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ORIGINAL ARTICLE

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Dynamics of methane in mesotrophic Lake Biwa, Japan

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Abstract As a part of a core project of IGBP (International Geosphere-Biosphere Programme), distribution, production, oxidation and transport processes of methane in bottom sediments and lake water in a mesotrophic lake (Lake Biwa) have been studied with special reference to the spatial heterogeneity of each process. In this study, we attempted to synthesize previously reported results with newly obtained ones to depict the methane dynamics in the entire lake. The pelagic water column exhibited subsurface maxima of dissolved methane during a stratified period. Transect observation at the littoral zone suggested that horizontal transportation may be a reason for the high methane concentration in epilimnion and thermocline at the offshore area. Tributary rivers and littoral sediments were suggested to be the source. Observations also showed that the internal wave caused resuspension of the bottom sediment and release of methane from the sediment into the lake water. The impact of the internal waves was pronounced in the late stage of a stratified period. The littoral sediment showed much higher methanogenic activity than the profundal sediments, and the bottom water of the littoral sediments had little methanotrophic activity. In the profundal sediment, most of the methane that diffused up from the deeper part was oxidized when it passed through the oxic layer. Active methane oxidation was also observed in the hypolimnetic water, while the lake water in the epilimnion and thermocline showed very low methane oxidation, probably due to the inhibitory effect of light. These results mean a longer residence time for methane in the epilimnion than in the hypolimnion. Horizontal inflow of dissolved methane from the river and/or littoral sediment, together with the longer residence time in the surface water, may cause the subsurface maxima, which have also been observed in other lakes and in the ocean.

Keywords Methane · Mesotrophic lake · Resuspension · Seiche · Subsurface maximum

Introduction

Methane is a terminal product of anaerobic carbon metabolism, and methanogenesis is a dominant biogeochemical process in anaerobic freshwater environments (Zehnder and Stumm 1988). Methane production and emission from various anaerobic ecosystems have been studied since methane is the most important greenhouse gas after CO_2 and adsorption of infrared radiation by methane is more effective than by CO_2 on a per-mol basis (e.g., Cicerone and Oremland 1988; Mitchell 1989).

Methane release from a lake depends on the balance between methane production and oxidation (e.g., Reeburgh et al. 1991). A decrease in oxygen supply and an increase in supply of organic matter on the surface of the bottom sediment in a lake both stimulate methane production, and both also diminish the oxic layer at the surface of the lake sediment. Methane produced in the sediment also contributes to oxygen

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consumption through its oxidation (Gelda et al. 1995). Methane release from a lake is, therefore, sensitive to the redox condition at the surface of the sediment. Eutrophication of the lake also accelerates methane release from lake sediment by increasing the supply of organic matter on the surface of the lake sediment. It can be said that methane release from the lake-bottom sediment is also an indicator of the trophic condition of the lake.

Research on carbon flow in the watershed of Lake Biwa, the largest freshwater lake in Japan, has been carried out as a part of the core project TEMA (Terrestrial Ecosystem in Monsoon Asia) under IGBP (International Geosphere-Biosphere Programme). Various studies on methane dynamics in this lake have also been carried out. The spatial distribution of methane concentration and its carbon isotope ratio (Murase and Sugimoto 2001), the temporal variations in concentration and isotopic composition of dissolved methane in the lake and tributaries (Murase et al. 2003), and the rate of production of methane in the bottom sediment (Murase and Sugimoto 2002) have been previously reported. Many interesting results, such as photoinhibition of methane oxidation in the water column of the lake (J. Murase and A. Sugimoto, submitted), methane release from the sediment by an internal seiche (Sakai et al. 2002), and storage of methane on the surface of the sediment particles by adsorption (Sugimoto et al. 2003), have also been reported.

In order to discuss methane dynamics in the entire lake, mechanisms of methane production, oxidation, and release at each part of the lake should be taken into consideration. We have already reported most of them except for the oxidation process at the surface of the sediment and the release mechanism of methane from the sediment by the internal wave. In this article, we show the observational and experimental results for these remaining problems, and discuss the methane dynamics in the entire lake together with the previously reported results.

