INTERNATL MICROBIOL (2000) 3:89–95

RESEARCH ARTICLE

Brian Duval
Steve Goodwin

Department of Microbiology, University
of Massachusetts, Amherst, MA, USA

Received 4 November 1999
Accepted 23 March 2000

Correspondence to:
Steve Goodwin. Department of Microbiology.
Box 35720. University of Massachusetts.
Amherst, MA 01003-5720, USA.
Tel.: +1-413-5454604.
Fax +1-413-5451578.
E-mail: sgoodwin@microbio.umass.edu

Methane production and release from two New England peatlands

Summary The rate of methane production and release to the atmosphere was determined for two New England peat bogs. Methane production rates from peat sediments, which were measured down to depths of 150 cm, ranged from 1 to 15 μmoles per liter per hour. The highest rates of methane production occurred at depths of 60–100 cm. Methane release from these same peats was quantified from various habitats on the bog using gas collection chambers. The chambers enclose a two-liter volume and cover an area of 0.02 m^2. Methane accumulation in the chambers was measured for periods of up to 18 days. Methane release was related to pH and habitat zone. The lowest rates of methane release were from those portions of the bogs that had pH values below 5.0. Peak methane release occurred during or immediately after ice melt in both wetlands with release rates as high as 34 $mmoles/m^2/d$. The overall estimate of yearly release of methane from these bog systems is 2,900 and 14,900 moles per year for Arcadia and Hawley Bogs respectively. Both of these bogs have pH environments close to the lowest limit for methanogenesis, and small differences in pH values can have a large impact on both the rate of methane production and the rate of methane release to the atmosphere.

Key words Methanogenesis · Acidic habitats · Bogs · Gas release ·*Sphagnum*

Introduction

Wetlands are a major source of atmospheric methane [43]. Methane is a radiatively active gas that is influential in the global radiation budget. The rates of methane production and release from Minnesota, USA, peatlands have been widely reported [10, 13, 21, 39, 47]. However, methane production and release from similar bog habitats in New England has received far less attention [17, 18, 22]. A recent survey of sources of atmospheric methane in New England suggests that as much as 36% of methane release to the atmosphere may be from wetlands [5].

The production of methane is dependent on the presence of anaerobic conditions, fermentable organic matter, and methanogenic bacteria. Many environmental conditions are known to impact the rate of methane production including temperature, the presence of alternative electron acceptors, and pH. The rate of release is controlled by the rate of production, the rate of consumption (primarily as methane oxidation), and the mechanisms of transport (primarily diffusion, gas bubble ebullition, and transport through plants).

Measurements of methane flux out of wetlands rely on variations of three basic techniques: the use of static chambers enclosing the atmosphere immediately above the wetland, micrometeorology towers, or calculations of diffusion based on the thin boundary layer equation. A recent study comparing static chambers to thin boundary layer equation methods discusses several advantages and disadvantages of these techniques [14].

Most closed-chamber studies that report methane flux use time intervals as short as twenty minutes. These studies are well suited to account for methane diffusion. However, the release of methane is influenced also by factors such as gas ebullition [18], differences in daytime and nighttime fluxes [41], and release during ice melt [29]. These processes vary over time intervals that are much longer than the typical closed-chamber flux study.

When measuring net methane flux from visually uniform sites, a high level of variability has often been encountered [7, 13, 32, 33, 44, 46]. Sources of variability can include: utilization of methane by methanotrophic bacteria, differences in oxygen concentrations and the availability of nutrients, temperature, barometric pressure and porosity [23, 40].

Acidic peatlands (pH < 5.0) represent a special class of wetlands from which methane production and release represents a paradox. Methanogens are strictly anaerobic bacteria that utilize a variety of simple carbon compounds. Methane production is the terminal step in the breakdown of organic matter in peat bog sediments. The optimum pH for growth of most methanogens is near neutrality [25, 35, 49]. Methanogenesis in peatlands is known to be inhibited by low pH. Peats with bulk pH values between 3.8 and 4.9 have been shown to have pH optima for methane production between 5.2 and 6.0 [20, 47]. Methane production in peat slurries can have pH optima two pH units above in situ pH values [4]. In spite of extensive attempts to isolate methanogenic bacteria capable of growth at low pH, there are only a few reports of methanogenic isolates at pH values below pH 6.0 [25, 36, 48], and no reports of growth below pH 4.3. And yet, in spite of low pH conditions, peat bogs are important environments for the production and release of atmospheric methane. Methane release estimates for low pH peat bogs [21, 38, 42] range between 0.02–119 mmoles/m^2/d. Other wetland types such as Cypress swamps and subarctic taiga, generally release less methane per unit area [9].

The purpose of this study is to explore the impact of pH on the rates of methane production and release from two acid peat bogs in New England.

