ARTICLE

Periphytic diatom community structure in thermokarst ecosystems of Nunavik (Québec, Canada)

Frédéric Bouchard, Valentin Proult, Reinhard Pienitz, Dermot Antoniades, Roxane Tremblay, and Warwick F. Vincent

Abstract: Climate change is causing rapid permafrost degradation across Arctic and subarctic regions, resulting in changes in the size, abundance, and structure of thermokarst (thaw) ponds and lakes. The main objectives of this study were to analyze periphytic diatom communities and their affinity to vegetation substrates in thermokarst ecosystems located in the eastern Hudson Bay region and to establish a first inventory of diatom assemblages and the associated littoral vegetation in these systems. Some generalist diatom species, including *Tabellaria flocculosa*, occupied all ecological niches in the water bodies. In contrast, genera such as *Eunotia* and *Pinnularia* were more specialized and generally concentrated on moss substrates. Shoreline vegetation and thermokarst pond/lake littoral morphology (slope) resulted in limnological conditions that differed between sites and ultimately affected diatom community structure. Our results show that both shoreline vegetation and diatom communities are diverse in thermokarst ecosystems, and their species composition depends mostly on site-specific properties (available microhabitats, local pond/lake morphology) rather than limnological conditions that are closely aligned with regional ecoclimatic conditions.

Key words: diatoms, limnology, permafrost, shoreline vegetation, thermokarst lakes.

Résumé : Le changement climatique est en train de causer la dégradation rapide du pergélisol à travers les régions arctiques et subarctiques, donnant lieu à des changements en regard de la grandeur, de l'abondance et de la structure des étangs et des lacs thermokarstiques (de dégel). Les principaux objectifs de cette étude étaient d'analyser des communautés de diatomées periphytiques et leurs affinités relativement aux substrats végétaux dans des écosystèmes thermokarstiques situés dans la région de la baie d'Hudson orientale, et d'établir un premier inventaire d'assemblages de diatomées et de la végétation littorale liée à ces systèmes. Certaines espèces de diatomées généralistes, y compris *Tabellaria flocculosa*, ont occupé toutes les niches écologiques des plans d'eau étudiés. Au contraire, les genres comme *Eunotia* et *Pinnularia* étaient plus spécialisés et généralement concentrés sur des substrats de mousse. La végétation et la morphologie du littoral (pente) des étangs et des lacs thermokarstiques ont donné lieu à des conditions limnologiques qui ont varié entre les sites et ont déterminé la structure des communautés de diatomées. Nos résultats montrent que tant la végétation littorale

F. Bouchard, V. Proult, R. Pienitz, D. Antoniades, and R. Tremblay. Département de géographie, Centre d'études nordiques (CEN) and Takuvik Joint International Laboratory, Université Laval, Québec, QC G1V 0A6, Canada.
W.F. Vincent.* Département de biologie, Centre d'études nordiques (CEN) and Takuvik Joint International Laboratory, Université Laval, Québec, QC G1V 0A6, Canada.
Corresponding author: Frédéric Bouchard (e-mail: frederic.bouchard@cen.ulaval.ca).
*Warwick Vincent currently serves as an Associate Editor; peer review and editorial descisions regarding this manuscript were handled by Julia Boike and Greg Henry.

que les communautés de diatomées sont diversifiées dans les écosystèmes thermokars-
tiques et que leur composition en nombre d'espèces dépend surtout de propriétés
spécifiques aux sites (microhabitats disponibles, morphologie locale et type de plan
d'eau) plutôt que des conditions limnologiques qui sont étroitement liées aux conditions
écoclimatiques régionales. [Traduit par la Rédaction]

Mots-clés : diatomées, limnologie, pergélisol, végétation riveraine, lacs de thermokarst.

Introduction

Permafrost is a major landscape feature across circumpolar regions, underlying one
quarter of the exposed land area of the Northern Hemisphere and half of the land
territory of Canada (Allard and Séguin 1987; Zhang et al. 1999). In Nunavik (northern
Québec), and more specifically along the eastern coast of Hudson Bay, permafrost is
mostly discontinuous and sporadic. The impacts of recent climate warming on northern
circumpolar landscapes have already included shrub expansion and permafrost degrada-
tion through thawing and erosion (e.g., Romanovsky et al. 2010; Myers-Smith et al. 2011).
Changes in permafrost distribution and stability can also affect northern communities
by modifying infrastructure durability as well as water quantity and quality through
the ecosystem services provided by freshwater landscapes (Rowland et al. 2010; Vincent
et al. 2017).

In fine-grained permafrost soils (silts, clays), ground ice aggradation results in surface
heaving and the related formation of cryogenic mounds (palsas and lithalsas) across low-
land areas (Seppälä 1986; Larrivée 2007). Palsas (i.e., organic mounds) have an overlying peat
cover up to several metres thick, whereas lithalsas are exclusively composed of mineral
material. Along the eastern shore of Hudson Bay, palsas are generally distributed within
the forest tundra ecozone, where mean annual air temperature ranges between 0 and
−5 °C, whereas lithalsas are mostly located in the shrub tundra, with mean annual air
temperature ranging between −3 and −7 °C (Pissart 2002). These two periglacial landforms
can coexist at certain subarctic sites, and some lithalsas are, in fact, former palsas from
which the peat cover has been eroded (Calmels et al. 2008). There is thus a "morphogenetic
continuum" between palsas and lithalsas.

Increasing mean annual temperature since the beginning of the industrial era, and the
accelerating of this warming in the last decade or so, has caused permafrost thawing and
related ground ice melting in Nunavik (Allard and Séguin 1987; Payette et al. 2004; Bhiry
et al. 2011). The degradation of palsas and lithalsas results in the formation of thermokarst
(thaw) ponds and lakes (hereafter referred to as lakes), which are among the most abundant
aquatic ecosystems in circumpolar regions (Pienitz et al. 2008). These thermokarst ecosys-
tems are critical places of rapid changes in energy and matter fluxes (Vonk et al. 2015;
Vincent et al. 2017 and references therein) that transfer large quantities of organic carbon
to the atmosphere in the form of greenhouse gases such as CO_2 and CH_4 (Walter et al.
2006; Laurion et al. 2010), although this may be offset by bacterial consumption processes
(Crevecoeur et al. 2015). As climate is the main driver of vegetation and aquatic ecosystem
dynamics in these systems, increasing air temperatures can have a strong impact on lake
spatiotemporal evolution and vegetation densification (Fallu and Pienitz 1999; Bouchard
et al. 2014; Beck et al. 2015).

Thermokarst lakes show distinct limnological and environmental properties depend-
ing on their ecoclimatic setting (Pienitz et al. 2008; Roiha et al. 2015; Deshpande et al.
2016; Bouchard et al. 2017). They are generally surrounded by peat deposits with site-
specific shoreline vegetation. The vegetation cover of the littoral zone generally
includes four groups: bryophytes (mosses), herbaceous plants, macrophytes, and

shrubs. These groups provide diverse habitats for a suite of photosynthetic algal communities. Diatoms (class Bacillariophyceae) are a major component of aquatic biota. They strongly influence primary production dynamics, nutrient cycling, carbon transport and processing, and oxygen concentrations (Smol and Stoermer 2010; Majewska et al. 2012 and references therein). Diatom assemblages are used around the world as accurate bioindicators of environmental conditions (e.g., Lowe 1974; Smol and Stoermer 2010) and have been used successfully in numerous shallow-lake studies to evaluate climate-driven changes in aquatic environments (Bennion et al. 2010; Lotter et al. 2010; Bouchard et al. 2017). Diatom-based paleoenvironmental reconstructions have been conducted in numerous sites across the circumpolar regions (Douglas et al. 2004), from subarctic (Ponader et al. 2002; Bouchard et al. 2013; Rühland et al. 2014) to high-Arctic Canada (Antoniades et al. 2005; Ellis et al. 2008; Douglas and Smol 2010) as well as in Siberia (Pestryakova et al. 2012; Biskaborn et al. 2013).

The geographic coverage of northern diatom studies is still sparse. There is a need to fill the knowledge gap about thermokarst systems and their littoral vegetation to generate a comprehensive understanding of these biotopes under future climate change scenarios. Vegetation and diatom biodiversity in thermokarst ecosystems, as well as diatom–vegetation affinities, are still poorly understood relative to similar work done elsewhere on northern lakes and rivers. In the present study, we analyzed diatoms and shoreline vegetation along a latitudinal transect crossing treeline to characterize the differences in diatom assemblages and vegetation along this gradient. We also established a first inventory of diatoms and vegetation in the littoral zone of these subarctic lakes to understand the resulting ecosystem differences between them.

Study site

The study area is located in subarctic Québec on the eastern shore of Hudson Bay (Fig. 1a). The region crosses treeline, covering a latitudinal gradient from 55°13.12′N to 56°55.42′N. The sampled thermokarst ecosystems are distributed in four lake-rich areas within a region stretching from the Great Whale River, south of the village of Kuujjuarapik–Whapmagoostui, to the Nastapoka River watershed north of treeline.

The closest meteorological stations are located near the villages of Kuujjuarapik–Whapmagoostui and Umiujaq. For Kuujjuarapik–Whapmagoostui, the climate was relatively stable between the 1960s and 2000, with a mean annual temperature of −4.4 ± 0.5 °C (Environment Canada 2010); temperature has, however, considerably increased during the last decade, with a value of −2.6 ± 1.2 °C for the period 2001–2010 (Environment Canada 2010; Bhiry et al. 2011). The coldest month is January, with a mean temperature of −23.4 °C and dry conditions (Environment Canada 2010). During summer, the proximity to Hudson Bay results in more humid conditions. The mean temperature of the warmest month (August) is 11.4 °C and the growing season spans from mid-May to late September. The annual freezing index is more than twice the annual thawing index: 2890 versus 1310 degree-days, respectively. Mean total annual precipitation is 670 mm, with 35% falling as snow (Environment Canada 2010). For the Umiujaq region, meteorological data for the 2002–2013 period indicate a mean annual temperature of −3.0 °C. February is the coldest month with a mean temperature of −20.6 °C, and the warmest month is August with a mean temperature of 11.6 °C (CEN 2017).

