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REVIEWS

Review

Roles of Thermokarst Lakes in a Warming World

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Permafrost covers a quarter of the northern hemisphere land surface and contains twice the amount of carbon that is currently present in the atmosphere. Future climate change is expected to reduce its near-surface cover by over 90% by the end of the 21st century, leading to thermokarst lake formation. Thermokarst lakes are point sources of carbon dioxide and methane which release long-term carbon stocks into the atmosphere, thereby initiating a positive climate feedback potentially contributing up to a 0.39°C rise of surface air temperatures by 2300. This review describes the potential role of thermokarst lakes in a warming world and the microbial mechanisms that underlie their contributions to the global greenhouse gas budget.

Highlights

Thermokarst lakes form as a result of permafrost thaw in predominantly ice-rich yedoma deposits and are therefore an ecosystem that is rapidly expanding with the onset of climate change.

Thermokarst lakes are net greenhouse gas sources as century-old carbon deposits become bioavailable and are mineralized to CO_2 and CH_4.

CH_4 is a more potent greenhouse gas than CO_2. Changed dynamics will therefore disproportionately affect global warming.

Methane emissions are the net result of methane production by methanogenesis and methane oxidation by aerobic bacteria or anaerobic archaea, with high levels of heterogeneity and intricate interactions.

Future climate change will have disproportionate effects on the Arctic, which implies potentially strong consequences for future greenhouse gas fluxes and thaw progression.

The Warming Arctic Faces Permafrost Degradation and Thermokarst Formation

Permafrost covers a quarter of the northern hemisphere land surface [1,2]. Its carbon (C) pools are estimated at 1300 Pg C (range 1100–1500 Pg C) which equals twice the amount of carbon that is present in the atmosphere [3,4]. The major fraction, about 1000 Pg, is present in the near surface (the upper 3 m) that is vulnerable to warming [3]. Warming leads to destabilization and degradation of permafrost landscapes [5]. The Arctic Climate Impact Assessment (ACIA) reported a two times higher rise in Arctic air surface temperatures compared with the global average [6,7], resulting in an average permafrost soil and sediment warming of 0.29 ± 0.12°C between 2007 and 2016 [8]. This disproportionate near-surface warming is known as the 'Arctic amplification' [9]. It has a pronounced effect on near-surface permafrost which is expected to be reduced by over 90% at the end of the 21st century [10]. Upon thaw, the increased biological availability of carbon leads to enhanced microbial greenhouse gas (GHG) production [11–14] and net GHG emissions which consist mainly of CO_2 and CH_4 [15–17].

One consequence of a warming Arctic and permafrost thaw is the formation of **thermokarst** (see Glossary) landscapes. These landscapes are associated with **pingos**, thermokarst troughs and pits that can collapse to form thermokarst lakes [18]. GHG emissions from these lakes can have disproportionate climate effects due to the rapid release of long-term stored carbon into the atmosphere, which initiates a strong positive climate feedback [17,19–22]. This review focuses on the role of thermokarst lakes in a warming world and the microbial mechanisms that underlie their contributions to the global GHG budget.

Thermokarst Lakes Are a Feature of Thawing Yedoma Deposits

About 40% (500 Pg) of the permafrost carbon stocks are found in ice-rich **Yedoma** deposits which have an organic carbon content ranging from 2% to 5% [23,24]. These deposits are found in Alaska and Siberia, and they originate from the late Pleistocene [25–27]. The ice-rich Yedoma deposits remained unglaciated during the last ice age and contain organic carbon deposits from alluvial plains, hillslopes, and polygonal lowlands [28]. Yedoma landscapes are highly sensitive to climate change as observed in Western Siberia, Alaska, and Québec [29–31]. In addition, global warming projections estimate a loss of all Yedoma by the end of the 21st century

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[10,32]. Gradual thawing of the ice-rich permafrost leads to the formation of thermokarst, of which thermokarst lakes are a characteristic feature [32,33].

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Nowadays, thermokarst landscapes are estimated to cover 20–40% of the northern permafrost regions, including the Yukon delta, the Alaska north slope, and the coastal regions of the Kara Sea, the Laptev Sea, and the East Siberian Sea [13,34,35]. Thermokarst lakes also occur with lower densities on the Qinghai-Tibetan Plateau, which covers 8% of the global permafrost surface [36].

