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LETTER

Methanogenesis exceeds CH_4 consumption in eutrophic lake sediments

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Scientific Significance Statement

In lakes and reservoirs, most microbially produced methane (CH_4) is efficiently consumed via CH_4 oxidation, and changes to the balance between these two processes would have important implications for future aquatic greenhouse gas emissions. However, previous syntheses of CH_4 measurements from lakes and reservoirs compile emission rates from the surface, while ignoring CH_4 production and oxidation rates in the water column and sediments below. Our data set brings together CH_4 production and oxidation rates from over 60 lakes and reservoirs for the first time. Systems with greater sediment CH_4 production had less efficient sediment CH_4 consumption, potentially driving greater emissions. Our results also link higher lake primary productivity (trophic status) to greater sediment CH_4 production, suggesting eutrophication may contribute to increasing emissions.

Abstract

Lakes and reservoirs collectively contribute significant amounts of methane (CH_4) to the global atmosphere. If CH_4 production were not at least partially balanced by consumption (oxidation) in most of these systems, they could potentially emit an order of magnitude or more CH_4. The impacts of environmental drivers such as trophic status, temperature, and latitude on CH_4 production, CH_4 oxidation, and the balance of the two processes influence current and future patterns of freshwater CH_4 emissions. Using CH_4 production and oxidation rates measured with a common methodology (incubations) from over 60 different lakes and reservoirs, we provide novel evidence for lower sediment CH_4 oxidation efficiency at high sediment CH_4 production rates. We also show a strong positive correlation between sediment CH_4 production and lake trophic status. Our results suggest that less efficient CH_4 consumption at high CH_4 production rates could help explain greater surface emissions often observed in eutrophic lakes globally.

Lakes and reservoirs are responsible for a significant portion of the global methane (CH_4) budget, with emission estimates for these systems ranging from 8 to 185 Tg CH_4 yr^{-1} (Saunois et al. 2020). Emissions from lakes occur when microbial CH_4 production outpaces microbial CH_4 oxidation (consumption). Lake CH_4 production is primarily thought to occur in sediments and anaerobic regions of the water column, where anoxic conditions and abundant organic matter favor methanogenesis (Winfrey and Zeikus 1979; Iversen et al. 1987; Biderre-Petit et al. 2011). Nevertheless, there are

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Additional Supporting Information may be found in the online version of this article.

some examples of significant production in oxic layers of the water column (Bogard et al. 2014; Günthel et al. 2019). High organic carbon availability, warmer temperatures, and anoxic conditions are considered important drivers of methanogenesis, resulting in a generally positive correlation between lake primary productivity (trophic status) and CH_4 production rates (West et al. 2016). As CH_4 passes through sediments and the water column, some CH_4 is consumed via aerobic (Frenzel et al. 1990; Guérin and Abril 2007) or anaerobic methane oxidation (Martinez-Cruz et al. 2018; Cabrol et al. 2020). Methane oxidation is considered highest in systems with abundant CH_4 and a sufficient supply of electron acceptors such as oxygen, nitrate, and sulfate (van Grinsven et al. 2020*b*), but evidence is conflicting for whether oxidation is significantly dependent on temperature (Utsumi et al. 1998; Duc et al. 2010; Sepulveda-Jauregui et al. 2018; Thottathil et al. 2019). In addition, the few studies comparing CH_4 oxidation rates among lakes of different primary productivity suggest that trophic status may also influence CH_4 oxidation (Sepulveda-Jauregui et al. 2018; Yang et al. 2018, 2019).

