Review

Comparison of biogenic methane emissions from unmanaged estuaries, lakes, oceans, rivers and wetlands

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HIGHLIGHTS

► We report maximal and yearly CH4 emissions in different latitudes, climates and ecosystem types.
► We outline how CH4 emissions vary among different wetland- and marine ecosystem types.
► Seasonality of emissions in different aquatic environments has been described.
► The influence of spatial variability on emissions has been taking into account.
► We assess the influence of abiotic factors in aquatic environments and how different types of plants affect emissions.

ABSTRACT

A literature review of quantitative data was carried out to conduct a cross-system study on methane emissions relating peak emissions (PE) and annual emissions (AE) in five types of non-managed ecosystems: estuaries, lakes, oceans, streams and wetlands. PE spanned eight orders of magnitude (0.015 to 300 mg CH4 m⁻² h⁻¹) while AE spanned seven (0.078 to 19044 g CH4 m⁻² yr⁻¹). PE and AE were strongly related worldwide ($r^2 = 0.93$). There was no relationship between AE and latitude, with highly variable PE across latitudes and climates. The coefficient of variation (CV) was greatest for emissions in oceans and estuaries, while the highest emission rate was recorded in wetlands and lakes. Efflux from coastal areas and estuaries was higher than that from upwelling areas and deep seas. Concerning wetland types, marshes showed the highest PE with the highest wetland emissions occurring in sites dominated by big helophytes. Non-stratifying- and eutrophic lakes displayed more emissions than other lake types, but there was no environmental variable that might predict methane emissions from lakes on a worldwide basis. Generally, most ecosystem types followed a seasonal pattern of emissions, with a maximum in summer, except in estuaries which did not show any distinct pattern. Regarding the importance of hot spots within most ecosystems, more spatial variability of CH4 emissions was observed in lakes than in wetlands and oceans; however, no relationship between emissions and spatial variability was found. A positive relationship, albeit weak, was found between methane flux and either temperature or irradiance in wetlands; a narrow range of both negative and positive values of the water table promoted CH4 emissions. Previously, little was known about the factors controlling efflux from river and marine environments. Our study suggests that local conditions are important in controlling CH4 emissions, because the variability explained by the more commonly studied abiotic factors is low worldwide. This precludes the use of these variables to develop models to predict emissions at regional scales or wider, despite the many attempts made in the past. This makes local assessments of emissions essential, particularly in warm, temperate and tropical areas of the world. Future research aiming to shed light on CH4 fluxes from estuaries, lakes, oceans, rivers and wetlands must: 1) produce more detailed data on controlling factors; 2) increase efforts to fully characterize spatial and temporal heterogeneity; 3) combine bottom-up (measurements) and top-down (modelling) approaches.

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1. Introduction

Methane (CH4) is a greenhouse gas, whose concentration increased in the atmosphere from 1950 (IPCC, 2007) until the
1990s, when emissions decreased; however, there is considerable inter-annual variation (Bousquet et al., 2006). The global warming potential of CH₄ is 25 times greater than that of CO₂ on a 100-year time horizon (IPCC, 2007). Indeed, despite its lower concentration (6 ppb CH₄ y⁻¹ from 1990 to 2005) compared to CO₂ (1.7 ppm y⁻¹ from 1990 to 2005), CH₄ contributed ~20% of the global warming effect (IPCC, 2007). The major sources of CH₄ are submersed soils (natural wetlands, mangroves and rice fields), oceans and fresh-water, CH₄ hydrates, fossil fuels, enteric fermentation, animal wastes, domestic sewage, landfills and biomass burning (Dalal and Allen, 2008).

Wetlands are the main type of aquatic ecosystem emitting biogenic CH₄ (Matthews and Fung, 1987). They cover between 4% and 9% of the global surface area (Matthews and Fung, 1987), but store nearly 37% of the global terrestrial carbon (Bolin and Sukumar, 2000). The role of wetlands in terrestrial carbon cycling is particularly complex, due to the fact that methane production and oxidation are a part of carbon cycling (Roehm, 2005), contributing nearly 40% of global atmospheric methane annually (Fung et al., 1991). Wetlands are the largest single source of atmospheric methane, even when considering all anthropogenic emissions (Christensen, 2011).

