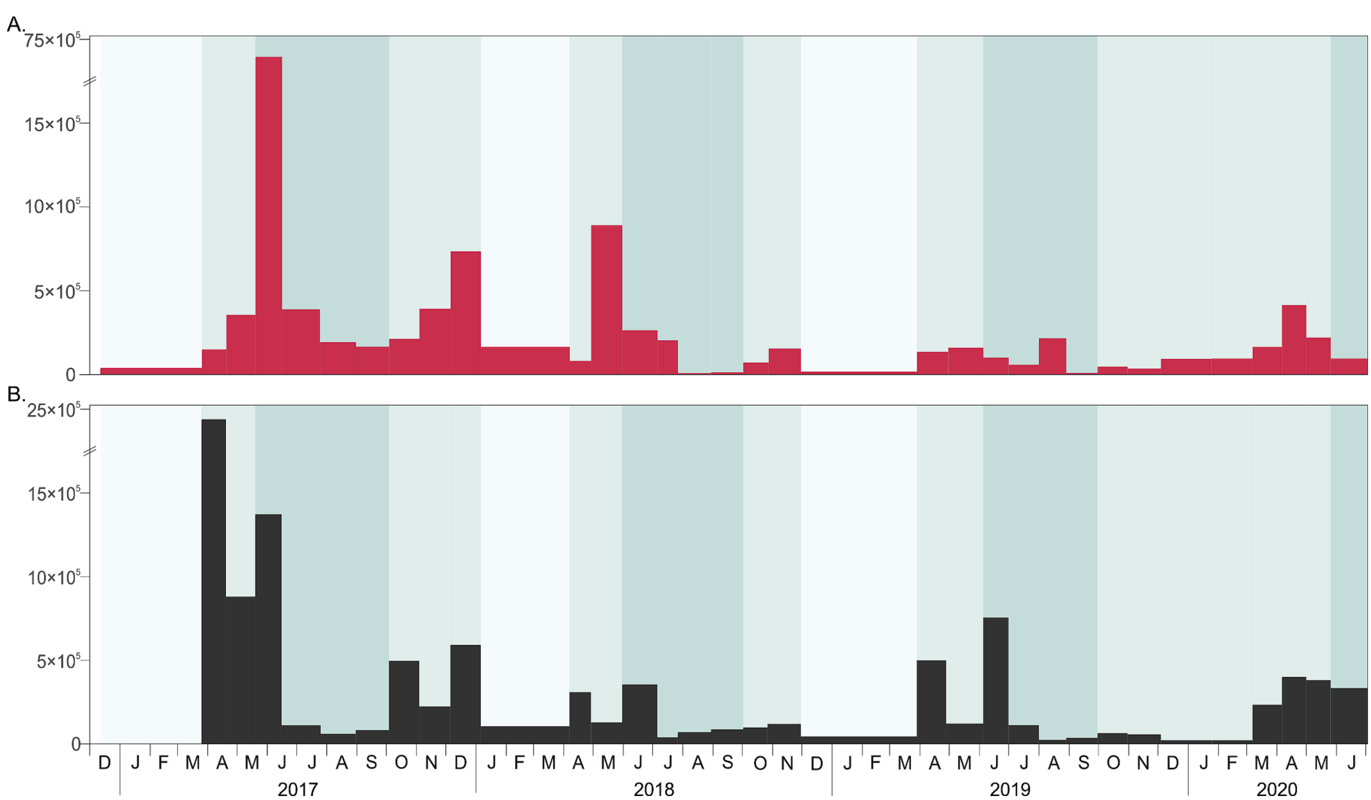

Fig. 4. Total fluxes of diatoms [valves g × cm^{-2} × day^{-1}] in lakes Łazduny (A) and Rzęśniki (B). The width of the bars represents the length of the exposure period of sediment traps. Colors of background as explained in Fig. 2.

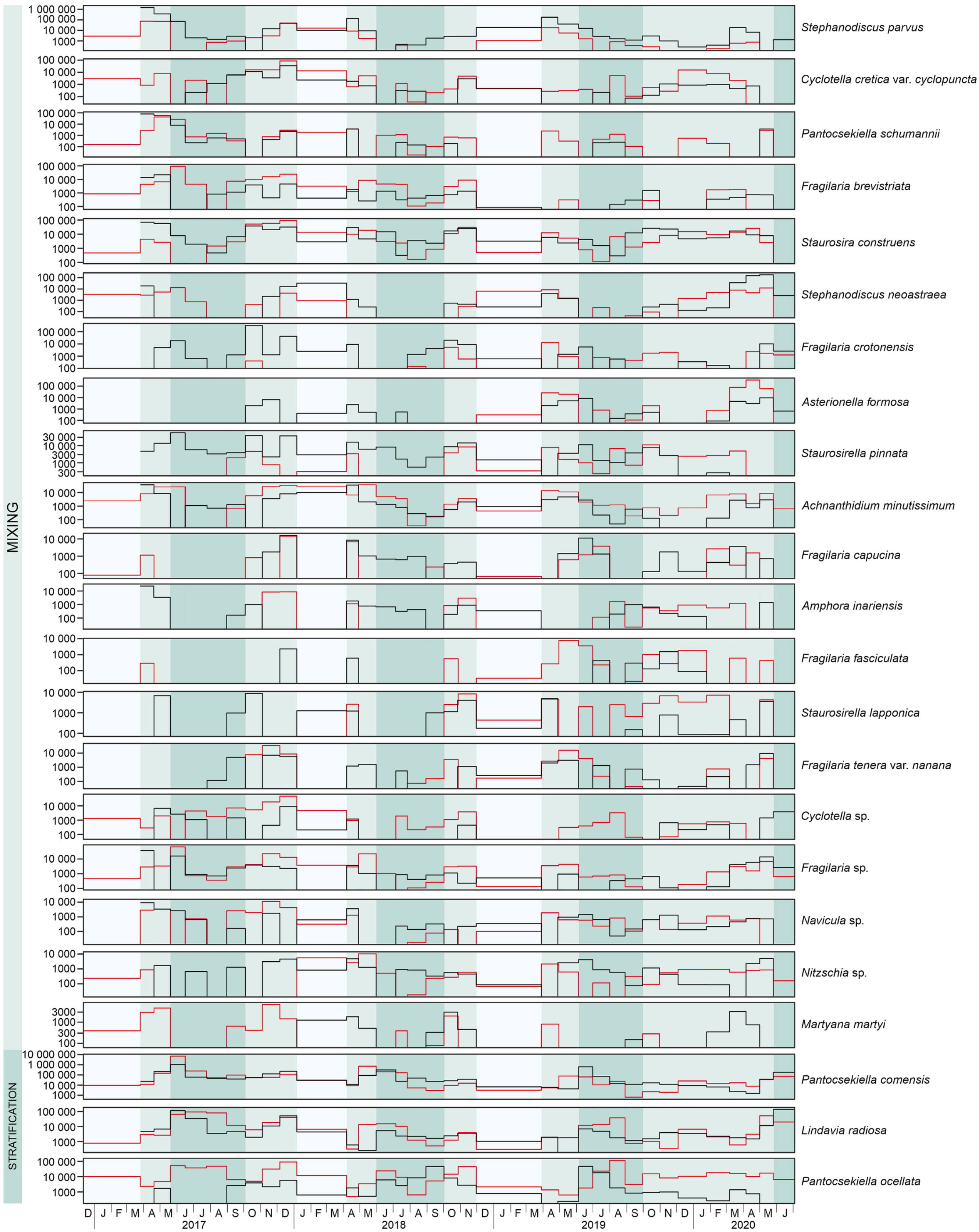

Fig. 5. Fluxes of diatom species [valves g × cm^{-2} × day^{-1}] with an abundance of 2 % or more in at least one sample present in Lake Łazduny (red line) and Lake Rzęśniki (black line). A logarithmic scale was used and taxa was divided into two groups: in mixing and stratification bloomers Colors of background as explained in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

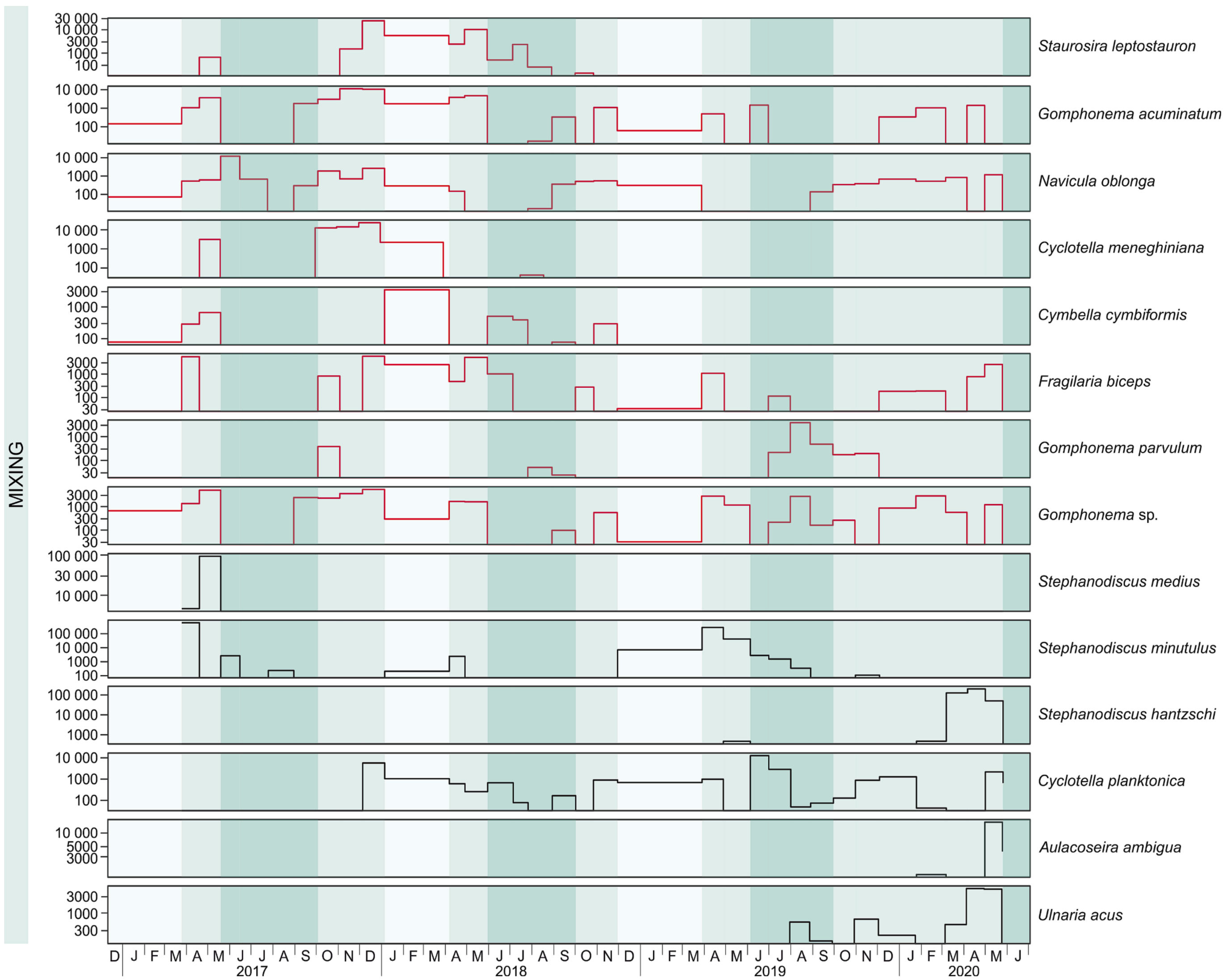

Fig. 6. Fluxes of diatom species [valves g × cm^{-2} × day^{-1}] with an abundance of 2 % or more in at least one sample present in Lake Łazduny (red line) or Lake Rzęśniki (black line). A logarithmic scale was used. Colors of background as explained in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

abundant in both lakes, while only 14 occurred in one of the lakes. The main differences referred to the seasonal succession of the specific diatom species and the values of their fluxes. We observed that the occurrences of some species were strongly connected to the pattern of total fluxes registered in both lakes, with fluxes maxima either in early spring or late spring and early summer (e.g. *Achnanthidium minutissimum)*. We recorded also species such as *Martyana martyi, Fragilaria fasciculata, Pantocsekiella oceallata, Staurosirella lapponica,* and *Staurosirella pinnata,* which were dominant in different parts of the observation period. *Staurosirella lapponica* and *Staurosirella pinnata* were dominant in Lake Rzęśnki in 2017, while in Łazduny the increase of their abundance was first recorded at the end of 2018. *Fragilaria fasciculata* showed the highest fluxes in 2019 in Łazduny, which decreased in 2020, while in Rzęśniki its values were low throughout the entire observation period. *Martyana martyi* were present in Łazduny from the beginning of the observation period, while the increase of their fluxes was observed at the turn of 2017/2018 in Rzęśniki. Other species such as *Cyclotella cretica* var. *cyclopuncta, Fragilaria tenera* var. *nanana, Lindavia radiosa* and *Pantocsekiella comensis*, had their highest fluxes during the same seasons, but differed in terms of their values in both lakes. Only four of 14 species pointed out as dominant in Lake Łazduny or Rzęśniki were present in only one lake, and these were *Cymbella cymbiformis, Aulacoseira ambigua, Stephanodiscus hantzschii* and *Stephanodiscus minutulus*.

3.3. Statistical relationships

The first and second DCA axis showed high eigenvalues ($\lambda = 0.74$, $\lambda = 0.68$) and separated samples of spring mixing periods from Lake Rzęśniki. These samples were characterized by high proportions of diatom species from the genus *Stephanodiscus*. DCA axes also separated samples from the spring mixing period of Lake Łazduny, which was characterized by high proportions of *Fragilaria* spp. (Fig. 7).

RDA conducted for the whole observation period explained 29.1 % of the variance in diatom data in both lakes. SC, AT, DO, TN, BGA.PC, and WS were indicated by forward selection as the most significant variables (*p-value* < 0.05 (Electronical Supplementary Materials Table S1.)). The analysis showed that all the samples can be divided into two categories related to the mixing and stratification periods (Fig. 8). In both lakes, samples from the mixing periods were correlated with higher values of wind speed, while samples from stratification were correlated with AT. To explain the interannual variability in diatom data we conducted an RDA analysis for each period separately.

The results of RDA conducted for mixing periods are presented in Fig. 9. Forward selection pointed to EC, AT, TN, BGA.PC and DO as the

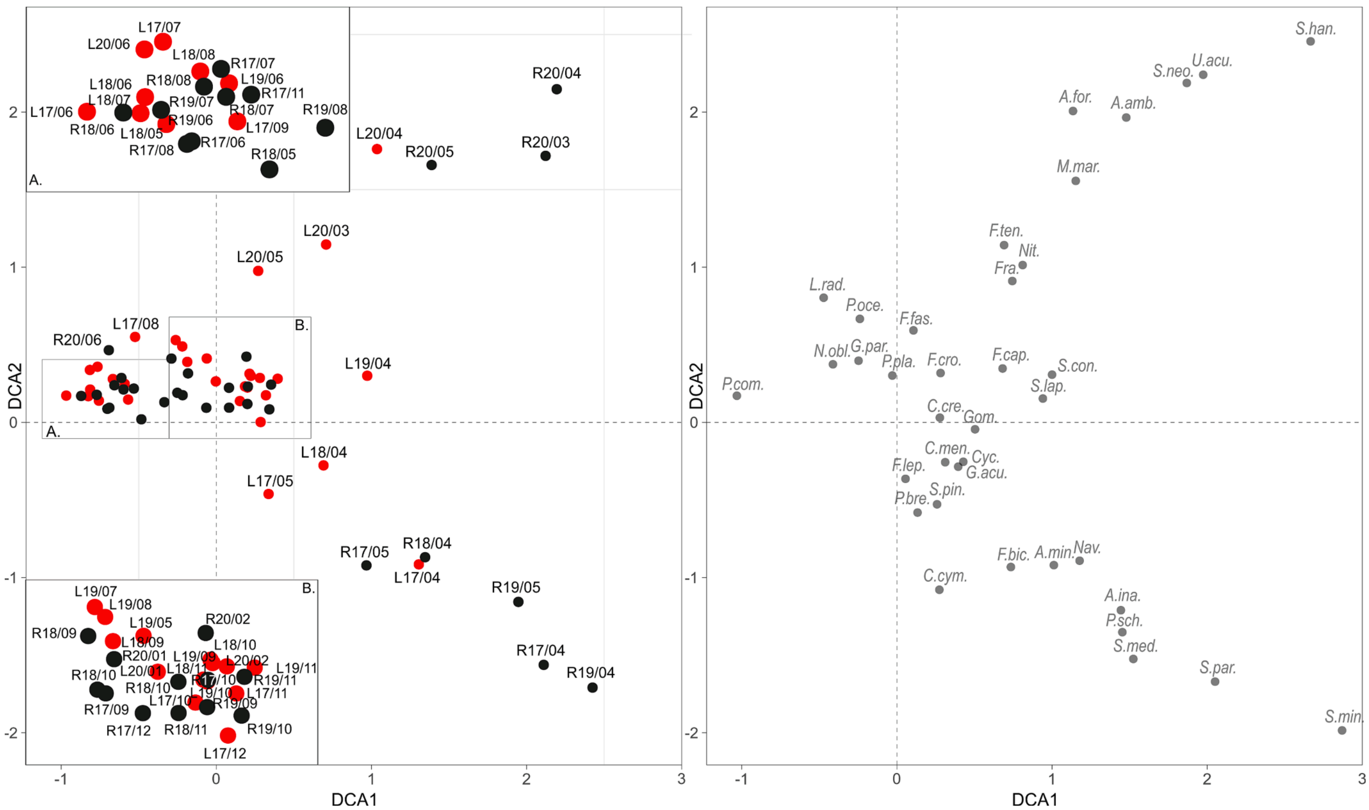

Fig. 7. DCA biplots of samples (right) and diatom species (left). Samples from lake Łazduny are presented in red, and from Rzęśniki in black. Diatom species abbreviations: *A.amb.–Aulacoseira ambigua, A.for.–Asterionella formosa, A.ina.–Amphora ineariensis, A.*min.*–Achnanthidium minutissimum, Cyc.–Cyclotella* sp., *C.cre.–Cyclotella cretica* var. *cyclopuncta, C.cym.–Cymbella cymbiformis, C.men.–Cyclotella meneghiniana, Fra.–Fragilaria* sp., *F.bic.–Fragilaria biceps, F.cap.–Fragilaria capucina, F.cro.–Fragilaria crotonensis, F.fas.–Fragilaria fasciculata, F.lep.–Staurosira leptostauron, F.ten.– Fragilaria tenera* var. *nanana, Gom.–Gomphonema, G.acu.–Gomphonema acuminatum, G.par.–Gomphonema parvulum, L.rad.–Lindavia radiosa, M.mar.–Martyana martyi, Nav.–Navicula, N.obl.–Navicula oblonga, Nit.–Nitzschia* sp., *P.com.–Pantocsekiella comensis, P.oce.–Pantocsekiella oceallata, P.sch.–Pantocsekiella schumanii, P.pla.–Pantocsekiella planktonica, P.bre–Pseudostaurosira brevistriata, S.con.–Staurosira construens, S.lap.–Staurosirella lapponica, S.pin.–Staurosirella pinnata, S.han.–Stephanodiscus hantzschi, S.med.–Stephanodiscus medius, S.neo.–Stephanodiscus neoastraea, S.par.–Stephanodiscus parvus, S.min.–Stephanodiscus minutulus, U.acu.–Ulnaria acus.* (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