Previous global assessments have highlighted important roles for trophic status, temperature, and latitude in determining CH_4 fluxes from lakes and reservoirs (Bastviken et al. 2004; Barros et al. 2011; Deemer et al. 2016; DelSontro et al. 2018; Beaulieu et al. 2019). These syntheses focus on net surface CH_4 emissions, not CH_4 processing rates (i.e., CH_4 production and oxidation in the sediments and water column). Although examining large-scale controls on net fluxes is useful, predicting future lake and reservoir CH_4 emissions requires understanding how the balance between production and oxidation changes with shifting climatic and anthropogenic drivers. Addressing this knowledge gap requires investigating controls on both CH_4 production *and* CH_4 consumption rates, as well as how these two processes interact. Here, we present a data set of sediment CH_4 production, sediment CH_4 oxidation, and water column CH_4 oxidation rates measured with a common methodology (incubations) from 42 peer-reviewed studies of 67 lakes. We analyze trends in CH_4 production and oxidation across systems as well as investigate potential environmental controls on lake and reservoir CH_4 cycling such as trophic status, temperature, and latitude.

Methods

Study selection

We compiled peer-reviewed studies measuring rates of sediment CH_4 production, sediment CH_4 oxidation, and/or water column CH_4 oxidation in freshwater lakes or reservoirs. Literature searches were done using online search engines (JSTOR, Web of Science, and ScienceDirect) in November 2020. Studies that measured production or oxidation using methods other than sediment or water incubations were excluded, as were lakes described as soda, saline, karst, acidic, or alkaline by the authors of the study. By focusing on studies using one common methodology (incubations), we ensure rate measurements between lakes are as comparable as possible.

Rate extraction

Production and oxidation rates were only used if presented by the authors in units that could be converted to per-area (μmol CH_4 m^{-2} d^{-1}), per-volume (μmol CH_4 L^{-1} d^{-1}), or per-mass (μmol CH_4 gram dry $sediment^{-1}$ d^{-1}) units. To compile a data set of rates as close to in situ conditions as possible, "potential" rates were excluded. Rates were considered potentials if reported as potentials by the authors or if the incubations were amended with nutrients or with carbon precursors for methanotrophy (supplemented CH_4) or methanogenesis (e.g., supplemented CO_2, bicarbonate, or acetate). By excluding potential rates from our analysis, we focus on controls of CH_4 processing in lakes and reservoirs close to in situ environmental conditions.

Rate averaging and subsetting

During our literature search, we extracted one mean rate of sediment CH_4 production, sediment CH_4 oxidation, and/or water column CH_4 oxidation for each lake in each study. If no mean rate for an individual lake was presented, the mean rates or range of rates were averaged between different sampling sites, times, and/or depths within the sediment or the water column. This approach occasionally required averaging across sediment or water column depths with differing oxygen conditions; therefore we do not distinguish between aerobic and anaerobic rates in our analysis.

In the online data file (D'Ambrosio and Harrison 2021), we present a data set of all sediment CH_4 production, sediment CH_4 oxidation, and/or water column CH_4 oxidation rates extracted during our literature search (77 studies of 107 lakes). The data set includes per-area (μmol CH_4 m^{-2} d^{-1}), per-volume (μmol CH_4 L^{-1} d^{-1}), or per-mass (μmol CH_4 gram dry $sediment^{-1}$ d^{-1}) rate measurements. Given the uncertainty associated with comparing per-area, per-volume, and per-mass units, we focus on per-area rates because this was the most commonly reported unit; our analysis therefore includes per-area rates of sediment CH_4 production (69 observations), sediment CH_4 oxidation (19 observations), and water column CH_4 oxidation (13 observations) from 42 peer-reviewed studies of 67 different lake and reservoir systems (Table 1, Fig. 1).

Incubation methodology

We focused our literature search on production and oxidation rates measured with incubations. Incubations typically involve sealing sediment and/or water in a gastight vial, incubating at a constant temperature in the lab or in situ, and monitoring the change in CH_4 concentrations over time to estimate net CH_4 production or oxidation rates (Kelly and Chynoweth 1980; Frenzel et al. 1990; Utsumi et al. 1998). Sediment incubations in our data set include those done with homogenized (slurried) sediment, intact sediment cores, and sediment subcores (slices from different layers of intact sediment cores). In order to focus on rates as close to in situ

Table 1. Statistical parameters of CH_4 processing rates across data set.

