Glacial lake outburst floods enhance benthic microbial productivity in perennially ice-covered Lake Untersee (East Antarctica)

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Benthic ecosystems of perennially ice-covered lakes in Antarctica are highly sensitive to climate-driven changes. Lake Untersee has been in hydrological steady-state for several hundred years with a high pH water column and extremely low levels of dissolved inorganic carbon. Here, we show that glacial lake outburst floods can replenish carbon dioxide-depleted lakes with carbon, enhancing phototrophic activity of the benthic ecosystem. In 2019, a glacial lake outburst flood brought 17.5 million m³ of water to Lake Untersee, the most substantial reported increase for any surface lake in Antarctica. High-resolution grain-size and carbon isotope analyses of microbial mats suggest that glacial lake outburst floods have occurred periodically over the Holocene and help explain the complex patterns of carbon cycling and sequestration observed in the lake. Our findings suggest that periodic flooding events may provide biological stimuli to other carbon dioxide-depleted Antarctic ecosystems and perhaps even icy lakes on early Mars.
Perennially ice-covered lakes are found in many regions of Antarctica, such as the McMurdo Dry Valleys (MDV), Buringer Hills, Vestfold Hills, Larsenmann Hills, Schirmacher Oasis, and the Söya Coast1–3. The majority of these lakes develop moats during the austral summer and are typically recharged annually by glacial meltwater that transports dissolved inorganic and organic carbon (DIC, DOC), cations and anions, nutrients, and sometimes allochthonous materials4,5. Fluctuations in thaw-degrees days in the upper catchment drive the production of meltwater influx thereby affecting the lake water levels4. For example, the summer of 2001–2002 in the MDV was exceptionally warm, and led to a glacial meltwater-sourced flooding of the lakes in Taylor Valley increasing their water level by 0.54–1.01 m4,6.

Lake levels in glacial regions can also be influenced by glacial lake outburst floods (GLOFs): the sudden drainage of ice-marginal, ice-dammed or subglacial lakes7–9. GLOFs are typically reported from Iceland and Greenland, where the high discharge (mega-GLOF > 106 m3) causes substantial damage to infrastructure and nearby communities10. Smaller magnitude GLOFs are also often reported from the Himalayas10,11 and Andean Patagonian lakes and fjord12,13. However, GLOFs in Antarctica have been rarely reported. The only descriptions have been of a small GLOF in the Larsemann Hills (76,320 m3) between 2017 and 2019, where ice-dammed lakes drained near the Russian Progress station14, and the catastrophic drainage of a surface meltwater lake (600–750 million m3) on the Amery Ice Shelf to the ocean below in East Antarctica in 20198. However, the potential impacts of GLOFs on water chemistry and productivity of benthic microbial ecosystems in Antarctic ice-covered lakes remain unknown. Here, we provide evidence from Lake Untersee, a large ultra-oligotrophic perennially ice-covered lake in Dronning Maud Land (East Antarctica), that GLOFs can replenish the water column with dissolved carbon dioxide (CO2) to help sustain the long-term primary production of benthic phototrophic communities.