There are many studies on methane dynamics in eutrophic lakes (Kiene 1991), while oligotrophic and mesotrophic lakes have been studied much less so far. Limited studies (Schmidt and Conrad 1993; Miyajima et al. 1997; Schulz et al. 2001) showed that, in a mesotrophic lake, methane concentration is higher in the upper layer of the water column than in the lower layer. This is in contrast to the eutrophic lake, where the bottom sediment is the most important source of methane in water, and the highest methane concentration is generally observed in the bottom water (Kiene 1991). The subsurface maxima of methane have also been observed in the sea and open ocean (Dafner et al. 1998; Seifert et al. 1999), but the mechanism is poorly understood. A diagnostic synthesis of our work on methane in mesotrophic Lake Biwa will be attempted in this study to elucidate the mechanism for subsurface maxima of dissolved methane in the lake.

Materials and methods

The series of studies on methane dynamics was conducted in Lake Biwa, in Japan. The sampling and observation sites are indicated in Fig. 1.

To determine the oxidation rate of methane diffused from sediment at the surface, sediment core samples were collected from the profundal zone (Station A) using a gravity corer (i.d. 5 cm). The surface part (0–10 cm) of the sediment was transferred to an acrylic tube (length 15 cm; i.d. 5 cm) keeping the structure of the sediment. Overlying water was removed with a syringe until 5 mm of water film was left on the sediment. The top of the tube was capped with a rubber stopper with a port for gas sampling. The headspace of the core was exchanged with N_2 for anaerobic incubation by flushing through the port. The core samples were incubated at the in situ temperature (8°C), and methane concentration in the headspace was monitored. Rate of methane oxidation at the surface layer of the sediment was estimated by comparing the rate of methane release from the sediment under oxic and anoxic conditions.

A microcosm experiment was done to estimate the impact of water current through the bottom water on release of methane from the sediments. Core samples were collected from Station A using a gravity corer (i.d. 5 cm), and the surface part (0–6 cm) of the core samples were transferred together with overlying water (5 cm deep) to an acrylic tube (i.d. 5 cm; length 20 cm) that

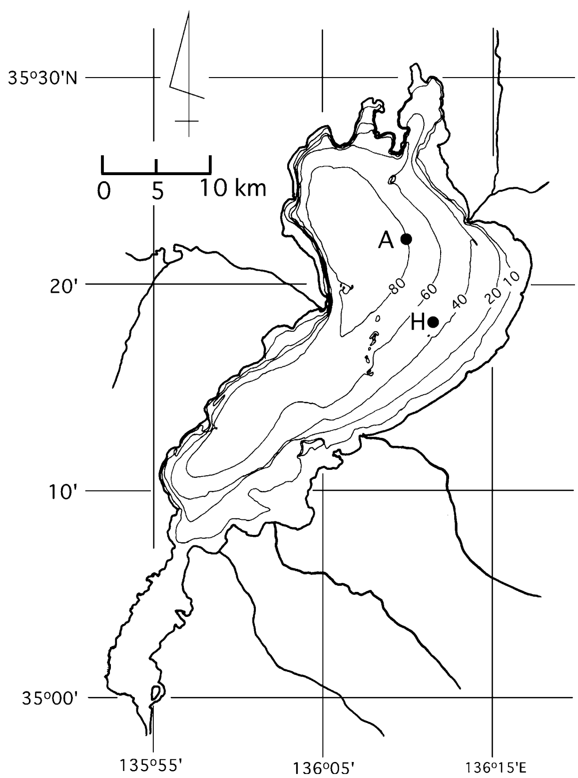

Fig. 1 Map of Lake Biwa

had holes on the side. The overlying water was removed with a syringe and the filtered (< 95 μm) surface water (10-m depth) collected in Station A was gently added above the sediment. The top of the tube was capped with a rubber stopper excluding bubbles inside the tube. Different rates (5.7 and 30 cm s^{-1}) of horizontal water flow were applied to the bottom part of the overlying water for 10 s from the side of the tube by a water pump. Concentration in the water was immediately determined by the headspace method (Kimura et al. 1992).