Studies on emissions from water-related ecosystems other than wetlands are less frequent. Streams are very poorly studied and ocean areas have been studied in more detail during the last two decades, but many unanswered questions still remain, concerning CH₄ origin, production, oxidation and advection, and controlling factors (Reeburgh, 2003, 2007). Studies on lake emissions have recently been undertaken (Bastviken et al., 2011), but they are still more geographically-restricted than those of wetlands.

Methane emissions from wetlands appear to be strongly influenced by environmental variables, such as soil temperature and inundation, at a local scale, and are likely to be influenced by climate change (Bartlett and Harris, 1993). Many studies have related methane flux changes with the capability of plants to transport gas depending on plant activity and environmental factors. Temperature, water table and irradiance all affect plant cycles, thereby affecting plant-mediated CH₄ emissions and even CH₄ emissions from vegetated soils (Kankaala et al., 2005; Käki et al., 2001; Kutzbach et al., 2004; Mikkelä et al., 1995). In addition, these abiotic factors affect emissions through control of microbial activity; therefore, they have been widely studied and used to estimate global emissions (Roehm, 2005; Walter et al., 1996). In lakes, regional studies suggest that shallow and small lakes release more methane per unit area than deep and large lakes (Bastviken et al., 2004; Juutinen et al., 2009); since there is a covariance between shallowness and eutrophication (Wetzel, 2001), it is not surprising that CH₄ efflux from eutrophic lakes is also higher (Juutinen et al., 2009).

Many global and regional reviews on CH₄ emissions from wetland environments have been carried out (Aselmann and Crutzen, 1989; Bartlett and Harris, 1993; Bridgham et al., 2006; Matthews and Fung, 1987; Roehm, 2005; Segers, 1998). Such reviews have analyzed yearly CH₄ emissions in wetlands, taking into account environmental variables and locations. Bastviken et al. (2004) and Juutinen et al. (2009) published global emission inventories of CH₄ from wetlands. It was restricted to measurements made in unmanaged ecosystems, without any external modification, thus disregarding man-made fertilization (e.g. rice fields). Potential emission rates and CH₄ oxidation rates were excluded from this analysis. For example, there were only 51 studies found on oceans, with a global area of 363 10⁶ km² (Bang et al., 1994) whereas there were 317 studies on wetlands, which have a much lower surface area (Aselmann and Crutzen, 1989). This could be because biogenic methane emissions in oceans are lower than those in wetlands; however the mechanisms regulating these emissions in the ocean are largely unknown due to the scarce number of studies carried out.

We conducted a cross-systems review compiling quantitative estimates of CH₄ emissions and their responses to controlling factors across estuaries, lakes, oceans, rivers and wetlands. This cross-system approach has enabled us to summarize research findings across different studies and quantitatively synthesize the ecological information about the process, as well as to explore general patterns among these ecosystems. More specifically, our aims are: (1) to report peak and yearly CH₄ emissions at different latitudes, climates and ecosystem types; (2) to outline how CH₄ emissions vary among different wetland and marine ecosystems; (3) to describe seasonality of emissions in these environments; (4) to consider the influence of spatial variability on emissions; and (5) to assess the influence of abiotic factors in these environments and how different types of vegetation affect emissions.

2. Methods

2.1. Data collection

This study was carried out by reviewing literature quantifying biogenic CH₄ emissions from estuaries, lakes, oceans, rivers and wetlands. It was restricted to measurements made in unmanaged ecosystems, without any external modification, thus disregarding man-made fertilization (e.g. rice fields). Potential emission rates and CH₄ oxidation rates were excluded from this analysis. Two main types of units appeared in the reviewed articles: weight area⁻¹ time⁻¹ and weight volume⁻¹ time⁻¹. Only studies using the first unit were chosen, which enabled comparisons of most emission data. The dataset was collected from texts, tables and figures of articles published from 1985 to December 2010, gathering information on the measurement site, dominant vegetation, maximal and annual CH₄ emission, spatial heterogeneity and seasonality of emissions as well as the factors controlling emissions (Appendices 1–4). Despite the fact that CH₄ emission can result from different processes (diffusion, ebullition, diffusion through aquatic plants), our compilation did not discriminate among them because most published studies did not attempt to make such a distinction; therefore, our reported data must be considered as “total emissions” from a given site, irrespective of the underlying process. Ebullition is negligible in most marine environments (McGinnis et al., 2006) and storage can also be overlooked in shallow lakes, wetlands and rivers due to the lack of thermal stratification.

