



# Paleolimnology of thermokarst lakes: a window into permafrost landscape evolution<sup>1</sup>

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**Abstract:** Widespread across northern permafrost landscapes, thermokarst ponds and lakes provide vital wildlife habitat and play a key role in biogeochemical processes. Stored in the sediments of these typically shallow and dynamic waterbodies are rich sources of paleoenvironmental information whose potential has not yet been fully exploited, likely because of concerns over stratigraphic preservation and challenges to develop reliable sediment core chronologies. Here, we present an overview of recently derived informative paleolimnological reconstructions based on multiparameter analysis of sediment archives from permafrost aquatic basins. We include examples from across the Canadian North, Alaska, and Siberia that illustrate their value for providing insights into temporal patterns of lake inception, catchment erosion, aquatic productivity, hydrological evolution, and land-scape disturbances. Although not captured in our survey, emerging research directions focused on carbon accumulation, storage, and balance hold much promise for contributing to global climate change science.

Key words: thermokarst lakes, permafrost, paleolimnology, lake sediments.

**Résumé :** Répandus d'un paysage de pergélisol septentrional à l'autre, les étangs et les lacs thermokarstiques fournissent un habitat essentiel à la faune et jouent un rôle clé dans les processus biogéochimiques. Accumulées dans les sédiments de ces plans d'eau typiquement peu profonds et dynamiques se trouvent des sources riches en informations paléoenvironnementales dont le potentiel n'a pas encore été entièrement exploité, probablement à cause des préoccupations concernant la conservation stratigraphique et les défis de développer des chronologies fiables à partir des carottes sédimentaires. Ici, nous présentons une vue d'ensemble des reconstitutions paléolimnologiques informatives récemment dérivées d'après l'analyse multi paramétrée d'archives de sédiments des bassins aquatiques du pergélisol. Nous incluons des exemples provenant du Nord canadien, de l'Alaska et de la Sibérie qui

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illustrent que ceux-ci peuvent offrir des perspectives sur les tendances temporelles de création de lacs, de l'érosion de bassins récepteurs, de la productivité aquatique, de l'évolution hydrologique et des perturbations du paysage. Bien que non mises en lumière dans notre enquête, les directions de recherche émergentes centrées sur l'accumulation carbonique, le stockage et l'équilibre s'annoncent bien quant à leur contribution à la science du changement climatique mondial.

Mots-clés : lacs thermokarstiques, pergélisol, paléolimnologie, sédiments lacustres.

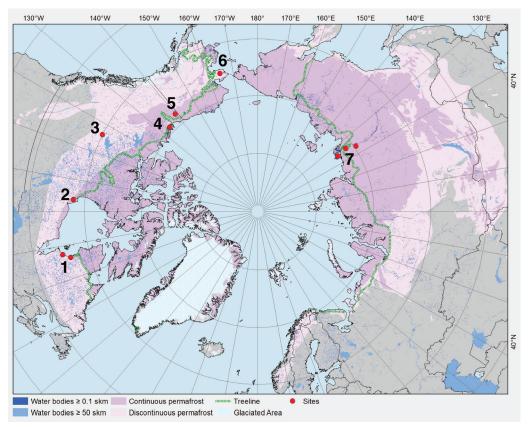
## Introduction

Thermokarst refers to a suite of landscape processes associated with the thawing of icerich permafrost, or melting of massive ground ice, which modify the local topography (Kokelj and Jorgenson 2013). Among the various landscape features resulting from permafrost thawing and erosion, thermokarst ponds and lakes (hereafter referred to collectively as lakes) are formed by localized ground subsidence resulting in water accumulation within closed topographic depressions. These aquatic systems form where excess ground ice is present, typically in soils where volumetric ice content is greater than 30% (Grosse et al. 2013). Permafrost thaw and related thermokarst processes transfer water, inorganic and organic matter, and dissolved chemical constituents from terrestrial to aquatic environments. These processes exert strong control on the physical (thermal and optical properties), geochemical (dissolved and particulate matter), and biological conditions in thermokarst lakes (Vonk et al. 2015, and references therein). Changes affecting the catchment and water column are filtered, integrated, and recorded in the lake bottom sediments as natural archives.

Thermokarst lakes are widespread across circumpolar regions, although detailed numbers and distribution maps are not available (Grosse et al. 2013) (Fig. 1). Smith et al. (2007) estimated that nearly 75% of all lakes north of 45.5°N are located in permafrost landscapes. with a cumulative area of >400 000  $\text{km}^2$  and representing nearly 150 000 lakes, most of which originate from thermokarst processes. However, these estimates only include waterbodies with surface areas between 0.1 and 50  $\text{km}^2$ , and because many thermokarst lakes are smaller, this number is likely underestimated. According to more recent estimates based on high-resolution remote sensing, the total number and cumulative surface area of lakes across the Arctic (north of 60 °N), regardless of their origin (i.e., not only thermokarst) and including smaller waterbodies (<0.1 km<sup>2</sup>), might range from 3.5 to 5.0  $\times 10^{6}$  and from 400 000 to 3  $\times 10^6$  km<sup>2</sup>, respectively (Verpoorter et al. 2014; Paltan et al. 2015). Indeed, thermokarst lakes vary greatly in surface area, from small ponds of a few metres across (Breton et al. 2009) to large lakes spanning many square kilometres (Côté and Burn 2002). Most thermokarst lakes are generally shallow, not deeper than 10 m, and frequently much less depending on ground-ice content and distribution, lake age, hydroclimatic conditions, and local topography (West and Plug 2008). However, some other lakes located within Pleistocene-age, ice-rich permafrost deposits underlying sectors of Siberia, Alaska, and western Canada ("Yedoma" deposits) can be much deeper (i.e., several tens of metres deep, e.g., Morgenstern et al. 2011; Schirrmeister et al. 2011). Thermokarst lakes provide important ecosystem services (e.g., fishing and hunting grounds, water supply to indigenous communities, habitat for wildlife) and also play a key role in water and biogeochemical cycles in northern landscapes. Numerous remote sensing studies have recently examined changes in the areal extent of thermokarst lakes during the past few decades, often as a means to determine hydrological consequences of climate change (e.g., Smith et al. 2005; Riordan et al. 2006; Labrecque et al. 2009; Jones et al. 2011a; Lantz and Turner 2015).

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**Fig. 1.** Circum-Arctic map of permafrost and lake distribution. Numbers refer to thermokarst paleolimnological studies highlighted in the text as follows: Western Nunavik, northern Quebec (1), Western Hudson Bay Lowlands, northern Manitoba (2), South Slave Taiga Plains, Northwest Territories (3), Mackenzie Delta Uplands, Northwest Territories (4), Old Crow Flats, northern Yukon Territory (5), Southern Seward Peninsula, Alaska (6), and Lena Delta transect, northeastern Siberia (7).



Temporal insight into hydrological and geomorphological processes influencing thermokarst lakes, and their drivers, can be obtained using a paleolimnological approach the analysis of physical, geochemical, and biological information preserved in their sediment records. However, their generally shallow depth can negatively affect the coherence of stratigraphic records as a result of wind-caused disturbance and desiccation. Also, thermo-erosion of shorelines can increase rates of supply of older organic and inorganic sediment to the coring location. This can confound the ability to date cores accurately using some radiometric methods (e.g., <sup>14</sup>C), although other dating techniques based on short-lived atmospheric radionuclides (<sup>210</sup>Pb, <sup>137</sup>Cs) or long-term luminescence can be applied with success (Appleby 2001; Lian and Huntley 2001). Furthermore, thermokarst lake sediments can be affected by post-deposition ("early diagenesis") processes such as organic matter mineralization (e.g., methane production) or trace element redistribution (Audry et al. 2011). These factors, as well as the often-brief existence and remoteness of thermokarst lakes, likely account for the relatively poor representation of thermokarst lake sedimentary records in the "northern paleolimnology" literature (Pienitz et al. 2004; MacDonald et al. 2012). A survey of papers published in the Journal of Paleolimnology during the past three decades (1987-2016) produced only three papers upon searching the term "thermokarst lake" (Dallimore et al. 2000; Biskaborn et al. 2013a; Frolova et al. 2014). Evidently, these

waterbodies remain virtually untapped for their paleolimnological potential, yet these shallow systems offer advantages for paleoenvironmental reconstructions in northern regions. Thermokarst lakes are widespread in permafrost landscapes, often possess relatively high sedimentation rates enabling highly resolved reconstructions, and contain great diversity of littoral habitats and shallow-water bio-indicators (Coulombe et al. 2016; Smol 2016).