The temporal change in the depth profiles of the water temperature was observed to determine the amplitude and frequency of internal waves in the lake. Measurement of water temperature was conducted in the late stage of a stratified period (from 29 November to 20 December in 2000) offshore of Hikone (Station H, water depth of 50 m; Fig. 1). A thermistor chain that had 22 thermistors at intervals of 3.5–4.5 m for epilimnion and 1.5 m for the deeper layer was set, and water temperature was measured at intervals of 30 min.

Observations which have been already published elsewhere are used for the discussion on the dynamics of methane in the entire lake. Spatial distribution of methane concentration and its stable carbon isotope ratio in the bottom sediment were obtained from the top-10-cm layer (Murase and Sugimoto 2001). Methane production rates of sediments were measured from the surface to 23 cm deep for the profundal area and from 2–8 cm for the littoral area (Murase and Sugimoto 2002). The amount of methane retained in the sediment (surface to 10 cm) were analyzed by Sugimoto et al. (2003) and Dan et al. (2004). Methane concentrations in the lake and tributary rivers were observed by Murase et al. (2003). Oxidation of the in situ methane in the lake water was determined by an incubation experiment, and the effect of light on methane oxidation was also examined (J. Murase and A. Sugimoto, submitted). Briefly, lake water samples, which were collected from the different depths of the pelagic area and from the bottom of the littoral area, were incubated in serum bottles at 15°C under dark and light conditions (57 μmol m^{-2} s^{-1} for 12 h day^{-1}), and temporal change in methane concentration was monitored.

Results

Methane oxidation in the surface layer of the sediment

Methane concentration in the headspace of the sediment core linearly increased with time when the headspace was exchanged with nitrogen (Fig. 2). The cores that were incubated with air in the headspace released much less methane into the headspace. The carbon isotopic composition of methane in the headspace was −70‰ under anaerobic conditions and −48‰ under aerobic conditions, suggesting that methane was oxidized in the oxic layer of the sediment under aerobic conditions.

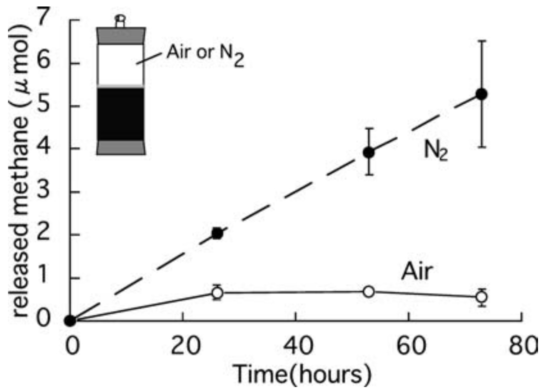

Fig. 2 Release of methane from profundal (Station A) sediment cores under oxic and anoxic atmospheres. *Bars* represent the error in duplicate

Based on the difference in release rate of methane from the sediment under oxic and anoxic conditions, approximately 90% of methane diffused from the deeper part of the sediment was considered to be oxidized when passing through the oxic layer of the surface sediment. High methane oxidation rates in the surface sediment of a mesotrophic lake have also been reported by Frenzel et al. (1990).

The effect of water current on release of methane from the sediment

Water current applied to the overlying water of the sediment core at 30 cm s^{-1} for 10 s resulted in a remarkable increase in methane concentration in the overlying water (Fig. 3). A water current of 30 cm s^{-1} is as high as the field data, and water currents higher than 200 cm s^{-1} have been observed in the lake (Endo, personal communication). Thus, our results reflect the impact of water current on release of methane from sediment. In the field, a rapid downward shift of the thermocline (5 m in depth in 3 h), probably due to an internal wave, was observed (Sakai et al. 2002). Turbidity and methane concentration synchronistically increased in the thermocline after the downward movement, suggesting that the water current of the internal wave caused resuspension of bottom sediment and release of dissolved methane (Sakai et al. 2002).

It is recognized that internal wave causes resuspension of bottom sediments of the lake (Shteinman et al. 1997). However, little attention has been given to the fact that considerable amounts of methane are released by an internal wave. Our observation is the first showing methane release caused by an internal wave.

