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Key Points:
- Multiyear lake methane flux monitoring reveals sampling only in summer (here: July, August) can overestimate ice-free emissions by 43–76%.
- Fluxes increase predictably with temperature and solar irradiance, enabling sampling bias correction via proxies based on energy input.
- Temperature proxies can be more cost-effective than measurements at estimating ice-free fluxes that are not greatly affected by hysteresis.

Supporting Information:
- Supporting Information S1

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Temperature Proxies as a Solution to Biased Sampling of Lake Methane Emissions

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Abstract
Lake emissions of the climate forcing trace gas methane (CH4) are spatiotemporally variable, but biases in flux measurements arising from undersampling are poorly quantified. We use a multiyear data set (2009–2017) of ice-free CH4 emissions from three subarctic lakes obtained with bubble traps (n = 14,677), floating chambers (n = 1,306), and surface concentrations plus a gas transfer model (n = 535) to quantify these biases and evaluate corrections. Sampling primarily in warmer summer months, as is common, overestimates the ice-free season flux by a factor 1.4–1.8. Temperature proxies based on Arrhenius functions that closely fit measured fluxes (R2 ≥ 0.93) enable gap filling the colder months of the ice-free season and reduce sampling bias. Eubillition (activation energy 1.36 eV) expressed greater temperature sensitivity than diffusion (1.00 eV). Resolving seasonal and interannual variability in fluxes with proxies requires ~135 sampling days for ebullition, and 22 and 14 days for diffusion via models and chambers, respectively.

1. Introduction

Inland waters are an important source of methane (CH4) to the atmosphere (Bastviken et al., 2011; Cole et al., 2007). The majority of the world’s lakes and ponds are located at northern latitudes and experience seasonal ice cover (Denfeld et al., 2018; Verpoorter et al., 2014). Thermal energy input is a key driver of variability in lake emissions during the ice-free season (Wik et al., 2014; Yvon-Durocher et al., 2014), in part due to the exponential temperature dependency of microbial CH4 production (Zeikus & Winfrey, 1976).

Resolving the flux variability in order to understand the ecological response to climate warming requires measuring consistently across a wide temperature range (Aguilera et al., 2016; Hampton et al., 2018). However, out of 733 northern lakes and ponds where ice-free season CH4 fluxes have been obtained (Wik, Varner, et al., 2016), a majority (60%) were sampled ≤3 months of the year and more than half (53%) were sampled exclusively in the warm summer months (June, July, August) when emissions tend to peak (Huttunen et al., 2003; Natchimuthu et al., 2016). Extrapolating from time series that omit the colder months of the ice-free season can lead to a significant overestimation of total flux. Only two studies have quantified the biases associated with parsimonious sampling strategies (Stanley et al., 2019; Wik, Thornton, et al., 2016).

Proxies enable low-cost upscaling or gap filling of manually sampled data using functional relationships with environmental covariates. Temperature proxies have been applied in regional and global assessments of carbon emissions from lakes (DeSontro et al., 2018; Hartery et al., 2018; Kraemer et al., 2017) and in process-based models to construct future emission scenarios (Bayer et al., 2019; Tan & Zhuang, 2015). They can be effective predictors of erratic bubble fluxes (Aben et al., 2017; Wik et al., 2014), which are expensive to monitor long-term (Wik, Thornton, et al., 2016). However, it is unclear how proxies are affected by timing biases in the underlying measurements, for example, through a dependence on history (hysteresis) (Updegraff et al., 1998) or a threshold response (Tveit et al., 2015). Moreover, differences in temperature sensitivity between the major CH4 emission pathways—ebullition (bubbling) and turbulence-driven diffusion—remain poorly understood (DeSontro et al., 2016). Here we use high-resolution, multiyear time series of CH4 fluxes from three subarctic lakes to quantify the biases associated with sampling only in the warmer summer months. We test the predictive capability of widely used temperature functions and identify mechanisms that modulate these relationships. We also compute the number of samples required to arrive at reasonably accurate estimates of ice-free fluxes with manual sampling and temperature proxies.
2. Materials and Methods

