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Methane oxidation in Lake Tanganyika (East Africa)

Abstract—Methane oxidation rates were measured at five stations on Lake Tanganyika. Oxidation occurred mainly within a narrow zone at the boundary of the seasonally mixed layer and the permanently anoxic monimolimnion. Whole lake methane oxidation rates were estimated to have varied seasonally from 3.8 to 5.8 mmol CH₄·m⁻²·d⁻¹. The annual rate was tentatively estimated to be about 3.1 mmol CH₄·m⁻²·yr⁻¹, equivalent to at least 10% of annual primary productivity. Certain differences and similarities of methane cycling in Lakes Tanganyika and Kivu are compared to those in lakes of other types.

Lake Tanganyika is in east central Africa between 3° and 9°S lat at an altitude of about 773 m. It is the largest (34,000 km²) and deepest (1,400 m) of several lakes situated along a 3,000-km system of rift valleys which runs across Africa from the Zambesi River in the south to the Red Sea in the north (Hecky and Degens 1973). The lake is meromictic, with an anoxic monimolimnion containing hydrogen sulfide below a depth of 100–200 m (Coulter 1963) which is considered to be a "relict hypolimnion" (Craig 1975; Hecky 1978) and is thought to have originated at least 700 years ago, on the basis of radiocarbon measurements (H. Craig pers. comm.), during a drier and cooler period than the present. There is a seasonal thermocline from about 25–75-m depth with periodic circulation to the depth of zero oxygen concentration (100–200 m) usually during May–September (Coulter 1963).

Methane is oxidized in lakes by a group of bacteria that convert methane and oxygen to cellular material and carbon dioxide (Rudd and Taylor 1980). In lakes with anoxic bottom water, methane is oxidized in a narrow zone at the upper boundary of the anoxic zone during periods of stratification (Jannasch 1975; Rudd and Hamilton 1975, 1978; Rudd et al. 1974, 1976; Welch et al. 1980). In such lakes the methane oxidizers consumed almost all of the methane

as it diffuses up to the oxic–anoxic interface, so that concentrations in the oxygenated portion of the water column are very low but increase rapidly below the depth of zero oxygen. A similar situation was expected in Lake Tanganyika even though previous Belgian expeditions had not detected dissolved methane (Dussart pers. comm.).

During October 1975 a Canadian research team in cooperation with the United Nations Food and Agriculture Organization (FAO) fisheries research station in Bujumbura, Burundi, surveyed the water chemistry of the lake and attempted to estimate rates of production of particulate carbon by methane-oxidizing bacteria and phytoplankton. These data should be useful in establishing guidelines for maximum sustainable yield for the developing fishing industry.

I report here on the activities of the methane-oxidizing bacteria as well as some aspects of the methane cycle of Lake Tanganyika and consider these results in conjunction with available information on methane cycling in other smaller, intensively studied lakes. The other data have been presented elsewhere (Hecky et al. 1978).

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Lake water samples were taken in 2-liter Niskin bottles. Subsamples were collected in three 125-ml ground glass-stoppered reagent bottles for dissolved oxygen analysis (Strickland and Parsons 1968) except that to minimize atmospheric gas exchange the bottle volume was

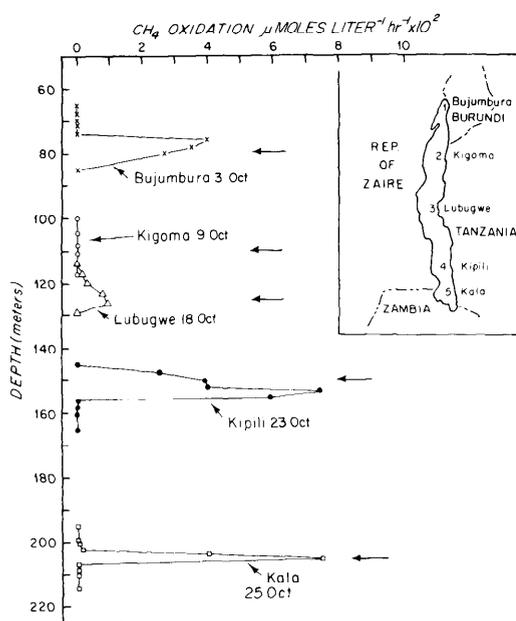


Fig. 1. Methane oxidation profiles and depth of zero oxygen concentration (horizontal arrows) at five sampling stations on Lake Tanganyika, 1975. Methane oxidation rates shown have been multiplied by a factor of 10^2 .