Frequency and amplitude of internal waves

The amplitude and frequency of internal waves in the lake were studied by monitoring the temporal change in the depth profiles of water temperature. Water temper-

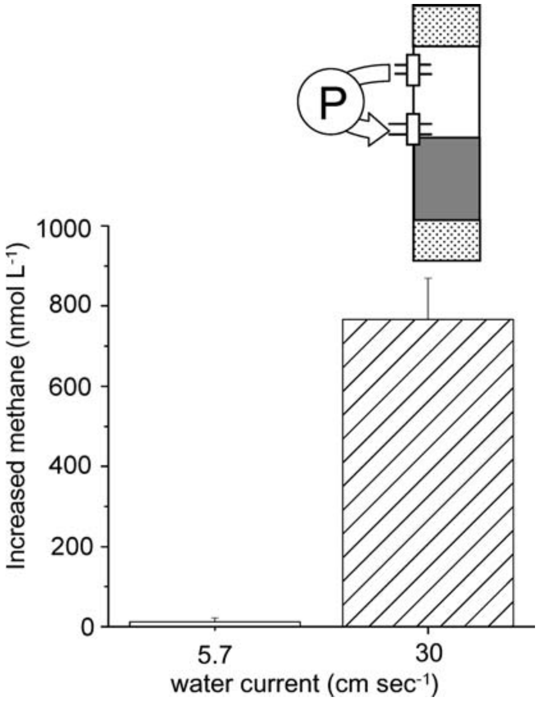

Fig. 3 The effect of water current on methane concentration in bottom water. The bottom water of the sediment core sample was circulated using a pump to provide water currents at the indicated speeds (see the illustration). *Bars* indicate the error of duplicate measurements

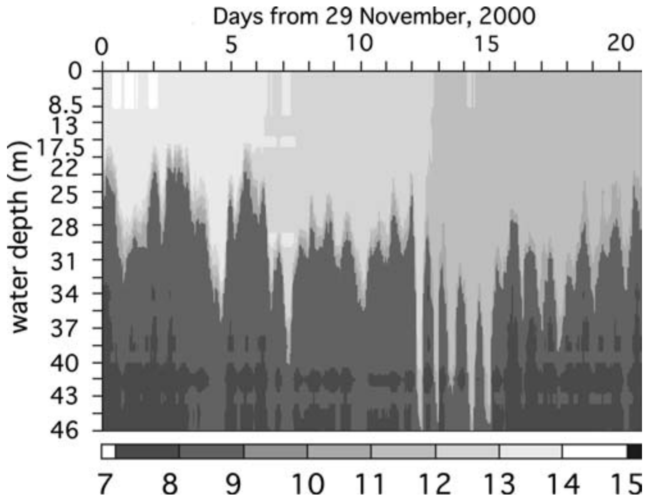

Fig. 4 Temporal change in depth profile of water temperature (°C) at the late stage of a stratified period offshore of Hikone at a water depth of 50 m (Station H)

ature in the epilimnion decreased from 14.0 to 11.4°C during the observation period (Fig. 4). Internal waves with amplitudes higher than 5 m were observed more than once a day on average, with a higher frequency in the late period. Internal waves with high amplitude (>20 m) occurred in a short time especially at the late stage, when the water temperature in the epilimnion decreased.

The amplitude of the internal waves was large. It is highly possible that considerable methane is released when the internal wave hits the bottom sediment. Actually, in the late stage of a stratified period (in December and January 2000), a high concentration of dissolved methane (100–140 nM) was observed in the bottom water of the site (Station B) where the thermocline was situated around the lake bottom (Murase et al. 2003).

Discussion

There are few studies on methane dynamics in oligo- to mesotrophic lakes, and little attention has been paid to the spatial heterogeneity of methane dynamics in an entire lake ecosystem. Our series of studies demonstrates that transport, production, and oxidation processes of methane differ among the subsystems of the lake; water versus sediment, littoral area versus pelagic area, and epilimnion versus hypolimnion, and the spatial heterogeneities characterize the methane dynamics of the entire lake. Methane dynamics in the subsystems of Lake Biwa are discussed below.

Methane production and release from the lake sediments

Methane content in the surface (0–10 cm) sediments of the north basin of the lake ranged from 0.06–2.4 mmol l^{-1} (Table 1). The carbon isotopic ratio of methane ranged from −71 to −80‰, and the apparent carbon fractionations between methane and inorganic carbon ranged from 1.064–1.084 (Murase and Sugimoto 2001), suggesting that CO_2 reduction is the major pathway of methanogenesis (Whiticar et al. 1986; Sugimoto and Wada 1993).