Lake Untersee is located within the Untersee Oasis in the Gruber Mountains, c. 150 km south of the Princess Astrid Coast (Fig. 1). The local geology consists of plagioclase of the Precambrian Eliseev anorthosite-norite complex2. The Oasis contains two large perennially ice-covered lakes: Untersee and Obersee15. Lake Untersee is a 6.5 km long and 2.5 km wide ice-dammed lake (volume of 5.21 × 108 m3) adjacent to the Anuchin Glacier and reaches a maximum depth of 169 m. A sill that cuts across the lake at 50 m depth separates the deeper northern basin from a smaller 100 m deep basin to the south. The North basin is nearly homo-thermal, well-oxygenated to the bottom, and well-mixed due to buoyancy-driven convection caused by melting of the ice-wall at the glacier-lake interface16,17. In contrast, the southern basin is density stratified below the sill depth and is anoxic at its bottom; the higher density prevents mixing with the overlyingoxic water column18,19. Except for a large boulder field at the south end of the lake and a few other boulders scattered across the ice cover (n ~ 350 and most of them greater than 2 < 2 m), the surface of the ice cover on Lake Untersee is smooth and free of any fine sediments. The presence of the boulders is evidence for the presence of a thick, continuous ice cover for at least the past hundred years or perhaps throughout the Holocene20. The lake is recharged entirely by subaqueous melting of glacial ice and subglacial meltwater21, and it has a Na(Ca)-SO4 geochemical facies with high pH (10.6) that reflects a heritage of recharge from glacial meltwater, with minor contribution of Ca2+–Na+ solutes from in situ weathering of plagioclase and aluminosilicate minerals22. The total inorganic carbon (TIC) and total organic carbon (TOC) concentrations in the lake are very low (0.3–0.4 mg C L−1)22, 1–3 orders of magnitude lower than in the MDV lakes and Antarctic subglacial lakes23–26. Despite the ultra-oligotrophic, low-light conditions, and lack of a seasonal moat, the lake hosts a benthic microbial ecosystem composed of photosynthetic microbial mats, small cuspate pinnacles, and large conical stromatolitic structures to depths of at least 130 m27–30 (Fig. 2). The top layer of the microbial mats comprises a carbon-fixing cyanobacteria community (Tychonema sp., Phormidium sp., Leptolyngbya sp., and Pseudanabaena sp.) that shift to a hetero- trophic community in the underlying layers (Actinobacteria, Verrucomicrobia, Proteobacteria, and Bacteroidetes)28,30,31. The phototrophic mats are growing in very low light conditions: c. 5% of incident photosynthetically active radiation (PAR) irradiance is transmitted through the lake ice and decreases to c. 0.1% at a 135 m depth27. The benthic microbial mats were sampled by a scientific diver using 5 cm diameter core tubes at depths of 13, 17, and 18.5 m for subsequent analysis of organic C content, δ13Corg, and δ14C22. The organic C abundance of the mats ranged from 1.0 to 5.8 wt%, with the organic carbon density calculated at 793 ± 264 g m−2. Despite showing some age reversals, the 14C age distribution in the mats suggests that they are slowly accumulating biomass at a rate of c. 2.5 mm per 100 years. Carbon isotope analyses show that the cyanobacteria in the top 1 mm layer of the mats are fixing carbon without the isotopic fractionation of bicarbonate (HCO3−) from the high pH water or the respired CO2 from heterotrophs in the layers of the underlying mat. As a result, it was inferred that the phototrophs growing in the upper-most layer of the mats are CO2-depleted22, resulting in lower gross photosynthesis and sequestration rates of organic carbon than the microbial mats in MDV lakes29.

Lake Obersee is a smaller ice-dammed lake (volume of 8.07 × 107 m3) located c. 6 km north-east of Untersee with a maximum depth of 83 m31. Like Untersee, Lake Obersee has a well-sealed ice cover with high pH (10–10.6) water and conductivity between 85 and 93 μS/cm−1. The lake’s water column has higher levels of dissolved nutrients and greater primary productivity than Untersee32.

Lake Untersee, among the largest lakes in East Antarctica, is a closed-basin lake that remains tightly sealed from the atmosphere with no open water along the margin that would enhance gas exchange33,34. Despite a relatively warm mean annual air temperature (~9.5 ± 0.7 °C) and thawing degree-days (ranging from 7 to 51)35,36, no surface streams have been observed entering the lake since work began there in 1969 due to the high ablation rate that limits surface melt of the Anuchin Glacier, as a result of cooling associated with the latent heat of sublimation33,35. Further, unlike lakes in the MDV and other regions in Antarctica, the water level of Lake Untersee has been stable for the past several decades35,36, and based on the δD–δ18O composition of the water column, the lake was likely in hydrological steady-state with no summer moating for at least the past 300–500 years34. However, during our field campaign in November–December 2019, we observed that the lake water level had increased by c. 2 m. This study aims to: (1) explain the cause of the increase in water level in Lake Untersee; and (2) examine the impact the large influx of water had on the lake chemistry and the benthic microbial ecosystem. These goals were achieved by: (1) reporting changes in lake level since 2004 using ICESat altimetry data; (2) determining changes in lake water chemistry (pH, major ions, δD–δ18O, TIC, TOC, and δ13C(TIC) and δ14C(TIC)); and (3) determining the amount of carbon stored in the lake to evaluate the effect of the large influx of water on the sustainability of the benthic ecosystem. This study provides important insight regarding the fate of this lake and other Antarctic lacustrine ecosystems impacted by the response of glaciers to a warming climate.
Results and discussion