It was deemed necessary to divide the study in two groups to tackle different time scales that might be important in CH₄ emission studies. The first group comprised those conducted over an annual cycle (AE) with at least monthly periodicity of sampling, and was used to study seasonal emissions in different ecosystems. However, most studies on CH₄ emission were restricted to shorter
periods. Therefore, we also compiled data collected over shorter time periods, focusing on emissions occurring in the most favourable month of the year (peak emissions, PE), namely, when environmental factors controlling emission were less limiting. When only monthly data over an entire year were supplied, AE was estimated by the numerical integration of these data (Appendix 3). The relationship between peak and annual emissions in the same sites was also studied. Moreover, the distribution of annual emission data has been studied and divided into two series, each analysed separately. Most comparisons and analyses among ecosystem types would be carried out for PE due to the fact that there were more degrees of freedom in the PE dataset.

Whenever available, data of environmental factors were collected. Thus the relationship was studied between water table, air temperature, soil temperature, PAR in wetlands and lakes. However, in the case of oceans, rivers and estuaries, data were insufficient to search for relationships between CH4 emissions and environmental factors.

2.2. Data analysis

We studied PE and AE vs latitudes and climate types, the latter following Köppen’s Climate Classification by FAO-SDRN-AgroMeteorology Group (1997). Five ecosystems were studied: estuaries, lakes, oceans, rivers and wetlands. Hopkinson and Smith (2005) define estuaries as “...those regions at the interface of the terrestrial and oceanic realm where seawater is measurably diluted by freshwater runoff from land.” The Ramsar Convention (2000) defines wetlands as “the site where water is at or near the soil surface for a significant part of the growing season.” The Merriam-Webster Dictionary (2011) defines river as “any natural stream of water that flows in a channel with defined banks.” And lakes are defined as “an inland body of standing water” while the definition of ocean is: “the whole body of salt water that covers nearly three fourths of the surface of the earth.”

There are some reports of emissions by impoundments, which refer to lakes, while emissions from the littoral fringe of lakes are included within wetlands. Ocean environments have also been studied specifically, splitting them into estuaries, coastal shelves, deep seas and upwelling areas. Likewise, wetlands have been further divided into other categories: peatlands, marshes, forested wetlands and coastal wetlands (estuaries have been considered as different from coastal wetlands when freshwater inputs were suspected to occur), following the outline by Mitsch and Gosselink (2001), who define peatland as “a generic term of any wetland that accumulates partially decayed plant matter”, and marsh as “a frequently or continually inundated wetland characterized by emergent herbaceous vegetation adapted to saturated soil conditions.” Forested or riparian wetlands are defined as “occurring along rivers and streams, which are occasionally flooded by those bodies of water but are otherwise dry for varying portions of the growing season.” Moreover, we classified wetlands as either ice-free or winter-frozen when the authors mentioned this in their articles. We analysed the relationship between PE and predominant vegetation, classifying them within the main physiognomic groups (hydrophytes, bryophytes, small helophytes, big helophytes and trees).

Thermal stratification and trophic status are the main drivers of lake ecological functioning (Wetzel, 2001). We compare PE in stratifying vs non-stratifying lakes and oligotrophic vs eutrophic lakes. Data on thermal regimes were obtained from the studies reporting lake emissions, whereas their trophic status was ascertained using yearly-averaged total phosphorus in the water column of each lake as an index, those lakes having more than 30 μg l⁻¹ were considered as eutrophic (OECD, 1982).

Due to the lack of both Gaussian distribution and homogeneity of variances for most variables, non-parametric tests were undertaken for comparisons (Siegel and Castellan, 1988). While a Mann–Whitney test was employed to compare medians of CH4 emission between two categories, a Kruskal–Wallis test was used to assess differences in CH4 emission among the categorized aquatic ecosystems when these exceeded two. Latitudinal, climatic, ecosystem types, wetland types and their main vegetation, marine ecosystems and lake trophic status (as total phosphorus in the mixed layer) and stratification types were considered to make comparisons.

The Kavvas and Delleur (1975) method to visualize periodicities in a time series was used with the annual dataset to study seasonality in different aquatic ecosystems and wetlands types. Seasonal dynamics in oceans could not be ascertained because of the lack of data. Seasonal data reported from the Southern Hemisphere were rearranged to enable comparisons with data taken in the Northern Hemisphere. An average over a constant time unit (year) was calculated and formed a new series as the new difference between the original series and the mean. For any CH4 emission time series, a scaled difference, MEt, was calculated to represent the observed rate, Xt on time t:

$$\text{ME}_t = 100^* (X_t - X)/X$$

(1)

where X was the yearly mean calculated for that series time. This procedure was repeated for each time series in all aquatic ecosystems of the annual database (Appendix 3).

