

1 **Effects of permafrost thaw on arctic aquatic ecosystems**

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31

32 **Abstract**

33 The Arctic is a water-rich region, with freshwater systems covering about 16% of the northern
34 permafrost landscape. Permafrost thaw creates new freshwater ecosystems, while at the same time
35 modifying the existing lakes, streams, and rivers that are impacted by thaw. Here, we describe the
36 current state of knowledge regarding how permafrost thaw affects lentic (still) and lotic (moving)
37 systems, exploring the effects of both thermokarst (thawing and collapse of ice-rich permafrost)
38 and deepening of the active layer (the surface soil layer that thaws and refreezes each year). Within
39 thermokarst, we further differentiate between the effects of thermokarst in lowland areas, versus
40 that on hillslopes. For almost all of the processes that we explore, the effects of thaw vary
41 regionally, and between lake and stream systems. Much of this regional variation is caused by
42 differences in ground ice content, topography, soil type, and permafrost coverage. Together, these
43 modifying factors determine (i) the degree to which permafrost thaw manifests as thermokarst, (ii)
44 whether thermokarst leads to slumping or the formation of thermokarst lakes, and (iii) the manner
45 in which constituent delivery to freshwater systems is altered by thaw. Differences in thaw-enabled
46 constituent delivery can be considerable, with these modifying factors determining, for example,
47 the balance between delivery of particulate versus dissolved constituents, and inorganic versus
48 organic materials. Changes in the composition of thaw-impacted waters, coupled with changes in
49 lake morphology, can strongly affect the physical and optical properties of thermokarst lakes. The
50 ecology of thaw-impacted lakes and streams is also likely to change, these systems have unique
51 microbiological communities, and show differences in respiration, primary production, and food
52 web structure that are largely driven by differences in sediment, dissolved organic matter, and
53 nutrient delivery. The degree to which thaw enables the delivery of dissolved versus particulate
54 organic matter, coupled with the composition of that organic matter and the morphology and
55 stratification characteristics of recipient systems will play an important role in determining the
56 balance between the release of organic matter as greenhouse gases (CO₂ and CH₄), its burial in
57 sediments, and its loss downstream. The magnitude of thaw impacts on northern aquatic
58 ecosystems is increasing, as is the prevalence of thaw-impacted lakes and streams. There is
59 therefore an urgent need to quantify how permafrost thaw is affecting aquatic ecosystems across
60 diverse Arctic landscapes, and the implications of this change for further climate warming.

61

62 **1. Introduction**

63 Permafrost is perennially frozen ground that underlies about a quarter of the landmass of the
64 Northern hemisphere (Brown et al., 1998). It consists of various soil types ranging from frozen peat
65 and frozen mineral soil to frozen Pleistocene deposits rich in massive ground ice. The distribution
66 of permafrost is generally divided into four zones based on the percentage of the land that is
67 underlain by permafrost: continuous (90-100%), discontinuous (50-90%), sporadic (10-50%), and
68 isolated (<10%) (Fig. 1). Terrestrial permafrost (we do not consider subsea permafrost in this
69 review) hosts about 1,330-1,580 Pg (1Pg = 10¹⁵ g) organic carbon (OC) of which about half is
70 deeper than 1 m (Schuur et al., 2015). Over the last few decades, permafrost ground temperatures

71 have been slowly increasing (Romanovsky et al., 2010) as a result of increased surface warming in
72 Arctic regions (IPCC, 2013).

73 The Arctic is extremely rich in water. Lakes, reservoirs, rivers, and various types of wetlands,
74 floodplains, bogs, fens, and mires, on average occupy 16% of the landscape underlain by permafrost
75 when considering water bodies larger than 0.1 km² in area (Fig. 1; Global Lakes and Wetlands
76 Database; Lehner and Döll, 2004) making this number a conservative estimate. Discontinuous,
77 sporadic, and isolated permafrost regions are relatively rich in surface water with 20, 23, and 18%
78 landscape coverage, respectively, compared to continuous permafrost with only 11%. Water, in all
79 its forms, connects all components of the landscape and plays a key role in the storage and
80 transport pathways of sediments, organic matter, nutrients, and other constituents (Battin et al.,
81 2009; Vonk and Gustafsson, 2013). The role of hydrology is therefore key in both the response and
82 the effects of permafrost thaw, and it strongly influences the balance of carbon dioxide (CO₂) and
83 methane (CH₄) emissions. At the same time, permafrost thaw will also create new aquatic
84 ecosystems and modify existing aquatic ecosystems. In this review we provide an overview of the
85 effects of permafrost thaw on aquatic ecosystems and their potential effects on climate, with a
86 consideration of all aquatic ecosystems located within the permafrost zones defined by Brown et al.
87 (1998; Fig. 1).

88 When permafrost thaws, the soil organic matter and minerals within it become available for
89 remobilization and introduction into aquatic systems. The type of thaw will largely determine the
90 rate and effects of this remobilization. Here, we will distinguish between two types of thaw: (i) thaw
91 of ice-rich permafrost, also called thermokarst, with a more abrupt or episodic character that tends
92 to manifest as a *pulse disturbance*, and (ii) thaw of permafrost with (relatively) low ground-ice
93 content, with a gradual but persistent and longer-term character that tends to manifest as a *press*
94 *disturbance* (Grosse et al., 2011). In this review we consider the effects of both pulse and press thaw
95 disturbances.

96 Thaw of ice-rich permafrost leads to a range of landscape features (Fig. 2) that are collectively
97 referred to as thermokarst, and that are typically divided into three primary groups based on where
98 and how they form (Kokelj and Jorgenson, 2013): (i) hillslope processes, (ii) wetland processes, and
99 (iii) thermokarst lake processes. *Hillslope processes* result in dramatic features such as
100 retrogressive thaw slumps (Fig. 2b), active layer detachment slides, and thermal erosional gullies
101 (Fig. 2c), which together we refer to as thermo-erosional features (TEFs). The scale of these
102 features is local and depends on landscape features, but the transport of sediment, nutrients, and
103 organic matter into aquatic ecosystems can be large, and these features may form in a matter of
104 hours and slowly grow for several years. *Wetland processes* include peatland collapse and the
105 development of bogs and fens. While wetlands store significant quantities of soil carbon (Tarnocai
106 et al., 2009) they are not specifically discussed in this review. *Thermokarst lake processes*, which
107 include lake and pond formation, expansion, and drainage, are the most abundant (10-50% of
108 permafrost-impacted landscapes; Jorgenson et al., 2006; Kokelj and Jorgenson, 2013) and most
109 easily recognizable form of thermokarst, and are particularly emphasized in this review.

110 Thaw of permafrost with lower ice content results in a more gradual top-down thawing process,
111 and occurs through active layer deepening and talik formation (Schuur et al., 2008). This type of

112 thaw is gradual but can occur over entire landscapes (Åkerman and Johansson, 2008; Shiklomanov
113 et al., 2013). Although its impact on aquatic ecosystems is harder to detect and requires long-term
114 (decades-scale) monitoring, such gradual thaw can cause striking changes to regional hydrology
115 and chemistry (e.g., in Alaska, Striegl et al., 2005; Keller et al., 2010; Walvoord et al., 2012). Talik
116 formation occurs under water bodies, but also when the active layer has deepened to such an extent
117 that the soil does not refreeze completely in winter. Taliks create new hydrological hotspots in the
118 landscape, and may increase groundwater flow and deeper flow paths, particularly in the case of
119 open taliks that fully penetrate the permafrost profile (Walvoord et al., 2012), and alter fluxes of
120 constituents (Walvoord and Striegl, 2007).

121 While ground ice content and topography are important modifying factors that determine how
122 permafrost thaw manifests itself within landscapes, factors such as the local composition of soils
123 and regional extent of permafrost will also play an important role in determining the effect of
124 permafrost thaw on aquatic ecosystems (Fig. 3). For example, continued permafrost degradation,
125 and in particular the transition from continuous to discontinuous permafrost, will considerably
126 lengthen flow paths, often enable greater inputs of groundwater to freshwater systems, and affect
127 the processing of water en route to aquatic systems (e.g., Striegl et al., 2005; Walvoord et al., 2012).
128 Thermokarst processes along with other climate-driven changes in, for example, vegetation and
129 precipitation, also determine local hydrological trajectories that affect the landscape in contrasting
130 ways (e.g., lake expansion vs. drainage) (Bouchard et al., 2013; Turner et al., 2014). Similarly, local
131 soil conditions (e.g., composition, porosity) will affect how permafrost thaw changes soil-water
132 interactions as water moves across landscapes, with the mobilization or exposure of organic versus
133 mineral soils being an important potential regulator of how thaw affects impacted aquatic systems
134 (Tank et al., 2012a).

135 In this review, we first describe the general impacts of permafrost thaw on aquatic ecosystems such
136 as changes in physical, optical, and chemical limnology and the release of materials from land to
137 water (section 2). We identify the various pathways of organic carbon and contaminant
138 degradation (bio- and photodegradation), and the resulting changes in microbial community
139 structure and gas fluxes from thaw-impacted systems (section 3). We then evaluate the broader
140 consequences of permafrost thaw for aquatic ecosystems considering the release of old carbon into
141 waters and the atmosphere, carbon burial, effects for ecosystem structure and functioning, and
142 exports to the ocean (section 4). We end this review with a summary of our findings, an overview of
143 potential climate effects and recommendations for future research (section 5).

144 **2. Impacts of thaw on aquatic ecosystems**

145 **2.1 Physical and optical limnology**

146 The land area above latitude 45.5°N totals 41.3 million km² and contains around 200,000 lakes
147 (sized 0.1 to 50 km²), with 73% of them occurring in permafrost landscapes (Smith et al., 2007;
148 Grosse et al., 2011; 2013). Thermokarst lakes and ponds, defined as water bodies that form in a
149 depression as a result of permafrost thaw, are among the most abundant water bodies in
150 permafrost landscapes, and can be found throughout the circumpolar north, from North America to

151 Europe and Russia. They encompass a wide range of physical characteristics, which in turn
152 contribute to the large variations in their biogeochemical properties. In this section, we focus on the
153 effects of thermokarst on the physical and optical limnology of ponds and lakes (Fig. 4). We
154 acknowledge, however, that thermokarst processes will also have significant effects on the physical
155 properties of stream and river systems, for example via the delivery of coloured or chromophoric
156 dissolved organic matter (CDOM) and sediments to these environments (see section 2.2).

157 Thermokarst lakes occur in cold, high-latitude environments that experience prolonged winters
158 with sub-zero temperatures for 8 months or more of the year, and short summers with air
159 temperatures that may rise well above 10°C depending on location. They tend to have minimal
160 hydrological connectivity given their frozen surroundings, which inhibit the infiltration and
161 exchange of water. As a result, the hydrological balance of these closed basins is strongly influenced
162 by snowmelt in spring, evaporation and precipitation in summer, and water inflow from local
163 permafrost soils as a result of thermokarst processes (Fig. 4; Dingman et al., 1980; Bowling et al.,
164 2003; Smith et al., 2007). Notable exceptions are the thermokarst lakes located in floodplain deltas,
165 where river waters may flood and connect the lakes each year, depending on their height above the
166 main stem of the river (McKnight et al., 2008). Thermokarst lake disappearance is a common
167 process throughout the Arctic (e.g., in Siberia, Smith et al., 2005; Kravtsova and Bystrova, 2009).

168 Thermokarst lakes vary greatly in surface area, from ponds that are only a few meters across
169 (northern Québec, Breton et al., 2009; Bouchard et al., 2011) to lakes that are several kilometres in
170 their maximum dimension (Alaska, Pelletier, 2005 and Arp et al., 2011; western Siberia, Pokrovsky
171 et al., 2011). In some thermokarst-impacted landscapes, ponds and lakes can cover up to 30% of
172 land surface area (estimated with remote sensing in NW Canada, Côté and Burn, 2002; and in
173 Alaska, Hinkel et al., 2005), although subpixel-scale water bodies could substantially increase the
174 total water surface area as was demonstrated in the Lena Delta of Siberia (Muster et al., 2013).
175 Their depth is limited by local geomorphology and thaw depth of the permafrost, resulting in
176 shallow waters in some areas, and much deeper systems in other regions. Depth is an important
177 feature in determining lake characteristics as it determines whether water bodies are frozen to the
178 bottom in winter. Typically, thermokarst lakes are rather shallow. For example, in northern
179 Québec, in a region extending from continuous to discontinuous and sporadic permafrost,
180 maximum lake depths range from 1 to 3.5 m (Breton et al., 2009; Laurion et al., 2010; Bouchard et
181 al., 2011; Crevecoeur et al., 2015). Similarly, lake depths range from 0.5 to 1.5 m on a discontinuous
182 permafrost tundra in western Siberia (Pokrovsky et al., 2013), from 0.4 to 2.6 m in an area of
183 continuous permafrost in northern Alaska (Arp et al., 2011), and from 1 to 3.5 m in continuous
184 permafrost of the Arctic Coastal Plain (Hinkel et al., 2012). However, thermokarst lakes
185 approaching 10 m depth can be found in interior Alaska (Sepulveda-Jáuregui et al., 2015) and lakes
186 deeper than 10 m can be found on the Seward Peninsula, Alaska (Hopkins, 1949) and northeast
187 Siberia (Walter Anthony and Anthony, 2013); thermokarst lakes as deep as 22 m exist on the Yukon
188 Coastal Plain of north-western Canada (West and Plug, 2008). The size and abundance of
189 thermokarst lakes are changing, but with pronounced differences between regions. In Russia,
190 thermokarst lake area has been increasing in mid-latitudes but decreasing in southern Siberia
191 (Kirpotin et al., 2008; Sharonov et al., 2012). However, High Arctic thermokarst lakes have also
192 been expanding (e.g. on the Yamal peninsula, Sannikov et al., 2012). Lake area changes may vary

193 substantially (i.e., both increasing and decreasing) even within smaller regions, for example in Altai
194 (Polishuk et al., 2013) or northwest Siberia (Bryksina et al., 2011). In summary, thermokarst lakes
195 and ponds occur in wide varieties (Fig. 2) depending on, for example, their formation process,
196 surface area, and depth; from here on we generally distinguish between ponds and lakes based on
197 their depth (ponds freeze to the bottom in winter, lakes do not), but also sometimes use 'lakes'
198 loosely for both systems when the distinction is less clear, or we follow the terminology used in the
199 studies we cite.

200 Ongoing thermokarst can result in variable inputs of dissolved organic carbon (DOC), inorganic
201 solutes (including nutrients and major ions), and particulate organic and mineral materials into
202 these lakes. Consequently, their limnological properties are highly influenced by their regional
203 surroundings (Fig. 4; Prowse et al., 2006; Bowden et al., 2008; Watanabe et al., 2011; see section 2.2
204 below). One of the expressions of that variability is the colour of the water, which although typically
205 brown, may sometimes be blue, green, black or even white. A study by Watanabe et al. (2011) on
206 water colour and light attenuation in the thaw waters of Nunavik, Québec (Fig. 2h), showed that the
207 lake surface colour (water-leaving spectral radiance) was dependent upon the combined
208 concentrations of CDOM and suspended non-algal particulate material, allowing certain
209 biogeochemical properties such as DOC to be estimated from satellite remote sensing. Waters rich
210 in CDOM (or in clays and silts) strongly attenuate solar radiation, and suppress primary production
211 (see section 4.3.1). In shallower and clearer waters, sufficient photosynthetically-active radiation
212 may penetrate to the bottom of the lakes to allow the development of aquatic macrophytes; for
213 example in lakes of the Mackenzie River Delta that are less affected by flooding with turbid river
214 water (Squires and Lesack, 2003).

215 Depending on their CDOM and particle content, the surface waters of thermokarst lakes may
216 strongly absorb solar radiation, and this can give rise to pronounced surface warming of the more
217 coloured lakes. In combination with the cooling of their bottom waters by the permafrost beneath,
218 this means that some thermokarst lakes have pronounced vertical thermal and density gradients in
219 summer (Fig. 4, Alaska, Sepulveda-Jáuregui et al., 2015). In winter, ice-cover reduces transfer of
220 energy with the atmosphere and eliminates potential wind mixing, although some transfer of heat
221 may result from the oxidation of organic matter in bacterial sediment processes if lakes are not
222 frozen to the bottom (Mortimer and Mackereth, 1958).

223 Many thermokarst lakes are likely to be cold polymictic, undergoing stratification events that
224 become established and then break down over diurnal, or several day, cycles (Alaska, Hinkel et al.,
225 2012; Canadian sub-Arctic, Deshpande et al., 2015). The increased use of high resolution,
226 automated temperature loggers is likely to yield new insights into these short term stratification
227 and mixing dynamics, even in those lakes currently considered to be well-mixed in summer. For
228 example, in western Siberia, an air-temperature increase of 15°C from an anomalous heat wave
229 resulted in increased surface-water temperatures of 10°C, and the formation of a strong
230 temperature gradient in the water column (Pokrovsky et al., 2013). Strong thermal stratification
231 during summer has been reported in shallow (<3 m maximum depth) thermokarst lakes and ponds
232 in sub-Arctic Québec (Laurion et al., 2010; Deshpande et al., 2015), the high Canadian Arctic
233 (Bouchard et al., 2015)), northern Siberia (Boike et al., 2015), and in lakes on yedoma-like

234 permafrost in a latitudinal transect in Alaska (Sepulveda-Jáuregui et al., 2015). In these shallow,
235 stratified systems, oxygen depletion is more prevalent especially in bottom waters (Deshpande et
236 al., 2015; Sepulveda-Jáuregui et al., 2015). On the other hand, lakes in non-yedoma permafrost or
237 non-permafrost catchments in Alaska tended to be less stratified, with well-oxygenated bottom
238 waters. In thermokarst lakes located at higher latitudes, particularly in tundra zones with reduced
239 vegetation, little or no stratification has been observed during summer (Yukon territory, Canada,
240 Burn, 2003; Alaska, Hinkel et al., 2012; western Siberia, Pokrovsky et al., 2013), possibly as a result
241 of greater wind exposure (a function of fetch and wind speed), the reduced tendency of cold waters
242 to stratify (the change in water density per unit °C is lower at lower temperatures), increased
243 convective mixing, and less near-surface light absorption and heating. Deep thermokarst lakes (>2
244 m; not freezing to the bottom in winter) show strong inverse stratification beneath their ice-cover
245 during winter (e.g., Canadian (sub-)Arctic, Breton et al., 2009; Laurion et al., 2010; Deshpande et al.,
246 2015; Alaska, Sepulveda-Jáuregui et al., 2015; Siberia, Boike et al., 2015), including those lakes that
247 show little or no stratification in summer (e.g., Yukon territory, Canada, Burn, 2003). Shallow water
248 bodies (depth <2 m) may freeze all the way to the bottom in winter; for example on the Arctic
249 Coastal Plain of Alaska, where the ice thickness reaches 1.5 – 2 m depths (Arp et al., 2011).

250 Stratification within lakes is also influenced by gradients in salinity and gas concentrations that
251 contribute to density differences down the water column (Kirillin et al., 2012). Such effects are also
252 likely in thermokarst lakes, but have received little attention to date. Thermokarst processes result
253 in inputs of eroded permafrost material into these water bodies, including POC and DOC, nutrients,
254 and ions (Mackenzie delta uplands, Kokelj et al., 2005; circum-Arctic, Prowse et al., 2006; Alaska,
255 Bowden et al., 2008), which are further concentrated with the lake freeze-up during winter
256 (Canadian Arctic, Grasby et al., 2013; Canadian sub-Arctic, Deshpande et al., 2015), in turn affecting
257 water column stability. The hydrodynamic effects of high dissolved CH₄ and CO₂ gradients under ice
258 in stratified thermokarst lakes and of the gas bubble trains associated with ebullition from
259 sediments (Siberia, Walter et al., 2006) have received little attention.