allowed to overflow at least three times. The subsamples were assayed as described by Rudd et al. (1974) and Rudd and Hamilton (1975). Briefly, $^{14}\text{CH}_4$ methane was equilibrated with the $^{12}\text{CH}_4$ present in the samples in the reagent bottles. The samples were incubated for 4 h at lake water temperature and killed after incubation by raising the pH to 11 with NaOH. Radiolabeled methane not oxidized during incubation was stripped from solution, combusted to $^{14}\text{CO}_2$, trapped in phenethylamine, and counted in a scintillation counter at the Freshwater Institute (in Canada). These counts plus in situ methane concentrations were used to calculate the methane specific activity. An aliquot of the killed samples was bubbled with air to rid it of dissolved $^{14}\text{CH}_4$; carbon-14 remaining in the solution was considered to be labeled cellular material and carbon dioxide produced via methane oxidation. A second aliquot was acidified to about pH 2 and bubbled with air to strip it of both $^{14}\text{CH}_4$ and

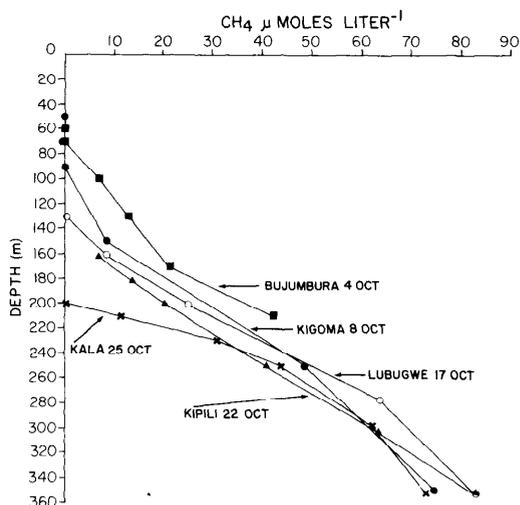


Fig. 2. Profiles of methane concentration at five sampling stations on Lake Tanganyika, 1975.

$^{14}\text{CO}_2$; activity remaining in this sample was considered to be cellular material. The ^{14}C cpm data were converted to dpm by the channels ratio method. The difference between the basic and acidic samples was the quantity of $^{14}\text{CO}_2$ produced during incubation. In situ methane oxidation rates were then calculated as described by Rudd et al. (1974). Replicate subsamples from a single lake water sample usually varied by $<10\%$.

Methane concentrations of the lake water were assayed according to Rudd et al. (1974) and Rudd (1977). Gas chromatographic analyses of the samples were done at the Freshwater Institute within 1 month of sampling. During transport the methane samples were sealed in serum vials which had been found to be gastight for at least 1 month. Dissolved oxygen was determined immediately by the azide modification of the Winkler method (Am. Public Health Assoc. 1965).

Plankton respiration was measured by determining oxygen consumption rates in 140- or 300-ml oxygen bottles kept in the dark. Two samples were fixed immediately after sampling with alkaline iodide and manganous sulfate; after 24 h (± 2 h) another two were fixed. Oxygen

concentrations were measured by titration to an electrometric end point (Golterman 1969); precision with this method was ± 0.02 ppm.

Bacteria were counted in samples preserved in 2% Formalin (Daley and Hobbie 1975).

In some cases methane oxidation occurred in samples that smelled of hydrogen sulfide. This was ascribed to contamination of the sample with atmospheric oxygen since methane-oxidizing bacteria do not oxidize methane anaerobically within the water column (Rudd unpubl.) and oxygen and hydrogen sulfide do not usually occur together. Therefore methane oxidation rates in all samples containing hydrogen sulfide were taken to be zero for the purpose of calculation of areal and annual methane oxidation rates.

During a north to south cruise on the lake, because of differing depths of seasonal mixing, the depth of zero oxygen concentration descended progressively at each of five sampling stations (Fig. 1). Methane concentrations in the oxygenated layer were very low ($< 0.5 \mu\text{M}$) but increased rapidly below that (Fig. 2).