2.1. Field Site

We measured CH₄ emissions from three lakes located around the Stordalen Mire, a subarctic permafrost peatland in northern Sweden (68°21’N, 19°02’E, 350 m above sea level). Lakes Villasjön, Inre Harrsjön, and Mellersta Harrsjön are of postglacial origin, are 0.17, 0.02, and 0.01 km² in area and have mean depths of 0.7, 2.0, and 1.9 m, respectively (Wik et al., 2013), as is typical of most lakes north of 50°N (Cael et al., 2017; Wik, Varner, et al., 2016). The ice-free period lasts from May through October (~161 days, 2009–2018), during which the lakes frequently mix to the bottom (Jansen et al., 2020). Ebullition accounts for 83%, 48%, and 66% of the ice-free CH₄ flux in Villasjön, Inre, and Mellersta Harrsjön, respectively, and the remainder by diffusion (2009–2017, Jansen et al., 2019). Both emission pathways display an exponential dependence on temperature (Jansen et al., 2019; Wik et al., 2014), and CH₄ emissions from the lakes are expected to rise under continued Arctic warming (Bayer et al., 2019; Thornton et al., 2015).

2.2. Fluxes Derived From Field and Laboratory Measurements

Flux measurements have been described in detail (Jansen et al., 2019; Wik et al., 2013) and are outlined here in brief. In all three lakes, between June and September, a total of 38–40 bubble traps were deployed across depth zones and sampled every 1–3 days to measure CH₄ ebullition (Fₑb, 2009–2017, n = 14,677). To obtain the diffusive CH₄ flux, 10–18 floating chambers with bubble-deflecting shields mounted underneath were deployed every 1–2 weeks and sampled 2–4 times over 24 hr, and fluxes were computed from the headspace concentration increase (Bastviken et al., 2004) (Fₕₑb, 2010–2017, n = 1,306). Continuous (Fₑcb) and 24-hr (Fₕₑcb) deployment integrated diel variability of the flux. Surface water samples were collected weekly between June and September at two to three locations in each lake (2009–2017, n = 606). Gas and water samples were collected with 10 and 60 ml polypropylene syringes capped with three-way stopcocks (Becton Dickinson). CH₄ concentrations were determined within 24 hr of sampling at the Abisko Scientific Research Station, 10 km west of the Mire, with a GC-2014 gas chromatograph (Shimadzu). Calibration standards of 2.059 ppm (Air Liquide) and 2010 ppm (AGA) CH₄ in N₂ bracketed sample concentrations (bubble samples were diluted with outdoor air) and were measured before and after each run. Headspace extraction was used to obtain dissolved gas concentrations (McAullife, 1971).

2.3. Modeled Fluxes

Turbulence-driven diffusive CH₄ fluxes were also estimated with a gas transfer model. The flux (Fₘₐₒᵈ) is defined as the product of the measured air-water concentration difference (Δ[CH₄]) and the gas transfer velocity (k) computed with a surface renewal model (Lamont & Scott, 1970):

\[ k = \alpha' (\nu)^{\frac{1}{2}} \frac{1}{\text{Sc}} \]

Here, k is a function of the molecular diffusivity of the dissolved gas (D₀) through the Schmidt number (Sc = ν/D₀) (Wanninkhof, 2014) and the dissipation rate of turbulent kinetic energy (ε) supplied to the surface mixed layer by wind shear and convection (Imberger, 1985; MacIntyre et al., 1995). ν is the kinematic viscosity of water. Scaling parameter α’ was determined empirically as 0.23 with independent estimates of k from chamber observations (Jansen et al., 2020). For ε we used a parameterization by Tedford et al. (2014), which has shown that wind shear, rather than thermal convection or stratification, controls gas transfer in the Stordalen lakes (Jansen et al., 2020). This implies that buoyancy effects do not modulate the temperature relation of the diffusive flux. Meteorological observations that informed the model (Equation 1) were collected at 30-min resolution on the Mire (Supporting Information S1).

2.4. Measurement of Energy Input

Water temperature loggers (HOBO Water Temp Pro v2, Onset Computer) were deployed in Villasjön and at the deepest points of Inre and Mellersta Harrsjön at 0.1, 0.3, 0.5, and 1.0 m depth, and further at 3.0, 5.0 m (IH and MH), and at 6.7 m (MH). Data were stored every 5 min. Sensors were intercalibrated in a well-mixed water tank to a precision of ≤0.05°C. Mean surface sediment temperatures (Tₑₙₑ) were computed using the lakes’ bathymetry, assuming each sensor depth was representative of a depth zone. We verified this approach with four logger moorings at 1.0 and 3.0 m water depth (IH and MH) in 2017. Net radiometers measured shortwave irradiance (SWₑₙₑ) on the Mire (CNR1, CNR4, Kipp & Zonnen).
2.5. Proxy Development