The inland regional geology consists of Archean granite and gneiss of the Superior Province, one of the main components of the Canadian Shield. Along the Hudson Bay shore, Proterozoic metasedimentary rocks of the Churchill Province form a series of cuestas with elevations ranging from 150 to more than 300 m a.s.l. (Lajeunesse 2008). Glacial retreat around the Hudson Bay region occurred during the early Holocene, at

Fig. 1. (*a*) Location of the four studied valleys within three ecozones: boreal forest, forest tundra, and shrub tundra (modified from Bouchard et al. 2013). (*b*) Permafrost distribution map of the study area, with studied valleys indicated with white stars. A, continuous permafrost; B, discontinuous and abundant permafrost; C, discontinuous and scattered permafrost; D, sporadic (isolated) permafrost (modified from Allard et al. 2012).
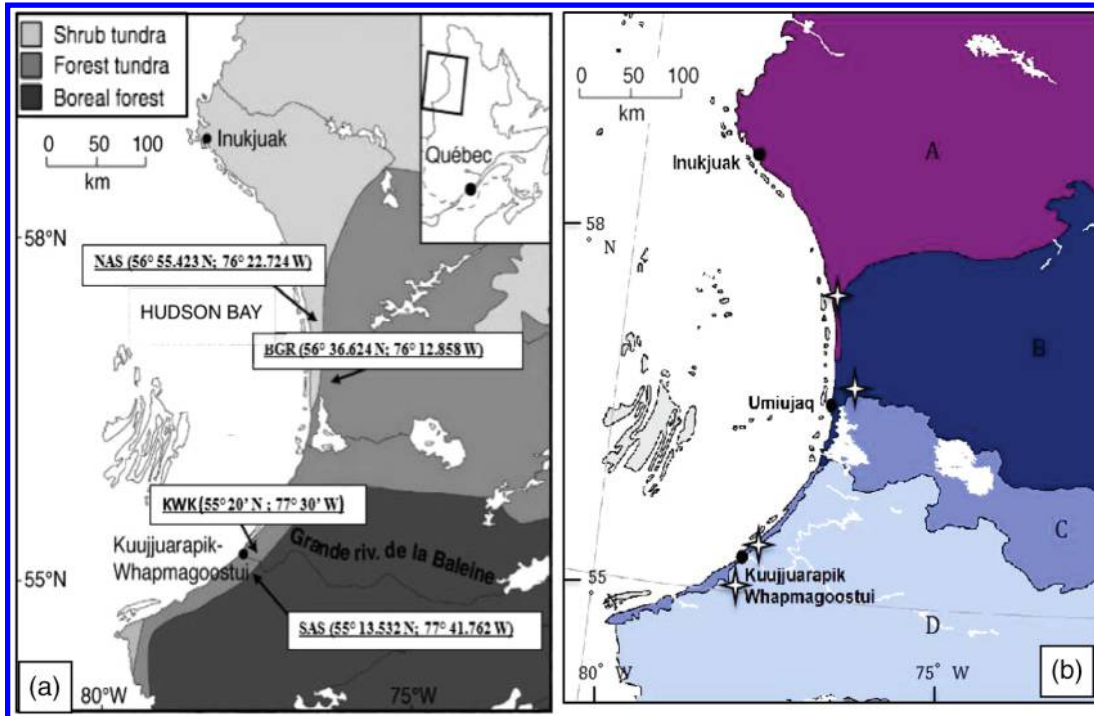
around 8000 years B.P. (Allard and Séguin 1985). This deglaciation was followed by a marine transgression episode (postglacial Tyrrell Sea), which covered the landscape with marine (silt–clay) and coastal (sand) deposits that are widespread today in topographic depressions (Saulnier-Talbot et al. 2003; Lavoie et al. 2008*a*). Following ice retreat, strong isostatic rebound (up to 9 m per century) affected the landscape, resulting in marine regression (Allard and Séguin 1987; Lafortune et al. 2006). The exposure of fine-grained sediments to the cold climate conditions of the late Holocene, especially during the Little Ice Age, gave way to permafrost inception and development in the region (Fig. 1*b*).

The eastern coast of Hudson Bay is dotted with a variety of periglacial forms that are currently located within the sporadic, discontinuous, and continuous permafrost zones (Fig. 1*b*) (Allard and Séguin 1987). Each studied area thus contains many thermokarst lakes and cryogenic mounds that are currently in a variable state of degradation (Bouchard et al. 2013; Jolivel and Allard 2013). A total of 11 thermokarst lakes were sampled in four valleys or survey areas. Two study sites were located in the "Sasapimakwananisikw" River (local Cree name) region and are referred to as SAS in this study. Four sites were located along the valley of the "Kwakwatanikapistikw" River (also a local Cree name) and are referred to as KWK. Four other sites were located along the Sheldrake River in the area known as BGR, named after an earlier permafrost study in the region by the "Bundesanstalt für Geowissenschaften und Rohstoffe" (Federal Institute for Geosciences and Natural Resources, Hannover, Germany). Finally, the

Fig. 2. Oblique aerial photographs representing different study sites in Nunavik: (*a*) SAS, (*b*) KWK, (*c*) BGR, and (*d*) NAS. Small water bodies vary between 5 and 10 m in diameter, whereas larger lakes can reach several tens of metres across. Photos: V. Proult and F. Bouchard.
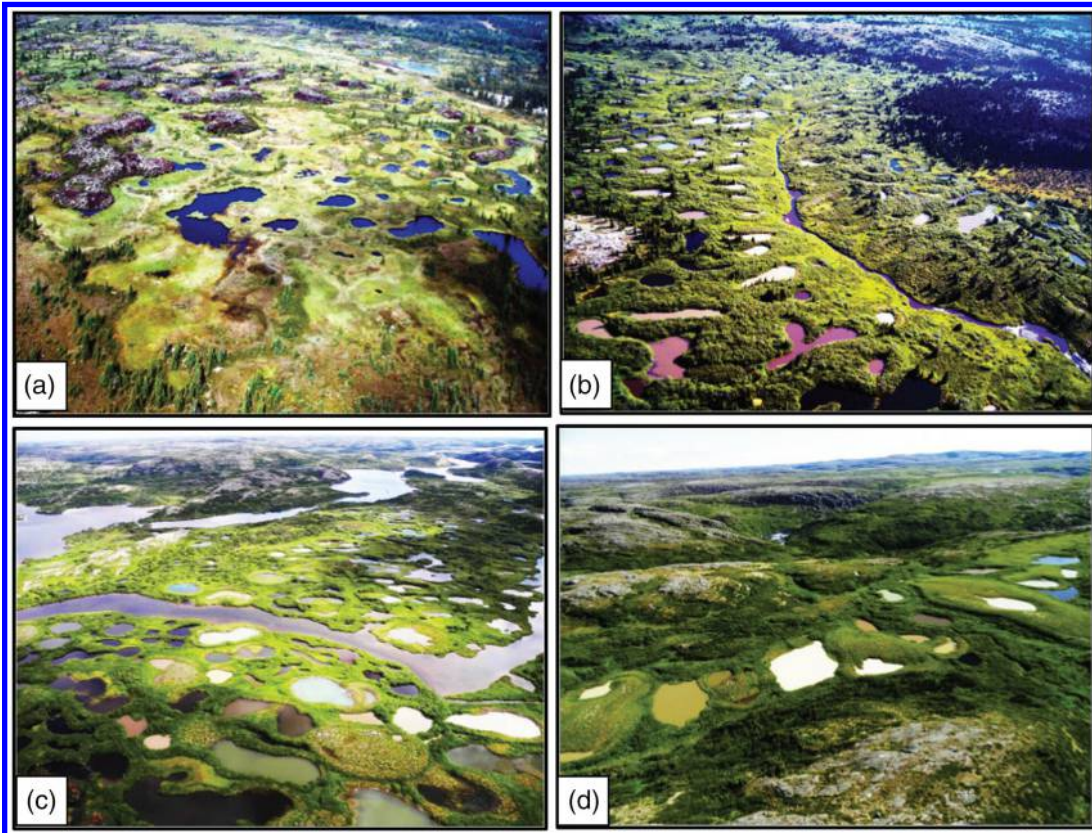
northernmost site was located along the Nastapoka River and is referred to as NAS (Fig. 2).

The study area covers three distinct ecoclimatic zones (Fig. 1*a*). The two southernmost studied valleys (SAS and KWK) are located within the taiga subzone of the boreal forest zone (with KWK being near/within the boundary with forest tundra). In this region, lichen–spruce vegetation is dominant from 52°N to 55°N. It is mainly composed of black spruce (*Picea mariana* Mill. Britton, Sterns & Poggenb.) above a thin lichen cover (*Cladina* and *Cladonia* spp.) (MRNF 2012). Balsam fir (*Abies balsamea* (L.) Mill.) and jack pine (*Pinus banksiana* Lamb.) are also present, but less abundant. These two areas are situated within the sporadic permafrost zone. The third valley (BGR) is located in the transition between the boreal and Arctic zones in the forest tundra subzone (MRNF 2012). The landscape of this region is characterized by limited forest patches in wind-protected depressions interspaced with shrub-dominated land. Dwarf or krummholz spruce (*P. mariana*) is the only tree species present at this latitude, with the northern limit of this region corresponding to treeline. Discontinuous permafrost underlies the landscape. The northernmost valley (NAS) is located in shrub tundra in the Arctic zone. Shrub willows (*Salix* spp.) and birches (*Betula* spp.) less than 2 m high characterize this zone. The lower-lying vegetation is mainly composed of herbaceous plants, mosses, and lichens (MRNF 2012). This area is located within the continuous permafrost zone.

Table 1. Physical properties of the 11 subarctic thermokarst lakes sampled in Nunavik.

Site	Latitude N	Longitude W	Ecozone	Z_{max} (m)	Area (m^2)	Origin
SAS-S1	55°13.128′	77°42.477′	BF	2.0	403.9	Palsa
SAS-N1	55°13.591′	77°41.815′	BF	2.6	78.5	Palsa
KWK-1	55°19.890′	77°30.241′	BF/FT	2.1	314.2	Palsa
KWK-6	55°19.937′	77°30.117′	BF/FT	3.6	415.5	Lithalsa
KWK-12	55°19.808′	77°30.239′	BF/FT	2.7	346.4	Palsa
KWK-23	55°19.947′	77°30.131′	BF/FT	3.2	254.0	Palsa
BGR-1	56°36.650′	76°12.900′	FT	3.5	962.1	Lithalsa
BGR-2	56°36.632′	76°12.937′	FT	1.1	200.0	Lithalsa
BGR-F	56°36.535′	76°12.983′	FT	4.3	706.9	Lithalsa
BGR-G	55°36.548′	76°12.996′	FT	2.7	1320.2	Lithalsa
NAS-1	56°55.434′	76°22.708′	ST	4.2	1963.5	Lithalsa

Note: BF, boreal forest; FT, forest tundra; ST, shrub tundra; Z_{max}, maximum depth measured at the time of sampling (August 2012).

Table 2. Limnological properties measured in the surface waters of the 11 sampled thermokarst lakes.

Site	TN (mg L^{-1})	TP (µg L^{-1})	DOC (mg L^{-1})	TSS (mg L^{-1})	T (°C)	Cond (µS cm^{-1})	DO (%)	pH	Trans (m)
SAS-S1	0.75	16.2	9.9	5.0	19.69	110	84.9	6.3	0.75
SAS-N1	0.70	10.9	14.9	2.6	20.50	95	56.2	5.3	0.60
KWK-1	0.55	67.9	12.0	26.1	11.35	62	66.6	6.1	
KWK-6	0.40	29.8	5.2	8.2	13.06	40	89.5	6.1	1.10
KWK-12	0.35	27.4	9.3	16.4	12.00	60	61.1	6.6	1.50
KWK-23	0.35	57.1	7.8	8.3	12.92	68	78.9	6.5	0.65
BGR-1	0.21	14.4	3.5	2.4	12.90	171	91.1	7.1	1.15
BGR-2	0.45	49.1	9.3	13.1	12.36	225	96.7	7.1	0.24
BGR-F					13.32	67	88.3	7.6	1.15
BGR-G					13.32	180	99.8	7.3	1.00
NAS-1	4.22	133.4	3.0	319.3	10.15	321	89.0	6.7	0.05

Note: TN, total nitrogen; TP, total phosphorus; DOC, dissolved organic carbon; TSS, total suspended solids; T, temperature; Cond, conductivity; DO, dissolved oxygen; Trans, water transparency (Secchi depth).