Materials and methods

Site description Arcadia Bog and Hawley Bog are sphagnum-dominated wetlands located in western Massachusetts, USA. Arcadia Bog is located in Belchertown, Massachusetts (42° 18’ 30’’ N, 72° 25’ 35’’ W) at an elevation of 95 m. Hawley Bog is located in the town of Hawley (42° 34’ 24’’ N, 72° 53’ 30’’ W) at an elevation of 534 m. Hawley Bog is the remnant of a glacial lake formed during the retreat of the last glacial period [31]. Arcadia Bog is a kettle hole bog formed by a remnant ice block after general glacial retreat [34]. Arcadia is the smaller of the two wetlands at 5000 m^2, while Hawley Bog covers an area of approximately 40,500 m^2. Both bogs are dominated by *Sphagnum* moss that overlies several meters of peat and glacial lake sediments. The active *Sphagnum* layer and the root systems of *Chamaedaphne* species extend to a depth of 40 cm at both bogs. Beneath the 40 cm depth are strata of denser fibrous peat that are waterlogged and predominantly anoxic.

Four vegetational zones can be distinguished in Hawley Bog. An open water pond remains at the center of the bog. The second zone is mat community dominated by *Sphagnum* and *Chamaedaphne* sp. growing on top of 9–10 m of consolidated peat. This zone is devoid of trees. A quaking mat of *Sphagnum* has encroached over the pond’s edge. The third zone is a shrub community consisting of a dense growth of high bush blueberry (*Vaccinium corymbosum*) and mountain holly (*Nemopanthus mucronata*). *Sphagnum* moss is the predominant ground cover. *Picea mariana* and *Larix laricina* are found at the shrub/mat transition. The fourth zone is the forest, a mature stand of conifer and northern hardwoods that was flooded by beaver impoundment.

Arcadia bog has three defined vegetational zones. The first zone is a central mat dominated by *Sphagnum* moss. The central mat is sparsely covered by *Picea mariana* and *Larix laricina*. There is not an open water region associated with Arcadia Bog. The shrub zone is similar to the shrub zone at Hawley Bog. The entire bog is surrounded by a lagg that is characterized by standing water and sparse vegetation. The lagg consists of shallow peat deposits (0–2 m) underlying 50–60 cm of water. Trees such as *Tsuga canadensis* and *Acer rubrum* shade the lagg zone, which can be up to 5 m in width.

A combination of color infrared aerial photography (University of Massachusetts 1985, 1:25,000) and ground measurements were used to determine the area of vegetational zones in Hawley Bog. Mapping done in a previous study [34] was used to determine the area of vegetational zones in Arcadia Bog.

Field measurements Water samples were pumped to the surface using a Masterflex peristaltic pump and collected after liberal flushing into biological oxygen demand bottles. A Yellow Springs Instruments model 51B dissolved oxygen meter was used in the field to establish the depth of oxic/anoxic sediment boundaries. Measurements of pore-water pH were made in the field using a Sargent-Welch model 4090 pH-meter or a Corning model 106 pH-meter. The pH was recorded across both wetlands at various depths at each of the methane monitoring sites.

Methane production rates Sediments from both wetland sites were collected at various depths to a maximum of 150 cm and transferred into extraction flasks. Pond sediments from Hawley Bog were collected by Eckman dredge. A bucket auger with 2 m of extension was used to sample the sediments beneath mat and shrub communities. A portable cylinder of nitrogen gas and a glove bag were used for media inoculation and sediment transfer into extraction flasks. Sediments transported to the laboratory were either homogenized in an anaerobic chamber or transferred directly into flasks using a Hungate apparatus.

Methane production was measured directly in the headspace of extraction flasks. Each 90 ml flask had a three-way stopcock that allowed sediment to be added to the flask in the field under a flow of nitrogen gas. Approximately 45 ml of sediment was added to each flask. After vigorous shaking, the headspace was sampled for methane through a rubber septum. When comparing methane production from bog sediments collected from different depths, the flasks were incubated in the dark at 20°C.

Methane analysis was performed using a Shimadzu Gas Chromatograph (GC 8A) equipped with a thermal conductivity detector (TCD). Methane was separated on a packed column of Carbosieve S-II, 80/100 mesh, at an injection/detection temperature of 100°C and a column temperature of 80°C, with purified He as a carrier gas. The total molar quantity of methane was determined from liquid and headspace volumes in accordance with Henry’s law.

Gas release chambers Rates of methane release were determined from the accumulation of methane within the headspace of sealed gas collection chambers transecting each wetland. These chambers were constructed by removing the bottom from two-liter glass bottles. With the bottoms removed, these chambers covered an area of approximately 0.02 m^2. A two-way valve at the top of each collector was fitted with a 21 g needle to collect headspace samples in evacuated 160 ml serum bottles with rubber stoppers. Between 8 and 14 identical chambers were spaced across both Arcadia and Hawley Bogs. Rates of methane release were determined over periods of 12–18 days.