Arrhenius-type temperature functions, widely used to express the temperature response of biogenic CH4 emissions (Yvon-Durocher et al., 2014), were fitted to ice-free flux and concentration measurements:

\[ J = e^{\frac{E_a}{k_B T} + b} \]  

Here, \( J \) is the predicted variable (e.g., flux), \( T \) is the temperature in kelvin, \( k_B \) is the Boltzmann constant \((8.62 \times 10^{-5} \text{ eV K}^{-1})\), and \( E_a \) the empirical activation energy in electron volts (eV) \((1 \text{ eV} = 96 \text{ kJ mol}^{-1})\).

We paired measurements with \( T_{\text{sed}} \) averaged over each sampling interval (bubble traps), sampling day (water samples), and deployment period (chambers). Multiyear time series of fluxes and \( \Delta[\text{CH}_4] \) were normalized by lake (e.g., \( J_{\text{norm}} = J \times J_{\text{lake}} \)), binned into 1°C bins, and the natural logarithm of Equation 2 was fitted by estimating the slope \( E_a' \) and intercept \( b \) via linear regression (OLS). Equation 2 could then be used as a proxy of \( F_{\text{ch}}, F_{\text{ch}}, \) and \( \Delta[\text{CH}_4] \), using \( E_a' \) and \( b \) values with \( T_{\text{sed}} \) time series. We also compared ice-free totals of fluxes and solar irradiance for each sampling year, extending the analysis of Wik et al. (2014).

2.6. Total Ice-Free Fluxes

In order to evaluate sampling biases, we compared two methods that estimate the total ice-free \( \text{CH}_4 \) fluxes:

1. Traditional: mean flux × ice free season length, defined as the number of days between a 3-day period with daily mean air temperatures \( (T_{\text{all}}) \) above 0°C and a 3-day period with \( T_{\text{all}} \) below 0°C.
2. Proxy: flux time series were constructed from \( E_a' \) values and Equation 2, using half-hourly series of \( T_{\text{sed}} \) \((F_{\text{ch}}, F_{\text{ch}}, T_{\text{sed}}) \) plus \( k_{\text{mod}} \) \((F_{\text{mod}}) \). The sum across ice-free periods represents the total flux.

We compared the two methods for each of the three flux estimation techniques as well each year.

2.7. Resampling Simulations

Proxies can remediate sampling bias if the required sampling effort is cost-effective. We ran resampling simulations (Bartlett et al., 1989; Sokal & Rohlf, 1995; Wik, Thornton, et al., 2016) to compare the number of sampling days required to accurately estimate the mean ice-free flux via measurements and proxies. Measurements were first averaged across locations to integrate spatial variability, and subsequently in bins of increasing size \( n \), such that the smallest bin contained the full range of sampling day means, and the largest bin the 8- or 9-year mean. We computed 200 binned means from \( n \) random subsamples for each sample size class. For the proxy-based flux estimates, \( n \) random measurements were paired with \( T_{\text{sed}} \) to compute the \( E_a' \) values using a nonlinear fitting algorithm (nlinfit in MATLAB R2018a); a total flux was computed via Method 2 (section 2.6). We determined the sample size \( n \) for which 95% of the computed means fell within 20% of the multiyear mean flux. We repeated the analysis with the measurements subdivided into \( n \) temperature bins within which random subsamples were picked to simulate an informed sampling strategy aimed at achieving a representative temperature range.

3. Results

Fluxes and concentrations were strongly related to energy input on daily-weekly (Figure 1a) and interannual time scales (Figure 1d), and closely fitted Arrhenius-type temperature functions (OLS: \( R^2 \geq 0.93, p < 0.01 \), Figure 1b). The ebullition pathway showed the greatest sensitivity to temperature \( (E_a' = 1.36 \pm 0.10 \text{ eV}) \), followed by the surface concentrations \( (E_a' = 1.10 \pm 0.12 \text{ eV}) \) and the diffusive emission pathway \( (E_a' = 1.00 \pm 0.17 \text{ eV}) \) (means ±95% CI). Bubble flux activation energies were greater in the vegetated littoral zones \((z \leq 2 \text{ m}, E_a' = 1.26 \pm 0.11 \text{ eV}) \) than in deeper waters \((z > 2 \text{ m}, E_a' = 1.11 \pm 0.16 \text{ eV}) \) (means ±95% CI), but we did not find depth differences for the concentrations or the diffusive fluxes. Emissions at \( T_{\text{sed}} \leq 6^\circ \text{C} \) did not fit the flux-temperature relationship (Figure 1b). Hysteresis occurred in the temperature response of the bubble flux, with lower fluxes in June relative to September within the same temperature range (Figure 1c). Concentrations and diffusive fluxes did not display hysteresis.