Process	Mean rate (mmol CH_4 m^{-2} d^{-1})	Median rate (mmol CH_4 m^{-2} d^{-1})	Range of rates (mmol CH_4 m^{-2} d^{-1})	Coefficient of variation (%)	Number of unique observations	Number of unique lakes
Sediment CH_4 production	2.98	0.936	0–21.8	181	69	53
Sediment CH_4 oxidation	0.341	0.05	0.001–2.65	200	19	14
Water column CH_4 oxidation	6.22	2.45	0.0237–32.5	146	13	13

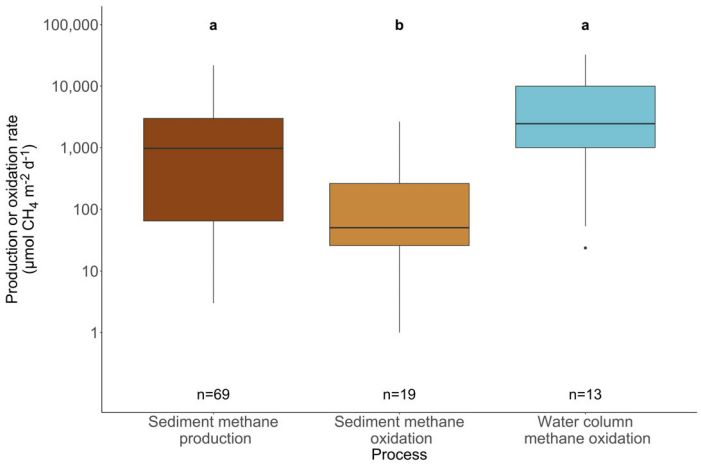

Fig 1. Distribution of CH_4 production and oxidation rates across data set. Number of unique observations is indicated underneath each boxplot. Letters above boxplots indicate significant groupings (Kruskal–Wallis test, $H = 15.362$, $p < 0.001$; Dunn's post hoc $p < 0.001$). Measurements of zero excluded from the graph. Upper and lower box hinges indicate 25th and 75th quantiles, respectively, and horizontal lines within boxes indicate medians.

conditions as possible, we excluded any incubations that injected an isotopic tracer (^{13}C- or ^{14}C-labeled CH_4, CO_2, etc.) unless the authors specified that such an addition did not significantly change ambient concentrations in the incubation.

Recent evidence demonstrates slurry incubations may suppress sediment CH_4 oxidation rates in lake sediments compared to intact cores or subcores (Su et al. 2019). In contrast, other work has suggested slurrying may stimulate higher rates of CH_4 production in lake sediments (Frenzel et al. 1990) or O_2 consumption in freshwater sediments (Flemming and Trevors 1990) compared to core incubations. The majority (75%) of our per-area sediment measurements derive from intact sediment core or subcore incubations, and therefore were unaffected by the potential effects of sediment homogenization. To ensure methodology did not bias our results, we repeated the analyses presented in this manuscript with slurry rates excluded.

Lake characteristics

Lake or reservoir latitude was taken as reported by the authors or estimated with Google Maps. Incubation temperature reported by the authors was used. If rates were averaged across multiple dates, sites, or depths with different incubation temperatures, temperature was classified as "Multiple." If incubations at multiple temperatures were performed, rates were extracted from the incubation within 5°C of the reported in situ temperature. Trophic status was taken as reported by the authors. In order to maintain sufficient statistical power, lakes and reservoirs were grouped into low trophic status (dystrophic, oligotrophic, or oligomesotrophic) or high trophic status systems (mesotrophic, eutrophic, or mesoeutrophic).

