# Is diatom richness responding to catchment glaciation? A case study from Canadian headwater streams

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#### ABSTRACT

Due to global change affecting glaciers worldwide, glacial streams are seen as threatened environments deserving specific scientific interest. Glacial streams from the Coast Range and Rocky Mountains in British Columbia and at the border to Alberta were investigated. In particular glacial streams and downstream sites in the Joffré Lakes Provincial Park, a near by mountain river and two large glacial streams in the Rocky Mountains (Kootenay Range, Jasper National Park) were studied. Regardless of a high variability of catchment glaciation (1 to 99%) thin organic biofilms with firmly attached diatom frustules of the genera Achnanthidium, Psammothidium, Encyonema, Gomphonema and fragilaroid taxa were found in all cases. In spite of fundamentally different geological conditions between the Coast Range sites and the Rocky Mountain sites, the pioneer taxon Achnanthidium minutissimum (with a slimy long ecomorph) was dominating quantitatively in most of the glacier stream samples together with the rheobiontic Hannaea arcus. Individual glacier stream samples were characterized by the dominance of Achnanthidium petersenii and Gomphonema calcifugum/Encyonema latens. The diatom community analysis (cluster analysis) revealed the expected separation of glacier stream sites and sites of the lower segments of the river continuum (e.g., dominance of Diatoma chrenbergii in the mountain river). In the Joffré area, the total species richness of turbid glacial streams close to the glacier mouth was significantly lower than in the more distant sites. The two largest glacial streams in the Rocky Mountains showed divergent results with a remarkable high species richness (43 taxa) at the Athabasca River origin (Columbia Icefield) and low diversity in Illecillewaet river (9 km downstream the glacier mouth). From the biogeographical point of view the dominant taxa comprised mainly widespread pioneer species coping best with the unstable conditions, while the subdominant taxa comprised taxa specific for pristine arctic-alpine or high altitude habitats (e.g., Psammothidium grischunum). Almost 50% of the taxa were classified as oligo- to oligo-mesotraphentic and approximately 20% as endangered or extremely rare.

Key words: hydrobiology, glacial streams, oligotrophy, diatoms, biodiversity.

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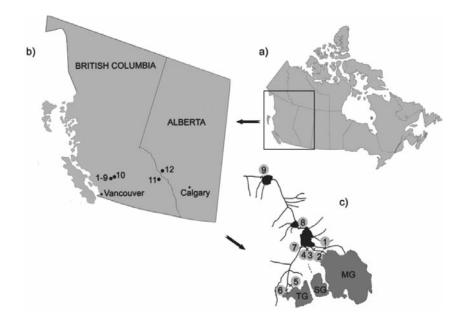
# INTRODUCTION

In mountain ranges worldwide the glaciation of drainage basins has a strong influence on the ecology of the adjacent glacial streams, specific high-alpine head-water types. Glacial streams show unique features, characterized by large seasonal and diurnal run-off fluctuations, strong longitudinal temperature gradients, restricted organic resources and temporarily enhanced sediment transport. They provide extremely harsh environments for benthic algae leading to the selection of a specific diatom species spectrum. Due to missing higher vegetation channel, shading is low and organic matter input limited (allochthonous of organic matter/nutrients). Eventual nutrient pulses originating from catchment washout are modified by temporal runoff pulses during snowmelt and/or from glacial flour during melting peak flows in summer (Rott et al. 2006).

Although several attempts were undertaken to extend the knowledge on alpine stream ecosystems (EU-funded projects: AASER – Arctic and Alpine Stream Ecosystem Research focusing on glacial stream ecosystems across Europe, Brittain et al. 2000; ARISE – A classification tool for

Alpine River and Stream Ecosystem, Brown et al. 2009, ACQWA-Assessing Climate impacts on the Quantity and quality of Water, http://www.acqwa.ch/), benthic algae are still a quite neglected component of investigations (e.g., Brittain, and Milner 2001, Cantonati et al. 2001). For high altitudes in the Alps mainly two major stream types can be differentiated, (A) kryal (glacialmelt dominated) and (B) krenal (groundwaterfed) streams (Ward 1994, Füreder 1999). The kryal stream section is characterised by constantly low temperatures (T<sub>max</sub><4°C) and extreme diurnal fluctuations of run-off in summer due to the diurnal air temperature variation in high altitudes of the glaciated areas. These run-off variations can be higher than the annual runoff variations. Additional typical features are extremely turbid waters from glacial silt and low channel stability close to the glacier mouth (Milner, and Petts 1994, Ward 1994). The glaciorhithral zone adjacent to the kryal segment is highly influenced by glacial runoff at some distance from the glacier mouth providing unstable substrate, high sediment loads and low summer temperatures (Füreder 1999).





**Fig. 1.** Geographic location of the sampling sites (1-12) in SW Canada (British Columbia, Alberta); a) overview, b) position of the sampling sites in the provinces of British Columbia and Alberta, c) detailed map of the sites 1-9 in Joffré Lake Provincial Park (MG – Matier glacier, SG – Stonecrop glacier, TG – Tszil glacier, black spots indicate Upper, Middle and Lower Joffré Lake).

Studies on benthic algae in alpine streams in general and glacial streams in particular are rare. Most recent studies were conducted in central and northern Europe dealing with the influence of glacial dynamics on benthic algae communities (e.g., Uehlinger et al. 1998; Cantonati et al. 2001; Bürgi et al. 2003; Gesierich, and Rott 2004; Hansen et al. 2006; Rott et al. 2010; Uehlinger et al. 2010) and the Himalaya (Jüttner et al. 2000). More studies on benthic algae and diatoms under extreme environment conditions were carried out in the Antarctic (e.g., Howard-Williams et al. 1986; Vincent, and Howard-Williams 1989) and Arctic region (Elster et al. 1997; Antoniades, and Douglas 2002), respectively. Although excellent expertises of diatoms from rivers in N-America have been accumulated in recent years (Anderson, and Carpenter 1998; Potapova, and Charles 2003; Bahls 2004, 2005; Carlisle et al. 2008; Potapova, and Carlisle 2011; USGS NAWQA Program 2011), small streams in pristine and remote areas, and especially glacial streams have not yet been in focus of interest, even though they can serve as remote lotic environment hotspots for biodiversity conservation (Cantonati et al. 2001). For the unglaciated Appalachians (East coast) an extended biodiversity inventory including diatoms has been made for the Great Smoky Mountains National Park (Johansen et al. 2004), representing data based on the survey of spring streams mainly from crystalline rocks serving as a reference to the present study. In multiple studies diatoms are widely used as indicators for environmental changes, in terms of climate change or acidification (e.g., Smol, and Störmer 2010), in this context complex information for low-alkalinity lakes throughout the NE United States and SE Canada are already given (Camburn, and Charles 2000).