260 The combination of high rates of bacterial metabolism, small lake volumes, and prolonged ice cover
261 means that thermokarst lakes (that do not freeze to the bottom in winter) can experience full water
262 column anoxia for much of the year, in striking contrast to the well-known deeper, non-
263 thermokarst lakes in the Arctic such as Toolik Lake, Alaska, and Char Lake, Canada (Deshpande et
264 al., 2015). In thermokarst lakes in sub-Arctic Québec, mixing in spring occurs during an extremely
265 short period of time (< 5 d) before the lakes restratify (Laurion et al., 2010). Mixing at that time
266 may be insufficient to completely re-oxygenate the water column, while in fall, prolonged mixing,
267 likely aided by convective processes, results in the transfer of oxygen to the bottom of the lake
268 (Deshpande et al., 2015). In a study near Mayo, Yukon Territory (Canada) by Burn (2003), a similar
269 pattern was observed, of prolonged, substantial mixing in fall but only a short period of mixing in
270 spring, which may favour the continuation of bottom water anoxia throughout summer. The fall
271 mixing period is likely to be especially important for gas exchange with the atmosphere, and for
272 stimulating aerobic processes such as bacterial respiration and methanotrophy throughout the
273 water column.

274 Presently, there are major gaps in our understanding of the physical and hydrological dynamics of
275 thermokarst lakes, including measurements of heat transfer from the sediments, the penetration of
276 solar radiation through winter ice cover, the potential for internal seiches in winter influenced by
277 floating ice, and the nature of groundwater flows (Kirillin et al., 2012). Advective transfer of liquid
278 water from shallower littoral zones to the pelagic bottom waters due to differential cooling may
279 also play a role in material transfer within these water bodies, as has been observed elsewhere
280 (MacIntyre and Melack, 1995); no studies to date have addressed the three dimensional
281 hydrodynamics of thaw waters.

282 **2.2 Chemical limnology and the transfer of materials from land to water**

283 Permafrost thaw and thermokarst processes can have a major effect on the chemistry of impacted
284 aquatic ecosystems. Particularly in thermokarst lakes, these changes may occur as a result of the
285 optical and physical processes described elsewhere. Where thermokarst affects lake stratification,
286 for example, changes in phosphorus remobilization from sediments could occur (e.g., Sondergaard
287 et al., 2003). However these effects have been little studied in thaw-impacted systems. Similarly,
288 changes in water column and sediment oxygenation will change the prevalence of redox reactions,
289 including the bacterially mediated processes described in sections 3.4 and 3.5, below. In addition to
290 these classic 'limnological' changes, permafrost thaw can also be expected to have a fundamental
291 effect on the transfer of sediments and chemical constituents from land to water. A recent review
292 by Frey and McClelland (2009) provides an in-depth discussion of how this change may play out for
293 nutrients, DOC, and major ions in stream and river systems. In this section, we update this previous
294 work, and add a consideration of the specific effects of thermokarst and permafrost thaw via active
295 layer deepening on lake water chemistry.

296 **2.2.1 Press vs. pulse disturbances**

297 The degree to which nutrients, organic matter, and sediments are released to aquatic systems is
298 likely to depend on the type of permafrost thaw. For example, the *press disturbance* of active layer
299 deepening (time scale of decades, and greater) will likely favour the delivery of soluble materials
300 (nutrients, base cations, DOC), although the mechanisms that deliver soluble materials to aquatic
301 systems are complex, as outlined below (see 2.2.3). In contrast, the *pulse disturbance* of thermo-
302 erosional processes (localized time scale of years to decades) is likely to favour the delivery of
303 particulate over soluble materials. In addition, hydrologic connectivity and landscape topography
304 are also likely to affect land-to-water constituent transfer (Abnizova et al. 2014), and further affect
305 carbon burial or transfer to the atmosphere. For example, high-gradient watersheds may
306 experience much more lateral constituent transfer, while in low-gradient watersheds with low
307 specific runoff the vertical emission of carbon as CO₂ and CH₄ may predominate.

308 The spatial distribution and life cycle of press and pulse disturbances will also govern the impact
309 that they have on the delivery of biogeochemical constituents to aquatic ecosystems. For example,
310 TEFs (thermo-erosional features) are discretely distributed across the landscape, following
311 variations in topography (affecting, for example, snow cover; Godin et al., 2015) and ground ice
312 content. While these features can be numerous in impacted areas (Lacelle et al., 2015) they take up
313 a relatively small percentage of the total landscape area (1.5% in Alaska; Krieger, 2012). Individual

314 TEFs have lifecycles on the order of decades (Kokelj et al., 2013; Pearce et al., 2014), and – while
315 they are active – may have intense local impacts on sediment and ionic fluxes to freshwater systems
316 (see below). They also seem likely to act as a population of features, however, only a small portion
317 of which will be active at any one time within the landscape. As a result, the observed significant
318 local effects may become more muted when averaged over wider landscapes. In contrast, the press
319 disturbance of active layer thickening occurs more universally across the landscape, but results in
320 changes that are much more subtle, and may require long-term (decades-scale) monitoring
321 programs to detect. Slow press changes can operate over many decades, altering aquatic
322 ecosystems (e.g., in Alaska, Keller et al., 2010, Walvoord et al., 2012), and causing entire landscapes
323 to slowly subside (Alaska, Shiklomanov et al., 2013).

324 **2.2.2 Sediment delivery to aquatic ecosystems**

325 Thermo-erosional features either directly adjacent to, or within the catchment of, aquatic systems
326 can significantly increase suspended sediment concentrations, particularly in streams and rivers
327 where turbulence causes materials to remain entrained. Thaw slumps and gullies directly adjacent
328 to streams have been shown to cause order-of-magnitude increases in suspended sediment
329 concentrations (Alaska, Bowden et al., 2008; Calhoun, 2012) that can continue to be seen for
330 considerable distance downstream (western Canadian Arctic, Kokelj et al., 2013). For example, one
331 small thermokarst gully that formed in 2003 and intersected a small, headwater beaded-stream
332 (the Toolik River) in a 0.9 km² Alaskan catchment delivered more sediment downslope to the river
333 than is normally delivered in 18 years from a 132 km² adjacent reference catchment of the upper
334 Kuparuk River (Bowden et al., 2008). Similarly, streams impacted by within-catchment active layer
335 detachments have been shown to exhibit elevated sediment levels at their outflow when compared
336 to non-impacted sites (Canadian High Arctic, Lamoureux and Lafrenière, 2014). Where slumping
337 occurs directly adjacent to lakes, however, slump-associated sediments can settle out of suspension
338 rapidly, depending on particle size. Thus, while lakes impacted by permafrost slumping experience
339 altered sedimentation rates (Mackenzie delta uplands, Deison et al., 2012), water column sediment
340 loads are generally not impacted (Mackenzie delta uplands, Kokelj et al., 2005; Canadian High
341 Arctic, Dugan et al., 2012). Similarly, increases in sediment loads are atypical in systems where
342 thermokarst causes landscape collapse without significant exposure of soils, such as in the creation
343 of thermokarst lakes in lowland regions. However, where postglacial silts and clays are present
344 (which have very low sedimentation rates), for example on the Eastern coast of Hudson Bay,
345 permafrost thaw can have profound consequences on sediment loads to lakes (Bouchard et al.,
346 2011; Watanabe et al., 2011).

347 **2.2.3 Organic matter delivery to aquatic ecosystems**

348 Increases in sediment delivery to aquatic ecosystems will in turn increase the flux of particulate
349 organic carbon (POC) to affected systems. In the active-layer detachment system described above,
350 increases in suspended sediments were accompanied by measured increases in POC (Canadian
351 High Arctic, Lamoureux and Lafrenière, 2014). In lakes, permafrost thaw can change the rate of
352 accumulation of organic matter in sediments, and depending on the composition of eroding
353 materials, either increase (sub-Arctic Sweden, Vonk et al., 2012a) or decrease (Mackenzie delta
354 uplands, Deison et al., 2012) the concentration of sediment organic matter. Notably, the POC that
355 travels to aquatic systems as a result of permafrost thaw may be only partially derived from

356 permafrost carbon, because the action of thaw and landscape collapse will also expose and mobilize
357 soils from the seasonally unfrozen active layer (e.g., Kokelj and Jorgenson, 2013). In a later section
358 (4.1.2), we review the effect of permafrost thaw on the mobilization of old organic carbon.

359 Where permafrost thaw enhances contact between water and organic soil horizons, increases in
360 DOC concentrations are likely to occur. Direct slumping of old, yedoma carbon into streams causes
361 striking increases in DOC in adjacent receiving waters in the Kolyma River watershed (Vonk et al.,
362 2013), while slumping adjacent to streams in the Alaskan Arctic is also associated with significantly
363 increased stream water DOC at the site of impact (Abbott et al., 2014). During thaw of ice-rich
364 permafrost, DOC stored in ice wedges and other ground ice (Fritz et al., 2015) is also released.
365 Thermokarst lakes that form in organic-rich terrains can have significantly elevated concentrations
366 of DOC as a result of direct contact between overlying water and recently submerged soils, and
367 continued thermokarst expansion into new soils at the lake margin (e.g., sub-Arctic Québec, Breton
368 et al., 2009; western Siberia, Shirokova et al., 2013). In regions where slumping increases delivery
369 of inorganic particles from land to water, however, aquatic DOC concentrations can decrease as a
370 result of the adsorption of organics onto sediment surfaces that settle after suspension (e.g.,
371 Mackenzie delta uplands, Kokelj et al., 2005; sub-Arctic Québec, Bouchard et al., 2012).

372 In addition, thaw-enabled changes in flow paths can also be expected to affect the transport of DOC
373 to aquatic ecosystems. Although there is little direct evidence for the effect of water interactions
374 with deeper soil layers as active layers deepen in organic-rich regions, there are parallels to be
375 drawn with more transitional (sub-Arctic) systems, where permafrost peatland plateaus are
376 associated with low annual export (2–3 g C/m²/yr) dominated by the snow melt period (~70%)
377 and non-permafrost fens are characterized by much higher DOC export (7 g C/m²/yr) due to more
378 sustained annual hydrological connectivity (sub-Arctic Sweden, Olefeldt and Roulet, 2014).
379 Conversely, where soils are characterized by shallow organic layers, growing season export of flow-
380 weighted DOC has been shown to decrease significantly between 1978–1980 and 2001–2003
381 (Yukon River, Alaska, Striegl et al., 2005), likely as a result of the combined effect of increased flow
382 paths (deeper active layer), residence time (Alaska, Koch et al., 2013), and microbial mineralization
383 of DOC in the unfrozen soil and groundwater zone. Permafrost thaw as a result of wildfire has been
384 shown to increase hydrologic connectivity between burned hillslopes and catchment surface
385 waters, such that burned soils can become a dominant source of water and solutes to streams
386 during summer, whereas unburned hillslopes provide longer term storage of water and solutes
387 (Alaska; Koch et al., 2014). Recent forest fires in central Siberia (Parham et al., 2013) however, led
388 to a decrease in stream DOC concentrations due to removal of a DOC source through combustion. In
389 these regions, it has been suggested that organic matter sorption onto newly thawed (due to forest
390 fires) mineral soils may also be important (Petroni et al., 2007). Over geographic gradients,
391 changes in permafrost extent appear to have regionally-variable effects on DOC flux from land to
392 water, with decreasing permafrost extent (and presumably increasing contact with deeper soils and
393 groundwater inflows) causing increasing DOC fluxes in organic rich regions, but decreasing DOC
394 fluxes in regions with poorly developed organic horizons (Frey and Smith, 2005; Prokushkin et al.
395 2011; Tank et al., 2012a). Controlled leaching experiments of soils from the Alaskan and western
396 Canadian Arctic have also found that regardless of temperature and leaching time, only small

397 amounts of DOC are released from permafrost-impacted soils, and that mobilization of OC occurred
398 largely in the POC phase (Guo et al., 2007).

399 **2.2.4 Nutrient delivery to aquatic ecosystems**

400 Similar to DOC, the effect of permafrost thaw on nutrient concentrations may also be region, or
401 landscape specific. For thermo-erosional processes, direct slumping into Alaskan streams has been
402 shown to increase dissolved inorganic and organic nutrient concentrations (Bowden et al., 2008;
403 Abbott et al., 2014), while in the western Canadian Arctic, total dissolved N and P can be lower in
404 shallow lakes directly impacted by permafrost slumping. This latter effect has been hypothesized to
405 occur as a result of the adsorption of organic nitrogen and phosphorus onto settling mineral
406 particles, or following rapid uptake and senescence, and then burial, of photosynthesizing cells
407 (Mackenzie delta uplands, Thompson et al., 2012). In lakes that remain turbid following
408 thermokarst disturbances, total phosphorus concentrations can be high, following phosphorus
409 adsorption onto clays that are transported into aquatic systems (sub-Arctic Québec, Breton et al.,
410 2009). Similarly, slumping can also increase sediment nutrient concentrations (Mackenzie delta
411 uplands, Mesquita et al., 2010), while shoreline expansion of thermokarst lakes in yedoma regions
412 can enable nutrient-rich yedoma soils, and the nutrient-rich plants that these soils support, to enter
413 lakes (Siberia, Walter Anthony et al., 2014).

414 Warming, coupled with landscape changes that decrease water contact with organic soils and
415 increase water contact with inorganic soils has been shown in several Arctic regions to lead to
416 higher nitrate concentrations in adjacent streams, as a result of decreased NO₃ uptake or increased
417 nitrification (e.g., Alaska, Jones et al., 2005 and Harms and Jones, 2012; Canadian High Arctic,
418 Louiseize et al., 2014). On the Alaskan North Slope, nitrate export from the upper Kuparuk River
419 increased over a period of several decades, via mechanisms that may be linked to warming and
420 permafrost thaw (McClelland et al., 2007). Conversely, deeper flow paths that increase contact with
421 mineral soils are expected to decrease dissolved organic nitrogen exports (Alaska, Walvoord and
422 Striegl, 2007; Harms and Jones, 2012; Koch et al., 2013). This may also lead to increased
423 phosphorus concentrations, because mineral weathering is the primary source of phosphorus in
424 soil waters (e.g., Frey and McClelland, 2009).

425 **2.2.5 Delivery of major ions**

426 Permafrost thaw is also expected to increase the concentration of weathering-derived ions in
427 receiving waters, as slumping or deepening flow paths increases the contact between water and
428 deeper mineral soil layers (see review in Frey and McClelland, 2009). For example, in the Alaskan
429 Arctic, increasing thaw depths have been associated with increasing surface water concentrations
430 of calcium and bicarbonate (Keller et al., 2010), while near-surface permafrost has been found to be
431 ion-rich in the western Canadian Arctic. In Siberia, and at multiple locations throughout the pan-
432 Arctic, decreasing permafrost extent has also been associated with increasing stream water
433 concentrations of major weathering ions (Frey et al., 2007; Tank et al., 2012a). This effect can be
434 pronounced when thermokarst slumping occurs directly adjacent to aquatic systems: both streams
435 (NW Canada, Malone et al., 2013) and lakes (Mackenzie delta uplands, Kokelj et al., 2005) can
436 exhibit strikingly elevated ionic concentrations when directly impacted by permafrost slumping.

437 **2.2.6 Mobilization of contaminants**

438 Contaminants reach polar regions following long-range atmospheric transport and deposition, as
439 well as through increased local waste production from marine transport and industrial or mining
440 activities. The frozen soils of permafrost have historically been considered a barrier to the
441 movement of contaminants and many waste and dump sites use containment strategies that rely on
442 the low mobility of contaminants in permafrost soils (Grannas et al., 2013). However, the warming
443 Arctic climate may lead to an increased mobility of contaminants, either stored in soils at waste
444 sites or historically-accumulated in permafrost, into Arctic surface waters (Armitage and Wania,
445 2013; Chételat et al., 2014).

446 Thawing permafrost may have major consequences for contaminant transport and transformations
447 in the Arctic due to: a) physical changes in the hydrological cycle leading to the remobilization of
448 contaminants from contaminated soils or sediments, b) chemical changes due to the release of
449 nutrients and organic carbon from previously frozen soils, and c) biological changes via the
450 microbial transformation of contaminants. Most studies on the interactions between contaminants
451 and permafrost soils have concentrated on fuel products, persistent organic pollutants (POPs), and
452 metals such as mercury (Hg) and lead (Pb).

453 Permafrost thaw may cause increased mobility of contaminants from catchment soils to surface
454 waters due to accelerated soil/peat erosion, altered hydrological flow (increasing hydrological
455 connectivity), and increased runoff leading to exposure of soluble contaminants (sub-Arctic
456 Sweden, Klaminder et al., 2008). Increased lateral hydraulic conductivity may accelerate the
457 downhill movement of contaminants through the large pores, lenses, and veins created in the active
458 layer by the thawing of ice-rich permafrost (Mackenzie delta region, Dyke, 2001). After thaw,
459 permafrost is no longer an impermeable barrier to contaminants, allowing for infiltration into soils
460 and aquatic systems (Grannas et al., 2013). The reduced surface area of thermokarst lakes in some
461 areas due to the creation of drainage channels may lead to increased contaminant concentrations in
462 the remaining surface waters (Macdonald et al., 2005).

463 Traditionally, the distinction is made between (i) organic contaminants, and (ii) inorganic
464 contaminants. Studies of *organic contaminants* (hydrocarbons or non-aqueous phase liquids)
465 predict lateral movement in the active layer with limited vertical transport in areas of continuous
466 permafrost (Mackenzie delta region, Dyke, 2001; Alaska, Carlson and Barnes, 2011). Vertical
467 migration is possible in some regions (Alaska, McCarthy et al., 2004) yet permafrost acts as a low-
468 permeability barrier in others (Antarctica, Curtosi et al., 2007). Organic contaminants may migrate
469 downwards into frozen soils in areas of discontinuous permafrost due to more variable distribution
470 (Alaska, Carlson and Barnes, 2011).

471 Studies of *inorganic contaminants* show that physical changes in permafrost affect contaminant
472 mobility. For instance, Manasypov et al. (2014) observed geographical gradients in trace metal
473 concentrations in surface waters from Siberia related to thermokarst lake evolution (from small
474 permafrost depressions to larger lakes), mainly due to peat leaching. They also described seasonal
475 differences in trace metal levels related to cycles of ice formation and melting (Manasypov et al.,
476 2015). Further, studies using mass-balance calculations and paleoecological techniques have linked
477 thermokarst erosion in peatlands and the release of Hg into lake surface waters (sub-Arctic

478 Sweden, Klaminder et al., 2008; Rydberg et al., 2010). Stable isotope analysis also suggests that the
479 weak recovery of Pb contamination in two sub-Arctic lakes (despite dramatically reduced
480 atmosphere inputs) may be linked to the subsidence of thawing permafrost soils (sub-Arctic
481 Sweden, Klaminder et al., 2010). Permafrost degradation may affect the mobility of inorganic
482 contaminants differently across different Arctic regions. Deison et al. (2012) found that Mackenzie
483 delta upland lakes impacted by the development of retrogressive thaw slumps in siliciclastic soils
484 had lower levels of Hg in surface sediments when compared to reference lakes. In this instance,
485 thaw slumping may have led to a dilution of organic material and associated mercury (Hg) due to
486 high inorganic sedimentation rates. On the other hand, MacMillan et al. (2015) showed that small
487 thermokarst lakes located in sub-Arctic and High Arctic Canada dominated by slumping of organic
488 soils showed elevated concentrations of Hg and toxic methylmercury. This was strongly related to
489 inputs of organic matter and nutrients into surface waters.

490 In summary, permafrost has historically been considered an impermeable barrier to the movement
491 of contaminants due to their low infiltration and mobility in frozen soils (Grannas et al., 2013).
492 However, ongoing and future climate warming will likely disrupt the sequestration of contaminants
493 in permafrost soils, which leads to enhanced leaching and mobility of organic and inorganic
494 contaminants to nearby aquatic systems. This, however, will not necessarily result in increased
495 contaminant concentrations due to a dilution effect by other materials transported along with the
496 contaminant.