Description of the 2019 GLOF at Lake Untersee. ICESat-1 and ICESat-2 laser altimetry data show that the water levels of Lake Untersee and Lake Obersee remained stable between October 22nd, 2003 (the first acquisition date of ICESat-1 data) and mid-December 2018 (Fig. 3). However, the laser altimetry data indicates that the water level of Lake Untersee increased by 2.0 m between December 12th, 2018 and February 7th, 2019 (Fig. 3), and images from the time-lapse digital camera installed on our meteorological station revealed the sudden release of water through the ice cover on Jan 14-15th, 2019 (Fig. 4). Between the same dates, the water level of Lake Obersee decreased by 11.3 m. Therefore, the partial drainage of Lake Obersee that caused the mid-January 2019 GLOF in Lake Untersee was likely due to a section of the Vangengejm Glacier that collapsed or shifted through a glacial tunnel, or by fast-moving ice-streams surrounding the Untersee Oasis (Fig. 5). The GLOF cannot be attributed to a surge or extensive surface melting of the Anuchin Glacier because the snout remained at the same location (Fig. 1). Further, the austral summer of 2018-2019 was not abnormally warm: the number of thawing degree days only reached 26.8 (ranking 6 out of 11 years). In fact, the water level of Lake Untersee has not been affected by annual fluctuations in thawing degree days (Fig. 3). Even at the maximum thawing degree days of 51, no surface melt was observed on the Anuchin Glacier due to the high ablation rate21. This contrasts with the lakes in the MDV, where water levels positively correlate with thawing degree days in the upper catchment area with increased contribution of glacial meltwater recharging the lakes.

The mid-January 2019 GLOF of Lake Untersee caused the most substantial single event increase in water level and volume of water for any surface lakes in Antarctica reported to date. In the MDV, a 1 m increase in water-level has a 100-years recurrence interval8. The 2017 and 2019 GLOFs at Larsemann Hills caused the water level of four lakes to increase by 0.4–1.5 m, which increased the water volume by a maximum of 76,320 m314. The GLOF at Lake Untersee

Cause and magnitude of the GLOF. The ice flowing around Untersee Oasis is heavily disturbed by local mountains and nunataks, with glaciers flowing in different directions (the Anuchin Glacier represents a counter-current flow to the north flowing East Antarctic Ice Sheet). The partial drainage of Lake Obersee that caused the mid-January 2019 GLOF in Lake Untersee was likely due to a section of the Vangengejm Glacier that collapsed or shifted through a glacial tunnel, or by fast-moving ice-streams surrounding the Untersee Oasis (Fig. 5). The GLOF cannot be attributed to a surge or extensive surface melting of the Anuchin Glacier because the snout remained at the same location (Fig. 1). Further, the austral summer of 2018-2019 was not abnormally warm: the number of thawing degree days only reached 26.8 (ranking 6 out of 11 years). In fact, the water level of Lake Untersee has not been affected by annual fluctuations in thawing degree days (Fig. 3). Even at the maximum thawing degree days of 51, no surface melt was observed on the Anuchin Glacier due to the high ablation rate21. This contrasts with the lakes in the MDV, where water levels positively correlate with thawing degree days in the upper catchment area with increased contribution of glacial meltwater recharging the lakes.

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increased the water level by 2 m over 21 days and added $1.75 \times 10^7$ m$^3$ of water to the lake (three orders of magnitude higher than the Larsemann Hills GLOF). We estimated the average discharge of the 2019 GLOF at ~ $9 - 10$ m$^3$ s$^{-1}$ (calculated from the increase in volume of water over 21 days), which is substantially lower than discharge rates associated with mega floods (>10$^6$ m$^3$ s$^{-1}$) or catastrophic flooding events (>10$^5$ m$^3$ s$^{-1}$) documented in Iceland$^{37-39}$. Further, in terms of total flood volume, the 2019 Untersee GLOF was much lower than typical Icelandic jökulhlaups$^7$. However, it was in the same range as some jökulhlaups recently inventoried in Greenland$^{40,41}$. Therefore, despite having a relatively low estimated average discharge, the 2019 GLOF contributed a substantial volume of water to Lake Untersee that was sufficient to affect the chemical composition of the water column.

GLOF and its impacts on water chemistry. The mid-January 2019th GLOF altered the chemistry of the oxic water column of Lake Untersee from its stable composition that we have periodically measured since 2011, and that has remained unchanged since the early 1980s (Supplementary Table 1). The GLOF caused the pH to decrease from 10.5 to 9.5, specific conductivity decreased from 505–520 to 485 µS/cm$^{-1}$, and D.O. decreased from 150 to 128% (Fig. 3). The $\delta^{18}$O composition showed little change (from $-37.8 \pm 0.3$ to $-37.4 \pm 0.5\%o$), but the D-{$\delta^{18}$O} shifted from being distributed above the local meteoric water line (LMWL) to now plotting below it (D-excess decreased from $14.1 \pm 0.7$ to $7.9 \pm 2.6\%o$). The TIC increased from $0.35 \pm 0.05$ mg C L$^{-1}$ to $0.5 \pm 0.02$ mg C L$^{-1}$ with $\delta^{13}$C$_{TIC}$ values decreasing from $-9.1 \pm 0.4\%o$ to $-14.5 \pm 1.9\%o$ and the F$^{14}$C$_{TIC}$ increasing from 0.4233 ± 0.02 to 0.5107–0.5481 (Fig. 3). The water that entered the lake in mid-January 2019 was not sampled because our field campaign ended in mid-December 2018. However, when we returned in late November 2019, a small stream was still flowing in the GLOF channel into the North-East corner of Lake Untersee; this stream had pH = 7.7, conductivity = 70 µS/cm$^{-1}$, $\delta^{18}$O = $-34.5\%o$, D-excess = 3.2%o, TIC = 1.8 mg C L$^{-1}$, $\delta^{13}$C$_{TIC}$ = $-18.5\%o$, and F$^{14}$C$_{TIC}$ = 0.5844.