Materials and methods

Field surveys, vegetation sampling, and identification

Eleven thermokarst lakes were sampled in August 2012 and July–August 2013 (Tables 1 and 2; Supplementary Table S3[1]). Bathymetric surveys were completed for the most representative sites ($n = 7$) of the four sampling areas. Maximum depths (Z_{max}) of the studied lakes were determined with a portable sonar. Lake surface areas were calculated based on field measurements. Lakewater transparency (depth of light penetration) was evaluated with a Secchi disk.

Peripheral substrate occurrence frequency was characterized for the most representative sites ($n = 7$) using "point-transect analysis" and quadrat sampling (as in Bowden et al. 1994). Sampled substrates included bryophytes, herbaceous plants, macrophytes, and shrubs. Nearshore (within <1 m of the water body) peripheral plant specimens were sampled using a 15 cm × 15 cm quadrat and occurrence frequency was determined by presence or absence at 50 cm intervals along a 5 m rope placed along the most representative vegetation zones (two or three zones per site). Samples were placed in a herbarium and then identified using several identification keys (Fasset 1957; Porsild and Cody 1980;

Fig. 3. Photographs representing different vegetation types present along thermokarst lake littoral zones: (*a*) *Carex aquatilis*, (*b*) *Sphagnum* cf. *fuscum*, (*c*) *Sparganium angustifolium*, and (*d*) *Salix glauca*. Photos: V. Proult.
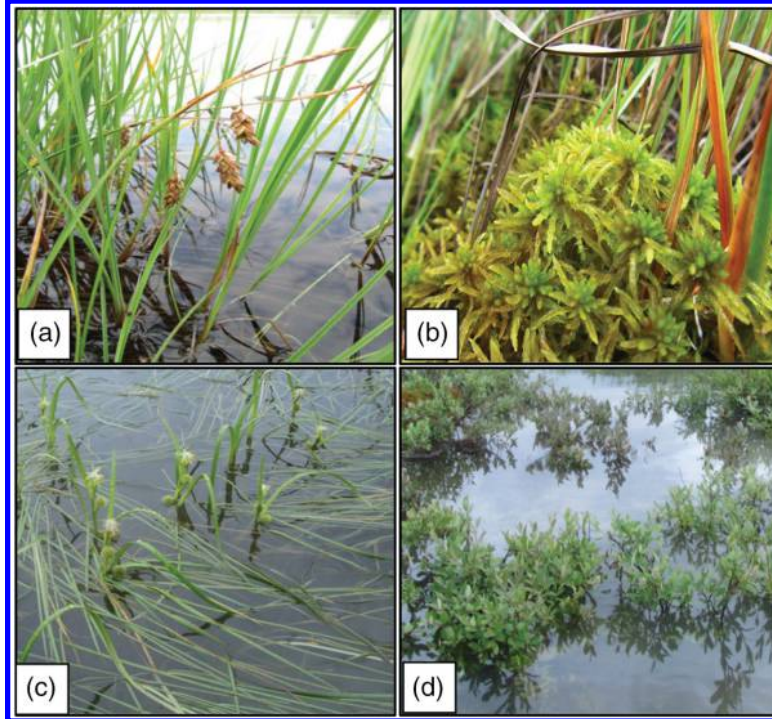
Howard and Lewis 1981; Ireland 1983) and floras (Lamoureux 1987; Blondeau et al. 2004). Occurrence frequency was calculated for each area and plotted on histograms.

Limnological analyses

A YSI water column profiler was used to measure temperature (Temp), pH, dissolved oxygen (DO), and conductivity (Cond) at each lake surface (Table 2). Dissolved organic carbon (DOC) was measured from 40 mL of filtered lake water (47 mm GF/F filter) using a Shimadzu TOC-5000A carbon analyzer calibrated with potassium biphthalate. Water samples were analyzed for total phosphorus (TP) and total nitrogen (TN) using methods described by Laurion et al. (2010). Total suspended solids (TSS) were extracted using 47 mm GF/F filters (preburned at 500 °C and preweighed). Filters were kept at −80 °C until analysis. They were dried for 24 h (60 °C), weighed, burned for 4 h (500 °C), and then weighed again. The difference between burned and dried masses gave the TSS mass. TN, TP, TSS, and DOC were not available for sites BGR-F and BGR-G; these ponds were therefore excluded from statistical analyses, although they are included in the diatom–substrate analyses.

Diatom analyses

Epiphytic diatoms were sampled on littoral substrates along lake shores (Fig. 3). All available vegetation groups were sampled at each site: bryophytes, herbaceous plants, macrophytes, and shrubs. Substrate samples were kept in the dark at 4 °C until further analysis. Diatom valves were extracted using hydrogen peroxide (30% H_2O_2) to remove organic matter. Samples were rinsed three times with distilled water to equilibrate pH. Diatom aliquots of different concentrations were then placed on slides using Naphrax mounting

medium ([Pienitz et al. 1995](#)). A total of 40 samples were analyzed from the 11 sites. Depending on the occurrence of different diatom taxa, we counted between 100 (only a few taxa present, i.e., <10) and 500 valves per sample.

A species occurrence inventory (presence–absence) was performed on each slide for the whole community. The mean taxonomic relative abundance of each diatom genus was calculated for separate sampling areas (i.e., SAS, KWK, BGR, and NAS) on each substrate type (bryophytes, herbaceous plants, macrophytes, and shrubs) and summarized in histograms using C2 software. Diatom valves were identified with a light microscope (Leica DMRX) at 1000× magnification. Selected specimens were photographed with a digital camera (Leica DFC 490) and identified using appropriate taxonomic references ([Krammer and Lange-Bertalot 1991](#); [Fallu et al. 2000](#); [Krammer 2000, 2002, 2003](#); [Lavoie et al. 2008*b*](#)).

Statistical analyses

A standardized principal component analysis (PCA) was performed with limnological variables to characterize their variability within and between the ecoclimatic zones. Bathymetric data (Bath) were obtained either using the above-mentioned sonar or from direct field observations. In the data set, slopes were denoted as "Bath1" (steep slope) or "Bath2" (gentle slope). Lakewater apparent color (ACo), which has a direct influence on light penetration within the photic zone, was noted as ACo1 (brown), ACo2 (beige), ACo3 (blue), or ACo4 (milky). To reduce the skewness of the frequency distributions and increase the linearity of the relationships, some environmental variables were ln-transformed (TN, TP, Temp, and TSS). Data ordination was done using the software CANOCO, version 5 ([ter Braak and Šmilauer 2012](#)). Another PCA was performed to examine relationships between diatoms and vegetation substrates. The Hellinger transformation was applied to the data ([Legendre and Gallagher 2001](#)). This transformation forces the PCA to preserve the Hellinger distance, which is a distance appropriate for the study of community composition data ([Legendre and Legendre 2012](#)). This distance is insensitive to double zeros in the data matrix.

Results and discussion

Limnology

The relationships among sites as a function of their limnological properties are shown on a PCA biplot ([Fig. 4](#)). The first two axes explained 62% of the limnological variation, with eigenvalues of 0.42 and 0.20 for axis 1 and 2, respectively (with NAS-1 accounting for a large part of the explained variance). Axis 1 illustrates the contrast between water bodies formed by the degradation of palsas (organic matter = peat), mostly located at the southern end of our gradient (SAS-S1, SAS-N1, KWK-1, KWK-12, and KWK-23), and those formed by the degradation of lithalsas (mineral matter), mostly located at the northern end (KWK-6, BGR-1, BGR-2, and NAS-1). The northernmost site had more turbid and nutrient-enriched waters (high TSS, TN, and TP) ([Table 2](#)) with higher conductivity related to the local mineral soils (marine silts and clays). During rain events, surface runoff transported substantial sediment loads to the aquatic ecosystems. Contrastingly, lakes located within the southernmost lake-rich area (SAS) were underlain and surrounded by organic-rich peaty soils and substrates that contributed to deeper infiltration of less turbid, DOC-rich surface water.

Similar to the findings of [Fallu et al. (2000)](#) from this region, lakes were segregated on the biplot according to their position along the ecoclimatic transect. The shrub tundra site (NAS) plotted in the upper right quadrant of the PCA and was associated with higher nutrient and ion concentrations (TN, TP, TSS, and Cond) as well as a milky (very turbid) apparent color. Forest tundra sites in the lower right corner (BGR) had relatively high pH due to a lack of peat deposits relative to SAS and KWK. Well-oxygenated water columns may have resulted partly from the sparse vegetation in the surroundings (near the shore),

Fig. 4. Principal component analysis (PCA) of studied sites ($n = 11$) and environmental variables ($n = 11$). Symbols refer to ecozones: boreal forest (green circles), forest tundra (blue squares), and shrub tundra (gray diamond). TN, total nitrogen; TP, total phosphorus; DOC, dissolved organic carbon; TSS, total suspended solids; Temp, temperature; Cond, conductivity; DO, dissolved oxygen; Z_{max}, maximum depth; ACo, apparent color; Bath, bathymetry.
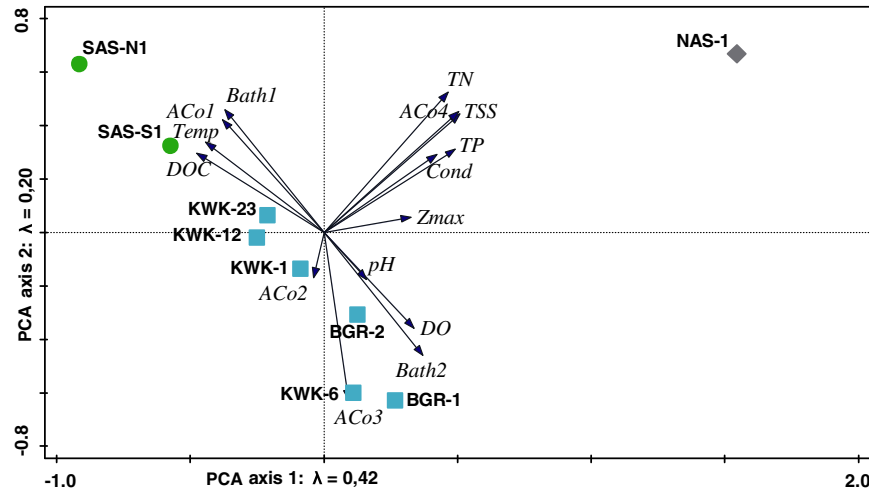
resulting in efficient wind-driven mixing and exchange with the atmosphere. Both NAS and BGR sites had a gentle slope bathymetry, potentially allowing the establishment of macrophyte substrates (see next section).