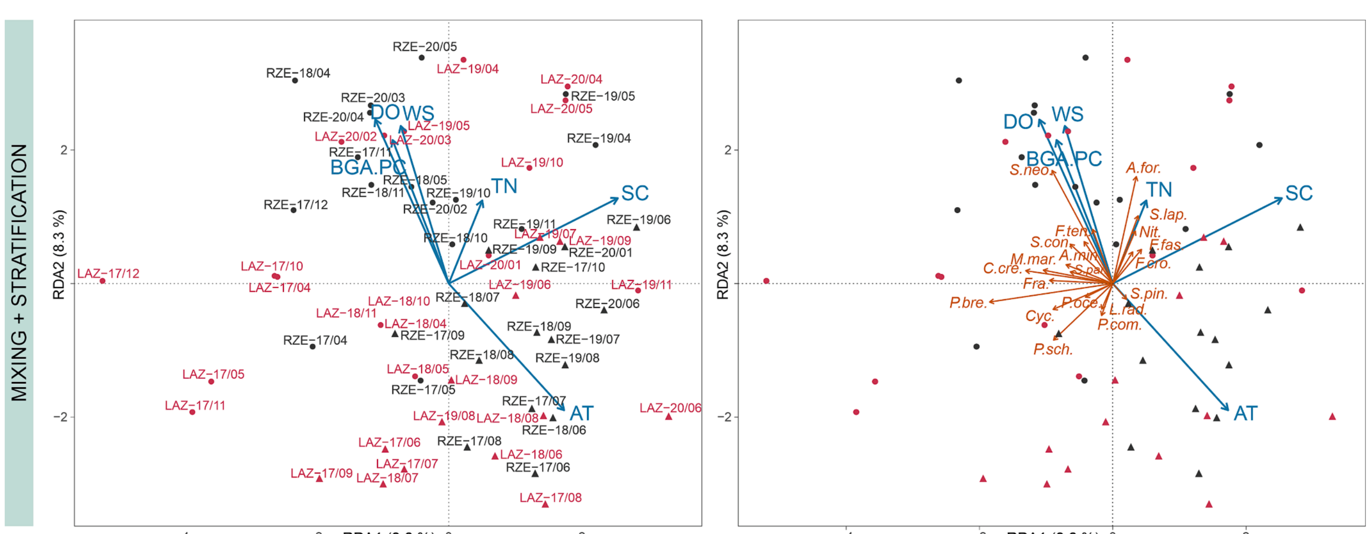

Fig. 8. RDA biplots of samples (left) and diatom species (right) with explanatory variables for the entire observation period (circles – samples from mixing period, triangles – samples from the stratification period). Diatom species abbreviations as explained in Fig. 7.

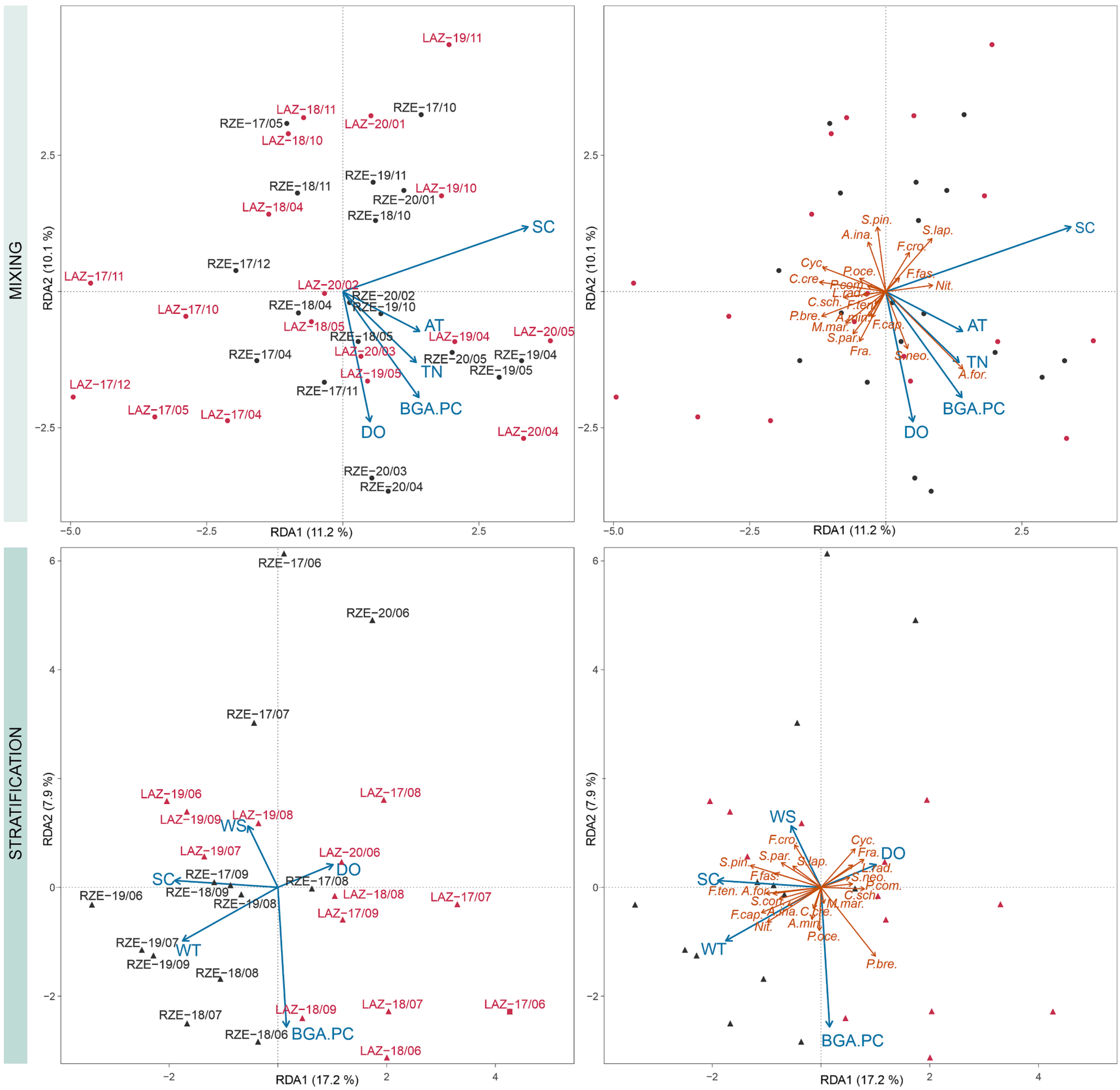

Fig. 9. RDA biplots of samples (left) and diatom species (right) with explanatory variables for the periods of mixing and stratification. Diatom species abbreviations as explained in Fig. 7.

most significant (Electronical Supplementary Materials Table S1.) variables, explaining in total 31.6 % of the variance in the diatom data, with SC explaining the highest variation – 8.8 %. RDA1 followed the gradient of EC, while RDA2 was more related to the gradient of DO. *Asterionella formosa* was strongly positively correlated with TN, in contrast to *Pantocsekiella comensis. Stephanodiscus neoastrea* showed a strong positive correlation to DO and a strong negative relationship to EC. Samples from fall 2019 and January 2020, were associated with the high EC, while those from the beginning of the observation period with low EC. Spring mixing samples from 2019 and 2020 were strongly correlated to high DO, AT and TN values (Fig. 9).

For the stratification period, RDA 1 and RDA2 explained 17.2 % and 7.9 % of the variance, respectively (Fig. 9). EC, wind speed, DO, BGA.PC and WT were indicated by forward selection as the most significant variables (Electronical Supplementary Materials Table S1.), which explained 37.2 % of the variance, with SC explaining the highest variation – 10.3 %. RDA 1 followed the gradient of SC and WT and was associated with *Pseudostaurosira brevistrata, Fragilaria capucina, Fragilaria tenera* var. *nanana* and *Staurosirella pinnata*. RDA 2 were strongly associated with BGA.PC, *Pseudostaurosira brevistrata* and *Pantocsekiella oceallata*. Species such as *Staurosira construens* and *Stephanodiscus neoastraea* were correlated with WT. *Pseudostaurosira brevistrata* and *Fragilaria fasciculata* showed a positive correlation with BGA.PC and SC, respectively. *Fragilaria capucina* was positively correlated with EC, while *Pantocsekiella schumanii* and *Lindavia radiosa* showed a negative correlation. Samples from Lake Łazduny showed a stronger correlation to BGA.PC, DO and wind speed, while those from Lake Rzęśnki showed a stronger correlation to SC and WT (Fig. 9).

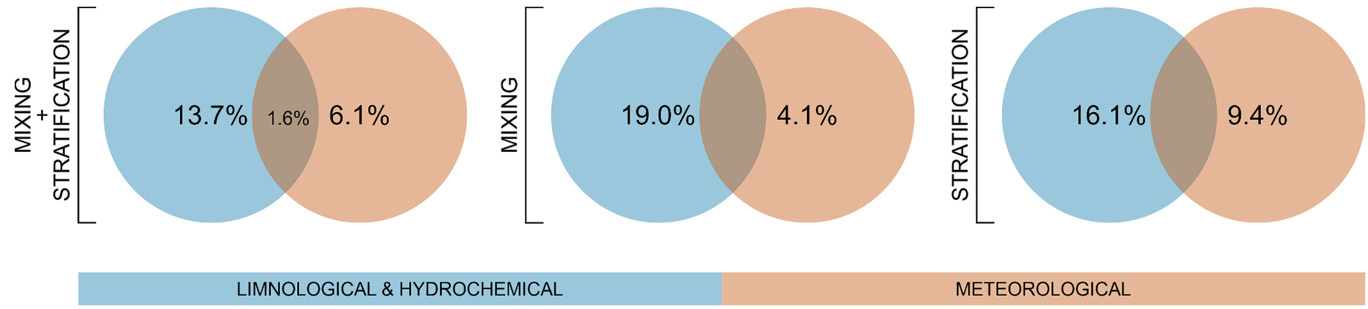

Fig. 10. Venn diagram representing the percentage of variance in diatom data explained by limnological and hydrochemical, and climate variables.

The variation partitioning analysis showed that the variation in diatom composition was better explained by combined limnological and hydrochemical variables than by meteorological variables. For the whole period they explained 13.7 %, for the mixing period 19 %, and for the stratification period 16.1 % of variance in diatom data. Meteorological variables were most important during the stratification period, and explained 9.4 % of variance in diatom data.

4. Discussion

4.1. Drivers of the seasonal and interannual variability of diatom fluxes and composition

A distinct seasonality of the diatom fluxes was observed in both lakes. Between 2017 and 2019 we recorded that an increase of diatom growth occurred in spring/early summer and during the fall (Fig. 4). In these years, the disappearance of the ice cover followed by spring mixing resulted in an improvement in nutrient and light supply to the surface waters, therefore creating favorable conditions for diatom blooms and generating distinctive peaks of diatom fluxes. The seasonal cycle of diatom blooms in the studied lakes is greatly dependent on the duration of the ice cover as it influences the intensity of the lakes' productivity in the spring. With longer ice-cover period the organic matter mineralization process takes longer, which reduces oxygen availability and increases the dissolved nutrient (phosphorus) pool in deep waters. On the other hand, when the ice-out occurs later, spring temperatures are high, which can result in rapid warming of lake water and development of summer stratification (Wetzel, 2001; Reynolds, 2006). In 2018, despite the longest duration of the ice cover, we recorded low total fluxes (Fig. 4.). It was a result of the most belated ice-out from the observation period combined with the warmest spring and rapid development of summer stratification. In 2017 and 2019, shorter ice cover periods and slower air temperature increases in spring resulted in longer mixing periods, with the one from 2017 much more intense and resulting in highest fluxes from the studied period (Fig. 4.). The observed diatom variability is consistent with the study of chrysophyte cysts in these lakes (Szczerba et al., 2021) as well as with similar studies of diatom assemblages seasonality conducted in Germany (Kirilova et al., 2008; Kienel et al., 2017), Finland (Korkonen et al., 2017) and Sweden (Maier et al., 2019). Recorded changes in the diatom fluxes are related to the mixing and stratification patterns that are in turn controlled by the meteorological conditions. Air temperature and windiness during the growing season are the major drivers of the diatom seasonality in lakes Łazduny and Rzęśniki (Fig. 9), thereby confirming the effect of meteorological conditions, observed also elsewhere (Winder and Sommer, 2012; Rühland et al., 2015).

The exceptional year of 2020 – without ice cover and with a prolonged mixing period lasting from fall 2019 to May 2020 – showed a different diatom response in comparison to the other years. Generally, the diatom fluxes did not show a distinct spring peak but rather a gradual increase starting from March 2020. This could have been caused by the gradual distribution of nutrients throughout the water column during a time of prolonged and intense mixing in contrast to the years with ice cover when nutrients are accumulated in the hypolimnion under the anoxic conditions and rapidly redistributed during the relatively short spring mixing. Lack of the quick increase of nutrients concentrations in spring resulted in a low peak of diatom fluxes in Łazduny and equally spread fluxes in spring and early summer in Rzęśniki. Other studies using sediment trap data also found that diatom fluxes can be dominated by seasonal peaks or be annually integrated (Kienel et al., 2017; Korkonen et al., 2017; Maier et al., 2019). Even though in 2020 the lakes were not covered with ice and nutrients were available, we observed a decrease of total fluxes in the winter months. In temperate lakes, light availability usually controls the timing of the spring diatom bloom and influences the plankton biomass. Winter seasons in Poland are characterized by the lowest mean relative sunshine duration (Bartoszek et al., 2020), ranging from seven to nine daylight hours only, which can result in a limitation of light for algae growth. Additionally, the intensity of lake mixing also affects the light conditions and would lead to higher turbidity and lower water transparency (the lowest Secchi disc values recorded during the mixing period were 1.35 m and 1.20 m in Łazduny and Rzęśniki, respectively – Figs. 2, 3) furthermore contributing to the low diatom fluxes during the winter of 2019/2020.

Statistical analysis revealed that the variability in diatom composition data was influenced by multiple factors. Variation partitioning showed that the majority of the variance in diatom data was explained by limnological and hydrochemical variables (Fig. 10). Of all the considered environmental variables, seven had a major influence on the diatom composition. RDA showed that SC alone explained the highest percentage of variation demonstrating its importance in structuring the diatom communities. Changes in conductivity may affect the physiological response and species composition of the lake biota, including diatoms (Bere and Tundisi, 2011). In the investigated lakes the present diatom species show a rather negative correlation to SC, confirming that present species are less tolerant to high SC. According to the review of Saros and Fritz (2000), salinity and anion composition, i.e., derivatives of conductivity, may influence the nutrient availability to primary producers. Increased conductivity allows more anion binding to phosphorus in the form of phosphate, which results in a limitation of phosphorus availability for phytoplankton growth. Since phosphorus is a critical nutrient for phytoplankton, such chemical interaction may prevent phytoplankton from accessing phosphorus and cause a decrease in its populations (Chouyyok et al., 2010). Nevertheless, we also recorded an increase in fluxes of a taxon characteristic of high specific conductance waters, namely *Fragilaria fasciculata* (Kociolek, 2011). Its increase was associated with increasing SC, further confirming the importance of conductivity in shaping the composition of species in the studied lakes.

Another important variable influencing the diatom assemblages in the investigated lakes during the mixing periods was TN, which is also a limiting factor in surface waters for algal growth (Reynolds, 2006). Except for the year 2020, increases in the diatom fluxes observed in Łazduny and Rzęśniki were correlated with the TN concentrations. We noted a strong relationship between *Asterionella formosa* and TN during the mixing period. This species is common in mesotrophic and eutrophic lakes globally and has been shown to be more abundant when phosphorus availability is very low and the supply of nitrogen is moderate to high (Saros et al., 2011). Such conditions faithfully describe the mixing periods in the investigated lakes when we observe the supply of TN. Both lakes also are generally characterized by low values of TP. Additionally, at the end of the observation period we noted elevated concentrations of TN, which were accompanied by the intensified growth of species from the genus *Stephanodiscus* such as *Stephanodiscus hantzschi,* which is widely regarded as an indicator species dominant in eutrophic lakes (Anderson, 1990; Hall and Smol, 1992). These elevated values of TN may be associated with the increase in EC, and are the result of the increase of ionic indicators of eutrophication, which limited the phytoplankton growth (lower diatom fluxes) and caused a shift in species composition, i.e., the appearance of eutrophic ones.

The concentration of DO in aquatic systems influences among others the nutrient biogeochemistry and biodiversity, as DO is essential to the respiratory metabolism of most aquatic organisms. Loss of deep-water DO promotes the release of accumulated nutrients from sediments into the water (Wetzel, 2001; Jane et al., 2021). Diatoms are very susceptible indicators for changes in the oxygen balance. Similarly to air temperature, DO can act as a proxy for more complex changes occurring in the water column, such as spring mixing and connected changes in nutrient availability. During the mixing period, species such as *Stephanodiscus neoastraea* and *Asterionella formosa* showed a positive correlation to DO, with species occurring in nutrient favorable conditions and the mixed water column (Saros et al., 2011; Wolf et al., 2011). Generally periods of summer stratification are characterized by lower values of DO and represent a time of water column stability. During this time we observed a negative correlation of DO with species from the genus *Fragilaria,* for which turbulent mixing creates a more suitable environment (Moreno-Ostos et al., 2009).