The littoral sediments showed much higher methane production rates than the profundal sediments (Table 2). One of the main reasons for the high activity of methanognesis in the littoral sediments was the high summer temperatures. Other factors such as quality of organic matter deposited may be also responsible, since the littoral sediment in winter showed a higher methanogenic activity than the profundal sediments (Murase and Sugimoto 2002).

The profundal sediments showed apparent methane production even in the deeper layers (23 cm depth) upon anaerobic incubation (Murase and Sugimoto 2002). However, part of the methane released by incubation may have been produced earlier by methanogenic bacteria and stored in adsorbed form in the sediment particles (Sugimoto et al. 2003). Dan et al. (2004) investigated the methane release and found that methane is released biotically and abiotically as well from the sediment slurry. Methane stored on the sediment particles can be desorped by release of hydrostatic pressure or decrease in the concentration of dissolved methane in

Table 1 Methane content and its carbon stable isotopic ratio in lake water, sediment, and tributary rivers of Lake Biwa

Site	Methane content (μmol l^{-1})	$\delta^{13}C$ (‰)	Remarks	Reference
Lake water				
Pelagic	0.004–0.17	−62.6 to −21.8	Station A	Murase et al. (2003)
Littoral	0.49–3.04	−57.3 to −47.6	Stations Y5 and Y10 (22 July 2000)	Murase et al. (2003)
Sediments				
North basin	60–2,400	−78.8 to −70.9	12–100 m	Murase and Sugimoto (2001)
South basin	40–710	−79.7 to −60.7	in water depth	Murase and Sugimoto (2001)
Tributary rivers			Distance from the river mouth (km)	
Echi	0.33–2.03	−54.4 to −46.8	1.2	Murase et al. (2003)
Hino	0.24–2.17	−59.5 to −47.6	1.8	Murase et al. (2003)
Yasu	0.24–3.43	−64.0 to −49.3	1.2	Murase et al. (2003)
Ado	0.014–2.29	ND	1.2	Murase et al. (2003)
Ane	0.015–0.26	ND	1.2	Murase et al. (2003)

ND no data

Table 2 Production rates of methane in the bottom sediments of Lake Biwa (Murase and Sugimoto 2002)

Site	Production rate (μmol l^{-1} day^{-1})	$\delta^{13}C$ (‰)
Profundal sediment		
Station A	0.02–12.3	−72.3 to −69.3
Station B	0.04–9.82	−78.0 to −73.3
Littoral sediments		
In situ temperature	11.4–88.0	−68.7 to −60.1
10°C	9.87–14.3	−69.8 to −67.4

the pore water. The amount of methane stored on the clay minerals in the Lake Biwa sediment was small compared to the total amount of methane in the sediment (Sugimoto et al. 2003). However, we should pay attention to the adsorption of methane on the surface of the sediment particles because clay minerals are universally observed in lake and ocean sediments, and high adsorption ability may be expected in some cases.

Methane in the sediment is the potential source of dissolved methane in the lake water, since the methane contents in the sediment were higher than those in lake water by 2–5 orders of magnitude (Table 1). However, the surface of the sediment is oxic in the mesotrophic lake, and active oxidation at the surface layer is a strong sink for methane produced in the deeper layer of the sediment. Consequently, only a small amount of methane is released to the lake water (Fig. 2). Rate of oxygen consumption by methane oxidation at the sediment surface was comparable to that by decomposition of organic matter in the surface layer of the sediment (0–5 mm) (A. Kametani, unpublished data). The active methane oxidation at the surface layer of the sediments implies that methane-oxidizing bacteria may significantly contribute to carbon flow in the sediment. Extremely low values of carbon isotope ratio observed in chironomid larvae suggest ingestion of microbial biomass of methanotrophs and flow of methane-derived carbon in the bottom sediment in Lake Biwa (Kiyashko et al. 2001).