As demonstrated in this review paper, thermokarst lakes represent more than just "by-products" of permafrost degradation; they are unique "sediment sinks" that can collect useful environmental archives over their life span (e.g., Dallimore et al. 2000; Pienitz et al. 2008; Edwards et al. 2016; Lenz et al. 2016). For example, using a set of thermokarst lakes spanning an ecoclimatic gradient at a given site, it is possible to gain knowledge about past environmental changes related to local geomorphological and hydrological processes, in addition to regional climate (Dallimore et al. 2000; Wolfe et al. 2011b). Most paleolimnological investigations that have focused specifically on thermokarst lakes are based on short sediment core analyses and generally report on recent (i.e., past several decades to centuries) environmental changes within thermokarst basins and their catchments. This includes documenting terrestrial vegetation change, transport of dissolved organic matter related to the thawing of peat-rich permafrost, and lake expansion and subsequent drainage caused by increased summer rainfall (e.g., Bouchard et al. 2011, 2013a, 2014; MacDonald et al. 2012; Coleman et al. 2015). Yet, some thermokarst lakes have persisted for several thousand years, spanning the Holocene and beyond, and their sediment records have yielded temporal information about the succession of cool and warm climate episodes, influence of thermokarst activity on sediment input to lakes, and carbon exchange with the atmosphere (e.g., Dallimore et al. 2000; Biskaborn et al. 2012, 2013a; Lenz et al. 2013, 2016; Walter Anthony et al. 2014; Edwards et al. 2016). Thus, sediments that accumulate in thermokarst lakes provide promising archives to examine a multitude of environmental changes, including temporal insights into permafrost landscape evolution. Knowledge gained can help place spatial analyses into a longer temporal context (e.g., MacDonald et al. 2012; Coleman et al. 2015; Farquharson et al. 2016), be used to test models of the consequences of climate change and related feedbacks from thawing permafrost (Stepanenko et al. 2011; Gao et al. 2013), and to anticipate future trajectories of thermokarst lake change (van Huissteden et al. 2011; Kessler et al. 2012).

Here, we first review processes that influence thermokarst lakes, which are important to consider in the interpretation of their sedimentary records. Then, we present an overview of key findings stemming from the recent use of paleolimnological data obtained from thermokarst lake studies to reconstruct hydrological conditions and sedimentological processes, organic matter and nutrient balance, catchment disturbances, and extreme hydroclimatic events affecting lake ecology and evolution in permafrost landscapes. We focus mostly on case studies from northern Canada (Nunavik, Hudson Bay Lowlands, South Slave region, Mackenzie Delta, and northern Yukon) and also include recent investigations from Alaska and Siberia. Finally, we comment on emerging research directions in thermokarst lake paleolimnology.

## Thermokarst lake formation and evolution

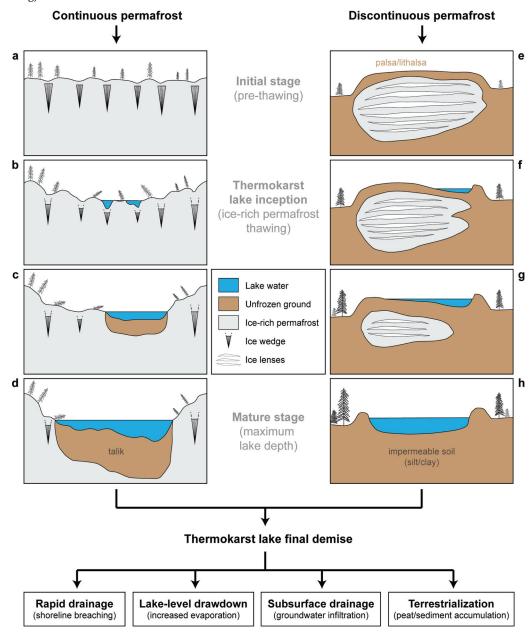
Conditions affecting lake-rich permafrost landscapes across the Arctic (e.g., climate, vegetation, geology, topography, frozen-ground properties such as ground-ice content) are strongly heterogeneous at the local to regional scales. There is thus a remarkable diversity of thermokarst lake formation processes, morphology, and hydrological and limnological conditions. In regions of continuous permafrost, thermokarst lake inception generally starts with the coalescence of polygonal and (or) ice-wedge trough pools overlying melting ice-wedge networks (Czudek and Demek 1970), whereas in the discontinuous permafrost

zone, initial lake formation often results from the thawing of ice-rich cryogenic mounds called palsas (organic) or lithalsas (mineral) (Luoto and Seppälä 2003; Calmels et al. 2008) (Fig. 2). Climatic factors (e.g., increasing temperature and (or) precipitation) and other drivers such as forest fires and human activity (e.g., active layer disturbance, inadequate drainage) can trigger thermokarst lake inception (e.g., Burn and Smith 1990; Burn 2002; Payette et al. 2004; Kokelj and Jorgenson 2013). When thaw depth exceeds the maximum thickness of winter ice cover, annual lake bottom temperatures above 0 °C enhance further thawing and subsidence and the formation of an unfrozen ground layer underneath a lake called a talik, or thaw bulb (Burn 2002; West and Plug 2008). Once initiated, thermokarst lakes also tend to develop laterally by thermal and mechanical erosion into the surrounding ice-rich permafrost soils, resulting in characteristic sedimentation patterns and lakewater chemistry (e.g., Murton 1996; Kokelj et al. 2009b). Active shoreline erosional processes (e.g., erosional niche development by wave action, mass wasting through thaw slumping and block failures, ice-shove during breakup) are typical in thermokarst basins and can lead to drainage as part of their hydrological evolution (Marsh et al. 2009; Jones et al. 2011a; Kokelj and Jorgenson 2013).

The final "demise" of thermokarst lakes generally involves one of the following: rapid drainage resulting from shoreline breaching after higher-than-average precipitation (Turner et al. 2010; Lantz and Turner 2015), lake-level drawdown due to factors that lead to increased evaporation (Riordan et al. 2006; Bouchard et al. 2013*b*), subsurface drainage (groundwater infiltration) through an open talik (Yoshikawa and Hinzman 2003), or terrestrialization via rapid peat accumulation and lake infilling (Payette et al. 2004; Roach et al. 2011). Local land-scape conditions and individual catchment characteristics (e.g., soil type, vegetation cover, topography) will interact with regional climate, resulting in a broad range of processes (both autogenic and allogenic, respectively) that influence the evolution of thermokarst lakes (Fig. 2).

Although some studies (summarized by Jorgenson and Shur 2007) have proposed that thermokarst lake stages from inception to termination may be cyclical, field observations focusing specifically on ground-ice content and aggradation prior to lake inception, rates of changes and associated processes during the Holocene, and diatom-based paleoecological reconstructions do not support such a recurrent succession (Jorgenson and Shur 2007; Ellis et al. 2008; Grosse et al. 2013; Lenz et al. 2016). Instead, these findings indicate that (1) geomorphological and limnological processes occurring in thermokarst terrain do not allow the surface to return to original conditions (i.e. prior to the onset of a cycle) and (2) such processes are too slow to counterbalance surface stabilization that occurred during the Holocene. Thermokarst lakes thus likely follow a complex sequential development, often characterized by distinct initial and secondary lake inception stages, lateral expansion accompanied by spatially heterogeneous sorting and redistribution of surface sediments. and lake stabilization and persistence possibly over millennia, contradicting a strictly cyclical succession. This complex development is further demonstrated by the co-existence – and sometimes overlapping — of multiple lake stages within a given region from the continuous to the sporadic permafrost zones (e.g., Jorgenson and Shur 2007; Ellis et al. 2008; Calmels et al. 2008: Bouchard et al. 2014).

Below, we show that thermokarst lakes can collect and record, over time, a broad spectrum of useful environmental information about hydrological and limnological processes, some of which are unique to permafrost aquatic systems (e.g., ground-ice melting triggering soil and lake bottom subsidence, thermal erosion of shorelines, thaw slump activity, and impacts on lakewater chemistry). We highlight key results from recent studies that utilized lake sediment properties to reconstruct processes and timing of thermokarst lake formation, as well as the temporal evolution of their limnological and hydrological conditions, **Fig. 2.** Thermokarst lake formation and evolution in ice-rich permafrost in the (a-d) continuous and (e-h) discontinuous zones (modified from Grosse et al. (2013) and Calmels et al. (2008), respectively). In continuous permafrost, where ice-wedge terrains dominate (a), thermokarst lake inception generally starts with water pooling above low-center polygons and melting ice wedges (b). These small ponds eventually merge to create shallow lakes (c), which further deepen and develop laterally by thermo-erosion, resulting in larger and deeper mature lakes with an underlying thaw bulb or talik (d). In discontinuous permafrost, where ice-rich cryogenic mounds (palsas and lithalsas) are widespread (e), the melting of segregation ice lenses results in surface subsidence and water pooling in topographic depressions (f and g). Once permafrost has completely thawed, a mature thermokarst pond/ lake surrounded by a peripheral ridge can stabilize if underlain by impermeable silts and clays (h). The final stage of thermokarst lakes can involve: rapid drainage (resulting from shoreline breaching after higher-than-average precipitation), lake level drawdown (due to factors that lead to increased evaporation), subsurface drainage (groundwater infiltration through an open talik), or terrestrialization (via rapid peat accumulation and (or) lake infilling). See text for details and references.