The use of gas collection chambers inherently disturbs the soil-plant-atmosphere continuum [33]. Therefore, the following precautions were taken to minimize disturbances at the sediment-atmosphere interface. (i) Chambers were wrapped in reflective Mylar to limit heating during summer months by minimizing the solar-trapping effect. Temperatures were recorded for two identical and adjacent chambers to determine the effect of using a reflective wrapping. During sunny days in July, chambers not enclosed in Mylar were as much as 8°C above ambient air temperatures. Temperatures inside the chambers wrapped in Mylar were within 2°C of the outside air temperature. (ii) The emplacement of chambers involved a slight insertion of the glass edge into the peat surface. After initial emplacement, any pressure changes were relieved by briefly removing the chamber and clearing it of gases that may have been evolved as a result of the disturbance [33]. The chamber was then returned to the initial location.

At Hawley Bog, collectors were placed on pond ice in early April. After ice melt, methane release was monitored at Hawley Bog pond by securing the glass collectors at the water level to brackets that were anchored into the sediment. Floating chambers have been shown to provide reasonable estimates of methane emissions [30].

Results and Discussion

Methane production Methane production was greatest from sediment collected between 60–100 cm in depth for both bogs (Fig. 1). Shallow sediments (< 60 cm in depth) produced less methane when incubated under anaerobic conditions, than did sediments taken from 60–80 cm and 80–100 cm depths. Beneath the 100 cm depth, methane production per unit volume decreased sharply. Dissolved oxygen dropped below 2 mg/l at a shallower depth in Arcadia Bog than in Hawley Bog and therefore the maximum rate of methane production occurred closer to the surface in Arcadia Bog than in Hawley Bog.

The rate of methane production was greater from sediments of higher pH. Rates of methane production remained linear over time, although slightly lower rates were usually measured during the first 36 hours. Sediments collected from pond, lagg, shrub, and mat habitats with characteristically different pH values are compared in Fig. 2. The highest rates of methane production are found in the pond sediments of Hawley Bog and the lagg sediments of Arcadia Bog. The lowest rates of methane production are found in the Hawley Bog mat, the Arcadia Bog mat and the Arcadia shrub. All three of these sites have pH values below 5.0 and methane production rates ranging from 1 to 5 µmoles/l/h.

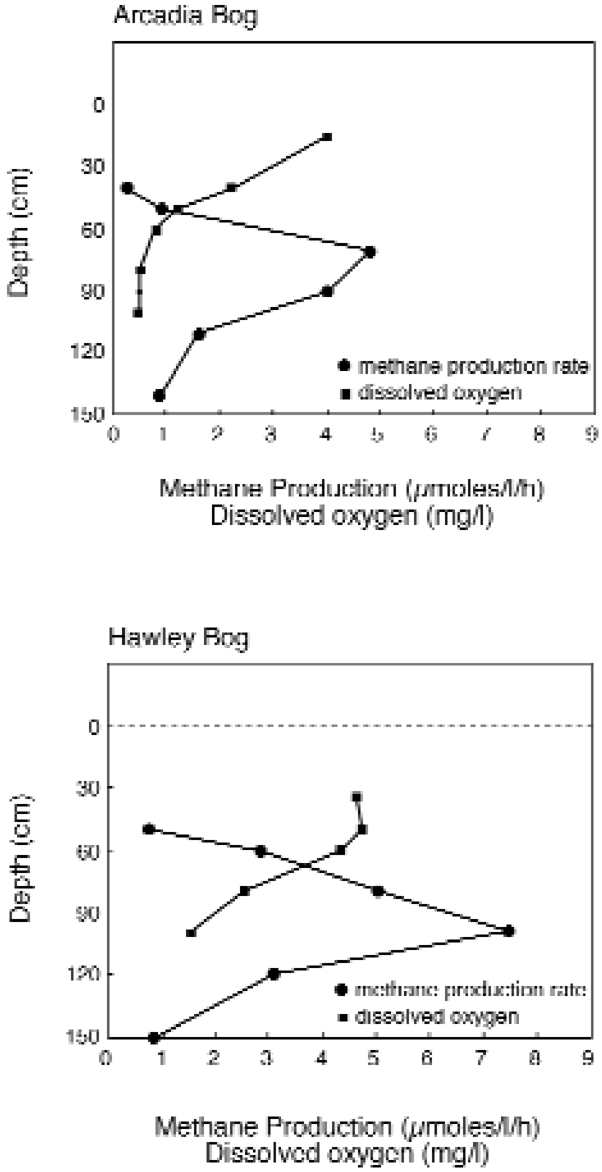

Fig. 1 Dissolved oxygen and methane production rates from the mats in Arcadia Bog and Hawley Bog, July 1993

Methane release Even when measured over extended periods of time (up to 18 days), rates of methane release did not always decrease with time, as would be expected if diffusion were the primary driving force for release (Table 1). In general, the highest rates of methane release were measured during the first day. In several cases however, the last sampling period had release rates that were nearly as high as the first sampling period.

