Diatom communities of lake/stream networks in the Tatra Mountains, Poland, and the Swiss Alps

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Abstract

Diatom communities in alpine-zone streams of the Tatra National Park and the Swiss National Park were heterogeneous with respect to species richness, abundance, Shannon diversity index, and ecological preference. Two groups of diatoms were distinguished. Group 1, inhabited streams in the upper Gąsienicowa Valley (Tatra Mts) and Macun Lakes region (Alps), and had high species richness and Shannon diversities (especially in the Tatra Mts streams) but low abundances. The most abundant and common diatoms were Psammothidium helveticum, Diatoma mesodon, Aulacoseira alpigena, Achnanthidium minutissimum, Psammothidium subatomoides, Psammothidium marginatum, and Gomphonema parvulum. Group 2 inhabited Tatra Mts
streams in the Five Polish Lakes Valley and lower Gąsienicowa Valley. Diatoms were highly abundant but species richness and Shannon diversities were relatively low. The most abundant were *Achnanthidium minutissimum*, *Diatoma mesodon*, *Fragilaria capucina gracilis* group and *Tabellaria flocculosa*. There was no clear difference between the diatom communities of the outlet streams of upper lakes and the inlet streams of adjacent downstream lakes. The high abundance of diatoms in the streams of the Tatra Mts suggests recent ecosystem changes related to lake eutrophication and partly by weather anomalies resulting from climate change.

**INTRODUCTION**

Although recent efforts have increased our ecological understanding of high elevation lakes and glacier-fed rivers (e.g., EU Projects: ALPE-Alpine lakes, Paleolimnology and Ecology, MOLAR-Mountain Lake Research, EMERGE-European Mountain Lake Ecosystems, AASER-Arctic and Alpine Stream Ecosystem Research), aquatic alpine environments have still been relatively little studied (but see Ward and Uehlinger 2003). Running waters in alpine areas consist primarily of spring-fed (krenal), glacier-melt-fed (kryal) and seasonal snowmelt/rainfall-fed (rhithral) systems (Ward 1994), although combinations of water sources are also common (Brown et al. 2003). In addition, streams fed by lakes (outlets) that store water from precipitation (rain and melting snow) or glacier melt are also frequent. These lake outlet streams are influenced by the origin of the lake water and form subclasses of rhithral and kryal systems (Hieber et al. 2002). Further, lake outlet streams often link lakes longitudinally along alpine stream networks (Wurtsbaugh et al. 2005, Robinson et al. 2007).

The aim of this study was to characterize diatom communities along lake/stream networks in the alpine zone of the Tatra Mountains (Tatra Mts) and the Swiss Alps. Special consideration was placed on lake outlet streams which constitute a transition zone (ecotone) between lake and stream habitats (Richardson and Mackay 1991, Hieber et al. 2002). Our objective was to test for community similarities between the different study areas, as literature comparing diatoms of different alpine lotic systems is scarce (Kann 1978, Kawecka 1971, 1980, 2008, Kownacki et al. 1997, Hieber et al. 2001, 2002).

**STUDY AREA**

The study was conducted in the high eastern part of the Tatra National Park (Poland) and in the Swiss National Park in Canton Graubunden (Switzerland) (Robinson and Kawecka 2005, 2007; Kawecka 2008). The examined streams flow over crystalline bedrock. The bedrock geology of the high Tatra Mts is granite, and that in the Alps study area is ortho-gneiss. Study streams are in the alpine zone above the tree line, which in the Tatra Mts is at around 1550 m above sea level (a.s.l.) and in the Alps around 2100 m a.s.l. The study streams
were above 1600 m a.s.l. in Poland and above 2600 m a.s.l. in Switzerland. Streams in the Tatra Mts interconnect adjacent lakes within high alpine cirques: in the Five Polish Lakes Valley (sample sites P1, P2, P3, P4) and the Gąsienicowa Valley (sample sites G1, G2, G3, G4, G6, G8) (Fig. 1, Table 1). These streams are fed by precipitation and flow from June to October. A loss of surface water is usually observed in the autumn, and during winter they are covered by snow. Streams between the lakes are generally <500 m in length.