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from their inception to the present (generally the past few centuries). The location of the study sites referred to in the text is indicated in Fig. 1.

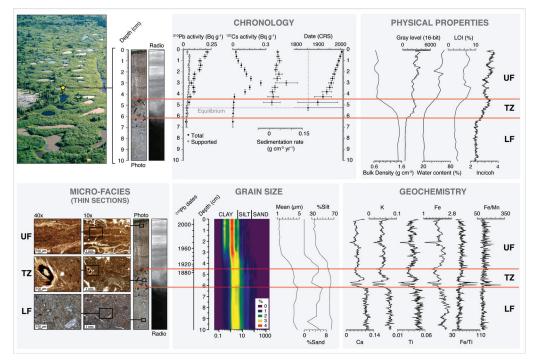
## Key paleolimnological findings from thermokarst lake archives

## Western Nunavik, northern Quebec

Nunavik (the Inuit territory in northern Quebec) encompasses, in its western part, most of the eastern coast of Hudson Bay and covers a latitudinal gradient crossing the treeline, ranging from isolated to continuous permafrost (Brown et al. 1998) (Fig. 1). Post-glacial land emergence of the area occurred around 6000 years ago, after which tree and shrub vegetation and peatlands started to colonize the underlying marine silty clays (Arlen-Pouliot and Bhiry 2005). Permafrost inception started in the mid- to late Holocene, culminating during the Little Ice Age. Palsas and lithalsas, formed by ground ice aggradation and related surface heaving, are widespread in the region and typical of the discontinuous permafrost landforms in subarctic Quebec (Allard and Seguin 1987). Recent increases in air/ground temperatures and snow cover along the eastern shore of Hudson Bay have contributed to widespread reduction of permafrost extent, resulting in increasing surface areas occupied by subarctic thermokarst ponds (Payette et al. 2004; Vallée and Payette 2007; Jolivel and Allard 2013). However, the exact timing of their inception as well as the processes controlling their sedimentological and limnological evolution in response to past paleoenvironmental changes in their vicinity were poorly known until recently.

Combining high-resolution X-ray scanning techniques (microfluorescence, microradiography) with more "classical" methods (e.g., grain size analysis, thin sections for microfacies analysis, loss-on-ignition), Bouchard et al. (2011) examined the physicochemical properties of sediments in small thermokarst systems covering a wide range of limnological properties near Kuujjuarapik-Whapmagoostui (Great Whale River) along the southeastern shore of Hudson Bay (Fig. 3). They were able to identify the main processes controlling sediment erosion, transport, and deposition and characterize lake inception and temporal evolution of sediment inputs and limnological conditions in the recent past. Identified sedimentary facies (or units) were, from oldest to youngest, (1) massive marine silts and clays deposited during the postglacial Tyrrell Sea transgression (~8000 to 6000 cal yr BP), subsequently emerged by glacio-isostatic rebound and more recently (~1500 to 400 cal vr BP) affected by permafrost inception and growth, (2) a transitional organic-rich unit containing macroand microscopic peat debris derived from ancient summits of palsas that were partially eroded and subsequently submerged, and (3) laminated organic-rich lacustrine muds deposited as a consequence of permafrost thawing and subsidence (i.e., since thermokarst lake inception) during the past few centuries. Moreover, down-core profiles of redox-sensitive elements (iron, manganese) documented the progressive development, since lake inception, of seasonal thermal stratification in the water column and anoxic/hypoxic conditions in bottom waters, a prominent feature of these limnologically diverse systems today (Breton et al. 2009). This pioneering lithostratigraphic work served as a baseline to further investigate permafrost landscape dynamics since the 1950s based on remote sensing images of the same study area (Bouchard et al. 2014) and also led to assessments of sediment inputs and the "life span" of shallow thermokarst ecosystems within the discontinuous permafrost zone based on sediment trap studies (Coulombe et al. 2016).

In a companion paper focused on biological aspects, Bouchard et al. (2013*a*) analyzed fossil diatom assemblages in thermokarst lake sediments, thereby confirming the occurrence and nature of the three distinct stratigraphic units mentioned above. They also used a diatom-based inference model (developed for western subarctic Quebec, including the eastern Hudson Bay region; Fallu and Pienitz 1999) to reconstruct past concentrations of dissolved organic carbon (DOC). Diatom-inferred DOC revealed decreasing concentrations during **Fig. 3.** Lithostratigraphic properties of thermokarst lake sediments in eastern Hudson Bay near Kuujjuarapik-Whapmagoostui along the Great Whale River (modified from Bouchard et al. 2011). Chronological (<sup>210</sup>Pb, <sup>137</sup>Cs), physical (bulk density, loss-on-ignition), sedimentological (thin sections, grain size), and geochemical (XRF) data are combined to distinguish three distinct lithostratigraphic facies from bottom to top: a marine lower facies (LF), an organic-rich (peat) transition zone (TZ), and a lacustrine upper facies (UF).



the past few centuries, in contrast with the general trend in this region (Saulnier-Talbot et al. 2003), suggesting the interplay of local drivers such as exhaustion of external DOC sources from small catchments and important peat inputs (from former palsa surfaces) as a source of organic carbon during the initial stages of lake formation. In the same study, Bouchard et al. (2013a) compared fossil diatom data to visible near infrared spectral sediment properties, which confirmed anoxia/hypoxia development in bottom waters following lake inception. These results indicate that, in the recent past, diatom community changes and limnological evolution of thermokarst ecosystems were controlled also by autogenic processes (e.g., local vegetation/soil development, peat accumulation and erosion, adsorption of organic matter onto settling clays) rather than by allogenic forcing mechanisms alone (e.g., precipitation and temperature, geochemical leaching of the surrounding catchment). Indeed, the optical diversity of these small and shallow thermokarst lakes was found to be mainly controlled by two optically active substances (DOC and settling mineral particles; Watanabe et al. 2011), which varied greatly among lakes in relation to surrounding landscape properties. This underscored the major influence of local geomorphological and ecological conditions on thermokarst lake inception and limnological evolution through time.

## Western Hudson Bay Lowlands, northern Manitoba

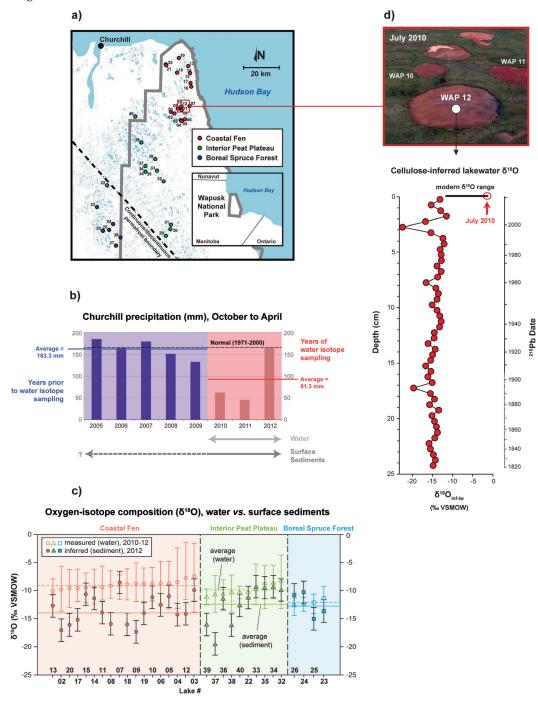
The Hudson Bay Lowlands (HBL) is the world's second largest contiguous wetland (Fig. 1). Continuous and discontinuous permafrost that underlies the western portion of the HBL impedes infiltration and, consequently, water pools on the surface creating thousands of lakes, ponds, and vast wetlands, which are mainly of thermokarst origin and serve a variety

of ecosystem services. These shallow waterbodies are a dominant feature of the land surface, which spans a vegetation gradient from boreal forest to coastal tundra.