Statistical analyses

All analyses were done in R version 3.6.1 with a threshold for significance of 0.05. For analyses of grouped data, rates were log-transformed then assessed for normality using a Shapiro–Wilk normality test and for constant variance with a Bartlett test. When log-transformed data were normally distributed and had constant variance, we analyzed for significant differences using a Welch's two-sample *t*-test ($n = 2$ groups) or an ANOVA ($n > 2$ groups). If ANOVA comparisons were significant, post hoc analyses were performed using Tukey's honest significant difference test. When log-transformed data were not normally distributed and/or did not have constant variance, we analyzed for significant differences using a Mann–Whitney *U*-test ($n = 2$ groups) or Kruskal–Wallis test ($n > 2$ groups). If Kruskal–Wallis comparisons were significant, post hoc analyses were performed using a Dunn's post hoc test. For correlation analyses, we used Spearman's rank correlation test on log-transformed rates.

Results and discussion

Comparing CH_4 production and oxidation

Explicit comparisons of production and oxidation rates in the same system are rare, but can provide insight into how emissions change in response to environmental variables. If future lake warming or eutrophication drives higher CH_4 production rates, we can expect little change in emissions if oxidation increases at a similar rate. However, if production and oxidation respond in different ways to changing environmental variables, accurate emission predictions require a more detailed understanding of how both processes are affected by environmental drivers and how they interact.

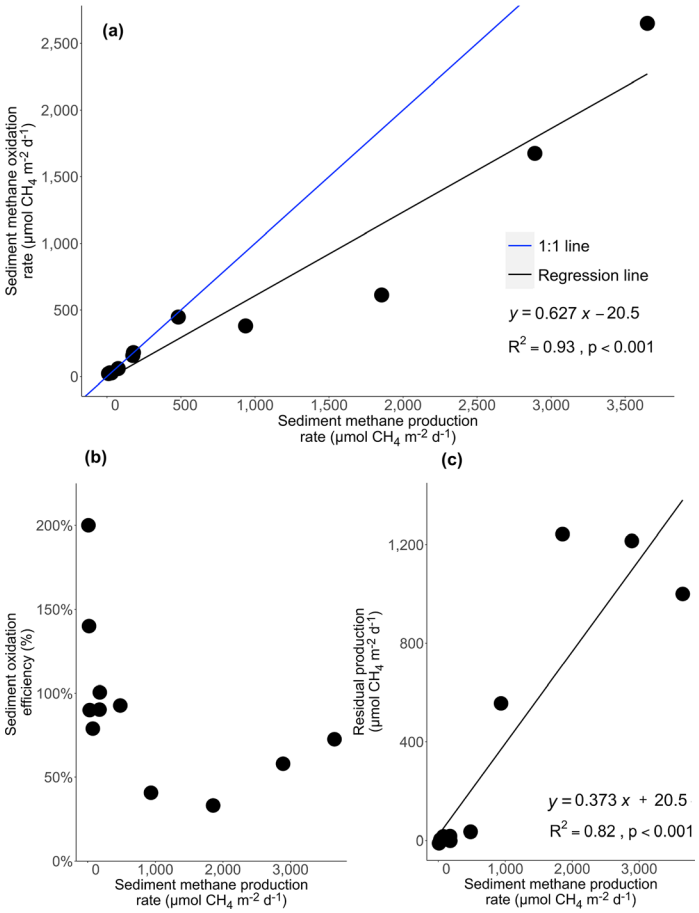

Fig 2. Comparing CH_4 production and oxidation in sediments. (**a**) Sediment CH_4 production vs. sediment CH_4 oxidation, with 1 : 1 line shown in blue and linear regression line shown in black. Regression line equation, R^2, and *p*-value shown in bottom right. (**b**) Sediment CH_4 production vs. sediment CH_4 oxidation efficiency (i.e., sediment oxidation rate/sediment production rate). (**c**) Sediment CH_4 production vs. residual production (i.e., sediment production rate – sediment oxidation rate). Linear regression line is shown in black, and regression line equation, R^2, and *p*-value appear at bottom right. All panels include data exclusively from lake and reservoir systems where both sediment CH_4 production and sediment CH_4 oxidation rates have been reported in the same units (n = 11 lakes).