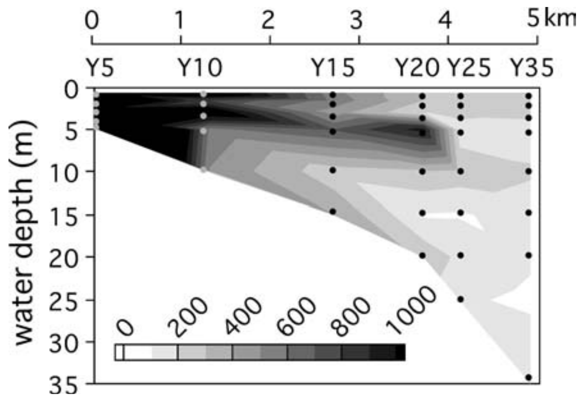

Fig. 5 Transect observation of distribution of dissolved methane (nmol l^{-1}) in the offshore of Yasu River (redrawn from Murase et al. 2003)

Methane dynamics in the littoral zone

The lake water in the near-shore area contained much higher amounts of methane than the pelagic water (Table 1) (Murase et al. 2003). The transect observation indicated that high concentrations of dissolved methane in the littoral zone were horizontally transported offshore (Fig. 5).

All the river waters examined were replete with dissolved oxygen, but were oversaturated with dissolved methane to the atmospheric concentration of methane (Murase et al. 2003). The water samples of the rivers located on the eastern side of the lake (Echi, Hino, and Yasu Rivers) contained much higher amounts of dissolved methane than the pelagic water column of the lake (Table 1). Thus, transportation from the tributary rivers may be a source of the dissolved methane in the lake water as reported in the coastal area (de Angelis and Lilley 1987; Jones and Mulholland 1998). River water can transport high concentrations of methane into the different depths of the water column in the lake according to seasonal changes in density current. That is, in the early stage of the thermal stratification period, when the water temperature of the river water is higher than that of the surface water of the lake, the river water is discharged onto the surface of the lake water and may contribute to the high methane concentration in the surface water. This was observed offshore of the Yasu River in July 1999 (Fig. 5). In the late stage of a stratified period, the temperature of the river water becomes lower than that of the surface water and the river water intrudes into the water column of the lake, probably onto the thermocline.

The high levels of microbial activities due to the high temperature in the littoral sediments and the diurnal thermal stratification of the lake water may cause depleted oxygen concentration in the bottom water in the littoral zone. Although methanotrophs may oxidize methane even at low O_2 concentrations (Rudd et al. 1974), some part of the methane diffused from the deeper sediment can diffuse into the lake water, passing through the less oxic surface layer of sediments without being oxidized. Decreased oxygen and increased methane concentrations were observed in the bottom water of the littoral zone of Lake Biwa in summer (Murase et al. 2003). The transect observations demonstrated that methane diffused from the littoral sediments was horizontally transported to the offshore of the lake like river water. This suggests that methane diffused from the littoral sediment is another potential source of methane in the epilimnion and thermocline of the pelagic water column.

Because the bottom sediments contain high amounts of methane compared to the lake water as described above, resuspension of the surface sediment causes release of methane from the sediment, which may be a source of methane in the lake water. Resuspension of the littoral sediments is induced by a surface wave, while an internal wave induces resuspension of the deeper sediments (Bloesch 1995). Our results demonstrate the potential importance of internal waves in release of methane from the "sub-littoral" sediments. The water depth of the thermocline seasonally shifts according to the change in the structure of water temperature. In the early to middle stage of a stratified period, the thermocline is situated at a depth of around 15–20 m in Lake Biwa. In the late stage, the thermocline moves down to 30–40 m accompanied by a decrease in the water temperature of the epilimnion until the lake water is overturned. The internal waves can cause resuspension of the bottom sediments over broad depths due to the vertical shift of the thermocline. Especially in the late stage of a stratified period, differences in the water temperature between the epilimnion and hypolimnion become smaller, and the amplitude of the internal wave consequently becomes larger (Fig. 4). The strong seasonal winds in winter may induce frequent occurrence of internal waves, which may also cause the resuspension of the sediment and release of methane from the sediment.