Two primary stressors influence thermokarst lakes in this region. Warming has occurred during the past century and models predict that mean annual temperatures will increase by a further 3.1 °C by 2070 (Macrae et al. 2014). Concomitant increases in the length of the ice-free season and open-water evaporation, as well as shifts in seasonality of precipitation, have the potential to strongly alter lake water balances. In the northwestern coastal region of the HBL, the population size and geographic range of the Lesser Snow Goose (LSG) (*Chen caerulescens caerulescens*) have increased rapidly during the past ~40 years (Jefferies et al. 2006). Grubbing and the removal of grasses, construction and occupation of nests, and deposits of feces are evident in catchments of many lakes in this region. As summarized below, paleolimnological results have shed new light on the sensitivity of thermokarst lakes to climate change and waterfowl disturbance in this region.

Snowmelt runoff is an important hydrological process that sustains water balance of shallow subarctic lakes (Schindler and Smol 2006). Yet, evidence suggests that spring snow cover extent over the Northern Hemisphere has declined substantially during the past four decades (Derksen and Brown 2012). Such trends are expected to continue, although models predict considerable spatial and temporal heterogeneity in snow cover (AMAP 2011; Derksen and Brown 2012; Krasting et al. 2013). Bouchard et al. (2013b) examined the consequences of low snowmelt runoff on shallow thermokarst lakes in the HBL, as well as in the Old Crow Flats, Yukon, using contemporary and paleolimnological isotopic approaches (Fig. 4). Measurement of lakewater  $\delta^{18}$  was systematically and positively offset from lakewater  $\delta^{18}$ O inferred from aquatic cellulose in recently deposited sediments from many lakes situated in low-relief, open-tundra catchments where snow cover is redistributed by wind (Figs. 4b and 4c). This isotopic offset was attributed to marked evaporation and  $^{18}$ O enrichment in surface waters, stemming from lower-than-average snowmelt runoff in recent years. These results demonstrated the potential for lake level drawdown in shallow thermokarst lakes that are situated in catchments lacking features (i.e., shrub vegetation, relief) that promote snowmelt runoff. Further paleolimnological investigations by Bouchard et al. (2013b) showed that recently observed near-complete desiccation of one open-tundra thermokarst lake in western HBL, following a year of particularly low snowmelt runoff, may be unprecedented during the past 200 years (Fig. 4d). Findings support the contention that reduction in snowmelt runoff could lead to widespread desiccation of shallow thermokarst lakes in these regions.

Although a number of studies have examined the effects of LSG disturbance on terrestrial ecosystems in the coastal region of the western HBL (e.g., Batt 1997; Handa et al. 2002; Jefferies et al. 2004, 2006; Abraham et al. 2005a, 2005b), comparatively less was known of the effects of LSG catchment disturbance on the numerous thermokarst lakes in their nesting grounds until recently. MacDonald et al. (2015) combined paleolimnological analyses with three years of water chemistry measurements to assess the dual effects of climate warming and LSG population expansion on three thermokarst lakes — two that were in catchments strongly disturbed by the LSG based on field observations and one that had no visual evidence of recent LSG disturbance in its catchment. Results identified limnological phases characterized by regime shifts in productivity, nutrient cycling, and aquatic habitat during the past two centuries (Table 1). Low productivity, turbid, and nutrient-poor conditions transitioned to higher productivity, low nitrogen availability, and development of a benthic biofilm habitat as climate warmed at the end of the Little Ice Age. A second regime shift beginning in the mid-1970s was uniquely recorded at the LSG-disturbed lakes. Accelerated productivity and increased nitrogen availability leading to high carbon demand occurred as a consequence of an increase in catchment-derived nutrients from **Fig. 4.** Hydrological sensitivity of shallow subarctic lakes to low snowmelt runoff in western Hudson Bay Lowlands, Manitoba (modified from Bouchard et al. 2013*b*). (*a*) Location of the study area, including sampled lakes colourcoded based on their classification. (*b*) Winter precipitation during years of water isotope sampling (red) and the five years prior (blue), including the 1971–2000 climate normal (dashed black line). (*c*) Comparison of measured (water, open symbols) with cellulose-inferred (sediment, solid symbols) lakewater oxygen isotope composition ( $\delta^{18}$ O). (*d*) Cellulose-inferred  $\delta^{18}$ O record from coastal fen lake WAP12, where near-complete desiccation occurred during the midsummer of 2010.



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Driver of limnological change	Limnology	Nutrient behaviour	Aquatic community
LSG catchment disturbance	Erosional input of dissolved nutrients and ions; ↑ sedimentation rate	Increase in C demand $\rightarrow CO_2$ invasion; $\downarrow \delta^{13}C_{org}$	Decrease in cyanobacteria; ↓ cyanobacteria pigments
	Increase in productivity; ↑ organic matter; ↑ chlorophyll <i>a</i>	Increase in N availability and rapid uptake; ↑ δ <sup>15</sup> N; ↓ C/N	
Climate warming	Increase in light availability; ↑ organic matter; ↓ mineral matter	Increase in C demand; ↑ δ <sup>13</sup> C <sub>org</sub>	Development of benthic biofilm; Benthic mat dwelling; Denticula kuetzingii dominate; ↑ Denticula kuetzingii; ↓ Fragilaria pinnata
	Increase in productivity; $\uparrow$ chlorophyll <i>a</i>	Increase in N demand $\rightarrow$ N limitation; $\delta^{15}N \approx 0\%;$ $\downarrow C/N$	Increase in cyanobacteria; ↑cyanobacteria pigments
Cool climate (Little Ice Age)	Low light availability; ↓ organic matter; ↑ mineral matter; low productivity; ↓ chlorophyll <i>a</i>	Low nutrient availability; $\uparrow C/N;$ $\downarrow N%;$ $\downarrow C_{org}\%;$ Low C demand; $\downarrow \delta^{13}C_{org}$	Episammic Fragilaria pinnata dominate; ↑ Fragilaria pinnata; ↓ Denticula kuetzingii

**Table 1.** Summary of limnological changes, nutrient behaviour, and aquatic community responses to climate warming and LSG catchment disturbance in the Hudson Bay Lowlands, Manitoba.

LSG disturbance in the catchment. Results distinguish the consequences of warming and LSG disturbance on limnological conditions of coastal tundra thermokarst lakes in HBL and provide a suite of sensitive measures that are being used to inform aquatic ecosystem monitoring (MacDonald et al. 2015; White et al. 2015).

## South Slave Taiga Plains, Northwest Territories

Permafrost in the South Slave Taiga Plains, Northwest Territories, is discontinuous and generally restricted to treed peat plateaus (Heginbottom and Dubreuil 1995) (Fig. 1). The presence of ice-rich permafrost raises soils above the surrounding wetland complexes, forming plateaus that are elevated by 1-3 m. The drier soil conditions on peat plateaus allow for the growth of spruce trees, and the landscape consists of a mosaic of forested permafrost plateaus and nonpermafrost bogs and fens. Permafrost thaw under peat plateaus causes the conversion of treed plateaus into wetlands. As ground ice melts, collapse scars form, either along the margins of the plateau, leading to the expansion and merger of bogs and fens, or isolated within the plateau, forming an ombrotrophic bog. The trees become waterlogged and die, and collapse scars are vegetated by hydrophilic taxa such as sedges and mosses (Beilman et al. 2001). Because peat plateaus act as barriers to the lateral flow of water, redirecting surface and subsurface flow into channel fens, the loss of permafrost peat plateaus leads to substantial hydrological changes (Quinton et al. 2009). Peat subsidence and the loss of permafrost plateaus generally promote increased connectivity of drainage networks and export of DOC to aquatic ecosystems (Quinton et al. 2009; Olefeldt and Roulet 2014). Permafrost thaw can be initiated by warming temperatures or landscape disturbances such as seismic cut lines and forest fires. Although permafrost thaw has been occurring in this region since the end of the Little Ice Age (Halsey et al. 1995), the rate of peat subsidence has accelerated in recent decades (Quinton et al. 2011).

