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## Integrating isotopic, microbial, and modeling approaches to understand methane dynamics in a frequently disturbed deep reservoir in Taiwan

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**Abstract** It has been estimated that more than 48% of global methane emissions from lakes and reservoirs occur at low latitudes ( $<24^\circ$ ). To improve this estimate, knowledge regarding underexplored ecosystems, particularly deep lakes and reservoirs in Asian monsoon regions, is needed because the magnitude of methane emissions is influenced by lake bathymetry and climatic conditions. We conducted long-term studies beginning in 2004 at Feitsui Reservoir (FTR) in Taiwan, a subtropical monomictic system with a maximum depth of 120 m to monitor seasonal and interannual variations of three key characteristics and to understand the mechanisms underlying these variations. Key characteristics investigated were as follows: (1) the balance of primary production and heterotrophic respiration as a determinant of vertical oxygen distribution, (2) methane production at the bottom of the reservoir, oxidation in the

water column, and emissions from the lake surface, and (3) the contribution of methane-originated carbon to the pelagic food web through methane-oxidizing bacteria (MOB). This review highlights major achievements from FTR studies integrating isotopic, microbial, and modeling approaches. Based on our findings, we proposed two conceptual models: (1) a model of methane dynamics, which addresses the differences in methane emission mechanisms between deep and shallow lakes, and (2) a spatially explicit model linking benthic methane production to the pelagic food web, which addresses the diversity of MOB metabolisms and their dependence on oxygen availability. Finally, we address why long-term studies of subtropical lakes and reservoirs are important for better understanding the effects of climate on low- to mid-latitude ecosystems.

**Keywords** Methane production · Methane oxidizing bacteria · Food web model · Isotope ecology · Environmental microbiology

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## Background

Growing evidence indicates that the global methane budget may be influenced by methane release from freshwater systems (e.g., Bastviken et al. 2004; Ciais et al. 2013; Hamdan and Wickland 2016) and shallow coastal areas in marine systems (Borges et al. 2016, 2017), whereas the open ocean (excluding areas with hydrates, especially in the arctic) is a minor contributor (Bates et al. 1996; Rhee et al. 2009). Freshwater studies encompassing arctic (Kling et al. 1992; Laurion et al. 2010), boreal (Bastviken et al. 2004; Huttunen et al. 2003), and temperate (e.g., Michmerhuizen et al. 1996) systems, have led to an estimated emission of 103 Tg methane year<sup>-1</sup> from lakes, reservoirs, and rivers (Bastviken et al. 2011). This estimate, which is equal to 0.65 Pg of C (expressed as CO<sub>2</sub> equivalent) and 25% of the estimated terrestrial greenhouse gas sink, would be even larger if more recent studies of rivers were considered (Borges et al. 2015a, b).

The magnitude of methane emissions from lake water surfaces is largely influenced by climate and lake bathymetry (i.e., depth and area) (Bastviken et al. 2004), which critically determine the vertical distribution of oxygen. For example, the duration of the thermal stratification period and lake bathymetry control the depth and stratification intensity of the mixed layer (Wilhelm and Adrian 2008), which, in turn, determine the balance of primary production (PP) and aerobic respiration (Ostrom et al. 2005), especially in surface layers. This balance affects the degree of oxygen depletion in deeper layers, which controls the production and oxidation of methane because these processes are regulated by oxygen availability (Murase et al. 2005). For these reasons, regional variations in freshwater methane emissions are important factors that must be considered to ensure reliable global estimates (Bastviken et al. 2004; Tranvik et al. 2009; Pacheco et al. 2013).

According to estimates based on several studies, more than 48% of global methane emissions from lakes and

reservoirs are due to methane released at lower latitudes (<24°) (calculated from Table 1 in Bastviken et al. 2011). However, most studies of methane emissions from lakes and reservoirs at lower latitudes concerned shallow lakes (i.e., Amazon floodplains; Bastviken et al. 2010), only five of which were located in Asia. Although this distribution is partly reasonable because most lakes are shallow (Wetzel 1990), more studies of deep lakes and reservoirs in Asian monsoon regions will improve the accuracy of such estimates.

Multiple factors influence methane biogeochemistry, with key determinants of methane oxidation being oxygen availability, oxygen-to-substrate ratio (Morana et al. 2015), and temperature (Lofton et al. 2014). The main determinants of anaerobic methane production are oxygen deficiency and substrate availability, which are also influenced by lake bathymetry (Bastviken et al. 2004, 2008). Anaerobic methane oxidation is believed to be coupled with denitrification, which is affected by nitrogen availability (Deutzmann et al. 2014). The phylogeny of archaeal and bacterial groups indicates their specific roles in methane production and oxidation (Borrel et al. 2011).

In addition to their role in biogeochemical cycling, methane-oxidizing bacteria (MOB), also known as methanotrophs, represent alternative carbon resources at higher trophic levels in benthic and pelagic food webs (Kiyashko et al. 2001; Deines and Fink 2011; Jones and Grey 2011). The contribution of methane-derived carbon via MOB to the pelagic food web changes seasonally in temperate regions (Taipale et al. 2009). However, this topic remains underexplored for lakes and reservoirs in subtropical and tropical regions (hereinafter referred to as “lower-latitude regions”).