The geochemical composition of the stream, assuming it originates from Lake Obersee, is very different from the high pH, low conductivity of Lake Obersee. Geochemical modeling using the PHREEQC hydrogeochemical software$^{42}$ suggests that the geochemical composition of the stream can be obtained following the drainage of Lake Obersee’s water, and the weathering of plagioclase and biotite-bearing gneisses morainic material in equilibrium with atmospheric CO$_2$ as the water flows along the 8 km channel into Lake Untersee (Supplementary Table 2). Considering that the GLOF contributed 3% vol of water to Lake Untersee, a two-component mixing of the stream water chemistry being added to the lake matches reasonably well the post-GLOF conductivity and $\delta^{18}$O values of the lake (Supplementary Table 3). However, parameters affected by exchanges with atmospheric gases, such as D.O., TIC, and F$^{14}$C$_{TIC}$, have mixing values that differ from those measured in the lake, which suggests additional interaction with the atmosphere. The lower D.O. is attributed to partial degassing of the water column of Lake Untersee through
the c. 50 m wide moat that formed just beyond the stream entering the lake, or along fractures in the ice cover that developed from the rapid rise in water level. The higher TIC and F14C in the water column of the lake are attributed to additional uptake of modern atmospheric CO2 from the small moat region. In fact, an additional uptake of 0.11 mg C L−1 (or 21%) of modern atmospheric CO2 (with F14C = 1) through the melt pool would be required to match both the measured post-GLOF TIC and F14C in the oxic water column of Lake Untersee. The dashed vertical line represents the timing of the 2019 glacial lake outburst flood. The scatter plots on the right side of the figure show elevation (m) data for Lake Untersee and Lake Obersee after the 2019 GLOF event.

Carbon stock and carbon mass balance of Lake Untersee. Based on the 2017 TIC–TOC measurements in the oxic water column and organic carbon content in microbial mats, Lake Untersee stores 5.42 to 6.71 × 109 g C, with >95% of the carbon pool residing in the microbial mats (Table 1). The TIC and TOC pools in the lake waters are 1.81 × 108 g C and 6.19 × 107 g C, respectively, with the organic C reservoir in the microbial mats reaching 5.17 to 6.47 × 109 g C. The latter was calculated from the average organic C content (793 ± 264 g m−2) of three cores collected near the push moraine, the surface area of the oxic lake bottom (8.15 km2) and scaling to the three scenarios of mat coverage along the oxic lake bed: 100, 90, and 80% mat coverage. On occasion, small carbonate spherules can be found within the mat layers; however, these are uncommon and excluded from the carbon reservoir.

A carbon mass balance approach was used to determine if the 5.42 to 6.71 × 109 g C stored in Lake Untersee is in equilibrium with the carbon inputs under its hydrological steady-state condition, or if GLOFs can contribute carbon to help enhance productivity and subsequent sequestration of organic carbon within the CO2-
depleted microbial mats. The carbon mass balance builds on the water mass balance of Lake Untersee21:

$$\Delta S = I_{sa} + I_{sg} - O_s,$$

where $\Delta S$ is the change in the volume of water, $I_{sa}$ and $I_{sg}$ are the contribution from subaqueous melting of terminus ice (originating from the melting of the submerged Anuchin Glacier at the ice–lake water interface) and subglacial meltwater (or other sources), respectively, and $O_s$ is the surface outflow (sublimation of the ice cover). Recharge from precipitation ($P$) and surface water ($I_s$) were ruled out because they do not contribute to the lake; direct precipitation does not contribute to the lake since it has been well-sealed for the past 300–500 years, and there is no evidence for the influx of surface water feeding the lake via melt streams. Therefore, Untersee is only recharged by subaqueous melting of the Anuchin Glacier and subglacial meltwater and annually loses 0.6–1.2% of its water through ablation of the ice. Using an energy mass balance, it was determined that the subaqueous meltwater contributes 40–45% of the annual recharge, and the subglacial meltwater accounts for the remaining 55–60%21.