As the southernmost sites, boreal forest lakes in the upper left quadrant (SAS) were characterized by more acidic and warmer waters that were particularly rich in DOC. They showed a steep slope bathymetry that was related to the presence of peripheral "floating moss edges" or mats, and their color was generally dark brown to "tea-like" yellowish–black. Sites located near the transition zone between the boreal forest and the forest tundra (KWK) plotted near the center of the graph and had midrange DOC concentrations. Because autochthonous DOC concentrations were generally low in northern aquatic ecosystems (Fallu and Pienitz 1999), the presence of denser vegetation around lakes from KWK and SAS valleys likely contributed to higher external DOC inputs from runoff (Watanabe et al. 2011). In contrast, more open northern sites of the forest/shrub tundra (BGR and NAS) and the only "lithalsa-lake" in the KWK area (KWK-6) (Table 1) all plotted with low DOC.

Qualitative analysis of shoreline vegetation

From thermokarst ecosystems located in the boreal forest (SAS and KWK) to the forest tundra and shrub tundra sites (BGR and NAS), there was a general decrease in DOC concentrations and (or) peat deposits and a corresponding increase in pH (Fig. 4). The SAS area was typical of palsa peatlands along the eastern shore of Hudson Bay (Arlen-Pouliot and Bhiry 2005). There was also a latitudinal gradient in permafrost state and related cryogenic forms: the KWK area (sporadic permafrost) showed the most mature thermokarst lakes (i.e., the most advanced state of permafrost degradation), generally formed by collapsed palsas (with the exception of KWK-6), whereas the BGR and NAS areas (discontinuous and continuous permafrost, respectively) comprised younger lakes, most of them still surrounded by degrading lithalsas.

The SAS sites (boreal forest, sporadic permafrost) were located within a very humid peatland valley, where mosses (*Sphagnum* spp.) overlay postglacial marine clays (Tyrrell Sea) and rocks of the Canadian Shield, resulting in a characteristic dark brown color.

Fig. 5. Diagram showing the occurrence frequency of the vegetation surrounding representative sites in each valley (SAS, KWK, BGR, and NAS).
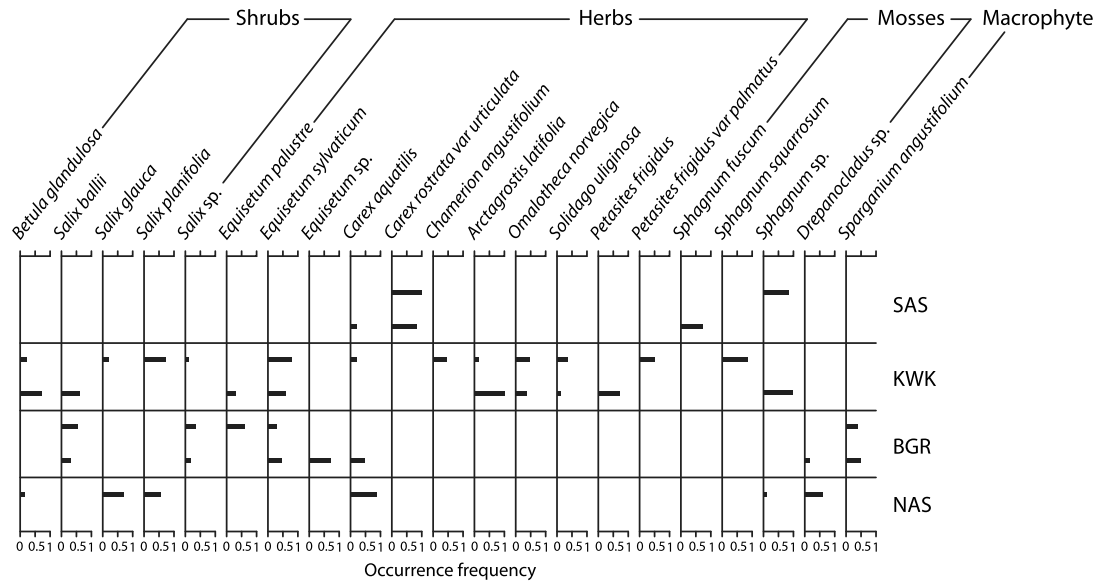
The surrounding vegetation, partly submerged, was mainly composed of grasses and mosses (*Carex rostrata* var. *urticulata* (Boott) J.H. Bailey and *Sphagnum* cf. *fuscum* Klinggräff) (Fig. 5). As reported by Arlen-Pouliot and Bhiry (2005), abundant floating peat blocks, often colonized by *Sphagnum* and *Carex* spp., can be observed at the lake surfaces in the SAS valley.

The KWK valley (boreal forest and forest tundra transition, sporadic permafrost) had a slight topographic slope running from the west (rocky hill) to the east (steeply embedded creek) (Fig. 2). This valley included many thermokarst lakes formed by the degradation of palsas and lithalsas (Bouchard et al. 2013). Remnants of palsas and peat debris found in lacustrine sediments at their bottom indicated the presence of a former peatland in the past. Lakewater apparent color ranged from brown to brown–beige, with one site (KWK-6) having a distinctly blue color related to low DOC concentrations (Table 2). Peripheral ridges surrounding the lakes were densely colonized by shrubs (*Salix planifolia* Pursh and *Betula glandulosa* Michx.) that limited light penetration along shorelines, thus restricting aquatic plant development. Underneath these shrubs, the vegetation was dominated by horsetail (*Equisetum sylvaticum* L.), sedge (*Carex* spp.), and grass (*Arctagrostis latifolia* (R. Br.) Griseb.). The surface of the peripheral ridges was mainly colonized by mosses (*Mnium* sp., *Sphagnum* spp.). This littoral vegetation heterogeneity (relatively high number of substrates) was typical of the KWK valley (Fig. 5).

The BGR valley (forest tundra, discontinuous permafrost) contained numerous lithalsas with ice-rich cores as well as some degrading palsas (Calmels et al. 2008; Jolivel and Allard 2013). The apparent color of these lakes ranged from brown–beige to blue, and most of them were surrounded by clay-rich peripheral ridges with inorganic soils on which vegetation was low-lying and scattered. A comprehensive stratigraphic record from this region (Calmels et al. 2008) has shown the presence of a thick (1.5 m) active layer composed of silty clay. On this substrate, shrubs were dominated by willows (*Salix* spp.), whereas herbaceous plants were represented by horsetail (*E. sylvaticum*) and sedge (*Carex aquatilis* Wahlenb.). Some moss patches (*Drepanocladus* sp.) were also present around the water bodies. Gentle

slopes and the sparse surrounding vegetation allowed the establishment of macrophytes, such as *Sparganium angustifolium* Michx. and *Potamogeton praelongus* Wulfen, along the littoral zone (Fig. 5).

NAS was the northernmost valley in this study, located within the shrub tundra zone and continuous permafrost. This valley was exclusively occupied by lithalsas (no palsas) and thermokarst systems. The surface of one such lithalsa, bordering site NAS-1, was covered by mudboils (convective clay-"upwelling" structures). The surrounding vegetation was included in three groups: shrubs, exclusively represented by willows (*Salix glauca* L. and *S. planifolia*), sedges (*C. aquatilis*), and mosses (*Drepanocladus* sp.) (Fig. 5).

Diatom taxonomic composition and substrate affinities

A total of 164 diatom taxa belonging to 26 genera were identified on vegetation substrates along the littoral zones of the thermokarst ecosystems (Supplementary Table S1[1]; Plates 1–4). Several genera (i.e., *Tabellaria*, *Achnanthes*, *Navicula*, *Pinnularia*, and *Nitzschia*) were found at all sampled sites. The taxon *Tabellaria flocculosa* was identified in all ecological niches and sites along the study transect. Diatom assemblages colonizing the southernmost sites generally displayed a higher variety of life strategies than those from the northern sites. Such a north–south contrast, although based on more sampling sites, was also observed in other regions spanning the treeline (Pienitz et al. 1995; Fallu and Pienitz 1999; Rühland 2001). However, there was a tendency for some diatom genera to be associated with specific substrate types (Fig. 6). Herbs and shrubs were colonized by a wide range of genera, whereas mosses and aquatic plants were more selectively occupied by specific genera (i.e., *Pinnularia*, *Eunotia*). A histogram representing the spatial distribution of diatom genera as a function of vegetation substrates is shown in Fig. 7. This rich diatom flora in the periphyton contrasted with summer phytoplankton communities in these waters, which contained few diatoms and were dominated by green algae, cyanobacteria, and phytoflagellates (Przytulska et al. 2016).

The steeply sloped morphometry of SAS lakes precluded the establishment of macrophytes along the littoral zone. *Eunotia* was the most frequent genus (40%), with species such as *Eunotia bilunaris* Mills occupying slightly acidic, low-conductivity peat-rich, and herbaceous littoral substrates (Bey and Ector 2013*a*) (Fig. 7). The acidophilous *Eunotia minor* Grunow and *Eunotia serra* Ehrenberg colonized *Sphagnum* peatlands in our study and appeared to be widespread in low-pH environments regardless of the underlying substrate (Lange-Bertalot 2001; Pienitz 2001; Sabater 2009). Limnological conditions thus appeared to override vegetation substrate availability in controlling the establishment of *Eunotia* spp. in these systems.

The greatest number of diatom taxa was observed on slides from the KWK area (boreal forest, sporadic permafrost zone), as revealed by a qualitative assessment. This area is where the highest number of vegetation substrates surrounding the lakes was found, with a total of 16 substrates compared to four, eight, and six for SAS, BGR, and NAS sites, respectively (Fig. 5). This is also where thermokarst systems were the most advanced in their development along our study transect, with a last remnant of a permafrost mound undergoing severe degradation during the last several years (Bouchard et al. 2013). This may have resulted in more fragmented habitats, leading to a greater variety of life strategies. Diatom genera typically established on shrubs here included *Gomphonema* (15% of samples), especially *Gomphonema parvulum* Van Heurck and *Gomphonema gracile* Ehrenberg, and the genus *Nitzschia*. On herbaceous substrates, the genera *Nitzschia* (20%), *Achnanthes* s.l. (10%), and *Eunotia* (15%) were the most frequent (Fig. 7), represented by *Nitzschia perminuta* Peragallo, *Eunotia bilunaris*, and *Eunotia michaelis* Guiry. Mosses were mostly colonized by *Pinnularia* spp. (25%), in particular *Pinnularia viridis* Ehrenberg and *Pinnularia subgibba* Krammer. *Pinnularia* spp. were also recorded to be frequent in peatland sites in northern Québec and Labrador (Pienitz 2001).