Thermokarst Lakes Accelerate Permafrost Thaw and Emit Old Carbon Stocks into the Atmosphere

Thermokarst lakes play a significant role in the current climate by functioning as point sources of GHG emissions in comparison with surrounding soils and sediments [32,37]. Thermokarst lake expansion therefore results in an increase in GHG emissions. Observation-based modeling predicts the largest methane (CH_4) emission rates of 50 Tg year^{-1} from newly thawed permafrost around 2050 compared with current rates of around 1 Tg year^{-1} [5,11]. This peak coincides with the expected highest expansion of thermokarst landscapes [5]. The expansion of thermokarst landscapes is accelerated by the physical phenomenon of rapid heat conduction through thawed water bodies leading to abrupt thaw beneath and around the thermokarst lakes. Modeled lake sediment temperatures are about 10°C higher than mean annual air temperatures [38], leading to vertical and radial expansion of thermokarst lakes. Therefore, heat conduction in thermokarst lakes significantly contributes to early (<100 years) thaw progression [39,40]. However, the heat conduction effects are different for shallow and deeper thermokarst lakes.

Shallow bedfast ice lakes completely freeze over during winter, whereas deeper floating ice lakes have a year-round unfrozen sediment [41,42]. Within the Arctic coastal plain of northern Alaska many bedfast ice lakes have transitioned to floating ice lakes since the 1980s [43]. This has direct consequences for cumulative heat storage in lake sediments. For floating ice lakes in Alaska, layers of unfrozen ground, called **taliks**, form underneath the lakes [44,45]. Similar observations were made for Siberian thermokarst lakes where field measurements showed an increase in thaw depth below lakes of 5–10 cm year^{-1} [46]. This thaw progression is generally rapid in the first years and slows down over time [44]. Overall, taliks facilitate rapid thaw beneath lakes and cause deeper carbon stocks to become bioavailable (Figure 1) [21,47–49]. Besides vertical

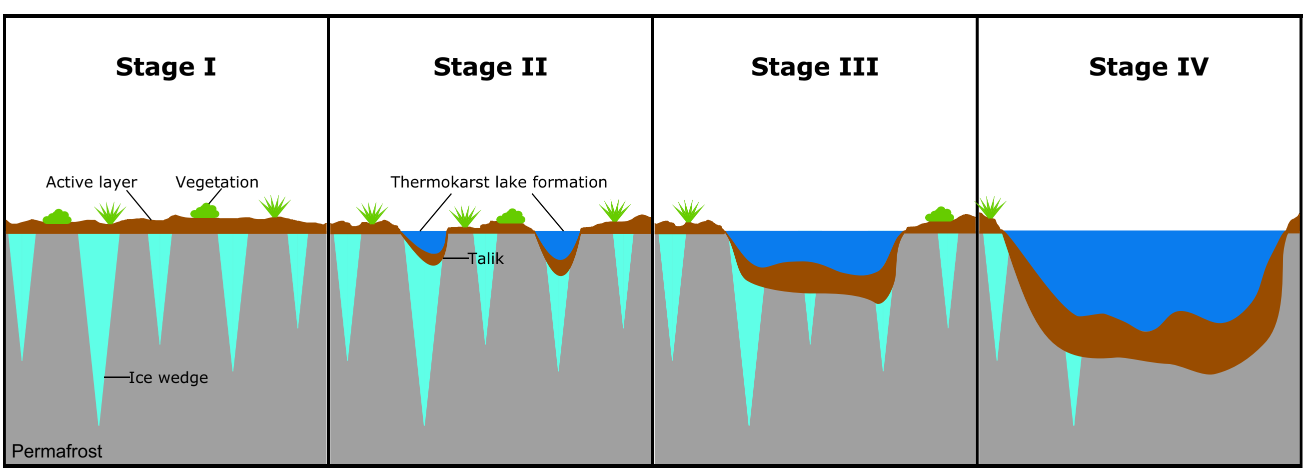

Figure 1. The Process of Thermokarst Lake Formation in Ice-rich Yedoma Permafrost. Stage I: Permafrost stage, Yedoma with major ice wedges. Stage II: Thaw processes lead to thermokarst lake formation. Stages III, IV: Thaw progression results in horizontal and vertical lake expansion. Figure based on data from [141,142].

growth, thermokarst lakes also undergo horizontal expansion (Figure 1). The collapse of surrounding Yedoma increases lake surface area, whereas slumping of adjacent sediment introduces organic material into the lake [45].