Air temperature and water temperature were other important variables influencing the diatom assemblages. Since they are strongly correlated (Livingstone and Lotter, 1998; Piccolroaz et al., 2015), the effect of air temperature is most likely mediated through changes in the water temperature. This is an important variable influencing seasonal changes in lake ecosystems affecting physiological factors, such as the growth rate of organisms. Each species additionally has its temperature optima and tolerances which will determine the occurrence of specific species (Battarbee et al., 2001). During the spring season, the pace of the temperature increase is of high importance, as it determines the length of the mixing period and its intensity, which in turn control the nutrient supplies to the photic zone. High temperatures during summer cause the development of thermal stratification and associated changes in the light and nutrient availability, which favors species from *Cyclotella* genus (Winder et al., 2009; Rühland et al., 2015). Our study shows that the dominant species in the investigated lakes, *Pantocsekiella comensis*, has its highest fluxes in the late spring or early summer when we observed the onset of summer stratification. Therefore, we believe that the influence of temperature on diatom assemblages in the investigated lakes is actually the surrogate for complex changes in the lakes' physical structure. Previous studies of the occurrence of *Pantocsekiella comensis* indicate that this taxa can be observed in a variety of light and mixing regimes. This include a stratification period as found in the Great Lakes (Stoermer et al., 1996; Bramburger and Reavie, 2016) in late winter, either under the ice or under ice-free winter conditions (Thackeray et al., 2008; Kienel et al., 2017). The study by Laird et al., 2021, conducted in two Canadian lakes, Seton and Anderson, showed the presence of various *Pantocsekiella comensis* morphotypes throughout the observation period in Anderson Lake, and during the fall in Seton Lake, and pointed out that increase in *Pantocsekiella comensis* can be linked to the ice-free conditions enabling this taxon to persist throughout the year. Additionally, the sediment trap study from the Swiss Alps showed that, *Pantocsekiella comensis* growth was recorded primarily during the ice-free period in summer (Lotter and Bigler, 2000). Similarly, the study from Lake Holzmaar in Germany, showed that *Pantocsekiella comensis* was a dominant taxa and noted its increase in April, with the blooms in summer samples (Raubitschek et al., 1999). All of these findings suggest that multiple site-specific drivers may be relevant for *Pantocsekiella comensis* growth, yet confirm the influence of temperature-induced changes in the physical structure of lakes on its deposition in sediment traps.

Wind speed proved to be an important variable during the stratification period. Wind can introduce major changes into the water column that could cause variations of thermocline if sufficiently strong. Strong wind events may induce internal loading if nutrients (particularly phosphorus) enter into the epilimnion and consequently enhance primary production (Jennings et al., 2012). Also, wind-induced turbulence influences the phytoplankton distribution, directly changing the community composition (Yang et al., 2016). Additionally, wind influence on diatom assemblages is associated with the influence of BGA.PC (cyanobacteria). During the stratification period, reduced vertical mixing will possibly shift the competitive advantage from buoyant cyanobacteria to the diatom that need higher turbulence. Cyanobacteria have a higher growth rate at higher temperatures (above 23 °C) and many have the ability to form intracellular gas vesicles, allowing them to exploit the habitat under the intensified stratification and outcompete other taxa (Winder and Sommer, 2012). Therefore, the summer decrease of wind speed values and, in turn, the decreased rates of turbulent mixing cause the general decrease in diatom fluxes and the appearance of more buoyant ones with an increase in BGA.PC. Higher turbulent mixing during the stratification period gives an advantage to fragilarioid species, while a more stable water column promotes species from *Cyclotella* genus (e.g., *Pantocsekiella comenisis/oceallata, Lindavia radiosa)* and cyanobacteria. This stays in agreement with our findings, as the summer diatom assemblages were dominated by centric diatoms.

4.2. Influence of local conditions on diatom fluxes and taxonomy

Lakes Łazduny and Rzęśniki are located in the same catchment at a distance of only about 2 km. The geological setting, lake basins' morphology, and morphometric parameters are also very similar. Minor differences between the lakes are related to the catchment topography and land use, their hydrological type and trophic status. The lakes share many similarities in the diversity of their diatom assemblages as well as in their seasonal variability. However, some significant differences in diatom composition and succession were recorded.

The general seasonal pattern points to two increases of diatom fluxes each year. We also observed that the fluxes reached rather similar values in both lakes. However, in 2017 the early summer peak in Łazduny exceeded the one from Rzęśniki by more than threefold. The high diatom fluxes in 2017 are connected to the increased supply of nutrients to the water bodies from the hypolimnion. We attribute the differences between the lakes to the intensity of the mixing, which in Łazduny reached the lake bottom. This deep mixing period could have resulted in a greater nutrient transport to the surface layer, therefore promoting the more intense diatom bloom.

The exact timing of diatom deposition peaks is also different in the investigated lakes. The spring maximum of diatom deposition in Łazduny is cumulated in one late spring/early summer peak, while in Rzęśniki we observed the occurrence of double peaks – right after the ice cover break-up and in early summer (Fig. 4). Our observations indicate that in Rzęśniki the diatom bloom development could have started prior to the ice break-up. This is confirmed by the increase in Chl-a concentrations under the ice, which we measured in 2019. Careful study of the location of the investigated lakes in the catchment and their sheltering showed that in Rzęśniki there is a greater possibility for the development of an under-the-ice diatom bloom. During most of the winter, the ice cover on the lakes is covered by snow, which prevents light penetrating the water column. However, the specific location of Lake Rzęśniki, i.e., and its much better exposure to sunlight due to the lower slopes from the east and south (Fig. 1), could result in a faster snow melt on the ice cover. In addition, Rzęśniki is supplied in nutrients by the incoming stream. The increased light availability and nutrient supply from the incoming stream could have promoted the early onset of the spring phytoplankton bloom under the ice and before the lake overturn. Additionally, careful study of the species dominating in the peaks showed that in the first peak benthic species increased, while the second one was created mainly by planktonic *Pantocsekiella comensis,* which is the dominant species occurring during the entire observation period. This cyclotelloid taxa prefers warmer temperatures and more stable conditions and in several studies is considered an indicator of well-stratified lake water in summer (Hausmann and Lotter, 2001; Rühland et al., 2008; Winder et al., 2009; Rühland et al., 2015; Saros and Anderson, 2015; Reavie et al., 2017). Moreover, in many temperate lakes planktonic diatom growth is initiated and usually completed before the lake-water temperature reaches its seasonal maximum (Anderson, 2000), and therefore the peaks of this dominant species are present in the early summer. For benthic diatom growing in the littoral zone with different nutrient sources and light climates, seasonal growth may reflect the higher temperatures associated with the shallower water of the littoral zone (Anderson, 2000). In Rzęśniki, the shallowest area of the lake with a depth of 5 m or less accounts for around 38 % of the lake's surface area, while in Łazduny it accounts for around 27 %. The presence of a greater shallow water zone in Rzęśniki, and the influence of the lake's exposure to external factors (sunlight, wind activity, input of nutrients from the incoming stream) resulted in creating favorable conditions for benthic diatom development in the early spring. Their presence in the sediment traps suggests that horizontal transport has occurred and sediment focusing may have influenced the observed seasonal dynamics. This indicates low water column stability and is part of diatom assemblages' response to the physical conditions in the lake. The presence of benthic diatoms with the early development of the diatom bloom before the ice-break contributed to the development of the first spring peak.

Also in the fall of 2017 we recorded a double peak of diatom fluxes in Rzęśniki – first at the beginning and second at the end of season. Monitoring of the hydrochemical properties of the water column recorded elevated values of TP in Rzęśniki at the end of the summer of 2017, which could have been delivered to the lake by the inflowing stream (Fig. 3). This supply of phosphorus triggered the development of the diatom deposition peak after the break-up of the stratification.

Along with the differences between the peaks of total fluxes, we observed differences in diatom composition that occurred mainly during periods of spring water column mixing. Samples from Łazduny and Rzęśniki differed in terms of presence of species from the genus *Stephanodiscus* and *Fragilaria* (Fig. 7.). These differences in diatom assemblages are connected to the different trophic state of the studied lakes. Due to more eutrophic character of Rzęśniki *Stephanodiscus* taxa are more abundant in lake Rzęśniki than in lake Łazduny. Additionally, we observed differences in the occurrence of benthic diatom species, e.g., *Achnanthidium minutissimum, Staurosirella pinnata,* and *Martyana martyi*. The benthic diatoms are common in shallower water where light penetration is able to reach the sediment–water interface (Stone and Fritz, 2004). Changes in the penetration of photosynthetically active radiation, ultraviolet radiation and nutrient supply, which are independent of lake depth, influence the aquatic macrophytes that are one of the habitats of benthic diatoms in lakes. Also, the water clarity, which is affected by different internal and external factors such as food web interactions, changes in nutrient supply, variations in turbulence, and changes in the dissolved oxygen concentration, influences the habitat available for benthic diatom growth (Dearing, 1997; Stone and Fritz, 2004; Pla-Rabés and Catalan, 2018). Łazduny and Rzęśniki differ slightly in terms of the extent of their littoral zone, water-level fluctuations and insolation. They also may differ in macrophyte composition and other factors influencing the benthic diatom. Investigations of these drivers would be needed to precisely define the main factor behind these differences. Nevertheless, here the differences in benthic communities between the lakes indicate the local environmental effect on the species' growth.

Other differences between the investigated lakes were connected to the timing of the occurrence of some of the planktonic species. Many studies have noted that there are certain diatom taxa which consistently stand out as important to the overall algal dynamics. At the end of the observation period we recorded an increase of *Aulacoseira ambigua* fluxes and a decrease of small-celled cyclotelloid species in Rzęśniki. Previous studies show that the *Aulacoseira ambigua* species was recorded during strong water mixing (Houk and Poulícková, 2003). Also, it has been shown that in Elk Lake, the increase in *Aulacoseira* spp. was a result of increased mixing of the water column connected to locally increased windiness and seasonally strong late-summer thunderstorms (Bradbury et al., 1993). The occurrence of *Aulacoseira ambigua* therefore may be connected to a prolonged water column mixing period recorded in the investigated lakes. Additionally, this species prefers nutrient-rich environments (Houk and Poulícková, 2003; Taylor et al., 2007). The supply of nutrients from the hypolimnion during the mixing phase and from the incoming stream created favorable conditions for its development in Rzęśniki. In the same period, we observed a decrease of the taxa from *Cyclotella* genus, which are characteristic in more thermally stable periods (Rühland et al., 2015). *Staurosirella lapponica, Staurosirella pinnata* and *Fragilaria fasciculata* are the common species showing higher abundances with increasing conductance. However, as their occurrence in our lakes does not show any clear pattern related to SC over the observation period, and is similar between the lakes, SC is most likely not the strongest environmental variable controlling their distribution We also recorded that the presence of *Martyana martyi* differed between the lakes. These species were present in Łazduny from the beginning of the observation period, while in Rzęśniki their occurrence was noted at the beginning of 2018. Additionally, their fluxes decreased over the time in Łazduny, and increased in Rzęśniki. Occurrence of these species was associated with the mixing periods, but no specific pattern between its occurrence and changes, for example in intensity of mixing, was recorded.

5. Conclusions

The study of the limnological and hydrochemical properties of lakes Łazduny and Rzęśniki as well as the dynamics of the diatom assemblages allowed us to investigate the diatom response to changes in the environmental conditions during the observation period of three and one-half years. Our study revealed that the distinctive seasonal patterns in diatom total fluxes depends largely on the changes in the lakes' physical structure induced by changes in meteorological conditions. As it has been shown, the ice cover and mixing intensity, which control the availability of nutrients and light, are the major drivers of the diatom seasonality, therefore confirming the indirect influence of changes in meteorological conditions. The response of diatoms to any changes in the water column proved to be very complex and none of the identified taxa responded solely to any of the variables. Nevertheless, our study showed the relationship between diatom assemblages and air temperature and wind speed. The first variable proved to be more important during the mixing periods, as the intensity and length of the overturn depends on the rate of air temperature increase. Wind speed had its major influence during the stratification periods due to the influence of increased windiness on the deepening of the epilimnion and therefore on its volume. We believe these variables represented more complex changes in the water column, therefore further confirming the indirect influence of the meteorological conditions. Site-specific differences between the investigated lakes created divergences in the taxonomic composition and total fluxes of the diatoms. Our study showed that depending on the availability of light, the onset of planktonic diatom blooms may occur when the lake is still covered with ice. Possible differences in the littoral zone and horizontal transport could also have contributed to observed dissimilarities.

Based on our observations, rather than focusing on the specific taxon response to any variable, more informative are the observations of species' succession and changes in the diatom total fluxes. Even small differences in the nutrient supply, mixing intensity, ionic composition or any other variable may introduce differences on the species level and cover the direct influence of meteorological variables. Nevertheless, the general patterns of diatom fluxes, and the succession of specific species, may give invaluable insight into which climate-related factors play an important role in shaping diatom assemblages' variability.

CRediT authorship contribution statement

Agnieszka Szczerba: Conceptualization, Investigation, Writing – original draft, Visualization. **Monika Rzodkiewicz:** Writing – review & editing. **Wojciech Tylmann:** Conceptualization, Investigation, Writing – review & editing, Funding acquisition.

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.

Data availability

Data will be made available on request.

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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.2023.110028.

References

Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W., Livingstone, D.M., Sommaruga, R., Straile, D., Van Donk, E., Weyhenmeyer, G.A., Winder, M., 2009. Lakes as sentinels of climate change. Limnology and Oceanography 54, 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283.

Anderson, N.J., 1990. Variability of diatom concentrations and accumulation rates in sediments of a small lake basin. Limnology and Oceanography 35, 497–508. https://doi.org/10.4319/lo.1990.35.2.0497.

Anderson, N.J., 2000. Miniview: Diatoms, temperature and climatic change. Eur. J. Phycol. 35, 307–314. https://doi.org/10.1080/09670260010001735911.

Bartoszek, K., Matuszko, D., Soroka, J., 2020. Relationships between cloudiness, aerosol optical thickness, and sunshine duration in Poland. Atmospheric Research 245, 105097. https://doi.org/10.1016/j.atmosres.2020.105097.

Battarbee, R.W., 2000. Palaeolimnological approaches to climate change, with special regard to the biological record. Quaternary Science Reviews 19, 107–124. https://doi.org/10.1016/S0277-3791(99)00057-8.

Battarbee, R.W., Jones, V.J., Flower, R.J., Cameron, N.G., Bennion, H., Carvalho, L., Juggins, S., 2001. Diatoms. Tracking environmental change using lake sediments. Vol 3: Terrestrial, algal and siliceous indicators. 3, 155–202. https://doi.org/10.1007/0-306-47668-1.

Battarbee, R.W., Kneen, M.J., 1982. The use of electronically counted microspheres in absolute diatom analysis. Limnol. Oceanogr. 27, 184–188. https://doi.org/10.4319/lo.1982.27.1.0184.

Bennion, H., Kelly, M.G., Juggins, S., Yallop, M.L., Burgess, A., Jamieson, J., Krokowski, J., 2014. Assessment of ecological status in UK lakes using benthic diatoms. Freshwater Science 33, 639–654. https://doi.org/10.1086/675447.

Bere, T., Tundisi, J.G., 2011. Influence of ionic strength and conductivity on benthic diatom communities in a tropical river (Monjolinho), São Carlos-SP, Brazil. Hydrobiologia 661, 261–276. https://doi.org/10.1007/s10750-010-0532-0.

Bigler, C., Hall, R.I., 2003. Diatoms as quantitative indicators of July temperature: a validation attempt at century-scale with meteorological data from northern Sweden. Palaeogeography, Palaeoclimatology, Palaeoecology 189, 147–160. https://doi.org/10.1016/S0031-0182(02)00638-7.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C., Braak, C.J.F.T., 1990. Diatom and pH reconstruction. Philosophical Transactions of the Royal Society of London 327, 263–278. https://doi.org/10.1017/CBO9781107415324.004.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the Spatial Component of Ecological Variation. Ecology 73, 1045–1055. https://doi.org/10.2307/1940179.

Bradbury, J.P., Dean, W.E., Anderson, R.Y., 1993. Holocene climatic and limnologic history of the north-central United States as recorded in the varved sediments of Elk Lake, Minnesota: A synthesis, in: Bradbury, J. Piatt, Dean, W.E. (Eds.), Elk Lake, Minnesota: Evidence for Rapid Climate Change in the North-Central United States. Geological Society of America. https://doi.org/10.1130/SPE276-p309.

Bramburger, A.J., Reavie, E.D., 2016. A comparison of phytoplankton communities of the deep chlorophyll layers and epilimnia of the Laurentian Great Lakes. Journal of Great Lakes Research 42, 1016–1025. https://doi.org/10.1016/j.jglr.2016.07.004.

Cantonati, M., Scola, S., Angeli, N., Guella, G., Frassanito, R., 2009. Environmental controls of epilithic diatom depth-distribution in an oligotrophic lake characterized by marked water-level fluctuations. European Journal of Phycology 44, 15–29. https://doi.org/10.1080/09670260802079335.

Chouyyok, W., Wiacek, R.J., Pattamakomsan, K., Sangvanich, T., Grudzien, R.M., Fryxell, G.E., Yantasee, W., 2010. Phosphate Removal by Anion Binding on Functionalized Nanoporous Sorbents. Environmental Science & Technology 44, 3073–3078. https://doi.org/10.1021/es100787m.

Dearing, J.A., 1997. Sedimentary indicators of lake-level changes in the humid temperate zone: a critical review. Journal of Paleolimnology 18, 1–14. https://doi.org/10.1023/A:1007916210820.

Dixit, S.S., Smol, J.P., Kingston, J.C., Charles, D.F., 1992. Diatoms: Powerful Indicators of Environmental Change. Environmental Science and Technology 26, 22–33. https://doi.org/10.1021/es00025a002.

Fritz, S.C., 2008. Deciphering climatic history from lake sediments. Journal of Paleolimnology 39, 5–16. https://doi.org/10.1007/s10933-007-9134-x.