497 **2.2.7 Overarching considerations**

498 Overall, the manner in which permafrost thaw affects surface water chemistry as a result of
499 changing land-to-water fluxes will be dependent on the constituent and the landscape. While
500 evidence suggests that constituents such as suspended sediments and weathering ions will
501 experience neutral to increasing effects in response to permafrost thaw, the effect on constituents
502 such as DOC and nutrients is likely to be more variable. As a result, we must consider local
503 conditions, including soil composition (mineral vs. organic-rich), the nature of thaw (e.g.,
504 thermokarst processes on hillslopes vs. within lowlands, vs. active layer deepening), and the
505 current extent of permafrost (continuous vs. discontinuous) to best understand the effects of thaw
506 on land-water fluxes of chemical constituents.

507 Particularly for streams, hydrological connectivity between sites of thaw and the stream system is
508 also an important consideration, because lateral inputs are typically more influenced by conditions
509 in the riparian and deeper subsurface zones than by conditions at ridge tops and the near surface
510 (Stieglitz et al., 2003; Rastetter et al., 2004). Thus, in areas where permafrost is thawing rapidly, the
511 proximity of thaw features to aquatic systems, and the hydrological conditions of local stream and
512 subsurface zones are likely to have a strong influence on the biogeochemical imprint of lateral
513 inputs to streams. While TEFs have the capacity to move large quantities of soils and nutrients
514 downslope, hydrological connectivity must be present to enable these constituents to reach the
515 stream for biogeochemical impact to occur.

516 **3 Pathways of degradation**

517 The carbon, nutrients, and contaminants that are delivered to aquatic ecosystems as a result of
518 permafrost thaw will have a critical effect on the functioning of these systems. Changes in biological
519 function (see section 4) will determine the relative balance between processing within freshwater
520 systems, versus loss via potential outflow pathways and the eventual delivery of these constituents
521 to sediments (see section 4.2) or ‘downstream’ to the Arctic Ocean (see section 4.5). In the case of
522 carbon, differences in quality will affect whether processing and uptake results in the release of
523 greenhouse gases (GHG), or C incorporation into microbially-based food webs. At the same time,
524 changes in stratification, redox, solubility, and oxygen availability (sections 2.1, 2.2, and 3.5.1) will
525 affect the balance between CO₂ and CH₄ release. In this section, we review the dominant pathways
526 of carbon and contaminant degradation in permafrost-thaw impacted systems. We focus
527 specifically on bio- and photo-degradation pathways, and the effect of permafrost thaw on GHG
528 emissions from thaw-impacted systems. The manner in which permafrost thaw affects nutrient
529 uptake within aquatic systems is addressed in section 4.3.

530 **3.1 Biodegradation of organic carbon**

531 In the Arctic, where transfers of organic C from soils to aquatic ecosystems can be especially strong
532 (Kling et al., 1991), C fluxes from surface waters to the atmosphere, and from land to ocean, may
533 represent up to 40% of the net land-atmosphere C exchange (maximum flux of ~0.16 Pg C/y
534 compared to a net terrestrial sink of 0.4 ± 0.4 Pg C/y; McGuire et al., 2009). In many cases, these C
535 fluxes from freshwaters to the atmosphere or to the coastal oceans are supported by the
536 degradation of terrestrially-derived DOC (e.g., Yukon River, Alaska, Spencer et al., 2008), although
537 DIC derived from weathering can also be an important CO₂ source (Yukon River, Alaska, Striegl et
538 al., 2012). Biological processing of DOC occurs prior to, and upon, hydrologic delivery to surface
539 waters (Alaska, Michaelson et al., 1998; NE Siberia, Spencer et al., 2015). The biodegradability of
540 DOC in various Arctic systems is dependent on several factors including DOC source and chemical
541 character (Michaelson et al., 1998; Wickland et al., 2007; 2012; Balcarczyk et al., 2009; Mann et al.,
542 2012; Olefeldt et al., 2013; Abbott et al., 2014), nutrient availability (Holmes et al., 2008; Mann et
543 al., 2012; Wickland et al., 2012; Abbott et al., 2014), water temperature (Wickland et al., 2012), and
544 prior processing (Michaelson et al., 1998; Wickland et al., 2007; Spencer et al., 2015). There are
545 strong seasonal patterns in DOC biodegradability in large Arctic rivers, where the relative amount
546 of biodegradable DOC (BDOC) is greatest in winter and spring, and generally declines through the
547 summer and fall (Holmes et al., 2008; Mann et al., 2012; Wickland et al., 2012; Vonk et al., 2015),
548 reflecting the influences of seasonal thaw depth on DOC sources and hydrologic connectivity. Soil
549 BDOC does not show a strong seasonality (Wickland et al., 2007; Vonk et al., 2015), supporting the
550 notion that changes in DOC residence time and processing in soils prior to delivery to surface
551 waters is a primary control on aquatic BDOC (Striegl et al., 2005; Vonk et al., 2015).

552 Permafrost presence and extent has direct and indirect influences on biodegradable DOC in aquatic
553 ecosystems through its controls on potential sources and on hydrologic pathways and rate of
554 delivery. A synthesis study by Vonk et al. (2015) of BDOC in circum-Arctic soils and surface waters
555 finds higher BDOC in soils and aquatic systems with increasing permafrost extent. In the absence of

556 direct slumping, sources of DOC in permafrost-impacted areas are restricted to surface litter and
557 modern active layer soils, which have relatively high total and labile C contents that are readily
558 accessible (e.g., Holmes et al., 2008), and thus are strong potential sources of BDOC. Deeper soils
559 having generally lower C content are more accessible in discontinuous permafrost areas, and
560 hydrologic flow paths with longer residence times allow for greater opportunity of DOC processing
561 during transport (Alaska, Walvoord and Striegl, 2007) generally resulting in lower potential BDOC
562 delivery to aquatic systems (Vonk et al., 2015). However, there are observations of increasing
563 delivery of biodegradable DOC to aquatic ecosystems in areas of decreasing permafrost extent
564 (western Siberia, Kawahigashi et al., 2004; Alaska, Balcarczyk et al., 2009), with one explanation
565 being the preferential sorption of more recalcitrant hydrophobic DOC constituents to increasingly-
566 exposed/accessible mineral soils (Kawahigashi et al., 2004). Therefore broad generalizations of
567 permafrost control on BDOC are still difficult to make with certainty.

568 Permafrost thaw and thermokarst formation can potentially impact biodegradable DOC in aquatic
569 ecosystems by altering sources, rates, and pathways of hydrologic delivery. Newly thawed soils are
570 potential DOC sources that can exceed DOC released from seasonally thawed active layer soils (sub-
571 Arctic Sweden, Roehm et al., 2009; Alaska, Waldrop et al., 2010). Studies of distinct DOC sources
572 suggest that non-permafrost-derived soil pore water DOC is moderately biodegradable (Wickland
573 et al., 2007; Roehm et al., 2009; Vonk et al., 2015), whereas certain permafrost soil-derived DOC can
574 be highly biodegradable, particularly Pleistocene yedoma DOC in NE Siberia and Alaska (Vonk et al.,
575 2013; Abbott et al., 2014; Spencer et al., 2015). These studies point to a high susceptibility of
576 permafrost DOC to degradation during transport from soils, and within surface waters, compared to
577 non-permafrost DOC, with aliphatic DOC originating in permafrost being preferentially degraded
578 (NE Siberia, Spencer et al., 2015). Surface waters contain a mixture of DOC from different sources,
579 and therefore it is difficult to isolate the relative biodegradability of permafrost soil vs. non-
580 permafrost soil (active layer) derived DOC within surface waters (Holmes et al., 2008; Balcarczyk et
581 al., 2009; Mann et al., 2012; Wickland et al., 2012). Frey et al. (2015) have shown a relatively
582 constant proportion of bioavailable DOC (~4.4%; based on five day biological oxygen demand
583 assays) along the flow-path continuum throughout the Kolyma River basin in Siberia. Actively
584 thawing permafrost features, however, release elevated amounts of BDOC to low order water tracks
585 and outflows (upt to 40% BDOC after 30-40 days incubation; NE Siberia, Vonk et al., 2013; Alaska,
586 Abbott et al., 2014), but significant biodegradation during transport to higher order streams and
587 rivers remove substantial amounts of permafrost DOC before reaching major Arctic rivers and the
588 ocean (NE Siberia, Mann et al., 2015; Spencer et al., 2015). Increasing hydrologic flow path lengths
589 and residence time in soils in some areas as a result of permafrost thaw likely promote DOC
590 processing and sorption within watersheds prior to discharge to surface waters (Yukon River,
591 Alaska, Striegl et al., 2005), further reducing the likelihood of biodegradable permafrost DOC
592 reaching aquatic systems.

593 Thermokarst can also release significant quantities of POC to aquatic ecosystems (section 2.2),
594 often substantially outweighing the amount of released DOC (assessed via direct measurements, or
595 assuming a 1-2% conversion between suspended sediments and POC; Bowden et al., 2008; Lewis et
596 al., 2012; Vonk et al., 2013; Abbott et al., 2015). In streams impacted by thermokarst, POC will
597 remain entrained for long distances downstream (NW Canada, Kokelj et al., 2013), and may

598 reasonably be subject to significant biological decomposition as a result of this entrainment, as has
599 been shown for other, temperate, systems (Richardson et al., 2013). Degradation of the POC
600 delivered to aquatic systems as a result of permafrost thaw, however, has received little attention to
601 date.

602 **3.2 Photodegradation of organic carbon**

603 Recent studies indicate that sunlight can play an important role in dissolved organic matter (DOM)
604 degradation in thermokarst-impacted lakes and ponds (Alaska, Cory et al., 2013, 2014; Canadian
605 High Arctic, Laurion and Mladenov, 2013; sub-Arctic Sweden, Koehler et al., 2014). To understand
606 why sunlight can be an important control on DOM degradation in these systems, we review controls
607 on DOM photo-degradation and the specific characteristics of thermokarst lakes that can maximize
608 opportunities for photo-degradation.

609 Sunlight breaks down DOM into three broad classes of products: (1) CO₂ (and CO that can be
610 subsequently oxidized to CO₂; photo-mineralization), (2) partially oxidized or degraded DOM that
611 bacteria can then readily respire to CO₂ (photo-stimulated bacterial respiration), and (3) partially
612 oxidized or degraded DOM that is more recalcitrant to bacteria (Alaska, Cory et al., 2010, 2013,
613 2014; Hong et al., 2014; Canadian High Arctic, Laurion and Mladenov, 2013). Where the presence of
614 thermokarst increases the transfer of old permafrost carbon from land to water, photochemical
615 conversion of DOC to CO₂ and photo-stimulated bacterial respiration may therefore increase old C
616 transfer to the atmosphere. This occurs on relatively short time scales (e.g. months to decades),
617 thus providing a positive climate effect with respect to global warming (e.g., Cory et al., 2013, 2014;
618 Laurion and Mladenov, 2013). The water column rate of DOM photo-degradation to CO₂ or to
619 partially oxidized DOM increases with increasing UV radiation, and also depends on the rate of light
620 absorption by DOM in the water column, and the lability of DOM to be converted to CO₂ or to
621 partially oxidized DOM during light exposure.

622 UV irradiance entering the water column depends on the extent and presence of snow and ice cover
623 (Vincent and Belzile, 2003), the solar zenith angle (i.e., latitude, date and time of day), and the
624 composition of the atmosphere (e.g., ozone, and the amount and type of clouds and aerosols)
625 (Vavrus et al., 2010; Bernhard et al., 2013). In surface waters across the Alaskan Arctic (from Toolik
626 Lake to Barrow, AK), the sun is above the horizon from approximately mid-May through mid-July,
627 but ~ 90% of the daily UV flux involved in DOM degradation reaches surface waters during the day
628 due to the low solar zenith angle overnight (Alaska, Cory et al., 2014). Clouds generally decrease
629 surface UV, but the effect of clouds can be offset by ozone levels, making it difficult to predict
630 surface UV based only on latitude and date across the Arctic (Vavrus et al., 2010; Bernhard et al.,
631 2013). Although less UV generally reaches surface waters in the Arctic compared to lower latitudes
632 due to lower solar zenith angles, thermokarst lakes and ponds can often have high concentrations
633 of light-absorbing DOM that is susceptible to photo-degradation, thus potentially counter-balancing
634 the lower UV (Alaska, Cory et al., 2014; sub-Arctic Sweden, Koehler et al., 2014).

635 The many shallow ponds and lakes across the Arctic often contain high concentrations of light-
636 absorbing CDOM (e.g., Alaska, Hobbie, 1980; NW Canada, Gareis et al. 2010; sub-Arctic Québec,
637 Watanabe et al., 2011; Alaska, Cory et al., 2014) as is consistent with high concentrations of light-

638 absorbing DOC draining from soils surrounding these lakes (Alaska, Judd et al., 2007; Merck et al.,
639 2012; NE Siberia, Frey et al., 2015). For example, absorption coefficients for CDOM were reported
640 to range from 9 - 17 m⁻¹ at 330 nm in lakes of the Mackenzie Delta (Gareis et al., 2010), while a
641 survey of 380 lakes in the Alaskan Arctic reported a mean of 11 m⁻¹ vs. 31 m⁻¹ at 320 nm for lakes
642 near the foothills of the Brooks Range vs. lakes on the coastal plain, respectively (Cory et al., 2014).
643 For small sub-Arctic thermokarst lakes at the southern limit of permafrost along the Eastern
644 Hudson Bay, Watanabe et al. (2011) present a large range of absorption coefficients at 320 nm (9.9
645 to 56 m⁻¹) at the southern limit of permafrost along eastern Hudson Bay, while even a wider range
646 was obtained by Breton et al. (2009) in the same region (reaching up to 171 m⁻¹), although these
647 systems are typically also affected by high levels of non-CDOM UV absorbance (see below).

648 Near-surface rates of DOM photo-degradation increase linearly with increasing CDOM, while the
649 depth-integrated rates of photo-degradation in the water column depend non-linearly on CDOM
650 concentrations due to the attenuation of light (Miller, 1998). In thermokarst lakes and ponds, CDOM
651 is often the main UV-absorbing constituent (e.g., Hobbie, 1980; Gareis et al., 2010; Cory et al., 2014),
652 and thus controls the depth of UV light penetration. However, non-algal particles and especially fine
653 inorganic particles can contribute a significant portion of UV attenuation in thermokarst lakes
654 influenced by marine clays and silts (Watanabe et al., 2011). In such cases, UV is attenuated to a
655 much larger extent, limiting photochemical reactions to the very surface under the strongly
656 stratified conditions observed for these systems (Laurion et al., 2010). Although CDOM
657 concentrations, and thus light attenuation, are often high in lakes and ponds across the Arctic, the
658 whole water column can still be exposed to UV because many of these systems are shallow (Gareis
659 et al., 2010; Cory et al., 2014; see also section 2.1). For example, a survey of CDOM and UV light in
660 thermokarst lakes of the Mackenzie River delta concluded that 19% and 31% of the water column
661 was exposed to UVB and UVA radiation, respectively (Gareis et al., 2010). For a series of
662 thermokarst lakes and ponds of the coastal plain in the Alaskan Arctic, up to 20% of the water
663 column was exposed to UVB while 30 - 100% was exposed to UVA (Cory et al., 2014). Exceptions
664 include turbid streams, ponds, and lakes impacted by thermokarst slumping (Bowden et al., 2008;
665 Gareis et al., 2010; Watanabe et al., 2011; Cory et al., 2013), or ponds with abundant macrophyte
666 production (Gareis et al., 2010), where UV penetration is low.

667 The degree to which DOM drained from catchment soils underlain by permafrost is susceptible to
668 photo-degradation, quantified as the apparent quantum yield for each major class of DOM photo-
669 products, has been measured to be on the high end of the range reported for aquatic DOM (Alaska,
670 Cory et al., 2013, 2014; Hong et al., 2014; sub-Arctic Sweden, Koehler et al., 2014). These findings
671 suggest that DOM originating from soils underlain by permafrost may be more labile to photo-
672 degradation relative to DOM in freshwaters outside the Arctic, consistent with prior studies
673 showing a high photo-reactivity of DOM in Arctic surface waters (NE Siberia, Mann et al., 2012;
674 Canadian High Arctic, Laurion and Mladenov, 2013) that is suggested to increase downstream in
675 the network (Frey et al., 2015). However, DOM leached specifically from the permafrost soil layer
676 sampled across the Arctic has a consistently lower concentration of aromatic, light absorbing
677 carbon (i.e., lower CDOM per DOC concentration), often quantified as lower SUVA₂₅₄ values (Mann
678 et al., 2012; Cory et al., 2013; 2014; Abbott et al., 2014; Ward and Cory, 2015), compared to DOM
679 draining from the active, organic surface layer. Despite lower concentrations of light-absorbing C,

680 permafrost DOM has been measured to be equally or more sensitive to photo-degradation in a
681 series of sites in the Alaskan Arctic (i.e., when comparing apparent quantum yields for
682 photochemical CO₂ production for example, corrected for differences in rates of light-absorption;
683 Cory et al., 2013). These results may suggest that the chemical composition of permafrost DOM
684 makes it more reactive to sunlight than expected based on aromatic C content alone.

685 Overall, the typical range of CDOM concentrations and the shallow water depths in thermokarst
686 lakes and ponds can mean that a greater fraction of DOM is exposed to UV in the water column
687 compared to deeper, non-thermokarst lakes. Especially for lakes and ponds with no outlet, the
688 residence time of DOM and its exposure to UV light is high, thus confining DOM to a thin boundary
689 layer where opportunities for photo-degradation are maximized (e.g., Alaska, Lougheed et al., 2011;
690 sub-Arctic Sweden, Olefeldt and Roulet, 2012). The alternation of stratification periods (intensive
691 UV exposure at the very surface) with night-time cooling and mixing (renewal of surface water
692 DOM) observed in many shallow thermokarst lakes may also offer a greater opportunity for
693 efficient DOM photo-degradation. With forthcoming climate change and deeper permafrost thaw, C
694 flux from peaty soils to thermokarst lakes may also be enhanced in some regions, and the released
695 DOM will be subject to UV-induced mineralization, especially as the summer season lengthens
696 (Erickson et al., 2015). On the other hand, a study of 73 lakes in the Mackenzie Delta uplands found
697 that slump-impacted lakes had significantly lower CDOM than unimpacted lakes (Kokelj et al., 2009;
698 Thompson et al., 2012; see section 2.2), indicating that photodegradation may decline in some
699 slump-impacted systems due to adsorption of CDOM to basic cations and clay particles. A strong
700 response in UVB attenuation to small changes in CDOM was observed in lakes of NW Finnish
701 Lapland, suggesting that even minor shifts in CDOM may largely change the UV radiation exposure
702 of high-latitude lakes, with likely consequences on the photochemistry and biota (Forsström et al.,
703 2015). To understand the role of sunlight in DOM processing in thermokarst waters, future work
704 must quantify UV irradiance in the water column, residence time of DOM in the UV-exposed portion
705 of the water, and identify the factors that control vertical losses of DOM and the lability of
706 permafrost DOM to photo-degradation.

707 **3.3 Photochemical and microbial transformation of contaminants**

708 There are likely to be multiple effects of permafrost thaw on the mobility and transformation of
709 contaminants in Arctic environments. The climate-triggered release of contaminants may increase
710 contaminant transport into aquatic systems through increased leaching and hydrological
711 connectivity. Thermokarst lakes with anoxic sediments may cause the remobilization of
712 contaminants, and may also allow enhanced microbial activity and hypolimnia, and bacterial metal
713 alkylation in the hypolimnion (e.g., production of the neurotoxin methylmercury). Here, we
714 examine the potential mechanisms that may allow Arctic warming to lead to increases in the
715 degradation and transformation of contaminants.