The undecomposed organic matter from permafrost is highly reactive upon thaw [5,50–52]. Freshly thawed permafrost soils release more nutrients than soils that have already been exposed to thawing, which boosts initial microbial activity leading to GHG production [53,54]. Radiocarbon age profiles, which were obtained by analyzing the ^{14}C composition of CH_4 **ebullition** seeps from Yedoma thermokarst lakes showed oldest CH_4-carbon origins at lake margins and younger profiles towards the center, indicating rapid degradation of freshly thawed old permafrost C associated with lake expansion [55,56]. A study of thermokarst lake taliks found the highest CH_4 production potentials in organic-rich lake sediments and freshly thawed permafrost soils [57]. In addition, the exposure of organic matter to sunlight within lakes transforms dissolved organic matter into microbiologically more easily accessible substrates [58]. These findings illustrate how the input of freshly thawed organic matter can lead to peak emissions of GHGs from thermokarst lakes [55].

Overall, the microbial degradation of organic matter is highly dependent on oxygen availability. Under oxic conditions microbial mineralization results mainly in CO_2 production, whereas anoxic conditions also lead to CH_4 production. Despite their shallow depths (<4 m) thermokarst lakes and ponds are generally stratified, which results in separation of oxic and anoxic habitats [59,60]. The constant input of organic matter during thaw stimulates microbial decomposition and leads to the formation of anoxic, methanogenic conditions toward the bottom [61]. Thermokarst formation therefore affects local hydrology and limits oxygen availability, which in turn enhances the CH_4 production potential [15,62,63].

Methanogenesis Pathways Are Highly Location-specific

CH_4 is produced during the final step in the anaerobic degradation of organic matter [64] (Figure 2). The main pathways for CH_4 production in permafrost environments are hydrogenotrophic methanogenesis, which uses hydrogen (H_2) and CO_2 as substrates, and acetoclastic methanogenesis, which uses acetate as substrate [65–70]. There is, however, conflicting evidence as to which methanogenic pathway is dominant in thermokarst lake sediments [56,57,71]. The availability of methanogenic substrates may differ between thermokarst lake regions, or even single lakes, due to differences in local physicochemical parameters such as pH and organic matter types and inputs [72]. A study on thaw lakes in the Arctic Foothills province of Alaska found that the acetoclastic pathway dominated over the hydrogenotrophic pathway with a 2:1 ratio that further increased with sediment depth [73]. A study on polygonal ponds, trough ponds, and lakes on Bylot Island, a continuous permafrost zone of the Eastern Canadian Arctic, also designated acetoclastic methanogenesis as the dominant process [74]. In contrast with the aforementioned studies, Blodau and coworkers showed that, for a thermokarst pond and adjacent thermokarst depressions in Igarka, Northern Siberia, CH_4 was produced mainly through hydrogenotrophic methanogenesis [75]. When thermokarst lakes develop into fully thawed thermokarst bogs, methanogenesis may shift from acetoclastic to hydrogenotrophic, as found in a microcosm study in peat bog samples from west Siberia by Kotsyurbenko and coworkers due to the low pH (3.8) of the bog [67].

A molecular survey, based on methanogenic marker genes, of thaw lakes that formed upon the collapse of **palsas** (frozen peat cores) and **lithalsas** (mineral core mounds) found both hydrogenotrophic Methanomicrobiales and versatile Methanosarcinales in near-bottom waters [76]. The dominance of Methanomicrobiales in **functional gene** (methyl-coenzyme M reductase, *mcrA*) transcript data on these thaw lakes indicates that hydrogenotrophic methanogenesis is the major pathway [76]. However, a study of transcriptional activity in methanogenic archaea showed

Glossary

16S rRNA gene: a molecular biological proxy with which the identity and phylogeny of a microorganism can be determined. Its gene product is part of the small subunit of the prokaryotic ribosome.

Active layer: the top layer of permafrost soil that is exposed to thaw during summer and freezes over during the autumn and winter seasons.

ANME: anaerobic methanotrophic archaea. These microorganisms oxidize methane either syntrophically with a sulfate-reducing partner, or independently of a syntrophic partner with nitrate, iron, or manganese as terminal electron acceptor.

AOM: anaerobic oxidation of methane. This process is performed by anaerobic methanotrophic archaea (ANME). The ANME are further subdivided into the clades ANME-1, ANME-2, and ANME-3.

Ebullition: a suddenly occurring flux of methane bubbles from sediments and water columns. These emissions are the result of methane building up over time, which leads to the formation of gas pockets that are released during bubbling events.

Functional gene: a region of DNA that contains the nucleotide sequence encoding a single protein with a function in an organism. These regions behave as single hereditary units.

GWP: global warming potential. This is a measure of the amount of heat that is trapped by a greenhouse gas in the atmosphere within a specific time period. The number is expressed relative to CO_2, whose GWP is standardized to 1.