The seasonal evolution of \( \text{CH}_4 \) emissions closely followed that of the sediment temperature, with a clear peak in the warmest months of July and August (Figure 2a). Temperature proxies generally matched the annual cycle of the manually measured fluxes. Differences were partly due to single-year outliers. Elevated bubble fluxes in July/August 2014 (the warmest period in our record) and September 2016 (autumn emission burst) skewed the multiyear means (orange dots, Figure 2a). Due to hysteresis (Figure 1c) the
bubble flux proxy estimates were offset from measurements by +41% in June and −37% in September (excluding 2016). These offsets canceled out to a multiyear mean difference of −0.3% (Table 1). Overall, differences between measured emissions and proxy fluxes computed over the same sampling periods were less than 8% of the three-lake multiyear means (Table 1). This implies that temperature proxies provide a reasonable estimate of total ice-free season flux.

Despite sampling over most of the ice-free season, we collected fewer samples in the colder months (less coverage in June and September, as represented by bottom bars in Figure 2a). The ice-free season lasted 5–6 months, yet only 40% of bubble fluxes and concentrations were measured outside of July and August, and 30% of chamber fluxes. The bias is reflected in sediment temperatures during bubble trap deployments, water sampling, and chamber deployments, which averaged 11.7, 11.4, and 11.9°C, respectively, compared to the ice-free mean of 9.3°C (2009–2018). This discrepancy led to overestimation of fluxes computed via traditional upscaling approaches compared to proxy fluxes computed over the full ice-free season (Table 1, Figure 2b). Total ice-free bubble fluxes were overestimated by 39%, and diffusive fluxes by 20% (model) and 40% (chambers). Had sampling been limited to July and August, the biases would have increased to 76%, 43%, and 65%, respectively. Hence, for chamber fluxes, a lower temperature sensitivity did not negate the sampling bias.

Sampling bias can be remedied with proxies (Table 1) or by collecting additional samples, but which approach is more effective? With resampling simulations (Figure 3) we compared the sample sizes needed to estimate multiyear mean ice-free fluxes with 20% accuracy for different sampling strategies. Erratic
EBULLITION REQUIRED THE GREATEST NUMBER OF SAMPLING DAYS (WIK, THORNTON, ET AL., 2016), AND PROXIES MORE SO THAN THE TRADITIONAL METHOD (FIGURE 3A) DUE TO HYSTERESIS AT LOW TEMPERATURES (FIGURE 1C). PROXIES WERE MORE EFFICIENT AT QUANTIFYING DIFFUSIVE FLUXES, WHICH DisplayED NO HYSTERESIS (FIGURES 3B AND 3C). GAS TRANSFER MODELS (FIGURE 3B) REQUIRED MORE SAMPLING DAYS THAN FLOATING CHAMBERS (FIGURE 3C), LIKELY DUE TO DIEL VARIABILITY OF $\Delta$CH$_4$ (JANSEN ET AL., 2020), WHICH WAS INTEGRATED BY THE 24‐HR CHAMBER DEPLOYMENTS BUT NOT RESOLVED WITH DISCRETE WATER SAMPLING. THE USE OF IN SITU CH$_4$ SENSORS WOULD MITIGATE THAT PROBLEM (ENCINAS FERNÁNDEZ ET AL., 2014; ERKKILÄ ET AL., 2018).

