Greenhouse gas production and lipid biomarker distribution in Yedoma and Alas thermokarst lake sediments in Eastern Siberia

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Abstract
Permafrost thaw leads to thermokarst lake formation and talik growth tens of meters deep, enabling microbial decomposition of formerly frozen organic matter (OM). We analyzed two 17-m-long thermokarst lake sediment cores taken in Central Yakutia, Russia. One core was from an Alas lake in a Holocene thermokarst basin that underwent multiple lake generations, and the second core from a young Yedoma upland lake (formed ~70 years ago) whose sediments have thawed for the first time since deposition. This comparison provides a glance into OM fate in thawing Yedoma deposits. We analyzed total organic carbon (TOC) and dissolved organic carbon (DOC) content, n-alkane concentrations, and bacterial and archaeal membrane markers. Furthermore, we conducted 1-year-long incubations (4°C, dark) and measured anaerobic carbon dioxide (CO2) and methane (CH4) production. The sediments from both cores contained little TOC (0.7 ± 0.4 wt%), but DOC values were relatively high, with the highest values in the frozen Yedoma lake sediments (1620 mg L−1). Cumulative greenhouse gas (GHG) production after 1 year was highest in the Yedoma lake sediments.
deposits (>25 m depth) are an important pool of permafrost OM (Schirrmeister et al., 2013; Strauss et al., 2017). In contrast, gradual topo- 
being ice- rich and susceptible to ground subsidence, deep Yedoma 
results in deep thaw and subsequent ground subsidence. Aside from 
development, could lead to an additional net OC release from perma-
(2020) estimated that abrupt thaw processes, such as thermokarst lake 
production during Holocene talik development. Furthermore, we found that drivers of CO₂ and CH₄ production differ following thaw. 
Our results suggest that GHG production from TOC-poor mineral deposits, which are 
spread throughout the Arctic, can be substantial. Therefore, our novel data are 
relevant for vast ice-rich permafrost deposits vulnerable to thermokarst formation.

KEYWORDS
anaerobic, greenhouse gases, incubation experiments, lipid biomarkers, organic matter 
degradation, permafrost thaw, talik, Yakutia

1 | INTRODUCTION

Rapid warming of the Arctic results in permafrost warming (Biskaborn et al., 2019) and thaw, enabling microbial decomposi-
tion of previously frozen organic matter (OM; Schuur et al., 2008; 
Walter Anthony et al., 2016). Soil organic carbon (OC) that has been 
stored for millennia could be released to the atmosphere as green-
house gases (GHGs). OC release from permafrost regions will con-
tinue gradually with ongoing warming, thereby accelerating warming (Schuur et al., 2015). Factors controlling GHG release from thawing 
permafrost are complex and therefore not fully considered by most 
climate models (Turetsky et al., 2020).

Thermokarst lake and talik formation is the most common expres-
sion of deep permafrost degradation (>10 m depth; Grosse et al., 2013). 
Ground subsidence following thawing of ice-rich ground beneath the 
lake leads to lake formation. A positive downward heat flux from the 
water further enhances thaw and leads to the formation of a talik. 
After lake drainage or desiccation, a subaerial thermokarst lake basin 
remains, which is called an alas (Soloviev, 1973). Consequently, the talik 
can refreeze and OC becomes freeze-locked again. Thermokarst and 
talik formation, especially in ice-rich Late Pleistocene Yedoma depos-
its, result in deep thaw and subsequent ground subsidence. Aside from 
being ice-rich and susceptible to ground subsidence, deep Yedoma deposits (>25 m depth) are an important pool of permafrost OM (Schirmmeister et al., 2013; Strauss et al., 2017). In contrast, gradual topo- 
down thawing, such as active layer deepening, affects only centimeters per decade (Grosse et al., 2011; Turetsky et al., 2020). Turetsky et al. (2020) estimated that abrupt thaw processes, such as thermokarst lake 
development, could lead to an additional net OC release from perma-
frost regions of 80 ± 19 Pg by 2300 under RCP 8.5. Thermokarst de-
velopment in Yedoma regions, therefore, contributes globally relevant 
GHG emissions to the active carbon cycle (Turetsky et al., 2020).

The amount of OM that can be mobilized upon thaw is highly 
dependent on the state of OM degradation. Several studies have 
analyzed permafrost OM on a molecular level using lipid biomarkers 
(226 ± 212 µg CO₂-C g⁻¹ dw, 28 ± 36 µg CH₄-C g⁻¹ dw) and 3 and 1.5 times lower in the 
Alas lake sediments, respectively (75 ± 76 µg CO₂-C g⁻¹ dw, 19 ± 29 µg CH₄-C g⁻¹ dw). The highest CO₂ production in the frozen Yedoma lake sediments likely results from 
decomposition of readily bioavailable OM, while highest CH₄ production in the non-
frozen top sediments of this core suggests that methanogenic communities estab-
lished upon thaw. The lower GHG production in the non-frozen Alas lake sediments 
resulted from advanced OM decomposition during Holocene talik development. Furthermore, we found that drivers of CO₂ and CH₄ production differ following thaw. 
Our results suggest that GHG production from TOC-poor mineral deposits, which are 

spread throughout the Arctic, can be substantial. Therefore, our novel data are 
relevant for vast ice-rich permafrost deposits vulnerable to thermokarst formation.

KEYWORDS
anaerobic, greenhouse gases, incubation experiments, lipid biomarkers, organic matter 
degradation, permafrost thaw, talik, Yakutia
Estop-Aragonés & Blodau, 2012; Waldrop et al., 2010) and only few studies have incubated permafrost sediments from >10 m deep (Dutta et al., 2006; Knoblauch et al., 2013; Lee et al., 2012). Even though several studies showed that aerobic decomposition released more OC than anaerobic decomposition over short time scales (months–years; Knoblauch et al., 2013; Lee et al., 2012; Schädel et al., 2016), CH$_4$ emissions from permafrost regions are projected to become more important on longer time scales (decades–centuries; Dean et al., 2018; Knoblauch et al., 2018). Furthermore, Knoblauch et al. (2018) showed that after multiple years, the production of carbon dioxide (CO$_2$) carbon equivalents is higher under anaerobic conditions when taking into account the much stronger global warming potential of CH$_4$ compared to CO$_2$ (28 over a 100-year timescale; Myhre et al., 2013). Moreover, increased thermokarst lake initiation, especially in the continuous permafrost zone (Nitze et al., 2017), might lead to a landscape-scale increase of anaerobic decomposition processes.