Our data set showed a positive correlation between rates of sediment CH_4 production and sediment CH_4 oxidation in studies where both rates are reported for the same lake (Fig. 2a). However, sediment oxidation efficiency (i.e., oxidation/production) declined at high sediment CH_4 production rates (Fig. 2b). As oxidation efficiency declines, there is larger residual CH_4 production (i.e., production—oxidation, Fig. 2c), presumably resulting in greater release of CH_4 from sediments. Low sediment CH_4 oxidation efficiency at high CH_4 production rates could be a result of two different factors. First, methanotrophs may become resource-limited as they deplete or are outcompeted for electron acceptors needed for oxidation (e.g., oxygen, nitrate, or sulfate). Second, low oxidation efficiency at high production rates is consistent with the common assumption that CH_4 oxidation follows Michaelis–Menten or Monod kinetics (Kuivila et al. 1988; Mayr et al. 2020*b*), meaning oxidation rate initially increases with CH_4 concentration as a first-order reaction, but approaches a maximum rate (V_{max}) after reaching high enough CH_4 concentrations (K_m). Indeed, a recent investigation of CH_4 oxidation in several northern temperate lakes across a wide range of CH_4 and O_2 conditions found specific oxidation rates (i.e., oxidation rate/CH_4 concentration) decrease with increasing CH_4 concentrations (Thottathil et al. 2019). Our results expand upon these kinetic studies by providing evidence across multiple systems that in some lake sediments, high CH_4 production rates may increase CH_4 concentrations past the point where methanotrophs can keep up. Our interpretation assumes that CH_4 production, which may also obey Michaelis–Menten kinetics (Strayer and Tiedje 1978; Jones et al. 1982), is relatively unaffected by resource constraints when compared to methanotrophs across the range of conditions shown in Fig. 2.

Simultaneous measurements of sediment CH_4 production, sediment CH_4 oxidation, and water column CH_4 oxidation rates from more lakes and reservoirs are needed to determine how shifts in sediment oxidation efficiency ultimately influence CH_4 emission. For example, aerobic and anaerobic methanotrophic communities in the water column are dynamic and may rapidly respond to shifting CH_4, O_2, and other electron acceptor concentrations (Graf et al. 2018; Rissanen et al. 2020; Mayr et al. 2020*b*). Stratified lakes may have sufficiently high rates of CH_4 oxidation at or near the oxycline (Morana et al. 2015) or in the anaerobic water column (Thalasso et al. 2020; van Grinsven et al. 2020*a*) to compensate for potentially low oxidation efficiency in sediments. Low sediment oxidation efficiency may be a less important control on emissions during seasonal overturn of stratified lakes, which can be a hot moment for CH_4 oxidation in the water column (Kankaala et al. 2007; Mayr et al. 2020*a*).

Future work can also examine how alternative pathways of CH_4 release influence emissions from lakes with low sediment CH_4 oxidation efficiency. For example, low sediment oxidation efficiency may support bubble formation and ebullition, a surface emission pathway that can largely bypass water column CH_4 oxidation given sufficiently shallow water (Bastviken et al. 2004; McGinnis et al. 2006; West et al. 2016). In addition, changes in sediment oxidation efficiency may not exert significant control on surface emission in lakes where water column CH_4 production, a process we do not consider here, is a more important source of CH_4 than anoxic sediments (Bogard et al. 2014; Günthel et al. 2019).

Trophic status as a driver of CH_4 processing

Clarifying whether greater CH_4 surface emissions observed in eutrophic lakes (Deemer et al. 2016; DelSontro et al. 2018; Beaulieu et al. 2019) is driven by higher sediment CH_4

production, less efficient CH_4 oxidation, or both is important for predicting how greenhouse gas emissions will change with eutrophication globally (Smith 2003). Multiple studies of small groups of lakes have demonstrated higher potential sediment CH_4 production rates in eutrophic compared to oligotrophic systems (Torres et al. 2011; West et al. 2016; Yang et al. 2017; Sepulveda-Jauregui et al. 2018; Bertolet et al. 2019). However, it is less clear how lake trophic status influences oxidation rates. The increased availability of CH_4 in eutrophic systems could drive higher CH_4 oxidation rates, as observed previously (Sepulveda-Jauregui et al. 2018). On the other hand, the ability of oxidizing microbes to utilize abundant CH_4 may be limited by the supply of oxygen and other electron acceptors.