DISTRIBUTING OBSERVATIONS ACROSS A TEMPERATURE RANGE (DASHED LINES IN FIGURE 3) OBTAINED ACCURATE AVERAGES MORE EFFICIENTLY THAN RANDOM SAMPLING (SOLID LINES IN FIGURE 3). IN PRINCIPLE, VARIABILITY OF FLUXES OVER THE FULL ICE‐FREE PERIOD CAN BE CAPTURED WITH A DISTRIBUTED SAMPLING STRATEGY ($n \leq 87$ DAYS, FIGURE 3) WITHIN A SINGLE ICE‐FREE SEASON (161 DAYS). THE TEMPERATURE RANGE OF EACH ICE‐FREE SEASON (2009–2018) COVERED 95% OF THE MULTIYEAR VARIABILITY OF $T_{sed}$ (2.5TH AND 97.5TH PERCENTILES). HOWEVER, THE NUMBER OF DAYS WE COLLECTED SAMPLES FROM BUBBLE TRAPS (45 DAYS PER FIELD SEASON, ON AVERAGE), SURFACE WATER (14 DAYS), AND FLOATING CHAMBERS (13 DAYS) WERE BELOW MINIMUM SAMPLING REQUIREMENTS. THUS, OUR SAMPLING COVERED A LIMITED TEMPERATURE RANGE. THE SAME RESAMPLING ANALYSIS THEREFORE RESULTED IN A LOWER SAMPLING THRESHOLD WHEN DONE SEPARATELY FOR INDIVIDUAL FIELD SEASONS; $n \leq 39$ ($F_{eb}$) AND $n \leq 11$ ($F_{ch}$) DAYS PER YEAR (WIK, THORNTON, ET AL., 2016).

### 4. Discussion

Energy input is a dominant control on ice‐free CH$_4$ emissions from the Stordalen lakes for $T_{sed}$ from 7°C to 22°C (THORNTON ET AL., 2015; WIK ET AL., 2014). Well‐fitting Arrhenius models (FIGURES 1A AND 1B) AND A ROBUST DEPENDENCE ON SOLAR IRRADIANCE (FIGURE 1D) SUGGEST A TIGHT COUPLING BETWEEN ECOSYSTEM‐LEVEL CH$_4$ EMISSIONS.
and the underlying temperature-dependent microbial processes within this temperature range (McCalley et al., 2014; Yvon-Durocher et al., 2014). At 6°C and below, both emission pathways were independent of temperature (Figure 1b), corresponding to shifts in microbial community structures and rate-limiting metabolic reactions associated with a threshold temperature of 7°C (Tveit et al., 2015).

Ebullition was more sensitive to temperature changes (1.36 eV) than turbulence-driven diffusion (1.00 eV) or pure-culture methanogenesis (1.10 eV, Yvon-Durocher et al., 2014), implicating modulating factors that depend on emission pathway. Changes in thermal energy input primarily affect ebullition rates because CH4 concentrations in bubble formation zones already approach the solubility limit; increased methanogenesis rates directly enhance the flux. The decrease of CH4 solubility with increasing temperature contributes ~14% to the mean increase in ebullition rates between 5°C and 20°C (Chanton et al., 1989). Compounding effects may include increasing microbial abundance and activity, and expansion of the production zone as heat and dissolved organic substrates diffuse deeper into the sediment over summer (Chan et al., 2005; Wilkinson et al., 2015; Zeikus & Winfrey, 1976).

The activation energies computed here (Figure 1b) fall within the broad ranges previously reported for ebullition: 0.42–1.75 eV (Aben et al., 2017; DelSontro et al., 2016; Wilkinson et al., 2019), and diffusive fluxes of CH4: 0.34–1.38 eV (Wilkinson et al., 2019, and references therein). Variability at ecosystem-level emerges from the compound effects of temperature-sensitive biogeochemical processes including methanogenesis (Fey & Conrad, 2000; Negandhi et al., 2016) and methanotrophy (Duc et al., 2010; Fuchs et al., 2016; Lofton et al., 2014) and physical processes such as the solubility of CH4 gas (Wiesenburg & Guinasso, 1979) and the lake mixing regime (Engle & Melack, 2000; MacIntyre et al., 2009). $E_a'$ values have been observed to vary with lake trophic state (Davidson et al., 2018; Sepulveda-Jauregui et al., 2018) and thermal history (Yvon-Durocher et al., 2017). Choice of temperature measurement (e.g., $T_{air}$ or $T_{sed}$) may shift $E_a'$ as well. Our data show for the first time that $E_a'$ can also vary substantially between years ($F_{eb}$: 0.87–2.16 eV, Δ[CH4]: 0.45–2.34 eV, $F_{ch}$: 0.25–2.28 eV; Table S2). The extent to which interannual variability of ecosystem processes contributed is unclear, but it partly resulted from greater uncertainty (Table S2) associated with fewer samples (Figure 3) and the limited temperature range of individual field seasons. Both environmental context (Seekell et al., 2018) and sampling strategy contribute to the reported variability in $E_a'$.