Due to high water temperature and meromixis, tropical lakes have high potential for methane production in anoxic deep waters and sediment (e.g., Abril et al. 2005; Pasche et al. 2011), resulting in characteristic methane accumulation near the bottom under reducing conditions. In contrast, monomictic subtropical lakes can recover from hypoxia in deep water by vertical mixing in winter or extreme weather events such as typhoons (e.g., Tanaka and Tsuda 1996; Yoshimizu et al. 2010) and hurricanes. This effect may decrease the potential for methane production by methanogens in the sediment, but can facilitate methane oxidation by MOB in the water column. Therefore, an understanding of these processes in subtropical deep lakes will provide insight into the mechanisms underlying the carbon budget, methane emissions, and MOB roles in food webs of lakes and reservoirs at lower latitudes, and will help improve estimates of global carbon and methane release.

This study was conducted to provide information to enable a better understanding of the mechanisms of methane dynamics at lower latitudes. First, we highlight the research questions, approaches, and some achievements from a long-term study of a subtropical deep reservoir. Second, we propose some perspectives, including a revised conceptual model for methane

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dynamics in lakes and reservoirs at lower latitudes and new research directions.

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### Research questions and approaches

With the aim of improving understanding of methane dynamics at lower latitudes, we specifically focused on three questions. (1) How do physical structure and seasonal disturbances alter the balance between PP and bacterial heterotrophy? (2) Under what conditions would methane production and oxidation be enhanced in lower-latitude lakes? (3) Under what conditions would the contribution of MOB to the food web increase? An answer to the first question would help address the subsequent two questions because these two counter biological processes (PP and bacterial heterotrophy) control the redox conditions that subsequently affect methane dynamics.

To address our research questions, we conducted a multiyear survey in which we observed the PP, aerobic respiration, and dynamics of methane in response to environmental changes. This study was motivated by the notion that small lake systems are particularly sensitive to different environmental conditions with interannual variations in climate.

Beginning in November 2004, we conducted field sampling at Feitsui Reservoir (FTR) (120.34E, 24.54N; maximal depth 120 m) in northern Taiwan. The FTR is a good model system for deep monomictic lakes in subtropical regions because (1) it is well-protected from anthropogenic pollution and therefore habitat destruction, and its nutrient status is oligotrophic to mesotrophic (Chang and Wen 1997); and (2) the region has substantial interannual variations in winter mixing intensity, degree of summer stratification, and thickness of hypoxic hypolimnion depending on weather conditions (Itoh et al. 2015; Ho et al. 2016). In addition, typhoons are a major disturbance of summer stratification in this region (e.g., Fan and Kao 2008). Extreme weather events such as typhoons, which typically occur at lower latitudes, affect water and material cycling in lakes. The strength and frequency of typhoons passing over or near the FTR change interannually; therefore, we can focus on and observe the ecosystem responses to changes in hydrodynamics.

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### Results of research on the FTR

R1: Disproportionate enhancement of bacterial over algal activity induced by typhoons

Using time-series data from 2004 to 2007, Tseng et al. (2010) showed that the ratio of bacterial production (BP) to PP (hereafter; BP/PP) in the FTR was higher in strong typhoon years (2004 and 2005:  $27 \pm 40\%$ ) than in normal typhoon years (2006 and 2007:  $12 \pm 9\%$ ),

indicating a disproportionate increase of BP relative to PP after typhoons. In the FTR, BP was twofold greater, but PP was only 20% greater in strong than in normal/weak typhoon years. Such disproportionate enhancement of heterotrophic bacterial activity by typhoons has seldom been described in freshwater ecosystems. Previous studies only focused on the effects of typhoons on autotrophic activity (PP) (Ko et al. 2016, 2017; and citations therein), whereas only a few studies quantified both PP and BP (Shiah et al. 2000; Tsuchiya et al. 2015).