Here, we studied GHG production, long-chain n-alkanes, branched GDGTs, and archaeal microbial markers in talik sediments to determine the OM characteristics of Yedoma sediments thawed under subaquatic conditions underneath two different thermokarst lakes. We focused on the following research questions: (1) can we characterize the OM degradability of thawed Yedoma deposits using biomarker analyses and (2) how much GHG is produced in these deposits after thaw? For the first time, to the best of our knowledge, we present OC turnover data from Siberian Yedoma talik sediments. Furthermore, the combination of biomarker degradation proxies and incubation data from >10 m deep permafrost sediments that are thawed underneath a thermokarst lake is unique so far.

### 2 MATERIALS AND METHODS

#### 2.1 Study area

The study site is located in Central Yakutia (Sakha Republic), East Siberia, about 80 km southeast from the city of Yakutsk (Figure 1a). The region is part of the continuous permafrost zone with permafrost reaching several hundred meters in depth. The Yukechi study site (61.76495°N, 130.46664°E) includes drained lake basins (alases) and thermokarst lakes formed in Yedoma uplands with ice-rich deposits tens of meters thick that cover about two thirds of the study area (Soloviev, 1973; Ulrich et al., 2019; Windirsch et al., 2020).

Taiga vegetation, predominantly larch trees and sparse pine and birch communities, dominate the region. Underneath the forest, the active layer reaches a thickness of ~1 m (Fedorov et al., 2014). The drained lake basins are covered by a steppe-like grass vegetation and are characterized by an active layer reaching >2 m thickness (Soloviev, 1959). The region is characterized by a strong continental climate with a mean annual air temperature of −10.7°C (mean January: −41°C, mean July: 18.5°C) and a mean annual precipitation of 246 mm (period: 1982–2012; Yakutsk Weather Station: RSM00024959; Climate-data.org, 2020).

Two different types of thermokarst lakes were selected for this study: an Alas lake and a Yedoma lake (Figure 1b). The Alas lake is located within the Yukechi Alas, which is a Holocene thermokarst basin of ~300–500 m in diameter and ~10–15 m lower compared to surrounding Yedoma uplands (Ulrich et al., 2019). The Alas lake has a diameter of ~57 m, a surface area of 1 ha and an average water depth.

![FIGURE 1](location of study sites. (a) Location of study area (pink square) in Central Yakutia close to Yakutsk in Siberia (globe in lower left corner). (b) Close-up of study area with coring location: YU-L7 below Alas lake (yellow circle) and YU-L15 below Yedoma lake (orange circle). (c) Digital elevation model of study area with core locations indicated. Source of (a) and (b): Sentinel-2 (ESA) 2018-08-03, (c): Ulrich et al. (2017))
of 1.9 m (measured in summer 2014). The Yedoma thermokarst lake is a younger lake and is located on the Yedoma uplands. Its lake level lies approximately 18 m higher than the Alas lake level (Figure 1c). With a diameter of ~43 m and surface area of 0.6 ha, the Yedoma lake is smaller than the Alas lake but deeper (average water depth of 3.7 m). Using historical aerial imagery, this lake was estimated to be about 70 years old and developed in a small forest-free grassland area (Ulrich et al., 2017).

Thermokarst lake development in the Yukechi Alas has been monitored by the Melnikov Permafrost Institute in Yakutsk since 1992 (Fedorov & Konstantinov, 2003). Previous research by Ulrich et al. (2017) included remote sensing as well as field and statistical analysis of thermokarst lake change in the Yukechi Alas. In addition, Windirsch et al. (2020) assessed the local sediment genesis and its effect on permafrost carbon storage by analyzing sediment cores taken from Yedoma upland sediments in the close vicinity of the studied Yedoma lake YU-L15 (140 m SSW) and Alas deposits adjacent to Alas lake YU-L7 (110 m NNE; Figure S1).

2.2 | Field work

During the field campaign to Yukechi in March 2015, we retrieved two sediment cores from the bottom of two thermokarst lakes (Figure 1b). Drilling was carried out from the lake ice using a URB2-4T drilling rig mounted on a truck. The cores were drilled with 15.7 cm diameter for the uppermost parts and 8 cm in diameter in the lower parts. The sediment cores were removed from the core barrel using compressed air. Sediment core YU-L7 was 17.7 m long and retrieved from the Alas lake (61.76397°N, 130.46442°E). At the sampling position, the Alas lake had an ice cover of 70 cm and a water depth of 2.3 m on March 23, 2015. The sediment core consisted entirely of unfrozen sediments, which are part of the talik underneath the thermokarst lake. Sediment core YU-L15 was 17.2 m long and taken from the Yedoma upland lake (61.76086°N, 130.47466°E). This lake had a 71-cm thick ice cover and a water depth of 4.3 m at the sampling position on March 23, 2015. The sediment core consisted of unfrozen talik sediments down to a depth of 8.1 m followed by frozen sediments below. The cores were described visually in the field, packed in plastic core wrapper, and kept frozen.

In both lakes, the ice was covered by ~35 cm snow. Directly underneath the ice cover, the pH and electrical conductivity of the lake water were respectively 8.0 and 2.45 mS cm$^{-1}$ for the Alas lake and 8.3 and 2.29 mS cm$^{-1}$ for the Yedoma lake.

2.3 | Laboratory analyses

We cut the sediment cores into halves with a band saw and cleaned the cutting surfaces by removing the material that was superficially thawed during the saw process. Then, we subsampled the cores for different biogeochemical laboratory analyses (Figure 2). Ten sediment samples were taken from each core (every 1–2 m according to the stratigraphy) and analyzed for total OC (TOC) content, lipid biomarkers, and anaerobic GHG production. Radiocarbon ages from both sediment cores were published separately (Jongejans et al., 2019). Sedimentological and geochemical data are being prepared for publication in an additional study.