The range (as difference between the minimum and maximum flux measured) statistic was used to study the spatial variability of emissions, an approach suggested by the lack of both Gaussian distributions and homogeneities of variances in these data. We chose studies reporting data of CH4 emission, measured at the same time but in different areas within the same study area (Appendix 4). We only used ranges of CH4 emissions in wetlands, lakes, estuaries and the ocean because of the lack of stream data. Moreover, since we suspected that the larger study areas corresponded to the higher variability in methane emission, we used the distance between the most distant sites in the studied areas as a surrogate of the spatial scale.

To study the relationship between peak CH4 emissions and abiotic factors (air and water temperature, water table and irradiance) we employed the Spearman correlation. For lakes, average and maximal depth and total phosphorus were also related with AE. All statistical analyses were performed using STATISTICA 6.1 (Statsoft Inc., 1997).

3. Results

3.1. Emissions and their ranges

Most continental studies were carried out in Canada, USA, Finland and China. Marine environments were more evenly covered throughout the world but only during PE (Appendix 1). Methane emissions were more commonly measured in the Northern Hemisphere, probably due to the abundance of environments related to water and the funding available to create the infrastructure needed to measure methane emissions. A total of 551 estimations were compiled for PE, of which 18 were estuaries, 143 were lakes and impoundments, 51 were oceans, 22 were rivers and 317 were wetlands. As concerning different wetlands, 179 were peatlands, 101 were marshes, 42 were forested wetlands and 8 coastal wetlands (Appendix 1, Table 1). Concerning AE, records were taken from 6 estuaries, 55 lakes, 12 rivers and 126 wetlands, but no annual data were available for any oceanic sites (Appendix 3, Table 1).
Boxes include 25 sites are 115, equatorial sites (E) 114, Mediterranean sites (M)-7, oceanic sites (O)-15, subarctic (S)-7, steppe sites (ST)-37, tropical sites (T)-71, and warm temperate sites (WT)-84.

Statistics of peak and annual emissions in different ecosystem types worldwide. Data for calculations are reported in Appendix 1 and 3 (Supplementary material). No data are available to estimate annual emissions from any oceanic site. CV: coefficient of variation; n: number of data; SD: standard deviation.

<table>
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<tr>
<th>Ecosystem Type</th>
<th>Annual CH4 Emission (g CH4 m$^{-2}$ yr$^{-1}$)</th>
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<tbody>
<tr>
<td>Estuary</td>
<td>Lake</td>
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<tr>
<td>Average</td>
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<tr>
<td>SD</td>
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<tr>
<td>Median</td>
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<tr>
<td>Max</td>
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<tr>
<td>Min</td>
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<table>
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<td>Median</td>
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<table>
<thead>
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<tbody>
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<tr>
<td>Min</td>
<td>0.009</td>
</tr>
<tr>
<td>n</td>
<td>51</td>
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</table>

There were no significant differences in CH$_4$ emissions between latitude or climate zone classes (Fig. 1). The highest emissions appeared in lakes between 0–20° and 60–80°, whereas highest emissions for wetland varied between 40 and 60°.

Annual Emissions differed among ecosystem types (Table 1). Efflux from lakes and wetlands was far more variable (CVs: 537 and 489%, respectively) than that from estuaries and rivers. All environments presented contrasting maximal values. The highest values occurred in wetlands, followed by those in lakes, rivers and estuaries. Mean values showed differences in different ecosystem types with maxima in estuaries and wetlands and minima in lakes and rivers (Table 1).

The scenario was different concerning PE (Table 1). It varied greatly in oceans and estuaries (CV: 630 and 259%, respectively), as compared with those from rivers, wetlands and lakes (CV: 187–198%). Ranges were wider in lakes and wetlands. Average values were roughly similar in inland waters, with those of the sea being much lower (Table 1).

Oceanic ecosystems differed in their biogenic PE, as judged by a Kruskal–Wallis test (P < 0.05; Fig. 2a). Coastal shelves (range: 0.0001–64.9 mg CH$_4$ m$^{-2}$ h$^{-1}$) appeared to be the most variable, whereas estuaries (mean ± STE 3.29 ± 11.04 mg CH$_4$ m$^{-2}$ h$^{-1}$) reached the highest PE averages.