Samples for methane-oxidizing activity were taken at close depth intervals above and below the depth of zero oxygen concentration. The oxidizers were active only within a zone of about 10 m at the oxic-anoxic interface (Fig. 1). The thickness of this methane oxidation zone was similar in depth to that given by Jannasch (1975) for Lake Kivu, but was about 10 times greater than that reported by Rudd and Hamilton (1975) for Lake 227, a small Canadian Shield lake. This large difference probably reflects higher rates of vertical mixing of dissolved substrates (CH_4 , O_2 , and nutrients) in the larger lakes. During summer stratification at the depth of zero oxygen concentration, Lake 227 has extremely low rates of vertical diffusion ($\approx 1.5 \times 10^{-4} \text{ cm}^2 \cdot \text{s}^{-1}$; P. Quay in prep.), as compared to an estimated Lake Tanganyika value of $\approx 3 \text{ cm}^2 \cdot \text{s}^{-1}$ calculated from methane concentration profiles (Fig. 2). As in Lake 227 (Rudd and Hamilton 1975), the rates and distribution of methane oxidizers in Lake Tanganyika

were ultimately controlled by the flux of oxygen and methane into the zone of activity.

Rates of methane oxidation were highest at both ends of the lake (Fig. 1). Toward the center of the lake rates were lower (Lubugwe station) or almost undetectable (Kigoma station). The reduced rates at the Lubugwe and Kigoma stations may be explained by the alternate periods of stratification and mixing of the upper layer of the lake during the dry windy season of May–September (Coulter 1963).

During a mixing period, the narrow zone of methane-oxidizing activity would be spread over a wider depth range and the rate per unit volume of water might be undetectable. When all of the methane had been oxidized down to the maximum depth of the mixed layer and restratification had occurred the rapid respiration rates, which averaged $13.3 \mu\text{g} \cdot \text{liter}^{-1} \cdot \text{h}^{-1}$ ($n = 36$; $\text{SD} = 4.4$) would lead to an anoxic zone containing negligible methane. Under these circumstances, methane would not be oxidized at any depth. There is some evidence that this is what happened at the Kigoma station on 9 October 1975 when the methane oxidation and oxygen profiles were taken. At that time the oxygen concentration of a 40-m-thick layer of water between 75 and 115 m was uniformly about $0.1 \text{ mg} \cdot \text{liter}^{-1}$. Consequently the depth of zero oxygen concentration would probably have risen quickly from 120 m to about 75 m as the remaining oxygen was consumed, and methane oxidation would not resume until methane had diffused upward to the new oxic-anoxic interface. Thus during the dry season methane oxidation may be intermittent and of variable intensity, depending on water circulation.

During the rainy season of October–April, the upper portion of the lake is thermally stratified without interruption (Coulter 1963) and the methane oxidizers would probably become well established at the depth of zero oxygen concentration. During this time methane-oxidizing activity would probably be similar to that

observed at the Bujumbura, Kipili, and Kala stations (Fig. 1). The average calculated rate for these stations was $5.8 \text{ mmol CH}_4 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ (Table 1). If this figure is taken as an average daily areal rate for the rainy season, then the total amount of methane oxidized during that period would be $2.5 \text{ mol} \cdot \text{m}^{-2}$ or $30.0 \text{ g C} \cdot \text{m}^{-2}$. During the dry season (May–September), when different parts of the lake are intermittently mixed to the depth of zero oxygen concentration, methane-oxidizing activity would probably be more closely approximated by all of the profiles shown in Fig. 2. On this basis I estimate that the average daily rate during the dry season was $3.8 \text{ mmol CH}_4 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ and the total amount of methane oxidized during the dry season would be $0.6 \text{ mol CH}_4 \cdot \text{m}^{-2}$ or $7.2 \text{ g C} \cdot \text{m}^{-2}$. A rough estimate of total annual methane oxidation in Lake Tanganyika is $3.1 \text{ mol CH}_4 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ or $37.2 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. Although these are crude estimates of seasonal and annual methane oxidation rates, it has nevertheless been useful to compare them with other lakes where crude (Kivu) and more precise (Lake 227, Frains Lake) estimates are available.