716 Photochemical transformations may affect both the mobility and availability of photoreactive
717 contaminants such as the DOC-driven photoredox transformations of As (Buschmann et al., 2005)
718 and Hg. Tseng et al. (2004) showed that Hg can be photoreduced and volatilized in Alaskan surface
719 waters, whereas the neurotoxin methylmercury in the same region can be photodegraded

720 (Hammerschmidt and Fitzgerald, 2010). Photochemical transformation of contaminants may
721 become more important in regions where the total area of non-turbid thermokarst ponds is
722 increasing, as these shallow ecosystems are irradiated constantly during the polar summer (e.g.,
723 Mann et al., 2014).

724 Changes in the release of DOC and POC into aquatic ecosystems may significantly affect the phase
725 partitioning and solubility of contaminants. In discontinuous permafrost regions, an increase in
726 labile organic carbon (i.e. DOC) with thawing may lead to enhanced microbial activity and hence
727 alter the microbial transformation of some contaminants (Roehm et al., 2009). Microbes can
728 influence contaminant cycling by degrading organic contaminants, alkylating metals, and creating
729 redox gradients that may modify the mobility and toxicity of toxic metals. Permafrost thaw can
730 affect microbial diversity and microbial activity. Microbial *diversity* typically is highest in the
731 surface active layer and decreases towards the permafrost table (NW Canadian Arctic, Frank-Fahle
732 et al., 2014), hence deepening of the active layer will likely modify microbial diversity. Changing
733 microbial diversity in combination with nutrient and temperature effects can affect the microbial
734 degradation of organic pollutants in thawing permafrost (Bell et al., 2013). Microbial *activity* can be
735 enhanced when permafrost thaw creates new environments such as warm, stratified thermokarst
736 lakes, which may be potential sites for bacterial metal alkylation (Stern et al., 2012) such as found
737 in two regions of NW Canada (MacMillan et al., 2015). Thermokarst lakes with hypoxic or anoxic
738 bottom waters may be sites that are highly conducive to microbial Hg(II) methylation, and
739 increasing inputs of organic matter and nutrients from thawing permafrost into these systems may
740 have potentially important consequences for the transport or *in situ* production of methylmercury
741 (MacMillan et al., 2015).

742 Manasypov et al. (2014) showed that thermokarst lakes in Siberia have close relationships between
743 diagenetic processes and the remobilization of contaminants from the sediments. This
744 remobilization is tied to diagenetic reactions occurring in these lakes due to the microbial
745 mineralization of natural organic matter. The anoxic conditions in lake sediments during the early
746 stages of thermokarst lake development result in microbe-mediated reactions causing authigenic
747 sulphide precipitation (i.e., the reduction of sulphate) that can create a sink for metals in the
748 sediments (western Siberia, Audry et al., 2011). Early diagenetic reactions in Siberian thermokarst
749 lakes and the resulting shift in redox conditions are responsible for the partitioning of trace
750 elements, including several major contaminants (As, Cu, Zn, Cd, Pb, Ni). During all stages of lake
751 development in this region, the sediments may be a source of dissolved Ni and As to the water
752 column (Audry et al., 2011).

753 As outlined in section 2.2.6, permafrost thaw may initially lead to a higher mobility of organic and
754 inorganic contaminants into aquatic systems across different Arctic regions. For instance, peat
755 leaching leads to higher levels of dissolved trace metal concentrations in Siberian thermokarst
756 lakes (Manasypov et al., 2014). However, the bioavailable metal pool will ultimately be controlled
757 not only by the importance of the dissolved fraction, but also by chemical and biological changes,
758 such as photodegradation and organic matter complexation. For inorganic contaminants, the
759 quantity, quality, and molecular weight of organic matter being released, photolyzed, and

760 microbially transformed from thawing permafrost during thermokarst lake evolution is likely a key
761 driver of metal bioavailability in these systems (Pokrovsky et al., 2011).

762 **3.4 Microbiology of thaw waters**

763 Biogeochemical data collected to date from thermokarst lakes, rivers, ponds, and wetlands point to
764 the importance of these environments as sites of intense microbial activity in the northern
765 landscape. As a result there is an increasing effort to apply molecular microbiological methods,
766 particularly next generation nucleic acid sequencing techniques, to understand the biodiversity,
767 network relationships, and biogeochemical capabilities of these microbial communities. This
768 research theme is still at an early stage of development, but the picture that is emerging is one of
769 complex microbial consortia, with all domains of life well represented, and dominance by certain
770 groups that play key biogeochemical roles (e.g., Negandhi et al., 2013; Crevecoeur et al. 2015;
771 Przytulska et al., 2015).

772 Methanogenic archaea occur in high abundance in the anoxic, CH₄-rich waters of permafrost thaw
773 waters and wetlands, and molecular techniques have revealed a variety of taxa. In the Canadian
774 High Arctic, gene signatures from acetoclastic and hydrogenotrophic methanogenic Archaea were
775 detected in ponds associated with ice-wedge polygons (Negandhi et al., 2013), while Mondav et al.
776 (2014) showed across a permafrost gradient in northern Sweden that partially thawed sites were
777 often dominated by a single taxon (*Methanoflorens stordalenmirensis*) that belongs to the
778 uncultivated archaeal lineage 'Rice Cluster II'. Metagenomic analysis showed that this micro-
779 organism has the genes for hydrogenotrophic methanogenesis. A subsequent molecular study by
780 McCalley et al. (2014) in sub-Arctic Sweden combined with isotopic analyses showed that the
781 abundance of this taxon is a predictor of the relative proportions of carbon released from the
782 thawing permafrost as CH₄ versus carbon CO₂.

783 There is now a rapidly growing DNA data base for bacteria in permafrost soils, which often contain
784 anaerobic groups such as sulphate reducers, Fe(III) reducers, and denitrifiers, and many aerobic
785 groups including actinobacteria and methanotrophs (Jansson and Tas, 2014). By comparison, much
786 less is known about the microbial constituents of thaw waters. Soil crusts in the High Arctic polar
787 desert have been shown to contain remarkably diverse communities of bacteria, with evidence that
788 their populations of cyanobacteria and acidobacteria are stimulated by water track flows over the
789 permafrost (Steven et al., 2013). High throughput analysis of bacterial samples from High Arctic
790 ponds showed that the planktonic sequences in these waters were dominated by carbon degrading
791 taxa in the Bacteroidetes, Betaproteobacteria and Actinobacteria (Negandhi et al., 2014). In
792 contrast, the sediment community had a higher alpha-diversity and the sequences included carbon
793 degraders (29–46 %), cyanobacteria (20–27 %), purple non-sulfur bacteria (6–13 %),
794 methanotrophs (11–20 %), and methanogen symbionts (1–2 %).

795 DNA clone library analysis of thermokarst lakes in a sporadic permafrost region in sub-Arctic
796 Québec revealed large differences in the assemblages inhabiting the different water layers, and the
797 presence of methanotrophic bacteria (Rossi et al., 2013). Subsequent analysis of lake communities
798 in the same region by high throughput RNA sequencing showed that the dominant bacterial taxa
799 were beta-proteobacteria, especially the genera *Variovorax* and *Polynucleobacter* (both known to

800 degrade a wide variety of organic compounds), and that methanotrophs (notably *Methylobacter*)
801 were also well represented (Crevecoeur et al., 2015). Methanotrophic taxa accounted for up to 27%
802 of the total bacterial sequences, indicating the importance of CH₄ as an energy source in these
803 ecosystems. A puzzling observation was that the anoxic bottom waters in most of these
804 thermokarst lakes had abundant methanotrophs, accounting for up to 23% of the sequences. This
805 could be the result of intermittent injection of oxygen into these bottom waters by mixing, or
806 sustained viability of the methanotrophs mixed down from the aerobic surface zone. Such mixing
807 occurs mostly during fall in these sub-Arctic lakes (Deshpande et al., 2015), which would imply
808 prolonged survival under anoxic conditions, and the availability of an inoculum for rapid response
809 to oxygen resupply during mixing. However, few data are available from thermokarst lakes further
810 north, and it is not known whether these sub-Arctic patterns occur elsewhere. A major unknown for
811 thermokarst lakes throughout the sub-Arctic and Arctic is the composition of winter microbial
812 communities beneath the ice, and this will require close attention in the future.

813 High-throughput DNA sequencing has also been used to examine biogeographical patterns. The
814 bacterial composition of thermokarst lakes was examined over a North-South gradient of
815 permafrost degradation in sub-Arctic Québec showed that greater differences occurred among
816 valleys across this gradient than among lakes within a valley, despite marked differences in
817 limnological properties among neighbouring lakes (Comte et al., 2015). This implies that the
818 taxonomic composition and perhaps also the biogeochemical functioning of thermokarst lake
819 bacterial assemblages are regulated by local landscape features, such as the extent of permafrost
820 thaw.

821 Phototrophic organisms in thaw waters include photosynthetic sulphur bacteria (sub-Arctic
822 Québec, Rossi et al., 2013; Crevecoeur et al., 2015), benthic cyanobacteria, purple non-sulphur
823 bacteria (Canadian High Arctic, Negandhi et al., 2014), and picocyanobacteria, as well as eukaryotic
824 algae of diverse phylogenetic groups (sub-Arctic Québec, Przytulska et al., 2015), however the
825 network associations among these organisms and other microbial taxa has yet to be explored. Such
826 analyses have been applied to temperate lake communities, combining bacterial DNA sequence data
827 with phytoplankton and zooplankton counts by microscopy, and these reveal highly connected,
828 potential keystone taxa in the mixed communities (Peura et al., 2015).

829 Large Arctic river systems receive thaw waters from throughout their catchments and can serve to
830 monitor large-scale patterns. Crump et al. (2009) reported that bacterial communities showed a
831 large spatial synchrony, along with clear seasonal community differences driven by shifts in
832 hydrology and biogeochemistry that reassembled annually. Furthermore, Crump et al. (2012)
833 observed a decreasing species diversity downslope in a soil-stream-lake sequence in Alaska. Soil
834 waters and headwater streams showed highest species richness, whereas lake waters show a lower
835 diversity. They suggest that bacterial and archaeal diversity in freshwaters is initially structured by
836 inoculation of soil microbes, and then subject to a species-sorting process during downslope
837 dispersal. Permafrost thaw could lead to a greater transfer of soil microbes into aquatic
838 communities.

839 A conspicuous gap in information available to date is the diversity and role of viruses in these
840 microbe-rich habitats. Viruses are likely to be the biologically most abundant particles in these

841 waters, as elsewhere, and may influence the species succession of microbes in all domains of life,
842 affect carbon cycling by their lytic activities, and have a controlling influence on evolutionary
843 processes via horizontal gene transfer (Suttle et al., 2007). New viral lineages are being discovered
844 in environments elsewhere (e.g. freshwaters in the Canadian High Arctic, Chénard et al., 2015), and
845 thermokarst lakes and ponds will likely yield additional new groups given the diversity of potential
846 host taxa.

847 **3.5 Aquatic gas fluxes**

848 **3.5.1 Emission of CO₂ and CH₄ from permafrost-thaw impacted systems**

849 In well-drained terrestrial environments, permafrost thaw leads to microbial decomposition
850 resulting in variable production and emission of CO₂ (e.g., Schuur et al., 2009; Schädel et al., 2014).
851 Thaw of ice-rich permafrost, particularly in poorly drained lowland areas, results in ground
852 subsidence and saturated soils that take the form of thermokarst lakes, wetlands, and slumping into
853 streams. Since waterlogging slows the diffusion of oxygen from the atmosphere into soils, this
854 results in anoxic conditions in sediments as well as in portions of the overlying water columns of
855 many thermokarst water bodies. Under anaerobic conditions, decomposition of organic matter also
856 produces CH₄ (e.g. Alaska, Wickland et al., 2006). Where soils surrounding thermokarst lakes are
857 anoxic, lateral inputs of CH₄ produced within the active layer can also occur (Alaska, Paytan et al.,
858 2015). Work in northern Siberia suggests that small water bodies may be particularly important
859 for CO₂ and CH₄ emissions (Repo et al. 2007; Abnizova et al. 2012). In a study on northern
860 Ellesmere Island, Canada, desert soils consumed CH₄ during the growing season, whereas the
861 wetland margin emitted CH₄, with an overall positive CH₄ flux over the landscape using, varying
862 with soil temperature (Emmerton et al., 2014). The CH₄ flux varied closely with stream discharge
863 entering the wetland and hence the extent of soil saturation.

864 In a study of 40 Alaskan thermokarst lakes (Fig. 5) that span large gradients of climate, vegetation,
865 geology, and permafrost regimes, Sepulveda-Jáuregui et al. (2015) found that all lakes were net
866 sources of atmospheric CH₄ and CO₂ (when integrated over a year) as also noted earlier by Kling et
867 al. (1991; 1992). On a C mass basis, CO₂ emissions from Alaskan lakes were ~6-fold higher than CH₄
868 emissions. However, considering the ~30-fold stronger global warming potential of CH₄ vs. CO₂
869 over 100 years (GWP₁₀₀; Myhre et al., 2013), CH₄ emissions had nearly twice the impact on climate
870 as CO₂ emissions in this region.

871 In the Eastern Canadian Arctic, a thermokarst lake (deep enough to have unfrozen water in winter
872 and likely a talik underneath) was shown to be a relatively small GHG emitter in July (Bouchard et
873 al., 2015), although its thermal structure suggests that GHG potentially stored in the hypolimnion is
874 transferred to the atmosphere at the autumnal overturn. Large variations in summertime CO₂ and
875 CH₄ fluxes were shown in smaller lakes and ponds from two sites located in the Canadian sub- and
876 High Arctic (Laurion et al., 2010). Turbid, sub-Arctic thermokarst lakes were all GHG emitters, but
877 showed on average a 530-fold higher CO₂ than CH₄ diffusive flux in summer, with strong GHG
878 gradients in the hypolimnion (summer storage). In the High Arctic, polygonal ponds over low-
879 centered ice wedge polygons were CO₂ sinks because of colonization by active cyanobacterial mats
880 (Laurion et al., 2010), while shallower ice-wedge trough ponds were identified as the main GHG

881 emitters (Negandhi et al., 2013), with summer CO₂ fluxes ~25-fold higher than CH₄ diffusive flux. At
882 this site, the CH₄ ebullition flux (likely background ebullition) was in the same range as the diffusive
883 flux (Bouchard et al., 2015).

884 In streams and rivers, emission of CO₂ is typically much greater than emission as CH₄ (Yukon River,
885 Alaska, Striegl et al., 2012). On a catchment scale, sub-Arctic and Arctic streams within permafrost
886 zones can emit relatively high amounts of GHG relative to their areal extent (sub-Arctic Québec,
887 Teodoru et al., 2009; Alaska, Striegl et al., 2012; Siberia, Crawford et al., 2013; Denfeld et al., 2013;
888 sub-Arctic Sweden, Lundin et al., 2013), and gaseous emissions can account for up to 50% of total C
889 exports (Striegl et al., 2012). For example, in northern Sweden streams accounted for 4% of the
890 aquatic surface area yet accounted for 95% of the total aquatic emissions (Lundin et al., 2013),
891 whereas in northern Québec streams accounted for 1% of the aquatic surface and accounted for
892 25% of the aquatic emissions (Teodoru et al., 2009). Stream CH₄ emissions can also be significant to
893 total catchment emissions; for example in interior Alaska stream CH₄ emission was estimated to be
894 up to 10% of catchment terrestrial emissions despite the very low surface area (<0.2% of
895 catchment area; Crawford et al., 2013). The relatively high emissions can be attributed both to
896 supersaturation relative to the atmosphere as well as high gas transfer velocities associated with
897 these more turbulent waters (Kling et al., 1992; Striegl et al., 2012; Denfeld et al., 2013; Lundin et
898 al., 2013). To date, however, there are no published studies to show how gas fluxes are affected by
899 the direct action of thermokarst slumping into streams.

900 A global-scale database of 4902 lakes have previously shown a significant relationship between
901 DOC and CO₂ (Sobek et al., 2005). This relationship has also been shown for a smaller set of Arctic
902 and sub-Arctic thermokarst lakes in Canada, especially for the chromophoric fraction of DOM
903 (Laurion et al., 2010). Sepulveda-Jáuregui et al. (2015) also found a significant relationship between
904 CH₄ diffusive flux and phosphorus concentrations in a series of thermokarst lakes over a N-S Alaska
905 transect. Therefore, we can assume that when thermokarst slumping leads to an associated
906 increase in DOM and nutrients, we can expect an overall rise in GHG emissions from aquatic
907 systems.

908 **3.5.2 Scale and distribution of GHG measurements**

909 Since the solubility of CO₂ exceeds that of CH₄, CO₂ evades aquatic ecosystems primarily by
910 diffusion, while CH₄ more readily comes out of solution, forming bubbles in sediments that escape
911 to the atmosphere by ebullition. Emission of CH₄ through diffusion from aquatic systems can,
912 however, also be high, particularly in wetlands, lakes, and other standing open water (Alaska,
913 Reeburgh et al., 1998; sub-Arctic Sweden, Lundin et al., 2013). Due to large heterogeneity in the
914 spatial and temporal dynamics of ebullition, this mode of CH₄ emission is less commonly studied
915 than diffusion (Bastviken et al., 2011; Wik et al., in review), although ebullition has been found to be
916 the dominant form of CH₄ emission in many thermokarst lakes (Bartlett et al., 1992, Walter et al.,
917 2006; Sepulveda-Jáuregui et al., 2015; see also discussion on the Eastern Canadian Arctic, above).
918 Recent studies focusing on ebullition dynamics in thermokarst lakes distinguished multiple sub-
919 modes of ebullition emission including seep ebullition, background ebullition, and ice-bubble
920 storage (Alaska and Siberia, Walter et al., 2006; Greene et al., 2014; Langer et al., 2015; Sepulveda-
921 Jáuregui et al., 2015; Fig. 5). Background ebullition is most commonly reported in the literature and

922 consists predominately of distributed bubbling from seasonally warm surface sediments. In
923 contrast, seep ebullition involves bubbling of CH₄ formed at depth in dense sediments (Fig. 4),
924 which are typically found in thaw bulbs beneath thermokarst lakes and streams (Walter Anthony et
925 al., 2014). Seep ebullition occurs repeatedly from the same point-source locations and occurs year-
926 round due to the thermal lag that results in warmer temperatures in deep sediments through the
927 fall to winter. Bubbling rates in hotspot seeps are high enough to maintain open holes in
928 thermokarst lake ice, resulting in the emission of CH₄-rich bubbles to the atmosphere throughout
929 winter (Zimov et al., 2001; Greene et al., 2014; Fig. 5). In thermokarst lakes where both seep and
930 background ebullition were measured, seep ebullition was found to dominate CH₄ emissions
931 despite occupying only a small fraction of the lake surface area (Walter et al., 2006). More recently,
932 ice-bubble storage, the release of ebullition bubbles seasonally trapped by winter lake ice upon
933 spring melt, was also recognized as an important, additional mode of ebullition. It contributed 9-
934 13% of total annual CH₄ emissions from thermokarst (and non-thermokarst) lakes in Alaska
935 (Greene et al., 2014; Sepulveda-Jáuregui et al., 2015) and was also recognized as an important
936 springtime emission mode in West Siberian lakes (Golubyatnikov and Kazanstev, 2013). Ice-bubble
937 storage is likely an important mode of emission in many Arctic systems since CH₄-rich ice-bubbles
938 have been observed in aquatic systems in Northeast Siberia (Walter et al., 2006; Langer et al.,
939 2015), Sweden (Wik et al., 2011; Boereboom et al., 2012), Finland (Walter Anthony et al.,
940 unpublished data); Greenland (Walter Anthony et al., 2012), Alaska (Walter et al., 2007; Brosius et
941 al., 2012; Sepulveda-Jáuregui et al., 2015) and Canada (Duguay et al., 2002; Brosius et al., 2012).