In the Swiss Alps, the study was conducted in the Macun Lakes region, a high alpine cirque (Fig. 2, Table 1). The drainage network of the Macun Lakes is represented by a northern and a southern basin. Water sources in the north basin originate primarily from precipitation (mostly as snow) and in the south basin by glacial melt from rock glaciers. The annual flow regime differs between basins with the south basin experiencing more extreme channel contraction from the freezing of glacial water in autumn. Study streams included sites in the north basin (sample sites M1, M2, M3, M4) and south basin (sample sites M5, M6, M7, M8), with stream segments being <500 m in length. As a result of the bedrock geology streams in both areas had low

<table>
<thead>
<tr>
<th>Site abbreviation</th>
<th>Lake/stream network</th>
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<tr>
<td><strong>Five Polish Lakes Valley (alt. 1670-1880 m.)</strong></td>
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<tr>
<td>P1</td>
<td>Zadni Polski outlet</td>
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<td>P2</td>
<td>Wołe Oko inlet</td>
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<td>P3</td>
<td>Czarny Polski outlet</td>
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<td>P4</td>
<td>Wielki Polski inlet</td>
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<td><strong>Gąsienicowa Valley (alt.1610-1840 m.)</strong></td>
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<td>G1</td>
<td>Zadni Gąsienicowy outlet</td>
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<td>G3</td>
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<td>Czerwony inlet</td>
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<td>G6</td>
<td>Zielony Gąsienicowy outlet</td>
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<td>G8</td>
<td>Litworowy outlet</td>
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<td><strong>Macun Lakes area (alt. 2620-2668 m.)</strong></td>
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<td>M3</td>
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<td>Immez-north inlet</td>
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<td>M6</td>
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<td>M7</td>
<td>Sura outlet</td>
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<td>M8</td>
<td>Immez-south inlet</td>
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Fig. 1. Location of sampling sites on streams in the Tatra National Park (Gąsienicowa Valley and Five Polish Lakes Valley). See Table 1 for explanation of site abbreviations (the numbers of the sites according to Kawecka 2008).

Fig. 2. Location of sampling sites on streams in the Macun Lakes area in the Swiss National Park. See Table 1 for explanation of site abbreviations.
conductivity (12.5-23.9 μS cm\(^{-1}\) in the Tatra Mts and 5.7-14.1 μS cm\(^{-1}\) in the Alps). The sampled streams were oligotrophic in character with low phosphorus levels (<0.001-0.003 DIP mg l\(^{-1}\) in the Tatra Mts and <5 PO\(_4\)-P μg l\(^{-1}\) in the Alps) (Robinson and Kawecka 2005, 2007; Kawecka 2008).

MATERIALS AND METHODS

Diatoms of the Tatra Mts streams were collected in 1994, 1997 (Gąsienicowa Valley) and 2001 (Five Polish Lakes Valley), and those of the Macun Lakes streams in the Alps in 2002. Algal material was collected from the surface of stones by scrubbing with a brush and rinsing into a collection bottle. Moss was also collected when present at a site. The material was fixed with formalin (2-4%). In the laboratory, each sample was macerated in a chromic acid cleaning solution (3:1 sulphuric acid to potassium dichromate) for 1-2 days, and then washed by centrifugation. Diatoms from each sample were embedded permanently on glass slides with the synthetic resin Pleurax, which has a refractive index of 1.75. Slides of diatoms were examined using a Nikon microscope (Eclipse 600). Water samples for chemical analyses were collected from each study site, returned to the laboratory, and analyzed using methods described in Robinson and Kawecka (2005, 2007) and Kawecka (2008).

Diatom identifications were based on the following literature: Bukhtiyarova and Round (1996), Czarnecki (1994), Krammer (2000, 2002), Krammer and Lange-Bertalot (1991, 1999a,b; 2001), Lange-Bertalot (2001), Lange-Bertalot and Moser (1994), Lange-Bertalot and Metzeltin (1996), Round et al. (1990), and Round and Bukhtiyarova (1996). Diatom species abundance was determined by counting the cells of each species in 10 microscopic fields of view (after Kawecka 1980), and the percentage of each species in the community was calculated. Species representing >5% of the community were considered as numerous, while species representing <5% of the community were regarded as sporadic. A diversity index was calculated according to the Shannon and Weaver (1949) formula using log\(_2\). Shannon diversity and ecological groups of diatoms based on pH and trophy were determined using “Omnidia” software (Version 3) (Lecointe et al. 1993), and the following groups were distinguished according to Van Dam et al. (1994): for pH 1 = acidobiontic (optimal occurrence at pH <5.5), 2 = acidophilous (mainly occurring at pH <7), 3 = circumneutral (mainly occurring at pH values about 7), 4 = alkaliphilous (mainly occurring at pH >7), 5 = alkalibiontic (exclusively occurring at pH >7), 6 = indifferent (no apparent optimum); and for trophic state 1 = oligotraphentic, 2 = oligo-mesotraphentic, 3 = mesotraphentic, 4 = meso-eutraphentic, 5 = eutraphentic, 6 = hypertraphentic, and 7 = oligo- to eutraphentic. Cluster analysis was completed following Ward’s method based
RESULTS