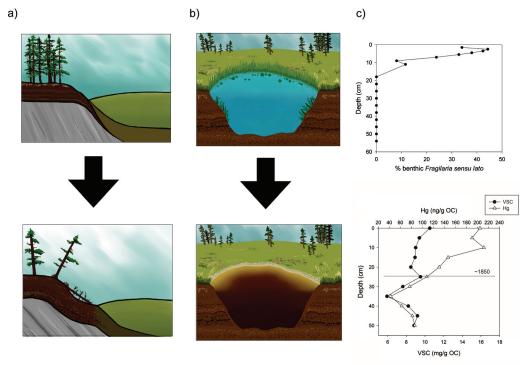
Two recently published paleolimnological studies have used multiple biological and biogeochemical sedimentary parameters to track peat subsidence in the South Slave Taiga Plains and assess implications for lake ecosystems (Figs. 5a and 5b). Coleman et al. (2015) integrated a diatom-based paleolimnological study of two lakes (informally named TAH-7 and KAK-1) located south of the community of Kakisa with a remote sensing investigation of landscape changes since ~1950 to understand how recent increases in peat subsidence have altered aquatic biota. In addition, they analyzed macroscopic charcoal in their sediment cores to investigate potential links between forest fires and the initiation of peat subsidence. Both lakes exhibited a substantial increase in the proportion of the landscape covered by collapsed peat scars between 1970 and 2012 based on remotely sensed images. In TAH-7, the appearance and increase in benthic Fragilaria diatom taxa after ~1930 indicated an increase in coloured DOC and decreased water clarity (Fig. 5c). No post-warming increases in chlorophyll *a* were observed in TAH-7, likely due to reduced light availability for photosynthesis. The authors concluded that recent (post-1970) peat subsidence is part of a longer-term trend that began prior to the earliest remote sensing records and has led to the crossing of an important ecological threshold for DOC. In contrast, no changes in diatom taxa were observed in KAK-1 that would indicate an increase in DOC.

Korosi et al. (2015) analyzed plant biomarkers (*n*-alkanes and lignin-derived phenols), stable isotopes, and mercury in the same sediment cores analyzed by Coleman et al. (2015) to investigate how the loss of permafrost-supported peat plateaus alters the transport of terrestrial organic matter to lakes. In both KAK-1 and TAH-7, organic matter biomarkers (specifically the  $C_{23}$  and  $C_{29}$  *n*-alkanes) tracked the changes in catchment vegetation that occur following peat subsidence (loss of spruce forests, colonization of collapse scars by wetland taxa). In general, however, KAK-1 and TAH-7 displayed differences in the timing and trajectory of sedimentary organic matter changes. In TAH-7, total yield of lignin-derived phenols was significantly and positively correlated with sedimentary mercury concentrations, suggesting that peat subsidence may increase the delivery of mercury to aquatic environments adsorbed onto terrestrial organic matter (Fig. 5c). Collectively, the findings of Coleman et al. (2015) and Korosi et al. (2015) showed that the integration of multiple paleolimnological parameters provides important insights into local variability in lake biological and biogeochemical responses to peat subsidence.

## Mackenzie Delta uplands, Northwest Territories

The Mackenzie Delta of Canada's western Arctic is the second largest Arctic delta globally, after the Lena River Delta in Siberia. The low-lying delta is bordered on the west by the Richardson Mountains and the east by elevated upland terrain. Permafrost in the uplands is thick and continuous, except where taliks exist under waterbodies (Rampton 1988) (Fig. 1). In addition, permafrost is ice-rich (Mackav 1963; Rampton 1988) and enriched in solutes (especially calcium and sulfate originating from glaciogenic carbonate and shalederived surficial deposits; Kokelj and Burn 2003, 2005). Thermokarst activity is common in the region (Mackay 1963), especially retrogressive thaw slumps, which occur on the margin of approximately 10% of lakes greater than 1 ha in area (Lantz and Kokelj 2008). The rate of growth as well as the size and area impacted by retrogressive thaw slumps have increased significantly in the western Canadian Arctic (Segal et al. 2016). In the Mackenzie Delta uplands region, lakes impacted by thaw slumping exhibit higher concentrations of major ions and anions, lower DOC concentrations (and thus much greater water clarity due to the chromophoric nature of DOC) (Kokelj et al. 2005, 2009b; Thompson et al. 2012), and lower nutrient (total phosphorus and total dissolved nitrogen) concentrations (Thompson et al. 2012) (Table 2). Lakes impacted by thaw slumping have also been shown to undergo significant changes to sediment and lake bottom processes (Kokelj et al. 2009a). These changes in water

**Fig. 5.** Generalized depiction of permafrost thaw under peat plateaus in the South Slave Taiga Plains and its potential downstream impacts based on the findings of Korosi et al. (2015). (*a*) As ground ice melts, the margins of peat plateaus collapse and tree roots are inundated. As trees die off, wetland taxa such as *Sphagnum* mosses colonize. (*b*) Peat subsidence may increase the transport of DOC to aquatic ecosystems, leading to a decrease in water clarity in the small ponds and lakes common in this landscape. (*c*) Summary of key results from paleolimnological analysis of Lake TAH-7, re-created from Korosi et al. (2015), that show that peat subsidence led to a long-term increase in mercury transport to the lake and the crossing of an ecological threshold for DOC. Top: the appearance and eventual dominance of the diatom assemblage by small benthic *Fragilaria* taxa adapted to low-light conditions (indicating ecological changes related to increased DOC); bottom: a positive correlation between total lignin yield (vanillyls plus syringyls plus vanillyls) and total mercury in the sediment core from TAH-7 indicates that a long-term increase in sedimentary mercury was related to increased runoff of terrestrial organic matter (line shows the approximate timing of the industrial revolution and enhanced mercury deposition). Drawings in Figs. 5*a* snd 5*b* by Jessica Korosi (University of Waterloo).



chemistry can result in rapid shifts in the sedimentary environment as well as for lake biota, which can be tracked through sediment-based analytical techniques. Deison et al. (2012) showed that sedimentation rate, in particular inorganic sedimentation, increased significantly coincident with the onset or reinitiation of thaw slumping. Likely related to this changing sediment accumulation, benthic macroinvertebrate abundance was found to be greater in lakes impacted by thaw slumps, driven primarily by increased abundances of nematodes and ostracods, although chironomids were found to be less abundant (Moquin et al. 2014) (Table 2).

Thienpont et al. (2013b) used sedimentary diatoms to infer the timing of slump initiation, an important step for reconstructing the limnological changes associated with this form of permafrost disturbance, since the precise time of slump initiation is often unknown, and the majority of inferences on the limnological impact of thaw slump activity are derived from modern-day comparisons of conditions in lakes impacted by slumps with unimpacted sites. They observed that the primary mechanism of diatom floristic change in response to slump development was an increase in diatom species associated with varied

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Landscape/geomorphic disturbance	Limnological changes	Biological responses	Impact on contaminants	
Retrogressive thaw slumping	↑ Ion concentrations/ conductivity <sup>a</sup>	↑ Benthic macrophyte production <sup>e</sup> ↑ Periphytic diatom diversity <sup>g</sup>	↑ PCB/pesticide concentrations (per gram organic carbon) <sup>n</sup>	
	$\downarrow$ DOC/water colour <sup><i>a,b</i></sup>	↑ Periphytic diatom diversity <sup>g</sup>	↓ Total mercury (per gram dry weight) <sup>d</sup>	
	$\uparrow pH^c$	$\uparrow$ Exposure to UV radiation <sup>b</sup>		
	$\downarrow \mathrm{TP}^b$	↑ Macroinvertebrate abundance <sup>f</sup>		
	$\downarrow \text{TDN}^b$	$\downarrow$ Water column <sup>b</sup> and sedimentary <sup>d</sup> chlorophyll <i>a</i>		
	$\uparrow$ Inorganic sedimentation <sup>d</sup>			
	↓ Sedimentary organic carbon <sup><i>d,e,f</i></sup>			

**Table 2.** Summary of limnological changes, biological responses, and changes in contaminants in lakes impacted by shoreline retrogressive thaw slumping in the Mackenzie Delta uplands, western Canadian Arctic.

<sup>a</sup>Kokelj et al. 2009a.

<sup>b</sup>Thompson et al. 2012.

<sup>c</sup>Kokelj et al. 2005. <sup>d</sup>Deison et al. 2012.

<sup>e</sup>Mesquita et al. 2012.

<sup>f</sup>Moquin et al. 2014.

<sup>g</sup>Thienpont et al. 2013a.

<sup>*h*</sup>Eickmeyer et al. 2016.

substrate colonization (greater periphytic abundance and diversity) as well as increased planktonic taxa. The mechanism for this diatom floristic response is likely due to the rapid increase in water clarity, resulting in colonization of open-water and periphytic habitats. Aquatic macrophyte biomass and production are known to be greater in lakes impacted by slumping (Mesquita et al. 2010). This paleolimnological change was found to be a strong indicator of the onset and (or) reinitiation of slump activity when compared to indirectly inferred methods (Thienpont et al. 2013*b*).