2.3.1 | Organic carbon content

Sediment samples ($n = 20$) were analyzed for total carbon (TC) and total nitrogen (TN) content with an elemental analyzer (VarioMAX Elementar Analyser). The total inorganic carbon (TIC) content was quantified from the amount of CO$_2$ that was released after sample treatment with phosphoric acid. The TOC content was calculated by subtracting the TIC from the TC and is expressed in weight percentage (wt%). We calculated the TOC to TN weight ratio, which will be referred to as the C/N ratio. This ratio can be used as OM content.
degradation proxy where the C/N ratio decreases with decomposition (e.g., Gundelwein et al., 2007).

In addition, we extracted 3–10 ml pore water from sediment samples from both cores (n = 57) that were thawed overnight at 20°C using rhizon samplers (membrane pore size: 0.12–0.18 μm). These samples were taken from different depths than the samples for lipid biomarkers and incubations but from same stratigraphic zones. The samples were acidified with 20 μl hydrochloric acid (35%) to pH 2 and kept cool at 4°C. The dissolved OC (DOC) content was measured as non-purgeable OC fraction using a Total Organic Carbon Analyzer TOC-VPCH/CPN (Shimadzu) and is expressed in mg L⁻¹.

2.3.2 | Lipid biomarkers

**Extraction and measurement**

Sediment samples (n = 20) from the main stratigraphic units were analyzed for n-alkanes and lipid biomarkers (Figure 2). Approximately 8 g of dried, ground sediments were extracted using accelerated solvent extractions (ASE) with dichloromethane/methanol (DCM/MeOH; 99:1 v/v) using a Dionex 200 ASE Extractor. Each sample was held in a static phase (5 min heating) for 20 min (75°C, 5 MPa). Afterward, the samples were concentrated using a TurboVap500 at 42°C. We removed asphaltenes by dissolving the extracts in DCM/MeOH (99:1 v/v) and adding a 40× excess of n-hexane, leading to precipitation of n-hexane-insoluble substances. Four internal standards were added for compound quantification: 5α-androstane, ethylpyrene, 5α-androstan-17-one, and erucic acid. We separated the maltene fraction (n-hexane soluble compounds) by medium pressure liquid chromatography (Radke et al., 1980) into an aliphatic, aromatic and NSO (nitrogen, sulfur, and oxygen containing) fraction using n-hexane.

The n-alkanes were measured in the aliphatic fraction by gas chromatography-mass spectrometry (GC-MS) using a Trace GC Ultra coupled to a DSQ MS (Thermo Electron Corporation) with helium as carrier gas (1 ml min⁻¹). The GC was equipped with a cold injection system and a BPX5 (SGE) column (50 m × 0.22 mm × 0.25 μm). The injector temperature was programmed from 50°C to 300°C at a rate of 10°C s⁻¹. The oven was heated from its initial temperature of 50°C (1 min isothermal) to 310°C with a heating rate of 3°C min⁻¹ (30 min isothermal). The MS was operated in the electron impact ionization mode at 50 eV. Full-scan mass spectra were obtained from m/z 50 to 600 Da with a scan rate of 2.5 scans s⁻¹. Compounds were identified and quantified using the software Xcalibur™.

The branched and isoprenoid GDGTs, as well as the dialkyl glycerol diether lipid (archaeol; Figure S2) were measured in the NSO fraction using a Shimadzu LC-10AD high-performance liquid chromatography coupled to a Finnigan TSQ 7000 mass spectrometer via an atmospheric pressure chemical ionization interface (corona current of 5 mA [5 kV], vaporizer T of 350°C, capillary T of 200°C, nitrogen sheath gas at 60 psi, no auxiliary gas). The sample was separated at 30°C in a column oven using a Prevail Cyano column (2.1 × 150 mm, 3 μm; Alltech) equipped with a pre-column filter. Compounds were eluted isocratically with n-hexane (99%) and isopropanol (1%) for 5 min, followed by a linear gradient to 1.8% isopropanol in 40 min and in 1 min to 10% isopropanol. It was held for 5 min to clean the column, set back to initial conditions in 1 min, and held for 16 min for equilibration. The flow rate was set to 200 μl min⁻¹. Mass spectra were obtained by selected ion monitoring in the positive ion mode and at a scan rate of 0.33 scans s⁻¹. Compounds were identified using the software Xcalibur™ and quantified using a daily-measured external archaeol standard. Here, we present the concentration of branched GDGTs, isoGDGT-0, and archaeol.

From both sediment cores, we selected five samples for open-system pyrolysis after Horsfield et al. (1989) and Stapel et al. (2018). The bitumen-free ASE residues were pyrolyzed (temperatures: 300–600°C) and the pyrosilates, which were trapped with liquid N₂, were measured on a pyrolysis gas chromatograph (Agilent GC 6890A chromatograph) equipped with a flame ionization detector (Py-GC-FID). The compounds were identified and quantified relative to n-butane external standard using the Agilent ChemStation software. We integrated short (C₁₋C₄), intermediate (C₅₋C₁₃), and longer (≥C₁₄) n-alkanes and n-alk-1-enes. In immature OM, these aliphatic compounds represent aliphatic side chains as well as alcohols and fatty acids formerly covalently linked via ether or ester bonds to the complex organic matrix.

**Lipid biomarker indices**

From the n-alkane concentrations, we calculated two indices. The ACL of n-alkanes is a measure of the chain length distribution (Poynter & Eglinton, 1990), and indicates the OM source. It was calculated according to Equation (1) where i is the carbon number.

\[
\text{ACL}_{23-33} = \frac{\sum C_i \cdot C_i}{\sum C_i}
\]

(1)

The CPI is an index for OM degradability. Higher values typically indicate better preserved OM and the ratio decreases with degradation (Bray & Evans, 1961; Marzi et al., 1993). The CPI was calculated according to Equation (2).

\[
\text{CPI}_{23-33} = \frac{\sum \text{odd } C_{23-31} + \sum \text{odd } C_{25-33}}{2 \cdot \sum \text{even } C_{24-32}}.
\]

(2)

2.3.3 | Incubations

From the 20 sediment samples, 17 samples were used in the incubation experiments to estimate GHG production from degrading OM. From each sample, we prepared three replicates for quality control. The frozen samples were thawed at 4°C overnight under an oxygen free atmosphere in a glovebox. After homogenization, approximately 10 g of sediment was weighed into 120 ml glass bottles and 10 ml
of autoclaved tap water added to each bottle with sediment. The 51 bottles were sealed with rubber stoppers and the headspace gas was exchanged with pure nitrogen to create an anaerobic atmosphere, comparable to the ambient conditions in the talik sediments below the thermokarst lakes. Samples were incubated anaerobically at 4°C for 1 year. CO₂ and CH₄ concentrations were measured biweekly in a 250-µl subsample using gas chromatography with an Agilent GC 7890A equipped with an Agilent HP-PLOT Q column. We used a thermal conductivity detector and flame ionization detector for measuring CO₂ and CH₄ concentrations, respectively, helium as a carrier gas, and an oven temperature of 100°C. From the concentrations, we calculated the average CH₄ and CO₂ production of the three replicates, which are expressed in µg CH₄-C and CO₂-C g⁻¹ dry weight and g⁻¹ TOC (an explanation of the calculations is provided in Supplement S1).