The baseline hypotheses for the present study that only specific adapted algae may grow in glacier streams has been derived from periphyton studies of glacier streams in the European Eastern Alps (Rotmoos, Ötztal and National Park Hohe Tauern, Austria) (Rott et al. 2006). Here most algae groups except diatoms were considerably reduced in richness at distances of less than 1 km from the glacier mouth (Rott et al. 2006).

This actual case study therefore follows five major questions: (1) How close to the permanent ice are diatoms found in glacier streams? (2) Which taxa are present? (3) Is the taxonomic composition specific or variable? (4) Is the taxonomic composition affected by glacier size or other factors? and (5) Can glacial segments be differentiated from other sites within the river continuum?

# MATERIALS AND METHODS

Twelve sites were sampled in August 2006 in SW Canada (British Columbia, Alberta) (Figs 1a and b). The sites comprise the uppermost sections of variable sized glacial streams (from a few l s 1 to more than 5 m<sup>3</sup> s<sup>-1</sup>), glacial lake outflows and a rhithral mountain river. Catchment areas and catchment glaciation varies along a broad range (1 to 99%) (Tab. 1). Most sites (sites 1-9) were situated in Joffré Lakes Provincial Park (14.6 km<sup>2</sup>) 70 km SW from Lillooet in the Eastern part of Coast Mountains region of British Columbia (Fig. 1c). The bedrock is composed mostly of cretaceous origin granite and granodiorite



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Site	Nr	Т	Latitude N	Longitude W	Alt (m)	Size (km <sup>2</sup> )	Glac (%)	Run (m3)
Matier Glacier Creek, NE	1	KT	50°20'39.77"	122°28'11.61"	1780	0.49	48.2	0.2
Matier Glacier Creek, upper part	2	KT	50°20'40.62"	122°28'26.00"	1780	0.89	92.4	0.1
Matier Glacier Creek, lower part	3	KT	50°20'40.62"	122°28'26.00"	1600	0.94	88.0	0.6
Stonecrop glacier, SW of campground	4	KR	50°20'40.48"	122°28'35.89"	1580	0.32	44.6	0.1
Tszil glacier stream NE, under waterfall	5	KT	50°19'59.94"	122°29'14.55"	1900	0.14	45.0	<<0.1
Tszil glacier mouth + snow field	6	KT	50°19'50.21"	122°29'20.98"	1920	0.10	47.3	<< 0.1
Tszil stream down near lake	7	GR	50°20'44.57"	122°28'47.53"	1580	1.27	8.9	0.2
Upper Joffre Lake outlet, cascade	8	GR	50°21'04.48"	122°28'49.65"	1490	3.88	33.9	1.0
Outflow Lower Joffre Lake, near parking	9	R	50°22'06.68"	122°29'56.59''	1210	5.47	24.0	1.0-2.0
Cayoosh Creek	10	R	50°36'53.67"	122°06'13.92"	950	100.00	1.0	3.0-5.0
Illecillewaet, near campground	11	KT	51°15'58.91"	117°29'59.03"	1240	239.20	34.6	3.0-5.0
Athabasca River origin	12	KT	52°12'45.30"	117°14'02.15"	2000	300.00	99.0	3.0-5.0

**Tab. 1.** Location and characteristics of the investigated sites (1-12). Nr: Number of the sampling site; T: stream type (GR – glaciorhithral, KR - krenal, KT - kryal turbid, R – rhithral); Alt: altitude; Size: catchment size; Glac: catchment glaciation; Run – runoff).

(British Columbia's Online Digital Geology Map, http://www.empr.gov.bc.ca/Mining/Geoscience/BedrockM apping/Pages/BCGeoMap.aspx).

Most of these sites are strongly affected by glacial silt that is suspended in the water. Matier glacier, the largest glacier in the Joffré Group, is the origin to waters of sites 1-3, whereas site 4 is apparently indirectly influenced by the small Stonecrop rock glacier, at 1 km distance from the origin with less glacial silt particles than the others. Sites 5-6 are influenced by Tszil glacier to various extend. Two sites (8 and 9) were sampled downstream the existing lake basins of Middle and Lower Joffré Lakes within pine forests. Elevation gain from site 9 at the outflow of the lowest Joffré Lake near the parking area to site 6 near the glacier mouth of Tszil Glacier is about 710 m. The sampling area is characterised by the three small, turquoise blue Joffré lakes situated right below the massive Joffré Glacier Group.

Site 10 is located approx. 30 km NE of Joffré area, around 10 km SW from Lillooet in the Cayoosh Range, the northernmost section of the Lillooet Ranges in the Coast Mountains in British Columbia. Cayoosh Creek is a NE flowing tributary of the Seton River and represents a clear water mountain stream with minor glacial influence (1% catchment glaciation) sampled at an altitude of 950 m a.s.l. The Illecillewaet River (site 11) as part of the Columbia River watershed, is fed by Illecillewaet Glacier in Glacier National Park (1349 km<sup>2</sup>) in the NW part of the Kootenay Rocky Mountains. The catchment is a mixture of marble, dolomite, limestone and shists of Cambrian to Devonian and Upper Proterozoinc to Cambrian origin bedrocks and alluvial formations in the valley including proterozoic origin diorites (British Columbia's Online Digital Geology Map, http://www. empr.gov.bc.ca/Mining/Geoscience/ BedrockMapping/ Pages/BCGeoMap.aspx).

Athabasca Glacier is positioned in Jasper National Park (10,878 km<sup>2</sup>), known as the largest National Park in the Canadian Rockies in Alberta. The geology of the site is re-

lated to Paleozoic Cambrian to Ordovician strata of the Rockies (limestone, dolomite, quartzite and other carbonaceous minerals). Site 12 is situated approx. 100 m downstream the glacier mouth of Columbia Icefield at an altitude of 2000 m a.s.l. and is characterised by 99% catchment glaciation from a total icefield of 300 km<sup>2</sup>.