Modeled and measured bubble fluxes diverged early and late in summer (Figure 2a). Differences stem in part from seasonal hysteresis of the flux (Figure 1c) and transient storage of CH4 gas, heat, or substrates. Time lags introduced by storage-and-release cycles can temporally dissociate the flux from its drivers. For example, bubble gas can build up in sediments until a hydrostatic pressure drop triggers its release (Mattson & Likens, 1990); here, a delayed emission burst in late September 2016 constituted 6–14% of that year’s ice-free flux (Jansen et al., 2019). Low bubble fluxes in early summer (Figure 2a) may be caused by a...
delay between the initial warming pulse and microbial abundance or substrate concentrations (Chan et al., 2005; Jerman et al., 2009; Updegraff et al., 1998). Conversely, thermal inertia of the lake sediments (Fang & Stefan, 1996) would maintain methanogenesis in autumn. Hysteresis was not observed in diffusive fluxes (Figure 1c). This could be because frequent wind mixing limits the accumulation of gas in the hypolimnion (Jansen et al., 2020), or because whole-lake diffusive emissions are driven by production in shallow sediments (DelSontro et al., 2017), for example, due to organic substrate of higher quality (Wik et al., 2018). If the latter, the development and application of temperature proxies for diffusive fluxes may not be confounded by hysteresis effects, even in lakes deeper than ours which mix less frequently.

Temperature proxies can accurately estimate total ice-free fluxes, even when emissions are affected by seasonal temperature hysteresis (Table 1). If they are however, it is more cost-effective to avoid sampling bias via additional field days in colder months (Figure 3a). Alternatively, $E_a'$ values from the literature may be used for bias correction. While replacing our ebullition $E_a'$ (1.36 eV) with literature values (0.42–1.75 eV) in Equation 2 would introduce substantial errors in the mean flux estimate—ranging between −27% and +26% depending on the $E_a'$ value used—this is smaller than our sampling bias (+39%). This suggests that existing flux estimates may be corrected for sampling bias using published $E_a'$ values and in situ temperature data. An additional benefit of proxies is that the impact of climate change on past, current, and future emissions can be evaluated via automated observations or existing meteorological data sets (Marotta et al., 2014; Thornton et al., 2015). This study provides guidelines for temperature proxy development:

1. calibration of the Arrhenius model ($E_a'$ and $b$ in Equation 2) for each unique site and emission pathway;
2. paired observations of flux and temperature that integrate or resolve spatiotemporal variability; and
3. a minimum of 14 distributed sampling days for diffusive fluxes and 135 days for ebullition.

Our proxies apply under ice-free conditions at $T_{sed}$ = 7–22°C. Drivers other than temperature govern CH$_4$ dynamics under ice and emissions in spring (Jammet et al., 2015; Jansen et al., 2019).

## 5. Summary and Implications

On a global scale, biased sampling contributes to the gap between upscaled measurements (bottom-up) and inverse models constrained by the atmospheric growth rate of CH$_4$ (top-down) (Crill & Thornton, 2017; Saunois et al., 2016). The overestimation of the seasonal mean flux due to sampling only in the warmest months—a factor 1.4–1.8 in this study—was similar in magnitude to underestimation from omitting large storage fluxes in spring (Denfeld et al., 2018; Jansen et al., 2019) or autumn (Encinas Fernández et al., 2014; López Bellido et al., 2009). Distributed sampling over a longer period would help reduce these biases, even though study designs and available funds often constrain the duration and continuity of field projects (Nisbet, 2007).

Because sampling bias increases with the magnitude of the flux (Figure 2b) and the majority of northern lake emission studies report higher fluxes over shorter sampling periods (Wik, Varner, et al., 2016) compared to this study, our bias estimates should be considered conservative. Proxies based on energy input may contribute to computation of unbiased total ice-free emissions from seasonally ice-covered lakes and aid in the prediction of future emission rates. Our work shows that annual ice-free fluxes depend on total solar irradiance. The 21st century projections of lake CH$_4$ emissions thus depend on the ability of climate models to resolve Arctic cloud cover. Future studies could also be directed at understanding the variability of the flux temperature-sensitivity encapsulated in $E_a'$ and identifying the biogeochemical and physical processes that govern this relationship at the ecosystem level.

## Data Availability Statement

Data are available at this site (www.bolin.su.se/data/).