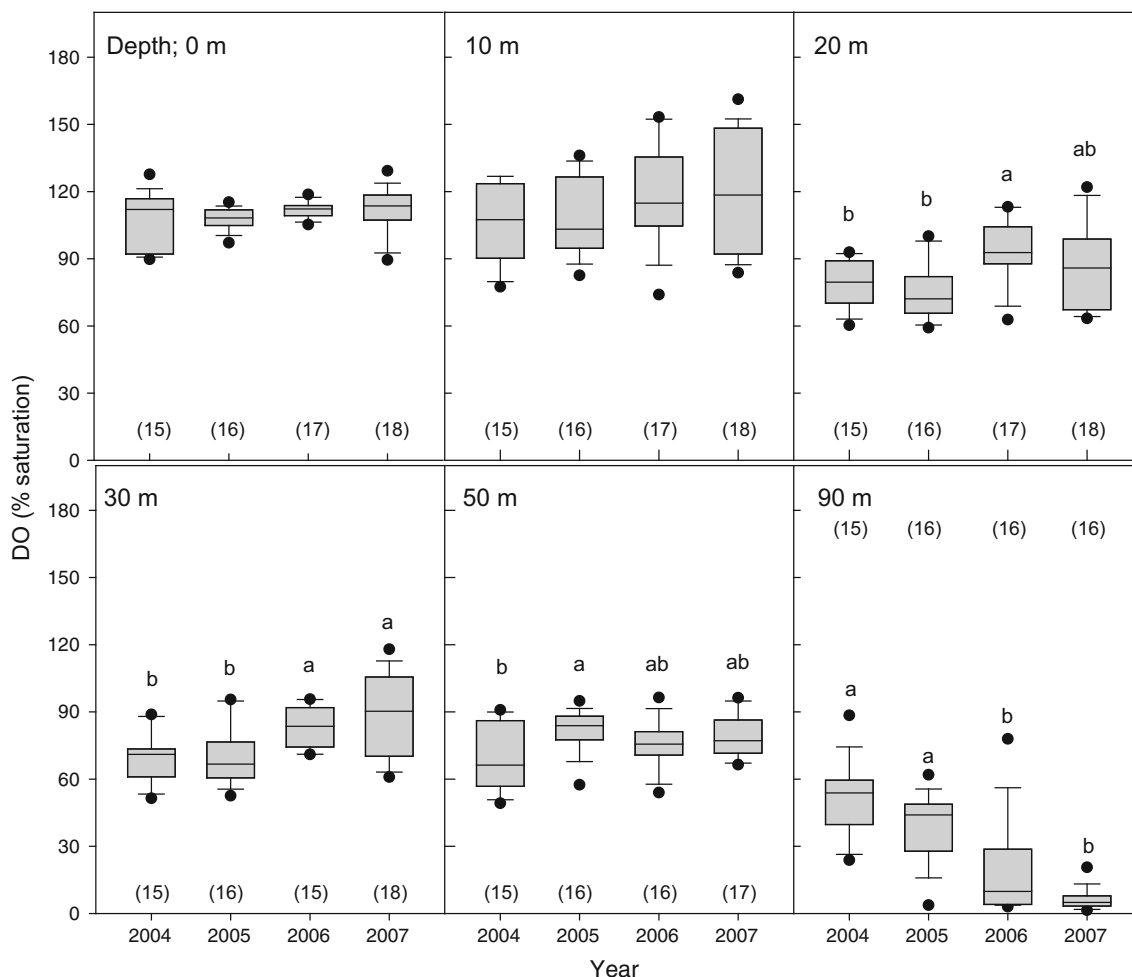
The increased BP/PP with typhoons in the FTR can be explained by the relative extent of the phosphorus (P) limitation in PP vs. BP. Whereas bioassay experiments demonstrated that autotrophic and heterotrophic activities are limited by P, but not carbon or nitrogen (Tseng et al. 2010), heterotrophic bacteria exhibited a faster response than algae to phosphate enrichment (Fig. 7 in Tseng et al. 2010). These findings suggest that, in the field, the P pulse introduced by typhoons might relieve bacteria from P limitation more than phytoplankton, which fits well with past empirical studies and theories indicating that bacteria are responsible for the major uptake of P due to their superior competition capacity in oligotrophic ecosystems (Currie and Kalff 1984; Thingstad et al. 1997; Vadstein 2000).

Strong typhoons may affect plankton activities in both euphotic and aphotic zones. Heavy rains caused by typhoons resulted in supply of P via hyperpynal flow. This P entered aphotic zones and enhanced bacterial production in aphotic and euphotic zones. Decoupling of BP and PP (i.e., increased BP/PP) in euphotic zones and increased BP in aphotic zones resulted in enhanced consumption and reduced concentration of dissolved organic carbon (DOC) in euphotic and deeper zones (Tseng et al. 2010).

R2: Distinct interannual variations of dissolved oxygen (DO) vertical profile between summer and winter

The vertical profile of DO is the key factor controlling aerobic and anaerobic respiration. Itoh et al. (2015) found that the interannual DO patterns in summer were different from those in winter in FTR, implying the presence of season-specific controlling mechanisms. In a typical monomictic lake, DO levels in the deep layer should be highest after vertical mixing of the water column in the coolest part of the year and lowest at the end of the stratification period. Dissolved oxygen levels at the bottom during the coolest period were negatively correlated with surface water temperature in 2005–2014 (Itoh et al. 2015). Higher surface water temperature led to weaker winter mixing and deficiency of DO at the bottom, which could last until the next stratification period.

During summer (June–September), when rainfall peaks with summer monsoon fronts and typhoons, interannual variation of DO levels (evaluated by the



**Fig. 1** Dissolved oxygen (DO) saturation (%) at each sampling depth from June to September of 2004–2007 (strong typhoon years 2004 or 2005 and weak typhoon years 2006 or 2007). Numbers in parentheses indicate numbers of samples. Box plots show the median (line), 25th–75th percentiles (box), 10th–90th percentiles