Plate 1. Selection of diatom taxa typical of moss (*Sphagnum*) substrates. 1, *Eunotia minor*; 2, *Eunotia pseudogroenlandica*; 3, *Eunotia incisa*; 4, *Eunotia exigua*; 5, *Eunotia fallax*; 6, *Eunotia neocompacta*; 7, *Eunotia hexaglyphis*; 8, *Eunotia tetraodon*; 9, *Eunotia valida*; 10, *Eunotia julma*; 11, *Eunotia nymanniana*; 12, *Eunotia bilunaris*; 13 and 14, *Brachysira brebissoni*; 15, *Brachysira microcephala*; 16, *Nitzschia fonticola*; 17, *Nitzschia perminuta*; 18, *Pinnularia rhombarea*; 19, *Pinnularia gibbba*; 20, *Pinnularia perspicua*; 21 and 22, *Pinnularia borealis*; 23 and 24, *Pinnularia subgibba*; 25, *Pinnularia julma*; 26, *Pinnularia microstauron*.
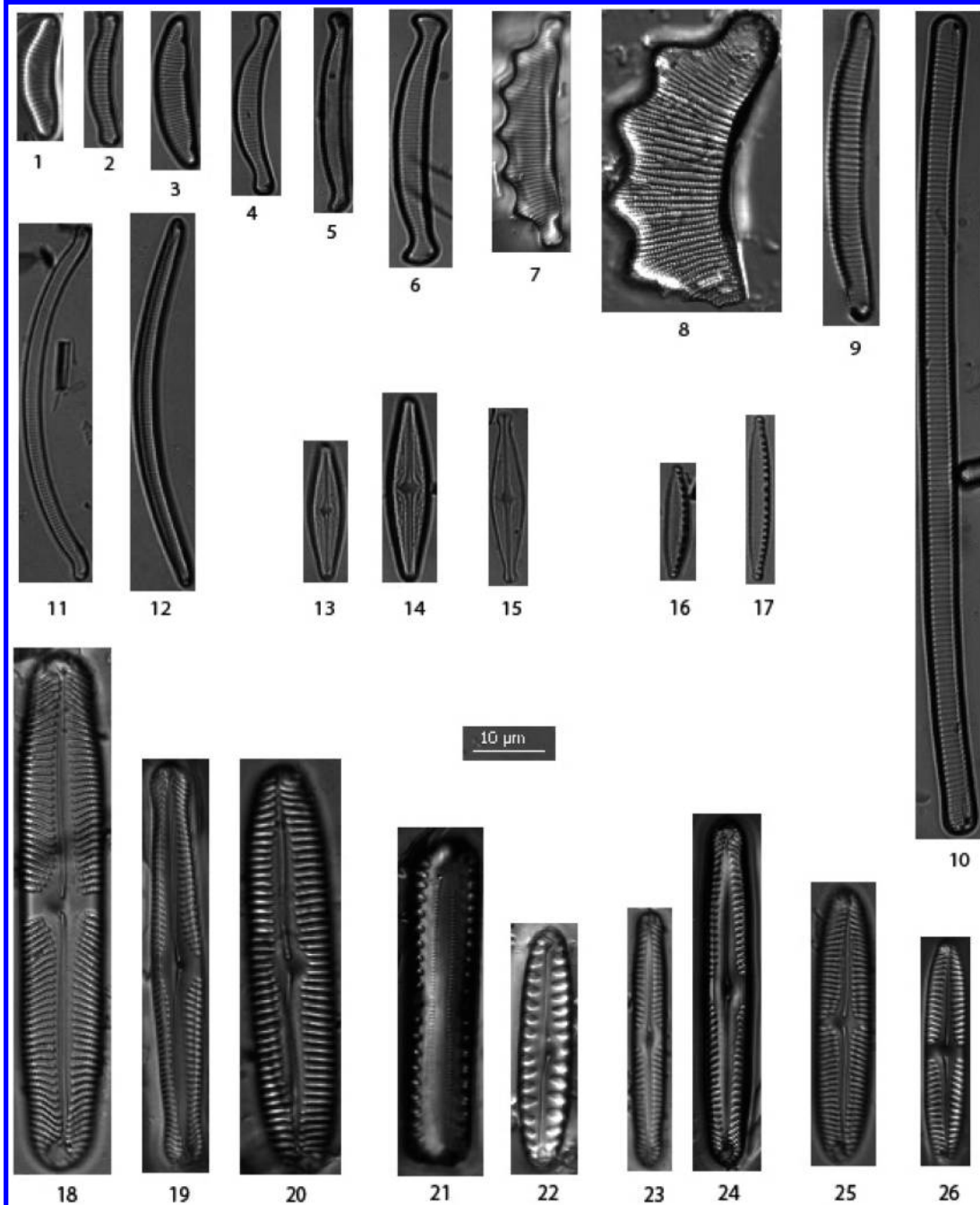
Plate 2. Selection of diatom taxa typical of herbaceous substrates. 1–3, *Frustulia crassinervia*; 4 and 5, *Frustulia rhomboides*; 6, *Frustulia amphipleuroides*; 7, *Encyonema silesiacum*; 8 and 9, *Encyonema neogracile*; 10, *Nitzschia perminuta*; 11, *Nitzschia radicula*; 12, *Nitzschia pura*; 13–16, *Tabellaria flocculosa*.
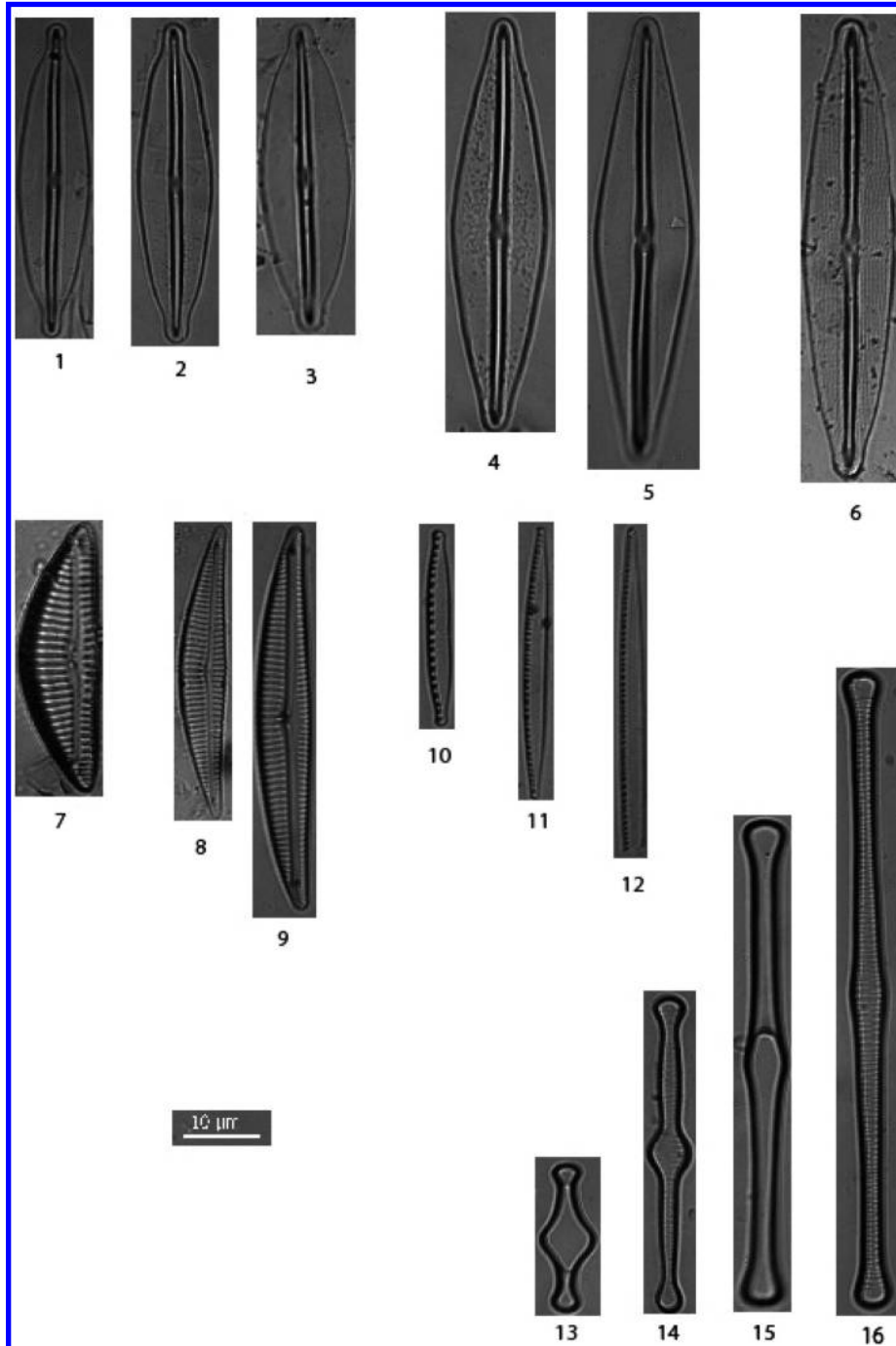
Plate 3. Selection of diatom taxa typical of shrub substrates. 1, *Staurosira construens* var. *venter*; 2–4, *Gomphonema parvulum*; 5, *Gomphonema gracile*; 6, *Gomphonema olivaceum* var. *calcareum*; 7, *Gomphonema acutiusculum*; 8–10, *Gomphonema acuminatum*; 11, *Gomphonema turgidum*; 12 and 13, *Gomphonema capitatum*; 14 and 15, *Gomphonema laticollum*; 16–18, *Navicula notha*; 19, *Sellaphora radiosa*.
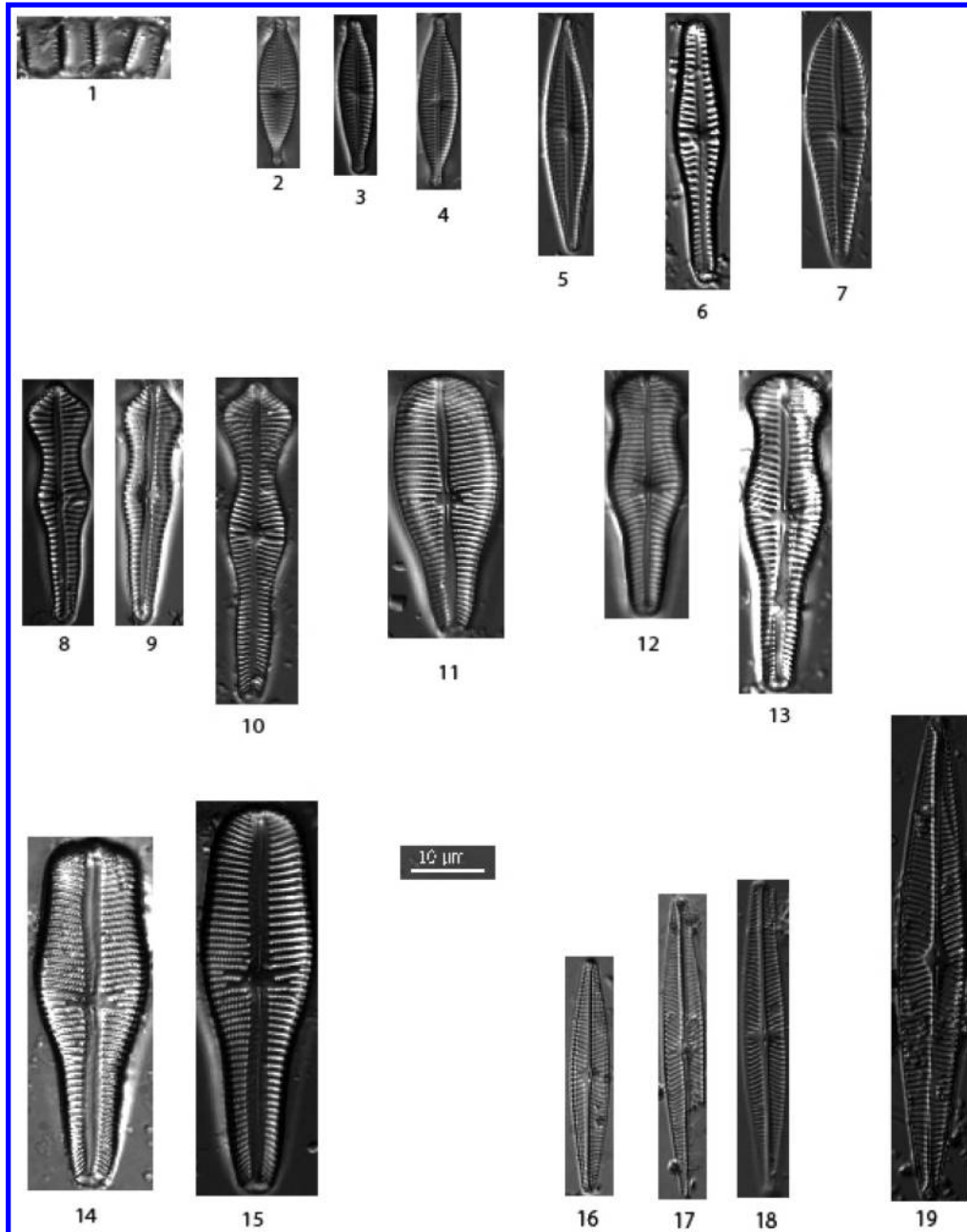
At BGR sites, epiphytic diatom assemblages colonizing partly submerged shrubs were dominated by taxa of the genera *Navicula* (approximately 15%) and *Gomphonema* (10%), whereas herbaceous substrates were mainly colonized by species of *Nitzschia* (15%), *Gomphonema* (15%), *Fragilaria* s.l., *Navicula*, and *Eunotia* (Fig. 7). Diatom genera associated with

