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Eutrophication exacerbates the impact of climate warming on lake methane emission

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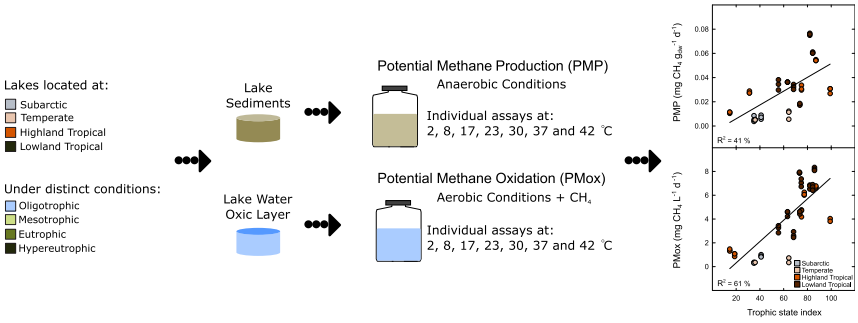
HIGHLIGHTS

- Net methane emission from lakes depends on methanogenesis and methanotrophy
- Methanogenesis is more sensitive to temperature increments than methanotrophy
- Rates of methanogenesis and methanotrophy are positively influenced by eutrophication
- A temperature buildup of 2 °C would lead to an increase in CH4 emissions by 47–183%

GRAPHICAL ABSTRACT



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ABSTRACT

Net methane (CH_4) emission from lakes depends on two antagonistic processes: CH_4 production (methanogenesis) and CH_4 oxidation (methanotrophy). It is unclear how climate warming will affect the balance between these processes, particularly among lakes of different trophic status. Here we show that methanogenesis is more sensitive to temperature than methanotrophy, and that eutrophication magnifies this temperature sensitivity. Using laboratory incubations of water and sediment from ten tropical, temperate and subarctic lakes with contrasting trophic states, ranging from oligotrophic to hypereutrophic, we explored the temperature sensitivity of methanogenesis and methanotrophy. We found that both processes presented a higher temperature sensitivity in tropical lakes, followed by temperate, and subarctic lakes; but more importantly, we found that eutrophication triggered a higher temperature sensitivity. A model fed by our empirical data revealed that increasing lake water temperature by 2 °C leads to a net increase in CH_4 emissions by 101–183% in hypereutrophic lakes and 47–56% in oligotrophic lakes. We conclude that climate warming will tilt the CH_4 balance towards higher lake emission and that this impact will be exacerbated by the eutrophication of the lakes.

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1. Introduction

Among the natural sources of CH_4 to the atmosphere, lakes represent a major source of uncertainty to the overall budget (Dean et al., 2018; Holgerson and Raymond, 2016; Saunois et al., 2016; Wik et al., 2016), with annual emissions ranging from 37 to 112 Tg CH_4 to the atmosphere (Saunois et al., 2016). Most lakes are found in northern latitudes, and are relatively small (Verpoorter et al., 2014). However, lakes located in tropical latitudes are highly dynamic, and despite their minor contribution to the overall lake area (~27%), they represent an important source of CH_4 to the atmosphere, contributing ~49% of the global lake and reservoir CH_4 emissions (Holgerson and Raymond, 2016; Bastviken et al., 2011).

Microbial methanogenesis in lakes mainly occurs in anoxic zones, with CH_4 being produced mostly in anoxic sediments, whereas methanotrophy in lakes primarily takes place in oxic zones, consuming CH_4 in the presence of oxygen (O_2). Methanogenesis in lakes is strongly dependent on the availability of labile substrates and is consequently affected by autochthonous (*e.g.* decaying aquatic biomass such as phytoplankton) and allochthonous (*e.g.* runoff from adjacent ecosystems) carbon inputs (Conrad, 1999; Grasset et al., 2018; Peura et al., 2014; Schulz et al., 1997; West et al., 2016). Methanotrophy depends on the availability of CH_4 and O_2, and thus primarily occurs in the oxic zones within the water column (Bastviken et al., 2008; Kankaala et al., 2007; Martinez-Cruz et al., 2015). Oxygenated water can be found throughout the entire water column in well mixed or shallow lakes or can be restricted to the epilimnion in some stratified lakes; but it is estimated that a large fraction of the CH_4 migrating through the water column in lakes is suitable for oxidation by methanotrophs (Bastviken et al., 2002; Bastviken et al., 2008; Kankaala et al., 2007). In addition, the availability of dissolved O_2 in lakes varies according to season, trophic state, stratification, and geomorphology; being the depth of particular relevance (Jenny et al., 2016; Lewis, 1996; Nürnberg, 1996), making methanotrophy spatio-temporally variable.