**2.4 Statistical analysis**

We identified the stratigraphical units of the two sediment cores by constrained hierarchical clustering of all measured parameters. We carried out this statistical clustering in R v. 3.6.1 using the "chclust" function in the package "rioja" with the method "coniss" (Juggins, 2020). We calculated the correlation (Pearson) between all parameters and reported the statistically significant correlations (p < 0.05). Also, we compared the two sediment cores and the units using Kruskal-Wallis and Mann-Whitney Wilcoxon nonparametric tests. Using a forward-selection stepwise multiple regression, we tried to identify what parameters explained the most variance in the cumulative CH₄ and CO₂ production. We carried out the regression in R using the package "MASS" with the function "stepAIC" (Venables & Ripley, 2002) and direction "forward". This method iterates the Akaike information criteria (AIC) for the regression model when taking out one parameter at the time. The AIC statistic is a method to evaluate how well the model fits. We calculated the relative importance of the significant variables with the function "calc.relimp" from the package "relaimpo" (Groemping, 2006).

**3 RESULTS**

**3.1 Organic matter characteristics**

**3.1.1 Alas lake sediment core YU-L7**

Core YU-L7 was divided into a bottom unit including sediments from 1769 to 1331 cm below the sediment surface (bss), a middle unit from 1125 to 518 cm bss and a top unit from 362 to 290 cm bss (Figure 3). This division was based on constrained hierarchical clustering of all measured parameters (Figure S3). The TOC ranged between 0.3 and 1.4 wt% (median: 0.5 wt%; Figure 4a). The TOC was slightly higher in the lowermost three samples (1713–1488 cm bss) and those at the top compared to the intermediate samples between 1315 and 778 cm bss. The C/N ratio had its maximum (13.2) as well as its minimum (8.9) in the top unit (Figure 4b). In the bottom unit, the C/N varied between 9.1 and 11.0 (core median: 9.7). The DOC concentration showed a lot of variation ranging from 51 to 1620 mg L⁻¹ with highest concentrations at the base of the core (1694–1185 cm bss; median: 448 mg L⁻¹; Figure 4c). In the top unit of YU-L15, DOC values were between 437 and 615 mg L⁻¹. The n-alkane concentration was lowest in the upper sample at 170 cm bss (2.2 µg g⁻¹ dw) and highest at 353 cm bss (median: 8.8 µg g⁻¹ dw; Figure 4d). The brGDGT concentration was highest in the upper sample (58.7 ng g⁻¹ dw) and lowest at 1315 cm bss (median: 993 µg g⁻¹ TOC). The archaeol concentration was highest at 591 cm bss (median: 8.8 µg g⁻¹ dw; Figure 4h) and isoGDGT-0 concentration (Figure 4i) showed a very similar pattern with the highest
concentration at 353 cm bss (26.1 and 6.1 ng g\(^{-1}\) dw, respectively) and a median of 2.8 and 1.1 ng g\(^{-1}\) dw, respectively. Per gram TOC, the maxima were 1861 and 433 ng g\(^{-1}\) for archaeol and isoGDGT-0, respectively. Following pyrolysis, samples with the highest TOC values (353-1488 cm bss) are also among those with the highest aliphatic character (Figure 5).
FIGURE 4  Biogeochemical parameters of Yedoma lake sediment core YU-L15. (a) Total organic carbon (TOC) content, (b) ratio of carbon to nitrogen content (C/N), (c) dissolved organic carbon (DOC) content of original pore water samples, (d) \( n \)-alkane concentration per gram dry weight (\( g^{-1} \) dw) and per gram TOC (orange triangles), (e) \( n \)-alkane average chain length, (f) \( n \)-alkane carbon preference index (CPI), (g) branched glycerol dialkyl glycerol tetraether (brGDGT) concentration \( g^{-1} \) dw and \( g^{-1} \) TOC (orange triangles), (h) archaeol concentration \( g^{-1} \) dw and \( g^{-1} \) TOC (orange triangles), and (i) isoGDGT-0 concentration \( g^{-1} \) dw and \( g^{-1} \) TOC (orange triangles). Units indicated on right: top (T) and bottom (B; gray area), boundary talik to permafrost (PF) indicated with gray dashed line.
3.2 | Greenhouse gas production

3.2.1 | Alas lake sediment core YU-L7

In total, we measured anaerobic GHG production of 10 samples from the Alas lake sediment core YU-L7 (Figure 6). CH₄ production after 1 year was highest (81.3 ± 38.2 µg CH₄·C g⁻¹·dw; mean ± standard deviation) in the sample closest to the sediment surface in the top part at 290 cm bss (Figure 6a). Furthermore, CH₄ production also exceeded 20 µg for the sediments at 1048 cm (54.5 ± 42.7 µg CH₄·C g⁻¹·dw) and 1769 cm bss (38.7 ± 66.3 µg CH₄·C g⁻¹·dw).

When normalized to gram TOC, CH₄ production was highest in the middle part of the core at 1048 cm bss (13.2 ± 10.4 mg CH₄·C g⁻¹·TOC). There was no trend in depth observed. For the three samples with the highest CH₄ production, the maximum production rates ranged from 0.62 to 0.91 µg CH₄·C g⁻¹·dw day⁻¹ (Figure 6b). After ~350 days, the rates of these samples decreased. In samples yielding higher CH₄ concentrations, CH₄ production started after ~200 days and increased exponentially. In 6 out of 10 samples, the CH₄ rates increased over time. Cumulative GHG production and rates for all replicates are shown in the supplement (Figures S6–S22).