The carbon mass balance can be calculated as:

$$\Delta \text{carbon (g C)} = I_{sa\text{TIC}} + I_{sa\text{TOC}} + I_{sg\text{TIC}} + I_{sg\text{TOC}} - O_{s\text{TIC}} - O_{s\text{TOC}},$$

where $I_{sa}$ and $I_{sg}$ are the annual inflows of subaqueous melting of the Anuchin glacier’s terminus ($1.98–2.23 \times 10^6$ m$^3$) and subglacial meltwater contributions ($2.68–2.92 \times 10^6$ m$^3$), and $O_s$ is outflow meltwater via ice cover ablation ($3.22–6.43 \times 10^6$ m$^3$).

As an initial scenario, the input of carbon into Lake Untersee assumes the lake is well-sealed and in hydrological steady-state (Supplementary Table 4). Subaqueous melting of the Anuchin Glacier at the lake-glacier interface ($I_{sa\text{TIC}}$ and $I_{sa\text{TOC}}$) releases occluded atmospheric CO$_2$ gas directly in the water column that contributes 0.0165 mg C L$^{-1}$ as TIC22. The TOC released by the Anuchin Glacier flowing over the crystalline bedrock is assumed to be similar to that measured in the Vostok ice core from the interior of the East Antarctic Ice Sheet (0.03 g C L$^{-1}$)43. The oxidation of the TOC in the water column and the oxidation of methane originating from the anoxic waters are not a substantial contributors to the TIC pool because $\delta^{13}$C$_{\text{TIC}}$ averages $-9.1 \pm 0.4$‰, similar to the $\delta^{13}$C$_{\text{CO}_2}$ of occluded gases ($-7.3$ to $-6.3$‰)44,45. We assume that the TIC–TOC concentrations in the subglacial meltwater recharging Lake Untersee ($I_{sg\text{TIC}}$ and $I_{sg\text{TOC}}$) are similar to those calculated for the subaqueous meltwater with little to no carbonate dissolution or oxidation of organic material. A major contribution from subglacial carbonate dissolution or oxidation of organic carbon in the Precambrian crystalline bedrock46,47 was ruled out in a previous study22, because these carbonates and organics would have $\delta^{13}$C values near 0 and c. $-25$‰, respectively48, and would be $^{14}$C dead, which would result in a very different $\delta^{13}$C$_{\text{TIC}}$ and $^{14}$C$_{\text{TIC}}$ in the

![Fig. 4 Time-lapse photography of glacial lake outburst flood in Lake Untersee, Antarctica. Glacial lake outburst flood started on January 14th-15th 2019, evidenced by the sudden release of water through the ice cover, which continued for many weeks.](image-url)
water column and older $^{14}$C age in the mats. In Lake Untersee, there is a minimal loss of carbon during the sublimation of ice cover ($O_{\text{TIC}}$, $O_{\text{TOC}}$): with the pH of the water column being 10.6, there is no CO$_2$ gas escaping through the sublimation of the ice cover (at pH 10.5, the DIC species are as bicarbonate and carbonate) and the soluble ions are segregated in the water column during freezing at the ice-water interface\textsuperscript{49}. Therefore, taking the TIC and TOC concentrations of the subaqueous and subglacial meltwaters and their respective volume of water added annually, these two water sources would contribute $2.28 \times 10^5$ g C year$^{-1}$ (Supplementary Table 5). Lake Untersee formed 12–10 ka B.P., and assuming it remained well-sealed and in hydrological steady-state throughout its existence, our calculations are unable to account for all the carbon in the lake, and there must be other sources that contribute $3.11 - 4.21 \times 10^5$ g C (57–62% of the total carbon stock) (Fig. 6a).

The δD–δ$^{18}$O composition of Lake Untersee suggests that the lake has been well-sealed with no summer moating for the past 300–500 years\textsuperscript{34}; however, a potential source for the missing carbon is the uptake of atmospheric CO$_2$ in the water column during a period when the lake possibly developed a summer moat along its margin. Paleo-temperature reconstructions show that the early Holocene in Dronning Maud Land was 1–2 °C warmer than today\textsuperscript{50}. The warmer temperature caused the rapid thinning of the East Antarctic Ice Sheet\textsuperscript{51}, and the retreat of the glacier.