942 One promising technique for measuring aquatic gas fluxes in permafrost-impacted systems is eddy
943 covariance (EC), but EC data on inland freshwater ecosystems are still rare. Currently, on-going EC
944 measurements focus on CO₂ and CH₄ fluxes over thermokarst lakes in Siberia (T. Sachs, personal
945 communication, 2015; L. Belelli-Marchesini, personal communication, 2015) or sub-Arctic lakes
946 within thawing permafrost environments (M. Jammet, personal communication, 2015). Using EC,
947 Eugster et al., (2003) found efflux rates of 114 mg C/m²/d over an Arctic Alaskan lake in late July,
948 which agreed well with two other continuous flux estimation techniques (boundary layer and
949 surface renewal models). In a Swedish boreal lake, CO₂ effluxes determined by episodic floating
950 chamber measurements were about 100% larger than fluxes measured with EC, suggesting
951 potential biases related to inadequate spatial and/or temporal sampling intervals of the chamber
952 method (Podgrajsek et al., 2014a).

953 While proving the feasibility of EC measurements in freshwater ecosystems, aquatic EC work also
954 highlights challenges related to the application of this terrestrially-optimized approach to aquatic
955 systems (Vesala et al., 2006; Eugster et al., 2011). Overall, EC shows great promise with respect to:
956 (1) integration of all gas flux pathways from the lake sediments to the atmosphere, (2) continuous
957 flux monitoring over time, enabling the capture of episodic ebullition events of CH₄ in lakes
958 (Eugster et al., 2011), and (3) the analysis of dynamic responses of lake-atmosphere carbon fluxes
959 to temporal (including diurnal) changes in environmental variables (Eugster, 2003; Vesala et al.,
960 2006; Podgrajsek et al., 2014b). A significant portion of gaseous carbon emissions from seasonally
961 ice-covered lakes appears to occur during spring ice-thaw (e.g. Karlsson et al., 2013), stressing the
962 importance of year-round carbon flux monitoring on thermokarst lakes.

963 3.5.3 Lake morphology and evolution

964 The morphological diversity of thermokarst lakes will have important consequences for hydrology,
965 physicochemistry, and thus ultimately the microbial processes responsible for GHG production and
966 evasion dynamics at the air-water interface. Within the context of permafrost soil organic carbon
967 content, thermokarst lakes have been classified depending on whether they are surrounded by
968 yedoma-type permafrost or non-yedoma substrates (Walter Anthony et al., 2012; Sepulveda-
969 Jáuregui et al., 2015). Yedoma is typically thick (tens of meters), Pleistocene-aged loess-dominated
970 permafrost sediment with high organic carbon (~2% by mass) and ice (50-90% by volume)
971 contents (Zimov et al., 2006). When yedoma thaws and ground ice melts, deep thermokarst lakes
972 with high CH₄ production potentials form (Zimov et al., 1997; Kanevskiy et al., 2011; Walter
973 Anthony and Anthony, 2013). Because these deep (>2m) lakes are often humic and underlain by a
974 talik, they are stratified for most of the year and are likely to have an anoxic hypolimnion
975 controlling GHG producers and consumers. These systems present large GHG seepage ebullition
976 throughout the year, with a characteristic seasonal pattern in GHG evasion (Walter et al., 2006;
977 Sepulveda-Jáuregui et al., 2015). Smaller but very turbid thermokarst lakes studied in the Eastern
978 coast of Hudson Bay also do not freeze to the bottom and can similarly be highly stratified and
979 anoxic (Laurion et al., 2010; Deshpande et al., 2015).

980 Some non-yedoma permafrost soils can also have high organic carbon and excess ice
981 concentrations within several meters of the ground surface; however, these organic- and ice-rich
982 permafrost horizons are typically thinner than yedoma deposits (Ping et al., 2008; Tarnocai et al.,
983 2009; Bouchard et al., 2015). As a result, thermokarst lakes formed in non-yedoma permafrost soils
984 are commonly shallower than yedoma lakes and have been shown to emit less CH₄ (West and Plug,
985 2008; Grosse et al., 2013; Walter Anthony and Anthony, 2013). For instance, CH₄ emissions from
986 thermokarst lakes formed in carbon-rich yedoma permafrost were 6-fold higher than emissions
987 from other lake types across Alaska (Sepulveda-Jáuregui et al., 2015).

988 Shallow thermokarst lakes (e.g., Yukon, Turner et al., 2014) may allow colonization by plants and
989 benthic photosynthesizing mats, creating CO₂ sink periods while they remain CH₄ emitters
990 (Mackenzie delta, Tank et al., 2009; Eastern Canadian High Arctic, Laurion et al., 2010; Negandhi et
991 al, 2014). These lakes can freeze to the bottom (no talik, depending on latitude), which limits active
992 GHG production to the unfrozen period of the year. In these shallow lakes there is less opportunity
993 for the dissolution of ebullitive CH₄ before it escapes to the atmosphere, and thus for its
994 consumption by methanotrophic bacteria. Furthermore, large and shallow lakes are generally
995 polymictic with GHG evasion largely influenced by winds, generating oxic conditions. For very small
996 water bodies (a few m²) such as ice-wedge trough ponds, microtopography will be the main
997 regulator of thermal structure, and gas exchange will be most affected by heat flux. Even though
998 trough ponds are very shallow systems (<1 m), they can be highly stratified with only occasional
999 mixing events during the summer (Bouchard et al., 2015), resulting in large periods of hypoxic to
1000 anoxic bottom waters, and evasion of GHG stored in bottom waters following changes in
1001 meteorological conditions. Depending on their erosional features these ponds can also be colonized
1002 by aquatic plants associated with efficient methanotrophic communities (e.g., Siberia, Liebner et al.,
1003 2011).

1004
1005 Finally, the evolution of thermokarst lake landscapes is a critical determinant of the overall carbon
1006 balance of these systems (van Huissteden et al., 2011; Walter Anthony et al., 2014). This landscape
1007 evolution can be observable at timescales on the order of 30-40 years (Smith et al., 2005; Bryksina
1008 et al., 2011; Polishuk et al., 2012) and is characterized by cyclical flooding of vegetated soils and
1009 recolonization of drained lake bottoms, and an evolution from strong CH₄ emission during the
1010 initial phase of lake formation, through a phase of carbon accumulation associated with higher
1011 within-lake primary production and the creation of terrestrial wetlands as lakes drain (Ovenden,
1012 1986; van Huissteden et al., 2011; Walter Anthony et al., 2014).

1013

1014 **4. Consequences**

1015 **4.1 Release of old permafrost OC into aquatic systems and the atmosphere**

1016 **4.1.1 Release of old permafrost OC into aquatic systems**

1017 A recent study of Eurasian Arctic river basins by Feng et al. (2013) concluded that climate change-
1018 induced mobilization of old permafrost OC is well underway in the Arctic. In this section we review
1019 the evidence that currently exists for the release of old permafrost OC into aquatic systems.

1020 Mobilization of old permafrost OC to surface waters could occur in the form of DOC, POC or gaseous
1021 C (CO₂ or CH₄). Release of old C can be measured with radiocarbon isotopes, either on bulk OC or on
1022 compound specific biomarkers. Since permafrost and Yedoma deposits contain organic C with ages
1023 of >30,000 yr BP (e.g. Zimov et al., 2006), radiocarbon could be an excellent marker to detect
1024 change in Arctic aquatic environments.

1025 Research that includes bulk radiocarbon measurements in rivers has largely focused on DOC and
1026 POC. Generally, DOC in larger river systems tends to be young. In large Arctic rivers, Amon et al.
1027 (2012) and Guo et al. (2007) measured ¹⁴C-DOC values ranging from 83 to 113% modern (1,440 to
1028 modern yr BP). Within large Arctic river basins there is significant spatial variability in riverine ¹⁴C-
1029 DOC values, reflecting dominant water and carbon source materials (Alaska, Aiken et al., 2014;
1030 O'Donnell et al., 2014). Export of contemporary DOC in rivers dominates the spring freshet, a time
1031 of year when the majority of water and DOC export occurs. In the Ob', Yenisey, Lena, Mackenzie, and
1032 Yukon rivers, Raymond et al. (2007) estimated that ~90% of DOC exported at this time was less
1033 than 20 years old. Later in the summer, DOC showed slight aging (675 yr BP, NE Siberia, Neff et al.,
1034 2006) which is likely related to OC input from deeper active layer thaw. Winter flow is most ¹⁴C-
1035 depleted, although there can be significant variation within a large river basin even in winter.
1036 O'Donnell et al. (2014) measured winter radiocarbon ages ranging from 35 to 445 yr BP, likely
1037 related to regional groundwater travel times.

1038 Whilst major Arctic rivers mostly seem to export large amounts of young semi-labile DOC, there are
1039 also examples of mobilization of old DOC, particularly within smaller systems. In the Sagavanirktok
1040 River, draining north Alaskan tundra, DOC age was 2,170-4,950 yr BP (Guo et al., 2007). Soil organic
1041 matter in the river basin was of similar age, and likely released old DOC from the active layer and
1042 through soil cryoturbation. The oldest DOC ever dated in surface waters is from small (first-order)

1043 sediment-rich thaw streams draining directly into the Kolyma River, Siberia (Vonk et al., 2013;
1044 Spencer et al., 2015). This Pleistocene-aged (>21,000 yr BP) DOC is being mobilized from old
1045 Yedoma deposits (aged up to 45,000 yr BP) into small DOC-rich streams. This old DOC also shows
1046 very high biodegradation potential (Vonk et al., 2013; Spencer et al., 2015; section 3.1), indicating
1047 that it may be degraded to CO₂ well before reaching the mouth of larger river systems (Kolyma
1048 River, Mann et al., 2015). Deep groundwater can also be a source of ancient DOC in large river
1049 systems (Yukon River, Aiken et al., 2014).

1050 There is abundant evidence of mobilization of old POC into Arctic lakes (e.g., Canada, Abbott and
1051 Stafford, 1996), rivers, and estuarine sediments associated with permafrost thaw, bank erosion,
1052 and transport of organic C. For example, Guo et al. (2007) reported ¹⁴C ages of sediment and
1053 suspended POC in large North-American Arctic rivers of 4430-7970 yr BP and concluded that POC
1054 release and age would increase in Arctic river systems subject to global warming. Additionally,
1055 there has been some work in smaller coastal watersheds in the Canadian High Arctic by Lamoureux
1056 and Lafrenière (2014) who concluded that recent permafrost disturbance delivered old (up to 6740
1057 yr BP) POC to the aquatic system. Yedoma-derived Pleistocene aged POC has also been identified in
1058 sediments from the Colville River Delta, which drains into the west Beaufort Sea (Schreiner et al.,
1059 2014; 10,000-16,000 yr BP), and in thaw streams draining Yedoma deposits, Siberia (Vonk et al.,
1060 2013; 19,000-38,000 yr BP). One caveat to studies in coastal or estuarine settings is that marine
1061 sediments and microfossils could potentially influence the ¹⁴C age of particulate material.

1062 Contrary to bulk measurements, compound-specific biomarkers can provide more source-specific
1063 information, and avoid many of the issues related to ¹⁴C dating of bulk OC. Spencer et al. (2008)
1064 found elevated lignin C-normalized yields during the spring freshet across the Yukon River basin,
1065 identifying surface vegetation as strong DOC sources. Amon et al. (2012) similarly found that
1066 biomarker abundance changed in six of the largest Arctic rivers according to season, with high
1067 concentrations of lignin phenols in the spring freshet (indicative of fresh vegetation) and elevated
1068 levels of p-hydroxybenzenes during the low flow season (indicative of moss and peat-derived OM).
1069 Concentration differences in source-tracing organic molecules, namely ¹⁴C-young, vascular plant-
1070 derived lignin phenols and ¹⁴C-old permafrost-derived waxy lipids, were found to show a
1071 relationship between ¹⁴C age and permafrost coverage (Feng et al., 2013). Drainage basins
1072 associated with increasing amounts of discontinuous permafrost were characterized by older OC,
1073 released from deeper conduits in the watershed. Likewise Gustafsson et al. (2011) found that the
1074 average age of *n*-alkanes in estuarine sediments increased (1140 to 6400 yr BP) from east to west
1075 across the Siberian Arctic, consistent with warmer climatic conditions and more discontinuous
1076 permafrost towards the west. Additional biomarkers such as membrane lipids (ex. glycerol dialkyl
1077 glycerol tetraethers, GDGTs; bacteriohopanepolyols, BHPs; and intact polar membrane lipids, IPLs)
1078 may have the potential to trace terrigenous OC stored in permafrost and remobilized along Arctic
1079 land-river-ocean transects (Rethemeyer et al., 2010; Doğrul Selver et al., 2012, 2015).

1080 **4.1.2 Release of old permafrost OC as greenhouse gases**

1081 The consequence of permafrost thaw beneath and adjacent to thermokarst lakes, wetlands, and
1082 streams is the potential mobilization and return of old carbon to the atmosphere. Schaefer et al.
1083 (2014) defined the permafrost carbon feedback as amplification of anthropogenic warming due to

1084 carbon emissions from thawing permafrost. Direct evidence for carbon emissions from thawing
1085 permafrost is found in the radiocarbon ages and deuterium values of CH₄ in bubbles and in spatial
1086 patterns of CH₄ emissions in thermokarst lakes. Zimov et al. (1997) first revealed that
1087 methanogenesis in deep, cold thaw bulbs where Pleistocene-aged yedoma is thawing beneath lakes
1088 in Siberia leads to the release of Pleistocene-aged CH₄. The release of permafrost-derived carbon to
1089 the atmosphere in ¹⁴C-depleted CH₄-rich bubbles contributes to climate warming, which in turn
1090 causes permafrost to thaw and more CH₄ to be produced in a positive feedback cycle (Walter et al.,
1091 2006). Field observations and modelling showed that permafrost-derived CH₄ emissions were
1092 highest along thermokarst margins in Siberian and Alaskan lakes, in younger stages of lake
1093 development where permafrost thaw is most active, and in small early-stage permafrost thaw
1094 depressions (Walter et al., 2006, 2007; Desyatkin et al., 2009; Kessler et al., 2012; Shirokova et al.,
1095 2013). This potential for permafrost thaw to augment climate change was affirmed in Alaskan
1096 thermokarst lakes by independent evidence from deuterium. Walter et al. (2008) and Brosius et al.
1097 (2012) found that δD values of ebullition CH₄ in yedoma-type lakes in Alaska and Siberia reflected
1098 CH₄ formation from Pleistocene-origin melt water, which has a highly negative isotopic signature.
1099 In contrast, bubbles emitted from the centres of older yedoma lakes where permafrost is no longer
1100 thawing (Alaska, Kessler et al., 2012), and from non-yedoma lakes, contained higher δD-CH₄ values
1101 and younger ¹⁴C-CH₄ ages, pointing to Holocene-aged meteoric water and carbon as the substrates
1102 for methanogenesis (Alaska, Brosius et al., 2012). On the other hand, recent work on an eastern
1103 Canadian thermokarst lake (Holocene deposits) shows a different trend, where ebullition CH₄
1104 emitted from the lakeshore was younger (~1550 yr BP) and had a more negative δD-CH₄ than from
1105 the lake centre (~3250 yr BP; Bouchard et al., 2015). Most interestingly, smaller thermokarst ponds
1106 at the same site emitted modern CH₄ even though they are exposed to peat slumping and erosion
1107 down at least to the active layer (base of active layer ~2,200 to 2,500 yr BP) with δD-CH₄ reaching
1108 down to -448 ‰ (Bouchard et al., 2015).

1109 It is important to note that the present-day effect of thermokarst lake evolution on climate warming
1110 is likely smaller than it was in the early Holocene when thermokarst lakes first formed on the
1111 permafrost landscape (Walter et al., 2007; Brosius et al., 2012). Walter Anthony et al. (2014)
1112 estimated rates of carbon loss from yedoma-type lakes (in North Siberia, Alaska and northwest
1113 Canada) to the atmosphere from 20 ky ago to the present. Their results indicate widespread lake
1114 formation between 14-9 ky ago, generating a major northern source of ¹⁴C-depleted atmospheric
1115 CH₄ during deglaciation. The subsequent slow-down of first-generation thermokarst-lake formation
1116 throughout the Holocene combined with the acceleration of other negative effects on global climate
1117 (e.g. carbon sequestration by lakes, see next section) results in lower present-day CH₄ emissions, a
1118 smaller permafrost carbon climatic effect, and a net negative radiative forcing of carbon exchange
1119 between lakes and the atmosphere on climate.

1120 **4.2 Carbon burial**

1121 **4.2.1 Carbon burial in Arctic aquatic ecosystems**

1122 Inland waters receive large quantities of organic matter from their watersheds, but, globally, less
1123 than half of this carbon reaches the ocean (Battin et al., 2009). The loss en route is attributed to (i)

1124 mineralization to CO₂ and CH₄ (see section 3), and (ii) and sequestration into sediments of lakes
1125 and reservoirs (Cole et al., 2007). Sediment sequestration of carbon can be substantial in relatively
1126 lake-rich boreal and Arctic landscapes (Lehner and Döll, 2004; Fig. 1), but still receives little
1127 attention.

1128 Generally, total carbon mineralization rates exceed carbon burial (Battin et al., 2009; Tranvik et al.,
1129 2009), but there are some exceptions, for example in the case of deep thermokarst lakes (see sec.
1130 4.2.2). Lake shape is a key regulator of carbon burial; small and deep lakes (boreal Finland,
1131 Kortelainen et al., 2004; northern Québec, Ferland et al., 2012) bury carbon more efficiently than
1132 large and shallow lakes. This is explained by a higher benthic metabolic capacity to process
1133 incoming carbon and greater particle resuspension in large, shallow, and thus well-mixed lakes.
1134 Prior to burial, degradation occurs in the water column and the uppermost sediment layers. This
1135 can be substantial with, for example, averages up to 75% of the OC mineralized over the first few
1136 decades following sediment deposition in boreal lakes in Québec (Ferland et al., 2014). Long-term
1137 (century-scale to full Holocene) accumulation rates in sediments of Arctic and boreal non-
1138 thermokarst lakes ranged between 0.2 and 13 g C/m²/yr across sites in Greenland, boreal Québec,
1139 and boreal Finland (Anderson et al., 2009b; Ferland et al., 2014; Kortelainen et al., 2004; Sobek et
1140 al., 2014). Thermokarst lakes in yedoma regions, however, show much larger long-term sediment
1141 accumulation rates (47±10 g C/m²/yr; Walter Anthony et al., 2014; see section 4.2.2).

1142 Similarly, coastal shelf regions bordering yedoma-rich Eastern Siberia receive rather large amounts
1143 of carbon with accumulation rates of 36±17 g C/m² annually (Vonk et al., 2012b). Long-term
1144 (Holocene) carbon accumulation rates in this region, however, vary between 0.1 and 2.7 g C/m²/yr
1145 (Stein and Fahl, 2000; Bauch et al., 2001) suggesting significant decomposition in the sediments
1146 after deposition and/or increases in recent accumulation rates. Furthermore, recent studies in this
1147 region suggest that permafrost-derived carbon is preferentially buried, when compared with
1148 marine or modern terrestrial carbon (Siberian shelf, Vonk et al., 2014). This appears to contrast
1149 with high initial biodegradability of (yedoma) permafrost DOC upon aquatic release (see section
1150 3.1). We hypothesize that this apparent contrast can be explained by the parallel thaw-release of
1151 different pools of organic matter in permafrost (Vonk et al., 2010; Karlsson et al., 2011). On the one
1152 hand, DOC and buoyant, non-mineral bound POC are released that are highly sensitive to
1153 biodegradation (e.g. NE Siberia, Vonk et al., 2013; Alaska, Abbott et al., 2014) leading to rapid
1154 removal in aquatic systems (Spencer et al., 2015), whereas mineral-bound, ballasted POC is
1155 resistant to degradation and preferentially transported to (and buried in) coastal shelf sediments
1156 (Karlsson et al., 2011; Vonk et al., 2011).