Thermokarst processes, such as retrogressive thaw slumping, lead to the translocation of terrestrial material to downstream aquatic ecosystems. Thus, in addition to the limnological change and subsequent biological response, potential exists for contaminants that may have been trapped in the terrestrial environment to enter aquatic ecosystems. However, Deison et al. (2012) showed that total and methyl mercury were lower in lakes with retrogressive thaw slumping, due to dilution with inorganic material, and concluded that thaw slumps were not a significant source of mercury to lakes of the Mackenzie Delta uplands. On the other hand, polychlorinated biphenyls (PCBs), a banned class of persistent organic pollutant, as well as organochlorine pesticides were found in greater concentrations in sediment cores taken from lakes with retrogressive thaw slump activity in their catchments (Eickmeyer et al. 2016). The dilution by inorganic matter was implicated by the elevated PCB concentrations observed in sediments, as these hydrophobic organic contaminants were associated with and concentrated on the smaller pool of available organic carbon in slump-impacted lakes (Eickmeyer et al. 2016).

In the Mackenzie Delta uplands region, the thawing of permafrost has also been shown to have an influence on indirect sources of contaminants to aquatic ecosystems through the loss of containment of materials associated with hydrocarbon exploration (Thienpont et al. 2013*a*). Drilling mud sumps, relict pits excavated into the permafrost to house the wastes associated with oil and gas exploratory well development, were previously thought to be a permanent containment mechanism for these by-products. However, as permafrost thaws,

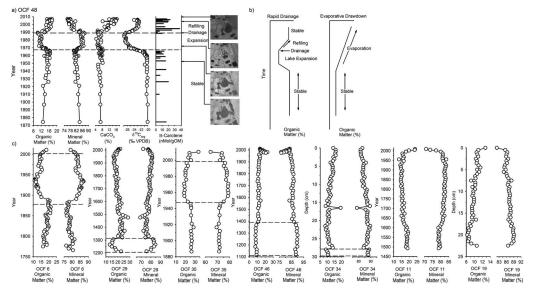
and due to poor construction practices, it has become clear that these sumps are leaching their contents (Dyke 2001). One of the major constituents of the slurry deposited in slumps is saline-rich cuttings, and elevated salt concentrations have been observed beyond the boundaries of drilling sumps previously (Dyke 2001). Using paleolimnological techniques, Thienpont et al. (2013*a*) showed that cladoceran assemblages became dominated by a taxon known to be tolerant of elevated ionic concentrations (and observed to be decreasing in other northern regions). Paleolimnological techniques appear effective for tracking both the direct and indirect inputs of contaminants due to thermokarst processes.

## Old Crow Flats, northern Yukon Territory

Old Crow Flats (OCF) is the largest (5600 km<sup>2</sup>) of three lake-rich permafrost landscapes across northern Yukon, centered ~45 km north of the village of Old Crow (Fig. 1). OCF is recognized as a Wetland of International Importance for its ecological integrity and cultural significance to the Vuntut Gwitchin First Nation (The Ramsar Convention 1982). Occupying the former lakebed of Glacial Lake Old Crow, over 2700 lakes, primarily thermokarst in origin, cover ~23% of OCF (Turner et al. 2014). The lakes, and the habitat they provide, have long been an important natural resource for wildlife while also supporting the traditional lifestyle of the Vuntut Gwitchin First Nation. In recent decades, local land users and managers have observed changes in the landscape, including drastically changing and unpredictable lake and river water levels that have negative effects on aquatic habitat and impede community member access to traditional territory. Of particular concern to the community of Old Crow are observations of lake level decline such as the drainage of Zelma Lake in 2007, formerly one of the largest lakes in OCF (Wolfe and Turner 2008; Turner et al. 2010). As part of a suite of multidisciplinary investigations into the natural history of OCF, supported by the Government of Canada International Polar Year Program (Wolfe et al. 2011a), paleolimnological studies were conducted to generate insight into hydrological variability and its causes. Although there was widespread evidence of recent lake level decline at many locations, it was unknown whether this was a result of drainage events and (or) evaporation. However, such knowledge is needed to better anticipate future lake hydrological responses to climate change.

MacDonald et al. (2012) investigated whether such evidence may be stored in the stratigraphic record of a lake in OCF ("OCF 48"), where historical images documented a marked decline in water level between 1972 and 2001. Utilizing physical, geochemical, and biological approaches, sediment core analyses identified four distinct hydroecological phases post-1870, with the most recent phases closely corresponding to evidence of lake level changes in the historical images (Fig. 6a). Phases included (1) a ~100-year stable interval (~1874–1967), (2) active thermokarst expansion (~1967–1989), (3) rapid lake drainage (~1989), and (4) lake refilling (~1989–2008). Notably, the drainage event was well preserved in the stratigraphic record of organic matter content, a simple measure derived from loss-on-ignition. Immediately above the inferred drainage event horizon, organic matter content abruptly increased (and mineral matter content decreased). This was interpreted to reflect an increase in concentration of nutrients in the residual shallow waterbody, and combined with greater light availability due to decreased shoreline erosion, aquatic productivity rapidly increased (as was also suggested by other indicators including an increase in the carbon isotope composition of organic matter). Given the clarity of this stratigraphic record for documenting a paleodrainage event, MacDonald et al. (2012) proposed that use of organic matter content in sediment cores may distinguish lake level drawdown due to drainage versus evaporation (Fig. 6b).

Here we employ the characteristic organic matter content stratigraphic profiles portrayed in Fig. 6*b* to speculate on past hydrological conditions for several additional lakes **Fig. 6.** (*a*) Summary of key paleolimnological indicators and historical images from MacDonald et al. (2012) for OCF 48 plotted versus time derived from <sup>210</sup>Pb analysis. (*b*) Expected sedimentary organic matter profiles for thermokarst lakes experiencing lake level drawdown by rapid drainage versus evaporation (from MacDonald et al. 2012). (*c*) Organic matter and mineral matter content from seven OCF lakes plotted versus time derived from <sup>210</sup>Pb analysis or depth. Dashed lines represent expansion (lower dashed line) and drainage (upper dashed line) events interpreted from the loss-on-ignition records.



in OCF (Fig. 6c). Of the seven additional organic matter content records shown, five appear to contain evidence of former drainage events following an interval of lake expansion analogous to OCF 48 and include Zelma Lake (OCF 6) as well as OCF 29, 34, 35, and 46. Notably, organic matter content at Zelma Lake does indeed increase following observed drainage in 2007 (the sediment core was obtained in 2010) providing additional support for the use of Fig. 6b, although other evidence suggests that aquatic productivity during the post-drainage phase has been much greater than prior to expansion (Tondu et al. 2017). It is notable that the timing of these drainage events, based on <sup>210</sup>Pb chronologies extrapolated downcore (where available), is highly variable, suggesting episodic occurrence. An exception is OCF 35 whose profiles display roughly similar timing as OCF 48. In contrast, OCF 11 and 19 appear to have experienced relatively stable hydrological conditions during the time captured by the cores. However, the increase in organic matter content at OCF 19 may reflect gradually increasing evaporative concentration of nutrients and subsequently increasing productivity (as depicted in the right-hand panel of Fig. 6b). Multiparameter paleolimnological analysis of these sediment core records would likely shed further light on past hydrological conditions. Nonetheless, these results suggest that thermokarst lake paleohydrology is highly individualistic in this landscape, akin to isotope-based assessments of contemporary hydrology (Turner et al. 2010, 2014), and is likely related to complex interactions over time among thermokarst evolutionary processes, meteorological conditions, and lake-specific catchment characteristics (e.g., area, relief, vegetation). Hence, this presents challenges to scale up to the landscape level with respect to both former hydrological conditions and predictions of future change.

#### Southern Seward Peninsula, Alaska

The landscape of the Southern Seward Peninsula (SSP) today is still heavily influenced by the last glacial period. Located on the eastern shore of the Bering Strait in Alaska, the region

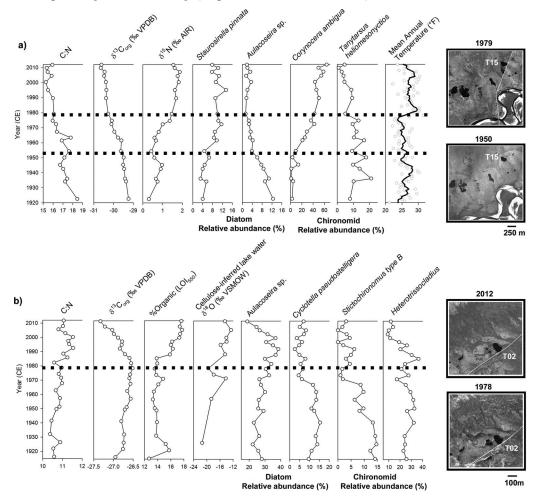
contains the transition from tundra to the boreal forest, which follows the transition from continuous to discontinuous permafrost (Jones et al. 2011*a*). The climate of the Seward Peninsula has been rapidly changing since deglaciation (Kaufman and Hopkins 1986; Calkin et al. 1998). Rising sea levels associated with decreased summer insolation, and a greater maritime influence, led to a reduction in seasonality and temperatures and an increase in moisture. However, there has been pronounced recent warming in the SSP, with an increase of ~2 °C in mean annual temperature since 1979 (Medeiros et al. 2014). As the SSP is exposed to prevailing winds from the south during the ice-free season, summer temperatures are warmer than in the northern Seward. Likewise, the southern region is primarily underlain by discontinuous permafrost, with continuous permafrost restricted to mountain ranges and adjacent valleys (Jones et al. 2011*a*).