### Table 1 Amount of carbon stored in the oxic water column and microbial mats of Lake Untersee, Antarctica.

| Reservoirs                | Volume/surface area | Carbon (g C)   |
|---------------------------|---------------------|----------------|
| Lake oxic water           | 5.16E+08 m$^2$      | 2.43E+08       |
| TIC (0.35 mg C L$^{-1}$)  |                     | 1.81E+08       |
| TOC (0.12 mg C L$^{-1}$)  |                     | 6.19E+07       |
| Mots                      |                     |                |
| S1 (1×)                   | 8.15E+06 m$^2$      | 6.47E+09       |
| S2 (0.9×)                 | 7.34E+06 m$^2$      | 5.82E+09       |
| S3 (0.8×)                 | 6.52E+06 m$^2$      | 5.17E+09       |
| Total                     |                     | 5.42–6.71E+09  |

The amount of carbon stored in mats was calculated using an organic carbon density of 793 ± 264 g m$^{-2}$ and a surface area for the lake’s oxic basin following three possible scenarios of mat coverage.

TIC total inorganic carbon, TOC total organic carbon.
from the valley subsequently filled the closed-basin valley and produced Lake Untersee 52. During the early formative stage of Untersee, the lake likely developed a summer moat, as evidenced from the 14C ages of bottom microbial mat layers (13–12 ka) that correspond to the timing of lake formation. This indicates that, at the time of lake formation, the cyanobacteria were fixing DIC under an open system with respect to CO₂ (F14CDIC ~ 1). Following cooling of regional air temperatures, the lake developed the tightly-sealed ice cover observed today. The water column likely became isolated from atmospheric CO₂ exchange shortly after 12 ka B.P., as indicated by the paucity of calcite observed in the mats 27. The microbial mats consumed the DIC reservoir in the water column while continuing to receive DIC – DOC contributions from subaqueous and subglacial meltwaters. Therefore, assuming the water column was in equilibrium with the atmosphere during the early formative stage of Lake Untersee, geochemical modeling predicts that the weathering of plagioclase minerals from glacial meltwater would generate pH near 10.5 with DIC reaching 1.3–1.5 mg C L⁻¹ (Supplementary Table 2). If the lake then became well-sealed shortly after it formed and was being recharge solely by the subaqueous and subglacial meltwaters, similar to hydrological conditions over the past few hundred years, carbon mass balance calculation indicates the lake would have accumulated 3.51 × 10⁹ g C, which is still 3–3.6 × 10⁹ g C lower than the estimated total carbon reservoir (Fig. 6).

**GLOFs and carbon mass balance of Lake Untersee.** The 2019 GLOF added c. 1.75 × 10⁷ m³ of water to Lake Untersee and replenished the oxic water column of Lake Untersee with c. 1.40 × 10⁸ g C (Supplementary Table 4). The amount of carbon added by this single GLOF event is, nevertheless, about an order of magnitude too low to explain the total carbon stored in Lake Untersee. However, high-resolution analyses in the microbial mat cores collected near the push moraine revealed individual matching layers with higher sand fraction, lower δ¹³Corg values and higher F14C values (Fig. 7). We suggest that these shared characteristics in the mats are due to previous GLOFs contributing carbon and other nutrients to Lake Untersee.

Unlike ice-covered lakes in the MDV 53–55, the surface ice cover of Lake Untersee is free of any fine sediments, and the main source of sediments is glacial flour derived from subaqueous and subglacial meltwaters 27. The 2019 GLOF, with an estimated discharge of 9–10 m³ s⁻¹, had sufficient velocity to transport sand-sized sediments that would be deposited into the lake. Observations of a potential thin layer of sand on the mats’ surface have yet to be made since the most recent samples in hand were collected in December 2017. Nonetheless, we did observe for the
first time a thin layer of fine sediment covering light sensors that we retrieved in December 2019. The 2019 GLOF also increased the TIC and F14CTIC in the oxic water column and decreased the δ13CTIC (Fig. 3), characteristics also observed in the δ13C and 14C of some layers in the mats. After a GLOF of this magnitude, the cyanobacteria in the top mat layer would be fixing the HCO3\(^-\) with this modified δ13C\(_{\text{TIC}}\) and F14C\(_{\text{TIC}}\) signatures, and that would be recorded in the δ13C\(_{\text{org}}\) and 14C of the microbial mat since fixation of the HCO3\(^-\) would likely still occur with no 13C fractionation due to the high pH (9.5) and still relatively low TIC (0.5 ppm C)\(^22\). In fact, the mats show these concurrent shifts in δ13C and F14C at distinct layers (sampled 1–2 mm layers which represent 50–100 years accumulation period). As the microbial mats progressively sequester the DIC reservoir in the water column, while continuing to receive DIC–DOC contribution from subaqueous and subglacial meltwaters with different δ13C\(_{\text{TIC}}\) and F14C\(_{\text{TIC}}\) compositions relative to the GLOF, the δ13C\(_{\text{TIC}}\) in the water column will, over time, evolve to those measured before the 2019 GLOF while the F14C\(_{\text{TIC}}\) will evolve following its decay. As a result, a shift in grain size and carbon isotopes within a single mat layer can be used as proxies of GLOF occurrences (Fig. 7). However, it should be noted that a change in grain size and carbon isotopes is unlikely to be identical in the mats throughout the 6.5 km long Lake Untersee due to limnological factors (e.g., water circulation, topography) and variations in metabolism and carbon assimilation within the mats due to differences in other stressors (i.e., light attenuation with depth, availability of other nutrients). A gradient in sediment deposition following a GLOF is expected with coarser material deposited in the North-East corner of the lake, where the GLOF entered the lake and fining of sediments with increasing distance. This is likely why only a thin layer of sand was observed in the mats sampled near the push moraine (3.5 km from the corner where the GLOF entered the lake). Thus, our results from the mats provide evidence that GLOFs sporadically recharged Lake Untersee over the Holocene, and the presence of multiple strandlines above Lake Untersee supports this assumption.