Plate 4. Selection of diatom taxa typical of macrophyte substrates. 1 and 2, *Surirella angusta*; 3, *Caloneis lewisi*; 4 and 5, *Navicula pupula*; 6–8, *Sellaphora radiosa*; 9 and 10, *Fragilaria capucina*; 11 and 12, *Fragilaria tenera*.
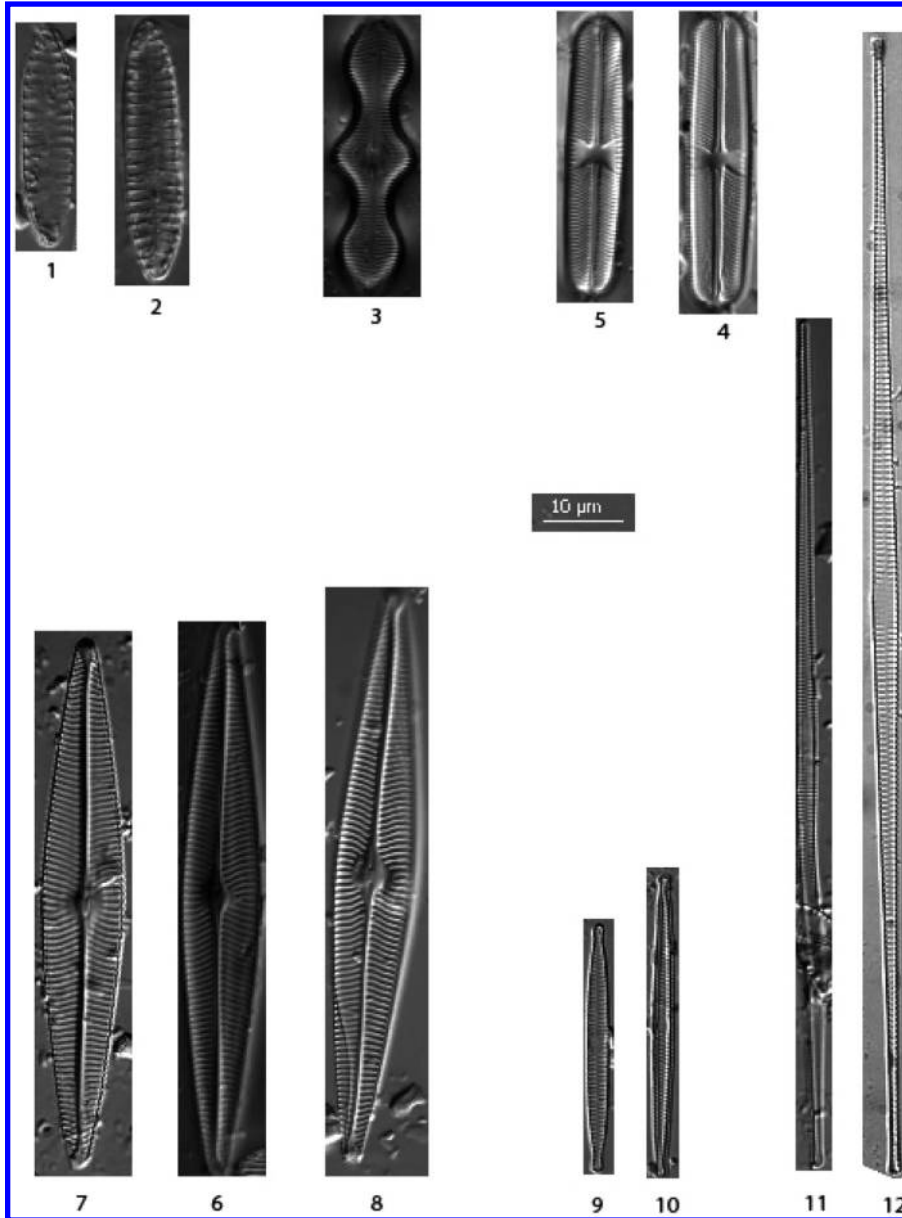
macrophytes included *Fragilaria* s.l. (15%), *Navicula* (15%), and *Nitzschia*. Finally, mosses were mostly colonized by the genus *Pinnularia* (25%), especially *Pinnularia borealis* Ehrenberg, an aerophilous species that is common in well-oxygenated, near-neutral, and low-conductivity waters (Pienitz 2001; Ellis et al. 2008; Bey and Ector 2013*b*). Moreover, lithalsa littoral morphology observed at BGR (more gentle slopes, in sharp contrast with the steep slopes around palsas such as at SAS) provided more extensive substrate space for the establishment of aquatic macrophytes and plants in general, which in turn would provide a greater variety of habitat types for diatoms to exploit, thus affecting their abundance.

Fig. 6. Principal component analysis of diatom genera (grouped from the observed taxa) and vegetation substrate types. See Supplementary Table S2[1] for genus abbreviations and the number of taxa within each genus.
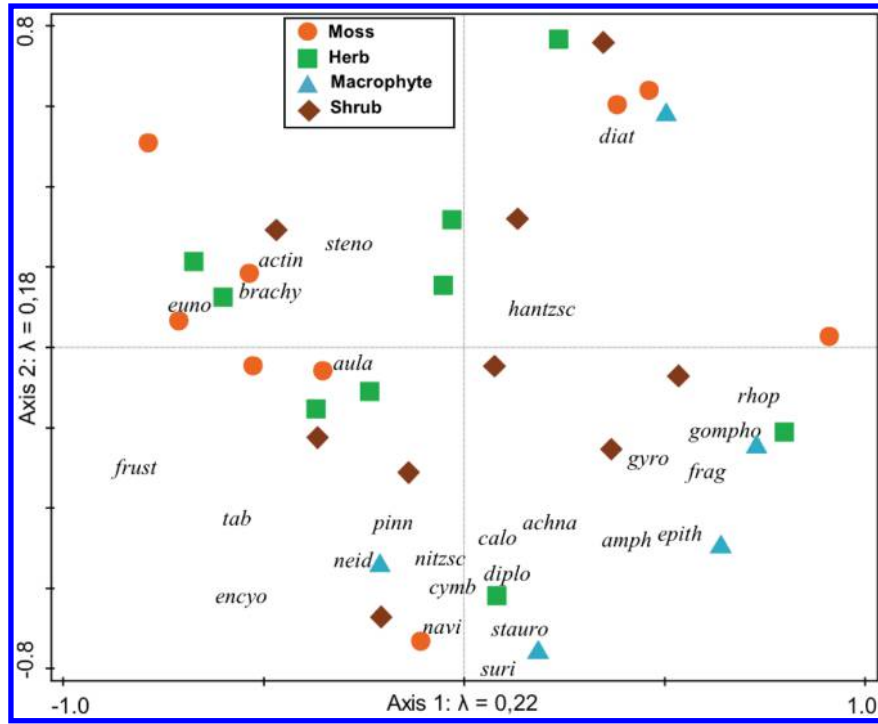
Fig. 7. Histogram representing the average taxonomic abundance of diatom genera (grouped from the observed taxa) on different vegetation substrates around sites SAS, KWK, BGR, and NAS.
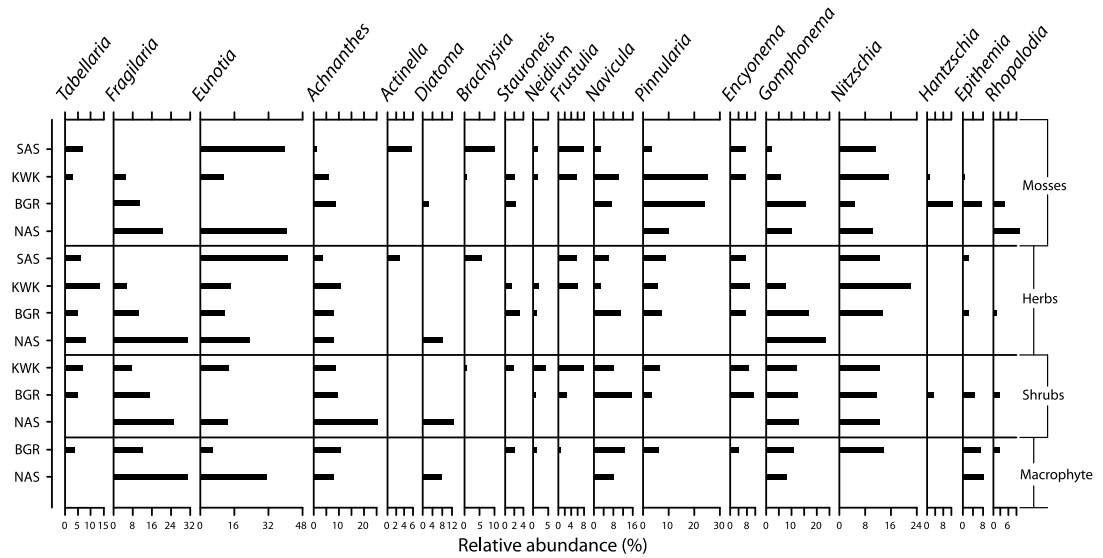
The epiphytic flora of the NAS site was mainly represented by *Achnanthes* s.l. (25%) and *Fragilaria* s.l. spp. on shrubs (*Salix*), *Fragilaria* s.l. (30%) and *Gomphonema* spp. on herbaceous plants (*C. aquatilis*), *Eunotia* (40%) on mosses, and *Fragilaria* s.l. (30%) and *Eunotia* spp. on aquatic plants (Fig. 7). Clay soils were widespread in this valley and provided high quantities of suspended particles into water bodies such as NAS-1 (Fig. 2*d*). This resulted in turbid (milky color), light-limited waters, as shown by the extremely low transparency (Secchi depth) of no more than 5 cm (Table 2). This also likely limited littoral vegetation diversity, i.e., with only a few types of sampled substrates (*Salix*, *Carex*, and *Drepanocladus*).