Epilithic diatoms were collected following standard procedures (e.g., European Committee for Standardization 2004), based on combined wash-samples from stones. Samples were cleaned using hydrochloric acid and 30% hydrogen peroxide. For light microscopy (LM) the mounting of the cover slips was done using Naphrax<sup>®</sup>, a mountant with a high refractive index ([R.I.]=1.74). An Olympus BX50-microscope equipped with a micro-camera (Olympus PM-C35B) was used for documentation. For scanning electron microscopy (SEM), subsamples of the diatom suspension were air-drying on glass cover slips and fixed on aluminium stubs with silver seal. The stubs were sputtercoated with gold and examined in a Hitachi S-4700 Field Emission Scanning Electron Microscope (FESEM) as well as in a Hitachi S-2600N Variable Pressure Scanning Electron Microscope (VPSEM).

The LM examinations were carried out at  $\times 1000$  magnification and at the lowest taxonomical level. A minimum of 300 valves were counted per slide for calculation of the relative abundance, with the exception of Site 6, near Tszil Glacier mouth, which was extremely poor in diatom valves (count of 100). The whole cover slip was screened after counting to characterise the actual species spectrum present at each site, and every new taxon was added to the species list with an absolute count of 1 individual (see Guidelines for biological water quality assessment in Austria: Part Phytobenthos, Pfister, and Pipp 2010). The relative abundance of each taxon was then indicated with: e - eudominant (>50%), d - dominant (50–20.1%), a - abundant (20–5.1%), o - occasional (5–1%) and s - scarce (<1%).

The standard literature was primarily used for species identification (Krammer, and Lange-Bertalot 1986-2004,



Lange-Bertalot, and Krammer 1989, Lange-Bertalot, and Moser 1994, Lange-Bertalot, and Metzeltin 1996, Krammer 1997a/b, Lange-Bertalot 2001) since the largest part of diatoms were widely distributed especially the artic alpine (circumpolar) taxa. In some cases of doubtful identification, the Monography on the diatoms of the United States was consulted (Patrick, and Reimer 1966). The thorough work on *Achnanthidium* taxa was largely based on Potapova, and Ponader (2004), Potapova, and Hamilton (2007), Ponader, and Potapova (2007) and the new online diatom identification guide of diatoms of the US (Spaulding et al. 2010, http://westerndiatoms. colorado.edu).

To provide taxonomic consistency with projects carried out in the US, terminology was based on the ANSP-2011 taxonomic system (The Academy of Natural Sciences of Philadelphia; Phycology Section, http://diatom.ansp.org/ taxaservice/). For those taxa not included in this list (9 taxa), taxa names were given according to Hofmann et al. (2011) and marked with an asterisk in the Appendix. For 2 taxa (*Achnanthes pusilla, Achnanthes petersenii*), we followed the taxonomy acc. to Hoffmann et al. (2011) and did not transfer them to the genus *Rossithidium*.

The distance from the glacier and the percentage of glaciation was calculated from geographic maps. Statistical analysis was based on SPSS 18.0 analytic software. Squared Euclidean distance was used as a measure of similarity between all cases based on presence / absence data (all 118 species). Hierarchical cluster analysis of the 12 investigated sites was carried out with Ward's linkage and Pearson's correlation coefficient has been used to measure the strength of the association between diatom richness and catchment glaciation/distance from the glacier.

# RESULTS

#### Diatom species spectrum

Diatom identification has yielded a total of 118 diatom taxa belonging to 38 genera, several characteristic taxa are illustrated in Figs 2 and 3. The genera richest in diatom taxa were Achnanthes related taxa (21 taxa), Navicula related taxa (14 taxa) and Cymbella related taxa (12 taxa). Generally a high percentage of diatom taxa (65%, 77 taxa) occurred only once (41 taxa) or twice (36 taxa) in the data set. Most taxa found in this study (92%, 108 taxa) were recorded in the ANSP-2011 taxonomic system (The Academy of Natural Sciences of Philadelphia; Phycology Section, http://diatom.ansp.org/ taxaservice/). The most frequent taxa in the data set were the oligotraphentic taxa Hannaea arcus, Achnanthidium minutissimum, Psammothidium grischunum, Tabellaria flocculosa and the oligomesotraphentic taxon Encyonema minutum (detected in at least 83% of the samples). Firmly attached small specimens of the genera Achnanthidium, Psammothidium, Encyonema, Fragilaria and Gomphonema were common at all

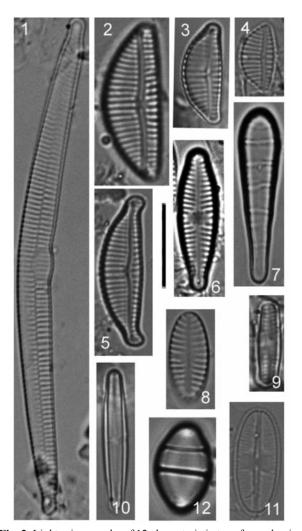
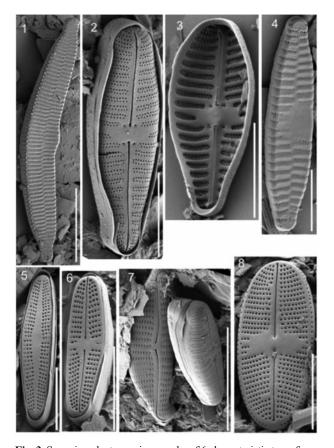


Fig. 2. Light micrographs of 12 characteristic taxa from gla-cier streams of SW Canada; 1 - Hannaea arcus, 2-4 - Encyonema minutum, 5 - Encyonema latens, 6 - Gomphonema calcifugum, 7 - Meridion circulare, 8 - Karayevia oblongella, 9 - Achnanthidium kriegeri, 10 - Achnanthidium minutissimum, 11 - Psammothidium grischunum; 12 - Diatoma mesodon, scale bar=10 µm.

sites. The quantitatively dominating taxa at most sites *Achnanthidium minutissimum* and *Hannaea arcus* were present in all the samples up to maximum relative abundances of 72% and 55%, respectively (Tab. 2). Species numbers ranged from 16 in the upper site of Matier Glacier creek (site 2) and in the site near Tszil Glacier mouth (site 6) to 50 in the outflow of the lowest Joffré Lake near the parking lot (site 9) (Fig. 4).