CO₂ production was highest in the top part of the sediment core at 362 cm bss (227.15 ± 248.8 µg CO₂·C g⁻¹·dw), closely followed by the sample at 1446 cm bss in the bottom unit (197.6 ± 225.7 µg CO₂·C g⁻¹·dw; Figure 6c). In the middle unit, CO₂ production was very low. The CO₂ production per gram TOC was highest at 1446 cm bss (30.5 ± 34.8 mg CO₂·C g⁻¹·TOC). In contrast to CH₄, CO₂ was produced from the start of the incubation and after which the rates decreased (e.g., Figure S6). Maximum rates of all samples varied between 1.52 and 3.17 µg CO₂·C g⁻¹·dw day⁻¹ (Figure 6d).

3.2.2 | Yedoma lake sediment core YU-L15

Anaerobic GHG production was measured on seven samples from the Yedoma lake sediment core YU-L15 (Figure 7). CH₄ production in the Yedoma lake sediment core YU-L15 was highest in the top of the core (Figure 7a). The maximum was at 353 cm bss with 87.0 ± 44.0 µg CH₄·C g⁻¹·dw. The sample at 170 and 966 cm bss also showed substantial CH₄ production (64.1 ± 57.2 and 41.6 ± 26.9 µg CH₄·C g⁻¹·dw, respectively). The CH₄ production normalized to gram TOC was highest in the sample at 966 cm bss (18.8 ± 12.2 mg CH₄·C g⁻¹·TOC). Like in the Alas lake core, CH₄ production started after 200 days for most samples and increased exponentially (e.g., Figure S6). In five samples, the CH₄ production rates increased over time and were highest at the end of the incubations from 300 days and onward. The three samples with the highest cumulative CH₄ production (353, 170, and 966 cm bss) also had the highest rates ranging from 0.56 to 1.15 µg CH₄·C g⁻¹·dw day⁻¹ (Figure 7b).

The CO₂ production was highest in the bottom of the core (Figure 7c). The maximum CO₂ production was observed in the sample at 1488 cm bss (561.5 ± 527.4 µg CO₂·C g⁻¹·dw). In the
sample at 1076 cm (407.7 ± 680.1 µg CO₂-C g⁻¹ dw) and 170 cm bss (350.2 ± 346.9 µg CO₂-C g⁻¹ dw). CO₂ production was also high. All samples produced more than 50 µg CO₂-C, except for the sample at 1594 and 966 cm bss. The production per gram TOC was highest at 1076 cm bss (120.6 ± 201.2 mg CO₂-C g⁻¹ TOC). CO₂ production started at the beginning of the incubation and increased gradually over time. Maximum CO₂ production rates ranged from 1.05 to 7.67 µg CO₂-C g⁻¹ dw day⁻¹ (Figure 7d).

3.2.3 | Carbon mineralization

Total anaerobic C production ranged from 0.02 to 0.23 mg g⁻¹ dw in YU-L7 (max: 0.08 mg C g⁻¹ dw as CH₄) and from 0.02 to 0.56 mg g⁻¹ dw in YU-L15 (max: 0.09 mg C g⁻¹ dw as CH₄). After 1 year, on average, 2.3 ± 3.1% of the initial carbon was mineralized to CO₂ and 0.4 ± 0.6% to CH₄ (Figure S4). In the first 100 days, 10 ± 21% of the cumulative CH₄ was produced. Production of CH₄ commenced after 200 days and CH₄ production rates were highest after 300 days in most samples. In six samples (YU-L7: 1125, 1446, and 1652 cm bss; YU-L15: 778, 1076 and 1488 cm bss; Figures S10, S12, S14, S18, S20, and S22), the CH₄ production was higher in the first week compared to the following weeks.

The CO₂ production rates were highest in the first 100 days in 8 out of 17 samples. In four samples, the rates were highest after 300 days. Within the first 100 days, 49 ± 28% of the cumulative CO₂ was produced. CO₂ production was generally highest at the beginning of the incubations and gradually decreased over time.

3.3 | Statistical correlation and regression

Considering both cores, the TOC correlated positively with n-alkane, brGDGT, archaeol, and isoGDGT-0 concentration (p < 0.01; Figure S5). The CO₂ production was correlated with the ACL (R: −0.56, p < 0.05) and with the DOC content in adjacent samples (R: 0.58, p < 0.05). The CH₄ production was negatively correlated with the depth (R: −0.58, p < 0.05).

Using the forward-selection stepwise multiple regression method, we found that the CH₄ production could not be explained by our data; no fitting model was found. The cumulative CO₂ production can be explained by a generalized linear regression model as shown in Equation (3). This model describes 73.5% of the variance of the cumulative CO₂ production, of which 58.5% is explained by the DOC content and the ACL alone. This clear relation of the CO₂ production with a high DOC and low ACL is also shown in Figure 8.
The rate and efficiency of hydrolysis from POC to DOC as well as the size and quality of the DOC pool are of utmost importance for GHG production since microbes mainly metabolize DOC size fractions (Battin et al., 2008). Therefore, DOC in pore water is readily bioavailable for microbial degradation upon talik formation and hence a very important OM fraction in GHG production process. Recent studies showed that DOC from thawing permafrost is highly biodegradable with the biolabile fractions composing ~20%–53% for Alaskan sites (Drake et al., 2015; Ewing et al., 2015) and 34%–50% for Siberian sites (Spencer et al., 2015; Vonk et al., 2013). These studies found that the biolabile DOC fraction was lost mainly in the first 1–2 weeks upon thaw. Furthermore, it was shown that ancient DOC originating from Pleistocene permafrost was more susceptible to decomposition than modern DOC (Mann et al., 2015; Vonk et al., 2013). The relatively high DOC contents in the Pleistocene Yedoma sediments in the bottom of core YU-L15 in combination with the generally high biolability of Yedoma OM could therefore be a reason for the substantial GHG production observed. The generally higher GHG production per gram TOC in contrast to unfrozen or Alas lake sediments (Figures 3 and 4) supports the relatively high bioavailability of Yedoma OM. Whereas the decomposition of labile DOC seems to contribute to the GHG production upon initial talik formation, GHG production at later stages of talik formation is primarily driven by the breakdown of the POC fraction. Only very few studies focus on the breakdown of DOC, and the interaction between POC and DOC decomposition is not well understood. Nevertheless, it was shown that POC turnover is relevant for DOC decomposition (Attermeyer et al., 2018; Richardson et al., 2013).