Even though the expansion of thermokarst lakes has likely been occurring for centuries to millennia since deglaciation (Lenz et al. 2016), increases in the extent of permafrost degradation have been observed in the northern Seward (Jones et al. 2011*a*) and the interior of Alaska (Jorgenson et al. 2006). Likewise, several studies have also noted a recent expansion of tall woody shrubs in response to earlier snowmelt, a deeper and drier active layer, and longer growing seasons linked to permafrost degradation throughout the Seward Peninsula (Sturm et al. 2001; Lloyd et al. 2003; Tape et al. 2012). Changes in the density of vegetation in lake catchments can influence the contribution of snowmelt to lakes (Pomeroy et al. 2006), which can alter water balances (Turner et al. 2014), influence nutrient cycling (Stewart and Lamoureux 2011), and shift the trophic structure of aquatic systems (Taylor et al. 2016).

Thermokarst ecosystems in the SSP are thought to be especially sensitive to warming due to the fragile and discontinuous extent of the underlying permafrost horizon in this region. The ecological trajectory of these thermokarst systems in a warming future is uncertain; however, shifts in their biotic communities are already occurring. Taylor et al. (2016) noted widespread establishment and expansion of boreal aquatic zooplankton predators in newly formed thermokarst lakes across the SSP. This shift in trophic structure, despite top-down controls of established endemic keystone predators, may signal the threshold at which a tundra-to-boreal metacommunity occurs (Taylor et al. 2016). Medeiros et al. (2014) compared the influence of catchment condition, specifically thermokarst development and shrub growth, in Alaskan lakes of the SSP in the context of recent warming using a multiproxy paleolimnological approach. The sediment record of a thermokarst lake examined indicated a shift from a high input of terrestrial organic matter (i.e., high C/N ratios), yet nitrogen-limiting conditions ( $\delta^{15}$ N values ~0%) (Fig. 7a), to decreasing aquatic productivity and a lower nitrogen demand from the 1920s to 1960s. This also marked a major shift in the biotic community (Fig. 7a). For example, a decline in the abundance of acidophilus diatoms, and a large increase in the abundance of productivityassociated chironomids in the 1960s, corresponded to an increase in  $\delta^{15}$ N and decline in  $\delta^{13}C_{org}$  values. Both diatom and chironomid assemblages were also observed to have a similar second transition at ~1985, where further reductions of the cold-water-adapted chironomids and increases of epiphytic diatoms suggest warmer water temperatures and the development of a more diverse benthic habitat. The shift observed in the biological and geochemical records occurred prior to a prominent increase in temperature in 1979 (Fig. 7a) and was likely associated with increasing supply of dissolved inorganic carbon and nitrogen to the lake from active shoreline thermokarst processes. This is consistent with Jones et al. (2011a), who noted that a majority of thermokarst lakes in the northern Seward Peninsula have expanded since the 1950s and that elevated nitrogen export occurs from thawing permafrost (Jones et al. 2011b).

Medeiros et al. (2014) contrasted this thermokarst-driven change in nutrient supply and biotic response with that of a lake whose catchment has experienced substantial shrub

**Fig. 7.** Relative abundance of selected geochemical parameters and chironomid and diatom taxa from the core of (*a*) a thermokarst lake and (*b*) a shrub-dominated kettle lake in the Southern Seward Peninsula, Alaska, plotted using the <sup>210</sup>Pb estimated age–depth profile. Historical images (indicated on the profiles by dashed lines) and a present-day image (2012) showing surrounding catchment conditions at different periods are displayed on the right (source: US Geological Survey's Earth Resources Observation and Science (EROS) Center). The mean annual temperature record from the nearest climate station (Nome, Alaska) is plotted in Fig. 6*a*. Note that *x*-axis scaling varies as a percentage of the assemblage (adapted from Medeiros et al. 2014).



development since the 1980s. Nutrient input to the shrub-dominated lake in the early part of the record highly contrasted that of the thermokarst lake, reflected by low C/N ratios throughout the record until the 1980s, indicating ample supply of nitrogen to support aquatic production (Fig. 7b). A shift in the geochemical and biological record was not observed until after ~1986, when a trend to lower  $\delta^{13}C_{org}$  values and higher C/N ratios likely reflected an increase in terrestrial particulate organic matter deposition and corresponding increasing aquatic production following enhanced shrubification of the lake catchment. Prior to ~1970, the lake was mainly represented by cold-water-adapted stenothermic chironomids; however, an increase of *Aulacoseira* sp. diatoms following ~1970 may indicate an increase in terrestrially derived particulate organic matter inputs and humic conditions. A reduction in planktonic habitat beginning ~1973 was inferred by a marked decrease in small planktonic diatoms consistent with increasing evaporation as suggested by an

increase in cellulose-inferred lakewater  $\delta^{18}$ O (Fig. 7*b*). Subsequently, large reductions of coldwater stenotherms at ~2000 indicate an increase in water temperature.

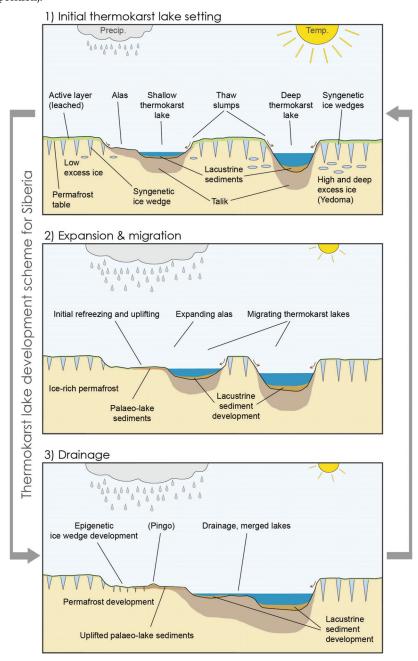
These results suggest that the evolution of aquatic ecosystems in the SSP is variably influenced by catchment-mediated processes, in addition to the direct effects of climate, as documented on a different, much longer time frame in northern Seward Peninsula (Lenz et al. 2016). In the study by Medeiros et al. (2014), an increase in supply of dissolved inorganic carbon and nitrogen related to shoreline erosion appeared to be associated with enhanced productivity in an otherwise nutrient-limited thermokarst lake. In contrast, increase in supply of particulate organic matter following an increase in shrub growth in the catchment of another lake had less apparent influence on aquatic biota, whereas more direct responses were linked to warming and hydrological changes.

## Lena Delta transect, northeastern Siberia

Arctic Russia experienced severe winters during the last ice ages. As most of the ground was not protected by an ice sheet, cold air deeply penetrated into the soils, forming continuous permafrost of up to 1600 m thick (French 2007) (Fig. 1). The investigated area, extending from the Lena River Delta towards central Yakutia, is typical of the continuous permafrost zone in northern Siberia, ranging in thickness from 500 to 700 m (Romanovskii et al. 2004). In this area, fluvial sediments of spatially variable stages of the Lena River are overlain by Quaternary loess-like syngenetic permafrost material, the so-called Yedoma complex, with high organic and ice contents (Schirrmeister et al. 2011). The landscape is dominated by thermokarst depressions as a result of varying degrees of permafrost thaw, subsidence, and reworking processes of the initial Pleistocene sequences. Associated with alases (depressions caused by thawing of ice-rich permafrost), numerous thermokarst lakes provide insight into the landscape dynamics typical of ice-rich permafrost. The majority of thermokarst lakes in Siberia started to form during the early Holocene Thermal Maximum (HTM), and lake–landscape dynamics include lake initiation, expansion, drainage, and reinitiation of thermokarst lakes (Morgenstern et al. 2011) (Fig. 8).