Assuming GLOFs of similar magnitude and chemical composition occurred on several occasions over the Holocene (at least five times), with the lake being recharged solely by subaqueous and subglacial meltwater during that period, we can explain the total carbon reservoir using the carbon balance calculation (Fig. 6a). In addition, numerical modeling of the evolution of F14C\(_{\text{TIC}}\) in the oxic water column and the 14C age distribution in the microbial mats following the addition of younger carbon to the lake by the GLOF also agrees well with the measurements (Fig. 6b, c). Therefore, our findings demonstrate that GLOFs can contribute substantially to the long-term accumulation of biomass and overall productivity of CO2-depleted perennially ice-covered lakes, such as Lake Untersee, by periodically
supplying them with carbon sources. Our findings contribute to the body of literature that GLOFs increase the productivity of lacustrine or fjord ecosystems. GLOFs were also found to be beneficial to phototrophs in Patagonian lakes, where floods decreased turbidity and increased light penetration due to a reduction in clays into the lake.13

In the Northern Patagonian Ice Field, GLOFs increased terrestrial particulate organic carbon and populations of Munida gregaria, which connects organic carbon to the higher trophic levels.12

Our findings also have relevance for the potential habitability of CO₂-depleted lakes on early Mars. As suggested by previous studies,19,20,21 well-sealed perennially ice-covered lakes in Antarctica provide relevant analogs that may help explain the lack of observed carbonates in the paleolacustrine sediments of Gale Crater (which was likely an ice-covered lake during the Hesperian)21 despite a higher CO₂ level in the atmosphere during that early period of Martian history. As shown in Lake Untersee, with its CO₂-depleted water column, and sediments nearly carbonate-free, such lakes can still sustain robust benthic microbial communities. This light CO₂-depleted aquatic environment provides a useful analog for assessing the habitability of other planetary bodies, and to inform and improve strategies for the search for life beyond Earth.

Methods
Changes in elevation and water volume for Lake Untersee and Lake Obersee. Surface elevation changes of lakes Untersee and Obersee during the 2004–2020 period were assessed using ICESat and ICESat-2 (ATL06 products) datasets available on the Open Altimetry web-based application.22,23 ICESat and ICESat-2 altimetry data have vertical precisions of 14 and 0.4 ± 2 cm, respectively.24

Although the altimetry data represents a composite of many discrete altimetry points, we assume in our temporal analysis that the elevation of the ice cover is constant across the surface of the lakes. Changes in lake water volume were subsequently determined from digitized, georeferenced bathymetric maps of Lake Untersee and Lake Obersee produced with measurements made during previous field seasons25,26, volume and surface area calculations were made with the Surface Volume tool in the ArcGIS pro 2.4 software.

Lake water analyses. During the field season at Lake Untersee in November 2019, measurements of pH, temperature, specific conductivity, total dissolved solids (TDS), dissolved oxygen (DO), and chlorophyll a were made using a calibrated Hydrolab DS5 Water Quality Sonde lowered through 25 cm holes drilled in the ice cover with a 10 m cable (Fig. 3f). Lake water samples were collected at 5–10 m intervals from the same locations of previous years using a clean 2.5 L Niskin bottle. The water samples were immediately transferred into sampling bottles unfiltered due to the ultra-clear and low-particulate content in the waters, and the sensitivity of the high pH waters to the rapid absorption of atmospheric CO₂. The samples were immediately de-aerated (N₂) to avoid pH and dissolved inorganic carbon (DIC) loss. Water samples for TIC-TOC analyses were collected in 40 mL amber glass vials with butyl septa caps. Radiocarbon samples were collected in pre-baked (500 °C for 3 h) 1 L amber glass vials with butyl septa caps. Radiocarbon samples were collected in pre-baked (500 °C for 3 h) 1 L amber glass vials.