(bars), and individual values <10th or >90th percentile (points). Differences were detected by one-way ANOVA and Tukey's multiple comparison tests. Different letters indicate significant differences ( $P < 0.05$ )

saturation level required to normalize temperature dependence) was complex and tended to depend on depth. This result was attributed to an increase in lateral water flow from upstream rivers and hillslopes with intensive rainfall and its effects on microbial activities. In the mid-depth layers (20–30 m), DO levels tended to be lower in strong typhoon years (2004 or 2005) than in weak typhoon years (2006 or 2007) (Fig. 1). There were no differences in DO levels at 0, 10, and 50 m among years during summer. In the summer of 2004, typhoons might have induced lateral turbid flow from upstream, with movement of eroded soils or suspended sediments into mid-depth layers (20–50 m) (Fan and Kao 2008). Particles suspended in turbid lateral flow would contribute to oxygen consumption in mid-depth layers. Therefore, these results imply that DO levels at mid-depth layers might be affected by typhoons and subsequent disproportionate increases in bacterial activity over algal growth. However, at the same time, the vertical profile of DO in strong typhoon years (2004 and

2005) indicated that the turbid lateral flow provided external DO to deeper layers (90 m; Fig. 1). Dissolved oxygen levels at the bottom would not only be caused by typhoons, but would also be influenced by the legacy of winter mixing in the previous year (Itoh et al. 2015).

### R3. Role of winter mixing in determining anaerobic methane production in lake sediment

Observations in FTR indicated that: (1) stratification can be maintained, even during winter, when mixing is weak because of high surface water temperature, and (2) lower surface water temperature in winter leads to more intense mixing. Reducing conditions in the bottom layer caused by incomplete vertical mixing in winter decreased profundal DO and  $\text{NO}_3^-$  concentrations the following summer. Oxygen was depleted during the subsequent thermal stratification period, which facilitated  $\text{NO}_3^-$  consumption by denitrifiers. Based on seasonal varia-



tions in the vertical profiles of methane concentrations and stable isotope signal ( $\delta^{13}\text{C}$ ) values from 2012 to 2014, weak winter mixing can increase sedimentary methane production and therefore profundal methane storage through hypoxia during the thermal stratification period (Itoh et al. 2015). Unfortunately, we did not observe methane dynamics in 2004–2007 and were therefore unable to directly investigate the effects of typhoons on methane production (see section above). This situation is analogous to a study of an Amazonian tropical lake conducted by Marotta et al. (2014), in which winter mixing was not expected. Overall, the results demonstrated that anaerobic biological methane production in the sediments increased exponentially in response to increased temperature.

#### R4: Effects of methane oxidation in the water column on methane release from the surface

Although a long strong stratification period increased the amount of methane that was produced and accumulated in the bottom layer, this process did not directly enhance the amount of methane emitted from the surface. With a maximum depth of 120 m, the FTR is deep enough so that most methane produced in the profundal layer is consumed and oxidized by MOB (Itoh et al. 2015). Such decoupling of methane accumulation in the bottom layer from methane emission at the surface has also been observed in strongly stratified tropical meromictic lakes (e.g., Borges et al. 2011). Methane oxidation in the water column was evidenced by a decrease in methane concentration with increasing distance from sediment (mostly within 20–30 m above the sediment) in tropical (Rudd 1980; Guérin and Abril 2007; Borges et al. 2011), subtropical, and temperate lakes (Eckert and Conrad 2007; Bastviken et al. 2008; Chanudet et al. 2011; Roland et al. 2017). Other studies directly demonstrated methane oxidation in the water column using water incubation experiments (e.g., Utsumi et al. 1998).

In the FTR, substantial methane oxidation in the water column was initially revealed by investigating the  $\delta^{13}\text{C}$ -methane profile in water samples with low methane concentrations (Itoh et al. 2015). The same method was used in tropical Lake Kivu (Morana et al. 2015). The  $\delta^{13}\text{C}$ -methane values were consistently negative in the near-bottom layer, reflecting that large isotope fractionation occurred during methanogenesis. The  $^{13}\text{C}$ -methane values were higher in the oxic/anoxic boundary layer (especially up to 30 m above the sediment surface). These results suggest that much of the enrichment of dissolved  $^{13}\text{CH}_4$  was a result of methane oxidation because MOB consume  $^{12}\text{CH}_4$  slightly faster than  $^{13}\text{CH}_4$ . Anaerobic and aerobic methane oxidation would be involved in methane consumption. Even during the stratified period, MOB were the predominant component of the whole bacterial community near the bottom of the water column, where oxygen was almost depleted, as shown by Kojima et al. (2014) using catalyzed re-

porter deposition fluorescence in situ hybridization (CARD-FISH) analysis.

#### R5: Major types of methanotrophs in FTR

Molecular analysis of bacterial communities in FTR revealed eight species-level operational taxonomic units (OTUs) of Type I MOB (gammaproteobacteria, commonly found in temperate lakes), one OTU of Type II MOB (alphaproteobacterial, commonly found in tropical lakes), and one *Methylomirabilis*-like OTU belonging to candidate phylum NC10 (Kojima et al. 2014). *Methylomirabilis oxyfera* is a nitrite-dependent methane oxidizer (Ettwig et al. 2010).