Regarding wetland types (Fig. 2b), marshes presented the highest range of methane release (range: 0.007–280 mg CH$_4$ m$^{-2}$ h$^{-1}$) and the highest mean emission (mean ± SD 20.026 ± 41.98 mg CH$_4$ m$^{-2}$ h$^{-1}$). Wetlands, where big helophytes predominate (Fig. 2c), showed the highest range of emissions (range: 0.003–288 mg CH$_4$ m$^{-2}$ h$^{-1}$) and also the highest mean emission (mean ± SD 27.75 ± 45.67 mg CH$_4$ m$^{-2}$ h$^{-1}$).

CH$_4$ emission in lakes depended upon the lake type. Eutrophic lakes (Fig. 2d) showed more PE variability than oligotrophic ones (range: 0.009–300 mg CH$_4$ m$^{-2}$ h$^{-1}$) (Mann–Whitney test, P < 0.05). Mean values were higher in eutrophic lakes (mean ± SD 25.53 ± 50.64 mg CH$_4$ m$^{-2}$ h$^{-1}$) than in oligotrophic ones (mean ± SD 61.9 ± 14.13 mg CH$_4$ m$^{-2}$ h$^{-1}$), as judged by a Mann–Whitney test (P < 0.05). Variability in CH$_4$ fluxes also

![Fig. 1. Methane emissions worldwide in different latitudes and climate types according to Köppen’s climate classification](image-url)
depended on lake stratification (Fig. 2d); the range was smallest in stratifying lakes (range: 0.34 \text{e} 4.93 \text{mg CH}_4 \text{m}^{-2} \text{h}^{-1}). As a result, mean values were much higher in non-stratifying lakes (mean \pm SD 15.83 \text{e} 37.87 \text{mg CH}_4 \text{m}^{-2} \text{h}^{-1}) than in stratifying ones (mean \pm SD 1.24 \text{e} 1.64 \text{mg CH}_4 \text{m}^{-2} \text{h}^{-1}).

3.2. Seasonality and spatial heterogeneity of emissions

Lakes and wetlands usually showed a peak in summer (Fig. 3a), with a maximum in August and February in the Northern and Southern hemispheres, respectively. Meanwhile, rivers presented three maxima of CH$_4$ emission, the first at the beginning of spring and the highest at the end of summer, with a short peak at the beginning of the autumn season. Estuaries did not show any distinct pattern of seasonality (Fig. 3a). Regarding wetland types (Fig. 3b), seasonal patterns of CH$_4$ fluxes in frozen and ice-free wetlands were similar as both presented a peak in August, higher in winter-frozen wetlands.

The range of spatial variability of CH$_4$ emission in lakes (0.546 \text{e} 233.6 \text{mg CH}_4 \text{m}^{-2} \text{h}^{-1}) was higher than those of wetlands (0.02 \text{e} 216.63 \text{mg CH}_4 \text{m}^{-2} \text{h}^{-1}) and oceans (0.00003 \text{e} 0.0109 \text{mg CH}_4 \text{m}^{-2} \text{h}^{-1}), as judged by a Kruskal–Wallis test ($P < 0.05$; Fig. 4). However, no statistically significant relationship was found when we studied how varied methane emissions depended on the distances between the measured sites.

![Figure 2](image1.png)

**Fig. 2.** (a) Peak emissions in different marine ecosystems in coastal shelf (CS, $n = 26$), deep sea (DS, $n = 20$), estuary (E, $n = 18$) and upwelling (U, $n = 5$) ecosystems. Outliers in estuaries ($n = 2$) and coastal shelves ($n = 1$) have not been represented; see Appendix 1 (Supplementary Material) for their values. (b) Peak emissions in different wetland types: coastal wetlands (CW, $n = 9$), forested wetlands (FW, $n = 43$), marshes (M, $n = 102$), and peatlands (P, $n = 179$). (c) Peak emission in wetlands with different plant dominance. Bryophyte-(B, $n = 75$), big helophyte-(BH, $n = 60$), hydrophyte-(H, $n = 14$), small helophyte-(SH, $n = 128$) and tree-dominated (T, $n = 53$) wetlands are shown. (d) Peak emission in lakes as related with eutrophication and thermal regime (separate by a dashed line). Oligotrophic (O, $n = 98$), eutrophic (E, $n = 44$), non-stratifying lakes (NS, $n = 132$) and stratifying lakes (S, $n = 10$). Plots as in Fig. 1.