## References

Aaben, R. C. H., Barros, N., van Donk, E., Frenken, T., Hill, S., Kazanjian, G., et al. (2017). Cross continental increase in methane ebullition under climate change. *Nature Communications*, 8(1), 1682. https://doi.org/10.1038/s41467-017-01535-y

Aguilera, R., Livingstone, D. M., Maréc, R., Jennings, E., Pèira, J., & Adrian, R. (2016). Using dynamic factor analysis to show how sampling resolution and data gaps affect the recognition of patterns in limnological time series. *Inland Waters*, 6(3), 284–294. https://doi.org/10.1002/IW.13948
Lament, J. C., & Scott, D. S. (1970). An eddy cell model of mass transfer into the surface of a turbulent liquid. AIChE Journal, 16(4), 513–539. https://doi.org/10.1002/aic.690160403

Lofton, D. D., Whalen, S. C., & Hershey, A. E. (2014). Effect of temperature on methane dynamics and evaluation of methane oxidation kinetics in shallow Arctic Alaskan lakes. Hydrobiologia, 721(1), 209–222. https://doi.org/10.1007/s10750-013-1663-x

López Belido, J., Tulonen, T., Kankaala, P., & Ojala, A. (2009). CO₂ and CH₄ fluxes during spring and autumn mixing periods in a boreal lake (Päijätjärvi, southern Finland). Journal of Geophysical Research, 114, G04007. https://doi.org/10.1029/2009JG000923

Machtneyre, S., Clark, J. F., Jellison, R., & Fram, J. P. (2009). Turbulent mixing induced by nonlinear internal waves in mono Lake, California. Limnology and Oceanography, 54(6), 2255–2272. https://doi.org/10.4319/lo.2009.54.6.2255

Natchimuthu, S., Sundgren, I., Gålfalk, M., Klemedtsson, L., Crill, P., Danielsson, Å., & Bastviken, D. (2016). Spatio-temporal variability of lake CH₄ fluxes and its influence on annual whole lake emission estimates. Limnology and Oceanography, 61(51), S13–S26. https://doi.org/10.1002/lio.10222

Negandhi, K., Laurion, I., & Lovejoy, C. (2016). Temperature effects on net greenhouse gas production and bacterial communities in arctic thaw ponds. FEMS Microbiology Ecology, 92(8), 1, fiw117–12. https://doi.org/10.1093/femsec/fiw117

Nisbet, E. (2007). Cinderella science. Nature, 450(7171), 789–790. https://doi.org/10.1038/450789a

Saunois, M., Bousquet, P., Poulter, B., Peregon, A., Ciais, P., Canadell, J. G., et al. (2016). The global methane budget 2000–2012. Earth System Science Data, 8(2), 697–751. https://doi.org/10.5194/esd-8-697-2016

Seekell, D. A., Lapierre, J.-F., & Cheruvellil, K. S. (2018). A geography of lake carbon cycling. Limnology and Oceanography Letters, 3(3), 49–56. https://doi.org/10.1002/lol.10078

Sepulveda-Jauregui, A., Hoyos-Santillan, J., Martinez-Cruz, K., Walter Anthony, K. M., Casper, P., Belmonte-Izquierdo, Y., & Thalasso, F. (2018). Eutrophication exacerbates the impact of climate warming on lake methane emission. Science of the Total Environment, 636, 411–419. https://doi.org/10.1016/j.scitotenv.2018.04.283

Sokal, R. R., & Rohlf, F. J. (1995). Biometry: The principles and practice of statistics in biological research, (3rd ed.). San Francisco: Freeman.

Stanley, E. H., Collins, S. M., Lottig, N. R., Oliver, S. K., Webster, K. E., Cheruvelil, K. S., & Soranno, P. A. (2019). Biases in lake water quality sampling and implications for macroscale research. Limnology and Oceanography, 64(4), 1572–1585. https://doi.org/10.1002/lio.11136

Tan, Z., & Zhuang, Q. (2015). Arctic lakes are continuous methane sources to the atmosphere under warming conditions. Environmental Research Letters, 10(5), 054016. https://doi.org/10.1088/1748-9326/10/5/054016

Telford, E. W., MacIntyre, S., Miller, S. D., & Czikowsky, M. J. (2014). Similarity scaling of turbulence in a temperate lake during fall cooling. Journal of Geophysical Research: Oceans, 119, 4689–4713. https://doi.org/10.1002/jgrc.2011035