Diatom communities inhabiting lake/stream networks in the Tatra Mts and the Alps were heterogeneous with respect to species richness, abundance, Shannon diversity and ecological preference. Kawecka (2008) and Robinson & Kawecka (2005, 2007) provide a list of diatoms identified in each of the study streams in the Tatra Mts and Macun Lakes, respectively.

In the streams of the Gąsienicowa Valley 174 species of diatom were found, and the number differed considerably between the study sites from 46 to 87 (Fig. 3). In the upper Gąsienicowa Valley (sample sites G1-G4) diatoms communities had mainly low abundances but high Shannon diversities. The following diatoms occurred most frequently: *Achnanthidium minutissimum, Eunotia exigua, Fragilaria capucina gracilis group, Psammothidium marginulatum* and *Tabellaria flocculosa*. Acidophilous and circumneutral groups of diatoms were dominant in these communities, with a relatively high percentage of acidobiontic species also present. With respect to trophy, oligomesotraphentic, oligotraphentic and oligotraphentic-eutraphentic groups of species prevailed. In the lower Gąsienicowa Valley (sample sites G6 and G8) Shannon diversities were lower than in the upper valley streams, and the abundance of *Fragilaria capucina gracilis* group substantially increased. The relative contribution of *Achnanthidium minutissimum* and *Brachysira intermedia* to communities also increased. The majority of diatoms in these streams were circumneutral and oligo-mesotraphentic.

In the diatom communities of the lake/stream systems in the Five Polish Lakes Valley, 81 species were found, ranging from 23 to 52 species at any individual site (Fig. 3). Species richness and Shannon diversities were generally low. In the upper valley (sample sites P1 and P2), *Diatoma mesodon* developed in masses (sometimes occurring as a monoculture). In the lower valley (samples sites P3 and P4), *Achnanthidium minutissimum* formed large assemblages, often occurring with *Fragilaria capucina gracilis* group, *Tabellaria flocculosa* and *Gomphonema clavatum*. With respect to pH the circumneutral group of diatoms was predominant and, with respect to trophy, oligo-mesotraphentic, oligo-eutraphentic and mesotraphentic diatoms dominated.

Diatom communities of the lake/stream network of the Macun Lakes comprised 112 species with species richness in the north and south basins equal, at 82 species each (Fig. 4). The number of species varied between sites from 19 to 51. In north basin streams, the diatom communities were relatively species rich. Communities were rather sparse but had high Shannon diversities. The
Fig. 3. Diatom community structures of lake/stream networks in Tatra Mts streams (Gąsienicowa Valley and Five Polish Lakes Valley). The most common species (>5% of the assemblage at each site) and their abundances are shown in the upper graph. Key = A - 200 cells, B - few cells, counted in 10 microscopic fields. The relative abundances of diatom groups based on the pH and trophic state classification systems are shown in the lower graph (after Van Dam et al. 1994).
Fig. 4. Diatom community structures of lake/stream networks in the Macun Lakes area. The most common species (>5% of the assemblage at each site) and their abundance are shown in the upper graph. Key = A - 200 cells, B - few cells, counted in 10 microscopic fields. The relative abundances of diatom groups based on the pH and trophic state classification systems are shown in the lower graph (after Van Dam et al. 1994).
most common diatoms were *Aulacoseira alpigena*, *Gomphonema parvulum*, *Tabellaria flocculosa* and, locally, *Luticola goeppertiana*. The species richness and Shannon diversities of diatom communities in the south basin streams were similar to those in the northern basin, most diatoms also occurring in low abundances. The contribution of *Diatoma mesodon*, *Psammothidium helveticum*, *P. marginulatum* and *P. subatomoides* increased in this area. With respect to pH, acidophilous, circumneutral, and alkaliophilous groups of diatoms were common in both basins. With respect to trophy oligotraphentic and eutraphentic groups of diatoms dominated in north basin streams and mesotraphentic and oligo-mesotraphentic groups dominated in south basin streams.