In contrast to the TOC, the DOC values from the frozen Yedoma sediments of YU-L15 are very high (median: 373 mg L$^{-1}$, max: 1620 mg L$^{-1}$; Figure 3), yet comparable to pore water from Yedoma deposits on Buor Khaya, northeastern Siberia (median: 317 mg L$^{-1}$, max: 1371 mg L$^{-1}$; Schirrmeister et al., 2017). In addition, Ewing et al. (2015) reported high maximum DOC values in Alaskan Yedoma pore water (median: 618 mg L$^{-1}$, max: 1551 mg L$^{-1}$). For comparison, other studies from northeastern Siberia reported much lower pore water DOC values such as for early to middle Weichselian sediments on the Cape Mamontov Klyk, ranging from 4 to 305 mg L$^{-1}$ (Mitzscherling et al., 2019), or for Samoylov Island, ranging from 57 to 288 mg L$^{-1}$ (Liebner et al., 2008).

The characteristics of the sediments directly below alas lakes are often the result of several subsequent lake generations at a location with sometimes lacustrine and subaerial deposition alternating (Katsanov et al., 1979; Lenz et al., 2016; Soloviev, 1959). In many thermokarst lake regions, multiple thermokarst lake generations over the past centuries to millennia led to repeated thawing and refreezing of the sediments (e.g., Jones et al., 2012) and therefore likely also recurring talik formation (Grosse et al., 2013). For the Yukechi Alas, the domination of long-chain alkanes ($n$-C$_{29}$ and $n$-C$_{31}$) throughout both cores, indicating OM from higher terrestrial plants, suggests that the Alas lake sediments are primarily thawed Yedoma sediments. However, dated macrofossils at 290 cm bss yielded a Holocene age (3.75 ± 0.12 cal kyr BP; Jongejans et al., 2019), suggesting a recent productivity signal in these sediments. The sediments at 518 cm bss had an age of 13.53 ± 0.66 cal kyr BP and all dated sediments below yielded $^{14}$C ages >24 cal kyr BP.

With thaw and talik formation at our Alas site, microbial decomposition of OM led to GHG production. Furthermore, the drying of the basins could have favored aerobic conditions and OM cycling as well as potentially permafrost re-aggradation (Lee et al., 2012). This, in combination with the low TOC in the Yukechi Alas, could explain
the low DOC values in the Alas core. During phases of intensified lake formation, interactions between pore water and the mineral phase could have led to liberation of DOC and the microbial transformation of the most biolabile fraction into GHG.

The sediments underneath the Yedoma lake have been thawed from the top down only for the last ~70 years for the first time since deposition (Ulrich et al., 2017), explaining the rather shallow talik compared to the Alas lake. The sediments at 778 cm bss of the Yedoma lake core, which was part of the talik, were attributed to the bottom cluster. This suggests that the studied OM characteristics in this sample are still more similar to the frozen sediments underneath than to the talik sediments above.

The frozen sediments in the bottom part have likely not been thawed since permafrost formation in the late Pleistocene. This suggests OM was better preserved in the permafrost sediments of the Yedoma lake compared to the top of the Alas lake sediments (Schuur et al., 2009). This was corroborated by a higher C/N ratio in the Yedoma lake sediments and in the bottom of the Alas lake sediments compared to the top and middle of YU-L7 (p < 0.05; Figures 3 and 4). However, we found no significant correlation between the OC loss (Figure S4) and the C/N ratio. This might be the result of the low TOC content in the Yukachi sediments; consequently, TOC and the C/N ratio. This might be the result of the low TOC content in the Yukachi sediments; consequently, TOC and the C/N ratio.

We did not see the better preservation signal of the OM in the Yedoma lake core compared to the Alas lake core (Figures 3 and 4). Potentially, not enough time has passed since deposition for maturation (Bray & Evans, 1961). The CPI must hence be a result of the original signal and depositional environment of the OM rather than permafrost thaw history (Jongejans et al., 2020).

Stapel et al. (2018) showed that the OM from Yedoma deposits on Bol’shoy Lyakhovsky Island had a relatively high aliphatic proportion, which suggests the OM is more easily degradable compared to more aromatic OM. Our pyrolysis experiments showed a clear connection between the TOC content and the aliphatic character, which suggests that these samples might contain more biolabile OM.

### 4.1.3 Presence of methanogenic communities

Archaeol and isoGDGT-0 concentrations were significantly higher in the Alas compared to the Yedoma lake sediments (p < 0.05 and p < 0.01, respectively; Figures 3 and 4). Archaeol and isoGDGT-0 are breakdown products of intact polar membrane lipids and represent the past archaeal biomass as a degradation product (Bischoff et al., 2013; Stapel et al., 2018). Archaeol, one of the main core membrane lipids of archaea, was used to infer methanogenic abundance specifically before (Bischoff et al., 2013; Pancost et al., 2011). Increased isoGDGT-0 and archaeol concentrations in thawed sediments can indicate a mixture of past and present archaea including methanogens. The higher archaeal marker concentration in the Alas lake core suggests that the methanogenic communities were likely established after talik formation.

In previous studies, a positive correlation was found between CH$_4$ production in thawing permafrost and the presence of methanogenic archaea (Carnevali et al., 2015; Holm et al., 2020; Knoblauch et al., 2018). In our study, the CH$_4$ production was higher in the talik sediments of the Yedoma lake core. Lower CH$_4$ and CO$_2$ production in YU-L7 compared to YU-L15 suggests that the biolabile fraction of OM was already largely decomposed in a talik in previous thermokarst lake stages. This is corroborated by the lower C/N ratio in the Alas lake sediments. The moderate concentrations in the Yedoma lake core between 1161 and 966 cm bss might result from microbial activity during sedimentation (Bischoff et al., 2013). Holm et al. (2020) showed that microbial communities established prior to freezing could lead to an earlier start and stronger CH$_4$ production compared to sediments where no prior communities were established. Further research is needed to study the interactions between present and past microbial communities, and the factors controlling GHG production in thawing permafrost.