![Figure 3](image2.png)

**Fig. 3.** Seasonality of methane emission in (a) ecosystem types and (b) in either ice-free or winter-frozen wetlands, as shown by the Kavvas and Delleur (1975) approach (see text). Estuary (E), lake (L), river (R), and wetland (W). No seasonal data are available for ocean sites. All time series for each ecosystem-year have been scaled by expressing emission as the percent difference from the annual mean. All ecosystems are either located in the Northern Hemisphere or their time course of emissions has been Fig. 2 changed accordingly to enable seasonal comparisons. The horizontal line represents the mean.
4. Discussion

4.1. Emissions and their ranges

We did not find any geographical pattern when we studied the relationship between climate types or latitude and methane emission (Fig. 1), higher emissions occurred in warm temperate climates rather than in tropical or equatorial ones, but also in cold continental sites. The most outstanding feature that emerged from our analyses was the strong variability of methane emissions in these non-managed environments across latitudes and climates.

The highest CH4 emission in different ecosystem types during PE occurred in lakes, whereas the highest AE were recorded in wetlands (Table 1). Areal rates of PE varied over eight orders of magnitude and AE spanned over seven orders of magnitude (Table 1). However, it is likely that the latter range would widen if some oceanic oligotrophic sites were studied for a year. Ranges and maximum rates reported here were much higher than those described in some recent, albeit regional, reviews (Reeburgh, 2003; Roehm, 2005; Bridgham et al., 2006). This discrepancy arose from the fact that we undertook a worldwide analysis of the data, thereby increasing environmental variability which usually resulted in a wider range of emissions.

Estuarine and coastal shelves were shown to depict more emissions than upwelling areas and deep seas (Fig. 2a). A part of the estuarine and coastal emission may be augmented by increases in their methane content delivered by rivers (Sarnat and McShane, 1991; Rehder et al., 1998; Semiletov, 1999). Both estuarine and coastal areas are richer in organic matter of continental origin than other marine ecosystems, thereby being better methane-producing places, provided they have more anoxic sites to promote CH4 production (Ward et al., 1987; Naqvi et al., 2010; Zhang et al., 2008).

Marshes were the wetland type presenting the highest CH4 flux, followed by peatlands (Fig. 2b). Their warm and waterlogged soil provides ideal conditions for methanogenesis (Roehm, 2005). These data suggest that marshes are a substantial source of atmospheric CH4. The deep standing water in marshes could not only provide enough C for CH4 production by inundating more surface area covered with plant litter, but could also create an anaerobic environment favouring CH4 production (Ding and Cai, 2007). Gorham (1991) estimated that peatlands contained approximately one-third of the global terrestrial C pool; thus, peatland is an important source of CH4 to the global C cycle, contributing an estimated 25–30% of global CH4 released to the atmosphere every year (Aselmann and Crutzen, 1989; Alvarez-Cobelas and Ortiz-
Llorente, unpublished data). However, wetland emissions were not explicitly considered in global climate models and hence, when included in predictions of future climate warming, such models will likely change (IPCC, 2007).

Some studies relate the changing fluxes of CH$_4$ with the capability of plants to transport the gas depending on plant activity (Käki et al., 2001), photosynthesis (Sutton-Grier and Mегonigal, 2011), decaying plant organic matter accumulating in the sediment (Kankaala et al., 2004) and plant biomass (Käki et al., 2001). Deep rooting helophytes with aerenchymatous cell structure are generally associated with high CH$_4$ flux rates (Bubier, 1995), supporting our results which show that the highest CH$_4$ emission occurred in soils whose dominant vegetation either comprised big helophytes or hydrophytes (Fig. 2c); these are the plant species with the highest root-system development in wetlands (Cronk and Fennessy, 2001).

Eutrophic lakes presented higher emissions than oligotrophic ones (Fig. 2d) due to the fact that more organic matter was available for methane production and increased anoxia. However, these relationships are of a qualitative nature since no statistically significant relationship was found between either lake depth or total phosphorus (as a surrogate of eutrophication) and PE or AE. Such relationships have been demonstrated at a regional scale (Juutinen et al., 2009); therefore, it seems such relationships with lake variables were of a very broad nature, losing significance as the geographical scope of the study increased.