Conclusions

Climate warming in northern landscapes drives important changes in freshwater ecosystem properties and catchment vegetation dynamics. The vegetation surrounding thermokarst systems is specific to these aquatic environments and differs from elsewhere in the subarctic ecoclimate zone. Our data reveal that environmental as well as biological conditions vary distinctly among study sites, rather than showing a latitudinal gradient of change. Allogenic factors (soil substrate and climate) affect the geomorphological evolution and limnological properties of these aquatic ecosystems, as southern sites are generally richer in DOC and peat and show darker colors and have steep slopes (palsas), whereas northern sites are richer in TSS (NAS), show lighter colors (BGR), and have more gentle slopes (lithalsas). However, autogenic factors (shoreline vegetation and microhabitats) exert a major control on the variety of diatom life forms. For example, SAS and KWK sites, with extensive floating peat blocks (*Sphagnum* moss), showed dominance of *Eunotia* and *Pinnularia* spp. On the other hand, BGR and NAS sites, surrounded by lithalsa-derived gentle slopes with abundant littoral vegetation, were mostly colonized by *Fragilaria* and *Gomphonema* spp. Water bodies in the most advanced stage of development (KWK sites) showed the greatest diatom abundance and variety due to more heterogeneous substrate types and limnological conditions. Our results provide a baseline against which future shifts in diatom biodiversity and community composition may be assessed.

Acknowledgements

References

Allard, M., and Séguin, M. 1985. La déglaciation d'une partie du versant hudsonien québécois: bassins des rivières Nastapoka, Sheldrake et à l'Eau Claire. Géogr. Phys. Quat. **39**: 13–24. doi: 10.7202/032581ar. PMID: 25242907.
Allard, M., and Séguin, M. 1987. Le pergélisol au Québec nordique: Bilan et perspectives. Géogr. Phys. Quat. **41**: 141–152. doi: 10.7202/032671ar. PMID: 25242907.
Allard, M., Lemay, M., Barrette, C., L'Hérault, E., Sarrazin, D., Bell, T., and Doré, G. 2012. Permafrost and climate change in Nunavik and Nunatsiavut: importance for municipal and transportation infrastructures. *In* From science to policy. An Integrated Impact Study (IRIS) of climate change and modernization. *Edited by* M. Allard and M. Lemay. ArcticNet Inc., Québec City, Qué. pp. 171–197.

Antoniades, D., Douglas, M.S.V., and Smol, J.P. 2005. Quantitative estimates of recent environmental changes in the Canadian High Arctic inferred from diatoms in lake and pond sediments. J. Paleolimnol. **33**: 349–360. doi: 10.1007/s10933-004-6611-3.

Arlen-Pouliot, Y., and Bhiry, N. 2005. Palaeoecology of a palsa and a filled thermokarst pond in a permafrost peatland, subarctic Québec, Canada. Holocene. **15**: 408–419. doi: 10.1191/0959683605hl818rp.

Beck, I., Ludwig, R., Bernier, M., Lévesque, E., and Boike, J. 2015. Assessing permafrost degradation and land cover changes (1986–2009) using remote sensing data over Umiujaq, sub-Arctic Québec. Permafr. Periglac. **26**: 129–141. doi: 10.1002/pp.1839.

Bennion, H., Sayer, C.D., Tibby, J., and Carrick, H.J. 2010. Diatoms as indicators of environmental change in shallow lakes. *In* The diatoms: applications for the environmental and earth sciences. *Edited by* J.P. Smol and E.F. Stoermer. 2nd ed. Cambridge University Press, Cambridge, UK. pp. 152–173.

Bey, M.-Y., and Ector, L. 2013*a*. Atlas des diatomées des cours d'eau de la région Rhône-Alpes. Araphidées, Brachyraphidées, 2. Direction régionale de l'Environnement, de l'Aménagement et du Logement Rhône-Alpes, Lyon, France. pp. 184–330.

Bey, M.-Y., and Ector, L. 2013*b*. Atlas des diatomées des cours d'eau de la région Rhône-Alpes. Naviculacées: Naviculoidées, 4. Direction régionale de l'Environnement, de l'Aménagement et du Logement Rhône-Alpes, Lyon, France. pp. 532–749.

Bhiry, N., Delwaide, A., Allard, M., Bégin, Y., Filion, L., Lavoie, M., Nozais, C., Payette, S., Pienitz, R., Saulnier-Talbot, E., and Vincent, W.F. 2011. Environmental change in the Great Whale River region, Hudson Bay: five decades of multidisciplinary research by Centre d'études nordiques (CEN). Ecoscience. **18**: 182–203. doi: 10.2980/18-3-3469.

Biskaborn, B.K., Herzschuh, U., Bolshiyanov, D., Savelieva, L., Zibulski, R., and Diekmann, B. 2013. Late Holocene thermokarst variability inferred from diatoms in a lake sediment record from the Lena Delta, Siberian Arctic. J. Paleolimnol. **49**: 155–170. doi: 10.1007/s10933-012-9650-1.

Blondeau, M., Cuerrier, A., and Roy, C. 2004. Atlas des Plantes des Villages du Nunavik. Éditions Multimondes, Sainte-Foy, France.

Bouchard, F., Pienitz, R., Ortiz, J.D., Francus, P., and Laurion, I. 2013. Palaeolimnological conditions inferred from fossil diatom assemblages and derivative spectral properties of sediments in thermokarst ponds of subarctic Quebec, Canada. Boreas. **42**: 575–595. doi: 10.1111/bor.12000.

Bouchard, F., Francus, P., Pienitz, R., Laurion, I., and Feyte, S. 2014. Subarctic thermokarst ponds: investigating recent landscape evolution and sediment dynamics in thawed permafrost of northern Québec (Canada). Arct. Antarct. Alp. Res. **46**: 251–271. doi: 10.1657/1938-4246-46.1.251.

Bouchard, F., MacDonald, L.A., Turner, K.W., Thienpont, J.R., Medeiros, A.S., Biskaborn, B.K., Korosi, J., Hall, R.I., Pienitz, R., and Wolfe, B.B. 2017. Paleolimnology of thermokarst ponds: a window into permafrost landscape evolution. Arct. Sci. **3**: 91–117. doi: 10.1139/as-2016-0022.

Bowden, W.B., Finlay, J.C., and Maloney, P.E. 1994. Long-term effects of PO_4 fertilization on the distribution of bryophytes in an arctic river. Freshw. Biol. **32**: 445–454. doi: 10.1111/j.1365-2427.1994.tb01138.x.

Calmels, F., Allard, M., and Delisle, G. 2008. Development and decay of a lithalsa in Northern Quebec: a geomorphological history. Geomorphology. **97**: 287–299. doi: 10.1016/j.geomorph.2007.08.013.

CEN. 2017. Climate station data from the Umiujaq region in Nunavik, Quebec, Canada, version 1.4 (1997–2016). Nordicana. **D9**. doi: 10.5885/45120SL-067305A53E914AF0.

Crevecoeur, S., Vincent, W.F., Comte, J., and Lovejoy, C. 2015. Bacterial community structure across environmental gradients in permafrost thaw ponds: methanotroph-rich ecosystems. Front. Microbiol. **6**: 192. doi: 10.3389/fmicb.2015.00192. PMID: 25926816.

Deshpande, B.N., Crevecoeur, S., Matveev, A., and Vincent, W.F. 2016. Bacterial production in subarctic peatland lakes enriched by thawing permafrost. Biogeosciences. **13**: 4411–4427. doi: 10.5194/bg-13-4411-2016.

Douglas, M.S.V., and Smol, J.P. 2010. Freshwater diatoms as indicators of environmental change in the High Arctic. *In* The diatoms: applications for the environmental and earth sciences. 2nd ed. *Edited by* J.P. Smol and E.F. Stoermer. Cambridge University Press, Cambridge, UK. pp. 227–244.

Douglas, M.S.V., Hamilton, P., Pienitz, R., and Smol, J.P. 2004. Algal indicators of environmental change in arctic and antarctic lakes and ponds. *In* Long-term environmental change in Arctic and Antarctic lakes. *Edited by* R. Pienitz, M.S.V. Douglas, and J.P. Smol. Developments in Paleoenvironmental Research. Vol. 8. Springer-Verlag, Dordrecht, the Netherlands. pp. 117–157.

Ellis, C.J., Rochefort, L., Gauthier, G., and Pienitz, R. 2008. Paleoecological evidence for transitions between contrasting landforms in a polygon-patterned High Arctic wetland. Arct. Antarct. Alp. Res. **40**: 624–637. doi: 10.1657/1523-0430(07-059)[ELLIS]2.0.CO;2.

Environment Canada. 2010. National archives of climate data and information. Environment Canada. www.climate.weatheroffice.gc.ca/ [accessed October 2012].

Fallu, M.-A., and Pienitz, R. 1999. Diatomées lacustres de Jamésie–Hudsonie (Québec) et modèle de reconstitution des concentrations de carbone organique dissous. Ecoscience. **6**: 603–620. doi: 10.1080/11956860.1999.11682553.

Fallu, M.-A., Allaire, N., and Pienitz, R. 2000. Freshwater diatoms from Northern Québec and Labrador (Canada). Species–environment relationships in lakes of boreal forest, forest–tundra and tundra regions. Bibliotheca Diatomologica, Band 45. J. Cramer, Berlin, Germany.

Fasset, N.C. 1957. A manual of aquatic plants. The University of Wisconsin Press, Madison, Wis.

Howard, A.C., and Lewis, E.A. 1981. Mosses of eastern North America. Vol. 2. Columbia University Press, New York.