Gasse, F., 2002. Diatom-inferred salinity and carbonate oxygen isotopes in Holocene waterbodies of the western Sahara and Sahel (Africa). Quaternary Science Reviews, Interactions between arid and humid records of Quaternary change in drylands (IGCP 413) 21, 737–767. https://doi.org/10.1016/S0277-3791(01)00125-1.

Gautam, S., Pandey, L.K., Vinayak, V., Arya, A., 2017. Morphological and physiological alterations in the diatom Gomphonema pseudoaugur due to heavy metal stress. Ecological Indicators 72, 67–76. https://doi.org/10.1016/j.ecolind.2016.08.002.

Guiry, M.D., Guiry, G.M., 2022. AlgaeBase. World-wide electronic publication, National University of Ireland.

Hall, R.I., Smol, J.P., 1992. A weighted—averaging regression and calibration model for inferring total phosphorus concentration from diatoms in British Columbia (Canada) lakes. Freshwater Biology 27, 417–434. https://doi.org/10.1111/j.1365-2427.1992.tb00551.x.

Hausmann, S., Lotter, A.F., 2001. Morphological variation within the diatom taxon Cyclotella comensis and its importance for quantitative temperature reconstructions. Freshwater Biology 46, 1323–1333. https://doi.org/10.1046/j.1365-2427.2001.00752.x.

Hausmann, S., Pienitz, R., 2007. Seasonal climate inferences from high-resolution modern diatom data along a climate gradient: a case study. Journal of Paleolimnology 38, 73–96. https://doi.org/10.1007/s10933-006-9061-2.

Houk, V., Poulícková, A., 2003. Atlas of freshwater centric diatoms with a brief key and descriptions: part 1. Palacký University Olomouc, Faculty of Science, Olomouc, Melosiraceae, Orthoseiraceae, Paraliaceae and Aulacoseiraceae, Czech phycology supplement.

Institute of Meteorology and Water Management - National Research Institute, 2022. https://danepubliczne.imgw.pl/ [WWW Document] (accessed 10.06.22).

Interlandi, S.J., Kilham, S.S., Theriot, E.C., 1999. Responses of phytoplankton to varied resource availability in large lakes of the Greater Yellowstone Ecosystem. Limnology and Oceanography 44, 668–682. https://doi.org/10.4319/lo.1999.44.3.0668.

Jane, S.F., Hansen, G.J.A., Kraemer, B.M., Leavitt, P.R., Mincer, J.L., North, R.L., Pilla, R.M., Stetler, J.T., Williamson, C.E., Woolway, R.I., Arvola, L., Chandra, S., DeGasperi, C.L., Diemer, L., Dunalska, J., Erina, O., Flaim, G., Grossart, H.-P., Hambright, K.D., Hein, C., Hejzlar, J., Janus, L.L., Jenny, J.-P., Jones, J.R., Knoll, L.B., Leoni, B., Mackay, E., Matsuzaki, S.-I.-S., McBride, C., Müller-Navarra, D.C., Paterson, A.M., Pierson, D., Rogora, M., Rusak, J.A., Sadro, S., Saulnier-Talbot, E., Schmid, M., Sommaruga, R., Thiery, W., Verburg, P., Weathers, K.C., Weyhenmeyer, G.A., Yokota, K., Rose, K.C., 2021. Widespread deoxygenation of temperate lakes. Nature 594, 66–70. https://doi.org/10.1038/s41586-021-03550-y.

Jennings, E., Jones, S., Arvola, L., Staehr, P.A., Gaiser, E., Jones, I.D., Weathers, K.C., Weyhenmeyer, G.A., Chiu, C.-Y., De Eyto, E., 2012. Effects of weather-related episodic events in lakes: an analysis based on high-frequency data. Freshwater Biology 57, 589–601. https://doi.org/10.1111/j.1365-2427.2011.02729.x.

Juggins, S., 2013. Quantitative reconstructions in palaeolimnology: New paradigm or sick science? Quaternary Science Reviews 64, 20–32. https://doi.org/10.1016/j.quascirev.2012.12.014.

Kienel, U., Kirillin, G., Brademann, B., Plessen, B., Lampe, R., Brauer, A., 2017. Effects of spring warming and mixing duration on diatom deposition in deep Tiefer See, NE Germany. Journal of Paleolimnology 57, 37–49. https://doi.org/10.1007/s10933-016-9925-z.

Kirilova, E.P., Bluszcz, P., Heiri, O., Cremer, H., Ohlendorf, C., Lotter, A.F., Zolitschka, B., 2008. Seasonal and interannual dynamics of diatom assemblages in Sacrower See (NE Germany): a sediment trap study. Hydrobiologia 614, 159–170. https://doi.org/10.1007/s10750-008-9504-z.

Kociolek, P., 2011. Tabularia fasciculata. In Diatoms of North America. [WWW Document]. URL https://diatoms.org/species/tabularia_fasciculata.

Korkonen, S.T., Ojala, A.E.K., Kosonen, E., Weckström, J., 2017. Seasonality of chrysophyte cyst and diatom assemblages in varved Lake Nautajärvi – implications for palaeolimnological studies. J. Limnol. 76 https://doi.org/10.4081/jlimnol.2017.1473.
Köster, D., Pienitz, R., 2006. Seasonal diatom variability and paleolimnological inferences - a case study. Journal of Paleolimnology 35, 395–416. https://doi.org/10.1007/s10933-005-1334-7.
Krammer, K., Lange-Bertalot, H., 1986. Bacillariophyceae 1. Teil: Naviculaceae, in: Ettl, H., Gerlof, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora von Mitteleuropa Band 2/1. Jena, p. 876.
Krammer, K., Lange-Bertalot, H., 1991a. Bacillariophyceae 3. Teil: Centrales, Fragilariaceae, Eunotiaceae, in: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora von Mitteleuropa Band 2/3. Gustav Fischer Verlag, Stuttgart, p. 576.
Krammer, K., Lange-Bertalot, H., 1988. Bacillariophyceae 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora Von Mitteleuropa, Band 2/2. Gustav Fischer Verlag, Stuttgart, p. 596.
Krammer, K., Lange-Bertalot, H., 1991b. Bacillariophyceae 4. Teil: Achnanthaceae. In: Ettl, H., Gärtner, G., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora Von Mitteleuropa, Band 2/4. Gustav Fischer Verlag, Stuttgart, p. 437.
Laird, K.R., Barouillet, C., Cumming, B.F., Perrin, C.J., Selbie, D.T., 2021. Influence of glacial turbidity and climate on diatom communities in two Fjord Lakes (British Columbia, Canada). Aquat Sci 83, 13. https://doi.org/10.1007/s00027-020-00767-3.
Leavitt, P.R., Fritz, S.C., Anderson, N.J., Baker, P.A., Blenckner, T., Bunting, L., Catalan, J., Conley, D.J., Hobbs, W.O., Jeppesen, E., Korhola, A., McGowan, S., RÜhland, K., Rusak, J.A., Simpson, G.L., Solovieva, N., Werne, J., 2009. Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. Limnology and Oceanography 54, 2330–2348. https://doi.org/10.4319/lo.2009.54.6_part_2.2330.
Legendre, P., Legendre, L., 2012. Numerical Ecology, Volume 24 - 3rd Edition. Elsevier Science.
Livingstone, D.M., Lotter, A.F., 1998. The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. Journal of Paleolimnology 19, 181–198. https://doi.org/10.1023/A:1007904817619.
Lotter, A.F., Bigler, C., 2000. Do diatoms in the Swiss Alps reflect the length of ice-cover? Aquatic Sciences 62, 125. https://doi.org/10.1007/s000270050002.
Luoto, T.P., Nevalainen, L., Kauppila, T., Tammelin, M., Sarmaja-Korjonen, K., 2012. Diatom-inferred total phosphorus from dystrophic Lake Arapisto, Finland, in relation to Holocene paleoclimate. Quaternary Research 78, 248–255. https://doi.org/10.1016/j.yqres.2012.05.009.
Maier, D.B., Diehl, S., Bigler, C., 2019. Interannual variation in seasonal diatom sedimentation reveals the importance of late winter processes and their timing for sediment signal formation. Limnol. Oceanogr. 64, 1186–1199. https://doi.org/10.1002/lno.11106.
Moreno-Ostos, E., Cruz-Pizarro, L., Basanta, A., George, D.G., 2009. The influence of wind-induced mixing on the vertical distribution of buoyant and sinking phytoplankton species. Aquat Ecol 43, 271–284. https://doi.org/10.1007/s10452-008-9167-x.
Piccolroaz, S., Toffolon, M., Majone, B., 2015. The role of stratification on lakes' thermal response: The case of Lake Superior. Water Resources Research 51, 7878–7894. https://doi.org/10.1002/2014WR016555.
Pla-Rabés, S., Catalan, J., 2018. Diatom species variation between lake habitats: implications for interpretation of paleolimnological records. J. Paleolimnol. 60, 169–187. https://doi.org/10.1007/s10933-018-0017-0.
Poikane, S., 2009. Water Framework Directive intercalibration technical report. Part 2: Lakes. OPOCE, Luxembourg.
R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [WWW Document]. URL https://www.R-project.org/.
Raubitschek, S., Lücke, A., Schleser, G.H., 1999. Sedimentation patterns of diatoms in Lake Holzmaar, Germany - (on the transfer of climate signals to biogenic silica oxygen isotope proxies). Journal of Paleolimnology 21, 437–448. https://doi.org/10.1023/A:1008022532458.
Reavie, E.D., Sgro, G.V., Estepp, L.R., Bramburger, A.J., Chraïbi, V.L.S., Pillsbury, R.W., Cai, M., Stow, C.A., Dove, A., 2017. Climate warming and changes in Cyclotella sensu lato in the Laurentian Great Lakes. Limnology and Oceanography 62, 768–783. https://doi.org/10.1002/lno.10459.
Reynolds, C.S., 2006. The Ecology of Phytoplankton. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511542145.
Rühland, K., Paterson, A.M., Smol, J.P., 2008. Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. Global Change Biology 14, 2740–2754. https://doi.org/10.1111/j.1365-2486.2008.01670.x.
Rühland, K.M., Paterson, A.M., Smol, J.P., 2015. Lake diatom responses to warming: reviewing the evidence. Journal of Paleolimnology 54, 1–35. https://doi.org/10.1007/s10933-015-9837-3.
Saros, J.E., Anderson, N.J., 2015. The ecology of the planktonic diatom Cyclotella and its implications for global environmental change studies. Biological Reviews of the Cambridge Philosophical Society 90, 522–541. https://doi.org/10.1111/brv.12120.
Saros, J.E., Fritz, S.C., 2000. Nutrients as a link between ionic concentration/composition and diatom distributions in saline lakes. Journal of Paleolimnology 23, 449–453. https://doi.org/10.1023/A:1008186431492.
Saros, J.E., Michel, T.J., Interlandi, S.J., Wolfe, A.P., 2011. Resource requirements of Asterionella formosa and Fragilaria crotonensis in oligotrophic alpine lakes: implications for recent phytoplankton community reorganizations. Canadian Journal of Fisheries and Aquatic Sciences. https://doi.org/10.1139/f05-077.
Smol, J.P., Cumming, B.F., 2000. Tracking Long-Term Changes in Climate Using Algal Indicators In Lake Sediments. Journal of Phycology 36, 986–1011.
Smol, J.P., Stoermer, E.F., 2010. The diatoms: application for the environmental and earth sciences. Cambridge University Press. https://doi.org/10.1016/S0022-0981(01)00239-8.
Smol, J.P., 2008. Pollution of Lakes and Rivers: A Paleoenvironmental Perspective, 2nd Edition. Willey, Blackwell. https://doi.org/10.1002/aqc.571.
Stenger-Kovács, C., Buczkó, K., Hajnal, É., Padisák, J., 2007. Epiphytic, littoral diatoms as bioindicators of shallow lake trophic status: Trophic Diatom Index for Lakes (TDIL) developed in Hungary. Hydrobiologia 589, 141–154. https://doi.org/10.1007/s10750-007-0729-z.
Stoermer, E.F., Emmert, G., Julius, M.L., Schelske, C.L., 1996. Paleolimnologic evidence of rapid recent change in Lake Erie's trophic status. Can. J. Fish. Aquat. Sci. 53, 1451–1458. https://doi.org/10.1139/f96-067.
Stone, J.R., Fritz, S.C., 2004. Three-dimensional modeling of lacustrine diatom habitat areas: Improving paleolimnological interpretation of planktic : benthic ratios. Limnology and Oceanography 49, 1540–1548. https://doi.org/10.4319/lo.2004.49.5.1540.
Szczerba, A., Pla-Rabes, S., Żarczyński, M., Tylmann, W., 2021. The relationship between chrysophyte cyst assemblages and meteorological conditions: Evidence from a sediment-trap study in northeast Poland. Ecol. Indic. 133, 108395 https://doi.org/10.1016/j.ecolind.2021.108395.
Taylor, J.C., Harding, W.R., Archibald, C.G.M., 2007. An Illustrated Guide to Some Common Diatom Species from South Africa. WRC report, Water Research Commission.
Thackeray, S.J., Jones, I.D., Maberly, S.C., 2008. Long-term change in the phenology of spring phytoplankton: species-specific responses to nutrient enrichment and climatic change. Journal of Ecology 96, 523–535. https://doi.org/10.1111/j.1365-2745.2008.01355.x.
Thompson, R., Price, D., Cameron, N., Jones, V., Bigler, C., Rosén, P., Hall, R.I., Catalan, J., García, J., Weckstrom, J., Korhola, A., 2005. Quantitative calibration of remote mountain-lake sediments as climatic recorders of air temperature and ice-cover duration. Arctic, Antarctic, and Alpine Research 37, 626–635. https://doi.org/10.1657/1523-0430(2005)037[0626:QCORMS]2.0.CO;2.
Tylmann, W., Głowacka, P., Szczerba, A., 2017. Tracking climate signals in varved lake sediments: research strategy and key sites for comprehensive process studies in the Masurian Lakeland. Limnological Review 17, 159–166. https://doi.org/10.1515/limre-2017-0015.
Weckström, J., Korhola, A., 2001. Patterns in the distribution, composition and diversity of diatom assemblages in relation to ecoclimatic factors in Arctic Lapland. Journal of Biogeography 28, 31–45. https://doi.org/10.1046/j.1365-2699.2001.00537.x.
Wetzel, R., 2001. Limnology. Lake and River Ecosystems, 3rd ed. Academic Press, San Diego.
Wiltse, B., Paterson, A.M., Findlay, D.L., Cumming, B.F., 2016. Seasonal and decadal patterns in Discostella (Bacillariophyceae) species from bi-weekly records of two boreal lakes (Experimental Lakes Area, Ontario, Canada). Journal of Phycology 52, 817–826. https://doi.org/10.1111/jpy.12443.
Winder, M., Reuter, J.E., Schladow, S.G., 2009. Lake warming favours small-sized planktonic diatom species. Proceedings of the Royal Society B: Biological Sciences 276, 427–435. https://doi.org/10.1098/rspb.2008.1200.
Winder, M., Sommer, U., 2012. Phytoplankton response to a changing climate. Hydrobiologia 698, 5–16. https://doi.org/10.1007/s10750-012-1149-2.
Wolf, M., Scheffler, W., Nicklisch, A., 2011. STEPHANODISCUS NEOASTRAEA AND STEPHANODISCUS HETEROSTYLUS (BACILLARIOPHYTA) ARE ONE AND THE SAME SPECIES 17, 445–451. https://doi.org/10.1080/0269249X.2002.9705561.
Yang, Y., Colom, W., Pierson, D., Pettersson, K., 2016. Water column stability and summer phytoplankton dynamics in a temperate lake (Lake Erken, Sweden). Inland Waters 6, 499–508. https://doi.org/10.1080/IW-6.4.874.
Zolitschka, B., Francus, P., Ojala, A.E.K., Schimmelmann, A., 2015. Varves in lake sediments - a review. Quaternary Science Reviews 117, 1–41. https://doi.org/10.1016/j.quascirev.2015.03.019.
Zou, Y., Wang, L., Zhang, L., Liu, Y., Li, P., Peng, Z., Yan, Y., Zhang, J., Lu, H., 2018. Seasonal diatom variability of Yunlong Lake, southwest China–a case study based on sediment trap records. Diatom Research 33, 381–396. https://doi.org/10.1080/0269249X.2018.1541823.

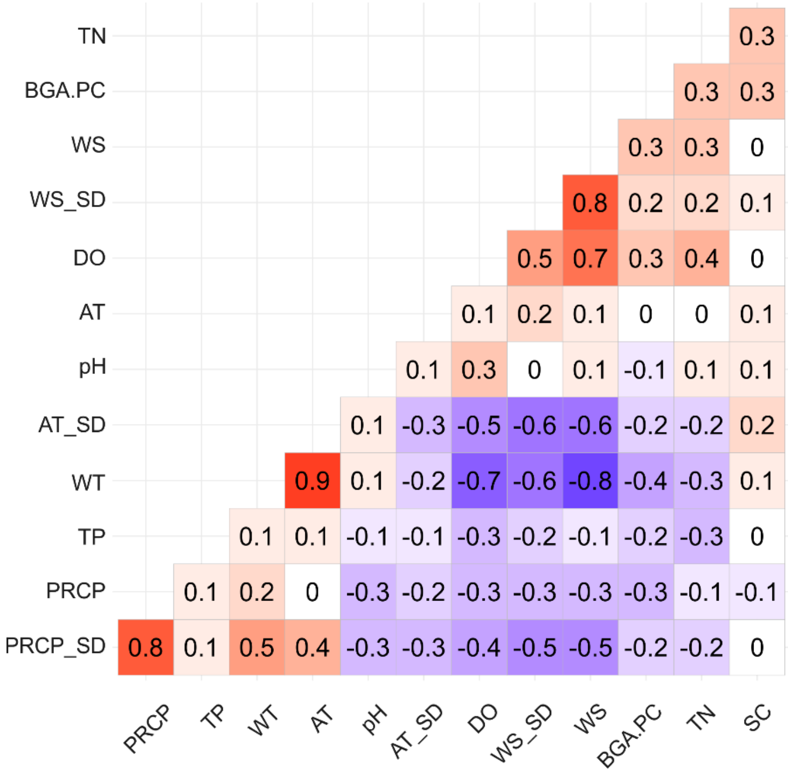

Fig. S1. Correlation matrix of normalized explanatory variables.