Those diatoms reaching more than 4% relative abundance in at least 1 sample (20 taxa) were chosen to represent the species spectrum (Tab. 2). Besides *Achnanthidium minutissimum* and *Hannaea arcus* were several *Achnanthes* related taxa (6 taxa) and *Encyonema* (4 taxa) characterizing the species spectrum. The oligo-mesotraphentic taxa *Encyonema minutum* and *Encyonema silesiacum* oc-



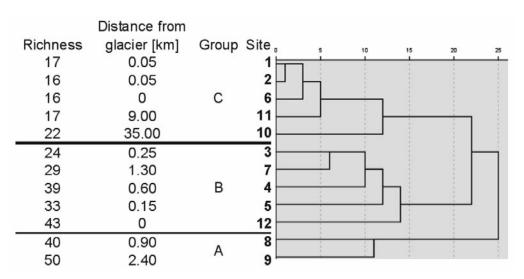


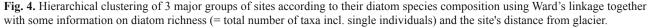
**Fig. 3.** Scanning electron micrographs of 6 characteristic taxa from site 4 (Stonecrop Glacier site) and 12 (Athabasca River) respectively, site numbers appear in brackets after the taxon name; 1 - *Hannaea arcus* (12), 2+3 - *Gomphonema calcifugum* (4), 4 - *Fragilaria vaucheriae* (12), 5+6 - *Achnanthidium minutissimum* (4), 7 - *Encyonema latens* (4), 8 - *Psammothidium grischunum* (4), scale bar = 5 µm (for numbers 1, 2, 7 the scale bar equals 10 µm).

curred in more than 2/3 of the sampling sites with maximum relative abundances of 6.8% and 11.0%, respectively. *Encyonema latens* was restricted to 3 sites only, most common at the Stonecrop Glacier site (site 4) with a relative abundance of 35.6%; this scarcely recorded taxon is known from Iceland, Spitzbergen, Alaska, Lake Michigan and the highlands of Venezuela (Krammer 1997a). *Encyonema neogracile* is restricted to two sites only, it was found in Tszil Glacier stream in higher abundances (11.2%).

Several small and firmly attached species of Achnanthes related taxa were found at all sites, but mainly or exclusively (15 taxa) in relative abundances <5%. The more frequent taxa Achnanthidium rivulare (5.8%) and Achnanthidium kriegeri (8.7%) were mostly found near the Tszil Glacier mouth (site 6), the latter occurred also in the upper part of Matier Glacier creek (site 2) with a proportion of 12.1%. Psammothidium grischunum (24.4%) and Achnanthes pusillum (5.4%) were characterizing the diatom assemblage further downstream in Tszil Glacier stream (site 5). Achnanthes petersenii was the dominating taxon in Illecillewaet River (site 11) with a relative abundance of 65.8%, a rarely recorded taxon at calcareous oligotrophic (up to mesotrophic) sites. In addition to these taxa Gomphonema calcifugum (oligo-mesotraphentic) and Fragilaria vaucheriae as well as Diatoma ehrenbergii/D. vulgaris are worth mentioning, the latter were restricted to Cayoosh Creek (site 10, 42.4% and 5.5%). Gomphonema calcifugum was found at various sites, reaching highest abundances near the Stonecrop glacier (site 4, 25.4%), whereas Fragilaria vaucheriae was frequent in the Upper Joffré Lake outlet (8.2%) and in Athabasca River (6.5%).

Trophic preferences were found from the literature for







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**Tab. 2.** Diatom species composition of 12 Canadian glacier streams. Ordination of samples and species according to cluster analysis (sample cluster see Fig. 4; taxa with relative abundance >4% in at least 1 sample); abundances given as 5 abundance classes: e - eu-dominant (>50%); d - dominant (50-20.1%); a - abundant (20-5.1%); o - occasional (5-1%); s - scarce (<1%); for explanation of site numbers see Tab. 1.

Site	1	2	6	11	10	3	7	4	5	12	8	9
Hannaea arcus	e	S	а	0	0	e	d	а	0	d	d	s
Achnanthidium minutissimum	а	e	e	а	а	а	а	а	d	d	d	а
Psammothidium grischunum	0	0	0	S		S	S	0	d	S	S	S
Encyonema minutum	а	0	0	S	0		0	0	а	0	S	s
Tabellaria flocculosa	S	0		0		S	а	S	S	0	S	e
Achnanthidium kriegeri	0	а	а	0			S	S	0			S
Encyonema silesiacum	S				а	S	а	0		а	S	S
Meridion circulare	а					S	S	S	S	S	S	S
Achnanthidium rivulare		0	а			S		S	S	S	S	
Gomphonema calcifugum						S	S	d	0	0	0	s
Achnanthes pusilla			0					S	а	S	S	S
Fragilaria vaucheriae					0	S	S			а	а	0
Achnanthidium linearioides		0		S			S					S
Achnanthes petersenii				e		S	0					
Encyonema latens						0		d		а		
Encyonema neogracile			0						а			
Gomphonema olivaceum					0					s		
Nitzschia fonticola					0					S		
Diatoma ehrenbergii					d							
Diatoma vulgaris					а							

78% of the diatom taxa (93 taxa). Half of the taxa (49%) were classified as oligotraphentic (4% ultraoligo-traphentic, 27% oligotraphentic, 18% oligo-mesotraphentic) and mesotraphentic (16%), another 27% as mesoeutraphentic (15%) and eutraphentic (12%). Only a very small proportion was classified with a preference for eupolytraphentic (5%) and polytraphentic conditions (2%) (Rott et al. 1999). Based on the Red List of algae for Germany (Lange-Bertalot, and Steindorf 1996) 103 diatom taxa (87%) could be classified with 21% (22 taxa) as endangered to various extend (critically endangered - 1 taxon, strongly endangered - 1 taxon, endangered - 1 taxa). A large proportion of arctic-alpine diatom species in the subdominant taxa was characterizing the data set.

# Classification of sites based on diatom species composition

From hierarchical cluster analysis of all sites based on presence / absence data including all 118 species found, three distinct groups (A-C) of sites were classified (Fig. 4). This differentiation of the major groups displays characters reflected mainly by the relative proportions of the different hydrological stream types: lake outlet, glacial (kryal) streams and krenal (spring fed) streams, respectively.

# GROUP A - lake outlets

The first group of sites, separated from the other sites on the first division level, was formed by the two lake outlets of Middle and Lower Joffré Lakes (sites 8, 9). These sites were characterised by the highest diatom richness within the Coast Mountain samples. The species spectrum from both sites showed beside typical stream taxa as *Achnanthidium minutissimum* and *Hannaea arcus*, small amounts of planktonic centric taxa (mostly *Cyclotella* species) and a dominance of *Tabellaria flocculosa*, a common littoral diatom, at the lower lake outlet (site 9).