Vertical analysis of 16S rRNA gene-based clone libraries demonstrated that Type I and II MOB were distributed in the hypoxic layer at 90 m, even during the summer stratification period, and in the oxic surface layer at 10 m (Kojima et al. 2014). Clone libraries of *pmoA* genes encoding particulate methane monooxygenase confirmed their presence at 90 m in the winter. This result is inconsistent with the conventional hypothesis that Type I and II MOB are aerobic. The number of 16S rRNA gene clone libraries analyzed was not sufficient to permit discussion of the seasonal or interannual variations in relative abundances of Type I and II MOB. However, CARD-FISH analysis of bacteria in the 90 m layer during winter (December 2013) demonstrated the dominance of *Methylomirabilis*-like OTUs (Kojima et al. 2014). These records represent the first evidence of anaerobic methane oxidizers in the water column of lake ecosystems, although many studies have reported the presence of anaerobic methane oxidizers coupled with denitrification in freshwater sediment (Raghoebarsing et al. 2006; Ettwig et al. 2009, 2010; Deutzmann et al. 2014; Noröi and Thamdrup 2014).

These results have two implications. First, spatial distributions of Types I and II MOB imply that they are involved in carbon flow under both oxic and hypoxic conditions, relying on distinct biochemical pathways (Vecherskaya et al. 2009; Kits et al. 2015). Second, the presence of the NC10 OTU close to the anaerobic nitrite reducer *Candidatus M. oxyfera* implies that methane oxidation would be coupled with nitrogen cycling in the water column of FTR. Further study of anaerobic methane oxidizers in lower-latitude lakes will be needed for a thorough understanding of MOB activities in lake ecosystems.

#### R6: Interannual variations in the MOB contribution to the pelagic food web

Results of isotope analyses based on the MixSIR Bayesian mixing model demonstrated interesting seasonal and interannual (2010–2013) variations in the contributions of MOB to the pelagic food web (Ho et al. 2016). The MOB contribution tended to be highest in winter, consistent with patterns in other climatic regions,

including boreal (Taipale et al. 2011) and tropical lakes (Morana et al. 2015). Interannual MOB contribution variations during winter may be influenced by two contrasting mechanisms. On one hand, deficient profundal DO in summer enhances methanogenesis and accumulation of profundal methane toward winter, supplying more substrate to MOB and resulting in a higher contribution of MOB during winter. However, oxygen supply for profundal waters caused by winter mixing enhances aerobic methane oxidation, resulting in a higher contribution of MOB to the food web during winter. The former mechanism would be the case if MOB were more limited by methane availability than oxygen availability, which is clearly the case in the FTR.

The results of a vertically structured food web model using reaction–advection–diffusion equations predicted that deeper disturbance during summer would suppress the contribution of MOB during winter (Ho et al. 2016). Although winter mixing could have positive and negative effects on the contribution of MOB over the year, stronger mixing in winter resulted in weaker deficiency of profundal DO in the next summer, leading to lower MOB contribution in the following winter. These findings are consistent with the methane accumulation pattern (Itoh et al. 2015) and estimates from the stable-isotope mixing model (Ho et al. 2016).

Molecular analyses of bacterial communities indicated that the taxonomic composition of MOB (i.e., anaerobic MOB phylogenetically close to NC10 and aerobic Types I and II) changed seasonally and vertically (Kojima et al. 2014; Kobayashi et al. 2016). However, because of the limited availability of quantitative data, MOB functional activity in the food web model was parameterized following an earlier experimental study (Harris and Hanson 1980). The activity of MOB was assumed to be suppressed by low or high oxygen availability and to be highest at an oxygen level of around 200  $\text{mmol O}_2 \text{ m}^{-3}$ . This model is a black box approach to represent the diverse functionality of MOB implicitly by assuming that the community is a mixture of aerobic and anaerobic MOB. If we assumed much lower optimal DO levels (with predominance of anaerobic MOB), then the model would be unable to explain the higher contribution of MOB observed in winter than summer when oxygen availability is high because of vertical water mixing. Therefore, we argue that both aerobic and anaerobic reactions are responsible for sustaining food web productivity, especially during winter.