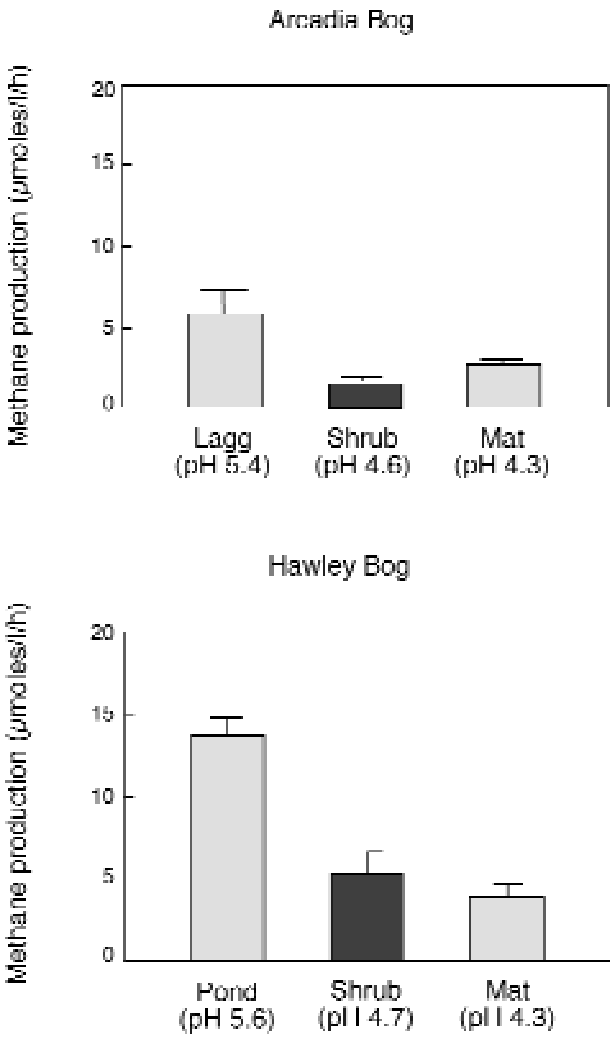

Fig. 2 Relationship between methane production rates and pH for various vegetational zones for July and August 1993

Figure 3 displays methane flux from Arcadia and Hawley Bogs between February and December. The average methane release from all vegetational zones during ice-free conditions (calculated from the data in Table 2) was 2.3 and 1.6 mmoles/m^2/d, at Arcadia and Hawley Bogs respectively. Methane release at both wetlands was greatest during the spring. The largest flux occurred at ice melt or shortly thereafter. The overall estimate of release from these bog sediments is 2,900 and 14,900 moles per year for Arcadia Bog and Hawley Bog respectively. These calculations are based on 250 ice-free days per year at Arcadia Bog and 230 ice-free days per year at Hawley Bog and correspond to 46 kg of methane released from Arcadia Bog and 238 kg of methane released from Hawley Bog per year.

Table 1 Methane accumulation rates (mmoles/m^2/d) in static collection chambers for Arcadia Bog

Habitat	Date	Day 1	Day 2	Day 6	Day 8	Day 13
Shrub	Aug 10–24	9.0	2.6	3.4	5.0	6.3
Shrub	Aug 10–24	5.8	3.3	2.1	3.7	4.4
Mat	Sep 2–16	4.6	3.3	2.2	2.3	1.6
Lagg	Sep 2–16	130.0	10.0	1.6	15.0	2.0
Lagg	Sep 2–16	80.0	1.0	0.0	5.0	5.0
Shrub	Sep 2–16	25.0	15.0	3.5	5.0	5.0
Shrub	Oct 8–22	14.9	10.2	8.6	4.6	5.1
Mat	Oct 8–22	12.1	3.8	0.9	0.9	1.4
Mat	Oct 8–22	4.6	3.3	2.3	2.4	1.6
Lagg	Oct 8–22	8.1	3.1	4.8	2.3	4.4
Mat	Nov 1–15	7.7	3.0	2.5	2.1	1.6
Lagg	Nov 1–15	57.4	10.1	6.5	1.7	23.4
Lagg	Nov 1–15	10.5	9.7	2.6	1.0	9.0
Shrub	Nov 16–Dec 1	1.9	1.6	1.0	1.3	0.1
Lagg	Nov 16–Dec 1	3.1	1.3	1.3	2.3	0.5

Note also that ice was not a perfect cap for methane. Collectors set over melting ice in several bog locations evidenced slight methane release (days 50–100). Methane release rates as high as 3.0 mmoles/m^2/d were measured through as much as 25 cm of ice and values as high as 14.5 mmoles methane/m^2/d were detected through the soft ice layer above the Hawley Bog pond just prior to ice melt.