In addition, our study showed that shallow lakes appeared to produce more emissions than deep lakes, in contrast with Kiene (1991). The latter stated that sediment methanogenesis was limited in shallow aquatic systems that were well mixed and oxygenated during summer periods. This could be explained taking into account that while CH$_4$ produced in hypolimnetic sediments could mostly be oxidized to CO$_2$ by methanotrophic microbes in the water table (Striegl and Michmerhuizen, 1998), much of the sediment in non-stratifying lakes was in contact with the upper mixed water layer, in contrast to stratifying lakes. This situation enhanced mineralization over burial, and CH$_4$ produced in shallow sediments largely escaped oxidation by methanotrophic bacteria and entered the atmosphere (Bastviken et al., 2008).

4.2. Seasonality and spatial heterogeneity of emissions

Seasonal CH$_4$ emissions in lakes and wetlands (Fig. 3a) showed a step-function response to soil temperature, emissions being zero or near zero during winter and much higher in summer with rapid shifts between both seasons. While lakes presented a sharp increase in summer and lower values throughout the year, CH$_4$ release by wetlands remained steadier throughout the year (Fig. 3a). The same results were reported by Dise et al. (1993), Kang and Freeman (2002) and Xing et al. (2005). The three riverine peaks shown here were also reported by Alford et al. (1997). The spring peak was the result of labile organic material accumulating over winter months when low temperatures reduced microbial activity. The summer peak appeared to match the physiological activity of plants when the release of organic material by root systems was increased. Autumn maxima were attributed to the dramatic influx of organic carbon-rich leaf litter to the system, which was readily converted into organic substrates by CH$_4$ producing bacteria. These results are in agreement with those by Bergström et al. (2007), who demonstrated that lake littoral plant cover and the distribution of littoral plant species must be taken into account when estimating regional CH$_4$ budgets.

Emission differences between winter ice-free and frozen-wetlands (Fig. 3b) could be explained by the fact that ice cover did not enable bacterial activity to begin, and that methane bubbles were trapped within the ice, so the increased emission in non-frozen wetlands started earlier. When high temperatures promoted ice-cover thaw, bacteria could resume their activity and methane was released to the atmosphere.

The preliminary spatial study demonstrates that there is no relationship between CH$_4$ emission variability and the spatial scale. It seems the larger the ecosystem, the smoother the variability of methane emissions, with areas of high and low emissions canceling each other out. Thus, successful scale-up is difficult. Hot spots of methane emission, however, appear to be the rule in spatially heterogeneous environments (Bastviken et al., 2010; Bianchi et al., 1996; Kock et al., 2008; Linke et al., 2010; Moore et al., 1994).

A positive relationship between PE and AE was found (Fig. 5) in lakes and wetlands (Alvarez-Cobelas and Ortiz-Llorente, unpublished data). This could enable optimization of the duration of experiments and related costs, thus diminishing work effort and saving money.

4.3. Factors controlling emissions

Relationships tested between environmental variables and CH$_4$ emissions, however, have poor explanatory power. We studied these relationships in wetlands and lakes, first individually and then together. Both attempts gave the same results. A statistically significant, albeit weak, positive relationship emerged between irradiance and CH$_4$ emission, which has also been reported in other studies (Mikkela et al., 1995; Käki et al., 2001). Concerning other abiotic factors, we found a complex relationship between the depth of water table and CH$_4$ emission because its maximum values were recorded within a short range of negative and positive values.

The water table position determines the relative extent of oxic and anoxic horizons within soils and, consequently, the ratio between CH$_4$ production and CH$_4$ oxidation, the fundamental microbial processes underlying the CH$_4$ cycle (Christensen et al., 2001). The effect of the water table position on CH$_4$ emissions can be compared with an on-off switch. When the depth of water table falls well below the soil surface, microbial CH$_4$ oxidation is increased and CH$_4$ emission is hence reduced, as occurs when water table level is increased above the sediment. Methane emissions in water-related ecosystems are partly controlled by water table, a parameter closely related with climate. Rainfall decrease, temperature increase and an elevated extraction of water from groundwater led to decreased water table and increased methane emissions from lakes and wetlands. Ringeval et al. (2010) stated that over the period 1993–2000, the variability in wetland areas strongly influenced the seasonal and inter-annual variability of CH$_4$ emissions. On a seasonal timescale, the variable flooded area mainly plays a role in controlling variable fluxes at boreal latitudes (≈ 30%). The difference with other studies (Shannon and White, 1994) is the strength of these relationships. While these authors have found very strong correlations between water table and methane emissions, worldwide data have shown a much lower statistical relationship.