Dynamics of dissolved methane in the water column in the pelagic zone

Methane concentration in the pelagic water column ranged from 4.3–166 nmol l^{-1} (Table 1). During the stratified period, methane concentration was higher in the epilimnion and thermocline than in the hypolimnion (Murase et al. 2003). The peaks in methane concentration were observed in the thermocline in the middle of a stratified period. The transportation of dissolved methane from the littoral and sub-littoral zones described above may be the most important source of dissolved methane. The highest methane concentration in the pelagic water column was recorded during the late stage of a stratified period (Murase et al. 2003). The river inflows may not explain this maximum methane content because no significant increase in methane concentration in the major river waters was observed in this period (Murase et al. 2003), nor in the amount of water discharge (data not shown). The littoral sediment had a lower methane production activity in winter than in summer (Murase and Sugimoto 2002). Therefore, release of methane from sediment resuspended by internal waves is the possible source of the increased methane. This conclusion is supported by the observational result that the maximum methane content in the pelagic water column was observed just before the overturn of the lake water in the late stage of the stratified period, when the bottom water of the sub-littoral zone (30-m depth) showed the highest methane concentration probably due to the internal waves (Murase et al. 2003).

Active oxidation of dissolved methane was observed in the hypolimnion of the pelagic area (Fig. 6). This is in agreement with the stable carbon isotope data of methane which showed a seasonal increase in the

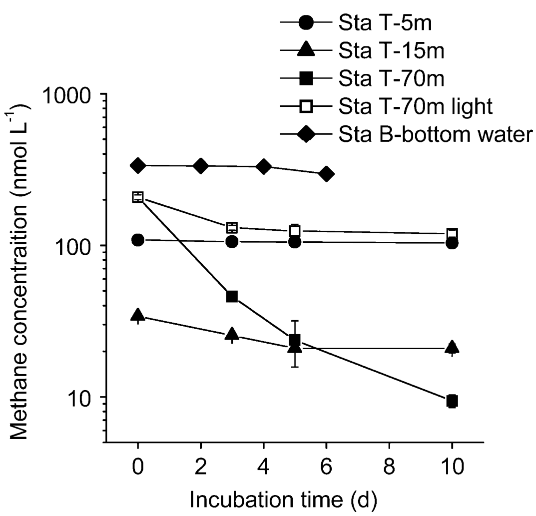

Fig. 6 Methane oxidation in lake water collected from different depths of the pelagic water column [Station T (*Sta T*)] and bottom water in the littoral zone [Station B (*Sta B*), 10 m depth]. Water depths of 5, 15, and 70 m in the pelagic water column correspond to epilimnion, thermocline, and hypolimnion, respectively

hypolimnion during a stratified period (Murase et al. 2003). Methane in the water column has been reported to be a carbon source for the lake pelagic food webs (Bastviken et al. 2003). Methane oxidation in the water samples from the epilimnion and thermocline (Station T, 5 and 15 m depth) was insignificant. Methane oxidation in the hypolimnetic water was insignificant when the water was incubated under light. Epilimnion water incubated under dark conditions showed methane oxidation after a long-term incubation period (> 1 month). These results indicate the inhibitory effect of light on methane oxidation in the lake water (J. Murase and A. Sugimoto, submitted).

The bottom water of the littoral area (Station B) also showed little methane oxidation (Fig. 6) (J. Murase, unpublished data). Because of the low methane oxidation and the high methane production rate in the sediment, the concentration of dissolved methane may be high in the littoral zone. This may be one of the strong sources of dissolved methane in the pelagic water column.

Methane dynamics in the entire lake

Based on data obtained, the dynamics of methane in the lake are summarized in Fig. 7. The horizontal inflow of dissolved methane from the river and littoral sediment is an important source of dissolved methane in the epilimnion and thermocline. Release of methane from the sub-littoral sediment caused by internal waves is another important source, especially at the end of a stratified period. Profundal sediment may be a minor source of methane in the hypolimnion because of the active oxidation of diffused methane in the sediment surface.