# GROUP B – upper stream segments with different runoff sources

Group B was characterised by higher relative abundances of *Achnanthidium minutissimum* and *Hannaea arcus* accompanied by several taxa defining the subgroups. The small proportions of the crenophilous taxa *Meridion circulare* and *Diatoma mesodon* as well as *Tabellaria flocculosa*, typical for low mineral content, indicated the influence of different runoff sources (ground water?).

Sites 3 and 7 (Matier glacier creek lower part, Tszil stream downstream near lake) showed highest relative abundances of *Hannaea arcus* dominating at site 3, but H. arcus accompanied by *Diatoma mesodon*, *Tabellaria flocculosa* and *Encyonema silesiacum* at Site 7. Site 4 fed by stonecrop rock glacier was characterised by *Encyonema latens* and *Gomphonema calcifugum*. The species spectrum at site 5 (Tszil stream NE) was dominated by *Achnanthidium minutissimum*, *Psammothidium grischunum* and *Encyonema neogracile*, whereas at site 12 (Athabasca River) *Achnanthidium minutissimum* was prevailing together with *Hannaea arcus*.



#### GROUP C - hypokryal/glaciorhithral stream segments

All sites in Group C showed varying abundances of the typical stream taxa Achnanthidium minutissimum, Encyonema minutum and Hannaea arcus. Sites 1, 2 and 6 located directly at or close by the glacier mouth (site 1 and 2 adjacent to Matier Glacier, site 6 close to Tszil Glacier mouth) were characterised by higher amounts of Achnanthidium kriegeri and Psammothidium grischunum. Site 1 might have been influenced by spring (ground) water input indicated by higher abundances of Meridion circulare. Adjacent to these three hypokryal sites there was a grouping of site 11 (Illecillewaet River) and site 10 (Cayoosh Creek), both represented the most distant sites from the glacial outflow. Site 11 was dominated by the oligotraphentic taxon Achnanthes petersenii. Site 10 reflected changes of diatom communities along alpine rivers with a shift from small, adhesive taxa of the Achnanthes related taxa group (except Achn. minutissimum 12% rel. abundance at site 10) to a dominance of the chainforming taxa Diatoma spp. (Diatoma ehrenbergii dominant, D. vulgaris) and a sub-dominance of Encyonema spp. (Encyonema silesiacum, Encyonema minutum), Nitzschia spp. (Nitzschia fonticola, Nitzschia dissipata), Fragilaria vaucheriae, Reimeria sinuata and Gomphonema olivaceum (these 9 taxa account for 80% rel. abundance).

#### Longitudinal variation in species richness

For analysing the relationship between diatom species richness and glaciation of the catchment as well as distance from glacier, sites 1 to 6 in Joffré Lakes Provincial Park have been chosen, for their geographic position is <1 km from the glacier mouth (Fig. 1). The existing lake basin downstream the Upper Joffré Lake had a specific effect in alteration of diatom species composition, therefore site 8, although less than 1 km from the glacier mouth, was excluded from the data set. The total number of diatoms species for the small streams close to the glacier mouth displayed a significant positive relationship with distance from the glacier (Fig. 5) irrespective of catchment glaciation (r=0.176).

# The Athabasca River origin - a special habitat

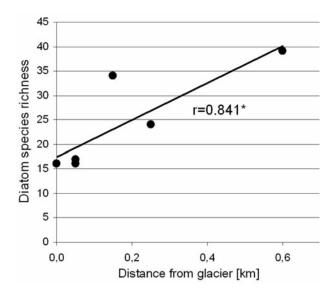
The taxa richness in Athabasca River at the glacier mouth (site 12) exceeded the expected results from the Austrian Alps with 43 diatom taxa recorded. It is most likely that the actual number of diatoms may be even higher than the one detected, since most of the taxa were detected only once in the slide (59%, 26 taxa). Nine species occurred in relative abundances >1% with *Achnanthidium minutissimum* dominating, accompanied by the rheophilous taxon *Hannaea arcus*, the nordic taxon *Encyonema latens*, *Encyonema silesiacum* and *Fragilaria vaucheriae* (Tab. 3).

Five taxa were restricted to this glacial outflow



(Achnanthidium jackii, Amphora inariensis, Encyonema mesianum, Diploneis ovalis, and Staurosirella pinnata group). Encyonema mesianum is a rarely found taxon in oligotrophic, electrolyte-poor habitats in high alpine regions.

The most species rich group amongst the 35 taxa reaching relative abundances <1% are the Achnanthes related taxa with 6 different genera (*Psammothidium grischunum*, *P. helveticum*, *Eucocconeis laevis*, *Planothidium lanceolatum*, *P. dubium*, *Achnanthidium jackii*, *A. rivulare*, *Karayevia oblongella*, *Achnanthes pusillum*) and *Nitzschia* spp. (*Nitzschia bryophila*, *N. cf. perminuta*, *N. dissipata*, *N. fonticola*, *N. pura*, *N. sublinearis*).



**Fig. 5.** Relationship between total species richness of diatoms and distance from glacier mouth in km for the 6 glacial stream sites in Joffré Lakes Provincial Park at distances of <1 km from the glacier mouth (sites 1 to 6); r- Pearson's Correlation Coefficient, \*=significant (p<0.05).

**Tab. 3.** Diatom composition (>1% relative abundance) and their relative abundance (%) from Athabasca River origin at Columbia ice field.

Taxon	%
Achnanthidium minutissimum	30.8
Hannaea arcus	25.9
Encyonema latens	8.7
Encyonema silesiacum	8.2
Fragilaria vaucheriae	6.5
Encyonema minutum	2.7
Gomphonema calcifugum	1.9
Fragilaria tenera	1.6
Tabellaria flocculosa	1.1

#### DISCUSSION

The findings from Canadian glacial streams confirmed our hypothesis that environmental conditions in turbid glacial streams seem to select specific attached algal communities (Gesierich, and Rott 2004). Although rarely recorded until now (*e.g.*, Jüttner et al. 2000; Cantonati et al. 2001; Gesierich, and Rott 2004; Rott et al. 2006), diatoms were well represented in all types of glacier streams even with peak flows in summer (with very variable runoff!) and very close to the glacier mouth.