We compared production and oxidation rates across lakes and reservoirs classified as low or high trophic status (see "Methods" section). We report significantly greater sediment CH_4 production rates in high trophic status lakes than in low trophic status systems (Fig. 3). In contrast, rates of CH_4 oxidation were statistically indistinguishable between trophic statuses (Fig. 3), although this may be influenced by the small sample size for sediment oxidation measurements in high trophic status systems ($n = 2$). The correlation between trophic status and sediment CH_4 production, but not oxidation, again supports the idea that sediment CH_4 oxidation efficiency falls as sediment production rises (Fig. 2). Water column oxidation

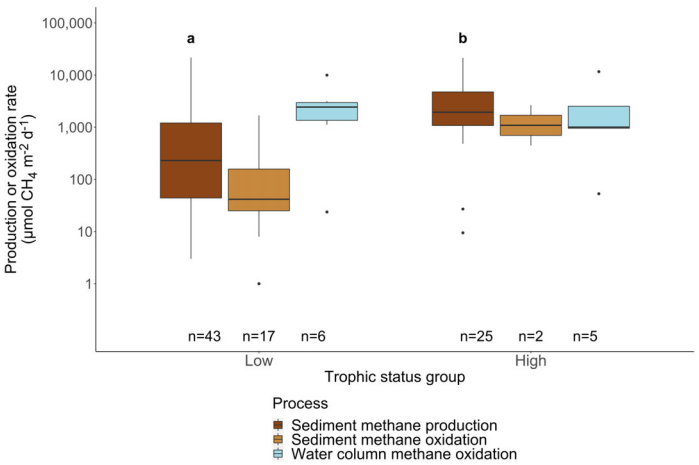

Fig 3. Comparing CH_4 production and oxidation rates across lakes of different trophic status. Number of unique observations indicated underneath each boxplot. Letters above boxplots indicate significant difference between sediment CH_4 production in the low vs. high trophic status group (Welch's two-sample *t*-test, test statistic = 3.79, $p < 0.01$). No significant difference between low and high trophic status lakes was detected for sediment CH_4 oxidation (Welch's two-sample *t*-test, test-statistic = 3.10, *p*-value = 0.12) or water column CH_4 oxidation (Welch's two-sample *t*-test, test statistic = 0.15, $p = 0.88$). Rate measurements of zero and observations from lakes with unclear trophic statuses are excluded from the graph. Upper and lower box hinges indicate 25th and 75th quantiles, respectively, and horizontal lines within boxes indicate medians.

efficiency may also be lower in eutrophic lakes, given trophic status correlated with greater sediment production but not water column oxidation (Fig. 3). Low CH_4 oxidation efficiency at high sediment CH_4 production rates therefore may help explain widespread evidence for greater surface CH_4 emissions in eutrophic lakes, and both support and elaborate upon the hypothesis that lake and reservoir CH_4 emissions will rise with continued eutrophication globally (Beaulieu et al. 2019).