Table S1. Results of the Monte Carlo permutation test on variables chosen for RDA.

RDA run:	***Variables***	***p-value***
Mixing	EC	0.001***
	BGA.PC	0.002**
	DO	0.016*
	Air temperature	0.002**
	TN	0.029*
Stratifcation	EC	0.001***
	WT	0.008**
	BGA.PC	0.012*
	DO	0.010**
	Wind speed	0.007**
Mixing & stratification	EC	0.001***
	Air temperature	0.001***
	DO	0.001***
	TN	0.001***
	BGA.PC	0.006**
	Wind speed	0.025*

Statement of Co-Authorship

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I hereby confirm my contribution to the scientific paper: "Modern diatom assemblages and their association with meteorological conditions in two lakes in northeastern Poland" (Ecological Indicators, 2023, 147, 110028) being a part of the doctoral dissertation "Tracking climate signals in lakes of northeastern Poland: modern sedimentation studies using chrysophyte cysts and diatoms".

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Publication 3

Szczerba A., Pla-Rabes S., Tylmann W., submitted

Control of diatoms and chrysophyte cysts dynamics by a meteorological-driven mixing regime in eutrophic Lake Żabińskie, northern Poland, Freshwater Biology

Control of diatoms and chrysophyte cysts dynamics by a meteorological-driven mixing regime in eutrophic Lake Żabińskie, northern Poland

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Keywords
climate change, seasonality, species turnover, sediment trap, sediment flux

Abstract

Ongoing climate warming has strong moderating controls of aquatic processes, such as ice cover duration, length of the growing season, vertical mixing patterns, thermal stratification, and the availability of light and nutrients. These fundamental mechanisms in turn influence the population dynamics of aquatic organisms such as diatoms and chrysophyte cysts. In our study, for three and half years with contrasting meteorological conditions, we investigated eutrophic Lake Żabińskie located in northeast Poland. By combining observational data of meteorological conditions, the physicochemical parameters of the water column, and modern sedimentation, we sought to explain the relationships between changes in meteorological conditions and dynamics of total fluxes and the taxonomic composition of diatoms and chrysophyte cysts. Our results show the direct influence of meteorological conditions on physicochemical conditions and their indirect influence on total diatom and chrysophyte cyst fluxes and species/types succession. The former refers to the importance of air temperature and wind speed in shaping the mixing regime of Lake Żabińskie, while the latter refers to the nutrients cycling driven by changes in the mixing regime, which in turn influences biotic sediment signal formation. Our study also reveals that the biotic response to unusual meteorological conditions that occurred in 2020 (i.e., warm winter without ice cover) differed from "typical" years in terms of diatom and chrysophyte cyst blooms phenology. Yet, this response was not as pronounced as in lakes with lower productivity and can be attributed to the already turbid and nutrient-high conditions, which alter the threshold for noticeable changes to occur. The reorganization of the taxonomic composition of diatoms and chrysophyte cysts was also a response to changes in meteorological conditions.

1. Introduction

Exploring the magnitude of the impact of climate change on aquatic ecosystems and their responses is crucial as they are critical components of the global environment and have a variety of uses for the human population (Woolway and Merchant, 2019). Climate has a profound effect on the thermodynamics of lake water, and observational studies revealed that inland water bodies are rapidly warming throughout the world (Schneider and Hook, 2010). Lakes under ongoing climate warming experience changes in the duration of ice cover, the strengthening and extension of summer stratification, and changes in mixing patterns (Råman Vinnå et al., 2021). These alterations impact aquatic organisms, especially phytoplankton, which are highly sensitive to any occurring changes. This issue has been studied for many years, and it has already been established that the annual fluctuations of temperature, water column mixing, resource availability, and consumption play a key role in phytoplankton population dynamics (Meis et al., 2009). Changes in the mixing regime are by far the most impactful, as they influence nutrients and light distribution in the water column. With climate warming, decreasing ice cover has lengthened the period of open-water conditions, providing a longer growing season and inducing alterations in recognized patterns of phytoplankton succession and dynamics (Winder and Sommer, 2012; Råman Vinnå et al., 2021).

Studies of phytoplankton communities with short generation times and strong seasonal replacement, such as diatoms and chrysophyte cysts, bring us closer to understanding lakes' biota responses to climatic and meteorological conditions under ongoing climate change (Reynolds 2006; Pla-Rabes and Catalan 2011). Diatoms (Bacillariophyceae) are often dominant primary producers, and therefore the most frequently used biological proxies to assess environmental changes (Dixit et al., 1992; Pla et al., 2005; Rühland et al., 2015). These unicellular organisms are characterized by silicon oxide cell walls, which ensure their good preservation in sediments. Diatoms have been proven invaluable indicators of ongoing global change due to their wide distribution, sensitivity to environmental changes, and taxonomic diversity (Dixit et al., 1992; Catalan et al., 2002; Rühland et al., 2015). Lake sediment diatom composition has been linked with atmospherically driven changes to lake stratification patterns, late winter processes such as under-ice stratification, light and nutrient availability, timing of over-turn and ice break-up (Maier et al., 2019), length of ice-cover (Lotter and Bigler, 2000), and length of spring mixing (Kienel et al., 2017).

Chrysophycean cysts, also known as golden or golden-brown algae, are an essential part of algal communities in lakes all over the world. They produce siliceous resting stages called stomatocysts or simply cysts, which ensure the survival of the population under unfavorable conditions. Similar to diatoms, they are widely distributed and well preserved in lake sediments. Several studies showed the application of these organisms in climatic studies, pointing to both direct and indirect relationship with meteorological conditions through changes in the lake stratification patterns (Pla and Catalan, 2005; Pla-Rabes and Catalan, 2011; Hernández-Almeida et al., 2015a, 2015b; Szczerba et al., 2021, 2023).

Even though studies of complex reactions of lake biota to changes in climatic conditions have advanced considerably in recent years (Catalan et al., 2013; Rühland et al., 2015), still further investigations are needed to fully understand the direct and indirect relationships and their impact on the transfer of environmental information to the sediments (Bonk et al., 2014; Maier et al., 2018). In this respect, seasonally collected and long term observational data are still scarce. In particular, there have been very few studies presenting diatom and chrysophyte cysts seasonality (Interlandi et al., 1999; Hausmann and Pienitz, 2007; Pla-Rabes and Catalan, 2011;

Korkonen et al., 2017). Having in mind this research gap, for three and a half consecutive years, with contrasting meteorological conditions, we conducted a high-resolution observational study of Lake Żabińskie. The research aimed at answering following research questions: 1) Can we establish linkages between changes in meteorological conditions and the seasonality of diatoms and chrysophyte cysts in a eutrophic lake? 2) How does ongoing global warming alter "typical" (with spring and fall peaks) seasonal patterns and the taxonomic composition of diatoms and chrysophyte cysts?

We hypothesize that, under eutrophic conditions, direct influences of meteorological conditions on lake biota are masked by complex relationships with physical and chemical conditions, e.g., light and nutrient availability, and thus the effects of global warming on diatom and chrysophyte cysts seasonality are difficult to predict. In this study, we will show how seasonal and interannual changes in meteorological conditions are reflected in physical and chemical properties of the water column as well as in the variability of diatom and chrysophyte cyst blooms. We will also indicate key processes regulating diatoms and chrysophyte cysts dynamics in a eutrophic temperate lake.

2. Materials and methods

2.1. Study site

Lake Żabińskie (54˚07'54.2"N, 21˚58'56.5"E, 117.0 m a.s.l.) is located in the postglacial landscape of the Masurian Lake District in northeastern Poland (Fig. 1). Climatic conditions in the region are characterized by strong seasonality (cold winters and warm summers) and continentality. Mean monthly air temperatures at Kętrzyn meteorological station, located about 40 km from Lake Żabińskie, range from -3.3°C in January to 18°C in July, while mean annual precipitation amounts to 600 mm, with a maximum in July, i.e. ca. 80 mm (https://danepubliczne.imgw.pl/). Typically, Lake Żabińskie is covered by ice between December and March (Żarczyński et al., 2022).

Lake Żabińskie is slightly elongated in the W-E direction and occupies a glacially eroded depression formed during the Vistulian glaciation (ca. 15.2 ka BP). This kettle hole lake is 44.4 m deep and has a surface area of 41.6 ha. Lake Żabińskie has two permanent and one periodic inflow. The outflow drains westward into Lake Gołdopiwo (Fig. 1). The catchment (24.6 km^2) is composed mostly of glacial tills, sands and gravels (Tylmann et al., 2017). Elevations in the eastern part of the catchment exceed 200 m a.s.l. and decrease generally westward to a minimum level of 117 m a.s.l., that corresponds to the water level of Lake Żabińskie (Fig. 1). In the northern and southwestern parts, the area surrounding the lake is covered by pine forests with spruce and birch trees. Fields and meadows dominate in eastern and southeastern parts. The lake is located near recreational and agricultural areas. Mean values of nutrients (total phosphorus, total nitrogen), chlorophyll-a, and Secchi disc depth for the observation period classify Lake Żabińskie as a eutrophic lake, according to limits presented by the Organization for Economic Cooperation and Development (OECD) (Supplementary Materials, Tab. S1).

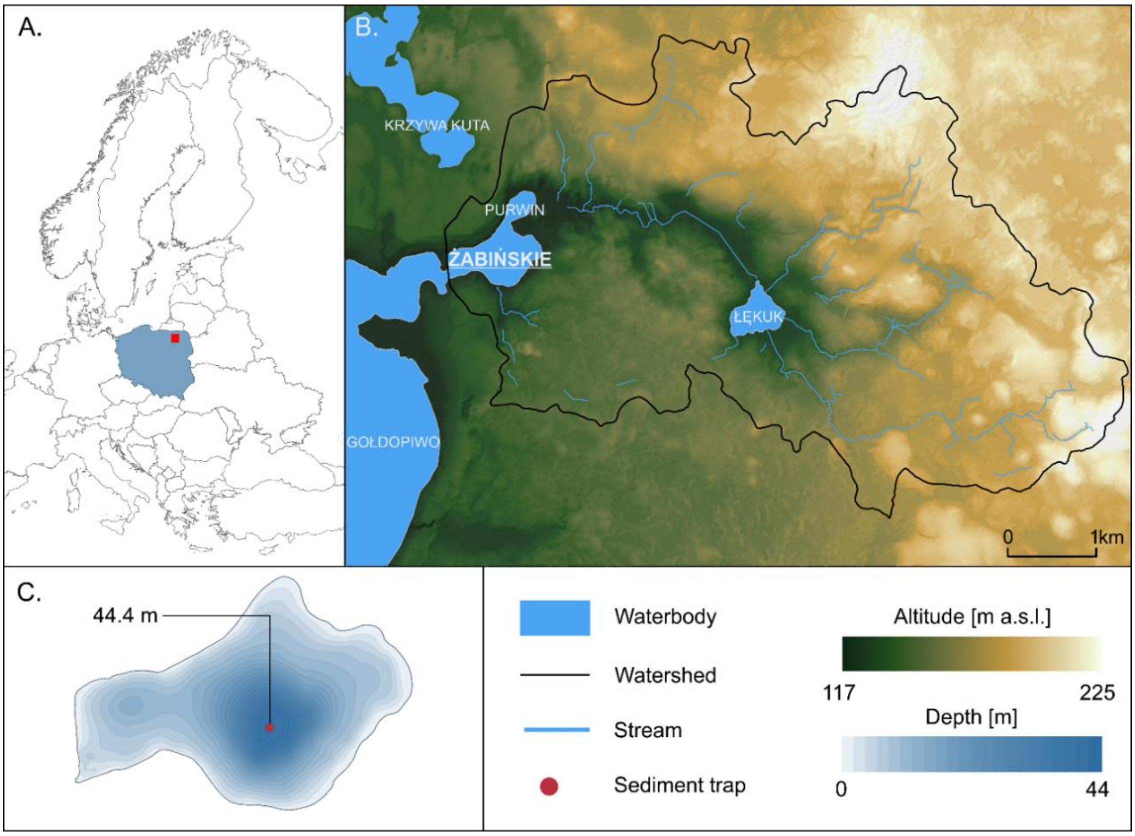

Fig. 1. Location of Lake Żabińskie in Europe and Poland (A), topography and hydrography of the catchment (B), and bathymetric map with the location of sediment trap (C).

2.2. Environmental variables

To assess the impact of environmental variables on biological assemblages, Lake Żabińskie was monitored biweekly from December 2016 to July 2020. Water temperature (WT), specific conductance (SC), dissolved oxygen (DO), and chlorophyll-a concentrations (Chl-a) were measured for the entire water column at 1m intervals using an EXO 2 Multiparameter Sonde (YSI, USA). Additionally, water temperature was measured every 15 minutes by HOBO Water Temperature Pro v2 loggers (ONSET) at a depth of 1, 5, 10, 20, 30 and 40 meters. Water transparency was measured with a Secchi disk. Water samples for chemical analysis were collected from the depth of 1 m, 10 m, and 40 m. The measurements included total phosphorus (TP) and total nitrogen (TN), measured on a UV/VIS spectrophotometer (Spectroquant Prove 600 Spectrophotometer, Merck, Germany), and major ions were measured with ion chromatograph ICS 1100, Dionex, USA.

Meteorological data, such as daily air temperature (AT), wind speed (WS), and precipitation (PRCP) for the closest meteorological station, i.e., Kętrzyn (about 40 km distant), were obtained from the Institute of Meteorology and Water Management–National Research Institute database (https://danepubliczne.imgw.pl/). Ice-cover dates were established based on field observations and satellite imagery.

2.3. Modern sedimentation

A sediment trap was deployed in the center of Lake Żabińskie (Fig. 1) to record the seasonal changes in accumulation and species composition of diatom and chrysophyte cyst assemblages. The trap consisted of four 80 cm-long plastic tubes with an inner diameter and total active area of 86 mm and 232.4 cm^2 respectively. The trap was moored 1 meter above the sediment surface and sampled monthly, apart from the periods when the lake was covered by ice. These periods were represented by one sample collected each year right after the ice out.

2.4. Chrysophyte cysts and diatoms analyses

Samples for diatom and chrysophyte cyst analyses were prepared following the methods of Battarbee et al. (2001). In the first step, samples were oxidized and cleaned by heating around 0.5 g of freeze-dried sediment material with HCl and subsequently with H_2O_2 to remove carbonates and organic material respectively. Slides were prepared by mounting with Naphrax. Diatoms and cysts were identified under oil immersion at x1000 magnification, using Zeiss Axio Imager A2 and Delta Optical Genetic Pro light microscopes. In each sample, at least 500 diatom valves and 100 cysts were counted along the random transects. Identification of diatom species followed mainly Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b). Diatom species names were updated according to the AlgaeBase (Guiry and Guiry, 2022). Cyst identification followed Duff et al. (1995), Wilkinson et al. (2001), and Pla (2001). To determine fluxes of both diatoms and chrysophyte cysts, microspheres were counted alongside (Battarbee and Kneen, 1982).

2.5. Data preparation and visualization

Processing and visualization of the data were performed with R 4.1.3 (R Core Team, 2022). Environmental variables, taken into account in data visualization and interpretation, represent the mean values for the photic zone, estimated as Secchi disc depth multiplied by 2.5 (Poikane, 2009). Data from thermistors were firstly assessed through presence of outliers, which were removed from dataset, and then homogenized. After homogenization, the 15-minute measurements were used to calculate the daily average. Using thermistor data and the package 'rLakeAnalyzer' (version 1.11.4.1), we estimated epilimnion and metalimnion depths. Calculations of the length of stratification and mixing periods were conducted according to the method provided by Żarczyński et al. (2022). On their basis, we divided the observational period and classified each sample into one of three phases, i.e., reverse stratification (winter with ice cover, usually recorded between December and March), mixing (spring and fall isothermy, recorded between April–May, and October–November, respectively) and stratification (the ice-free period except mixing, recorded between June–September).

Due to difficulties with chrysophyte cysts identification by light microscopy, the unornamented types were merged into 'collective groups' according to size: ≤5.9 µm (S1, S29, and S46); 6.0–8.9 µm (S9, S120, and S189); and ≥9.0 µm (S15, S42, and S150). In some cases, the sizes of individual cysts were on the border between the two types; therefore, we distinguished two additional groups (group 1–S1/S9, S29/S120, and S046/S189; group 2–S9/15, S120/42, and S189/150). Furthermore, two ornamented types, D114 and D115, which can be easily confused under light microscopy, were merged into the 'collective group' D114/115.

3. Results

3.1. Environmental conditions

Between 2017 and 2019, during the winter AT values were below 0°C and rose above the freezing point at the end of February and in March (Fig. 2). In February 2018, we observed the lowest AT values from the entire observation period, which reached -15.5°C. In winter 2020, which was the warmest winter in the last 200 years in Poland, most of the measurements showed AT above 0°C, with only nine days with AT below freezing point, and lowest reaching -1.6°C. Each year, during the spring, we noted an increase of the AT with the highest rate noted in 2018, reaching 7.7°C for daily temperatures, and around 14°C for the mean monthly values. During that year, also the summer was the warmest from the entire observation period, and the maximum temperature recorded that season reached 25.9°C in July. Increased WS was recorded in spring periods, and decreased in the summer, with the highest values observed in 2020. Each year, we noted highest growth of WS rate in the fall months, with the greatest in November 2019. Contrary to WS, the main pattern of seasonal variability in PRCP, showed an increase of the values in the summers, with the ones from 2017 as the greatest (Fig. 2).

The differences in weather conditions during the observation period were accompanied by changes in the water column properties (Fig. 2). During winters from 2017 to 2019, Lake Żabińskie was covered with ice and reverse stratification developed. The longest period of ice cover was recorded in 2018, while in 2017 and 2019, the length was similar (Supplementary Materials Tab. S2). In early spring, the mixing of the water column took place and was accompanied by gradual transport of the oxygen to deeper parts of the water column. The spring mixing periods differed between years in terms of duration and depth of effective transport of oxygen in the water column (Supplementary Materials Tab. S2). The mixing period was followed by the development of summer stratification, during which only epilimnion was oxic, and oxygen concentrations below 1 mg O_2 L^{-1} developed below ca. 5 m in depth (Fig. 2). In late summer, the thermocline broke down, and the water column gradually started to mix. The length of fall mixing periods was similar between years, yet differed in depth, with the deepest observed in fall 2019 (Fig. 2, Supplementary Materials Tab. S2). In the exceptional year of 2020, when the ice cover was not present, we registered the longest period of homothermy and good oxygenation in the whole water column, lasting from the end of January till May 2020 (Fig. 2). The maximum DO concentration at the bottom recorded during that period was 11.5 mg l^{-1}.