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## Perspectives

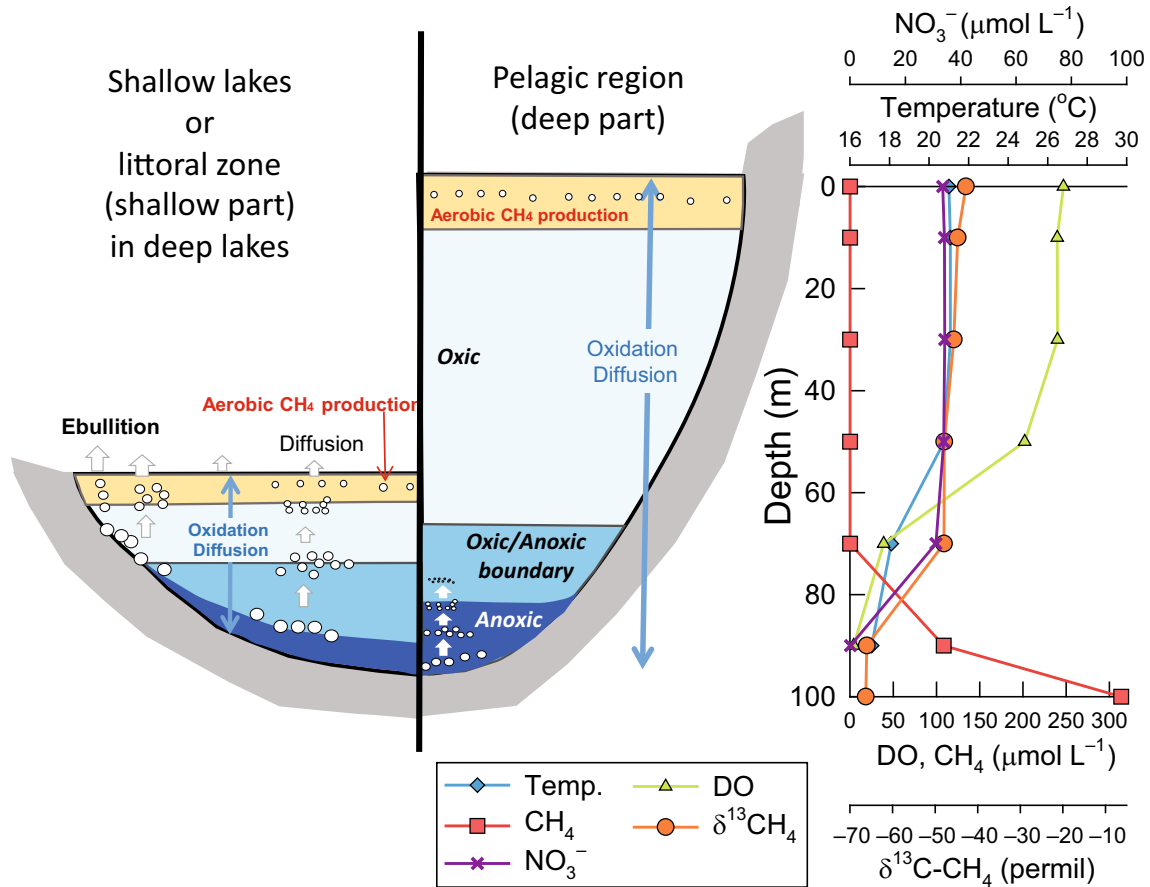
Perspective 1: Vertical distribution of methane in deep lake/reservoir at lower latitudes

Here, we propose a conceptual model for the vertical patterns of methane and its related elements in a deep lake during the stratification period (Fig. 2). This model

includes stable isotope signatures for methane compared with the shallow lake illustration modified from Bastviken et al. (2004).

Methane production, originating from organic matter and  $\text{CO}_2$ , mainly occurs in the anaerobic sediment. Production of sedimentary methane (by methanogenesis) and  $\text{CO}_2$  (by heterotrophic respiration) is controlled by profundal DO. The vertical distribution of DO depends on differences in the intensities of stratification and mixing, which are affected by climatic conditions. Despite the high profundal methane concentration in the stratified period, most of the dissolved methane can be oxidized within 20–30 m above the sediment layer (see “R4: Effects of methane oxidation in the water column on methane release from the surface”) in deep lakes. This fact suggests that sedimentary methane production is not a main source of methane emissions from lakes with sufficient depth (right diagram in Fig. 2). In contrast, methane produced in the sediment of shallow lakes affects methane flux at the water surface as both ebullition and diffusion flux while being oxidized incompletely (left diagram in Fig. 2). This phenomenon is also true for methane produced in sediment of the shallow part of a deep lake. For example, findings in German lakes showed that the ratio of the surface area of the shallow water zone to the entire lake area was a better predictor of surface methane concentration than the total surface area (Encinas Fernández et al. 2016). Nevertheless, studies of the distinct methane dynamics in shallow vs. deep parts of lakes at lower latitudes are needed to confirm the robustness of their conclusion.

Methane emissions from deep lakes could potentially be explained by subsurface methane production. The maximum amount of subsurface methane reported in some oceans and lakes implies in situ methane production in oxic waters (Bogard et al. 2014; Tang et al. 2014; Itoh et al. 2015; Yao et al. 2016). Therefore, subsurface rather than profundal methane production may account for a portion of the methane emitted from the water surface. As frequently occurs in well-stratified tropical lakes (Verburg et al. 2003), cyanobacterial blooms occur during summer in the FTR. It may be that the subsurface cyanobacteria bloom in summer plays a neglected role in the production of methane and the vertical distribution of oxygen and therefore regulates anaerobic methanogenesis in the bottom layer. Although interactions between cyanobacteria and bacteria/archaea can result in methane production in oxic layers (Bogard et al. 2014), the mechanism for this process is not fully understood (summarized in Tang et al. 2016). Another controversy is whether methane produced in the oxic subsurface layers makes a large (Bogard et al. 2014) or small (Encinas Fernández et al. 2016) contribution to the amount of methane emitted from the lake surface. Finally, the possible production of  $\text{CH}_4$  under aerobic conditions (Karl et al. 2008; Damm et al. 2008) in marine systems has been debated. Although this process could explain the very low concentration ( $< 4 \text{ nM}$ ) of  $\text{CH}_4$  in open and deep oceanic regions, it cannot explain