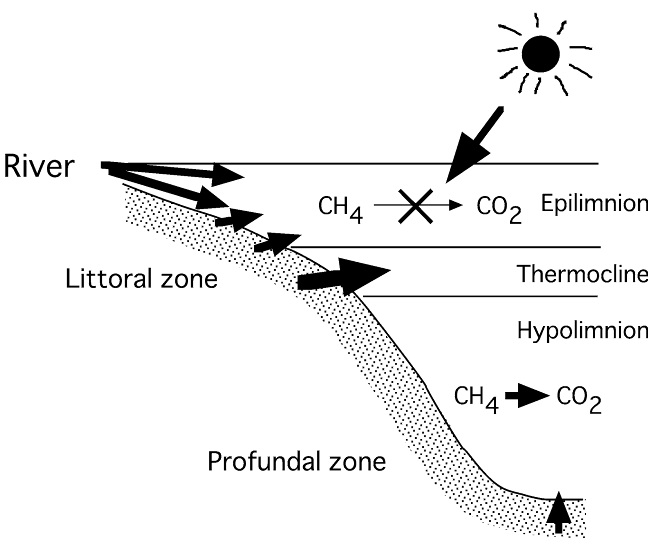

Fig. 7 A schematic model of the dynamics of methane in Lake Biwa. Methane in the lake water is supplied from the subsystems of the lake (rivers, littoral and profundal sediments) at different strengths (indicated with *arrows*). Dissolved methane is oxidized in the hypolimnion but not in the epilimnion because of the inhibitory effect of light

Methane oxidation is very low in the epilimnion and thermocline due to the inhibitory effect of light. Methane in the surface water is oversaturated to the atmospheric methane level and released to the atmosphere without oxidation in water. In contrast, methane is actively oxidized in the hypolimnion. The high loading and inactive oxidation of methane cause higher methane concentration in the epilimnion and thermocline than in the hypolimnion with the low loading and active oxidation of methane. This may be a mechanism for subsurface maxima of dissolved methane in the lake water, which have been observed in other lakes and in the ocean.

Other possible sources of dissolved methane in the lake water

A correlation between biomass of zooplankton and methane concentration has been observed in the near surface of marine environments (Traganza et al. 1979; Brooks et al. 1981; Conrad and Seiler 1988), and methane production by zooplankton (copepods) during grazing on marine phytoplankton has been reported (de Angelis and Lee 1994). However, methane production by zooplankton in freshwater environments has still not been clarified. Miyajima et al. (1997) detected no methane production by copepods in Lake Biwa. We also found no correlation between methane concentration and abundance of zooplankton (J. Murase, unpublished data). de Angelis and Lee (1994) reported methane production by zooplankton was species specific.

The presence of methane in the oxic open ocean is often explained by methanogensis in the anaerobic microsites inside particulate organic matter such as fecal pellets of copepods or marine snow. Karl and Tilbrook (1994) reported that the sinking particles released methane to seawater, explaining in part the in situ production of methane in the oxic seawater. Evidence of methanogenic archaea was revealed by analyses of lipid (King et al. 1998) and 16S rRNA genes (van der Maarel et al. 1999). The significance of methanogenesis from particulate matter in the methane budget of lakes remains to be studied.

Submarine groundwater discharge is often reported as a significant source of dissolved methane in the coastal oceans (e.g., Bugna et al. 1996; Bussmann and Suess 1998; Corbett et al. 2000). There is no study on the effect of groundwater discharge on methane budget in a lake. However, groundwater may be a possible source of dissolved methane in the lake water, because Taniguchi (2001) reported that the internal seiche enhanced the groundwater seepage in Lake Biwa.

Concluding remarks

Oxygen uptake by microbial metabolisms including methane oxidation in the profundal sediments may be accelerated by an increase in temperature at the lake bottom due to global warming (Hayami and Fujiwara 1999). Excessive depletion of benthic oxygen may release much more methane from the sediment to the lake water. Phosphorus can be also released from the sediment to the lake water due to oxygen depletion. Accelerated eutrophication of the lake by release of phosphorus may cause a catastrophic change in the methane dynamics in the lake.

The fact that methane is produced/released from the deeper layer (> 20 cm from the surface) of the profundal sediments suggests that the methane originated from organic matter deposited in the past (more than 100 years ago if the sedimentation rate is assumed to be 2 mm year^{-1}), and that this "old" methane contributes to the present carbon flow and oxygen budget of the sediments. The organic matter in the deeper layer of the profundal sediments as well as the littoral sediments is suggested to be relatively dominated by the allochthonous (terrestrial) origin in comparison to the surface layer of the profundal sediments (Murase and Sakamoto 2000). Further study is needed to elucidate the link between terrestrial organic matter and methane dynamics in lake sediments.

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