1157 **4.2.2 Carbon burial in yedoma thermokarst lakes**

1158 Since the last deglaciation (the past 14.7 ky), about 70% of all yedoma deposits has thawed through
1159 the formation of thermokarst lakes and streams (Strauss et al., 2013). This has released GHG to the
1160 atmosphere and OC to lake basin sediments and downstream export. Formation of thermokarst
1161 systems, however, has also caused atmospheric CO₂ to be absorbed through contemporary plant
1162 photosynthesis, senescence, and burial. While initial thermokarst basin formation caused
1163 significant efflux of CO₂ and CH₄ as these basins evolved, nutrient-rich sediments facilitated
1164 terrestrial and aquatic plant proliferation, leading to sequestration of OC in sediments of drained

1165 lake basins during the Holocene. The long-term organic carbon accumulation rate in deep, yedoma
1166 thermokarst lakes was found to be on average five times higher than in other northern lakes
1167 throughout the Holocene (Walter Anthony et al., 2014). The anomalously high carbon sequestration
1168 in yedoma thermokarst lakes was attributed to (a) thermokarst-related shore erosion and
1169 deposition of terrestrial organic matter in lake bottoms; (b) high aquatic productivity enhanced by
1170 nutrient supply from thawing yedoma; and (c) unique preservation conditions in deep thermokarst
1171 lakes.

1172 Since GHG emissions and carbon sequestration have counteractive effects on climate (warming vs.
1173 cooling, respectively), the radiative impacts of both processes must be upscaled to understand their
1174 overall impact over long time scales. Walter Anthony et al. (2014) developed trajectories of
1175 thermokarst-basin carbon flux (for yedoma landscapes) from the last major glaciation to present,
1176 based on estimates of contemporary CH₄ flux, total yedoma carbon lost as CO₂ and CH₄, total
1177 accumulated carbon, and thermokarst-lake initiation dates. Model results indicated that yedoma
1178 thermokarst lakes caused a net climate warming at the peak of their formation during deglaciation,
1179 driven primarily by CH₄ release from thawed, decaying yedoma. However, high carbon
1180 accumulation in existing basins and a slowdown of lake formation caused thermokarst lake impact
1181 on climate to switch from net warming to net cooling around 5 ky ago, such that these basins are
1182 now net GHG sinks. Notably, similar trajectories to describe the climatic effects of non-yedoma
1183 thermokarst lakes and ponds have not yet been extensively investigated, despite the fact that non-
1184 yedoma permafrost stores 75% of the global carbon permafrost pool (Zimov et al., 2006; Schuur et
1185 al., 2015).

1186 **4.3 Ecosystem structure and function**

1187 While there is a growing body of literature quantifying the nature, timing, and extent of permafrost
1188 thaw in the Arctic, there is considerably less literature on the direct effects of permafrost thaw on
1189 the structure and function of aquatic ecosystems, especially streams. The likelihood that permafrost
1190 thaw will substantially affect major ecological functions (e.g., photosynthesis, respiration, nutrient
1191 uptake) or food web characteristics (e.g., benthic algal biomass, macroinvertebrate community
1192 structure) is dependent on several factors, most notably the intensity, spatial extent, temporal
1193 duration, and hydrological connectivity of the disturbance associated with permafrost thaw. Here,
1194 we provide an overarching review of the potential effects of permafrost thaw on aquatic ecosystem
1195 structure and function.

1196 **4.3.1 Lakes**

1197 Arctic regions contain numerous lakes with large differences in abiotic and biotic conditions
1198 (Hamilton et al., 2001; Rautio et al., 2011), suggesting that the consequences of permafrost thaw on
1199 ecosystem function are likely to vary across systems. Thawing permafrost and associated changes
1200 in export of nutrients and DOM is expected to have pronounced effects on the productivity and food
1201 web dynamics of recipient lake ecosystems. Input of nutrients per se will increase primary
1202 production (mainly via effects on pelagic algae) (e.g., Alaska, Levine and Whalen, 2001 and O'Brien
1203 et al., 2005), yet input of sediments and DOM will decrease primary production if it leads to
1204 suboptimal conditions for photosynthesis, mainly affecting benthic algae but also planktonic algae

1205 when lakes are very turbid (northern Sweden, Ask et al., 2009; northern Québec, Roiha et al., 2015).
1206 In regions where thaw increases *both* nutrients and DOM we may expect stimulation of total
1207 primary production in clear and shallow lakes but suppression of primary production in more
1208 coloured or deeper lakes (Sweden and Alaska, Seekell et al., 2015). In regions where retrogressive
1209 thaw slumping delivers mineral-rich sediments to lakes (Mackenzie delta region, Thompson et al.,
1210 2008 and Mesquita et al., 2010), permafrost degradation has led to significantly greater dissolved
1211 ion content, lower DOC concentrations following mineral adsorption, and increased water
1212 transparency. This has led to enhanced macrophyte development and higher abundance of benthic
1213 macroinvertebrates (Mackenzie delta region, Mesquita et al., 2010 and Moquin et al., 2014) and
1214 higher abundance and diversity of periphytic diatoms (Canadian Arctic, Thienpont et al., 2013).
1215 Further, DOM released following thaw is relatively labile and could support bacterial metabolism
1216 (northern Sweden, Roehm et al., 2009; NE Siberia, Vonk et al., 2013), resulting in increasing rates of
1217 bacterial respiration and production relative to primary production (northern Québec Breton et al.,
1218 2009 and Roiha et al., 2015; sub-Arctic Sweden, Karlsson et al., 2010;).

1219 These changes at the base of the food web are expected to result in a shift in the relative importance
1220 of different OC resources supporting higher consumers, by decreasing the importance of benthic
1221 algae and increasing the reliance on pelagic and terrestrial resources with increasing DOM.
1222 Heterotrophic bacteria transfer DOM to mixotrophic algae and heterotrophic protozoans, to
1223 zooplankton and zoobenthos feeding on bacteria, and via predation to higher trophic levels
1224 (Jansson et al., 2007). Another consequence of thaw and increased DOM export is an increasing
1225 degree of net heterotrophy, i.e., a decrease in the ratio between gross primary production and
1226 community respiration (northern Sweden, Ask et al., 2012). Heterotrophic bacteria benefit from
1227 fresh and high carbon inputs from the catchment and the high nutrient concentrations below the
1228 thermocline (northern Québec, Breton et al., 2009, Roiha et al., 2015). Respiration rates can be very
1229 high in thermokarst lakes, favouring rapid oxygen depletion and prolonged anoxia (also northern
1230 Québec, Deshpande et al., 2015). This has implications for GHG production and exchange with the
1231 atmosphere (see section 3.5). Oxygen depletion following permafrost thaw may also affect the
1232 resource supply and abundance of higher consumer populations. CH₄-oxidizing bacteria, relatively
1233 abundant in many stratified thermokarst lakes (northern Québec, Crevecoeur et al., 2015), may
1234 play an important role in the carbon transfer through the food web. These bacteria are known to
1235 occur in environments where both oxygen and CH₄ are available, and they have been suggested to
1236 contribute to the zooplankton diet (Jones, 2000; northern Finland, Kankaala et al., 2006).
1237 Permafrost thaw may stimulate this C pathway but it is not clear if this could override the likely
1238 negative effect on higher consumers by oxygen depletion (Craig et al., 2015; Karlsson et al., 2015)

1239 **4.3.2 Streams**

1240 In section 2.2 we describe how permafrost thaw is likely to affect the delivery of sediment and
1241 nutrients to aquatic ecosystems. Sediment and nutrient concentrations are two of the fundamental
1242 factors that influence the structure and function of streams. However, as in lakes, there is a trade-
1243 off between the negative effects (smothering, shading, and scouring) caused by elevated levels of
1244 sediment loading versus the positive effects (fertilization) caused by elevated concentrations of
1245 soluble nutrients. Locally, and over the years-to-decades timescale of TEF disturbance, if these

1246 features intersect a stream they are likely to have significant impacts caused by massive inputs of
1247 sediment. While in some systems, TEFs have impacts that can be seen over broad catchment scales
1248 (e.g., NW Canada, Kokelj et al., 2013), in others, the long-term and regionally-averaged effect of
1249 TEFs on suspended sediments may be relatively small (see section 2.2). At the same time, ongoing
1250 active layer deepening (and long-term, deep impacts from older TEFs) may add low levels of
1251 nutrients to Arctic streams over longer time scales. Currently there is very little literature to
1252 support these potential impacts.

1253 Even subtle increases in the loading of limiting nutrients can have profound impacts on highly-
1254 oligotrophic, Arctic stream ecosystems. A whole-ecosystem nutrient fertilization experiment on the
1255 Kuparuk River has shown that long-term (30 year), low-level increases in soluble reactive
1256 phosphorus alone can have important influences on benthic autotrophic and macroinvertebrate
1257 community structure and can significantly increase primary and secondary production (Peterson et
1258 al., 1985; Bowden et al., 1994; Cappelletti, 2006). On the other hand, sediment loading may offset
1259 the stimulatory effects of introduced nutrients and interfere with benthic stream structure and
1260 function. Adverse effects of sediment influx to streams include damage to primary producers,
1261 especially from scour during storms, which can reduce primary production and ecosystem
1262 respiration. Increased sediment loading may clog the interstices among streambed particles, which
1263 could reduce the connectivity between the hyporheic zone and surface waters, interfering with
1264 exchange of nutrients and dissolved oxygen (Kasahara and Hill, 2006). Sediment loading may also
1265 lead to instability on the stream bottom, affecting the ability of benthic macroinvertebrates to
1266 establish and feed (Uehlinger and Naegeli, 1998).

1267 Recent studies have evaluated the higher order effects of sediment and nutrient loading from
1268 thermokarst and detected significant impacts on some aspects of the biological function of receiving
1269 waters. Daily rates of riverine production and respiration decreased by 63% and 68%, respectively,
1270 in the Selawik River in northwest Alaska in response to elevated turbidity levels that increased by
1271 several orders of magnitude below a massive thaw slump (Calhoun, 2012). Larouche et al.
1272 (submitted) studied biogeochemical characteristics of a tundra stream on the North Slope, Alaska
1273 over a period of three summer seasons (2009-2011) after a gully thermokarst feature impacted this
1274 stream several years earlier (2005). They found that 4-6 years after the initial disturbance the TEF
1275 still caused modest increases in the loading of sediment and dissolved solutes. Furthermore, rates
1276 of ecosystem production and respiration and benthic chlorophyll-a in the impacted reach of this
1277 stream, were significantly lower during the driest of the three summers. Rates of ammonium and
1278 soluble reactive phosphorus uptake were consistently lower in the impacted reach.

1279 Benthic macroinvertebrates are typically the dominant vector of energy flow in stream ecosystems,
1280 connecting primary production to higher trophic levels (e.g., Hynes, 1970; Merritt et al., 2008).
1281 Species diversity of macroinvertebrate communities has been shown to be sensitive to minor
1282 disturbances in running waters (Lake, 2000) while allochthonous sediment has been shown to
1283 significantly impact habitat composition, leading to profound effects on the distribution of
1284 individual organisms (Alaska, Parker and Huryn, 2006). As discussed above, lakes affected by thaw
1285 slumps in the Canadian Arctic (Mackenzie delta region) have been shown to have significantly
1286 greater dissolved ion content, lower DOC concentrations and increased water transparency

1287 (Thompson et al., 2008), that have in-turn led to enhanced macrophyte development and higher
1288 abundance of benthic macroinvertebrates (Mesquita et al., 2010; Moquin et al., 2014) and higher
1289 abundance and diversity of periphytic diatoms (Thienpont et al., 2013). We are not aware of any
1290 published studies that document impacts of thermo-erosional events on the benthic community
1291 structure of Arctic stream ecosystems. In the study conducted by Larouche et al. (submitted) initial
1292 macroinvertebrate richness and diversity in Alaska was low but increased late in the season
1293 (August). Overall, the shifts in stream community structure were subtle.

1294 It appears that Arctic headwater streams may be resilient and regain considerable functionality as
1295 local disturbance features begin to repair, particularly in the case of smaller features such as gully
1296 thermokarst disturbance that experience stabilization by re-vegetation (Jorgenson et al., 2006).
1297 While the acute impacts of slumping are obvious and notable, it is the chronic impacts of long-term,
1298 elevated nutrient and sediment loading that are of greater interest. There is growing evidence that
1299 subtle differences in sediment and nutrient delivery to Arctic headwater streams can still be
1300 apparent many years after disturbance, and that thermokarst slumping may significantly affect
1301 primary producer biomass, benthic organic nutrients, benthic invertebrate community structure
1302 and key ecosystem functions such as whole-stream metabolism and nutrient update. Averaged over
1303 thaw-impacted landscapes as a whole, these effects may often be subtle (e.g., Alaska, Larouche et al.,
1304 submitted). However, it is less clear how long-term nutrient and sediment loading will change in
1305 thaw-impacted stream systems (Frey and McClelland, 2009; Lewis et al., 2012; Lafrenière and
1306 Lamoureux, 2013; Malone et al., 2013).

1307 **4.4. Export to ocean**

1308 Permafrost degradation can lead to clear changes in the biogeochemical flux of constituents from
1309 land to water (see section 2.2). Beyond the immediate site of impact, however, this constituent flux
1310 can be expected to have effects that range well into downstream environments. In many cases,
1311 changes on land can have clear impacts on coastal ocean processes, as has been shown within the
1312 estuarine zones of many large, southern rivers (Bianchi and Allison, 2009). In permafrost-impacted
1313 systems, understanding how changes in constituent flux at the terrestrial-aquatic interface will
1314 translate to changing export to the Arctic Ocean is still a challenging task. In this section, we
1315 describe the potential effects of permafrost thaw on land to ocean constituent flux, highlighting
1316 some major knowledge gaps in our current understanding of this process.

1317 Scaling changes that are being observed at the small catchment scale to changes in ocean-bound
1318 transport requires an understanding of the rates of deposition, uptake, and decomposition of
1319 various thaw-released constituents, both in absolute terms and relative to their non-permafrost
1320 derived counterparts. These rates will vary considerably among constituent types. For example,
1321 nutrients released as a result of permafrost thaw may be taken up rapidly following release to
1322 aquatic environments (Alaska, Bowden et al., 2008), while major ions released following the
1323 exposure of mineral soils are largely conservative, and can be detected far downstream (NW
1324 Canada, Kokelj et al., 2013 and Malone et al., 2013). Similarly, in some regions, sediment pulses
1325 associated with thermokarst disturbances decline markedly with movement downstream (Alaska,
1326 Bowden et al., 2008), while in others, thaw-associated sediment signatures are elevated across
1327 broad, catchment-wide scales (NW Canada, Kokelj et al., 2013). The signature of permafrost thaw-

1328 origin sediments and particulate organics has also been detected at the mouths of several large,
1329 Arctic rivers (Guo et al., 2007; Gustafsson et al., 2011), and in increasing concentrations in some
1330 Arctic coastal sediments (Feng et al., 2013).

1331 Where direct observational evidence does exist to indicate changing biogeochemical flux at the
1332 mouths of Arctic rivers, it appears that some constituents are changing relatively synchronously
1333 across Arctic regions, while others may show significant regional differences in their trends. For
1334 example, flow-weighted bicarbonate fluxes appear to be increasing modestly in some Arctic
1335 regions, such as at the mouth of the Yukon River (Striegl et al., 2005). This trend is further
1336 corroborated by studies examining variation in riverine bicarbonate flux across Arctic watersheds
1337 with differing permafrost coverage (Tank et al., 2012a; Tank et al., 2012c; Pokrovsky et al., 2015).
1338 In contrast, the downstream transport of DOC to coastal areas appears to be increasing in some, but
1339 decreasing in other, regions, based both on direct river-mouth measurements over time and sub-
1340 watershed comparisons across permafrost gradients (Kawahigashi et al., 2004; Striegl et al., 2005;
1341 Tank et al., 2012a). Furthermore, DOC originating in old permafrost may be preferentially degraded
1342 within stream networks, and thus may not be detectable at the river mouth (Yedoma-rich eastern
1343 Siberia; Spencer et al., 2015). It therefore remains difficult to attribute the few documented changes
1344 at the mouths of Arctic rivers to either up-catchment permafrost degradation or, for example, to the
1345 more widespread effects of changing temperature and precipitation patterns. For example, fluxes of
1346 DOC will be affected by changes in the composition and overall production and decomposition of
1347 vegetation (e.g., across northern regions, Laudon et al., 2012), in addition to the exposure of organic
1348 soils via permafrost thaw. Similarly, fluxes of bicarbonate will be affected not only by the thaw-
1349 mediated exposure of deeper mineral soils, but also by increases in root respiration that affect
1350 weathering rates (Beaulieu et al., 2012). For many constituents, changes in the seasonality of
1351 precipitation may also affect constituent flux and concentration (northern Canada, Spence et al.,
1352 2011). Research to explore how permafrost thaw affects aquatic biogeochemistry across nested
1353 spatial scales, and to further elucidate the mechanisms of changing chemistry at scales where
1354 direct, mechanistic, observations are possible, will greatly aid our ability to understand how up-
1355 catchment permafrost degradation affects biogeochemical flux to the coastal ocean.

1356 The effect of changing riverine fluxes on coastal ocean processes cannot be considered without also
1357 considering thaw-induced changes in coastal erosion. Rates of coastal erosion vary by region, in
1358 part because of regional differences in ground ice content and bluff height (Lantuit et al., 2013).
1359 Overall, however, the impact of coastal erosion on biogeochemical flux to the ocean appears to be
1360 significant. Estimates of carbon release by coastal erosion vary significantly, and range between 5-
1361 14 Tg OC/year for the entire Arctic combined (Rachold et al., 2004; Jorgenson and Brown, 2005;
1362 Vasiliev et al., 2005; Couture, 2010; Vonk et al., 2012b) with highest delivery rates in the Laptev and
1363 East Siberian Seas (Vonk et al., 2012b). This value is nearly a third of the combined, circum-Arctic,
1364 estimated delivery of DOC (34 Tg; Holmes et al., 2012) and POC (6 Tg; McGuire et al., 2009) via
1365 rivers each year. Rates of coastal erosion, however, appear to be increasing both in the Russian and
1366 the Alaskan Arctic (Jones et al., 2009; Günther et al., 2013) which is due to decreasing sea ice
1367 content, allowing for higher storm intensity and wave fetch, along with increasing summertime sea
1368 surface temperature and a rising sea (IPCC, 2013).