Stemming from a long-term strategy based on high-resolution lake-sediment-core analyses spanning a north-south transect along the Lena River, the "SibLake-Programm" at the Alfred Wegener Institute (Potsdam, Germany) investigates the potential of thermokarst lake sediment sequences for reconstructing regional climate change in the past and the impacts of local thermokarst phenomena on aquatic ecosystem dynamics. The main objective is to detect and explain the spatial pattern of the onset and termination of the HTM across Russia. The studied lakes mentioned in this review comprise small, oligotrophic, and cold-monomictic thermokarst basins in the Lena Delta, the open Lena hinterland tundra, and the northern taiga zone of central Yakutia (Fig. 1). Studied lakes are usually shallow (~3 m) but can sometimes be deeper than 10–20 m in upland permafrost settings with high excess ground ice in deep permafrost layers (Yedoma). Lake bathymetry can also vary significantly within a lake, related to (1) spatial variability in ice content and associated differential subsidence rates, (2) restriction of talik development within unfrozen areas during winter, and (3) spatial differences in sedimentation rates associated with river input and permafrost-specific processes such as thaw slumping. Yedoma thermokarst lakes generally penetrate directly into the surrounding ice complex often surrounded by steep slopes, thermo-erosion gullies, and retrogressive thaw slumps associated with alluvial fans (Biskaborn et al. 2013a, 2013b).

Based on multiple parameters, mainly aquatic (diatoms) and terrestrial (pollen) bio-indicators and sediment geochemical proxies from radiocarbon dated sediment cores, several studies (synthesized in Biskaborn et al. 2016) revealed the timing and magnitude of the onset of the HTM. These authors documented a temporal delay from north to south along **Fig. 8.** Generalized compilation of typical northeastern Siberian thermokarst development in "Yedoma" deposits (Pleistocene-age, ice-rich loess) considering the findings of Soloviev (1973), French (2007), and van Huissteden et al. (2011). Thermokarst processes depend upon temperature and precipitation as well as local permafrost characteristics (i.e., excess ice and geomorphology). Initial thermokarst lake development (1) results from the melting of excess ground ice, generally in the form of syngenetic ice wedges (i.e., formed at the same time as sediment deposition). Lake depth is controlled by ice-wedge depth as well as local factors (especially excess ground ice content). An underlying talik (thaw bulb) forms underneath when lake depth is greater than winter lake-ice cover thickness. Lake expansion and migration (2) proceeds through shoreline erosion, while former lake sediments can be exposed to atmospheric conditions, thus refrozen and uplifted. Finally, partial or complete lake drainage (3) can result in the new development of permafrost, including epigenetic ice wedges (i.e., formed after sediment deposition).



the lower Lena River due to climatic teleconnections with the Laurentide Ice Sheet in North America. Such a southward delay in HTM onset appeared to be up to 3000 years, although the termination of the HTM is still under debate. Based on bio- and lithostratigraphic reconstructions, Biskaborn et al. (2012, 2013*a*, 2016) reported that climate warming in the Lena Delta hinterland caused major changes in aquatic ecosystems (e.g., decrease in lake-ice cover extent and duration, decrease in alkalinity, increase in habitat availability). Furthermore, these studies demonstrated that use of bio-indicators for climate reconstruction requires differentiation between summer and winter seasons. In cold continental environments in particular, seasonal lake-ice cover can have a significant impact on the distribution of diatom species (Rühland et al. 2015), whereas terrestrial vegetation (e.g., pollen) likely reflects summer conditions.

Alas-stage succession in Siberia led to complex lake evolution (Bosikov 1991; van Huissteden et al. 2011; Schleusner et al. 2015). No general temporal pattern in alas cycles has been found, suggesting that thermokarst lake development is highly dependent on local morphological, lithological, and hydroclimatic properties. Accordingly, sedimentological investigations of thermokarst lakes in the Lena Delta region revealed that limnogeological processes are not driven by climate changes alone but also reflect differential permafrost degradation (Fig. 8). For example, drainage processes associated with lakeshore thermoerosion in northwestern Lena Delta caused strong fluctuations in water level, changing the abiotic and biotic lake status. Dramatic short-term lake level shifts were evidenced by changes in fossil diatom species assemblages around 1300 cal yr BP (Biskaborn et al. 2013a). In a thermokarst setting within ice-rich Yedoma, Biskaborn et al. (2013b) tracked block failure events from retrogressive thaw slumping in sediment cores from Lake El'gene Kyuele using end-member modeling of grain size and elemental composition. Their results indicated repetitive phases of bluff stability and instability along the shoreline associated with differential degradation of the orthogonal oriented ice-wedge pattern. As a consequence, in geomorphologically pronounced catchment settings with steep slopes and active thaw slumping, thermo-erosion of ice- and carbon-rich permafrost (i.e., Yedoma) significantly contributed as a sediment source, resulting in challenges for establishing reliable age-depth models. Including sedimentological and geochemical impacts of patterned cryological permafrost features (i.e., ice wedges) in the interpretation of abiotic and biotic sedimentological indicators is thus essential for yielding sound paleoenvironmental implications.

## **Emerging research directions**

Knowledge of short- and long-term environmental change in high-latitude regions has substantially advanced during the past few decades, partly due to significant methodological and conceptual progress in paleolimnology. Since rising temperature in subarctic and Arctic regions will increase active-layer thickness, enhance microbial activity, and increase supply of dissolved and particulate carbon and other nutrients to lakes (Hobbie et al. 2002; Fritz and Anderson 2013), knowledge of changing catchment condition is crucial for anticipating aquatic ecosystem responses. Although we provide a few recent examples in this review paper, there is a wealth of research potential and thermokarst lake archives still untapped. As we demonstrate above, these shallow aquatic ecosystems can indeed provide useful archives for paleolimnological investigations. Furthermore, when coupled with carbon balance and remote sensing approaches, these two emerging axes of research have great potential to significantly enhance our understanding of thermokarst lake evolution through space and time and their response to ongoing and future climate changes.

Long-term patterns in carbon storage and emissions in the past are of great relevance to the scientific community, and paleolimnology is now showing great promise to occupy a central position in global change research (Heathcote et al. 2015; McGowan et al. 2016, and references therein). Because of the enormous quantities of carbon stored in permafrost compared to the atmosphere (Hugelius et al. 2014), thermokarst lakes have been identified as a potentially major global source of greenhouse gas such as methane if mobilized to the atmosphere (Walter et al. 2007a, 2007b). Conversely, widespread mineral (organic-poor) Arctic soils may rather consume methane under a warmer climate (Lau et al. 2015). Moreover, some thermokarst ecosystems may have shifted from carbon sources to sinks during the past millennia (Walter Anthony et al. 2014). Hence, many uncertainties remain about carbon cycle modeling and upscaling to the global scale, as shown for example by the strong spatial heterogeneity of greenhouse gas fluxes from permafrost aquatic systems, including thermokarst lakes (Bouchard et al. 2015). Yet, useful information about carbon dynamics within permafrost landscapes in the past can be obtained from thermokarst lake archives. Key potential measures include carbon inventories and accumulation rates (through the loss-on-ignition technique), fossil biomarkers (e.g., pigments, fatty acids) indicating the presence of methanogenic or methanotrophic bacteria, and sedimentary geochemistry related to the different fractions and sources of organic matter (e.g., organic carbon and nitrogen elemental and stable isotope composition, organic matter biomarkers; Korosi et al. 2015; MacDonald et al. 2015; McGowan et al. 2016). Moreover, sources and accumulation rates of mineral and organic particles in lakes can be characterized by sediment trap techniques, which have not yet been widely used in thermokarst aquatic systems (Coulombe et al. 2016). There is thus a need to foster such approaches based on the study of thermokarst lake sediments with a special focus on carbon dynamics in aquatic systems.

Several remote sensing studies, based on historical air photos and satellite imagery. have documented recent lake level drawdown and widespread occurrence of drainage events in lake-rich thermokarst landscapes, although with notable differences between continuous and discontinuous permafrost regions (e.g., Yoshikawa and Hinzman 2003; Smith et al. 2005; Riordan et al. 2006; Plug et al. 2008; Jones et al. 2011a). It is not clear if such major hydrological shifts are driven solely by climate or thermokarst activity or a combination of both (Lantz and Turner 2015). Yet, identifying the processes responsible for water level changes in thermokarst landscapes is important to better anticipate ecological consequences that will affect local wildlife species and traditional lifestyle of northern communities. Investigations combining remote sensing imagery and multiproxy paleolimnological analyses are scarce (MacDonald et al. 2012; Edwards et al. 2016) but offer great promise for disentangling factors controlling hydrological trajectories of thermokarst lakes. Moreover, key findings stemming from such studies could help to better inform modeling and lake surface mapping efforts. We therefore anticipate that future progress in thermokarst knowledge will result from a better integration of remotely sensed data and lake sediment archives.

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