The rates of methane release were never uniform within a single vegetation zone. Local pH and methane release rates varied considerably even between collectors spaced approximately 30 cm apart within the mat community at Arcadia Bog. In both Arcadia and Hawley Bogs, pH is influenced primarily by vegetational zone and only slightly by depth of sediment. Throughout the field season, the pH was consistently higher (pH 4.9–5.6) in the lagg community. The

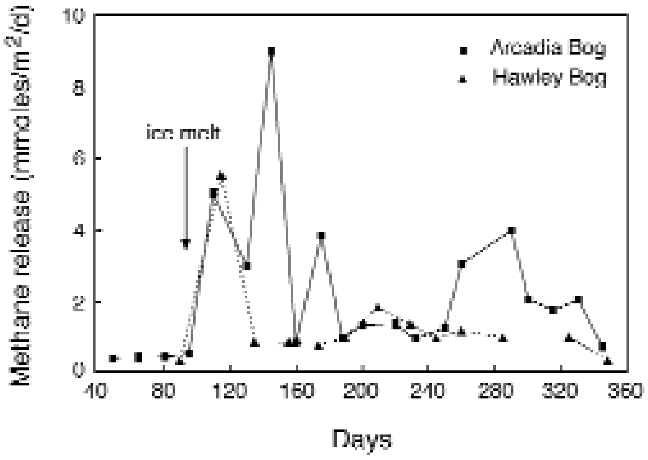

Fig. 3 Average methane release rates from Arcadia Bog and Hawley Bog. Ice melt occurred between day 105 and 110 for both bogs

Table 2 Average methane release from Arcadia Bog and Hawley Bog as a function of vegetational zone

Site	Zone	n[(*)]	CH_4 release (mmoles/m²/d)		Area (m²)	Total CH_4 flux (moles/d)
			Range	Mean		
Arcadia	lagg	56	0–11.2	2.1	1000	2.1
	shrub	54	0–34.1	3.8	1500	5.7
	mat	65	0–33.7	1.5	2500	3.9
	Totals	175			5000	11.7
Hawley	pond	16	1.4–15.4	5.5	4500	24.8
	shrub	60	0–27.7	1.0	15000	15.0
	mat	56	0–31.2	1.3	10500	13.7
	forest	10	0–1.0	0.1	10500	1.1
	Totals	142			40500	54.6

(*) Number of replicates.

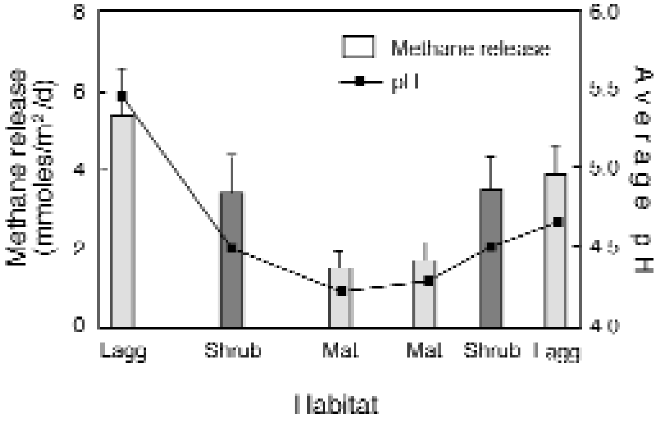

Fig. 4 Methane release from Arcadia Bog as a function of vegetational zone in the fall of 1992

pH was lowest in the central mat portion of each bog that is dominated by a *Sphagnum* mat with typical pH values between 3.9 and 4.4.

Figure 4 depicts methane release rates for a transect across the width of Arcadia Bog during the autumn of 1992. Each site represents the average of eight measurements. The highest release rates occurred at the edge of the bog, where pH is the highest. The central mat has both the lowest pH and the lowest methane release rates. Methane release and pH are depressed in the *Sphagnum*-dominated, central portions of Arcadia Bog. Examining the rates of methane release across all vegetational types for the fall of 1992 further emphasizes the effect of pH on the rates of methane release in the pH range from 3.8 to 4.8 (Fig. 5).

The contribution to the total methane flux over the study period was estimated for each vegetational zone for both bogs (Table 2). More than 300 individual measurements of methane release are represented in these averages. The mean methane release rate for each habitat was multiplied by the area of that habitat to estimate total methane flux from both bogs. The lowest mean methane release rates are for the mat, the portion of the bog with the lowest pH. The only exceptions are the low rates from the forested portion on the edge of Hawley Bog (pH 5.0). Lower methane production and release rates in forested versus open peat lands have been noted previously. The average methane release rate weighted for area for Arcadia Bog is 2.3 mmoles/m²/d (36.8 mg/m²/d) and for Hawley Bog is 1.6 mmoles/m²/d (25.6 mg/m²/d). If only the open portions of Hawley Bog are considered, the average methane release rate rises to 1.8 mmoles/m²/d (28.8 mg/m²/d). These estimates are in line with other estimates of methane release from temperate bogs that range from 10 to 870 mg/m²/d [1, 10, 13, 15, 19, 21, 39, 45].