### 4.2 Greenhouse gas production

The 1-year-long incubation experiments showed distinct differences between the first-generation and multiple-generation thermokarst lake sediments. Both CH$_4$ and CO$_2$ production were higher in the Yedoma lake sediments compared to the Alas lake sediments (3 and 1.5 times higher mean, respectively). The GHG production did neither correlate with the TOC content nor with the biomarker concentrations and indices. Previous incubation studies of permafrost sediments found a positive correlation between CO$_2$ production and TOC (Knoblauch et al., 2013; Lee et al., 2012; Walter Anthony et al., 2016). These studies, however, analyzed sediment samples with higher TOC contents compared to our study (median: 1.2, 5.0, and ~4 wt%, respectively). Furthermore, we compared sediment samples that have undergone different depositional conditions and thaw legacy, which might explain the lack of correlation between TOC content and GHG production.

#### 4.2.1 Carbon dioxide production

CO$_2$ production was highest in the bottom of YU-L15 (Figure 4). This is likely because the sediments were thawed for the first time since deposition, and the presence of readily bioavailable DOC after thaw. The latter is corroborated by the positive correlation between the initial DOC values in samples adjacent to the incubation samples and the CO$_2$ production, supporting the rapid turnover of biolabile DOC fractions (Vonk et al., 2013). The CO$_2$ production from the still frozen Yedoma sediments in our core (1713–996 cm bss) is in the same order of magnitude as from Pleistocene sediments in the Lena Delta (0.13 ± 0.06 mg CO$_2$·C g$^{-1}$ dw; Knoblauch et al., 2013) and from mineral soils in Alaska and Siberia (0.34 ± 0.13 mg CO$_2$·C g$^{-1}$ dw; Lee et al., 2012). When expressed on a bulk carbon basis, however, the CO$_2$ production in the permafrost sediments of the Yedoma lake
This means that despite the low carbon content of these sediments, the overall mineral OM has a high potential for being degraded into CO₂. Nevertheless, the percentage of initial C that was mineralized to CO₂ was low in comparison with -year-long incubation studies of organic-rich active layer sediments as reported by Schädel et al. (2014; 6% loss) and Faucherre et al. (2018; 8% loss).

The median CO₂ rates over time in the bottom unit of the Yedoma lake core was 50 µg CO₂-C g⁻¹ TOC day⁻¹. While some anaerobic incubations studies with permafrost samples had much lower CO₂ production rates, median: 1.6–3.6 µg CO₂-C g⁻¹ TOC day⁻¹; Knoblauch et al., 2013; Zona et al., 2012), other studies found rates in the same order of magnitude as our data such as Lupascu et al. (2012) and Santruckova et al. (unpublished data; median 37.8 and 68.6 µg CO₂-C g⁻¹ TOC day⁻¹, respectively). However, of these studies, only Knoblauch et al. (2013) reported CO₂ production in sediments >1 m bss (i.e., down to 25 m depth).

The relatively high GHG production at the uppermost sample (290 cm bss) of the Alas lake sediment core might be explained by the input of Holocene OM (see Section 4.1.2) during a previous thermokarst lake stage where methanogenic communities were established, which might have a priming effect on the older carbon in these sediments (Wild et al., 2014).

4.2.2 Methane production

In most of our samples, a significant start of CH₄ production could be recognized only after 200 days (Figures S5 and S6). Previous incubation studies also observed this lag phase and explained it as the result of the low initial abundance of methanogens in the sediments, which increases with thaw (Knoblauch et al., 2013, 2018; Treat et al., 2014; Waldrop et al., 2010). Interestingly, the frozen sample below the talik boundary in the Yedoma lake core (996 cm bss), showed the highest CH₄ production rate (252.2 µg CH₄-C g⁻¹ TOC day⁻¹). As these sediments were frozen continuously since deposition and permafrost incorporation, these findings suggest that methanogenic communities were established here prior or during deposition and survived while being freeze-locked (Holm et al., 2020). In this particular sample, methanogenic taxa were likely present that produce CH₄ using very low substrate TOC concentrations as reported from low-temperature incubations of Arctic soils (Blake et al., 2015), but further detailed microbial analyses are required to substantiate this hypothesis.

CH₄ production was highest in the top of Yedoma lake core (Figure 7), which is corroborated by a negative correlation between CH₄ production and the depth bss in this core. This fits well to thaw front migration with talik formation and subsequent gradual population of methanogenic communities. In their study of methanogenesis response to permafrost thaw, Holm et al. (2020) found that CH₄ production was not correlated to C content, but rather to paleoenvironmental conditions. They argued that CH₄ production is more vulnerable to disturbance than anoxic CO₂ production, because methanogenesis is restricted to a very small group of archaea whereas there are many different groups of microorganisms producing CO₂ under anoxic conditions. Their findings show that anaerobic GHG release from thawing permafrost is complex and not yet well understood.

To our knowledge, Heslop et al. (2015) present the only other CH₄ production rates from Yedoma deposits that were thawed in a talik. They measured C release rates as CH₄ along a talik profile below an Alaskan first-generation thermokarst lake. In contrast to our data, Heslop et al. (2015) found highest CH₄ production rates in the recently thawed sediments (59.6 ± 51.5 µg CH₄-C g⁻¹ TOC day⁻¹) compared to the transitional permafrost (15.3 ± 9.1 µg CH₄-C g⁻¹ TOC day⁻¹) and the thawed Yedoma sediments (17.9 ± 13.6 µg CH₄-C g⁻¹ TOC day⁻¹). Our data did not show such a trend: sediments from the recently thawed permafrost (778 cm bss) had a low maximum CH₄ production rate (2.5 µg CH₄-C g⁻¹ TOC day⁻¹). However, the rates from the top of YU-L15 (81.8-135.1 µg CH₄-C g⁻¹ TOC day⁻¹) were much higher. Nevertheless, the CH₄ production is not necessarily directly linked to CH₄ release, since a part of the produced CH₄ might be oxidized in the sediment column before being released into the atmosphere (Winkel et al., 2019).