Temperature and latitude

Determining how temperature influences the balance between CH_4 production and oxidation is important given the ongoing warming of many lakes globally (O'Reilly et al. 2015). The temperature dependence of sediment CH_4 production is well documented through lab experiments that expose microbes from one lake, or small groups of lakes, to a wide range of temperatures (Zeikus and Winfrey 1976; Duc et al. 2010; Lofton et al. 2014; Marotta et al. 2014; Sepulveda-Jauregui et al. 2018). Similar experiments with CH_4 oxidation provide mixed results, with some studies reporting a correlation between oxidation rates and temperature (Lofton et al. 2014; Sepulveda-Jauregui et al. 2018; Thottathil et al. 2019) and others failing to detect temperature dependence (Utsumi et al. 1998; Duc et al. 2010). We found no significant correlation between temperature and rates of sediment CH_4 production (Fig. 4a), even within lake productivity class (Supporting Information Fig. S1). There was also no detectable correlation between temperature and sediment CH_4 oxidation (Fig. 4a). Although the temperature dependence of methanogenesis is often cited as part of the reason for greater CH_4 surface emissions observed in some low-latitude, tropical lakes (Barros et al. 2011; Prairie et al. 2017), we found no significant correlation between latitude and rates of CH_4 production or oxidation (Fig. 4b).

The lack of a detectable correlation between incubation temperature and CH_4 production or oxidation may be surprising given the previously demonstrated temperature dependence of sediment methanogenesis (and sometimes methanotrophy) in lab settings (Yvon-Durocher et al. 2014; Sepulveda-Jauregui et al. 2018; Thottathil et al. 2019). The range of temperatures at which incubations in our data set occurred (~ 5–25°C, Fig. 4a) should result in about a 10-fold increase in CH_4 production rates (Yvon-Durocher et al. 2014). Such a temperature effect may have been masked given rates of CH_4 production varied by 3–4 orders of magnitude within our data set (Fig. 4a). In addition, microbial adaptation to local in situ temperatures can affect the optimum temperature for microbially mediated reactions (Canion et al. 2014; Robador et al. 2016). A similar local adaptation may affect lake sediment methanogenic and/or methanotrophic communities, resulting in the apparent lack of a temperature effect when rate measurements are compared from different communities close to in situ temperature (as done in our analysis).