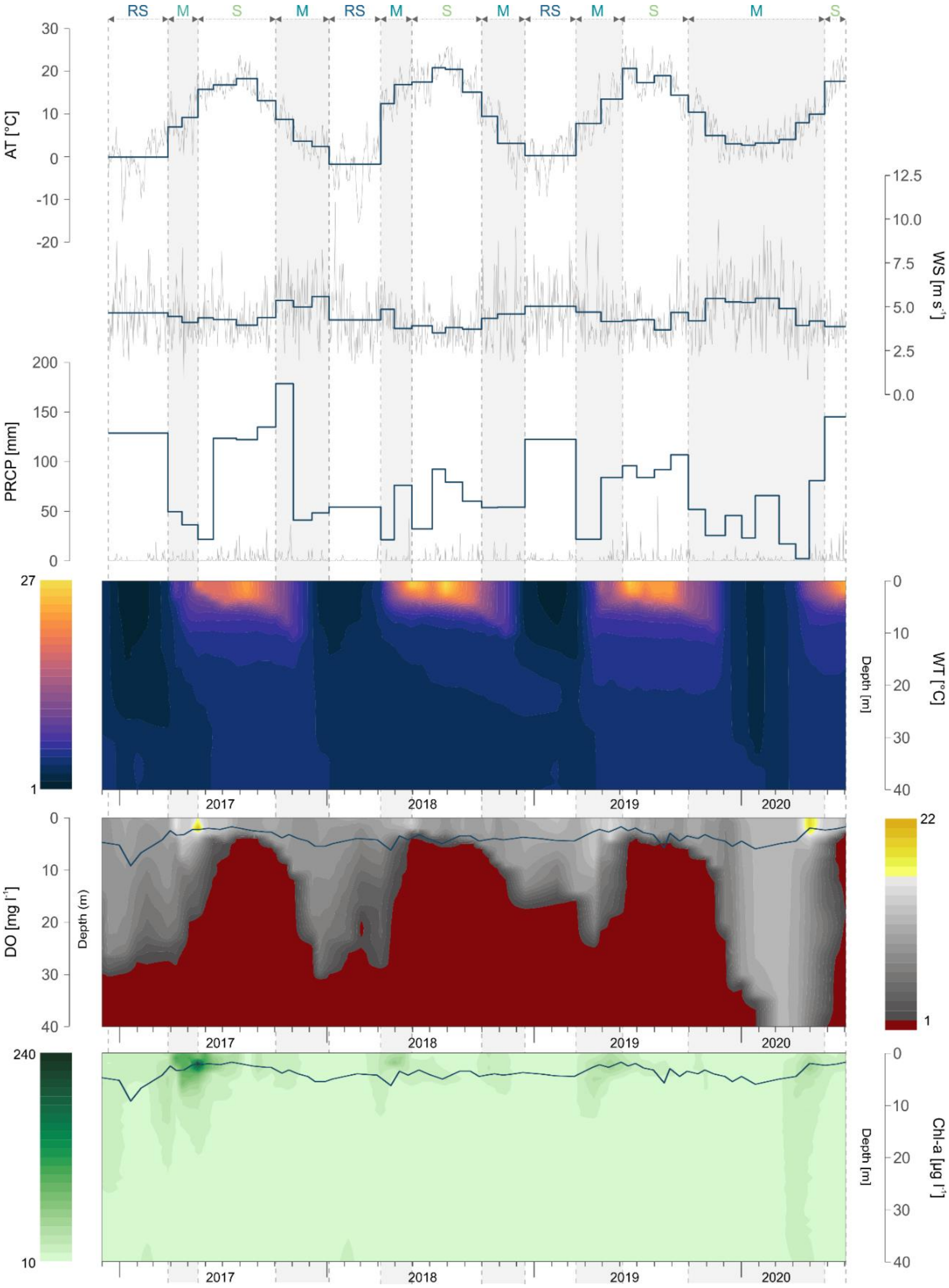

Fig. 2. Daily values of meteorological variables (grey lines) with mean values of AT and WS and sum of PRCP for the periods of the sediment trap exposure time (blue lines) and depth profiles of WT, DO and Chl-a concentrations with the depth of photic zone (blue line). “RS” stands for reverse stratification, “M” for mixing, and “S” for summer stratification.

Along with the weather and mixing regime data, seasonal and interannual differences in nutrients and Chl-a concentrations occurred (Fig. 2, 3). The values of TN and TP were related to the mixing periods, with the greatest values of TN recorded in the spring of 2017, and TP in the springs of 2018 and 2019. Along with the increased nutrients concentrations, we recorded elevation of Chl-a values, with the highest peak observed in spring 2017 (Fig. 2, 3). Summer stratification periods had lower concentrations of both nutrients and Chl-a. Values of N:P ratio also varied seasonally and interannually, with the highest values recorded in the spring of 2017 and 2018 and the summer of 2017. Winters from the observation period were generally characterized by elevated TN values. Furthermore, the depth of photic zone varied over the observation period, with the lowest value reaching 2 m in spring and the highest 9 m in the winter in 2017. Shortly after ice-out we observed increases of the photic zone depth, which decrease with the intensification of plankton growth expressed by elevation of Chl-a concentrations (Fig. 2).

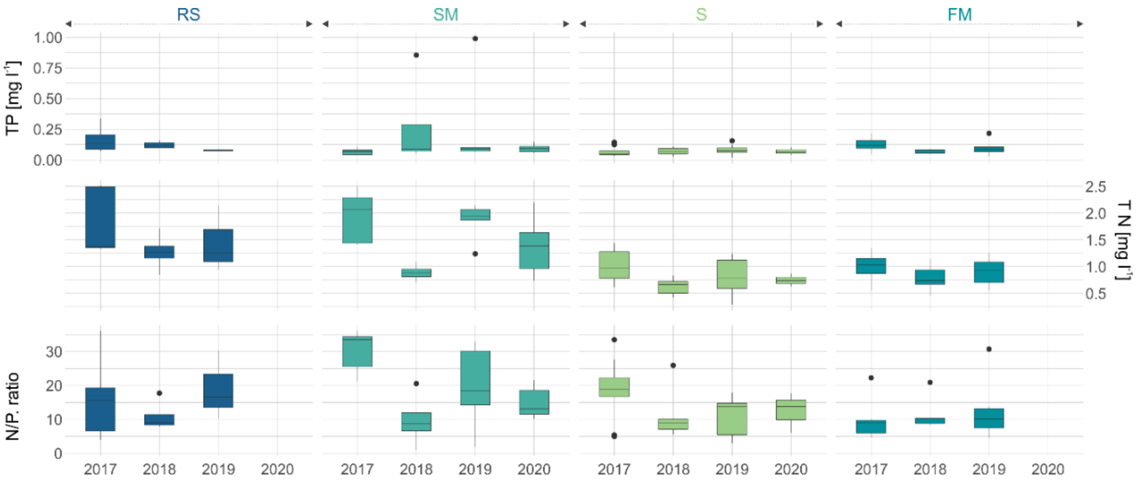

Fig. 3 Mean values of TP and TN for the depth of photic zone, and N:P ratio. “RS” stands for reverse stratification, “SM” for spring mixing, “S” for summer stratification, and “FM” for fall mixing.

3.2. Diatom and chrysophyte cyst composition and total fluxes

In 35 samples, we identified 123 diatom taxa, 34 of which obtained abundance equal or more than 2% in at least one sample. Dominant species were: *Fragilaria crotonensis* (7.8%), *Stephanodiscus parvus* (7.3%), *Pantocsekiella comensis* (7%), *Sephanodiscus neoastraea* (5.9%), *Stephanodiscus hantzschi* (5.7%), *Fragilaria tenera* var. *nanana* (4.4%), *Stephanodiscus medius* (4%), *Aulacoseira granulata* (3.9%), and *Pantoseckiella oceallata* (3.2%), which accounted for almost half of the identified individuals (Fig. 4).

From 109 cyst morphotypes or ‘collective categories identified in 35 samples, 39 morphotypes had abundance equal or more than 2% in at least one sample. Dominant morphotypes or ‘collective groups’ were: unornamented 6–8.9 µm (14.3%), unornamented ≤ 5.9 µm (11%), group 2 (8.4%), D114/115 (6%), S128 (5.3%), S118 (3.9%), S041 (3.6%), S161 (3.2%), unornamented ≥ 9 µm (3.1%), group 1 (2.7%). They accounted for 61.5% of all identified cysts (Fig. 5).

Fig. 4. Bubble matrix of main diatom taxa fluxes.

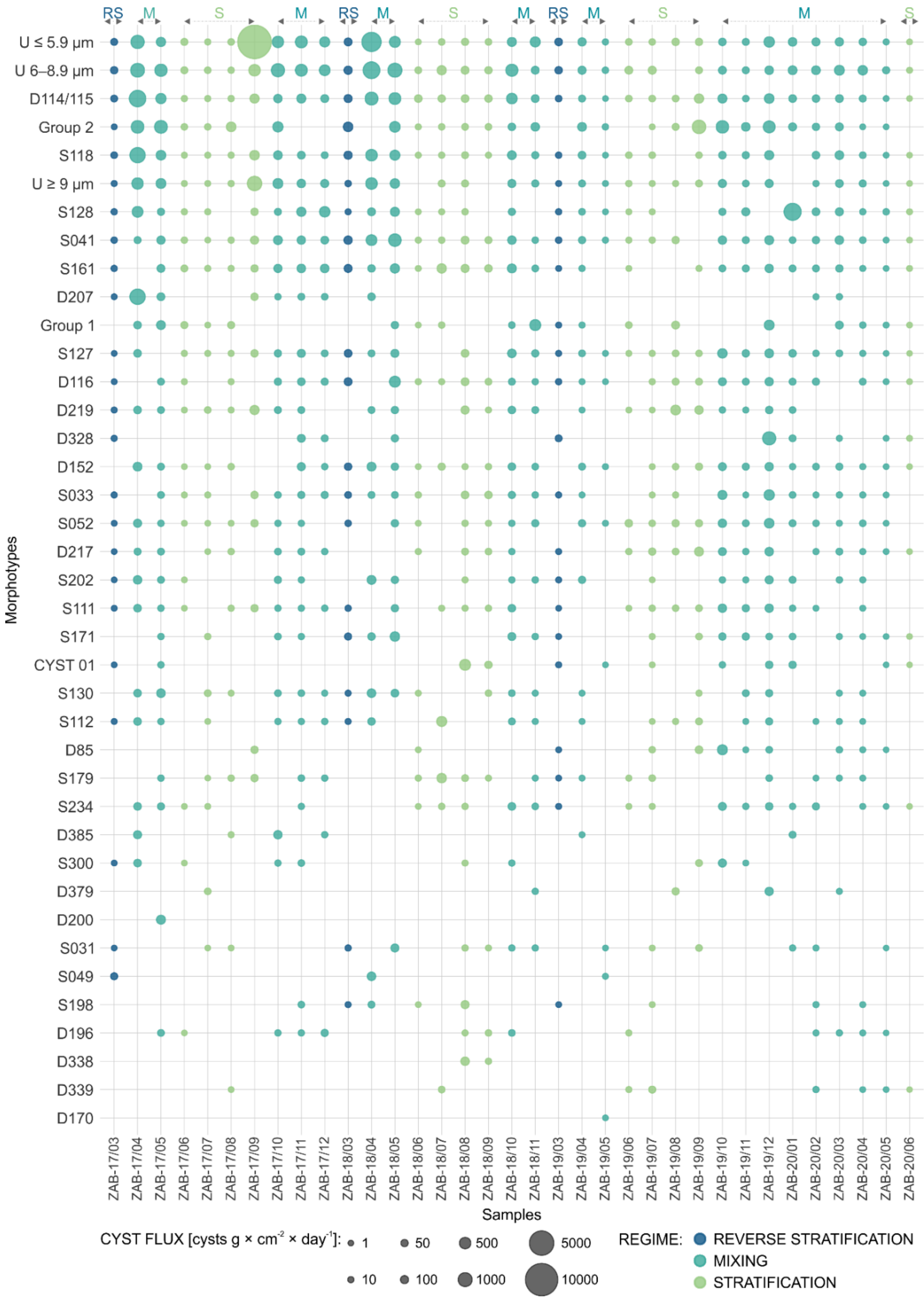

Fig. 5. Bubble matrix of main cyst morphotypes or ‘collective categories’ fluxes (“U” stands for unornamented, CYST 1 possible new morphotype; further research is needed to confirm this).

The highest peaks in diatom and chrysophyte cyst total fluxes between 2017 and 2019 were mainly recorded in spring and fall samples, and the magnitude of the maxima varied from year to year (Fig. 6). As a general trend, fluxes showed a seasonal pattern, with the maximum fluxes during the winter–spring transition. The exception was the sample from the end of the summer 2017 when the cysts fluxes obtained the greatest value from the entire observation period. In the exceptional year 2020, without ice cover during the winter, we recorded a slight increase of both diatom and cyst fluxes in the January, followed by a decrease in February and a further increase in March and April. In May and June 2020, fluxes decreased. Although diatoms and cysts presented a similar pattern of total fluxes pulses, diatoms dominated during the study period, and their fluxes were ca. an order of magnitude greater than the chrysophyte cysts (Fig. 6).

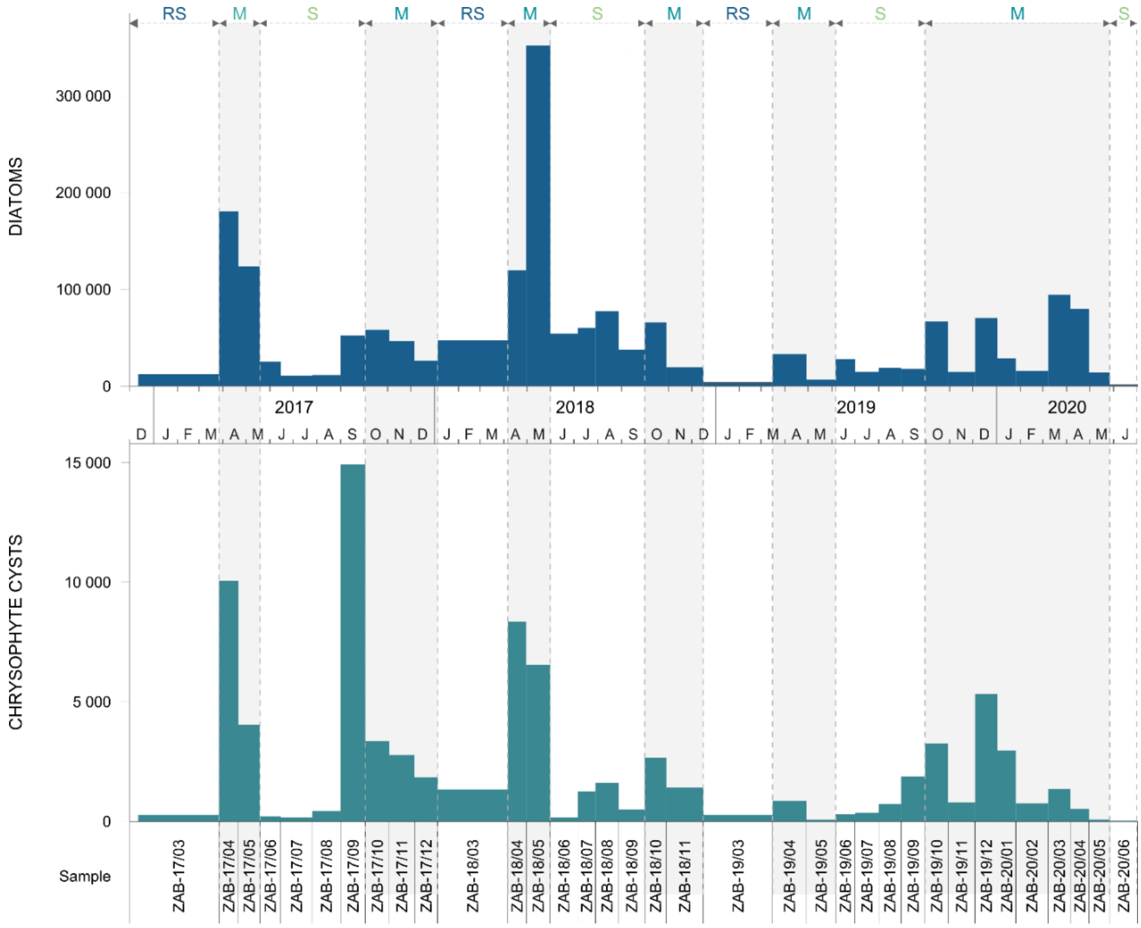

Fig. 6. Total fluxes of diatoms [valves g × cm^{-2} × day^{-1}] and chrysophyte cysts [cysts g × cm^{-2} × day^{-1}]. The width of the bars represents the length of the exposure period of sediment traps.