The CH₄ production rates in the bottom unit of the Yedoma lake core (median: 0.02 µg CH₄-C g⁻¹ TOC day⁻¹) were much lower compared to previously published CH₄ rates in 4°C permafrost incubation studies (0.12–0.56 µg CH₄-C g⁻¹ TOC day⁻¹; Knoblauch et al., 2013; Lupascu et al., 2012; Santruckova et al., unpublished data; Zona et al., 2012).

4.3 GHG links with other parameters and outlook

Using the generalized linear regression models, we found that CO₂ production was mainly explained by the ACL and the DOC content: sediments with the lowest ACL and highest DOC content produced the most CO₂ (Figure 8). This suggests that these parameters describe the lability of the OM best for our study. While the DOC seems to indicate the abundance of bioavailable OM (see Section 4.1), the ACL signal might represent a more labile OM source fraction from the respective surrounding ecosystem.

In some cases, we did find high archaeal markers or a strong aliphatic character corresponding to a higher CH₄ production, but in other samples, this was the exact opposite. We did not find significant correlations between biomarker distribution and CH₄ production (Figure S5). Therefore, we assume that the variation must be explained by a complex interplay of different external factors controlling GHG production. The varying sedimentation history of the Yukichi sediments might play an important role in this, as different depositional mechanisms could have resulted in OM from different sources (e.g., transported vs. in situ, different types of plants) leading to a mixture of labile and recalcitrant OM. This could have led to an activation of OM in some (sub-)samples but not in others. For the
samples with increased bacterial and archaeal markers but low GHG production, the biomarkers might indicate past microbial activity rather than the presence of active methanogenic communities. The reactivation of such paleo-active horizons depends on factors which are not yet fully understood, but intense remineralization in the past as indicated by the high lipid biomarker concentrations might have strongly depleted labile organic compounds from the overall OM pool. Further research into intact polar lipids could help to quantify the interaction between present and past microorganisms (Bischoff et al., 2013; Stapel et al., 2018).

In contrast to our incubation experiment, external factors could influence the oxygen content of the sediments as well as the soil microbial communities under in situ conditions. Differences between the temperature used in our incubations (4°C) and the actual temperature in talik sediments, which varies seasonally depending on the depth and probably ranges from ~0°C to about 4°C (Heslop et al., 2015), might lead to over- or underestimation of GHG production. Earlier incubations (e.g., Tanski et al., 2019) and modeling research (e.g., Knoblauch et al., 2013) considered GHG production for 4 months per year, which represents the summer thaw season. GHG production in talik sediments, however, continues year-round, which is why we incubated our samples for one entire year.

Thermokarst lake initiation and expansion in a warming climate will continue to set free OM. Even though initially microbial abundances might be low in permafrost soils, long-term thawing of ice-rich sediments underneath thermokarst lakes will promote anaerobic conditions and activate methanogenic OM degradation, leading to substantial GHG production. Walter Anthony et al. (2016) showed that anaerobic carbon release from thermokarst lakes was directly proportional to the amount of carbon found by thawing of sediments. They calculated that, since the 1950s, 0.2–2.5 Gt permafrost carbon was released as GHG in thermokarst expansion zones of pan-Arctic lakes. Converted to annual release, they found a mean CH$_4$ production of 0.50 ± 0.09 mg CH$_4$-C g$^{-1}$ TOC year$^{-1}$, which is much lower than the mean of all our samples after 1 year (3.80 ± 5.66 mg CH$_4$-C g$^{-1}$ TOC). Our findings underline the vast potential of thermokarst lake formation and subsequent GHG release. Considering the importance of this input for the global climate system, this topic should receive continued attention.

5 | CONCLUSION

In this study, we analyzed GHG production and lipid biomarker distributions in two 17-m-long thermokarst lake sediment cores taken in Central Yakutia, Russia. We found that the sediments in both cores were relatively OC poor, which is in agreement with previous research in the Yukechi region. We found substantial differences between the well-preserved sediments below a young Yedoma lake, and the heavily thermokarst-affected sediments below an Alas lake. Both CH$_4$ and CO$_2$ production were higher in the Yedoma lake deposits compared to Alas lake deposits. The highest CO$_2$ production was measured in the deepest, in situ still frozen part of the Yedoma lake core, which shows that potential CO$_2$ production in newly thawed sediments strongly depends on the decomposition of readily available DOC. In contrast to previous research, we found no correlation between CO$_2$ production and TOC content. However, CO$_2$ production could mainly be explained by the ACL and DOC content, suggesting that OM source and quality is the main driver for CO$_2$ production. CH$_4$ production showed a different pattern: most CH$_4$ was produced in the talik sediments below the Yedoma lake, suggesting that methanogenic communities were established in the thawed sediments but not yet in the frozen sediments in the bottom of the core. We assume that the variable depositional history of the Yukechi region led to the accumulation of OM from a different source and quality in different sediment layers, which explains the variation in GHG production in the sediments. The lower GHG production in the Alas lake core is a result of a degradation legacy that led to OM decomposition during earlier thermokarst lake generations. GHG production from thawed permafrost was substantial even from OC-poor sediments, highlighting the importance of thermokarst formation in general, and thaw of mineral permafrost in particular for the climate system. Therefore, our study presents novel insights that are relevant for mineral-dominated deposits with generally low TOC contents, which are widespread throughout the Arctic.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

Loeka L. Jongejans wrote the initial draft of the manuscript. Loeka L. Jongejans and Jens Strauss designed the lab studies. Guido Grosse, Mathias Ulrich, Jens Strauss, Alexander N. Fedorov, and Pavel Ya. Konstantinov selected the field sites and conducted the drilling expedition. Loeka L. Jongejans, Susanne Liebner, and Christian Knoblauch conducted the incubation experiments. Loeka L. Jongejans and Kai Mangelsdorf carried out the lipid biomarker analysis. All authors contributed to the manuscript drafts and to manuscript finalization.
DATA AVAILABILITY STATEMENT

All results were published in the PANGAEA research data repository, specifically the biogeochemical parameters, n-alkane and brGDGT concentrations, cumulative GHG production, and DOC content (Jongejans et al., 2021a, 2021b, 2021c, 2021d, 2021e). The supplement includes additional images and tables illustrating the methods and results, including graphs of the GHG of all replicates.

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