**Fig. 2** Schematic of methane dynamics in shallow lakes and coastal parts of deep lakes (modified from Bastviken et al. 2004) and pelagic parts of deep lakes (modified from Itoh et al. 2015) during the stratification period. Right panel shows vertical profiles of

temperature, DO, methane concentration, methane carbon isotope ratio, and nitrate concentration at the end of the stratification period (Dec 2013) in FTR (Itoh et al. 2015)

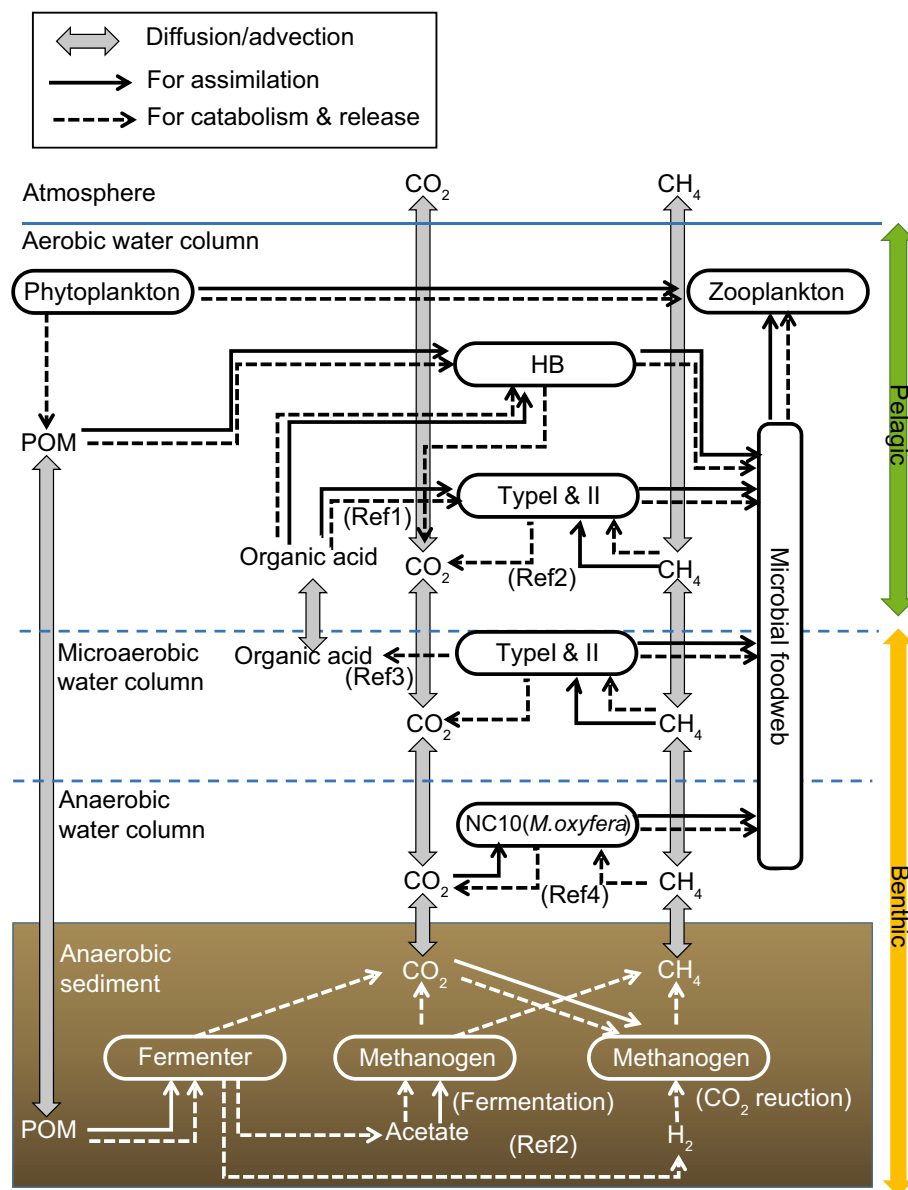
the much larger concentration of CH<sub>4</sub> (10–1000 nM) in shallow coastal areas, where CH<sub>4</sub> undoubtedly comes from sediments (Borges et al. 2016, 2017).

#### Perspective 2: Roles of diverse methanotrophs (MOB) in food web dynamics

From a food-web perspective, MOB are key players in a new mode of pelagic–benthic coupling in lake ecosystems (Schindler and Scheuerell 2002). In the broadly accepted view of pelagic–benthic coupling in deep lakes, sedimentation of organic matter produced by pelagic production is the basal resource of benthic invertebrates and fish, which act as alternative resources of pelagic mobile predators such as zooplankton and fish. In the new mode of pelagic–benthic coupling in deep lakes, summer pelagic PP is transferred to the benthic layers, ultimately supporting the secondary production of pelagic zooplankton mediated by methane-based food webs along the water column.