The structure of diatom communities in streams in the outlets of upstream lakes and inlets of adjacent downstream lakes was similar or varied with respect to the dominance of certain species. In Macun Lakes' streams, for example, *Luticola goeppertiana*, *Aulacoseira alpigena*, and *Pinnularia subcapitata* were abundant in lake outlets, whereas *Psammothidium helveticum*, *P. marginulatum* and *Fragilaria capucina* were abundant in the inlets of lower adjacent lakes.

Two groups of diatoms were evident when comparing all sites (Fig. 5). Group 1 included diatoms in most sites in the upper part of the Gąsienicowa Valley as well as those in the Macun Lakes region. In this group the diatom

![Dendrogram](https://www.oandhs.org)

**Fig. 5.** Dendrogram of similarities of diatom communities between the study sites in the Tatra Mts and Alps using 1-Pearson r correlation coefficient and Ward's method. See Table 1 for explanation of site abbreviations.
communities were mostly species rich, had low abundances, and high Shannon diversities (especially in the Tatra Mts). The most numerous diatoms in group 1 were *Psammothidium helveticum*, *Diatoma mesodon*, *Aulacoseira alpigena*, *Achnanthidium minutissimum*, *Psammothidium subatomoides*, *Psammothidium marginulatum*, *Gomphonema parvulum* and locally *Luticola goeppertiana*. Group 2 included diatoms inhabiting streams in the Five Polish Lakes Valley and in the lower part of the Gąsienicowa Valley. Diatoms had high abundances (especially in the Five Polish Lakes Valley), but relatively low species richness and Shannon diversities. The most numerous diatoms were *Achnanthidium minutissimum*, *Diatoma mesodon*, *Fragilaria capucina gracilis* group and *Tabellaria flocculosa*.

**DISCUSSION**

The structures of diatom communities in the examined lake/stream networks of the Tatra Mts and Alps differed with respect to species richness, abundance, Shannon diversity and proportion of groups showing ecological preferences. Lake outlet streams in the upper part of the Gąsienicowa Valley (subclass rhithral) and in the Macun Lakes region (subclass rhithral and kryal) had diatom communities with low abundance but generally high species richness and Shannon diversities (especially in the Tatra Mts streams). These streams had diatoms found in group 1. Species richness of diatoms in kryal lake outlets was higher than in kryal streams, a finding also reported by Hieber et al. (2001, 2002). In general, the richness of algal species, including diatoms, in kryal streams is considerably reduced (Kawecka 1974, 1980; Kawecka and Leo 1985; Cantonati et al. 2001, Gesierich & Rott 2004, Kawecka & Olech 2004). However, Rott et al. (2006) suggested that the reduction of algal species does not refer to diatoms, which may grow under the most severe conditions of the hypo-kryal reaches of glacial streams. The lower algal richness in kryal streams is caused by the harsh environmental conditions such as low temperature, diel and seasonal fluctuations in flow regime, high turbidity, and nutrient limitation (Kawecka 1980, Brittain and Milner 2001, Hieber et al. 2002, Ward and Uehlinger 2003, Rott et al. (2006). In contrast, lakes act as thermal and hydrological regulators that mitigate pronounced seasonality in the physico-chemical characteristics of kryal outlet streams (Brittain and Milner 2001, Hieber et al. 2002), resulting in habitat conditions that are more favorable for algal development and higher diversity.

Diatoms belonging to group 1 (e.g., *Psammothidium marginulatum* and *P. subatomoides*), that is species with preferences for northern Alpine conditions (Krammer and Lange-Bertalot 1991), were numerous in streams in the south basin of the Macun Lakes region, which were fed by glacial meltwater.
Psammothidium marginulatum was also reported as being characteristic of diatom communities inhabiting other (non-glacial) types of streams in the alpine zone of the Tatra Mts (Kawecka 2008). Diatom communities in these Tatra Mts streams were also characterized by low abundances but relatively high species richness and generally high Shannon diversities. These features indicate that these communities, and the habitat in which they have developed, are undisturbed. They form stable structures, which was confirmed by long-term observations. For example, the diatom communities of streams in the upper part of the Gąsienicowa Valley have had low abundances and high Shannon diversities over many years with a prevalence of acidophilous, and oligo- and oligo-mesotrophic groups of diatoms (Kawecka 2008).