1369 Documented changes in riverine biogeochemistry and coastal erosion rates may in turn have a
1370 significant effect on carbon and nutrient cycles in the near shore ocean. Where the delivery of DOC
1371 and POC increase, the attenuation of light will reduce photosynthetic uptake of CO₂ (NW Canada,
1372 Retamal et al., 2008). Concomitantly, increases in both bacterial production, and the
1373 decomposition of this organic matter to carbon dioxide CO₂ may occur. On the East Siberian Shelf,
1374 for example, large zones of CO₂ outgassing have been shown to occur alongside plumes of DOC that
1375 have a clear terrestrial isotopic signature (Anderson et al., 2009a). In addition, increases in light
1376 caused by sea ice retreat could also increase photochemical degradation of riverine DOM to CO₂
1377 (e.g., Tank et al., 2012b). If changing delivery of organic matter does affect coastal CO₂ saturation,
1378 this could combine with changes in bicarbonate flux to have a significant impact on nearshore
1379 aragonite saturation, compounding the effects of temperature and sea ice melt on ocean
1380 acidification in the Arctic (Steinacher et al., 2009; Yamamoto-Kawai et al., 2009). In much of the
1381 Russian Arctic, organic carbon transport from land to ocean is already high (Holmes et al., 2012;
1382 Vonk et al., 2012b) when compared to the North American Arctic, and rivers are relatively
1383 bicarbonate-poor (Tank et al., 2012c). Thus, increasing delivery of organics to coastal zones, and
1384 the resultant CO₂ production, could further reduce aragonite saturation in a region where near
1385 shore regions are already poorly buffered (Anderson et al., 2011; Tank et al., 2012c). For these, and
1386 other constituents such as nutrients, we still have much to learn about how fluxes to the coastal
1387 ocean are changing, and how this change may affect near shore biogeochemical function (Tank et
1388 al., 2012b; Le Fouest et al., 2013; Letscher et al., 2013). Understanding the effect of these changing
1389 fluxes in general, and the specific importance of permafrost thaw for changing biogeochemistry in
1390 the coastal Arctic, remains a clear priority for future research.

1391 **4.5 Broad-scale climatic effects**

1392 In addition to the numerous climate-related effects described above, thermokarst can be expected
1393 to have effects on climate that range beyond those that are directly related to aquatic processes. For
1394 example, thermokarst-enabled increases in inundated landscape area can be followed by loss of
1395 tree cover in the area surrounding thaw depressions, and a shift towards sedge-dominated fen
1396 vegetation (e.g. Jorgenson et al., 2001). The resulting change in albedo could subsequently affect
1397 regional radiative forcing, in a direction which will depend upon the manner in which vegetation
1398 changes affect snow cover (Notaro and Liu, 2007), and the relative change in cover of peat, forest,
1399 and water, because of the differences in albedo between these land cover types (e.g. Lohila et al.,
1400 2010). Additionally, energy partitioning into latent and sensible heat fluxes may be altered
1401 significantly upon thaw, as lake surfaces would be increasingly more important in certain regions,
1402 creating a distinct microclimate with high evapotranspiration and low sensible heat flux (e.g. Rouse
1403 et al., 2005). Lake energy balance varies widely with depth (e.g. Eaton et al., 2001), adding
1404 importance to the temporal changes in thermokarst lake sizes. Finally, thermokarst-enabled
1405 changes in the emission of biogenic volatile organic compounds (BVOCs) through landscape shifts
1406 could also affect regional climate, because secondary aerosols originating from BVOCs facilitate
1407 cloud formation (e.g. Ehn et al., 2014). Taken as a whole, permafrost thaw and the occurrence of
1408 thermokarst will produce diverse and contra-directional climatic effects at different landscape,
1409 regional, and global scales. An approach that considers these multiple effects is therefore needed to
1410 understand how thermokarst feeds back to regional and global climates.

1411

1412 **5. Summary, and future research needs**

1413 **5.1 Summary**

1414 Ground-ice content, topography, and soil type are the main drivers for both types of permafrost
1415 thaw (press vs. pulse) and associated release of constituents into aquatic systems: (i) When thaw is
1416 manifested as a pulse disturbance, this leads to thermokarst lakes (lowland terrain) or slumping
1417 (hillslope terrain). For both features, *the soil type of the pulsed material* generally determines the
1418 release and effect of constituents; a pulse of OC-rich soils will colour thermokarst lakes (affecting
1419 stratification etc.), will cause low transparency (high turbidity) in aquatic ecosystems after thaw,
1420 and will lead to increasing OC export. A pulse of mineral-rich soils, however, might lead to clearer
1421 thermokarst lakes and decreasing OC in the water column, due to sorption of matter to mineral
1422 surfaces. (ii) When thaw is manifested as a press disturbance, this generally leads to longer flow
1423 paths and increasing residence time in soils. Here, *the soil type of the thawed material* generally
1424 determines the release and effect of constituents; thaw of OC-rich soils will lead to higher OC export
1425 whereas thaw of mineral-rich soils will lead to lower OC export.

1426 The fate of released constituents and their effect on climate depends on the propensity of these
1427 constituents for degradation versus burial, which is determined by environmental parameters as
1428 well as intrinsic properties. Also, it is important to distinguish between thaw-mobilization of old
1429 permafrost OC versus contemporary OC, when considering the climatic effect potential. The
1430 degradability of released OC, representing the most direct carbon-climate "linkage", can be divided
1431 into a dissolved and a particulate fraction; the biodegradability of DOC is determined by source,
1432 chemical character, nutrient availability, temperature, and prior microbial and photochemical
1433 processing. Furthermore, DOC is generally more degradable when flushed from continuous
1434 permafrost regions, surface litter, active layer soils, and yedoma, but less degradable when flushed
1435 from deeper mineral soil layers. Photodegradation of DOC is relatively high in thaw-impacted
1436 systems that are shallow, rich in light-absorbing DOM, or that undergo short-term (days to weeks)
1437 stratification events. Photodegradation can however be hampered by slumping of OC-rich soils
1438 (decreasing transparency) or slumping of mineral-rich soils (adsorbing CDOM). Our understanding
1439 of degradation of POC and the factors influencing it is still remarkably poor. Burial of OC is
1440 generally lower than total OC remineralisation to CO₂ and CH₄, particularly in large and shallow
1441 lakes, but can be higher in small and deep lakes, thermokarst-yedoma lakes, and on the coastal
1442 shelf.

1443 There are few studies on the effects of permafrost degradation on the ecology and food web
1444 structure of aquatic ecosystems. Thus, we can only speculate about future ecological conditions
1445 based on our current understanding of the function of high latitude systems and the effects of
1446 permafrost degradation on the physics and chemistry of impacted systems. The impact of
1447 permafrost thaw on foodwebs and ecosystem functioning appear likely to be driven by changes in
1448 the inputs of nutrients, DOM, and sediments. Primary production is stimulated by nutrient input but
1449 can be hindered by light suppression following increasing input of CDOM or OC-rich sediments,

1450 particularly when DOM concentrations are great enough that the positive effect of increasing
1451 organic nutrients is overwhelmed by the negative effect of decreasing light penetration (Seekell et
1452 al., 2015). Benthic communities can be destabilized by high sediment loading but may thrive when
1453 slumping of mineral-rich sediment leads to increasing water clarity. Overall, food web changes may
1454 lead to shifts in (i) OC resources supporting higher consumers, and (ii) the net heterotrophy of
1455 systems. Increasing terrestrial DOM input may be transferred to zooplankton and zoobenthos via
1456 increased heterotrophic bacterial production. On the other hand, in response to elevated turbidity
1457 levels, production, and respiration may decrease.

1458 **5.2. Gaps in understanding, and future needs for research**

1459 Aquatic ecosystems are widely recognized as locations of active processing and burial of the
1460 organic matter they receive (Cole et al., 2007; Battin et al., 2009), and, lately, also receive more
1461 attention in climate-carbon interactions in the Arctic (e.g. Sobek et al., 2003; Feng et al., 2013; Vonk
1462 and Gustafsson, 2013; Olefeldt and Roulet, 2014). However, in this review we have also identified
1463 numerous gaps in our knowledge of the diverse effects of permafrost thaw on aquatic ecosystems
1464 and the consequential effects on climate. We therefore make the following recommendations for
1465 future research directions, where we make the division into general directions, directions specific
1466 to streams and rivers, directions specific to thermokarst lakes, and the use of specific techniques:

1467 **5.2.1 General future research directions**

- 1468 • Fluxes and degradation of particulate OC from thawing permafrost

1469 Permafrost thaw, particularly when manifested as a pulse disturbance, can deliver substantial POC
1470 inputs to aquatic systems by exposing and rapidly thawing deep permafrost deposits. However,
1471 studies focusing on OC fluxes from thawing permafrost have to date mostly focused on DOC.
1472 Whereas DOC from collapsing permafrost is among the most biodegradable reported in natural
1473 systems (Vonk et al., 2013a; Abbott et al., 2014; Spencer et al., 2015), the biodegradability of POC,
1474 released in far larger quantities, has never been properly assessed.

- 1475 • The relative mobilization and degradability of old versus contemporary carbon

1476 As thawing permafrost increases shoreline contact between lakewater and soils, and increases
1477 direct slumping into lake and stream systems, the carbon that is introduced to aquatic systems will
1478 be from both shallow, contemporary, soil layers and from older, permafrost soils. Although
1479 permafrost DOC derived from yedoma appears to be highly degradable (see section 3.1), there is
1480 also evidence that some thermokarst lakes emit modern carbon (see section 4.1.2). Understanding
1481 the relative susceptibility of OC pools with permafrost-origin versus contemporary-origin to bio-
1482 and photodegradation, and the relative mobilization of these two pools as a result of permafrost
1483 thaw across various regions and aquatic ecosystems, will help our ability to quantify the effect of
1484 carbon mobilization on climate across thaw-impacted systems. The priming effects generated by,
1485 for example, light and photosynthetic exudates on the consumption of old OC also needs to be
1486 further explored.

- 1487 • Influence of permafrost thaw on fluxes to coastal ocean

1488 Our understanding of the effect of changing constituent fluxes following permafrost thaw on the
1489 optical characteristics, primary production, and biogeochemistry of coastal Arctic systems is still
1490 limited and remains a clear priority for future research.

1491 • Resiliency of stream ecosystems to direct thermokarst impacts

1492 Very few studies have reported on the intensity or the duration of thermokarst impacts on the
1493 structure of biological communities or the function of key ecological processes (e.g., photosynthesis,
1494 respiration, and nutrient uptake) in Arctic streams (Calhoun, 2012; Larouche et al., submitted). It is
1495 impossible, therefore, to do more than speculate about how the ecosystem services provided by
1496 Arctic streams and rivers are changing in response to this regional impact of climate change.

1497 • Trophic structure and food web processes

1498 The effect of permafrost thaw on aquatic autotrophic and heterotrophic communities, and their
1499 interaction, remains poorly studied. For example, resource use and growth by consumers in
1500 thermokarst lakes has not been quantified to date. Long-term effects of nutrient and sediment
1501 loading in thaw-impacted stream systems are still understudied, but are vital for effects on and
1502 shifts in receiving foodwebs.

1503 • Microbial diversity and processes

1504 Microbial diversity studies have only recently begun, and there are many gaps in understanding.
1505 For example, the diversity and roles of viruses, likely the biologically most abundant particles in
1506 thaw waters, have not received attention to date. The composition of winter microbial communities
1507 in ice-covered thermokarst lakes and ponds is at present unknown, and only minimally studied in
1508 rivers (Crump et al., 2009) and the microbial processes operating under the ice have been little
1509 explored. These deserve special attention, given the long duration of ice-cover in northern lakes,
1510 and the evidence of prolonged anoxia in these waters that favour anaerobic processes such as
1511 methanogenesis. The spring period of ice melt and partial mixing, and the prolonged period of
1512 mixing in fall, may be important for gas exchange as well as key aerobic microbial processes such as
1513 methanotrophy, and these transition periods also require closer study.

1514 • Improved assessment of underwater UV irradiance

1515 To specifically understand photodegradation of both old and contemporary DOM in thaw waters
1516 (see also bullet above), we further recommend work to (i) quantify UV spectral irradiance in thaw-
1517 impacted water columns, (ii) understand the residence time of DOM in the UV-exposed portion of
1518 the water column and its variability with changing mixing regimes, and (iii) identify the factors that
1519 control vertical losses of DOM and the lability of permafrost DOM to photo-degradation.

1520 • Inclusion and prioritization in models

1521 The export of OC and other constituents from Arctic aquatic systems remains poorly represented in
1522 ecosystem, landscape, and permafrost models. Generally, linkages between permafrost thaw and
1523 changes in surface hydrology (i.e. whether the Arctic landscape becomes wetter or drier after
1524 permafrost thaw), are poorly understood (Schuur et al., 2015). In the terrestrial ecosystem model
1525 (TEM) presented in McGuire et al. (2010), a riverine DOC export component is included which
1526 stems from simulating production and export of DOC from land. However, processing within rivers
1527 is not accounted for, which would ideally be needed to couple observed DOC data to input of DOC
1528 from soils. In addition, there are many other components that are currently not included in global
1529 or landscape-scale models, such as the release of DOC from pulse disturbances, the release and
1530 transport of POC from permafrost thaw (by pulse and press disturbances), or the release and

1531 transport of OC into thermokarst systems. Non-OC constituents (nutrients, sediment) are even
1532 more poorly represented in these models. Improving aquatic constituent fluxes, processing and
1533 transport should be a key prioritization in future model development.

1534

1535 **5.2.2 Research directions specific to streams and rivers**

1536 • Watersheds of small and intermediate size

1537 Research to date has been somewhat skewed towards large rivers basins and estuaries; small
1538 watersheds and headwater streams where processes and change are easier to elucidate remain
1539 under-studied, meaning that it is often difficult to link measurements to clear source areas or
1540 processes.

1541 • Sediment erosion versus delivery to streams

1542 Streambank erosion effectively delivers 100% of eroded sediments to streams. But TEFs that form
1543 at some distance from streams may deliver far less sediment mass, C, N, and P to streams. To scale
1544 the effects of hillslope thermokarst to aquatic systems at broad spatial scales, we must better
1545 quantify how the position of various TEF features in the landscape moderates their effect on aquatic
1546 ecosystems.

1547 • Influences of hyporheic processes

1548 It is well known that the hyporheic zone (region below and alongside the stream) contributes
1549 substantially to nutrient and carbon processing in temperate and tropical streams (e.g., Boulton et
1550 al., 1998). Recent research has shown that despite the presence of permafrost, the hyporheic zone
1551 is equally important to the ecological functions of Arctic streams (e.g., Zarnetske et al., 2008).
1552 However, we do not know how thermokarst impacts will affect hyporheic processes or vice versa
1553 (Edwardson et al., 2003).

1554

1555 **5.2.3 Research directions specific to thermokarst lakes**

1556 • Thermokarst lake processes in non-yedoma systems

1557 The emission and burial of thaw-released OC in yedoma thermokarst lakes has been a relatively
1558 large focus of research attention (e.g. Walter Anthony et al., 2007; 2014; Sepulveda-Jáuregui et al.,
1559 2015), but the fate of thaw-released OC in thermokarst lakes in non-yedoma regions is still
1560 understudied. Considering that the yedoma region holds 210-456 Pg C and the total permafrost
1561 region holds 1330-1580 Pg C (Schuur et al., 2015), this makes non-yedoma regions holding 66-87%
1562 of the total permafrost C important to consider, particularly where non-yedoma regions are also
1563 lake-rich.

1564 • Physical and hydrological dynamics of thermokarst lakes

1565 Current gaps in our understanding of the physical and hydrological dynamics of thermokarst lakes
1566 include the quantification of sediment heat transfer, penetration of solar radiation through ice
1567 cover, modelling of diffusive GHG exchange in small lakes, wave and energy dynamics associated
1568 with floating ice, and the extent of groundwater flow (Kirillin et al., 2012). Furthermore, material
1569 transport caused by advective water transfer between shallow zones to bottom waters such as
1570 found in MacIntyre and Melack (1995) in other systems has not been addressed in thaw waters.

1571 • Hydrodynamic effects of high CH₄ and CO₂ concentrations

1572 Gradients in gas concentrations (particularly during ice-covered periods) can cause density
1573 differences in the water column that can modify stratification such as suggested by Deshpande et al.
1574 (2015) but these effects have been little studied to date. Also, the effects on stratification by gas
1575 bubble trains associated with ebullition from sediments (Walter et al., 2006) have received little
1576 attention.

1577 • Role of CH₄ oxidation in thermokarst systems

1578 The emission of CH₄ from aquatic ecosystems is significantly offset by microbial oxidation of CH₄
1579 (Trotsenko and Murrell, 2008). For example, in northern lakes, up to 88% of CH₄ produced in
1580 sediments is oxidized by microbes (e.g., Bastviken et al., 2008) and abundant methanotrophs have
1581 been observed in thermokarst lakes. Oxidation of CH₄ has recently been detected through
1582 laboratory incubation studies of thermokarst lakes in the boreal and tundra zones of Alaska
1583 (Martinez-Cruz et al., 2015), however, numerous questions remain to be answered with respect to
1584 (i) the extent to which CH₄ oxidation offsets whole-lake emissions in thermokarst-lake systems, (ii)
1585 which CH₄-carbon pools are subject to oxidation (contemporary vs. old carbon), (iii) microbial
1586 community dynamics, and (iv) biogeochemical and ecological controls over CH₄ oxidation among
1587 different thermokarst lake types.

1588 • Lake carbon burial

1589 Our knowledge of the relative role of burial versus processing in northern lakes remains poor.
1590 Tranvik et al. (2009) project that carbon burial in polar lakes will decrease whereas carbon burial
1591 in boreal lakes will increase. This review, however, points out that other factors such as permafrost
1592 type (yedoma vs. non-yedoma; Walter Anthony et al., 2014) or lake shape (small and deep vs. large
1593 and shallow; Ferland et al., 2012) strongly affect burial efficiencies and may overrule the distinction
1594 between boreal and polar regions. More research is needed to shed light on these processes.

1595

1596 **5.2.4 The use of specific techniques in future research**

1597 • Usage of high-resolution automated loggers in thermokarst lakes

1598 Many thermokarst lakes undergo rapidly cycling stratification events (i.e. diurnal or several day)
1599 that are hard to capture with sparse measurements. The increased use of high resolution,
1600 automated temperature and O₂ loggers is likely to yield new insights into short term (single to
1601 several day) stratification and mixing dynamics, even in those lakes currently considered to be well
1602 mixed in summer.

1603 • Remote sensing

1604 We recommend increasing usage of high-resolution satellite remote sensing to assess (i) local
1605 landscape conditions that affect thermokarst formation, (ii) the changing areal coverage of
1606 thermokarst lakes and ponds in both discontinuous and continuous permafrost regions, as well as
1607 (iii) changing DOC lake concentrations (e.g. Watanabe et al., 2011) derived from changing lake
1608 surface colour as a result of permafrost thaw.

1609 • Radiocarbon dating

1610 The Arctic aquatic system should provide an early and sensitive signal of change in the cycling of OC
1611 in the terrestrial environment. The development of new direct methods to date aquatic dissolved
1612 CO₂ (Billett et al., 2012; Garnett et al., 2012) has significantly increased our capacity to measure the
1613 source and age of CO₂ released from Arctic landscapes; these along with existing dating tools for
1614 POC, DOC, and CH₄, provide researchers with a strong methodological basis to quantify and detect

1615 the release of aged C into the aquatic environment. This will allow us to detect change or rates of
1616 change in areas of the Arctic undergoing differential rates of climate warming and address the key
1617 issue of whether “old” carbon (fixed 100s or 1000s of year BP) is being released directly or
1618 indirectly into the atmosphere.

1619 • *Eddy correlation flux measurements on thermokarst lakes*

1620 Given its general applicability for studying lake-atmosphere exchanges of carbon (e.g. Vesala et al.,
1621 2012), we recommend increasing the application of eddy covariance on thermokarst lakes. We
1622 suggest that particular attention be paid to: (i) eddy flux footprint analysis: because the flux
1623 footprint often consists of a mixture of terrestrial and aquatic fluxes (Wille et al., 2008), it is
1624 important to use an appropriate footprint model (Vesala et al., 2008) supplemented with localized
1625 flux measurements (Sachs et al., 2010; Pelletier et al., 2014). (ii) usage of recently developed, low-
1626 maintenance instrumentation, such as robust, low power, open-path and enclosed-path gas
1627 analysers for CO₂ and CH₄ (Burba et al., 2012). (iii) the development of harmonized data processing
1628 protocols, as past efforts to compile datasets from large, terrestrial eddy covariance networks, such
1629 as FLUXNET (Baldocchi et al., 2001) have shown the importance of consistent data processing
1630 protocols to ensure comparability between sites. Processing protocols should be revised for
1631 application over lakes due to significant differences in surface processes of aquatic and terrestrial
1632 ecosystems (e.g. Vesala et al., 2012). Given the wide range of thermokarst lake sizes and types, a
1633 network of several flux towers has a great potential to better understand lake-atmosphere
1634 interactions of these ecosystems.