This study emphasizes the major role of pH as a variable for the control of methane production and consequent methane release from temperate bogs. The complex effect of pH on methane production in boreal mires has also been recently stressed [4]. At low pH, differences of 1 pH unit or less can have a sizeable impact on the rate of methane production. The bulk pH in most portions of an acid peat bog is well below the pH optimum for methane production. In fact, bulk pH in portions of these bogs is often below the minimum pH at which any methanogenic bacterium has been reported to be capable of methane production [25, 36, 48]. The production of much of the methane that is ultimately released from low pH wetlands may occur in localized, higher pH microniches and within the neutral pH niche inside endosymbiotic eukaryotic microorganisms, but the role of pH in influencing the release of methane from such ecosystems requires continued attention.

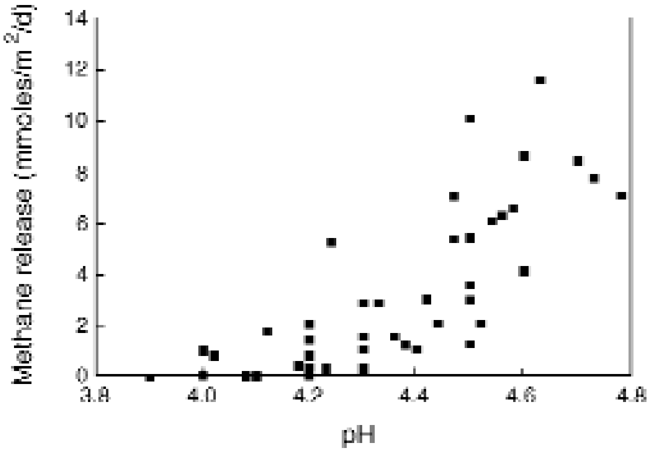

Fig. 5 Methane release rates as a function of pH in Arcadia Bog in the fall of 1992

The large methane release pulse that occurred upon ice melt was an unexpected finding of this study, but Boeckx and van Cleemput [6] report a similar methane profile with maximal flux occurring at 160 days with a smaller resurgence of methane flux in the fall. Phelps et al. [37] report similar phenomena from high altitude lakes and suggest that this spring flux could be relevant in bogs as well. Other studies have reported high methane concentrations building up under winter ice [27–29]. For several small lakes in Minnesota, 40% of the total yearly release of methane was shown to occur at the time of ice melt [29].

The goal in using methane flux chambers is to obtain measurements that approximate the flux that would have occurred if the chamber was not in place. It is widely acknowledged that there are limitations to the use of chambers. Chambers can only cover a small area relative to the spatial variation that occurs in most environments. The use of chambers also eliminates natural air turbulence that would normally occur at the interface. With time the presence of the chamber alters the microenvironment, temperature may differ in and out of the chamber, and the composition of the gas within the chamber changes. The latter is especially important for its impact on diffusion; as methane accumulates in the chamber, the concentration gradient decreases and methane diffusion can be expected to decrease. This is the primary reason that chamber studies of methane flux have almost universally used very short sampling periods (less than one hour). It has been estimated that closed chamber measurements over a period as short as twenty minutes may underestimate diffusional transport by as much as 55% due to changes in the concentration gradient [26]. Another concern with longer sampling periods is the possibility that higher concentration of methane within the chamber will lead to elevated rates of methane oxidation.

On the other hand, gas bubble ebullition is a discontinuous process. It is clear that gas bubble storage and ebullition accounts for some of the high spatial and temporal variability seen in methane flux measurements [3, 8, 18]. Gas bubbles can be stored within the mat or sediment and are released through discrete channels resulting in spatial variability. In a study of a New England bog it was demonstrated that gas bubble storage is frequently large enough to serve as a significant buffer between methane production and methane release [18] and it was suggested that changes in atmospheric pressure, temperature and water table levels can lead to discontinuities in ebullition on the order of hours and even days. Previous studies have demonstrated that ebullition accounted for between 39 and 89% of total methane flux from a variety of environments [2, 3, 8, 12, 24].

A significant contribution from gas bubble ebullition may be missed by discrete static chambers. The closed-chamber flux measurements over several days reported in this study clearly underestimate the diffusional flux and cannot account for possible increased methane oxidation caused by elevated methane concentration in the chamber. These measurements should be considered minimum estimates of methane flux. On the other hand, the extended measurement periods employed in this study may help to average out the effects of gas bubble storage and intermittent ebullition. It also helps to average out differences between daytime and nighttime fluxes [16, 41]. Note that, despite the limitations of the long sampling periods, the measured fluxes are comparable to those determined in other short-sampling-period chamber studies from similar environments.