Lagoon: a shallow body of water that is separated from a larger body of water, for example the sea, by barrier land or reefs. Water bodies separated by barrier land are called coastal lagoons; those separated by reefs are called atoll lagoons.

Lithalsa: frost-induced landscape elements that are elevated due to freeze-expansion effects during ice lens formation. Upon partial thaw these bodies can form characteristic ring-like structures.

MOB: methane-oxidizing bacteria. These are bacteria that oxidize methane at the expense of oxygen using the enzyme methane monooxygenase.

Palsa: frost heaves that occur in permafrost landscapes with permanently frozen ice lenses. They co-occurrence of Methanomicrobiales and Methanosarcinales in thawed permafrost, but only an increase in transcriptional activity in thawed permafrost for acetoclastic Methanosarcinales [77]. A study based on **16S rRNA gene** amplification by Matheus Carnevali and coworkers showed that the archaeal population of thermokarst lakes on the north slope of Alaska is highly diverse and not yet characterized properly with possibly novel taxa with poorly characterized metabolism involved in methanogenesis [78]. These findings stress the need for activity-based studies to gain insight into methanogenesis dynamics in the field.

One interesting aspect of thermokarst GHG emissions is that CO_2 and CH_4 production respond differently to warming. A study of 40 Alaskan lakes across a longitudinal transect that includes lakes formed in continuous, discontinuous, and isolated permafrost showed that all were net sources of CO_2 and CH_4, but that the warming impact on CH_4 production was twice as high compared with CO_2 [79]. Metje and Frenzel showed the highest methanogenesis rates between 26°C and 28°C, and 17% of the maximum activity at 4°C [80]. Little is known about the effects of seasonality, and only few studies have addressed year-round measurements in the field due to logistic and sampling limitations. It has been shown that floating ice lakes have a year-round **active layer** and that CH_4 is trapped in ice bubbles during winter and released in spring, causing seasonal peak emissions [43,79]. A study on thermokarst lakes on the Qinghai-Tibetan Plateau showed highest methanogenesis rates in July and lowest rates in September, which indicates a positive temperature dependency [36]. However, although methanogens show a positive response to warming, the methanogenesis rates seem mainly affected by labile organic matter and substrate availability in lakes [72]. A study on a thermokarst bog in interior Alaska showed a general substrate limitation as controlling factor of microbial GHG production rates [81]. Similarly, laboratory-based experiments on the sediment of a small Alaskan Arctic lake showed that acetate availability limited methanogenesis rates [70]. A similar observation was made by de Jong and coworkers with incubations of thermokarst lake sediments from Utqiagvik, Alaska, in which substrate amendment stimulated acetoclastic and methylotrophic methanogens, indicating substrate limitation in the sediment [82].

Aerobic Methanotrophs Function as an Important Methane Filter in Thermokarst Lakes

Methanotrophs function as a methane sink by oxidizing CH_4 to CO_2 (Figure 2). CH_4 is oxidized by both aerobic bacteria and anaerobic prokaryotes that can use a suite of alternative electron acceptors. Aerobic methanotrophy is thought to function as the main CH_4 filter in permafrost environments [11]. Aerobic methanotrophic bacteria belong to the Alphaproteobacteria (type II), Gammaproteobacteria (type I), and the Verrucomicrobia phylum [83–85]. A study on a stratified humic, boreal lake in southern Finland showed that methanotrophs can function as an efficient CH_4 filter, consuming up to 80% of the CH_4 produced in the lake sediment [86]. A study on thermokarst lakes that formed on collapsing lithalsas aligned in a north–south transect showed that methanotrophy in a northern lake was 10% of the CH_4 emission rate, whereas at the southernmost lake it accounted for 60% of the CH_4 emission rate. Even though total emissions of GHG were still higher at the southernmost lake, these data indicate that warmer temperatures have a disproportionate positive effect on methanotrophic activity [87]. Besides temperature, aerobic methanotrophic activity is dependent on dissolved oxygen and CH_4 concentrations. A study of 30 Alaskan lakes, including thermokarst and nonthermokarst lakes along a latitudinal transect, showed that the overall winter methanotrophic activity was controlled mainly by oxygen availability, whereas summer methanotrophic activity was limited by CH_4 availability [88]. In a comparative study on different lake types, Yedoma thermokarst lakes showed highest methanotrophy rates, which is linked to their relatively higher carbon inputs [79]. This is in line with the link between high methanogenesis rates and high methanotrophy rates, as found in a study on a small Alaskan lake [70].

consist of a frozen ice core that is covered by a layer of soil. Palsas are comparable to pingos, but they are generally smaller in size.