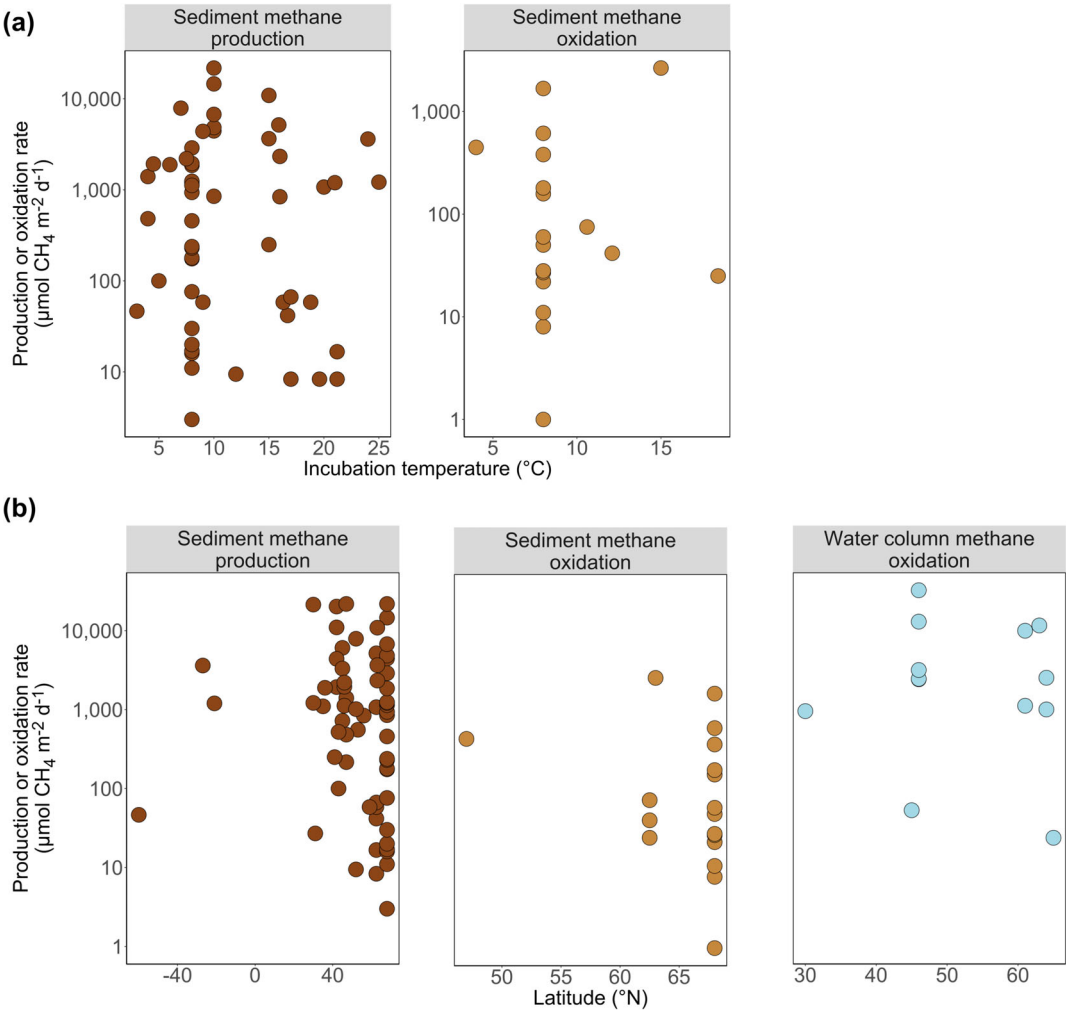

Fig 4. Comparing lake latitude, incubation temperature, and CH_4 processing rates. (**a**) Temperature plotted against sediment CH_4 production (left panel) or sediment CH_4 oxidation (right panel). No significant correlations between rates and temperature were detected (Spearman's rank correlation test; sediment CH_4 production: rho = −0.059, *p*-value = 0.67; sediment CH_4 oxidation rho = −0.012, *p*-value = 0.96). Water column oxidation measurements were excluded because most measurements were averaged across multiple temperatures (see Methods). **(B)** Latitude plotted against sediment CH_4 production (left panel), sediment CH_4 oxidation (center panel), or water column CH_4 oxidation rates (right panel). No significant correlation between rates and latitude was detected (Spearman's rank correlation test; sediment CH_4 production rho = −0.18, *p*-value = 0.14; sediment CH_4 oxidation rho = −0.22, *p*-value = 0.36; water column CH_4 oxidation rho = −0.037, *p*-value = 0.90). Rate measurements of zero are excluded from all graphs.

Similarly, a clear temperature dependence of methanogenesis and/or methanotrophy may be apparent when maximal potential rates are measured (Sepulveda-Jauregui et al. 2018), but less obvious in our analysis of rates measured at close to in situ conditions. Lastly, it is important to note that other studies have observed a strong relationship between temperature and sediment ebullition, a CH_4 emission pathway we do not examine here (Aben et al. 2017; Davidson et al. 2018; McClure et al. 2020).

Conclusions

Our analysis is the first to compile CH_4 production and oxidation rates close to in situ conditions across a wide range of lakes and reservoirs. We provide evidence for decreasing CH_4 oxidation efficiency in sediments at high rates of CH_4 production. Furthermore, we show a strong and positive relationship between sediment CH_4 production rates and system trophic status. Somewhat surprisingly, we did not detect significant correlations between CH_4 processing rates and either lake latitude or temperature. Taken together, our results suggest factors that could potentially increase sediment CH_4 production—such as lake eutrophication—may result in less efficient CH_4 consumption, ultimately driving a greater release of CH_4 from lake sediments into the water column. Given sediment oxidation efficiency can vary from about 50% to over 99% in our data set (Fig. 2b) and other lakes (Bastviken et al. 2008), decreasing oxidation efficiencies

could potentially increase the supply of CH_4 to the water column up to an order of magnitude or more. This phenomenon could help explain why eutrophic lakes often emit more CH_4 than oligotrophic or mesotrophic systems, and future work is needed to examine how oxidation efficiency changes with CH_4 production rates across lakes of different trophic statuses.

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