1635

1636 **5.2.5 Inclusion and prioritization in models**

1637 The export of OC and other constituents from Arctic aquatic systems remains poorly represented in
1638 ecosystem, landscape, and permafrost models. Generally, linkages between permafrost thaw and
1639 changes in surface hydrology (i.e. whether the Arctic landscape becomes wetter or drier after
1640 permafrost thaw), are poorly understood (Schuur et al., 2015). In the terrestrial ecosystem model
1641 (TEM) presented in McGuire et al. (2010), a riverine DOC export component is included which
1642 stems from simulating production and export of DOC from land. However, processing within rivers
1643 is not accounted for, which would ideally be needed to couple observed DOC data to input of DOC
1644 from soils. In addition, there are many other components that are currently not included in global
1645 or landscape-scale models, such as the release of DOC from pulse disturbances, the release and
1646 transport of POC from permafrost thaw (by pulse and press disturbances), or the release and
1647 transport of OC into thermokarst systems. Non-OC constituents (nutrients, sediment) are even
1648 more poorly represented in these models. Improving aquatic constituent fluxes, processing and
1649 transport should be a key prioritization in future model development.

1650

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1666

1667

1668

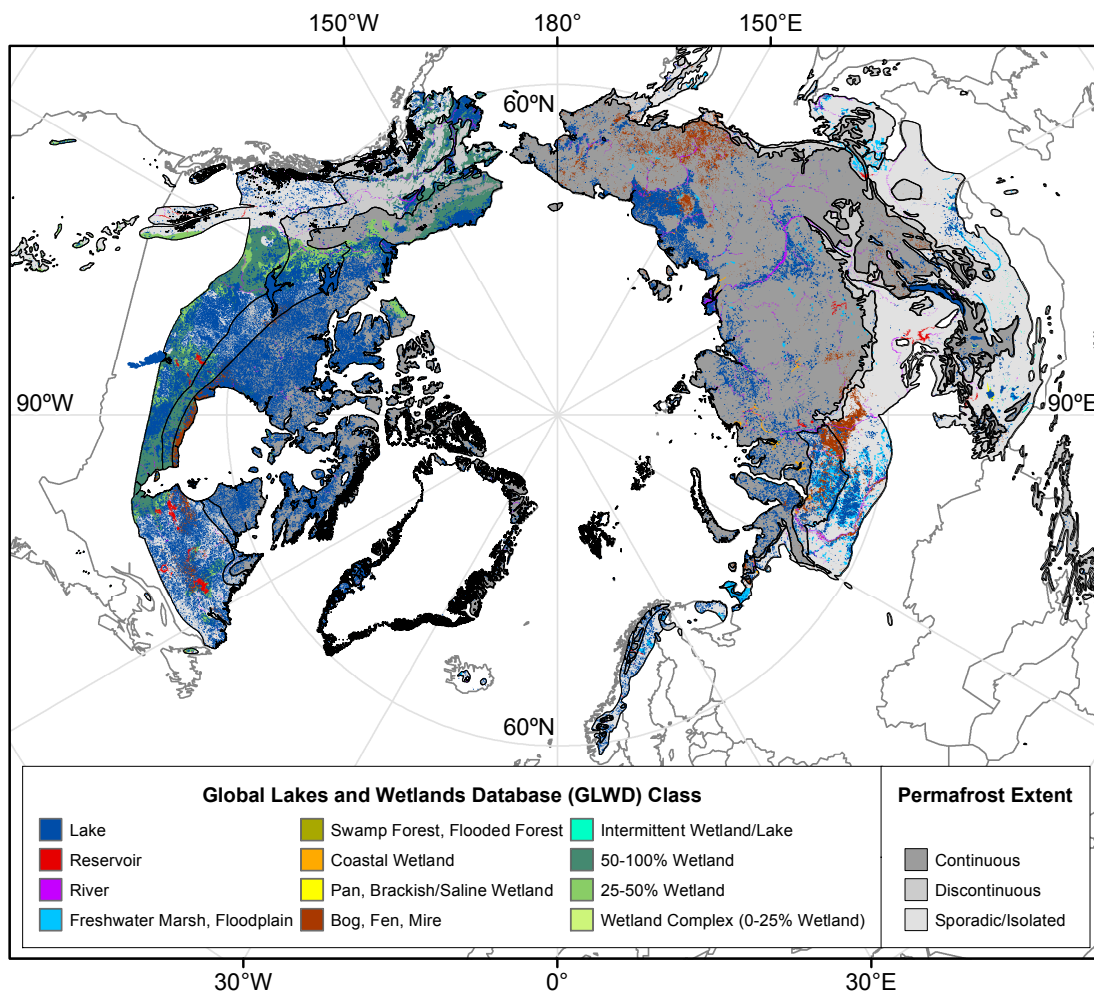
1669 **Figures**

1670

1671 **Figure 1:**

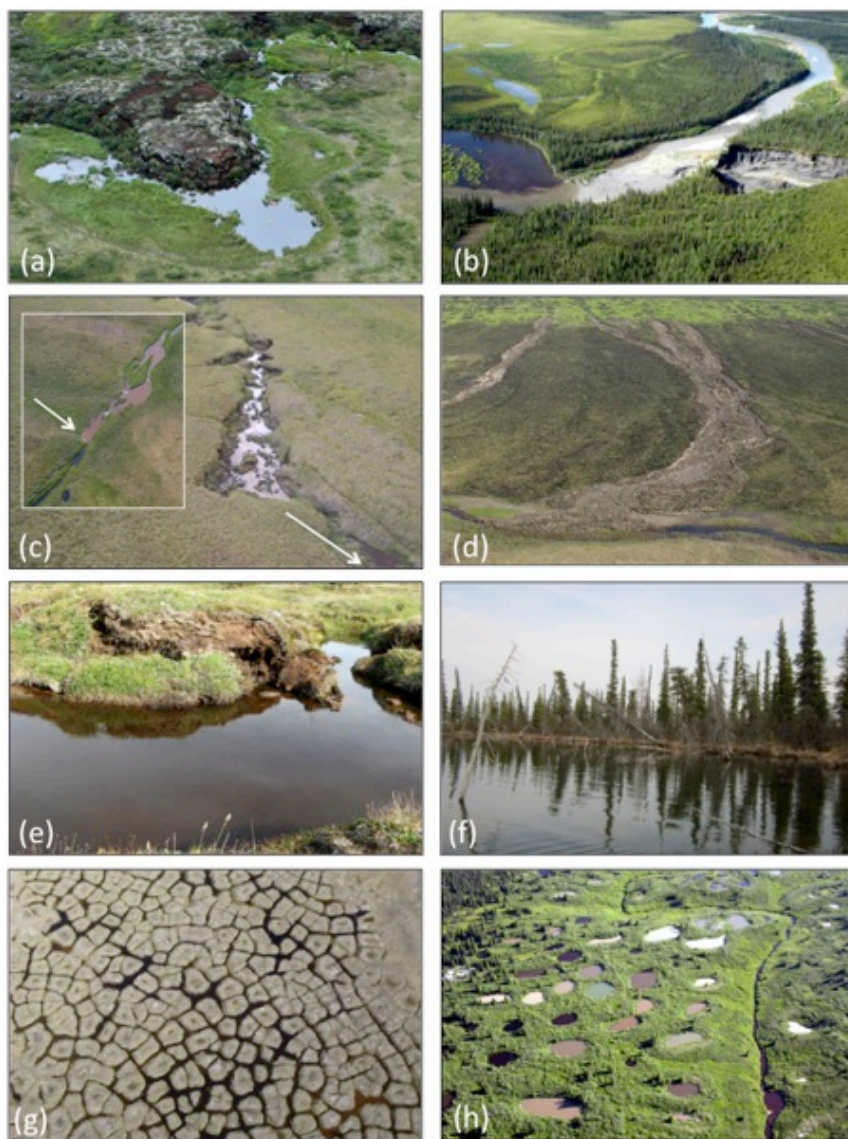
1672 Map of the permafrost zones in the northern hemisphere (grey scale; Brown et al., 1998)
1673 superimposed on water bodies from the Global Lakes and Wetlands Database (Lehner and Döll,
1674 2004).

1675



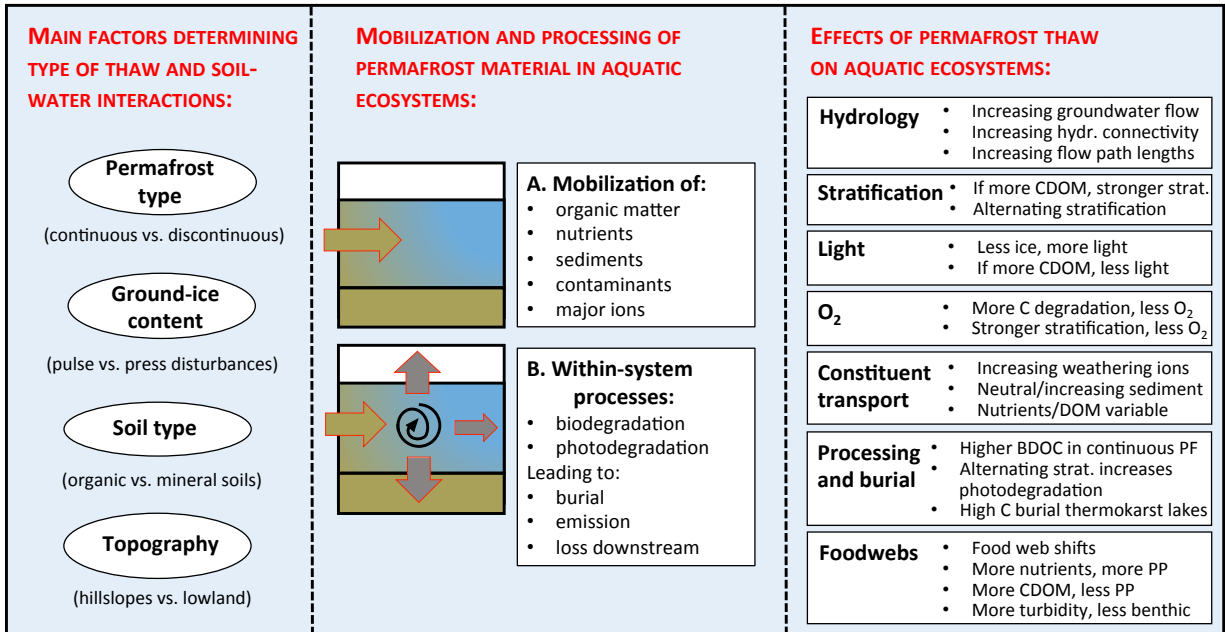
1676

1677 **Figure 2**
 1678 Photos of typical thermokarst processes: (a) Thermokarst lake SAS1, located in a sub-Arctic peat
 1679 bog near Kuujjuarapik-Whapmagoostui, Québec, Canada. The water body lies next to a thawing,
 1680 organic-rich palsa (permafrost mound), and is 25 m in its maximum dimension. (b) Massive thaw
 1681 slump on the Selawik River near Selawik, Alaska, US. Sediment discharge from the feature has
 1682 entirely blocked the river. Note the turbidity downstream. (c) Gully thermokarst on the Toolik
 1683 River, Alaska, US, and impact on receiving stream (inset), (d) active layer detachment slides near
 1684 the Anaktuvuk River burn area on the North Slope of Alaska, (e) trough pond on Bylot Island,
 1685 Nunavut, Canada featuring active erosion, (f) thermokarst lakes in Mackenzie Delta, Northwest
 1686 Territories, Canada, showing active shoreline slumping, (g) polygonal landscape on Bylot Island,
 1687 showing ice-wedge trough ponds, and (h) thermokarst lakes and ponds with a wide range in colour
 1688 near Kuujjuarapik-Whapmagoostui, Québec, Canada. Photo credits: a, Bethany Deshpande; b, Ben
 1689 Crosby, c, d, William Breck Bowden; e, g, and h, Isabelle Laurion; f, Suzanne Tank.
 1690



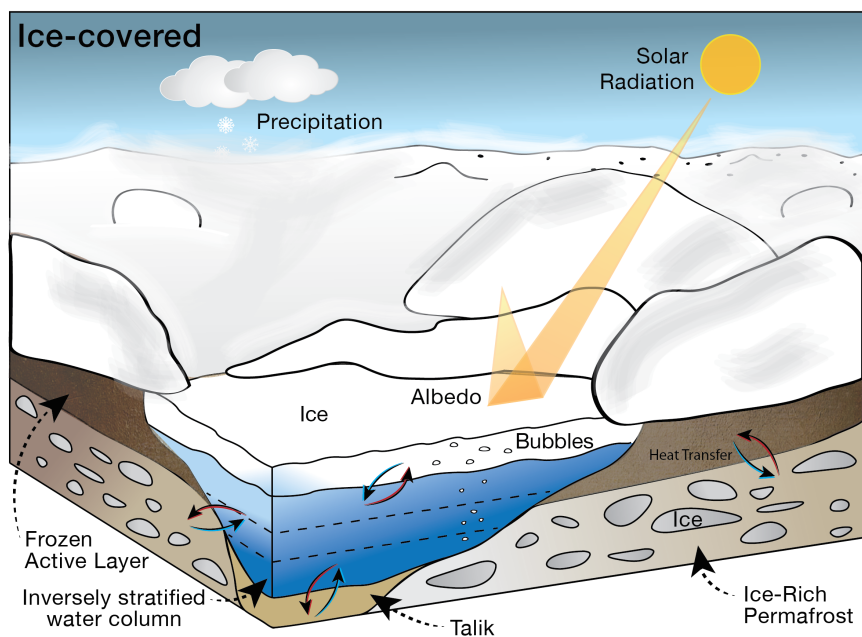
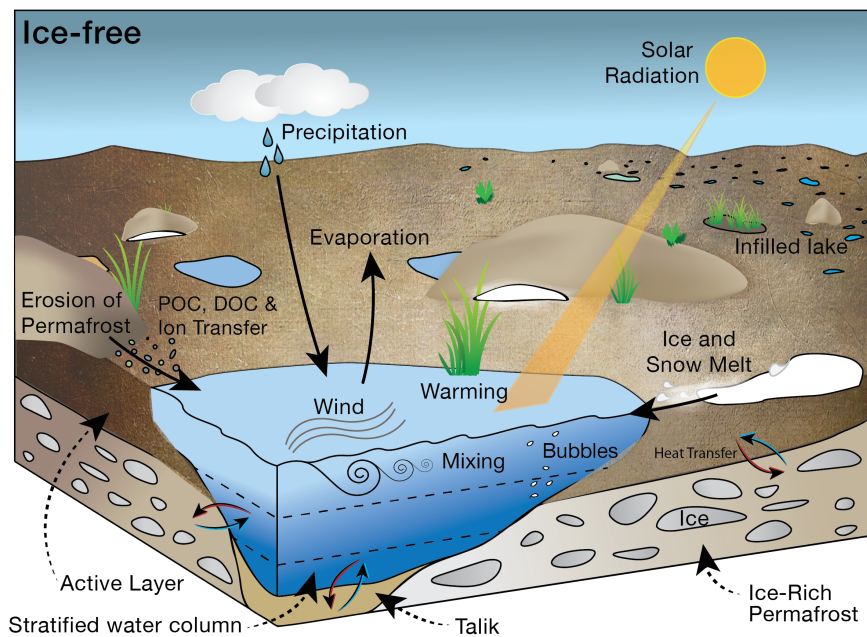
1691

1692 **Figure 3**
 1693 Conceptual diagram of (left) factors determining thaw type and soil-water interactions, (middle)
 1694 mobilization and processing of permafrost material into aquatic ecosystems, and (right) effects of
 1695 permafrost thaw on aquatic ecosystems.
 1696



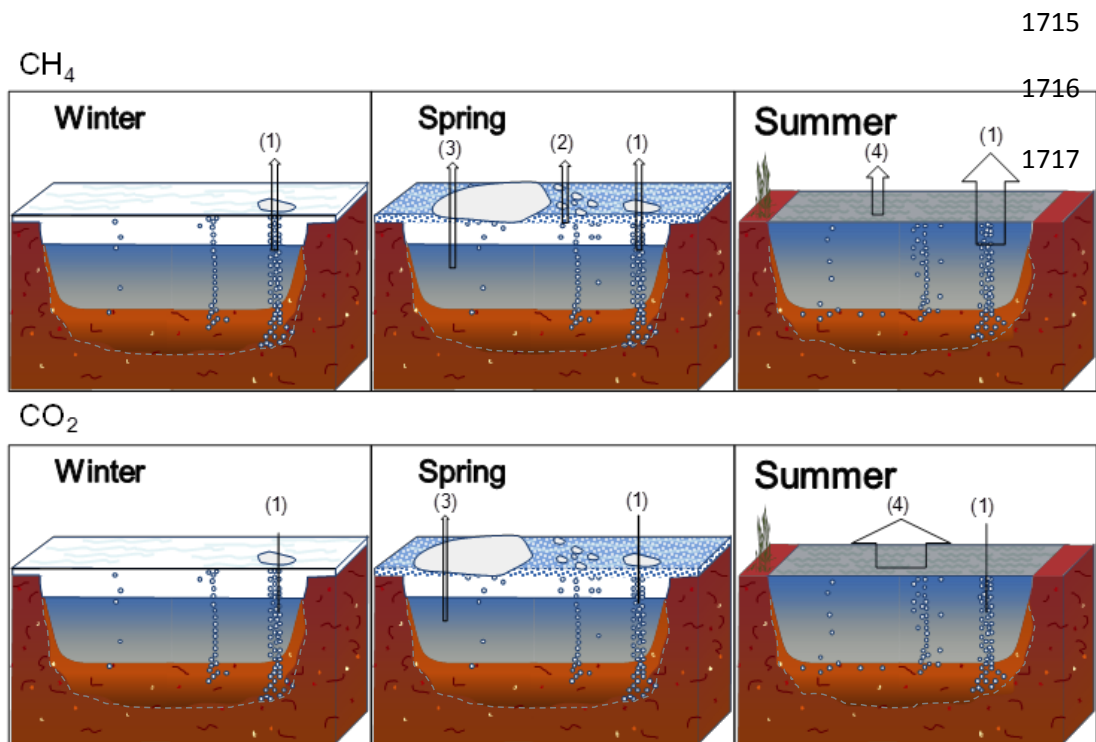
1697

1698 **Figure 4**
1699 Physical limnological characteristics of permafrost thaw lakes in the ice-free and ice-covered
1700 seasons. Note that shallow ponds and lakes that freeze to the bottom in winter are not considered
1701 in this schematic.



1702
1703
1704

1705 **Figure 5**
 1706 Schematic of CH₄ and CO₂ emission pathways during different seasons in thermokarst lakes. The
 1707 thickness of arrows indicates the relative magnitude of contribution from each pathway according
 1708 to a study of 40 Alaskan lakes (Sepulveda-Jáuregui et al., 2015): (1) Direct ebullition through ice-
 1709 free hotspot seeps in winter and from all seep classes during the last month of ice cover in spring
 1710 and in summer; (2) ice-bubble storage emission during spring ice melt; (3) Storage emission of
 1711 dissolved gases accumulated under lake ice when ice melts in spring; (4) Diffusion emission from
 1712 open water in summer. The background ebullition mode, discussed in the text, is not shown. The
 1713 dashed line indicates the boundary between the thaw bulb under lakes and the surrounding
 1714 permafrost. Figure modified from Sepulveda-Jáuregui et al., 2015.



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