4. Discussion

4.1. Meteorology and water column characteristics

Over the course of this study, we observed three and a half meteorologically different years, which confirmed the influence of meteorological conditions on the mixing regime in Lake Żabińskie. Across both meteorological and physical parameters, we observed marked differences between specific seasons and years. Spring mixing in Lake Żabińskie starts after the ice cover break up, as in a typical temperate lake. Winters characterized by long lasting ice-cover usually result in short spring overturn followed rapidly by summer stratification. This relationship is firmly visible in data obtained between 2017 and 2019 (Fig. 2., Supplementary Materials Tab. S2). In 2018, we recorded the development of the ice cover in January, which lasted till the beginning of April, and was the longest ice-cover period with the lowest air temperatures and highest numbers of days with the air temperatures below the freezing point. This period was followed by rapid warming, which resulted in the short, yet quite intensive spring mixing reaching 28 m water depth (Fig. 2, Supplementary Materials Tab. S2). The shorter ice cover periods in 2017 and 2019, with a cooler spring and a slow rate of air temperature increase, resulted in the longer spring overturn periods (Fig. 2, Supplementary Materials Tab. S2). The gradual increasing trend in air temperatures and the decreasing trend in wind speed during the spring season caused the development of the thermal stratification period. The sharp temperature gradient developed during summer stratification formed a contact zone between the warm and oxygenized waters of epilimnion and cold and anoxic waters of hypolimnion. Over the stratification period, epilimnion thickness increased gradually (Supplementary Materials Fig. S1). In 2017, the thermocline reached the deepest point on record (more than one meter deeper than in other years). The highest wind speed values and coolest air temperatures contributed to the deepening of the thermocline during summer stratification (Supplementary Materials Fig. S1). Due to cooling after the summer, the density of surface water increased sufficiently to start the fall overturn. The length of the fall mixing period is strictly correlated to the timing of the ice cover formation. The shallowest mixing in Lake Żabińskie occurred in 2018. That fall was characterized by a rapid decrease in air temperature, which allowed lake water to attain the freezing point at the earliest point from the observation period, i.e. in the second half of December (Fig. 2, 7). Fall mixing in 2018 was also characterized by the lowest mean wind speed values among investigated fall seasons (Supplementary Materials Tab. S2).

Ongoing global warming causes significant alterations in the temperatures across the globe and introduces an element of unpredictability. One of the lake ecosystems' most widespread physical responses has been the shortening of ice cover periods. Changes in the ice cover and mixing dynamics will most probably lead to regime shifts in lakes (Woolway and Merchant, 2019; Pilla and Williamson, 2022). The winter of 2020 was the warmest one in the last 200 years in Poland, with only 10 days with temperatures below freezing point recorded at the meteorological station in Kętrzyn, therefore not allowing for the formation of stable winter ice-cover. Such a meteorologically unusual winter resulted in a complete water column overturn with very good oxygenation of near-bottom waters, which lasted almost five months (Fig. 2, 7). This observed change in the mixing pattern may be a prelude to the transition of Lake Żabińskie from a dimictic to a monomictic regime under ongoing global warming. Recognized seasonal and interannual fluctuations in the meteorological and in turn physical conditions of Lake Żabińskie substantially affected the formation of the biotic sediment signal.

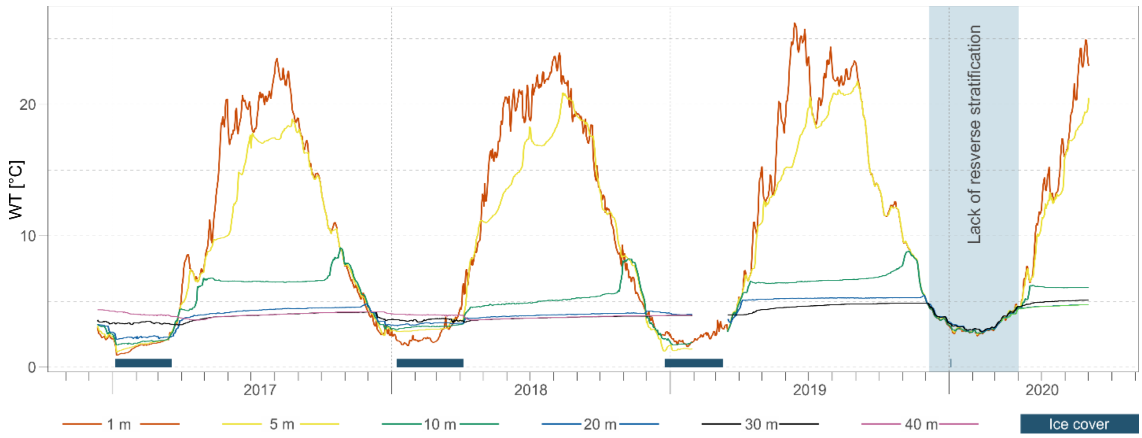

Fig. 7. Daily mean water temperature values over the observation period measured with thermistors at different water depths. Discontinuous data during the winter of 2018/2019, due to thermistor failure. Note the difference in development of winter inverse stratification between the years, especially the lack of winter stratification in 2019/2020.

4.2. Biotic response to changes in mixing regime

Meteorological conditions can directly and indirectly, control the biophysical processes of lakes. Contrasting meteorological conditions and mixing regimes among the studied years allowed us to register different biotic responses in the seasonality of diatoms and chrysophyte cysts. In 2020, we registered an exceptional year without ice cover due to the high winter air temperatures. During that period, the biotic response in Lake Żabińskie exposed the most apparent differences from the ones registered between 2017 and 2019 and was related to differences in taxonomic composition and phenology.

The observed response between 2017 and 2019 is characteristic of dimictic lakes. Winter ice cover periods reduce lake productivity regarding the total diatoms and cysts flux (Fig. 4, 5, 6) and Chl-a concentrations. The limited light availability and nutrient delivery from hypolimnion cause unfavorable conditions for plankton development. Additionally, during winter, external input from the catchment is strongly limited due to reduced runoff resulting from lower precipitation, snow cover and soil freeze (Jeppesen et al., 2005). With the onset of spring overturn, we recorded maximum of Chl-a concentrations and diatom and chrysophyte cyst fluxes (Fig. 2, 6). The spring mixing period proved to be determinant of nutrient availability during the growing season. In that period, nutrients released during organic matter decomposition in winter in the anoxic hypolimnion are transported to the photic zone, inducing planktonic organisms' growth (Reynolds, 2006; Winder and Sommer, 2012). After spring maximum, the summer seasons are characterized by rather low TP and TN concentrations (Catalan and Fee, 1994), which decrease diatom and chrysophyte cyst fluxes (Fig. 4, 5, 6). During summer stratification the phosphorus released under anoxic conditions from sediments is restricted to the aphotic hypolimnion, phytoplankton production is supported mostly by the external load (Jeppesen et al., 2005). However, the overall low summer total fluxes indicate that nutrients delivered from the catchment have a minimal effect on diatom and chrysophyte cyst growth in Lake Żabińskie. Following summer stratification, the fall mixing period is characterized by higher availability of nutrients, higher Chl-a concentrations and a related increase in total fluxes (Fig. 6). This is due to the distribution of nutrients from the hypolimnion after the break-up of the thermocline. The seasonal signal in fluxes is strong, yet chrysophyte cysts showed slight deviations from this rule. In summer 2017, we observed the highest peak of cysts from the entire observation period, which could have been caused by high N:P ratio values during that time, which favored cyst growth and created their highest peak (Liu et al., 2022).

The interannual differences in diatom and chrysophyte cyst fluxes are related to interannual variability in the mixing regime of Lake Żabińskie. When released from the anoxic hypolimnion, nutrients may reach the epilimnion only during the mixing phase; its intensity has straightforward relationships with TN and TP pools in surface waters after mixing. The mixing that occurred in 2017 and 2018 reached similar water depths, yet in 2018, we observed diatom fluxes two times higher than in 2017. That was related to the much higher input of TN in 2017, resulting in the highest values of the N:P ratio, while in 2018, the opposite conditions were observed (Fig. 3). High N:P ratios could have acted as a limiting factor for diatom growth and thus resulted in lower fluxes (Liu et al., 2022).

Seasonal and interannual changes in the mixing regime are the primary factors impacting nutrients concentrations and N:P ratio fluctuations in Lake Żabińskie. Inputs of nutrients from the catchment could modify the N:P ratio in epilimnetic waters, which can be important for diatoms and chrysophyte cysts development, especially during summer stratification periods, when delivery of nutrients from hypolimnion is not possible due to the development of a thermocline (Luttenton and Lowe 2006). Despite the catchment of Lake Żabińskie having been anthropogenically transformed (by recreational and agricultural areas), and external nutrient supplies from lake catchment are present, we did not detect their substantial influence on diatom and chrysophyte cyst growth and seasonal dynamics. The dominance of in-lake dynamics show that present anthropogenic influence has a secondary effect on studied organisms, therefore allowing us to recognize climate signals in the lake primary producers. Obtained results also highlight the importance of season dependent N:P ratio fluctuations in explaining changes in diatom and chrysophyte cyst dynamics. Freshwater phytoplankton assemblages are sensitive to changes in the N:P ratio, and any reductions of TN and TP may introduce a compositional turnover in phytoplankton (Vrede et al., 2009). In high N:P ratio environments, competition for phosphorus is more intense, as it becomes a limiting factor for phytoplankton growth (Reynolds, 2006). Diatoms, being able to utilize phosphorus (P) more effectively under eutrophic conditions and being able to increase their P uptake under P-limited environment, are better able to compete with chrysophytes (Alipanah et al., 2018), which explains their higher observed fluxes in Lake Żabińskie. Furthermore, according to our findings, even small enrichments of TP, and therefore decrease of N:P ratio, can increase diatom production, which is manifested by their interannual total flux change following the N:P ratio pattern.

The general pattern found in the seasonality of the studied organisms is in agreement with previous studies of temperate lakes, confirming the importance of ice cover and mixing regime in shaping their seasonal succession patterns. Pla and Catalan (2011) indicated that the relationship between chrysophyte cysts and ice cover length is a result of the impact of winter/spring air temperature on the onset and strength of the spring mixing period. Furthermore, studies from Austria (Kamenik and Schmidt, 2005), the Pyrenees (Pla and Catalan, 2005), and the Swiss Alps (R. De Jong et al., 2013) showed that cyst composition is closely related to winter/spring temperatures. Seasonality of diatoms was also associated with meteorological conditions and mixing regime. Changes in diatom assemblages were attributed to the availability of light and nutrients which are correlated to spring warming and the length of water column mixing (Kienel et al., 2017), late winter conditions (e.g., light and nutrient availability, under-ice stratification, timing of ice break-up and lake turnover) (Maier et al., 2019), or the length of ice-cover (Lotter and Bigler, 2000). Most importantly, Witak et al. (2017) showed that during the last century, water column stability and TP cycling played an important role in developing diatom communities in Lake Żabińskie, which is consistent with our findings.

In this context, we asked the question as to whether lack of ice cover in a eutrophic lake will substantially influence biotic signals in sediments. Ongoing climate warming impacts low-trophy lakes, inducing an increase in lake throphy, which subsequently affects the seasonality of the lakes' biota structure and composition (Nazari Sharabian et al., 2018). Our study shows that in an already eutrophic lake, the lack of ice cover in 2020 impacted the timing of diatoms and cysts production. The diatom and chrysophyte cysts peak occurred earlier than in other years (i.e. during the winter months), due to higher temperatures and the lack of ice cover (Fig. 6). More intense water mixing, high turbidity, changes in nutrients balance and light conditions in the water column, associated with the lack of ice cover, were not strong enough to induce more pronounced changes in total fluxes, which, in contrast, were observed in lower-trophy lakes. Szczerba et al. (2021, 2023) demonstrated that in two Polish lakes, Łazduny and Rzęśniki, which are characterized by lower productivity than Lake Żabińskie, diatom and chrysophyte cyst fluxes were more profoundly influenced by exceptional conditions from 2020. Not only were total fluxes very low, but no distinctive peaks were recorded, and diatom and chrysophyte cysts sediment signals were seasonally integrated. Thus, the higher trophy can indeed mask the effect of global warming. This can be especially true for chrysophyte cysts, which are more abundant and dominant in oligotrophic lakes. Hence, high trophic conditions are generally limiting their growth (Duff et al., 1995; Eloranta, 1995).

Nonetheless, the compositional response of diatoms and cysts revealed the greater impact of meteorological conditions (Fig. 4, 5, 8). Similar to findings from Lake Redo (Catalan et al. 2002), our study points to the threshold-like response of planktonic diatom to changes in air temperature, here acting through changes in the water column and nutrient cycling. In 2020, along with the major changes in water column characteristics, we observed the transition in taxonomic composition to the dominance of the diatom species *Stephanodiscus neostraea,* and *Stephanodiscus hantzshi* (Fig. 4, 8). Due to warmer near-bottom waters favoring phosphorus release from sediments in 2019, followed by the intense water column mixing in 2020, elevated TP values in the epilimnion created good conditions for *Stephanodiscus hantzshi* growth. This species was also present in the paleo record in Lake Żabińskie and was also connected with the high levels of TP concentrations, yet had been induced by an inflow of nutrients from the agricultural catchment (Witak et al., 2017). Furthermore, Reavie and Kireta (2015) found that

Stephanodiscus hantzshi served as an indicator of high phosphorus levels in the Laurentian Great Lakes. In March 2020, we also observed the peak of *Pseudostaurosira brevistriata,* which in 2017 and 2019 was recorded in samples accumulated during deep mixing periods in fall (Fig. 4, 8). In 2020, an appearance of *Aulacoseira ambigua* was registered (Fig. 4, 8). In previous studies this species was recorded during strong water column mixing (Bradbury et al., 1993). Furthermore, this characteristic increase in *Aulacoseira ambigua* was also observed in the same time period in the nearby Lake Rzęśniki and was connected to the whole water column mixing and induced by the nutrient rich environment present at the same time (Szczerba et al., 2023). A study of the sediment record from Lake Żabińskie also pointed to an increase in the abundance of *Aulacoseira ambigua* alongside nutrient enrichment (Witak et al., 2017). For chrysophyte cysts, the most characteristic was the appearance of type S128, with the start of whole water column mixing in 2019, and its peak in January 2020, and peaks of types D328 and D379 in December 2019 (Fig. 5, 8). Registered changes in the taxonomic composition and dynamics of the dominant diatoms and cysts confirm the indirect influence of changes in meteorological conditions on biotic sediment signal formation. Observed compositional turnover in both diatoms and chrysophyte cysts show the possibility of using these organisms to infer past lake dynamics and climate variability over time. The observed changes in dominant species, and appearance of new taxa during the unprecedented winter of 2020 can be used to recognize periods of lack of ice cover and intensified overturn periods in sediment records and infer past nutrient dynamics and temperature trends. These findings emphasize the importance of collecting seasonal data, which allows us to recognize the factors responsible for compositional changes and will enable us to properly infer past variability and understand processes occurring in aquatic ecosystems

Most recent studies concerning diatom and cyst seasonality pointed to changes in patterns of total fluxes in lakes of various trophy, from dystrophic to mesotrophic (Kienel et al., 2017; Maier et al., 2019; Szczerba et al., 2021, 2023). In eutrophic Lake Żabińskie, initial diatoms and chrysophyte cysts composition consist of species tolerant to high nutrient level, high turbidity, and limited light availability. Since adaptation thresholds for organisms living in eutrophic conditions are different than in low productivity lakes, the consequences of mild winter without the ice cover include detectable shifts in the taxonomic composition and flux dynamics, yet the latter are less profound than in lakes with lower productivity.

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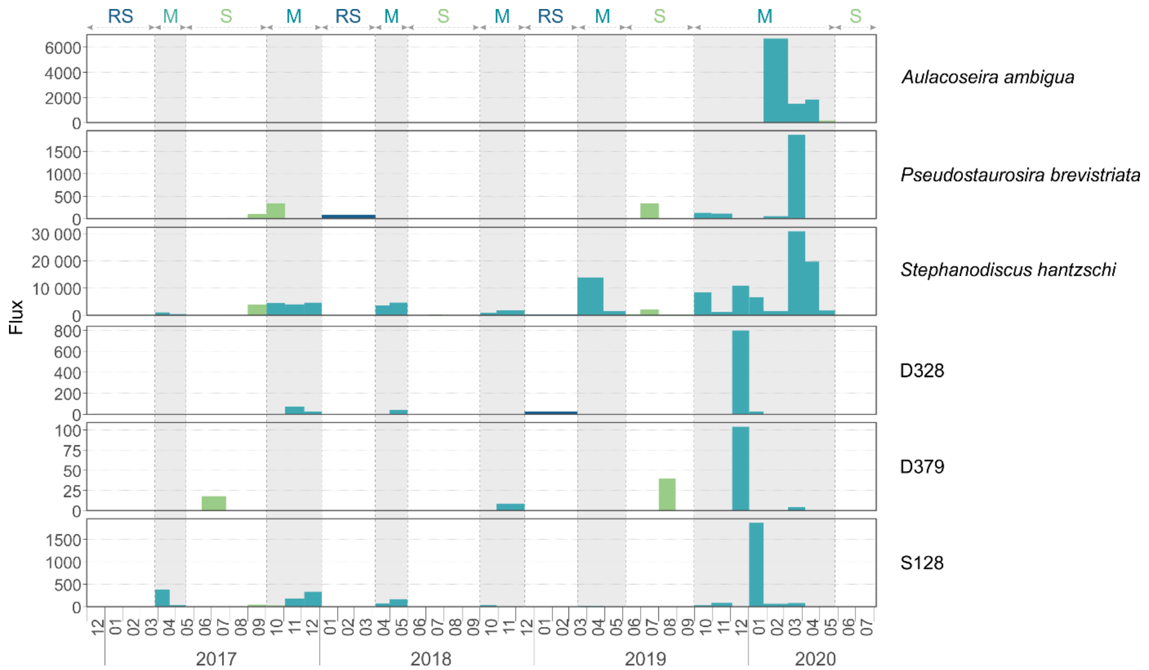

Fig. 8. Selected diatom and chrysophyte cyst taxa, highlighting compositional turnover during 2020.

5. Conclusions

We investigated Lake Żabińskie to explore the links between changes in meteorological conditions and fluxes of diatoms and chrysophyte cysts and to find out whether ongoing global warming alter recognized patterns of diatom and chrysophyte cyst seasonality and taxonomic composition. This study allowed us to confirm the hypothesis that under eutrophic conditions, direct influences of meteorological conditions on lake biota are masked by complex relationships with physical and chemical conditions. Nevertheless, combined meteorological, limnological, hydrochemical, and sediment trap data allowed us to identify a direct relationship between changes in weather and the mixing regime of the investigated lake as well as indirect responses of lake biota. Air temperature and wind speed proved to be major factors influencing the variability in physicochemical parameters in Lake Żabińskie.

According to our findings, nutrient cycling, steered by mixing regime, played a primary role in seasonal and interannual dynamics of diatoms and chrysophyte cysts, confirming that, despite anthropogenic impact, eutrophic Lake Żabińskie responds to climate change. Furthermore, our study revealed that unprecedented conditions connected to ongoing global warming, recorded in 2020 in the form of lack of ice cover, impacted the phenology of studied lake biota through changing the timing of their blooming. Species tolerance to already high-nutrient, turbid and low-light eutrophic conditions resulted in shifting the point at which the changes in seasonality will occur. We also recognized that changes in meteorological conditions induce community composition turnover.