Pingo: alternatively named 'hydrolaccolith' or 'bulgunniakh', pingos are frost heaves that occur in permafrost landscapes with permanently frozen ice lenses. These heaves can reach a height of up to 70 m and are much larger than palsas.

Q_{10} values: temperature coefficient. A measure of the rate of change of a system as a result of a temperature rise of 10°C.

Talik: year-round unfrozen ground that occurs within permafrost, often below thermokarst lakes, streams, and rivers.

Thermokarst: a landscape characterized by irregularities including hummocks and hollows caused by the thaw of ice-rich permafrost.

Wetland: an ecosystem that is temporarily or permanently flooded with water, causing anoxic sediment conditions.

Yedoma: ice-rich permafrost with an organic matter content between 2% and 5%.

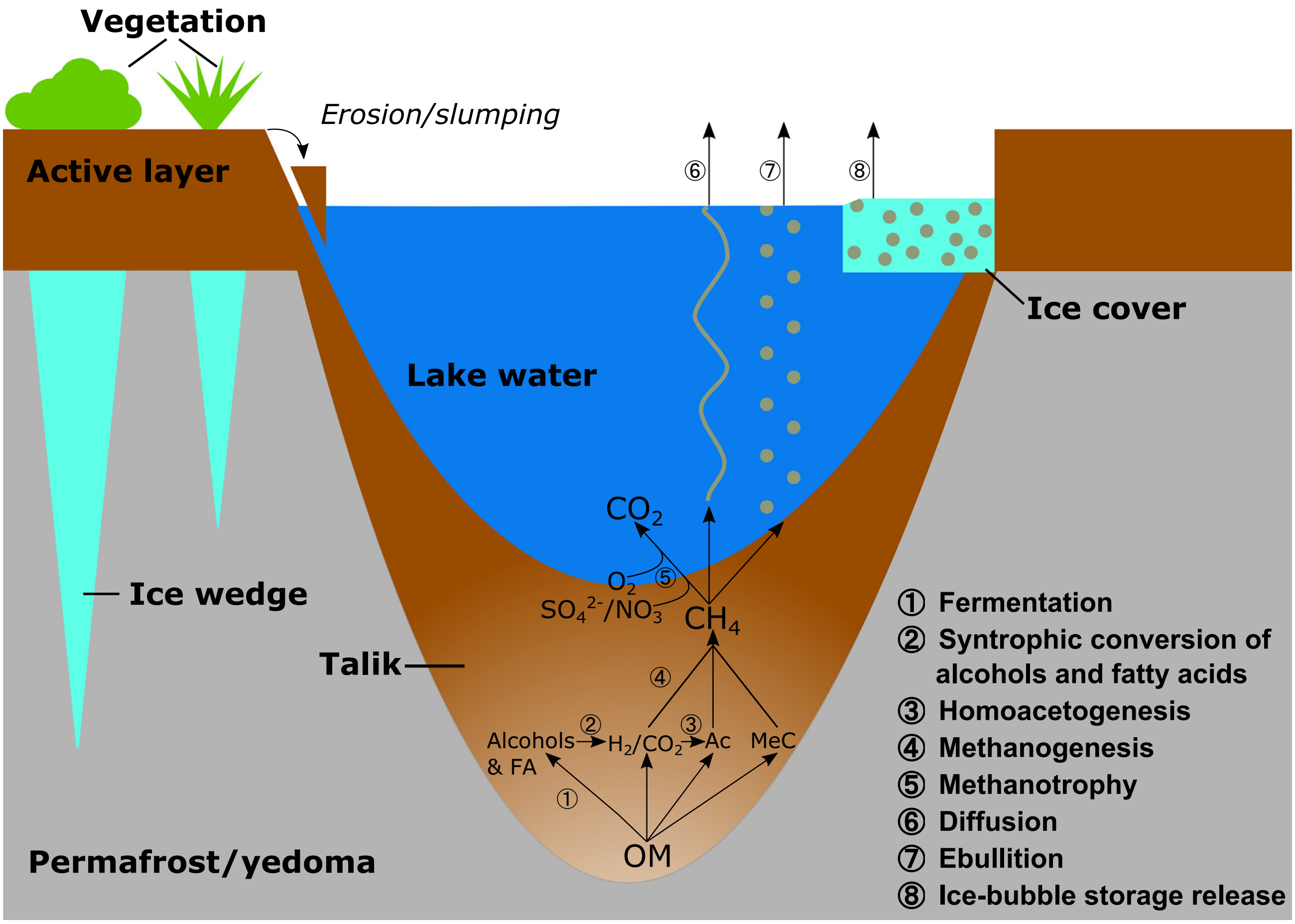

Figure 2. Scheme Illustrating the Thermokarst Lake Microbial Carbon Cycle within Ice-rich Yedoma Deposits That Are Characterized by Ice Wedges. The microbial community within the unfrozen ground layer (Talik) degrades organic matter (OM) to CH_4 through fermentative and syntrophic processes (①-④). CH_4 can be oxidized to CO_2 by aerobic and anaerobic methanotrophs (⑤). The non-oxidized fraction of CH_4 can escape via diffusion, ebullition, and the release of ice-bubble storage (⑥-⑧).