Two aspects of this new mode of pelagic–benthic coupling need to be addressed. First, the contribution from the benthic (methanotrophs) to pelagic (zoo-

plankton) habitats mainly occurs during winter. The coupling effect has a time delay because of the time required for sedimentation of particulate organic matter from the pelagic zone to the benthic zone and for subsequent biogeochemical processes in benthic habitats (sediment plus deep water column), which supply resources to zooplankton through methane-based food webs (Ho et al. 2016). Second, our microbial ecology studies (Kojima et al. 2014; Kobayashi et al. 2016) and other existing evidence (refs. in Fig. 3) indicate that the sources of biomass carbon from MOB to the microbial food web are more diverse than previously believed (Fig. 3). Methane is not always *directly* integrated into the microbial food web via assimilation of methane by MOB through aerobic methane oxidation. For example, carbon biomass of *M. oxyfera* (NC10) is assimilated by fixation of CO<sub>2</sub>, but not directly by carbon from methane (Rasigraf et al. 2014). Therefore, dominance of the *M. oxyfera*-like phylotype in anoxic layers of FTR (Kojima et al. 2014) implies that methane is completely respired as CO<sub>2</sub>. Some of the CO<sub>2</sub> assimilated into the bacterial biomass could have originated from methane oxidation; thus, carbon from methanogenesis is only *indirectly* incorporated into MOB biomass and the



**Fig. 3** Schematic diagram illustrating our new conceptual model of pelagic–benthic coupling mediated by vertically structured diverse MOB groups. Some arrows are omitted for simplicity (e.g., release of  $\text{CO}_2$  from zooplankton). Distribution of microbes in benthic habitats (from microaerobic water column to anaerobic sediment) was not clearly separated in the FTR (FeiTsu Reservoir) project, although it is conceptually separable. Microbial members in

sediment (fermenter and methanogen) were not targets of observation in this project. HB represents heterotrophic bacteria that utilize photosynthetic products (POM) and *M. oxyfera* represents *Methylomirabilis oxyfera*. Ref1: Belova et al. (2011); Im et al. (2011), Ref2: Borrel et al. (2011), Ref3: Vecherskaya et al. (2009) and Kalyuzhnaya et al. (2013), Ref4: Ettwig et al. (2010) and Rasigraf et al. (2014)

microbial food web. In addition, the presence of Type I and II MOB (Methylocystis) in the deep layers (anaerobic or microaerobic condition) implies that fermentative reactions support their activities, which are coupled with the release of organic acids such as acetate (Vecherskaya et al. 2009; Kalyuzhnaya et al. 2013). These organic acids are substrates for the growth of some bacteria, including *Methylocystis* (Belova et al. 2011; Im et al. 2011), and are finally incorporated into the microbial food web (i.e., indirect incorporation of methane-originated carbon).

These diverse types of MOB and metabolic pathways from methane should be further explored to better understand the importance and mechanisms of methane-based food web dynamics. The next version of the dynamic model coupling methane processes and food web dynamics should incorporate these diverse processes. In addition,  $\text{CO}_2$  would be repeatedly recycled within the anaerobic food chain in the sediment and sediment–water column boundary (Fig. 3). Therefore, isotopic analysis of  $\text{CO}_2$  and MOB together with analysis of phospholipid fatty acids (e.g., Belova



et al. 2011) will be necessary to elucidate the dominant reactions and estimate the timescale of interactions between CO<sub>2</sub>, methane, and MOB and, thus, the new pelagic–benthic coupling.

### Perspective 3: Importance of studying underexplored tropical/subtropical lakes

Lakes in subtropical regions are highly dynamic in terms of their interannual climate variations and strength/frequency of disturbances. These factors are determinants of the vertical, seasonal, and interannual variations in microbes and biogeochemical processes. Such variations control the (1) balance of PP and aerobic respiration, (2) production and oxidation of methane, and (3) incorporation of methane-originated carbon into the pelagic food web (Figs. 1, 2, 3). Our multiple approaches to understanding methane dynamics targeted a subtropical reservoir (FTR) with an essentially monomictic pattern. As is the case in some reported subtropical lakes, FTR occasionally undergoes not only incomplete vertical mixing during winter, but also stronger and longer thermal stratification periods, resulting in profundal hypoxia (e.g., Sahoo and Schladow 2008; Yoshimizu et al. 2010). In contrast, intensive winter mixing can be observed during cold winters. These findings indicate that long-term studies of deep monomictic lakes and reservoirs at lower latitudes can reveal aspects of both meromictic and monomictic lakes.

Our study sheds new light on other important controlling factors of biogeochemical cycles, such as the disruption of stratification by heavy-rain events. Lower-latitude areas experience a higher frequency of heavy precipitation than mid- or high-latitude regions (Dai 2012). Under recent warming conditions, the frequency of heavy precipitation and the temperature of mid-latitude regions have been increasing and are predicted to increase further (e.g., Meehl et al. 2005). Knowledge of the response of methane dynamics in lower-latitude lakes to climate variations will make it possible to predict the future condition of mid-latitude lakes. Our case study showed that the effects of typhoons in summer on the ratio of PP to aerobic respiration and, thus, DO levels were depth-specific. Long-term comparative studies of other mero/monomictic lakes at the tropical/subtropical boundary (e.g., Okuda et al. 2017) will provide a more comprehensive understanding of mechanisms in lakes at a wide latitudinal scale in a changing world.

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