Identified links between changes in meteorological conditions, lake dynamics and diatom distribution suggest that the utility of diatoms in climate related studies of modern sedimentation and paleoclimatic reconstruction in eutrophic lakes is limited only to some aspects. Although we recognized the indirect relationships between chrysophyte cysts and meteorological conditions, their overall low total fluxes and susceptibility to even small deviations in lake conditions suggest that their quantity should not be used in inferring climatic variability. Nevertheless, we observed compositional turnover associated with weather variability between studied years, thus suggesting that changes in cyst types dominance and composition indicate a response to different weather conditions even under eutrophic conditions. Our study suggests that future research should focus on investigations of the seasonality of biological proxies, and, in particular, investigations of the patterns of total fluxes and species succession, as they can reveal the impact of climate change on biota in high trophy lakes.

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Authorship Contribution Statement

Conceptualization, conducting the research: AS, SPR, WT. Data analysis, preparation of figures and tables, writing-original draft: AS. Writing-review & editing, supervision: SPR, WT. Funding acquisition: WT.

Data Availability Statement

Data are available from the authors upon reasonable request.

Conflict of Interest Statement

The authors have no conflict of interest to declare.

References

Alipanah L., Winge P., Rohloff J., Najafi J., Brembu T. & Bones A.M. (2018). Molecular adaptations to phosphorus deprivation and comparison with nitrogen deprivation responses in the diatom Phaeodactylum tricornutum. PLoS ONE 13, e0193335. https://doi.org/10.1371/journal.pone.0193335

Battarbee R.W., Jones V.J., Flower R.J., Cameron N.G., Bennion H., Carvalho L., et al. (2001). Diatoms. In: Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators. Developments in Paleoenvironmental Research, (Eds J.P. Smol, H.J.B. Birks, W.M. Last, R.S. Bradley & K. Alverson), pp. 155–202. Springer Netherlands, Dordrecht.

Battarbee R.W. & Kneen M.J. (1982). The use of electronically counted microspheres in absolute diatom analysis. Limnol. Oceanogr. 27, 184–188. https://doi.org/10.4319/lo.1982.27.1.0184

Bonk A., Tylmann W., Amann B., Enters D. & Grosjean M. (2014). Modern limnology, sediment accumulation and varve formation processes in Lake Żabińskie, northeastern Poland: comprehensive process studies as a key to understand the sediment record. J. Limnol. 73. http://dx.doi.org/10.4081/jlimnol.2014.1117

Bradbury J.P., Dean W.E. & Anderson R.Y. (1993). Holocene climatic and limnologic history of the north-central United States as recorded in the varved sediments of Elk Lake,

Minnesota: A synthesis. In: Elk Lake, Minnesota: Evidence for Rapid Climate Change in the North-Central United States. (Eds J.P. Bradbury & W.E. Dean), Geological Society of America.
Catalan J. & Fee E.J. (1994). Interannual variability in limnic ecosystems: origin, patterns, and predictability. In: Limnology Now: A Paradigm of Planetary Problems. pp. 81–97. Elsevier Science, New York.
Catalan J., Pla S., Rieradevall M., Felip M., Ventura M., Buchaca T., et al. (2002). Lake Redó ecosystem response to an increasing warming the Pyrenees during the twentieth century. J. Paleolimnol. 28, 129–145. https://doi.org/10.1023/A:1020380104031
Catalan J., Pla-Rabés S., Wolfe A.P., Smol J.P., Rühland K.M., Anderson N.J., et al. (2013). Global change revealed by palaeolimnological records from remote lakes: a review. J. Paleolimnol. 49, 513–535. https://doi.org/10.1007/s10933-013-9681-2
De Jong R., Kamenik C. & Grosjean M. (2013). Cold-season temperatures in the European Alps during the past millennium: variability, seasonality and recent trends. Quat. Sci. Rev. 82, 1–12. https://doi.org/10.1016/j.quascirev.2013.10.007
Dixit S.S., Smol J.P., Kingston J.C. & Charles D.F. (1992). Diatoms: powerful indicators of environmental change. ES&T 26, 22–33. https://doi.org/10.1021/es00025a002
Duff K., Zeeb B.A. & Smol J.P. (1995). Atlas of Chrysophycean Cysts. Springer Netherlands, Dordrecht.
Eloranta P. (1995). Biogeography of chrysophytes in Finnish lakes. In: Chrysophyte Algae: Ecology, Phylogeny and Development. pp. 214–231. Cambridge University Press, Cambridge.
Guiry M.D. & Guiry G.M. (2022). AlgaeBase. World-wide electronic publication, National University of Ireland.
Hausmann S. & Pienitz R. (2007). Seasonal climate inferences from high-resolution modern diatom data along a climate gradient: a case study. J. Paleolimnol. 38, 73–96. https://doi.org/10.1007/s10933-006-9061-2
Hernández-Almeida I., Grosjean M., Przybylak R. & Tylmann W. (2015a). A chrysophyte-based quantitative reconstruction of winter severity from varved lake sediments in NE Poland during the past millennium and its relationship to natural climate variability. Quat. Sci. Rev. 122, 74–88. https://doi.org/10.1016/j.quascirev.2015.05.029
Hernández-Almeida I., Grosjean M., Tylmann W. & Bonk A. (2015b). Chrysophyte cyst-inferred variability of warm season lake water chemistry and climate in northern Poland: training set and downcore reconstruction. J. Paleolimnol. 53, 123–138. https://doi.org/10.1007/s10933-014-9812-4
Institute of Meteorology and Water Management-National Research Institute https://danepubliczne.imgw.pl/. Public data of IMWR-NRI
Interlandi S.J., Kilham S.S. & Theriot E.C. (1999). Responses of phytoplankton to varied resource availability in large lakes of the Greater Yellowstone Ecosystem. Limnol. Oceanogr. 44, 668–682. https://doi.org/10.4319/lo.1999.44.3.0668
Jeppesen E., Søndergaard M., Jensen J.P., Havens K.E., Anneville O., Carvalho L., et al. (2005). Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. Freshw. Biol. 50, 1747–1771. https://doi.org/10.1111/j.1365-2427.2005.01415.x
Kamenik C. & Schmidt R. (2005). Chrysophyte resting stages: a tool for reconstructing winter/spring climate from Alpine lake sediments. Boreas 34, 477–489. https://doi.org/10.1080/03009480500231468
Kienel U., Kirillin G., Brademann B., Plessen B., Lampe R. & Brauer A. (2017). Effects of spring warming and mixing duration on diatom deposition in deep Tiefer See, NE Germany. J. Paleolimnol 57, 37–49. https://doi.org/10.1007/s10933-016-9925-z

Korkonen S.T., Ojala A.E.K., Kosonen E. & Weckström J. (2017). Seasonality of chrysophyte cyst and diatom assemblages in varved Lake Nautajärvi – implications for palaeolimnological studies. J. Limnol. 76. https://doi.org/10.4081/jlimnol.2017.1473

Krammer K. & Lange-Bertalot H. (1986). Bacillariophyceae 1. Teil: Naviculaceae. In: Süßwasserflora von Mitteleuropa Band 2/1. (Eds H. Ettl, J. Gerlof, H. Heynig & D. Mollenhauer), p. 876. Jena.

Krammer K. & Lange-Bertalot H. (1988). Bacillariophyceae 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. In: Süßwasserflora von Mitteleuropa, Band 2/2. (Eds H. Ettl, J. Gerloff, H. Heynig & D. Mollenhauer), p. 596. Gustav Fischer Verlag, Stuttgart.

Krammer K. & Lange-Bertalot H. (1991a). Bacillariophyceae 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. In: Süßwasserflora von Mitteleuropa Band 2/3. (Eds H. Ettl, J. Gerloff, H. Heynig & D. Mollenhauer), p. 576. Gustav Fischer Verlag, Stuttgart.

Krammer K. & Lange-Bertalot H. (1991b). Bacillariophyceae 4. Teil: Achnanthaceae. In: Süßwasserflora von Mitteleuropa, Band 2/4. (Eds H. Ettl, G. Gärtner, J. Gerloff, H. Heynig & D. Mollenhauer), p. 437. Gustav Fischer Verlag, Stuttgart.

Liu X., Li Y., Shen R., Zhang M. & Chen F. (2022). Reducing nutrient increases diatom biomass in a subtropical eutrophic lake, China–Do the ammonium concentration and nitrate to ammonium ratio play a role? Water Res. 218, 118493. https://doi.org/10.1016/j.watres.2022.118493

Lotter A.F. & Bigler C. (2000). Do diatoms in the Swiss Alps reflect the length of ice-cover? Aquat. Sci. 62, 125–141. https://doi.org/10.1007/s000270050002

Maier D.B., Diehl S. & Bigler C. (2019). Interannual variation in seasonal diatom sedimentation reveals the importance of late winter processes and their timing for sediment signal formation. Limnol. Oceanogr. 64, 1186–1199. https://doi.org/10.1002/lno.11106

Maier D.B., Gälman V., Renberg I. & Bigler C. (2018). Using a decadal diatom sediment trap record to unravel seasonal processes important for the formation of the sedimentary diatom signal. J. Paleolimnol. 60, 133–152. https://doi.org/10.1007/s10933-018-0020-5

Meis S., Thackeray S.J. & Jones I.D. (2009). Effects of recent climate change on phytoplankton phenology in a temperate lake. Freshw. Biol. 54, 1888–1898. https://doi.org/10.1111/j.1365-2427.2009.02240.x

Nazari Sharabian M., Ahmad S. & Karakouzian M. (2018). Climate Change and Eutrophication: A Short Review. Engineering, Technology & Applied Science Research 8, 3668–3672. https://doi.org/10.48084/etasr.2392

Pilla R.M. & Williamson C.E. (2022). Earlier ice breakup induces changepoint responses in duration and variability of spring mixing and summer stratification in dimictic lakes. Limnol. Oceanogr. 67, S173–S183. https://doi.org/10.1002/lno.11888

Pla S. (2001). Chrysophycean cysts from the Pyrenees. Bibliotheca Phycologica.

Pla S. & Catalan J. (2005). Chrysophyte cysts from lake sediments reveal the submillennial winter/spring climate variability in the northwestern Mediterranean region throughout the Holocene. Clim. Dyn. 24, 263–278. https://doi.org/10.1007/s00382-004-0482-1

Pla S., Paterson A.M., Smol J.P., Clark B.J. & Ingram R. (2005). Spatial Variability in Water Quality and Surface Sediment Diatom Assemblages in a Complex Lake Basin: Lake of the Woods, Ontario, Canada. J. Great Lakes Res. 31, 253–266. https://doi.org/10.1016/S0380-1330(05)70257-4

Pla-Rabes S. & Catalan J. (2011). Deciphering chrysophyte responses to climate seasonality. J. Paleolimnol. 46, 139–150. https://doi.org/10.1007/s10933-011-9529-6

Poikane S. (2009). Water Framework Directive intercalibration technical report. Part 2: Lakes. OPOCE, Luxembourg.

Råman Vinnå L., Medhaug I., Schmid M. & Bouffard D. (2021). The vulnerability of lakes to climate change along an altitudinal gradient. Commun. Earth Environ. 2, 1–10. https://doi.org/10.1038/s43247-021-00106-w

Reavie E.D. & Kireta A.R. (2015). Centric, Araphid and Eunotioid Diatoms of the Coastal Laurentian Great Lakes. Bibliotheca Diatomologica 62.

Reynolds C.S. (2006). The Ecology of Phytoplankton. Cambridge University Press, Cambridge.

Rühland K.M., Paterson A.M. & Smol J.P. (2015). Lake diatom responses to warming: reviewing the evidence. J. Paleolimnol. 54, 1–35. https://doi.org/10.1007/s10933-015-9837-3

Schneider P. & Hook S.J. (2010). Space observations of inland water bodies show rapid surface warming since 1985. Geophys. Res. Lett. 37. https://doi.org/10.1029/2010GL045059

Szczerba A., Pla-Rabes S., Żarczyński M. & Tylmann W. (2021). The relationship between chrysophyte cyst assemblages and meteorological conditions: Evidence from a sediment-trap study in northeast Poland. Ecol. Indic. 133, 108395. https://doi.org/10.1016/j.ecolind.2021.108395

Szczerba A., Rzodkiewicz M. & Tylmann W. (2023). Modern diatom assemblages and their association with meteorological conditions in two lakes in northeastern Poland. Ecol. Indic. 147, 110028. https://doi.org/10.1016/j.ecolind.2023.110028

Tylmann W., Głowacka P. & Szczerba A. (2017). Tracking climate signals in varved lake sediments: research strategy and key sites for comprehensive process studies in the Masurian Lakeland. Limnol. Rev. 17, 159–166. https://doi.org/10.1515/limre-2017-0015

Vrede T., Ballantyne A., Mille-Lindblom C., Algesten G., Gudasz C., Lindahl S., et al. (2009). Effects of N : P loading ratios on phytoplankton community composition, primary production and N fixation in a eutrophic lake. Freshw. Biol. 54, 331–344. https://doi.org/10.1111/j.1365-2427.2008.02118.x

Wilkinson A.N., Zeeb B.A. & Smol J.P. (2001). Atlas of Chrysophycean Cysts: Volume II. Springer Netherlands, Dordrecht.

Winder M. & Sommer U. (2012). Phytoplankton response to a changing climate. Hydrobiologia 698, 5–16. https://doi.org/10.1007/s10750-012-1149-2

Witak M., Hernández-Almeida I., Grosjean M. & Tylmann W. (2017). Diatom-based reconstruction of trophic status changes recorded in varved sediments of Lake Żabińskie (northeastern Poland), AD 1888-2010. Oceanol. Hydrobiol. Stud. 46, 1–17. https://doi.org/10.1515/ohs-2017-0001

Woolway R.I. & Merchant C.J. (2019). Worldwide alteration of lake mixing regimes in response to climate change. Nat. Geosci. 12, 271–276. https://doi.org/10.1038/s41561-019-0322-x

Żarczyński M., Zander P.D., Grosjean M. & Tylmann W. (2022). Linking the formation of varves in a eutrophic temperate lake to meteorological conditions and water column dynamics. Sci. Total Environ. 842, 156787. https://doi.org/10.1016/j.scitotenv.2022.156787

Supplementary materials – Publication 3

Tab. S1. Information about the concentration of nutrients and chlorophyll-a in the photic zone, and Secchi depth during the observation period.

Variable:	*Total, P* *($\mu g\ l^{-1}$)*	*Total, N* *($\mu g\ l^{-1}$)*	*Chl-a* *($\mu g\ l^{-1}$)*	*Secchi depth (m)*
Mean:	*118.89*	*1121.82*	*19.51*	*1.52*
Minimum:	*21.00*	*290.00*	*1.40*	*0.70*
Maximum:	*990.00*	*2510.00*	*126.57*	*3.70*

Tab. S2. Summary of meteorological conditions and water column characteristics during the observation period.

Variable:	*2017*	*2018*	*2019*	*2020*
Mean AT during spring mixing [°C]:	*8.14*	*14.80*	*10.37*	*5.27*
Mean AT during fall mixing [°C]:	*4.89*	*5.46*	*6.13*	-
Mean WS during spring mixing [m s⁻¹]:	*3.36*	*3.38*	*3.60*	*3.99*
Mean WS during fall mixing [m s⁻¹]:	*3.91*	*3.63*	*4.15*	-
Ice cover length [days]:	*75*	*88*	*77*	*2*
Spring mixing depth [m]:	*28*	*28*	*24*	*44*
Fall mixing depth [m]:	*30*	*17*	*36*	-

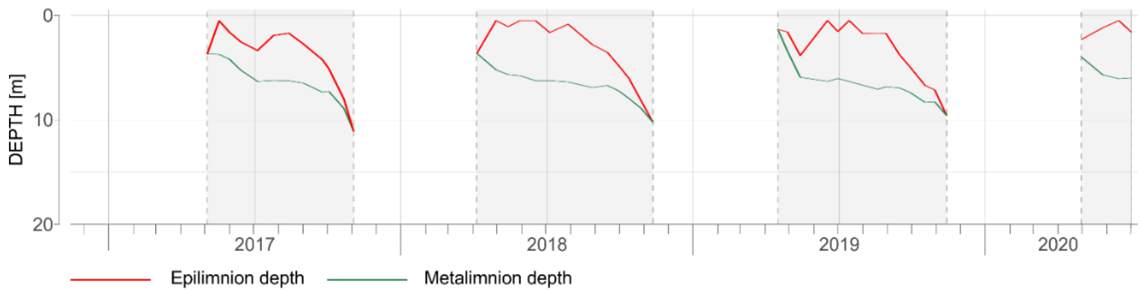

Fig. S1. Depths of epilimnion and metalimnion during the observation period.

Statement of Co-Authorship

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I hereby confirm my contribution to the submitted manuscript: "Control of diatoms and chrysophyte cysts dynamics by a meteorological-driven mixing regime in eutrophic Lake Żabińskie, northern Poland" (Freshwater Biology, 2023) being a part of the doctoral dissertation "Tracking climate signals in lakes of northeastern Poland: modern sedimentation studies using chrysophyte cysts and diatoms".

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Wojciech Tylmann

Appendix

OŚWIADCZENIE

Ja niżej podpisana Agnieszka Szczerba, absolwentka Środowiskowych Studiów Doktoranckich na Wydziale Oceanografii i Geografii (Uniwersytet Gdański) oświadczam, że przedłożona przeze mnie praca doktorska pt.: „Tracking climate signals in lakes of northeastern Poland: modern sedimentation studies using chrysophyte cysts and diatoms" („Poszukiwanie sygnału klimatycznego w jeziorach północno-wschodniej Polski: badania współczesnej sedymentacji z wykorzystaniem cyst złotowiciowców i okrzemek") jest oryginalna, została wykonana samodzielnie, przedstawia wyniki badań wykonanych pod kierunkiem Prof. dr hab. Wojciecha Tylmanna oraz Dr hab. Moniki Rzodkiewicz, Prof. UAM, a także nie narusza praw autorskich, interesów prawnych i materialnych innych osób.

Gdynia, 05.05.2023..........

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Agnieszka Szczerba