Methanotrophs are also detected in low-oxygen bottom waters and lake sediments [89]. The study of Crevecoeur and coworkers, using *pmoA* gene transcripts, found the presence of methanotrophs regardless of local oxygen conditions [89]. Osudar and coworkers report on a correlation between CH_4 oxidation rates and CH_4 concentrations in Siberian lakes and rivers that were all emitting CH_4 [90]. These findings indicate that even thermokarst lakes that have a large potential for methanotrophy remain net CH_4 sources.

A 16S rRNA gene-based study of Crevecoeur and coworkers on shallow ponds of the Nunavik subarctic region in Québec showed that methanotrophs were the most abundant bacterial group in all water bodies (median 4.9%, maximum 27%) [91]. This is in line with a 16S rRNA gene-based study on four subarctic thermokarst ponds near the coast of Hudson Bay, Canada, which found that 20% of clone library sequences belonged to methanotrophic bacteria (*Methylobacter*, *Crenothrix*, and *Methylocystis*) [60]. A *pmoA* transcript-based quantification study on thermokarst ponds in subarctic Québec showed dominance of type I methanotrophs, belonging mainly to *Methylobacter* species [89]. *Methylobacter* is a dominant member of the aerobic methanotrophic community in many permafrost-affected landscapes, both in soil and lake environments [92–95].

Verrucomicrobial methanotrophs have also been detected in ponds of sporadic and discontinuous permafrost in Québec, Canada (1–6% of bacterial community 16S rRNA gene reads) [91,96]. Their diversity in thermokarst lakes might be underestimated due to the fact that Verrucomicrobial methanotrophs are not picked up by standard primers [94]. During permafrost thaw progression, submerged or floating peat mosses can cover the water surface giving rise to a more effective methane filter due to methane-oxidizing bacteria (**MOB**) colonizing the peat moss [75,97]. In lakes formed within low-centered polygons on Samoylov Island in the Lena Delta, a symbiotic association between submerged brown mosses and aerobic methanotrophs was shown to reduce CH_4 emissions by at least 5% [98]. In a thermokarst pond near Igarka, northern Siberia, methanotrophic activity was found mainly in floating mats consisting of *Sphagnum* peat moss and sedges in the top 20 cm of the water body [75]. This CH_4 filter can be more efficient at lower temperatures due to an increasing imbalance between methanogenesis and methanotrophy at higher temperatures [97]. The development of peat vegetation during thermokarst lake development could thus have pronounced effects on net CH_4 fluxes. This is, however, beyond the scope of this review.

Role of Nitrogen- and Metal-dependent Anaerobic Oxidation of Methane (AOM) in Thermokarst Lakes

Under anoxic conditions, anaerobic methanotrophic prokaryotes can oxidize CH_4 using a suite of alternative electron acceptors. The methane that passes this anoxic filter can be oxidized by aerobic methanotrophs. In a study on thermokarst lakes, Winkel and coworkers observed a high abundance of potentially cold-adapted *Candidatus* Methanoperedenaceae **ANME**-2d sequences in 16S rRNA gene data [99]. *Candidatus* Methanoperedens archaea can perform nitrate-, manganese-, or iron-driven **AOM** [100–103]. They are of terrestrial origin and occur in, amongst others, **wetland** and permafrost habitats [99]. Stable $\delta^{13}C\text{–}CH_4$ isotope calculations on pore water samples of Vault Lake, Alaska, indicated that 41–83% of the dissolved CH_4 is oxidized by AOM, but relative contributions of AOM activities with specific electron acceptors remain elusive [104]. *Candidatus* Methanoperedens archaea were also detected (0.3–2.1% of archaeal 16S rRNA gene reads) in a study by de Jong *et al*. in thermokarst lake sediments in Utqiagvik, Alaska, despite very low nitrate concentrations ranging from 0.8 to 2.4 μM [82]. Iron and manganese concentrations were not measured in this study. A study by Winkel and coworkers on deep sea permafrost found *Candidatus* Methanoperedens archaea sequences in deep layers, with nitrate concentrations in the millimolar range [105]. However, there is currently no experimental evidence on the activity of nitrate-, manganese-, or iron-dependent AOM in thermokarst lakes.