Streams in the lower Gąsienicowa Valley (sample site G6) and Five Polish Lakes Valley (sample sites P1-P4) were inhabited by markedly different diatoms, and so were placed in group 2. High abundances of diatoms such as Diatoma mesodon and Achnanthidium minutissimum as well as Fragilaria capucina gracilis group (diatoms typically uncommon in the alpine zone) were found along with generally low species richness and Shannon diversities in these streams. Similarly, in undisturbed Tatra Mts streams such as Mięguszowiecki and Mnichowy, high abundances of Encyonema minutum and Achnanthidium minutissimum, along with low species richness and intermediate Shannon diversities, were recorded (Kawecka 2008). Such changes in diatom community structures suggest a change in environmental conditions such as, for example the deterioration of trophic status observed in Tatra lakes over the last few decades (Bombówna and Wojtan 1996, Kasza et al. 1997, Kawecka 2008), which resulted from stocking the Tatra lakes with fish (Kasza et al. 1997). For instance, Lakes Zielony Gąsienicowy, Przedni and Czarny Polski in the Five Polish Lakes Valley are stocked with trout (Salmo trutta m. fario L.), which may have increased nutrient loads, and consequently increased the abundance of diatoms in their outlet streams (sample sites G6 and P3-P4). The high abundance of Fragilaria capucina gracilis group in these streams, diatoms preferring oligo-mesotrophic waters (Van Dam et al. 1994), are probably related to these environmental conditions. In fact, this species has spread widely and become quite abundant in Tatra streams over the last few years (Kawecka 2008).

The increased development of certain diatoms in streams of the Five Polish Lakes Valley (sample sites P1-P2), as well as in Miegszowiecki and Mnichowy streams, also may have been caused by weather anomalies, recognized as a symptom of global climate change. Since 2001, periods of drought and strong spates have become more frequent in the Tatra Mts. These weather anomalies might have stimulated the development of species tolerant to a wide range of environmental conditions, such as Encyonema minutum or
Achnanthidium minutissimum. *Achnanthidium minutissimum* is a widespread and abundant diatom in mountain streams (Kawecka 2008), and it often dominates communities on highly disturbed substrates due to its high resistance to scour (Robinson and Rushforth 1987, Petersen and Stevenson 1992). Further, it also appears to be resistant to drought, being regularly found in moist areas (Van Dam et al. 1994). The frequency of occurrence of *Diatoma mesodon*, may have been stimulated by heavy precipitation and an increase in the flow of groundwater in the Five Polish Lakes Valley. This diatom is typically found in great abundance in spring areas of streams (Krammer and Lange-Bertalot 2000).

The ecological preference groups of diatoms reflected the chemical character of the different streams. In the streams of the Tatra Mts, with respect to pH acidophilous and acidobiontic (streams in the Gąsienicowa Valley) and circumneutral (most streams in the Five Polish Lakes Valley) groups of diatoms were predominant. With respect to trophy oligo-mesotraphentic as well as oligo- and indifferent diatom groups prevailed. Mesotraphentic diatoms were dominant in the Five Polish Lakes Valley.

In the Macun Lakes region, in the north basin in particular (sample sites M1 and M4), a high percentage of eutraphentic species were found in the streams, suggesting possible disturbances caused by nutrient enrichment. However, phosphorus concentrations were low, so the result may be from the overlap of two ecological features of the diatoms dominating there. For example, *Luticola goeppertiana* is characterized as an eutraphentic species, however, it also regularly occurs on wet and moist sites (Van Dam et al. 1994) and is resistant to desiccation (Krammer and Lange-Bertalot 1999a). Similar ecological preferences are found for *Gomphonema parvulum* (Van Dam et al. 1994). Many streams in alpine areas often lose water, or can even become dry, especially during autumn-winter (Rüegg and Robinson 2004, Robinson and Matthaei 2007), thus diatoms showing resistance to desiccation may be common there.

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