Acknowledgments We thank Bruce Mobarry for technical assistance and helpful discussion and Robin Richards and Harold Hemond for critically reading the manuscript. Funding was provided by NSF Grant 9106773.

References

1. Bartlett KB, Harriss RC (1993) Review and assessment of methane emissions from wetlands. Chemosphere 26:361–320
2. Bartlett KB, Crill PM, Bonassi JA, Richey JE, Hariss RC (1990) Methane flux from the Amazon River floodplain: emissions during rising water. J Geophys Res 95:16733–16788
3. Bartlett KB, Crill PM, Sebacher DI, Harriss RC, Wilson JO, Melack JM (1988) Methane flux from the Central Amazon Floodplain. J Geophys Res 93:1571–1582
4. Bergman I, Svensson BH, Nilsson M (1998) Regulation of methane production in a Swedish mire by pH, temperature and substrate. Soil Biol Biochem 30:729–741
5. Blaha D, Bartlett K, Czepiel P, Harriss R, Crill P (1999) Natural and anthropogenic methane sources in New England. Atmos Environ 33:243–255
6. Boeckx P, van Cleemput O (1997) Methane emission from a freshwater wetland in Belgium. Soil Sci Soc Am J 61:1250–1256
7. Chan ASK, Prueger JH, Parkin TB (1998) Comparison of closed-chamber and Bowen-ratio methods for determining methane flux from peatland surfaces. J Environ Qual 27:232–239
8. Chanton JP, Martens CS, Kelly CA (1989) Gas transport from methane-saturated, tidal freshwater and wetland sediments. Limnol Oceanogr 34:807–819
9. Crill PM, Harriss RC, Bartlett KB (1991) Methane fluxes from terrestrial wetland environments. In: Rogers JE , Whitman WB (eds) Microbial production and consumption of greenhouse gases: methane, nitrogen oxides and halomethanes. American Society for Microbiology, Washington, DC, pp 91–109
10. Crill PM, Bartlett KB, Harriss RC, Gorham E, Verry ES, Sebacher DI, Madzar L, Sanner W (1988) Methane flux from Minnesota peatlands. Global Biogeochem Cycles 2:371–384
11. Crill PM, Bartlett KB, Wilson JO, Sebacher DI, Harriss RC, Melack JM, MacIntyre S, Lesack L, Smith-Morrill L (1988) Methane flux from Minnesota peatlands. Global Biogeochem Cycles 2:371–384
12. Devol AH, Richey JE, Clark WA, King SL (1988) Methane emissions to the troposphere from the Amazon Floodplain. J Geophys Res 93:1583–1592
13. Dise NB (1993) Methane emission from Minnesota peatlands: spatial and seasonal variability. Global Biogeochem Cycles 7:123–142
14. Duchemin E, Lucotte M, Canuel R (1999) Comparison of static chamber and thin boundary layer equation methods for measuring greenhouse gas emmisions from large water bodies. Environ Sci Technol 33:350–357
15. Edwards GC, Neumann HH, den Hartog G, Thurtell GW, Kidd G (1994) Eddy correlation measurements of methane fluxes using a tunable diode laser at the Kinosheo Lake tower site during the Northern Wetlands Study (NOWES). J Geophys Res 99:1511–1517