Nitrite-dependent CH_4 oxidation is carried out by *Candidatus* Methylomirabilis belonging to the bacterial NC10 phylum. These bacteria produce oxygen for CH_4 activation via an intra-aerobic pathway [106]. So far, these bacteria have not been detected in permafrost soils or thermokarst environments. However, primer-based studies are prone to miss bacteria of the phylum NC10, which stresses the importance for future metagenomics studies to identify the full microbial methanotrophic potential of these ecosystems [89,107].

Marine Influence Introduces Anaerobic Methanotrophic Archaea (ANME) Capable of Sulfate-dependent Anaerobic Oxidation of Methane

Due to rising sea levels, coastal thermokarst lakes and lacustrine depressions can be converted into thermokarst **lagoons** [108,109]. Projections of estimated sea level rise range between 0.18 and 0.59 m globally, and the Arctic Ocean is expected to face the greatest magnitude of increase

[110,111]. This change will affect both coastal erosion rates and salinification of coastal permafrost and thermokarst lakes [110]. Thermokarst lagoons form the transitional state between a freshwater and saltwater environment [112]. Such a transitioning process is nowadays visible on the Bykovsky Peninsula and the Yana River Delta in Siberia [108]. Within the Bykovsky Peninsula and the Khorogor Valley of Siberia, thermokarst processes have affected over half of the area, and around 4% of the area is covered by lagoons [113]. A marine connection introduces sulfate into CH_4-rich environments. Under anoxic conditions, spatial co-occurrence of CH_4 and sulfate can induce sulfate-dependent anaerobic oxidation of methane (sulfate AOM) (Figure 2) [114].

Schirrmeister and coworkers calculated that the Bykovsky Peninsula in Siberia contains 1.68 ± 0.04 Mt of organic carbon in the upper 6 m [112]. Observed CH_4 emissions from the Ivashkina Lagoon range between 5 and 24 g per m^2 per day and occurred through bubble seeps [115]. This finding indicates that methanotrophy could limit diffusive CH_4 emissions from the lagoon. Sequences for anaerobic sulfate-dependent AOM (ANME-2a,b archaea) have been detected in permafrost habitats, including drained lakes, permafrost soils, and deep submarine permafrost [105,116,117]. Sequence-based studies suggest that ANME-2a,b are of marine origin and are introduced into the lakes during lagoon formation. Sulfate-dependent AOM can form an important additional CH_4 filter in these lakes, and more research is needed to quantify their role in the mitigation of CH_4 emission.

Thermokarst Lakes Are Important Contributors to the Global GHG Budget

Thermokarst processes not only accelerate thaw but also stimulate the release of carbon, nitrogen, and other nutrients from deeper permafrost layers [118]. In turn, microbial activity can further accelerate the release of nutrients and greenhouse gases. Thermokarst lake waters are supersaturated with CO_2 and CH_4, indicating a constant input and turnover of terrestrial carbon stocks which is corroborated by dissolved organic matter signatures [119–121]. Both CO_2 and CH_4 are emitted into the atmosphere through diffusion and ebullition (Figure 2) [32,79,87,122]. Ebullition is suggested to be the major emission pathway of thermokarst lakes with an expected emission of 4.1 ± 2.2 Tg CH_4 $year^{-1}$ which equals 17%–26% of the 24.2 ± 1.5 Tg CH_4 $year^{-1}$ that is emitted from all northern lakes [19,55,87,122–125]. However, a study in Québec on lithalsas found that diffusion rates can exceed ebullition [87]. In addition, ice-bubble storage fluxes comprise a third emission pathway that occurs when seasonally ice-trapped bubbles are released upon thaw in the spring [79]. These bubble fluxes can account for 10% of CH_4 emissions, as observed in Yedoma thermokarst lakes in Alaska (Figure 2) [57]. Although increased permafrost thaw leads to greater gross primary production, large thaw sites in Alaska were found to be a net source of GHGs [15,126]. Increased primary production is therefore unlikely to offset net increases in GHG release from thawing permafrost.