The dominant species found in the Canadian glacier streams corresponded in most cases to findings from other glaciated mountain areas worldwide with two dominants: the pioneer taxon Achnanthidium minutissimum together with the rheobiontic Hannaea arcus (e.g., Cantonati et al. 2001), but contrasted to cryoconite holes dominated by other diatom taxa (e.g. Diadesmis, Mayamaea, Navicula, Luticola, Muelleria) more related to still water situations (Müllner et al. 2001; Yallop, and Anesio 2010). The nominate variety of the rheobiontic Hannaea arcus however is not an exclusive taxon of glacier streams since it was common in most other fast flowing streams in arctic, antarctic and Alaska (Milner et al. 1992; Beyens, and van de Vijver 2000). We did not encounter the expected variety recta of Hannaea arcus, although reported as fairly common for cold circumpolar situations and the Himalaya region (Cantonati et al. 2001). Although Achnanthidium minutissimum is supposed to be a widespread taxon, it comprises a variety of ecomorphs that have specific adaptive capacities to grow under oligotrophic cold water conditions (Potapova, and Hamilton 2007 - 6 morphotypes of A. minutissimum within a data set of 728 specimens of North American Rivers). Since the major taxonomic revisions of the Achnanthes related taxa, information on the autecological and biogeographical distribution of the new taxa is scarce. The presence of several Achnanthes related taxa (Achnanthes, Achnanthidium, Eucocconeis, Karayevia, Planothidium, Psammothidium) with variable ecological demands in the streams observed seemed to underpin the specific situation found here. For example, Achnanthidium minutissimum present at all sites, is preferring low nutrient and ionic content, whereas Achnanthidium rivulare, found with slightly higher abundances in two sites in the Coast Range, is mainly recorded from low calcium, high chloride, phosphorus poor soft waters (Potapova, and Ponader 2004; Ponader, and Potapova 2007).

Despite high variability of catchment glaciation and fundamentally different geological conditions between the Coast Range sites and the Rocky Mountain sites there was a specific diatom species composition in high altitude turbid glacial streams that corresponded to streams in the Eand SE-Alps (>60% of the most common diatoms from 42 high altitude turbid glacial streams in E- and SE-Alps match with the present study in Canadian glacial streams), including several characteristic taxa *e.g. Achnanthidium* minutissimum, Diatoma mesodon, Encyonema minutum, Gomphonema calcifugum, Hannaea arcus, Meridion circulare and Staurosirella pinnata (Rott et al. 2006).

A similarity of the characteristic taxa was even found when the present results were compared with the algal species records for the spring streams in the Great Smoky Mountains National Park (Johansen et al. 2004) with a lower proportion of 32% taxa in common. Specific arcticalpine elements of the diatom flora (Achnanthes petersenii, Encyonema latens and Gomphonema calcifugum) seemed to be common not only in glacier streams but also in arctic meltwater streams and small brooks (Van de Vijver et al. 2003) as well as in moss samples and shallow lotic sites with low current (pre-sumably being able to survive periods of desiccation, Antoniades, and Douglas 2002). Encyonema latens was also reported from a glacial pool formed by flooding of the surrounding area at high meltwater input from a glacial stream in the arctic (Elster et al. 1997), whereas Gomphonema calcifugum was prevailing at some sites in the Himalaya together with Diatoma mesodon (Cantonati et al. 2001).

It is known that algal assemblages are partly regulated by catchment characteristics (Pipp, and Rott 1993; Rott et al. 1997, 1999; Rott et al. 2006). Geology however seemed not to be of primary importance in these Canadian streams, since high variability of catchment glaciation and fundamentally different geological conditions between the Coast Range sites and the Rocky Mountain sites showed a quite similar diatom composition. Although clear changes of the diatom flora along the river continuum were observed in the Coast range, it was not primarily the size of the glacier and the geology but the site's distance from the glacier and the related changes in the hydrological regime that shaped diatom species composition most.

Apparently in those glacier streams, larger already at the outflow of the glacier, fast current and strong flow variations accounted for a more diverse community (see Athabasca River). Hydrology in turbid glacier streams including scouring by sediment load may have had a negative effect on benthic algal growth and species selection, whereas nutrient input (generally phosphorus), mainly washed out as glacial flour (produced by the mechanical action of the glacier ice to the ground) positively affected algae species in the Alps and other mountain ranges in moderate latitudes (Bürgi et al. 2003; Gesierich, and Rott 2004; Rott et al. 2006; Uehlinger et al. 2010). Particularly small celled diatoms with specific adaptation to live within the viscous sub layer close to the substrate (normally <<1 mm thick) can sustain these extreme environment conditions

Strong water level fluctuations, dynamic discharge patterns, flood pulses and instable substrate cause lower densities of algae and seem to favour small taxa with low

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biomass like the primary colonizer *Achnanthidium minutissimum* apparently firmly attached to stone substrates with the araphid valves (Peterson, and Stevenson 1992). Generally the diatoms at kryal sites (*e.g.*, *Achnanthidium*, *Psammothidium*, *Encyonema*, *Gomphonema*) are nonmotile and can resist the harsh hydraulic conditions with strong attachment abilities and their capability to live in the boundary layer near the surface or living attached to the substrate by mucilage or mucilaginous stalks. To some degree, due to their small size, they may be resistant to ingestion by grazers, like the cold-stenothermal chironomid species of the subfamily Diamesinae (Füreder et al. 2000, 2001).

# CONCLUSIONS

The results of this study and in particular the generally lower diatom species number close to the glacier mouth raise several open questions for future investigations in these remote areas.

- 1) How fast can diatom pioneers reach recently formed streams in glacier retreat areas? Which taxa arrive first?
- 2) Is the species spectrum a consequence of stream size and hydraulic conditions or other factors (channel features, nutrients from glacial flour, topography etc.)?
- Are the diatom taxa from glacier streams psychrophilic (=cold loving)? If diatoms restricted to low temperatures exist, climate change would cause a considerable threat (Harte et al. 2004; Thomas et al. 2004).
- What would happen if most glacier streams would dry off in summer? Essential elements of the diatom flora may disappear.
- 5) What are the effects of shrinking glaciers, decreasing melt-water input and increasing water temperature on diatom growth and closely related kryal grazers (*e.g.*, several species within the genus *Diamesa*)?

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#### APPENDIX

Overall diatom species list (118 taxa) including relative abundances (%) at sites 1-12 in SW-Canada; red list classification (RL) according to Lange-Bertalot, and Steindorf (1996) and trophic indication values (T) according to Rott et al. (1999); 1 – threatened with extinction; 2 - severly endangered 3 – endangered, G - probably endangered, R - rare, V – decreasing, \* - at present not considered threatened, \*\* - surely not threatened, • - to be expected within the area, D – data scarce; uo – ultraoligotraphentic, o – oligotraphentic, om – oligomesotraphentic, m – mesotraphentic, me – mesoeutraphentic, e – eutraphentic, ep – eupolytraphentic, p – polytraphentic; taxa names acc. to ANSP-2011 taxonomic system, taxa names marked with an asterisk are taken from Hofmann et al. (2011).