Maximum methane concentrations in the anoxic bottom waters of Lake Kivu, of similar maximum depth, are about 20 mM (Degens et al. 1973) as compared to Lake Tanganyika's maximum concentration of $<2 \text{ mM}$. Examination of the different methane profiles might be misleading in forming conclusions about the relative importance of methane cycling in the two lakes. Methane oxidation rates were similar in the two lakes ($2.6 \text{ mol CH}_4 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; Jannasch 1975) so the rates of flux of methane to the oxidation zone must be similar. This is possible even though the concentration gradient is steeper in Kivu, if the coefficient of vertical diffusion in Kivu were low enough to produce the same flux rate as in Tanganyika, which is probably the case since Kivu has a strong halocline (Degens et al. 1973) and is a much smaller lake than Tanganyika. Thus the absolute contribution of methane oxidation to oxygen consumption and to carbon diox-

Table 1. Areal rates of methane oxidation at five sampling stations on Lake Tanganyika, October 1975.

Station	mmol $\text{CH}_4 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$
Bujumbura	4.9
Kigoma	0.0
Lubugwe	1.5
Kipili	9.6
Kala	3.0

ide and particulate carbon production for the epilimnia of these two lakes is probably quite similar even though the "standing crop" of methane is much lower in Lake Tanganyika.

Because little dissolved methane was found above the depth of zero oxygen concentration in Lake Tanganyika, and no methane-oxidizing activity could be found in surface water samples in which the methane concentration had been artificially increased, it is unlikely that methane was bubbling out of the monimolimnion. Therefore diffusion of methane to the depth of zero oxygen concentration was the only means of escape from the anoxic bottom waters. If vertical diffusion of dissolved methane out of the monimolimnion was equivalent to its production rate, then the annual rate of methane production in the anoxic bottom waters should equal the annual rate of methane oxidation within the narrow zone of activity at the depth of zero oxygen concentration (i.e. $3.1 \text{ mol CH}_4 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ or $37.2 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$). This estimate is very close to the Jannasch estimate of methane production rates in Lake Kivu ($2.2 \text{ mol} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) and also agrees reasonably well with the Deuser et al. (1973) estimate for Lake Kivu of $8.8 \text{ mol} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. Thus methane cycling (i.e. both production and oxidation) may be influencing carbon cycling of these two rift lakes in a similar manner.

Methane production rates in shallow lakes are directly related to rates of particulate carbon input to sediments (Robertson 1979) and are about 10–13% of primary productivity (Robertson 1979; Rudd 1979). In deeper lakes a larger proportion of fixed carbon is mineralized before

reaching the sediments (Bloesch et al. 1977). This is probably particularly true for Lake Tanganyika: in addition to its great depth, temperature and euphotic zone respiration are high and bacterial counts are also very high ($7.6 \times 10^5 \text{ ml}^{-1} \pm 3.0$; $n = 30$). Because of this it seems likely that methane production should amount to $\ll 10\%$ of primary productivity in Lake Tanganyika. This is not the case however (*see below*), which suggests that methane production (and consequently methane oxidation rates) may not be directly related to present day rates of particulate carbon flux to the sediments. Hecky (1978) and Craig (1975) have suggested that Lake Tanganyika's monimolimnion may be a "relict" from a cooler, drier period. This suggestion is based upon distribution of stable isotopes, conservative salts, and carbon compounds. If this is true, methane cycling in Lake Tanganyika may be mainly driven at present by "old" carbon deposited during a previous period of the lake's history.

An average of 74% of the methane oxidized at all of the stations was converted to carbon dioxide, with the remainder being incorporated into bacterial cell material. This is relatively high in comparison to methane oxidizers in a north temperate lake. Rudd and Hamilton (1978) found that only 50% of the methane oxidized in Lake 227 was converted to carbon dioxide. Thus the Lake 227 methane oxidizers were twice as effective as the Lake Tanganyika oxidizers in converting methane carbon to cell material. This high respiration rate seems to be a general characteristic of the entire planktonic microbial community of Lake Tanganyika.

The annual estimates of whole lake methane oxidation and production rates reported here are probably conservative. Rudd et al. (1976) and Rudd and Hamilton (1978) found that whole lake methane oxidation rates in Lake 227 are highest during periods of overturn when large quantities of methane and nutrients are swept up from the anoxic hypolimnion and mixed with oxygenated surface waters. This set of circumstances is anal-

ogous to periods of upwelling that are known to occur in Tanganyika (Coulter 1963). The amounts of methane transported from the monimolimnion and oxidized during upwelling are not known but they would add to the present conservative estimate of annual methane oxidation which equals about 10% of the carbon flux through the photosynthetic process (Hecky et al. 1978).

John W. M. Rudd

Department of Fisheries & Oceans
Freshwater Institute
501 University Crescent
Winnipeg, Manitoba R3T 2N6

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