The Future of Thermokarst Lakes

Thermokarst lake dynamics are highly complex and less cyclic than often assumed [127]. For Siberia, it has been reported that thaw leads to initial lake formation and lake area expansion, which is followed by rapid drainage and lake disappearance [128]. Rapid lake drainage can also be observed in Alaska and the western Canadian Arctic [129,130]. Due to these dynamic processes, thermokarst is often considered to have a major impact in the short term [46]. However, its dynamic nature hampers accurate quantification of future thermokarst lake development, which stresses the need for field data [128,131]. Data on microbial CH_4 dynamics in thermokarst lakes are essential to better estimate CO_2 to CH_4 emission ratios. These ratios are a main input for current permafrost climate feedback models.

Major changes in water chemistry and microbiology occur when permafrost thaw results in small thermokarst water bodies (0.001–0.01 ha). These small lakes are often not included in global models but they have a significant contribution to the hydrology and GHG emissions of the ecosystem [29,132,133]. Future GHG emission models should therefore aim to include these small water bodies.

Concluding Remarks and Future Perspectives

Due to its large total wetland area, the Arctic is a significant source of atmospheric CH_4 (32–112 Tg CH_4 year^{-1}) [134]. The total permafrost carbon feedback could contribute up to 0.39°C to the rise of surface air temperature by 2300 [5]. Although the modeled CH_4 emission from permafrost ecosystems is relatively low within the total GHG budget (2.3% of GHG release) it contributes up to half of the expected climate forcing when taking the global warming potential (**GWP**) into account (34 times the GWP of CO_2 for 100 years) [135,136]. Increases in thermokarst features are an early indicator of enhanced permafrost loss which is linked to enhanced GHG emissions [118]. The balance in GHG emissions is determined by methanogenic and methanotrophic activity. Whereas methanogenesis and aerobic methanotrophy are included in most studies, there is limited knowledge of the potential of AOM to function as a CH_4 filter, especially for marine-influenced thermokarst environments. Since AOM can function as a significant CH_4 filter in marine and brackish environments, its role in coastal thermokarst landscapes should be further investigated. In addition, with the expected sea level rise, these transition ecosystems become increasingly relevant in the near future.

Furthermore, the effects of warming on methanogenic substrate production in the field remain understudied. **Q_{10} values** can be used to describe rate changes of GHG production and consumption in response to temperature increase. Q_{10} values are both substrate- and process-specific [82,131]. Published Q_{10} values from field studies in Alaska, Québec, and the Lena Delta, Siberia, range between 1.7 and 16, which furthermore stresses the heterogeneity of these ecosystems [137]. Besides spatial heterogeneity, seasonality also affects measured GHG fluxes and microbial community structure and potential [88]. This stresses the need for multiseason field data.

Few studies additionally measured nitrous oxide (N_2O) production in thermokarst lakes. Nitrous oxide is a potent greenhouse gas with an almost 300 times higher GWP than CO_2 [135]. Several studies indicated that subarctic tundra and thawed Arctic peatlands, ponds, and lakes are sources of N_2O [138–140]. Data on N_2O emissions from the Arctic are, however, scarce.

Future research on microbial GHG drivers is therefore needed to fill current knowledge gaps and to more accurately predict the fate and climate feedback of thermokarst lakes in a warmer world (see Outstanding Questions).

Outstanding Questions

Thermokarst lakes are transient environments that are features of permafrost thaw. How can their greenhouse gas releases be best incorporated into climate models and temperature scenarios? Which data need to be generated by biogeochemists and microbiologists to be useful for climate scenario development?

Thermokarst lakes are highly variable environments with regard to hydrological changes, sea water influence, carbon bioavailability, and other physicochemical parameters. Which molecular proxies can be used to estimate greenhouse gas fluxes, or to categorize thermokarst lakes with regard to their greenhouse gas emission potential? Which factors determine the type of methanogenesis and methanotrophy pathways?

Most GHG flux data are collected during the summer months, due to difficulties in accessing the area and measuring fluxes in a frozen landscape. What are the year-round greenhouse gas emissions from thermokarst lakes? How are microbial processes changing during winter, under the ice cover of these lakes? How do these processes change with different types of thermokarst lake landscapes?

Which are the microbial key players in methane production and methane oxidation? Are current molecular methods adequate for the detection of all relevant players?

Do anaerobic methanotrophic archaea contribute to mitigation of methane emissions? Which physicochemical parameters govern the type of anaerobic/aerobic methane oxidation in thermokarst environments?

The temperature sensitivity of an ecosystem is determined by geochemical and biological parameters. How can we best implement these parameters to improve Q_{10} values of thermokarst environments?

Nitrous oxide (N_2O) has an even higher global warming potential than CO_2 and CH_4. Do thermokarst lakes, specifically those with high organic nitrogen concentrations and the presence of ANME-2d archaea, also contribute to N_2O emissions?

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