Ireland, R.R. 1983. Moss flora of the maritime provinces. University of Chicago Press, Chicago, Ill.

Jolivel, M., and Allard, M. 2013. Thermokarst and export of sediment and organic carbon in the Sheldrake River watershed, Nunavik, Canada. J. Geophys. Res. Earth. **118**: 1729–1745. doi: 10.1002/jgrf.20119.

Krammer, K. 2000. Diatoms of Europe. The genus *Pinnularia*. A.R.G. Gantner Verlag, Ruggell, Liechtenstein.

Krammer, K. 2002. Diatoms of Europe. *Cymbella*. A.R.G. Gantner Verlag, Ruggell, Liechtenstein.

Krammer, K. 2003. Diatoms of Europe. *Cymbopleura*, *Delicata*, *Navicymbula*, *Gomphocymbellopsis*, *Afrocymbella*. A.R.G. Gantner Verlag, Ruggell, Liechtenstein.

Krammer, K., and Lange-Bertalot, H. 1991. Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. *In* Süsswasserflora von Mitteleuropa. *Edited by* H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer. Gustav Fischer Verlag, Stuttgart/Jena, Germany.

Lafortune, V., Filion, L., and Hétu, B. 2006. Émersion des terres et développement des sols bien drainés au lac Guillaume-Delisle, Québec subarctique. Géogr. Phys. Quat. **60**: 165–181. doi: 10.7202/016827ar. PMID: 25242907.

Lajeunesse, P. 2008. Early Holocene deglaciation of the eastern coast of Hudson Bay. Geomorphology. **99**: 341–352. doi: 10.1016/j.geomorph.2007.11.012.

Lamoureux, G. 1987. Plantes sauvages des lacs, rivières et tourbières. Guide d'identification. Fleurbec, Saint-Augustin, Portneuf, Qué.

Lange-Bertalot, H. 2001. *Navicula* sensu stricto. 10 genera separated from *Navicula* sensu lato, *Frustulia*. Diatoms of Europe **2**: 1–526.

Larrivée, E. 2007. Tomographie électromagnétique du pergélisol près d'Umiujaq, Nunavik (Québec). MSc. thesis, Département de Géographie, Université Laval, Québec, Qué.

Laurion, I., Vincent, W.F., MacIntyre, S., Retamal, L., Dupont, C., Francus, P., and Pienitz, R. 2010. Variability in greenhouse gas emissions from permafrost thaw ponds. Limnol. Oceanogr. **55**: 115–133. doi: 10.4319/lo.2010.55.1.0115.

Lavoie, C., Hill, P.R., Allard, M., St-Onge, G., and Lajeunesse, P. 2008*a*. High-resolution seismo-stratigraphy and sedimentological properties of late- and postglacial sediments in Lac Guillaume-Delisle Estuary and Nastapoka Sound, eastern Hudson Bay. Can. J. Earth Sci. **45**: 427–441. doi: 10.1139/E08-010.

Lavoie, I., Hamilton, P.B., Campeau, S., Grenier, M., and Dillon, P.J. 2008*b*. Guide d'identification des diatomées des rivières de l'Est du Canada. Presses de l'Université du Québec, Québec City, Qué.

Legendre, P., and Gallagher, E. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia. **129**: 271–280. doi: 10.1007/s004420100716. PMID: 28547606.

Legendre, P., and Legendre, L. 2012. Numerical ecology. 3rd English ed. Elsevier Science B.V., Amsterdam, the Netherlands.

Lotter, A.F., Pienitz, R., and Schmidt, R. 2010. Diatoms as indicators of environmental change in subarctic and alpine regions. *In* The diatoms: applications for the environmental and earth sciences. *Edited by* J.P. Smol and E.F. Stoermer. Cambridge University Press, Cambridge, UK. pp. 231–248

Lowe, R.L. 1974. Environmental requirements and pollution tolerance of freshwater diatoms. US Environmental Protection Agency, Cincinnati, Ohio. EPA-670/4-74-005.

Majewska, R., Gambi, M.C., Totti, C.M., Pennesi, C., and De Stefano, M. 2012. Growth form analysis of epiphytic diatom communities of Terra Nova Bay (Ross Sea, Antarctica). Polar Biol. **36**: 73–86. doi: 10.1007/s00300-012-1240-1.

MRNF. 2012. Zone de végétation et domaine bioclimatique du Québec. www.mrn.gouv.qc.ca/forets/connaissances/connaissances-inventaire-zones-carte.jsp. [accessed 8 June 2016].

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Levesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Menard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., and Hik, D.S. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ. Res. Lett. **6**: 045509. doi: 10.1088/1748-9326/6/4/045509.

Payette, S., Delwaide, A., Caccianiga, M., and Beauchemin, M. 2004. Accelerated thawing of subarctic peatland permafrost over the last 50 years. Geophys. Res. Lett. **31**: L18208. doi: 10.1029/2004GL020358.

Pestryakova, L., Herzschuh, U., Wetterich, S., and Ulrich, M. 2012. Present-day variability and Holocene dynamics of permafrost affected lakes in central Yakutia (Eastern Siberia) inferred from diatom records. Quat. Sci. Rev. **51**: 56–70. doi: 10.1016/j.quascirev.2012.06.020.

Pienitz, R. 2001. Analyse des microrestes végétaux: diatomées. *In* Écologie des tourbières du Québec–Labrador. *Edited by* S. Payette and L. Rochefort. Les Presses de l'Université Laval, Québec City, Qué. pp. 311–326.

Pienitz, R., Smol, J.P., and 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. doi: 10.1007/BF00678109.

Pienitz, R., Doran, P.T., and Lamoureux, S.F. 2008. Origin and geomorphology of lakes in the polar regions. *In* Polar lakes and rivers: limnology of Arctic and Antarctic aquatic ecosystems. *Edited by* W.F. Vincent, J.E. Hobbie, and J. Laybourn-Parry. Oxford University Press, New York. pp. 25–41.

Pissart, A. 2002. Palsas, lithalsas and remnants of these periglacial mounds. A progress report. Prog. Phys. Geog. **26**: 605–621. doi: 10.1191/0309133302pp354ra.

Ponader, K., Pienitz, R., Vincent, W.F., and Gajewski, K. 2002. Limnological conditions in a subarctic lake (northern Québec, Canada) during the late Holocene: analyses based on fossil diatoms. J. Paleolimnol. **27**: 353–366. doi: 10.1023/A:1016033028144.

Porsild, A.E., and Cody, W.J. 1980. Vascular plants of continental Northwest Territories, Canada. National Museum of Natural Sciences, Ottawa, Ont.

Przytulska, A., Comte, J., Crevecoeur, S., Lovejoy, C., Laurion, I., and Vincent, W.F. 2016. Phototrophic pigment diversity and picophytoplankton abundance in subarctic permafrost thaw lakes. Biogeosciences. **13**: 13–26. doi: 10.5194/bg-13-13-2016.

Roiha, T., Laurion, I., and Rautio, M. 2015. Carbon dynamics in highly heterotrophic subarctic thaw ponds. Biogeosciences. **12**: 7223–7237. doi: 10.5194/bg-12-7223-2015.

Romanovsky, V.E., Smith, S.L., and Christiansen, H.H. 2010. Permafrost thermal state in the polar Northern Hemisphere during the international polar year 2007–2009: a synthesis. Permafr. Periglac. **21**: 106–116. doi: 10.1002/ppp.689.

Rowland, J.C., Jones, C.E., Altmann, G., Bryan, R., Crosby, B.T., Hinzman, L.D., Kane, D.L., Lawrence, D.M., Mancino, A., Marsh, P., McNamara, J.P., Romanovsky, V.E., Toniolo, H., Travis, B.J., Trochim, E., Wilson, C.J., and Geernaert, G.L. 2010. Arctic landscapes in transition: responses to thawing permafrost. EOS Trans. Am. Geophys. Union. **91**: 229–230. doi: 10.1029/2010EO260001.

Rühland, K.M. 2001. Diatom assemblage shifts relative to changes in environmental and climatic conditions in the circumpolar treeline regions of the Canadian and Siberian Arctic. Ph.D. thesis, Department of Biology, Queen's University, Kingston, Ont.

Rühland, K.M., Hargan, K.E., Jeziorski, A., Paterson, A.M., Keller, W., and Smol, J.P. 2014. A multi-trophic exploratory survey of recent environmental changes using lake sediments in the Hudson Bay Lowlands, Ontario, Canada. Arct. Antarct. Alp. Res. **46**: 139–158. doi: 10.1657/1938-4246-46.1.139.

Sabater, S. 2009. Diatoms. Encyclopedia of inland waters. 1st ed. Elsevier, Oxford, UK. pp. 149–156.

Saulnier-Talbot, E., Pienitz, R., and Vincent, W.F. 2003. Holocene lake succession and palaeo-optics of a Subarctic lake, northern Québec, Canada. Holocene. **13**: 517–526. doi: 10.1191/0959683603hl641rp.

Seppälä, M. 1986. The origin of palsas. Geogr. Ann. A. **68**: 141–147. doi: 10.2307/521453.

Smol, J.P., and Stoermer, E.F. (Editors). 2010. The diatoms: applications for the environmental and earth sciences. 2nd ed. Cambridge University Press, Cambridge, UK.

ter Braak, C.J.F., and Šmilauer, P. 2012. CANOCO 5: software for multivariate data exploration, testing, and summarization. 1997–2012 Biometris, Plant Research International, Wageningen, the Netherlands.

Vincent, W.F., Lemay, M., and Allard, M. 2017. Arctic permafrost landscapes in transition: towards an integrated Earth system approach. Arct. Sci. **3**: 39–64. doi: 10.1139/as-2016-0027.

Vonk, J.E., Tank, S.E., Bowden, W.B., Laurion, I., Vincent, W.F., Alekseychik, P., Amyot, M., Billet, M.F., Canário, J., Cory, R.M., Deshpande, B.N., Helbig, M., Jammet, M., Karlsson, J., Larouche, J., MacMillan, G., Rautio, M., Walter Anthony, K.M., and Wickland, K.P. 2015. Reviews and syntheses: effects of permafrost thaw on Arctic aquatic ecosystems. Biogeosciences. **12**: 7129–7167. doi: 10.5194/bg-12-7129-2015.

Walter, K.M., Zimov, S.A., Chanton, J.P., Verbyla, D., and Chapin, F.S. 2006. Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming. Nature. **443**: 71–75. doi: 10.1038/nature05040. PMID: 16957728.

Watanabe, S., Laurion, I., Chokmani, K., Pienitz, R., and Vincent, W.F. 2011. Optical diversity of thaw ponds in discontinuous permafrost: a model system for water color analysis. J. Geophys. Res. Biogeosci. **116**: G02003, doi: 10.1029/2010JG001380.

Zhang, T., Barry, R.G., Knowles, K., Heginbottom, J.A., and Brown, J. 1999. Statistics and characteristics of permafrost and ground-ice distribution in the Northern Hemisphere. Polar Geogr. **23**: 132–154. doi: 10.1080/10889379909377670.