16. Fan SM, Wofsy SC, Bakwin PS, Jacob DJ, Anderson SM, Kebabian PL, McManus JB, Kolb CE, Fitzjarrald DR (1992) Micrometeorological measurements of CH_4 and CO_2 exchange between the atmosphere and the subarctic tundra. J Geophys Res 97:16627–16643
17. Fechner EJ, Hemond HF (1992) Methane transport and oxidation in the unsaturated zone of a *Sphagnum* peatland. Global Biogeochem Cycles 6:33–44
18. Fechner-Levy EJ, Hemond HF (1996) Trapped methane volume and potential effects on methane ebullition in a northern peatland. Limnol Oceanogr 41:1375–1383
19. Frolking S, Crill P (1994) Climate controls on temporal variability of methane flux from a poor fen in southeastern New Hampshire: measurement and modeling. Global Biogeochem Cycles 8:385–397
20. Goodwin S, Zeikus JG (1987) Ecophysiological adaptations of anaerobic bacteria to low pH: analysis of anaerobic digestion in acidic bog sediments. Appl Environ Microbiol 53:57–64
21. Harriss R, Gorham E, Sebacher D, Bartlett K, Flebbe P (1985) Methane flux from northern peatlands. Nature 315:652–654
22. Krumholz LR, Hollenback JL, Roskes SJ, Ringelberg DB (1995) Methanogenesis and methanotrophy within a *Sphagnum* peatland. FEMS Microbial Ecol 18:215–224
23. Laine J (1996) Effect of water-level drawdown on global climatic warming: northern peatlands. Ambio 25:179–184
24. Lansdown JM, Quay PD, King SL (1992) CH_4 production via CO_2 reduction in a temperate bog: a source of ^{13}C-depleted CH_4. Geochim Cosmochim Acta 56:3493–3503
25. Maestrojuán GM, Boone DR (1991) Characterization of *Methanosarcina barkeri* MS^T and 227, *Methanosarcina mazei* S-6^T, and *Methanosarcina*. *vacuolata* Z-761^T. Int J Syst Bacteriol 41:267–274
26. Matthias AD, Yarger DN, Weinbeck RS (1978) A numerical evaluation of chamber methods for determining gas fluxes. Geophys Res Lett 5:765–768
27. Melloh RA, Crill PM (1995) Winter methane dynamics beneath ice and snow in a temperate poor fen. Hydrol Process 9:947–956
28. Melloh RA, Crill PM (1996) Winter methane dynamics in a temperate peatland. Global Biogeochem Cycles 10:247–254
29. Michmerhuizen CM, Striegl RG, McDonald ME (1996) Potential methane emission from north-temperate lakes following ice melt. Limnol Oceanogr 41:985–991
30. Miller LG, Oremland RS (1988) Methane efflux from pelagic regions of four lakes. Global Biogeochem Cycles 2:269–277
31. Moizuk G, Livingstone R (1966) Ecology of red maple in a Massachusetts upland bog. Ecology 47:942–950
32. Morrissey LA, Livingston GP (1992) Methane emmision from Alaska arctic tundra: an assessment of local spatial variability. J Geophys Res 97:16661–16670
33. Mosier A, Andreae M (1989) Chamber and isotope techniques. In: Andrae MO , Schimel DS (eds) Exchange of trace gases. John Wiley and Sons, NY, pp 175–187
34. Motzkin G, Pattersen W (1991) Vegetation patterns and basin morphometry of a New England moat bog. Rhodora 93:307–321
35. O'Flaherty V, Mahony T, O'Kennedy R, Colleran E (1998) Effect of pH on growth kinetics and sulphide toxicity thresholds of a range of methanogenic, syntrophic and sulphate-reducing bacteria. Proc Biochem 33:555–569
36. Patel GB, Sprott GD, Fein JE (1990) Isolation and characterization of *Methanobacterium espanolae* sp. nov., a mesophilic, moderately acidiphilic methanogen. Int J Syst Bacteriol 40:12–18
37. Phelps AR, Peterson KM, Jeffries MO (1998) Methane efflux from high-latitude lakes during spring ice melt. J Geophys Res 103:29029–29,036
38. Sebacher DI, Harriss RC, Bartlett KB, Grice SS (1986) Atmosphere methane sources: Alaskan tundra bogs, an alpine fen, and a subarctic boreal marsh. Tellus 38B:1–10
39. Shurpali NJ, Verma SB, Clement RJ, Billesbach DP (1993) Seasonal distribution of methane flux in Minnesota peatland measured by eddy correlation. J Geophys Res 98: 20649–20655
40. Sugimoto A, Fujita N (1997) Characteristics of methane emission from different vegetations on a wetland. Tellus 49B:382–392
41. Suyker AE, Verma SB, Clement RJ (1996) Methane flux in a boreal fen: season-long measurement by eddy correlation. J Geophys Res 101:28637–28647
42. Svensson B, Rosswall T (1984) In situ methane production from acid peat plant communities with different moisture regimes in a subarctic mire. Oikos 43:341–350
43. Tyler SC (1991) The global methane budget. In: Rogers JE , Whitman WB (eds) Microbial production and consumption of greenhouse gases: methane, nitrogen oxides and halomethanes. American Society for Microbiology, Washington, DC, pp 7–38
44. van den Pol-van Dasselaar A, Corre WJ, Prieme A, Klemedtsson AK, Weslien P, Stein A, Klemedtsson L, Oenema O (1998) Spacial variability of methane, nitrous oxide, and carbon dioxide emissions from drained grasslands. Soil Sci Soc Am J 62:810–817
45. West AE, Brooks PD, Fisk MC, Smith LK, Holland EA, Jaeger CH, Babcock S, Lai RS, Schmidt SK (1999) Landscape patterns of CH_4 fluxes in an alpine tundra ecosystem. Biogeochemistry 45:243–264
46. Whalen SC, Reeburgh WS (1988) A methane time flux series for tundra environments. Global Biogeochem Cycles 2:399–409
47. Williams RT, Crawford RL (1984) Methane production in Minnesota Peatlands. Appl Environ Microbiol 47:1266–1271
48. Williams RT, Crawford RL (1985) Methanogenic bacteria, including an acid–tolerant strain, from peatlands. Appl Environ Microbiol 50:1542–1544
49. Zellner G, Bleicher K, Braun E, Kneifel H, Tindall BJ, de Macario EC, Winter J (1989) Characterization of a new mesophilic, secondary alcohol-utilizing methanogen, *Methanobacterium palustre* spec. nov. from a peat bog. Arch Microbiol 151:1–9