Since methanogenesis and methanotrophy are strongly dependent on temperature (Duc et al., 2010; Dunfield et al., 1993; Lofton et al., 2014; Zeikus and Winfrey, 1976), temperature changes throughout the year can influence the seasonal patterns of CH_4 net emission from lakes (Aben et al., 2017; Davidson et al., 2018; Marotta et al., 2014; Yvon-Durocher et al., 2014; Yvon-Durocher et al., 2017). Methanogenesis increases exponentially with temperature until reaching an optimal value and then declines rapidly due to inactivation and cellular decay (Schulz et al., 1997; Svensson, 1984). Moreover, methanogenesis is carried out by two coexisting biochemical pathways; *i.e.*, autotrophy and heterotrophy, which have different thermal dependencies and distinct temperature optima (Conrad, 1999; Schulz et al., 1997; Svensson, 1984). The thermal dependency of methanotrophy may be less complex. Lofton et al. (2014) reported a linear response of methanotrophy to temperature increase under substrate-saturated conditions, and Duc et al. (2010) and Dunfield et al. (1993) have observed that substrate availability (*i.e.*, CH_4 and O_2) positively affects methanotrophy rates in a stronger way than temperature. The response of methanogenesis and methanotrophy to temperature comprises a complicated matrix of factors, and its understanding is fundamental to predict how net CH_4 emission from aquatic ecosystems will respond to climate warming (Aben et al., 2017; Audet et al., 2017; Davidson et al., 2018; Marotta et al., 2014; Negandhi et al., 2016; Yvon-Durocher et al., 2014; Yvon-Durocher et al., 2017).

In this context, eutrophication, which has become a major problem affecting biodiversity and biogeochemical cycles in aquatic ecosystems (Moss et al., 2011; Schilder et al., 2017; Schindler, 2012), may play an important role in CH_4 cycling, because it modifies O_2 and substrate availability in lakes, regulating methanogenesis and methanotrophy. Furthermore, climate warming exacerbates some symptoms of eutrophication, such as deoxygenation of the water column and increased phytoplankton biomass (Moss et al., 2011). Currently, eutrophication in lakes, associated to climate warming and anthropogenic activities, has increased, with ecosystems showing scarce or null resilience (Jenny et al., 2016). Therefore, it is plausible that severe eutrophication could alter the magnitude and net balance of CH_4 production and oxidation in lakes (Aben et al., 2017; Adrian et al., 2016; Davidson et al., 2018).

Until now, it has been difficult to determine whether climate warming in conjunction with eutrophication will tilt the CH_4 balance in lakes towards higher or lower CH_4 emissions to the atmosphere. To address this question, we conducted anaerobic potential methanogenic (PMP) and aerobic potential methanotrophic (PMox) assays, using sediments and water samples, respectively. Samples were collected from ten lakes located in tropical, temperate and subarctic latitudes. These lakes varied in their trophic state, ranging from oligotrophic to hypereutrophic. The samples were incubated at temperatures ranging from 2 to 42 °C, and from these assays, the temperature dependence of both methanogenic and methanotrophic processes was determined and used to model the impact of a potential climate warming scenario on net CH_4 emission from lakes.

2. Materials and methods

2.1. Study sites and sampling

Incubations were conducted using sediment and water samples from 10 lakes located across different latitudes (Table 1). Two were located at high-latitude (Alaska), two at temperate latitude (Germany) and six at tropical latitude (Mexico). Among the six lakes located in Mexico, three were in highlands (altitudes between 2255 and 2840 m *asl*) and three in lowlands (0–20 m *asl*). The ecosystems were selected according to four main criteria: (i) lake characteristics that are typical from the region, (ii) availability of limnological and biogeochemical information, (iii) accessibility to the ecosystem, and (iv) priority was given to the selection of ecosystems with distinct nutrient regimes. For this purpose, the trophic state index (TSI) and physicochemical parameters, determined in previous studies, were considered for the selection of the study sites (Table 1). The physicochemical parameters discussed in this study included: Secchi disk depth (m), determined with a 0.2 m Secchi disk; ammonium-NH_4^+ (mg L^{-1}), nitrate-NO_3^- (mg L^{-1}), and soluble reactive phosphorous-SRP (mg L^{-1}), determined according to the Standard Methods for the Examination of Water and Wastewater (APHA, 2005); chlorophyll *a* (mg L^{-1}), determined in Mexico and Germany according to standard methods, while a calibrated multiparametric probe Hydrolab Data Sonde (Hach, Loveland, Colorado, USA) was used for the chlorophyll *a* analyses of the water samples from Alaskan lakes. Whereas total organic carbon-TOC (mg L^{-1}) and total nitrogen-TN (mg L^{-1}) were measured using carbon elemental analyzers (TOC Shimadzu-Vcsn + TN1 module, in Mexico and Germany; Aurora TOC 1030 W, O·I Analytical, in Alaska).

Surficial sediment samples (for incubation tests) were collected in the central region of each lake using a mud sampler (Ekman dredge for Alaskan and Mexican lakes, and a gravity core for German lakes), with the objective of obtaining samples of the most active anaerobic sediment layer (Marotta et al., 2014). Simultaneously, water samples were collected from the oxycline using a water sampler (2.2 L horizontal Van Dorn Bottle for Alaskan and Mexican lakes and a 2 L Limnos water sampler for German lakes). When the oxycline was absent, samples were taken from the epilimnion at 1 m depth (*e.g.*, Otto and Llano lakes samples), since it has been observed that methanotrophy rates are similar throughout the water column (Martinez-Cruz et al., 2015; Utsumi et al., 1998). Sediment and water samples were stored for about a day at 2 °C, until incubation tests where initiated. The estimation of aerobic and anaerobic methanotrophy occurring on surficial sediments was out of the scope of the present study.