Thornton, B. F., Wilk, M., & Crill, P. M. (2015). Climate-forced changes in available energy and methane bubbling from subarctic lakes. Geophysical Research Letters, 42, 1936–1942. https://doi.org/10.1002/2015GL063189

Tveit, A. T., Urich, T., Frenzel, P., & Svenning, M. M. (2015). Metabolic and trophic interactions modulate methane production by Arctic peat microbiota in response to warming. Proceedings of the National Academy of Sciences, 112(19), E2507–E2516. https://doi.org/10.1073/pnas.1420797112

Updegraff, K., Bridgham, S. D., Pastor, J., & Weishampel, P. (1998). Hysterisis in the temperature response of carbon dioxide and methane production in peat soils. Biogeochemistry, 43(3), 253–272. https://doi.org/10.1021/05009708826

Vespero, C., Kutser, T., Seekell, D. A., & Tranvik, L. J. (2014). A global inventory of lakes based on high-resolution satellite imagery. Geophysical Research Letters, 41, 6396–6402. https://doi.org/10.1002/2014GL060641

Wanninkhof, R. (2014). Relationship between wind speed and gas exchange over the ocean revisited. Limnology and Oceanography: Methods, 12(6), 351–362. https://doi.org/10.4319/lom.2014.12.351

Wiesenburg, D. A., & Guinasso, D. A. (1979). Equilibrium solubilities of methane, carbon monoxide, and hydrogen in water and sea water. Journal of Chemical & Engineering Data, 24(4), 356–360. https://doi.org/10.1021/je0003a006

Wick, M., Crill, P. M., Varner, R. K., & Bastviken, D. (2013). Multiyear measurements of ebullitive methane flux from three subarctic lakes. Journal of Geophysical Research: Biogeosciences, 118, 1307–1321. https://doi.org/10.1002/jgrg.20103

Wick, M., Johnson, J. E., Crill, P. M., DeStasio, J. P., Erickson, L., Halloran, M. J., et al. (2018). Sediment characteristics and methane ebullition in three subarctic lakes. Journal of Geophysical Research: Biogeosciences, 123, 2399–2411. https://doi.org/10.1029/2017JG004298

Wick, M., Thornton, B. F., Bastviken, D., MacIntyre, S., Varner, R. K., & Crill, P. M. (2014). Energy input is primary controller of methane bubbling in subarctic lakes. Geophysical Research Letters, 41, 555–560. https://doi.org/10.1002/2013GL058510

Wick, M., Richardson, L. W., Wilk, M., & Crill, P. M. (2016). Biased sampling of methane release from northern lakes: A problem for extrapolation. Geophysical Research Letters, 43, 1256–1262. https://doi.org/10.1002/2015GL066501

Wick, M., Varner, R. K., Walter Anthony, K. M., MacIntyre, S., & Bastviken, D. (2016). Climate-sensitive northern lakes and ponds are critical components of methane release. Nature Geoscience, 9(2), 99–105. https://doi.org/10.1038/ngeo2578

Wilkinson, J., Bodmer, P., & Lorke, A. (2019). Methane dynamics and thermal response in impoundments of the Rhine River, Germany. Science of the Total Environment, 659, 1045–1057. https://doi.org/10.1016/j.scitotenv.2018.12.424

Wilkinson, J., Mack, A., Alibhoul, Z., & Lorke, A. (2015). Continuous seasonal river ebullition measurements linked to sediment methane formation. Environmental Science & Technology, 49(22), 13,121–13,129. https://doi.org/10.1021/acs.est.5b05125

Yvon-Durocher, G., Allen, A. P., Bastviken, D., Conrad, R., Gudasz, C., St-Pierre, A., et al. (2014). Methane fluxes show consistent temperature dependence across microbial to ecosystem scales. Nature, 507(7493), 488–491. https://doi.org/10.1038/nature13164

Yvon-Durocher, G., Hulatt, C. J., Woodward, G., & Trimmer, M. (2017). Long-term warming amplifies shifts in the carbon cycle of experimental ponds. Nature Climate Change, 7(3), 209–213. https://doi.org/10.1038/nclimate3329

Zeikus, J. G., & Winfrey, M. R. (1976). Temperature limitation of methanogenesis in aquatic sediments. Applied and Environmental Microbiology, 31(1), 99–107. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/621196