The TIC-TOC concentration and stable isotope ratios ($^{13}$C$_{TIC}$, $^{13}$C$_{TOC}$) in lake waters were measured by a wet TOC analyzer interfaced with a Thermo DeltaPlus XP isotope-ratio mass spectrometer at the Ján Veizer Stable Isotope Laboratory (University Ottawa) using methods described in this study.64

The isotope ratios are presented as per mil deviation relative to VPDB and expressed using the delta notation. The 2σ analytical precision is 0.5 ppm for TIC and TOC concentrations and 0.03% for $^{13}$C$_{TIC}$ and $^{13}$C$_{TOC}$. Radiocarbon analysis of TIC-TOC in waters was performed at the A.E. Lalonde Accelerator Mass Spectrometry Laboratory, University of Ottawa. Sample preparation, extraction of inorganic and organic carbon from waters and graphitization were performed according to this study.65

Graphitized samples were analyzed on a 1MV tandem mass spectrometer. The $^{12}$C/$^{13}$C ratios are expressed as fraction of modern carbon ($^{12}$C/$^{13}$C) and corrected for spectrometer and preparation fractionation using the AMS measured $^{13}$C/$^{12}$C ratio.66,67 Radiocarbon ages are calculated as $\delta^{14}C$ years BP ($^{14}$C year B.P. (BP) = AD1950 + $\delta^{14}C$)68. The 2σ errors are reported with the results and <0.013 $^{14}$C (or <190 years).

Carbon mass balance. A carbon mass balance approach was used to assess if the amount of organic carbon stored in the microbial mats and the oxic water column of Lake Untersee is in equilibrium with carbon inputs into the lake. The carbon stored in the mats was calculated from the organic C content of three cores, the surface area of the oxic lake bottom (8.15 km²) and scaling to the three scenarios of mat coverage along the oxic lake bed: 100, 90, and 80% mat coverage (data from this study.22). The data for TIC-TOC, $^{13}$C$_{TIC}$, and $^{14}$C$_{TIC}$ in the oxic water before the mid-January 2019 GLOF is taken from Table 4 in this study22 and determined using the methods described in the previous section.

Based on the annual inputs of carbon to the lake, the cumulative mass of carbon in the lake ecosystem, and the evolution of $^{14}$C$_{TIC}$ in the oxic water column and $^{14}$C in mats over the past 12 ka (since the formation of the lake) were calculated for four different scenarios and compared to our measurements (Supplementary Table 5): (S1) the lake was always well-sealed and under hydrological steady-state, as observed presently; (S2) during the early formative stage, the water column of the lake was exchanging with atmospheric CO₂ with no weathering, but then switched to a well-sealed ice cover and was under hydrological steady-state; (S3) same as S2, but with additional TIC contribution from open system weathering of plagioclase minerals; (S4) same as S3, but with additional TIC contribution from GLOFs. The cumulative mass of carbon was calculated in 500-year time-steps. The evolution of $^{14}$C$_{TIC}$ follows the accumulation of carbon to the lake with $^{14}$C of 0.8 (estimated from the age of occluded CO₂ gases being released into the lake)44 and its decay over time using the half-life = 5730 years. The $^{14}$C profile in the mats assumed that mats are using the TIC solely in lake water as their carbon source, and $^{14}$C mats reflect the evolution of $^{14}$C$_{TIC}$ in the water column. However, due to the substantial carbon reservoir effect in the water column, the $^{14}$C ages of the mats cannot be calibrated to calendar years, and an age-depth model cannot be performed.

Data availability
The Lake Untersee water column and microbial mat biogeochemical data used in this study are available through the National Snow and Ice Data Center (nsidc.org). The ICESat-1 and ICESat-2 laser altimetry datasets used for this study are available at: https://openaltimetry.org/.

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Author contributions
B.F., D.L., and D.A. conceived the study; B.F., N.M., D.L., and D.A. acquired data; B.F., N.M., and D.L. developed the numerical modeling; B.F., N.M., D.L., D.A., L.J., and I.C. contributed to drafting; B.F., N.M., D.L., D.A., L.J., and I.C. revised the manuscript; and B.F., N.M., D.L., D.A., L.J., and I.C. approved the submission of the manuscript.

Competing interests
The authors declare no competing interests.

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