Taxon	RL	Т	1	2	3	4	5	6	7	8	9	10	11	12
Achaenthes related taxa						0.3	0.6							
Achnanthes acidoclinata Lange-Bertalot Achnanthes petersenii Hustedt					0.3	0.5	0.0		1.3				65.8	
Achnanthes petersenti Hustedi Achnanthes pusilla (Grunow) DeToni	2				0.5	0.3	5.4	2.9	1.5	0.3	0.3		05.8	0.5
Achanthes pushia (Grunow) Deroni Achanthes trinodis (Ralfs) Grunow	3	0	0.3			0.5	0.3	2.9		0.5	0.5			0.5
Achnanthidium caledonicum (Lange-Bertalot) Lange-Bertalot	3	0	0.5	0.7			0.5			0.9				
Achnanthidium jackii Rabenhorst	D	om		0.7						0.9				0.8
Achnanthidium kriegeri (Krasske) Hamilton, Antoniades, and Siver	•	om	1.9	12.1		0.3	1.6	8.7	0.9		0.3		3.6	0.0
Achnanthidium linearioides (Lange-Bertalot) Lange-Bertalot*	3	m	1.9	4.6		0.5	1.0	0.7	0.3		0.3		0.3	
Achnanthidium minutissimum (Kützing) Czarnecki	**	om	16.6		99	8.0	25.0	58.3	17.3	48.9		12.1	17.9	30.8
Achnanthidium pyrenaicum (Hustedt) Kobayashi	**	om	10.0	12.2	/./	0.0	20.0	50.5	17.5	10.9	0.3	1.3	17.9	50.0
Achnanthidium rivulare Potapova, and Ponader				3.3	0.3	0.3	0.3	5.8		0.3				0.5
Eucocconeis flexella (Kützing) Cleve	3	uo									0.3			
Eucocconeis laevis (Østrup) Lange-Bertalot	*	om				0.3				0.3	0.3			0.3
Karayevia oblongella (Østrup) Aboal	V	0	0.3	1.0			1.0				0.3			0.3
Planothidium delicatulum (Kützing) Round, and Bukhtiyarova	*	e				0.3								
Planothidium dubium (Grunow) Round, and Bukhtiyarova	*									0.3	0.3			0.5
Planothidium lanceolatum (Brebisson ex Kützing) Lange-Bertalot	**	ep			0.3	0.3								0.3
Psammothidium grischunum (Wuthrich) Bukhtiyarova, and Round	*	•	2.6	1.6	0.3	4.6	24.4	3.9	0.6	0.3	0.3		0.7	0.5
Psammothidium helveticum (Hustedt) Bukhtiyarova, and Round	*	0				0.3		1.0		0.3				0.3
Psammothidium rechtensis (Leclercq) Lange-Bertalot	R	om					1.6			0.3				
Psammothidium subatomoides (Hustedt) Bukhtiyarova, and Round	V	me									0.3			
Amphora inariensis Krammer	3	me												0.3
Amphora pediculus (Kützing) Grunow	**	e								0.3		0.3		
Aulacoseira cf. italica (Ehrenberg) Simonsen	V									0.3	0.3			
Brachysira brebissonii Ross	*	om					0.3							
Brachysira neoexilis Lange-Bertalot*	*	om								0.3	0.3		0.7	
Brachysira sp.									0.3					0.3
Brachysira vitrea (Grunow) Ross	3	0	0.3	0.3		1.0								
Caloneis cf. ventricosa var. truncatula (Grunow) Meister	D					1.2				0.0				
Cocconeis neodiminuta Krammer	R **					0.0				0.3				
Cocconeis placentula Ehrenberg	**	e				0.3				0.3		0.3		
Cocconeis placentula var. lineata (Ehrenberg) Van Heurck	*	me				0.3				0.2	20	0.5		
Cyclotella ocellata Pantocsek	**	om				0.5				0.3 1.1	2.6			
Cyclotella pseudostelligera Hustedt* Cymbella related taxa										1.1				
<i>Cymbella amphicephala</i> Nägeli	v					0.3								
Cymbella cistula (Ehrenberg) Kirchner	v	om me				0.5				0.3	0.3			
Cymbella helvetica (Kützing)	v	om								0.5	0.5	1.1		
Encyonema gaeumannii (Meister) Krammer	3	0										1.1	0.7	
Encyonema latens (Krasske) Mann	•	0			2.5	35.6							0.7	8.7
Encyonema tatens (Klasske) Mann Encyonema mesianum (Cholnoky) Mann	v	m			2.5	35.0								0.3
Encyonema minutum (Cholnoky) Mahn	*	m	6.8	1.0		3.7	5.4	1.9	1.6	0.6	03	3.9	0.3	2.7
		m	0.0	1.0		5.1	J.7	1.)	1.0	0.0	0.5	5.7	0.5	2.7