The factors controlling CH$_4$ emission in lakes and wetlands are difficult to determine on a worldwide basis. Locally, they have been related to water depth, dissolved organic carbon, total phosphorus and anoxic volume fraction (Bastviken et al., 2004; Juutinen et al., 2009). However, no such relationships hold when studying them on a worldwide basis. Not only do CH$_4$ emissions from lake environments appear to be more spatially heterogeneous than initially suspected (Bastviken et al., 2010) but also, temporal variations in efflux occur ranging from diel (Bastviken et al., 2010) to inter-annual changes (Bartlett and Harris, 1993; Pulliam, 1993; Shannon and White, 1994; Hughes et al., 1999). Thus, controlling factors are likely to change depending upon the spatial scale involved. This
makes us suspect that the relationship between methane emissions and either water table or sediment temperature are only valid at small scales, for individual study areas. By contrast, when we study an ecosystem type (lake or wetland) at the global scale these relationships disappear, and a more complex relationship may emerge among them.

The latitudinal variability is also striking (Fig. 1), thus preventing meaningful prediction of the factors controlling emissions worldwide. It seems that temperature, organic matter and anoxic conditions may be some of them, but there are not enough data to support this hypothesis on the worldwide scale.

It is more difficult to study the control of biogenic CH$_4$ efflux in the sea. Most reported studies do not address it causally, may be because the multivariate nature of controls and the expense of studying them all preclude a mechanistic approach. The picture is clearer in estuaries and closed basins, where CH$_4$ and organic matter inputs transported by incoming streams and anoxic conditions prevail at the sediment–water interface (Scranton and McShane, 1991; Zhang et al., 2008; Naqvi et al., 2010). Deep seas and upwelling areas are quite different because there are long, advective effects (Brüchert et al., 2009) and short-range effects, such as oxidation of methane (Reebergh, 2007), vertical transport associated to settling fecal pellets (Karl and Tilbrook, 1994), mixing of different water masses (Rehder and Suess, 2001) and oxicogenic methane production due to methylphosphorous derivatives arising from decomposition of algal blooms in phosphate-stressed waters (Damm et al., 2008; Karl et al., 2008). It is therefore not surprising that methane fluxes from the ocean are so poorly understood and that the ocean methane paradox (Reebergh, 2007) needs further investigation. Strong seasonality is also evident for marine environments (Zhang et al., 2008; Yang et al., 2010), but to obtain a good resolution of seasonal changes of methane efflux from the sea is very expensive. Observations of biogenic methane efflux from ocean areas with frequent sampling for a year or more, can hardly be accomplished by oceanographic vessels and would be better undertaken using remote sensing (Frankenberg et al., 2005) and surface drifters (Boutin et al., 2008).

4.4. Conclusions and recommendations

The global distribution of studies in methane emissions is not homogeneous. Countries like the USA, Brazil, Canada, Finland and China account for almost 70% of studies worldwide. India, Russia, arid and tropical regions. Reeburgh (2007) has recently reviewed novel techniques for studying methane metabolism in the ocean, which can also be used in freshwater. Notwithstanding, there is still a lot of intercomparison work on methane flux methodologies to be done. Particularly, the technique most widely used for studying CH$_4$ efflux in the sea is that of the water–air gradient, which relies upon accurate determination of the gas piston velocity. However, this mass balance method poses theoretical problems (Wanninkhof et al., 2009) and also wide discrepancies in results depending upon the exchange equation used to calculate that velocity (e.g. Zhang et al., 2008).

Furthermore, studies must be carried out highlighting short-range spatial heterogeneity including areas of the Earth that are virtually unknown as yet. Hence, bottom-up (incubation chambers, surface drifters, remote sensors, eddy covariance towers) and top-down (inverse modelling) measurements must be combined to enhance the global estimation of methane emissions to the atmosphere. The significance of methane as a greenhouse gas (IPCC, 2007) makes these improvements essential if a better and more accurate picture of global emission is to be found, which is a precondition to reducing methane emissions worldwide.

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Appendix A. Supplementary material

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References