# Diatom richness in glacial streams

# APPENDIX: Continuation

Taxon	RL	Т	1	2	3	4	5	6	7	8	9	10	11	12
Encyonema neogracile Krammer	3	0					11.2	1.0						
Encyonema silesiacum (Bleisch) Mann	*	m	0.6		0.3	3.4			11.0	0.3 0.3	0.3 0.3	9.2	1.6	8.2 0.3
Encyonopsis cesatii (Rabenhorst) Krammer Encyonopsis microcephala (Grunow) Krammer	*	o om							0.3	0.5	0.5		1.0	0.5
Reimeria sinuata (Gregory) Kociolek, and Stoermer	**	me			0.3	0.3			0.3			2.9		0.8
Diatoma anceps (Ehrenberg) Kirchner	*	uo							0.3		0.3			0.3
Diatoma ehrenbergii Kützing	**	m			0.6			1.0	6.0	0.0	0.0	42.4		0.5
Diatoma mesodon (Ehrenberg) Kützing Diatoma vulgaris Bory	* D	o m			0.6	2.2		1.9	6.0	0.3	0.3	5.5		0.5
Didymosphenia geminata (Lyngbye) Schmidt	1	0								0.3		5.5		
Diploneis ovalis (Hilse) Cleve	V	õ												0.3
Diploneis sp.							0.3				0.3			
Eunotia bilunaris (Ehrenberg) Souza	** V	0	0.6	0.2	0.3	0.3	0.3 2.6	1.9			0.3 0.3			0.2
Eunotia cf. paludosa Grunow Eunotia exigua (Brébisson) Rabenhorst	V **	uo	0.0	0.3 0.3	0.5	0.3	2.0	1.9			0.5			0.3
Eunotia implicata Nörpel, Alles, and Lange-Bertalot	G	0		0.5		0.3				0.3				
Eunotia incisa Smith ex Gregory	*	0											1.6	
Eunotia minor (Kützing) Grunow	*	e									0.3			
Eunotia muscicola Krasske	•												0.3	
<u>Fragilaria</u> related taxa Fragilaria capucina Desmazieres	**	m				0.3	0.3	1.0	0.6					
Fragilaria tenera (Smith) Lange-Bertalot	V	0	0.3	0.3		0.5	0.5	1.9	0.0	0.3	0.3	0.3		1.6
Fragilaria vaucheriae (Kützing) Petersen	**	m			0.6				0.3		1.4	4.2		6.5
Hannaea arcus (Ehrenberg) Patrick	**	0	55.5	0.7	81.1	6.2	4.8	6.8	41.8	27.8	0.6	2.1	2.3	25.9
Pseudostaurosira brevistriata (Grunow) Williams, and Round	**	e					0.3					0.3		0.0
Staurosirella pinnata – Group (Ehrenberg) Williams, and Round	**	me	0.3			0.3			0.6	2.0			0.7	0.3
Synedra rumpens Kützing Ulnaria ulna (Nitzsch) P. Compére	*	o ep	0.5			0.5			0.0	2.0	0.3		0.7	
Frustulia rhomboides (Ehrenberg) De Toni*		uo	0.3								0.3		2.0	
Gomphonema acuminatum Ehrenberg	**	me								0.3	0.3			
Gomphonema affine Kützing	R	m				0.3						0.3		
Gomphonema angustatum (Kützing) Rabenhorst Gomphonema cf. bipunctatum Krasske*	* R	0					1.6 1.0		0.3		0.3		0.3	0.3
Gomphonema cf. instabilis Hohn et Hellermann*	K				0.3	0.3	1.0							
Gomphonema micropus Kützing	*	m			0.3	0.3	0.3		0.3	0.3	0.3			0.3
Gomphonema olivaceum (Lyngbye) Kützing	**	e										4.2		0.3
Gomphonema calcifugum Lange-Bertalot et Reichardt*	*	om			0.3	25.4	2.6		0.3	1.4	0.3			1.9
Gomphonema parvulum (Kützing) Kützing	ale ale	e	0.3		0.0	0.2	0.0			0.0	0.0			0.5
Meridion circulare (Greville) Agardh Meridion circulare var. constrictum (Ralfs) Van Heurck	**	me om	12.0		0.3 0.3	0.3	0.3		0.3 0.3	0.3	0.3			0.3
Navicula related taxa		om			0.5				0.5					
Cavinula pseudoscutiformis (Hustedt) Mann, and Stickle	3	om									0.3			
Diadesmis perpusilla (Grunow) Mann	**	om			0.3	0.3	0.3							
Luticola mutica (Kützing) Mann	**	e			0.3	0.3	0.3	1.0						
Luticola ventricosa (Kützing) D.G. Mann Mayamaea atomus (Kützing) Lange-Bertalot	D **	ep				0.3		1.0		03	0.3			
Navicula cari Ehrenberg	**	p e				0.5				0.5	0.5	0.3		
Navicula cf. concentrica Carter et Bailey-Watts	2	°,			0.3							0.0		
Navicula cf. cryptocephala Kützing	**	ep		0.3										
Navicula cryptotenella Lange-Bertalot	*	me							0.3	0.3	0.3		0.3	0.3
Navicula elginensis (Gregory) Ralfs*	* **	me									0.3	0.2		
Navicula lanceolata (Agardh) Kützing Navicula radiosa Kützing	**	ep o									0.3	0.3 1.8		
Navicula rhynchocephala Kützing	**	me									0.3	1.0		
Navicula sp.								1.0			0.3			
Neidium ampliatum (Ehrenberg) Krammer	V	om									0.3			
Neidium bisulcatum (Lagerstedt) Cleve	3	0					1.3			0.2	0.2			
Nitzschia angustata (Smith) Grunow Nitzschia bryophila (Hustedt) Hustedt	Ğ	m								0.3	0.3 0.3			0.3
Nitzschia cf. perminuta (Grunow) Peragallo	*	me	0.6		0.3	0.3	1.9		0.6	0.3	0.3			0.3
Nitzschia dissipata (Kützing) Grunow	**	me							1.9	0.3	0.3	2.4		0.3
Nitzschia fonticola (Grunow) Grunow	**	m										4.7		0.5
Nitzschia gracilis Hantzsch	*	me				0.2			0.6	0.3		0.3		
Nitzschia pura Hustedt Nitzschia recta Hantzsch ex Rabenhorst	*	m				0.3			0.6	0.3				0.3
Nitzschia recta Hantzsch ex Kabelinoist Nitzschia sublinearis Hustedt	*	e e							0.3	0.5				0.3
Pinnularia biceps Gregory		C							0.5		0.3			0.5
Pinnularia borealis Ehrenberg		m						1.0	0.3					
Pinnularia cf. appendiculata (Agardh) Cleve	*	m							0.3		<i>.</i> .			0.3
Pinnularia cf. julma Krammer, and Metzeltin*	~					0.2					0.3			
Pinnularia cf. rupestris Hantzsch	G	0			0.3	0.3								0.3
Pinnularia hilseana Janisch Pinnularia microstauron (Ehrenberg) Cleve	V	0			0.3		0.3							0.5
Pinnularia subcapitata Gregory	*	0				0.3	1.3							
Stauroneis cf. alpina Hustedt	R	-					1.6							0.3
Stauroneis cf. prominula (Grunow) Hustedt	R			0.3			0.3							
Surirella angusta Kützing	*	р			0.3	0.3	0.6			0.2	1.4			0.3
Tabellaria fenestrata (Lyngbye) Kützing Tabellaria flocculosa (Roth) Kützing	V **	om	0.2	1.0	0.3	0.6	0.3		10.4		1.4 73.7		1.0	1.1
	* *	0	0.3	- L.U	0.5	0.0	U.5		10.4	0.5	121		10	

